

Research Article

Detailed analysis of prey taxonomic composition indicates feeding habitat partitioning amongst co-occurring invasive gobies and native European perch

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Abstract

One of the negative impacts of non-native invasive species on trophic interactions in an invaded ecosystem occurs via increased interspecific competition for food resources between the invader and local species of the same food niche. In freshwaters, there are usually several fish species that feed on similar food resources. Ponto-Caspian gobies are amongst the most successful and widespread invaders colonising European waterways. They have a wide food niche and an opportunistic feeding strategy, with a focus on benthic invertebrates and piscivory occurring occasionally mainly in the case of large individuals. Competition with native percids for food resources is predicted on the basis of high dietary overlap. However, studies published so far provide no unequivocal answer. In order to resolve this question, we conducted a comparative taxonomic analysis of gut content, with an emphasis on chironomids and amphipods, of the invasive monkey goby (Neogobius fluviatilis), racer goby (Babka gymnotrachelus) and the native Eurasian perch (Perca fluviatilis) occurring sympatrically in a large lowland European river, the Bug River in Poland. We found that each species forages in slightly different habitats, as indicated by the different composition of prey species in the gut content. This suggests feeding niche partitioning between the studied species facilitating their co-existence and reduction or avoidance of competition for food resources. Resource partitioning regarding prey types and foraging habitats is a mechanism for permitting the co-existence of closely-related alien gobies with similar food preferences in the invaded waters and co-occurrence with local species. This mechanism can contribute to their invasion success, as observed in European waters during the recent decades. We also demonstrate that precise prey identification to the lowest possible taxon is crucial to reveal the dietary overlap between co-occurring fish species and to predict the impact of alien invaders on native species through interspecific competition, as well as to recommend such an approach in studies upon fish foraging strategies.

Key words: Feeding niche, fish diet, non-native species, resource partitioning, trophic interactions

Introduction

Freshwater ecosystems, together with their biodiversity, are amongst the most threatened and altered environments on the planet, due to the intensive human exploitation of water resources. Widespread invasions of introduced non-native species are amongst the five main threats for such ecosystems (Dudgeon et al. 2006). Successful biological invasion depends on several factors, including interactions of



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the newcomer with the local biota that can be particularly critical for the further fate of an alien species. The arrival and establishment of non-native fish species leads to a number of changes in the ecosystem, particularly in the pre-existing food web. The ecological consequences of such interference depend on the trophic position of the invader and the abundance of species that belong to the same ecological guild in the recipient ecosystem, as well as the availability of resources they share. Piscivorous invaders have a high potential for harmful effects on the ecosystem, especially if native predators are rare or absent (Howeth et al. 2016). The other frequent assumption in fish invasion ecology is that negative impacts of invasions on trophic interactions occur via increased inter-specific competition for food resources (see, for example, Gozlan at al. (2010); Cucherousset and Olden (2011)). In freshwaters, there are usually several fish species that feed on similar food resources. Their co-existence is made possible by resource partitioning, such as different activity patterns or different use of space and food resources. Resource partition is an effective way of reducing competition and it applies also in the case of alien species introductions to recipient fish assemblages (Britton et al. 2010; Tran et al. 2015). Comparative studies on diet of functionally similar fish species in sympatry require detailed prey identification to conclude about resource partitioning or diet overlap (Dukowska et al. 2013; Lik et al. 2017). The identification of prey to the lowest possible taxon has potential value for determining the habitat preferences of both a prey and, based on that, its predator, as for fish, feeding habits and habitat preferences are often interconnected.

As fish species change their trophic status over the course of their lives, displaying ontogenetic niche shifts, many European freshwater fish do not fall into discrete trophic categories (Noble et al. 2007; Specziár and Rezsu 2009), but should rather be classified into collective groups, for example, insectivore/piscivore (Noble et al. 2007) or, according to other classifications, zoobenthivorous/piscivorous or zooplanktivorous/zoobenthivorous/piscivorous (Aarts and Nienhuis 2003). Macrozoobenthos is an important food for many species. The classification of fish that occur in the Rhine and Meuse rivers into ecological guilds showed that 49 out of 56 species included in the study had a zoobenthivorous phase in their life and they comprised ca. 40% of all species of fish there. A similar pattern can be found in other rivers belonging to the Central European biogeographical region (sensu Reyjol et al. (2007)). The region was distinguished by the composition of ichthyofauna and encompasses watersheds from the River Elbe in the west, through the Rivers Oder, Vistula, Neman to Narva in the east, as well as the Swedish and Finnish Baltic river systems. In recent decades, the rivers in this region have faced rapid invasion by five Ponto-Caspian goby species (Grabowska et al. 2008; Rakauskas et al. 2018; Kvach et al. 2021). The contribution of invasive gobies to local fish assemblages varies between watersheds and changes over time (Polačik et al. 2009; Borcherding et al. 2011; Janáč et al. 2018; Gaye-Siessegger et al. 2022). They are considered to have a wide food niche and an opportunistic feeding strategy. The diet differs between goby species, but benthic invertebrates, in particular amphipods and chironomid larvae, are their main prey, while piscivory occurs only in the case of larger individuals of some species (see review by Grabowska et al. (2023)). Their strong competition with native fish species was expected on the basis of high diet overlap, especially with native percids (Copp et al. 2008; Adámek et al. 2010; Kocovsky et al. 2011; Borcherding et al. 2019).

The racer goby *Babka gymnotrachelus* (Kessler, 1857) and monkey goby *Neogobius fluviatilis* (Pallas, 1814) are the first two invasive gobies that arrived in the Vistula River system, almost at the same time, in the mid-1990s and soon spread there rapidly (Grabowska et al. 2008). They were recorded for the first time in the Baltic Sea Basin in the Bug River, right tributary of the Vistula, being part of the central invasion corridor for the Ponto-Caspian aquatic fauna from the Black Sea Basin (Semenchenko et al. 2011). Until 2008, they were the only goby species present in the Vistula River system (Grabowska et al. 2008). The frequency of occurrence of racer and monkey goby in the Bug River (main right tributary of the Vistula) in 2007–2009 was 32% and 68%, respectively (Penczak et al. 2010), reaching even as much as 85% and 100%, if we consider only the lower section of that river, where their first expansion occurred. At all sites, alien gobies co-occurred with Eurasian (European) perch *Perca fluviatilis* Linnaeus, 1758, which was recorded in 96% of the 56 sites surveyed along 587 km of the river (Penczak et al. 2010).

The diet of racer and monkey gobies is similar and mainly comprises benthic macroinvertebrates, though chironomid larvae, other insects larvae, amphipods, molluscs and occasionally also small fish fry, predominate in their diet (Grabows-ka and Grabowski 2005; Kakareko et al. 2005; Grabowska et al. 2009; Didenko et al. 2017, 2021a, b, 2022a). It can be expected that these two alien gobies share food resources with native perch that feed on similar prey, at least during some stages of their ontogeny (Kornijów 1997; Rezsu and Specziár 2006; Kornijów et al. 2016). Considering that, at the time of sampling for our study, racer goby and monkey goby had already established abundant populations in the Bug River and had co-occurred there with European perch for around 10–15 years since their first arrival, we aimed to determine whether such co-existence is based on resource partitioning.

We hypothesised that the three fish species, although potentially feeding on the same type of prey, slightly vary the composition of their diet, for example, by exploring different foraging habitats to minimise interspecific competition when co-occurring in the same section of a river. We verified this prediction by comparative analysis of fish diet, based on the detailed taxonomic identification of selected prey taxa, focusing on chironomids and amphipods, which can differ in terms of the occupied microhabitats. We achieved this by analysing the gut content of racer goby, monkey goby and European perch occurring sympatrically in a large lowland river flowing through the East European Plain, which constitutes a crucial part of the Central Invasion Corridor for westward expansion of the Ponto-Caspian fauna, as defined by Bij de Vaate et al. (2002).

Materials and methods

Fish sampling and site description

All the three studied species, monkey goby, racer goby and perch, were sampled from three sites (Fig. 1) located in the Bug River (the Vistula River system's largest eastern tributary, Baltic Basin, Poland) in 11–14 August 2007. The Bug River maintained its natural character of a lowland, meandering river within a wide valley. It is 772 km long and the watershed covers 39,420 km². Its sources are in Ukraine, but after 185 km, a stretch of 363 km comprises the border be-



Figure 1. Location of sampling sites Z, R, B in the Western Bug River and places of first record of racer goby (red dot) and monkey goby (green dot) in Poland.

tween Poland, Ukraine and Belarus. Later, it turns to the west until it joins the Narew River, shortly before its confluence with the Vistula River. Sampling sites Z (52°23.57333'N, 22°42.25833'E), R (52°42.08667'N, 22°09.73333'E) and site B (52°37.41000'N, 21°35.03000'E) were situated in the lower Bug River, which flows entirely through the territory of Poland. The river in this section is more than 100 m wide and relatively shallow, but with a heterogeneous depth profile (pools and riffles), mainly with a sandy bottom, though with some contribution of gravel and stones (Table 1) and scattered submerged vegetation, such as Elodea canadensis, Potamogeton perfoliatus, Myriophyllum sp. The riverbed is naturally meandering with a sequence of eroded and deposited banks with some emerging macrophytes (Typha sp., Scirpus sp., Juncus sp., Sparganium sp., Glyceria maxima). Only in site B, there was a short section of the bank that had a limestone embankment and a paved area at a small bay and a platform created as a recreational area in the village. The racer goby was very abundant there, as it used such artificial structures as hiding places. The surrounding landscape mainly comprised pastures and other agricultural lands (Table 1).

Fish were sampled at depths from 0.5 m to 1.7 m, along the riverbank by electrofishing with a battery-powered unit, 350 V, 20–100 Hz, wading ca.100 m upstream along the bank and from the boat drifting 500 m downstream.

Table 1. Morphometry of sampling sites: Z, R, B in the Western Bug River. Explanations: a) – absent, + very little/few, ++ common, +++ abundant; b) % of bed cover; c) % of bank overgrown; d) pa- pastures, ł- meadows, cr- cropland, bl- buildings.

| | Site | Z | R | В |
|------------------|--|----------|------------|-----------|
| 1. | Distance from the mouth [km] | 176.7 | 108.2 | 46.0 |
| 2. | Mean width [m] | 120 | 109 | 114 |
| 3. | Mean depth in current [m] | 1.8 | 0.8 | 1.5 |
| | Maximal depth in the current [m] | > 3.0 | 1.5 | > 3.0 |
| 4. ^{a)} | Pools/riffles | +++ | + | + |
| 5. | Mud cover 0–100 [%] | 0 | 5 | 0 |
| | Bottom substrate: sand/gravel/stone [%] | 70/20/10 | 50/30/20 | 60/20/20 |
| 6. ^{b)} | Submerged plants | 10 | 20 | 10 |
| 7.°) | Emerged plants | 30 | 50 | 30 |
| 8. ^{a)} | Trees along banks | +++ | +++ | + |
| 9. ^{d)} | Adjacent area | pa, ł | cr, pa, bl | bl, ł, pa |
| 10. | Water temperature [°C] | 19.0 | 19.1 | 19.2 |
| 11. | pН | 8.62 | 8.75 | 8.89 |
| 12. | Dissolved oxygen [mg O ² dm ⁻³] | 13.4 | 5.9 | 9.26 |
| 13 | Conductivity [µS cm ⁻¹] | 509 | 502 | 476 |

Fish diet analysis

Fish were anaesthetised (MS-222) and preserved in 4% formaldehyde. In the laboratory, the fish were measured for total length (L_T ; to the nearest 1 mm) and weighed (with 0.01 g accuracy). Their alimentary tracts were dissected. The gut contents (in each fish, the same section of alimentary tract, i.e. stomach and first half of intestine) were weighed (to 0.0001 g accuracy) and prey items were identified under a stereomicroscope. Chironomidae larval stages can be identified to genera or groups of closely-related species, but only rarely to the species level. Their remains from the fish gut lack many features that are necessary for precise identification and, thus, following the main key used in this study (Brooks et al. 2007), they were identified to the morphotype cf. level.

Animal prey remains were identified to the lowest readily recognisable taxon, counted and the proportional weight was estimated. The percentage contribution by weight of each food category to the biomass of total stomach content was estimated visually (Hyslop 1980) and then recalculated into real weights, based on the weight of total gut content. The frequency of occurrence (defined as percentage of fish guts containing given prey category in relation to the total number of fish with guts containing any food: %F), percentage of biomass (weight of given food category in relation to total weight of gut content: %B) and relative abundance (number of given prey category in relation to total number of prey: %N) were quantified for each food category at each sampling site.

The Amundsen et al. (1996) modification of the Costello (1990) graphical method was applied to describe feeding strategy and to identify dominant prey items for the fish species, as well as feeding phenotypic plasticity.

Dietary overlap between each pair of fish species was calculated using Schoener's index (Wallace 1981): $\alpha = 1-0.5 [\Sigma_{n=1} (p_{ij} - p_{ik})]$, where p_{ij} is the proportion of the *i*th resource used by species *j* and p_{ik} is the proportion of the *i*th resources used by

species k; overlap values exceeding 0.6 were regarded as high or biologically significant (Wallace 1981). As the proportion in Schoener's index calculation, we used %N proportion: numbers of given prey type to the total number of prey found in fish gut. To show how the accuracy of prey identification influences the evaluation of dietary overlap, we estimated it based on protocol 1 – considering main food categories, i.e. prey pooled into taxonomic groups usually applied in fish diet studies, for example, Amphipoda, Chironomidae (called later Schoener's index 1) and protocol 2 – considering detailed food categories, i.e. prey identified to the lowest possible taxonomic level (called later Schoener's index 2).

To compare the taxonomic composition of the diet between fish species overall (all sites pooled) and at each sampling site, one-way permutation analysis of similarity (ANOSIM, Bray-Curtis similarity coefficient) was used, based on prey. ANOSIM is analogous to an ANOVA procedure, with non-parametric permutation applied to rank similarity matrix of samples. The similarity percentage procedure (SIMPER) was used to identify which prey taxa were most likely responsible for the patterns detected by ANOSIM. SIMPER provided the average dissimilarities between the species and identified which prey taxa made the greatest contribution to any dissimilarities between analysed categories (Clarke and Warwick 1994). All multivariate analyses were performed using PAST software (ver. 3.15; Hammer et al. (2001)).

Dietary niche width was calculated as a Simpson diversity index: $1 - D = 1 - \sum pi^2$ and Shannon diversity index: $H = -\sum pi \log_2 pi$, where *pi* is the proportion of different prey in the diet (Ghent 1991).

Results

The fish species recorded from the sampling sites were mainly bleak *Alburnus alburnus* and roach *Rutilus rutilus*. These two species constituted 45%–64% of all fish caught at the study sites and dominated in abundance along the whole middle and lower river course. The other species that occurred at all three sites were common bream *Abramis brama*, white bream *Blicca bjoerkna*, pike *Esox lucius*, chub *Squalius cephalus*, ide *Leuciscus idus*, common rudd *Scardinus erythrophtalmus*, spined loach *Cobitis taenia* and bitterling *Rhodeus sericeus* (Suppl. material 1). The contribution of studied fish species to the fish assemblages at studied sites Z, R, B was as follows: racer goby (2.8%, 1.6%, 4.3%), monkey goby (0.7%, 4.0%, 6.0%) and perch (7.3%, 6.4%, 5.2%), respectively. However, for further analysis we selected perch species of size range similar to gobies, i.e. almost all large perch (> 150 mm) were excluded in diet analysis and the majority of individuals were juveniles, i.e. in benthivorous stage of ontogeny.

In total, 63 individuals of racer goby, 77 of monkey goby and 62 of perch were caught in three sampling sites. In four out of 202 dissected individuals, the alimentary tracts were empty and not considered in further analysis.

In all three fish species, prey belonging to Amphipoda, Chironomidae larvae and pupae, Gastropoda, Trichoptera larvae, Coleoptera larvae, Oligochaeta and Hirudinea were found in the diet (Suppl. material 2). Odonata larvae and Pisces were not recorded from any monkey goby and Bivalvia were not eaten by perch. Altogether, we distinguished 11 main prey categories and, additionally, four accountable categories of fish gut content for which only biomass was estimated, the latter being Mollusca not identified, detritus, sand and fish eggs. The contribution

| Species | | Racer goby | | | | Monkey goby | | | | | European perch | | | | | | |
|---------------------|------------|-------------------|------|-------------------|------|-------------------|------|-------------------|------|-------------------|----------------|-------------------|------|-------------------|------|-------------------|--|
| Site | Z | | R | | В | | Z | | R | | В | | Z | | R | | |
| N of specimens | 3 | 34 | | 20 | | 27 | | 20 | | 32 | | 24 | | 31 | | 30 | |
| Mean TL [mm] | 70 (±14 | 70.24 (±14.50) | | 60.70 (±15.53) | | 74.65 (±14.50) | | 96.90 (±27.36) | | 92.36 (±14.68) | | 85.86 (±16.03) | | 95.24 (±29.95) | | 98.154 (±7.95) | |
| Min-max TL [mm] | 51- | -101 | 42- | -96 | 52- | -103 | 52- | -124 | 61- | -120 | 54- | -112 | 53- | -150 | 84- | -115 | |
| Food categories | %N | %B | %N | %B | %N | %B | %N | %B | %N | %B | %N | %B | %N | %B | %N | %B | |
| Amphipoda | 27.5 | 48 | 19.6 | 65 | 13.8 | 38 | 16.7 | 22 | 6.1 | 19 | | | 54.9 | 53 | 54.2 | 57 | |
| Chironomidae larvae | 43.7 | 12 | 67.4 | 29 | 78.8 | 17 | 39.7 | 8 | 76.2 | 44 | 76.1 | 17 | 20.4 | 6 | 23.8 | 5 | |
| Chironomidae pupas | 4.8 | 4 | 4.3 | 1 | | | 3.8 | 3 | 5.4 | 7 | 1.0 | 2 | 2.6 | 2 | 7.0 | 3 | |
| Trichoptera larvae | 0.6 | > 1 | | | | | 12.8 | 4 | 2.2 | 3 | 18.1 | 18 | 0.4 | > 1 | 0.5 | 2 | |
| Odonata larvae | 0.6 | > 1 | | | | | | | 0.5 | 6 | 1.0 | | 1.7 | > 1 | | | |
| Coleoptera larvae | 1.8 | 2 | | | 2.5 | 1 | | | | | 1.0 | 4 | 0.9 | > 1 | 1.9 | 2 | |
| Bivalvia | 14.4 | 19 | 2.2 | 1 | | | 11.5 | 26 | 7.9 | 5 | 1.9 | 6 | | | | | |
| Gastropoda | 5.4 | 4 | 6.5 | 4 | 2.5 | 10 | 12.8 | 27 | 1.8 | 2 | | | | | 1.4 | 2 | |
| Mollusca not ident. | | 6 | | | | | | | | 14 | | | | | | | |
| Oligochaeta | | | | | 1.3 | 1 | | | | | 1.0 | 6 | | | 0.9 | 6 | |
| Hirudinea | 0.6 | > 1 | | | | | 2.6 | 10 | | | | | | | | | |
| Pisces | 0.6 | > 1 | | | 1.3 | 21 | | | | | | | 19.1 | 34 | 10.3 | 23 | |
| Detritus (plant) | | | | | | 12 | | | | | | 23 | | 2 | | | |
| Sand | | | | | | | | | | | | 12 | | | | | |
| Fish eggs | | | | | | | | | | | 12 | 12 | | | | | |

Table 2. Diet composition of the European perch, racer goby and monkey goby (mean, minimum and maximum total length of fish – TL) expressed as relative abundance (%N) and relative biomass (%B) of main food categories in gut content at the three studied sites (Z, R, B).

of each food category varied between sites (Table 2), but Chironomidae larvae were the dominant prey for both goby species, considering both abundance and frequency of occurrence and of a secondary importance for perch (Fig. 2A–C), which fed predominantly on amphipods, which dominated in abundance and biomass of their food (Table 2). These crustaceans were also found in more than 50% of racer goby guts (Fig. 2B), constituted 38–65% of food biomass in that fish species (Table 2) and were subdominant prey, considering their contribution to the total prey abundance (Fig. 2B). Amphipods were less frequently eaten by monkey goby (Fig. 2C) and their contribution to prey abundance and total biomass depended on the site (Table 2).

The plot of prey specific abundance (%Nps) and frequency of occurrence (%F) of the main components of the diet showed that chironomid larvae were the prey of higher importance for gobies, while, for European perch, amphipods were more important (Fig. 2). The prey of high importance means that it has been eaten by more than half the individuals and have high contribution in specific abundance. Considering feeding strategy, both gobiid species and European perch are generalist feeders, relying on several prey taxa with a relatively low prey-specific abundance, being mainly located in the lower part of the diagram.

Diet overlap, as calculated for the 11 main food categories (Schoener's index 1), occurred amongst all three species if data for all sites were pooled, which indicated that their prey spectrum was very similar (Table 3). If analysed separately for each site, the dietary overlap was very high (ca. 0.8) only between the gobies at all three



Figure 2. Feeding strategy displayed using the Amundsen et al. (1996) modification of the Costello (1990) graphical method for **A** European perch **B** racer goby **C** monkey goby, in the Bug River (only main food categories included and data from sites pooled for species) **D** explanatory diagram (%Nps – prey specific abundance; %F – frequency of occurrence defined as percentage of fish guts containing given prey category in relation to the total number of fish with guts containing any food).

sites, moderate (0.5) between racer goby and perch, while there was no dietary overlap between monkey goby and perch at any site (Table 3).

Up to 56 taxa (including 28 chironomids and 4 amphipods) dominated the food categories shared by the three studied fish species. For the analysis, we rejected taxa that were found in only one fish, which reduced the number of prey taxa to 42 (including 24 chironomids). The values of Schoener's index 2 indicated that there was no dietary overlap between gobies and perch at any site, but there was also no dietary overlap between racer goby and monkey goby at site B or it was moderate (ca. 0.5) at the other two sites, Z and R (Table 3). ANOSIM similarity analysis showed that the mean abundance of Chironomidae, Amphipoda and other taxa in fish diets varied between fish species, when data from all individuals of each fish species from all sites were pooled, while

Table 3. The dietary overlap estimated, based on two protocols: calculated for general (Schoener's index 1) and detailed food identification (Schoener's index 2) categories. Pairwise comparisons (Bonferroni test) of fish diet following one-way ANOSIM and SIMPER analysis based on detailed identified food categories.

| Composisons | Schoener's index | Schoener's index | AN | SIMPER | |
|--------------------------------------|------------------|------------------|---------|--------|---------------|
| Comparisons | 1 | 2 | R | р | dissimilarity |
| Fish species (site pooled) | | | | | |
| perch vs racer goby vs. monkey goby | | | 0.1893 | 0.0001 | 91.08 |
| perch vs. racer goby | 0.826 | 0.424 | 0.1333 | 0.0060 | 87.82 |
| perch vs. monkey goby | 0.721 | 0.220 | 0.3520 | 0.0030 | 94.95 |
| racer goby vs. monkey goby | 0.818 | 0.480 | 0.1266 | 0.0030 | 91.22 |
| Site Z | | | ~ | | |
| perch vs. racer goby vs. monkey goby | | | 0.2953 | 0.0001 | 91.07 |
| perch vs. racer goby | 0.530 | 0.346 | 0.3543 | 0.0003 | 88.47 |
| perch vs. monkey goby | 0.400 | 0.175 | 0.0353 | 0.9140 | 97.26 |
| racer goby vs. monkey goby | 0.784 | 0.572 | 0.2656 | 0.0470 | 92.53 |
| Site R | | · | · | | |
| perch vs. racer goby vs. monkey goby | | | 0.1883 | 0.0010 | 91.47 |
| perch vs. racer goby | 0.491 | 0.274 | 0.1393 | 0.0003 | 84.30 |
| perch vs. monkey goby | 0.370 | 0.175 | 0.3250 | 1.0000 | 94.57 |
| racer goby vs. monkey goby | 0.816 | 0.556 | -0.0870 | 1.0000 | 90.53 |
| Site B | · | | | • | |
| racer goby vs. monkey goby | 0.790 | 0.389 | 0.3243 | 0.0130 | 88.83 |

if analysed between fish species within each site, showed some exceptions, for example, there were no differences between perch and monkey goby at sites Z and R and between racer goby and monkey goby at site R (Table 4). SIMPER identified the taxa that contributed the most to the overall dissimilarity between the diets of the fish species (Table 4).

Ten taxa, i.e. *Glyptotendipes* cf. *pallens*, *Dikerogammarus villosus*, *Chironomus* cf. *riparius*, Pisces, *Pontogammarus robustoides*, *Polypedilum* cf. *nubeculosum*, *Micro-tendipes pedellus*-type, gastropods, caseless larvae (*Hydropsyche* sp.) of Trichoptera and *Rheocricotopus* cf. *chalybeatus*, out of 56 analysed, contributed to 80% of the overall dissimilarity amongst the diets of perch, racer and monkey gobies, though the mean abundance of particular prey varied between sites (Fig. 3).

The perch mainly fed on amphipods, i.e. *P. robustoides* at site Z, *D. villosus* at site R and fish at sites Z and R. Amongst the Chironomidae larvae, the *G. cf. pallens* contributed the most to the perch diet at each site. This chironomid was the most abundant in the diet of racer goby at sites Z and B. *D. villosus* was also an important food item of racer goby at site Z. Sphaeridae were not recorded in the diet of perch, but contributed to the diet of both goby species, especially at site Z, where monkey goby fed also on gastropods. Contrary to the other two co-occurring fish species, monkey goby consumed many caseless trichopteran larvae, as well as the chironomids: *C. cf. riparius* at all sites and *P. cf. nubeculosum* at site B.

The prey diversity was lower for perch than for gobies. Concerning the latter, prey diversity tended to be higher for racer goby than for monkey goby at sites Z and R; however, it was equal at site B (Fig. 4A, B), where the contribution of various chironomid species to the diet of both gobies was very high.





Table 4. Results of SIMPER analysis identifying prey categories with the highest contribution to the overall dissimilarity amongst fish species diets and their mean relative abundance (%N) in diets of perch (PF), racer goby (BG) and monkey goby (NF).

| Taxon | Contribution % | Cumulative % | Mean PF | Mean BG | Mean NF |
|------------------------------------|----------------|--------------|---------|---------|---------|
| Glyptotendipes cf. pallens | 15.1 | 15.1 | 17.0 | 28.0 | 11.9 |
| Dikerogammarus villosus | 14.1 | 29.2 | 29.1 | 13.3 | 0.1 |
| Chironomus cf. riparius | 9.6 | 38.8 | 0.0 | 3.8 | 22.8 |
| Pisces | 7.8 | 46.6 | 21.0 | 1.3 | 0.0 |
| Pontogammarus robustoides | 6.4 | 53.0 | 14.6 | 2.3 | 1.3 |
| Polypedilum cf. nubeculosum | 4.8 | 57.8 | 2.8 | 5.1 | 6.1 |
| Sphaeriidae | 4.4 | 62.3 | 0.0 | 7.5 | 3.8 |
| Microtendipes cf. pedellus | 4.3 | 66.5 | 0.0 | 4.8 | 6.8 |
| Gastropoda not identified | 4.2 | 70.7 | 0.6 | 2.4 | 8.0 |
| <i>Hydropsyche</i> sp. larvae | 3.6 | 74.3 | 0.5 | 0.0 | 8.9 |
| Dikerogammarus not identified | 2.4 | 76.7 | 0.3 | 2.7 | 3.4 |
| Rheocricotopus cf. chalybeatus | 2.1 | 78.8 | 0.0 | 3.6 | 1.6 |
| Gammaridae not identified | 1.9 | 80.7 | 1.3 | 2.4 | 1.5 |
| Dicrotendipes cf. nervosus | 1.9 | 82.6 | 0.6 | 3.1 | 1.2 |
| Glyptotendipes cauliginellus pupae | 1.6 | 84.2 | 2.4 | 1.3 | 0.9 |
| Chaetogammarus ischnus | 1.5 | 85.7 | 1.8 | 2.2 | 0.0 |
| Cryptochironomus sp. | 1.4 | 87.1 | 0.0 | 0.0 | 3.6 |
| Dikerogammarus haemobaphes | 1.3 | 88.4 | 0.4 | 1.5 | 1.4 |
| <i>Rheotanytarsus</i> sp. | 1.2 | 89.6 | 0.0 | 1.3 | 1.8 |
| Coleoptera (Gyrinus sp.) | 1.1 | 90.7 | 1.7 | 1.2 | 0.0 |
| Lipiniella moderata | 1.1 | 91.8 | 1.2 | 0.3 | 1.5 |
| Tanytarsini not identified | 1.1 | 92.9 | 0.0 | 0.3 | 2.4 |
| Zygoptera larvae | 1.0 | 93.8 | 2.4 | 0.3 | 0.0 |
| Trichoptera larvae not identified | 0.9 | 94.7 | 0.0 | 0.0 | 2.3 |
| Coleoptera larvae not identified | 0.7 | 95.5 | 0.5 | 0.9 | 0.4 |
| Polypedilum cf. sordens | 0.5 | 95.9 | 0.0 | 1.2 | 0.0 |



Figure 4. Dietary niche width of European perch, racer goby and monkey goby at three study sites Z, R, B, in the Western Bug River calculated as A – Simpson diversity index: 1 – D and B – Shannon diversity index: H.

Discussion

The studied fish species, native European perch as well as non-native racer goby and monkey goby, fed on similar prey taxa, which suggests a high dietary overlap. Nevertheless, more detailed identification of taxa in the most abundant food categories, i.e. chironomid larvae and amphipods, revealed that they foraged on different prey at sites where they co-occurred. Thus, although the majority of prey taxa were recorded in guts of all the three studied fish species, their contribution to the diet at a given site was different. This supports the hypothesis of resource partitioning to avoid competition for food between native and non-native species.

Although several experimental studies showed the higher competitive ability of invader *versus* native species and the greater potential of the former to utilise resources (Kakareko et al. 2013; Grabowska et al. 2016; Mofu et al. 2019), there are mechanisms to avoid such antagonistic interactions in natural environments. One of observed functional responses to introduction of non-native species is trophic niche divergence to minimise the trophic interactions between competing species (Tran et al. 2015; Britton et al. 2018). It facilitates the integration of introduced species into food webs (Britton et al. 2018). Contrary to an expected negative impact of gobies on co-occurring native fish species of similar trophic position, there was no clear evidence for that from field surveys (Piria et al. 2016; Ramler and Keckeis 2019). Instead, spatial segregation between species of the same feeding guild was suggested, which was assumed to arise from different prey dominating the diet, for example, racer goby and native ruff and perch in the Vistula River (Grabowska and Grabowski 2005).

Moreover, our findings proved that accuracy in taxonomic identification of prey taxa is essential to provide reliable data for dietary overlap or resource partitioning assessment. It is especially crucial in the case of fish species, for example, racer goby and monkey goby, feeding on the same type of prey that is very diverse considering its body size and occupied microhabitats. Identification of prey to the lowest possible taxon also allows us to determine the habitat preferences of fish species based on the knowledge of their prey microhabitat preferences. Our results showed that, in the case of gobies, resource partitioning is realised by utilisation of different habitats.

Native perch vs. alien gobies

Both goby species and European perch fed on the macrozoobenthos. The perch is known to shift toward piscivory with its ontogenetic development (Hjelm et al. 2000; Rezsu and Specziár 2006). In our study, only a few individuals of perch, i.e. > 120 mm predate on juveniles of fish. Bleak *Alburnus alburnus*, bitterling *Rhodeus amarus* and unidentified fry of other cyprinids were recorded in its diet in the Bug River. In the case of the studied gobies, we recorded piscivory only in the racer goby, but identification of the prey species was impossible due to the advanced stage of the digestion process. Piscivory was already reported, both for racer goby and monkey goby, but such a food category was not considered important and generally occurred only in the largest individuals (Grabowska and Grabowski 2005; Grabowska et al. 2009; Grabowska et al. 2023).

In general, the diets were more similar between the goby species than between either of the gobies and perch. However, the diet of perch was more similar to that of the racer goby than to that of the monkey goby. Both the Eurasian perch and the racer goby fed on prey that indicated their association with macrophytes. Macrophyte patches are refuges for small fish, as well as hiding places or substrate for several macrozoobenthic groups, such as amphipods, insect larvae, for example, Diptera and Zygoptera larvae or gastropods, that are attractive food for many fish species (Gulati et al. 1990; Van den Berg et al. 1997; Dukowska et al. 2012; Dukowska and Grzybkowska 2014; Grzybkowska et al. 2020). In fact, they were common prey for perch and racer goby in our study.

Amphipods were especially important food items for perch and racer goby in the Bug River. Depending on the site, these fish mainly ate Pontogammarus robustoides or Dikerogammarus villosus and less D. haemobaphes. Field observations have shown that all three species are rather eurytopic (Bacela and Konopacka 2005; Grabowski et al. 2007; Żytkowicz and Kobak 2008). Nevertheless, they show some species-specific habitat preferences. For example, D. villosus and D. haemobaphes were reported to prefer stony substrates (Boets et al. 2010; Clinton et al. 2018). On the other hand, in comparison to adult individuals, juveniles of P. robustoides are known to prefer various macrophytes as their main habitat (Czarnecka et al. 2010). The high contribution of *P. robustoides* to the diet of the racer goby and the co-occurring European perch has also been reported in our earlier studies in the Włocławski Reservoir (Grabowska and Grabowski 2005). Amphipoda are known to be eaten by racer goby in the main channel of the Vistula River and in the large dam-reservoir built on it (Kakareko et al. 2005), as well as in its native range, i.e. in the middle Dnieper River (Pinchuk et al. 2003). Considering chironomid larvae, both perch and racer goby predated relatively large species, such as Glyptotendipens cf. pallens. This morphotype of Glyptotendipes spp. is common in various freshwater habitats (Moller Pillot 2009). Often, it is associated with macrophytes and coarse organic matter (Kornijów 1997; Moller Pillot 2009; Čerba et al. 2022). Glyptotendipes pallens is a plant tissues miner and scraper (Koperski 1998; Beiger 2004), but it also inhabits other types of substrates, for example, plant detritus, wood debris and mud (Moller Pillot 2009; Čerba et al. 2022). Macrophytes are traps for organic matter in running waters and create ideal microhabitats for bottom dwelling chironomids, thus, many Glyptodendipes spp. are common on macrophytes, as well as in mud gathered around them (Grzybkowska et al. 2020). Glyptotendipes sp. were also one of the most important Chironomidae taxa in the diet of racer goby in lowland rivers in the Dnieper River system (Didenko et al. 2021a) where, in line with our findings, the diet of racer goby also indicated its association with plants, as has been reported from the Vistula River (Kakareko et al. 2005). Epiphytic chironomids were found to be the main prey of perch in pondweed (Potamogeton spp.) patches, while typically benthic species were preferred by ruff (Gymnocephalus cernuus) in the lowland Warta River (Dukowska and Grzybkowska 2014). We did not record Chironomus riparius in the diet of perch at any site, while it was quite common in gut content of both goby species, however, with different contributions to the overall species diet. This sediment burrowing chironomid is probably more difficult to obtain by perch, contrary to both goby species, as they have a habit of hiding in sediments (Kakareko 2011), which may give them more opportunities to find C. cf. riparius larvae in mud. However, the European perch, considered to be an epi-benthic predator, was found to penetrate bottom sediments to some depth searching for food in lake littoral, where it fed on large individuals of Chironomus plumosus larvae (Kornijów 1997). Despite that, amongst the same lentic sedimentary benthos communities associated with littoral macrophytes, predation by perch was most intensive on motile invertebrates,

such as isopods and amphipods, while chironomids contributed less to perch diet (Kornijów et al. 2016). This is consistent with our results, suggesting that amphipods may be the most important prey for the European perch.

Both goby species and European perch feed on small gastropods, such as Bithynia sp., Valvata sp. and Potammopyrgus antipodarum, which are also associated with submerged macrophytes (Van den Berg et al. 1997). These gastropods were frequently recorded in the diet of the racer goby in the Włocławski Reservoir (Kakareko et al. 2005). Locally, they were even the dominant food category for that fish species (Kostrzewa and Grabowski 2003). In our study, in comparison with racer and monkey gobies, European perch rarely ate gastropods. Such prey was scarcely reported in previous studies on the diet of perch, even if they were abundant in the macroinvertebrate assemblages (Rezsu and Specziár 2006; Kornijów et al. 2016). Macroinvertebrates of such low mobility are not attractive prey for sight-dependent diurnal predators like perch (Craig 2008; Kornijów et al. 2016). Another food item that differentiated gobies and perch in terms of diet were the Sphaeridae bivalves. That typical benthic group of molluscs was found quite frequently in the diet of both racer and monkey gobies, while none was recorded from perch. Sphaeridae were also an important prey of both goby species in the Vistula River and in the Włocławski Reservoir (Kakareko et al. 2005). Coleopteran larvae were occasional prey of gobies and perch in the Bug River. In the gut content of racer goby, we even found an adult of Gyrinidae. The presence of pleuston organisms, such as whirligig beetles, suggests that racer goby utilised a wider range of microhabitats when searching for food, from the surface of the water to the riverbed. In fact, the diversity of the gobies' diets, especially in the case of racer gobies, was higher than in the case of perch.

In summary, alien gobies, in particular the racer goby, and European perch possibly used similar habitats for foraging, i.e. macrophyte patches in areas of more stagnant water and muddy bottom. However, perch with a body length similar to that of co-occurring gobies, was more piscivorous. The dietary overlap between perch and gobies usually comprised prey items that are very common in the riverine environment, such as amphipods and large chironomid larvae (Dukowska et al. 2012; Dukowska and Grzybkowska 2014). The two fish display different foraging strategies. Perch searches actively for prey, is a sight-dependent diurnal predator (Craig 2008) and prefers rather motile prey that are easier to detect (Kornijów et al. 2016). Activity of the prey seems to be less important for a nocturnal predator, such as the racer goby (Grabowska and Grabowski 2005; Kakareko et al. 2013). In experimental conditions, the racer goby fed equally effectively on immobilised and mobile amphipods, choosing prey species rather according to their quality than their mobility (Błońska et al. 2015), which suggests that, to detect food, the racer goby uses not only sight, but also other senses. Furthermore, perch is morphologically and anatomically better adjusted for active hunting and pursuing escaping prey than gobies that do not possess a swim bladder and have a less streamlined body shape.

Racer goby vs. monkey goby

Racer goby and monkey goby had similar diets. They fed mainly on Chironomidae larvae, on the basis of the relative abundance and frequency of this prey in the fish gut content. The detailed identification of taxa within this food category showed that, in fact, the gobies foraged in different microhabitats, even at the same sites and their mode of foraging was also slightly different. Our study shows that several taxa of chironomids contributed to 60% dissimilarity between the diet of the studied goby species. Chironomids are a prevalent group in the freshwater macrozoobenthos, often standing out in their abundance and species and functional diversity, which makes them key elements of freshwater food webs (Armitage et al. 2012). Their ecological characteristics allow them to fill many niches and serve as a varied functional groups in aquatic ecosystems. Different groups of chironomid larvae are associated with different types of substrate: mud, sand, gravel, stones, plants (Moller Pillot 2009). They inhabit periphytic communities that develop on various hard surfaces or exploit the substrate by drilling into plant or animal tissue, mining wood, burrowing into the sediment surface or attaching to the bodies of other invertebrates (Moller Pillot 2009; Grzybkowska et al. 2016; Antczak-Orlewska et al. 2021). Chironomid larvae, being such a diverse group of macroinvertebrates and important food for many aquatic organisms, can be used as an additional indicator of habitat preferences, based on their contribution to the predator's diet.

Glyptotendipes cf. pallens dominated amongst chironomid larvae in the diet of racer goby. In summer, this taxon can be found in silty tubes built on macrophytes, mining in their decaying parts, but also on other firm surfaces, such as decaying wood or stones. In large rivers, in particular, the larvae of this species are more numerous on stones than on plants. This taxon avoids fast running waters and prefers more stagnant parts of the river channel (Moller Pillot 2009). Similarly, racer goby is more abundant in lentic areas, where it prefers habitats with a muddy bottom and moderate macrophyte cover, but also stones, for example, rip-raps along the river banks (Kakareko 2011; Płąchocki et al. 2020) or single stones scattered on the bottom (Kakareko et al. 2016). Thus, the high abundance of G. cf. pallens in the racer goby diet derives from similarity in habitats occupied by the prey and its predator. In addition to Glyptotendipes cf. pallens, the other chironomids associated with macrophytes (Dicrotendipes nervosus and Polypedilum sordens) were found in the gut content of the racer goby more frequently and in higher abundance than in the gut of the monkey goby. Similar chironomid taxa also dominated the racer goby diet in the Dnieper River system (Didenko et al. 2021a, b). Another indicator of racer goby habitat preferences are chironomids that use stones as one of the possible substrates, such as *Rheocricotopus chalybeatus*, which also frequently settles on plants and uses stones if plants are unavailable (Moller Pillot 2013). The R. cf. chalybeatus was recorded in the gut of racer goby more often than in monkey goby at two out of the three sites. Compared to racer goby and perch, the monkey goby ate many large larvae of the Chironomus cf. riparius. This pelophilous species is very common in chironomid communities associated with mud and sand, but sometimes also with submerged aquatic plants, burrowing in soft sediment trapped by the roots (Dukowska and Grzybkowska 2014; Grzybkowska et al. 2020; Leszczyńska et al. 2021). The species can be very numerous also on stones or concrete bottoms covered by a thin layer of mud (Moller Pillot 2009). Chironomus riparius is often considered to be a characteristic inhabitant of flowing waters, also fast-flowing sections of brooks and streams and even rapids, providing that the organic silt is on the bottom, as it feeds on organic particles. It was also recorded as the dominant chironomid taxon in the diet of monkey goby in the Vistula River and less numerous in the gut content of the co-occurring racer goby, which eats mainly epiphytic species (Kakareko et al. 2005). The monkey goby is usually associated with sandy or gravelly bottoms in lotic parts of rivers, while it is less abundant at sites with moderate vegetation cover (Kakareko 2011; Płąchocki et al. 2020). It also prefers higher

water velocity in comparison to the racer goby, as has been shown experimentally (Kakareko 2011) and can be found more often in the main flow of the river, where there are spots with slower water velocity caused by varied obstacles, such as macrophytes or stones. The latter form refuges for several organisms that are prey for fish, for example, for monkey goby. Such patches of macrophytes and stones covered by periphyton and accumulating sediment rich in organic matter, are very productive (Grzybkowska et al. 2020). Besides C. cf. riparius, other chironomid bottom-dwellers are more frequent in monkey goby gut content than in racer goby, for example, Cladopelma gr. viridulum, Cryptochironomus, Lipiniella moderata, Microtendipes cf. pedellus, Stictochironomus cf. rosenschoeldi (Brooks et al. 2007; Moller Pillot 2009). Some chironomid taxa recorded in the diet of monkey goby are typically associated with a fast water current and stony gravel substrate (e.g. R. cf. chalybeatus, Rheotanytarsus sp.) or with sand like, for example, Lipiniella moderata (Moller Pillot 2009; Klukowska et al. 2011). Moreover, the considerable contribution of caseless Trichoptera larvae, for example, Hydropsyche sp., which use water current to catch suspended organic matter, is another indicator that monkey goby occurs in lotic habitats (Stuijfzand et al. 1999). This supports the hypothesis of niche separation between the monkey goby and the racer goby and concurs with previous findings that monkey goby consumed mainly sand- and mud-dwelling, burrowing chironomids, while the racer goby has a more diverse diet, including both bottom-dwelling burrowing and phytophilous morphotypes of Chironomidae, as well as other macrophyte-associated macroinvertebrates (Kakareko et al. 2005; Didenko et al. 2022b). Shift in diel feeding activity can be another way to avoid food competition between co-occurring alien gobies. The racer goby is predominantly a nocturnal feeder (Grabowska and Grabowski 2005; Kakareko et al. 2013), while the monkey goby is more active during the day (Didenko et al. 2017) or shows no difference between day and night (Grabowska et al. 2009). Similarly, the co-existence of the other invasive gobies, i.e. round goby (Neogobius melanostomus) and big head goby (Ponticola kessleri) in the middle Danube River was suggested to be possible by resource partitioning and slightly different feeding strategy (Števove and Kováč 2013). The previously published revisions of ecological interactions of five alien Ponto-Caspian gobies in their non-native range (Kornis et al. 2012; Grabowska et al. 2023) emphasised that they are a diverse group considering their ecological demands and functional ecology, including types of prey (e.g. Didenko et al. (2022b)) and diet shift with ontogeny (e.g. Števove and Kováč (2016)); thus, their invasions in European inland waters impact native biota in diverse ways.

To conclude, we show that detailed prey identification to the lowest possible taxon is crucial to properly justify the diet overlap between co-occurring fish species and to verify the suggested impact of alien invaders on native species through interspecific competition. Resource partitioning considering prey types and foraging habitats is one of the ways of allowing the co-existence of closely-related alien gobies with similar food preferences in the invaded waters and their co-occurrence with local fish species. Together with an opportunistic feeding strategy, it is likely to be a major factor behind their invasion success observed in European waters in the last decades. We therefore recommend that, in order to gain more detailed insights into the foraging strategy of fish, in future studies, researchers should not limit their dietary analysis only to the identification of higher taxa, but should identify prey down to the lowest possible level, especially in taxonomic groups consisting of species that differ in the microhabitats they occupy.

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

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Data availability

All of the data that support the findings of this study are available in the main text or Supplementary Information.

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Supplementary material 1

Relative abundance of species (%N) in fish assemblages found at sites Z, R, B in the Western Bug River in August 2007 (Penczak et al. 2010)

Authors: Joanna Grabowska, Mateusz Płóciennik, Michał Grabowski

Data type: xlsx

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Supplementary material 2

Relative abundance of prey categories (%N) (number of given prey category in relation to total number of prey) identified in fish guts at sites Z, R, B in the Western Bug River in August 2007

Authors: Joanna Grabowska, Mateusz Płóciennik, Michał Grabowski

Data type: xlsx

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Book Review

Wattles on the move

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Travelling through parts of South Africa or Iberia, such as north-western Portugal, it would be easy to imagine that one is in the heart of the Australian bush, such is the abundance, prominence and diversity of species of Australian acacias that are now found in these areas. *Acacia*, a genus of more than 1,000 species of shrubs and small to medium-sized trees – known generically in Australia as "wattles "– now dominate significant areas in parts of the world where they are introduced. In Portugal, alongside the wattles, are large-scale plantations of eucalypts, further accentuating just how 'Australian' some of these distant habitats have become. It is this process of the globalisation via introductions and invasions of wattles that is the focus of a new book: "Wattles. Australian *Acacia* Species Around the World", published by CABI in 2023, and edited by David Richardson, Johannes Le Roux and Elizabete Marchante, who appropriately work respectively in South Africa and Portugal.

While it is well-known that the large, mainly Australian, legume genus *Acacia* is now one of the planet's most widely spread plant genera, the sheer scale and extent of its anthropogenic translocation are quite staggering. As documented in this new book, 41% of the 1082 species of *Acacia*, i.e. 417 species, are known to occur as non-natives; introduced *Acacia* species have been recorded from 172 countries; 75



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species have established self-sustaining populations following introductions; 28 species are classified as invasive and causing substantial ecological and socio-economic impacts. This global tallying up of the history of introductions and their current status is an impressive achievement of this book, establishing a global database and baseline for future comparisons and analyses. It is also notable that the sheer scale of translocation of so many species of wattles to different regions across the world opens opportunities for understanding the drivers and trajectories of plant invasions via large scale comparative studies of species and regions. For example, what are the relative contributions of variation in intrinsic species biology versus extrinsic factors in dictating the outcomes of introductions? Similarly, why have the impacts of introduced species been apparently much more benign in some regions than others? This scope to address general questions make wattles a flagship group for understanding invasion biology. Quite simply, Australia's wattles are among the plants that are central to the unfolding story of neobiotic species in the Anthropocene.

This book explores in great depth and breadth the insights that can be gained from understanding these plants. With 122 authors from 17 countries, spanning a wide range of disciplines, this book represents a goldmine of knowledge about the ecology, evolutionary biology, biogeography and macroecology, utility and invasiveness of the genus *Acacia*, the second largest genus of legumes (Fig. 1), and its spectacular conquest of the world.

The book starts with a series of chapters that presents a synthesis of the taxonomy, environmental amplitudes and functional trait and genetic attributes of the vast natural species pool encompassed by the genus Acacia, linking that knowledge to the invasion status and invasiveness potential of species. This is followed by a set of chapters documenting the history of introduction, spread and invasion of acacias, dubbed the Anthropocene conquest of the globe by the wattles. This synthesis is based around detailed regional studies in Europe, California, Africa, Brazil/ Chile, and New Zealand, including data on the utility and perceptions of wattles by people around the world. Next, follow chapters on the biology of interactions between Acacia and other groups of organisms - symbionts, seed dispersers, pollinators, and pests and diseases - biology that underpins our understanding of why wattles are such successful invaders. It is this biological knowledge that also provides the basis for developing potential biological control and management options in areas where wattles have invaded. There are then chapters devoted to assessments of the impacts - social, economic and ecological - of Acacia introductions and invasions. The final section of the book is devoted to discussing ways to control, monitor, manage and model wattle invasions. The concluding chapter, entitled the 'Wattles' Invasion Syndrome, attempts to encapsulate the key elements of why acacias are such prominent travellers and invaders. This is neatly summed up in the book as Woody Australian Trees that Transform landscapes: Leguminous, Enemy-free, with persistent Seedbanks, i.e., WATTLES!, a syndrome that may be applicable to other groups of woody plant invaders.

In common with many invasive tree species and genera that have been moved around the globe, wattles stand out as conflict trees. This is because they were usually introduced deliberately for forestry, agroforestry, soil stabilisation and as ornamental garden plants and can confer important economic, environmental or aesthetic benefits, but at the same time bring with them environmentally transformative impacts in the form of species invasions. These impacts include even the establishment of novel ecosystems, so-called "wattle jungles" or thickets, following



Figure 1. A selection of the 28 species of Australian *Acacia* that are invasive where introduced, showing growth forms, leaves, flowers and fruits **A** tree of *Acacia mearnsii*, Bridgetown, Western Australia **B** tree of *A. dealbata* subsp. *dealbata* in full flower **C** phyllodes (modified leaves) and spicate inflorescences of *A. longifolia* subsp. *sophorae* **D** bipinnate leaves and capitate inflorescences of *A. dealbata* subsp. *dealbata* **E** fruits and seeds with fleshy arils of *A. auriculiformis*. Photos courtesy of Bruce Maslin (**A**), Alan Gibb (deceased) (**B**), Lachlan Copeland (**C**), Alan Gibb (D), Kym Brennan (**E**).

invasion or abandonment of *Acacia* plantations. This book achieves a well-balanced perspective on what can often be polarised views of such conflict trees, giving attention to both the positive benefits and negative impacts of introductions. In that context, the book includes chapters devoted to sociological, not just biological and ecological aspects. This is important in revealing, for example, that planting intensity and scale, especially for forestry, is one of the principal determinants of whether species become invasive or not, and that changing perceptions about the value and utility of species are likely key determinants of future invasive trajectories. Above all, what comes across is that the social-ecological dynamics of wattle introductions and perceptions of their utility and value, are indeed dynamic, are far from stable through time, and are likely to continue to change in a rapidly changing world.

This importance of history and shifting perceptions through time is also amply revealed by the contributions in this book. The successive waves of interest in exporting and importing species of wattles at different times in history in different parts of the world are documented. The most recent wave of spread has resulted in by far the largest wattle production areas on the planet spanning millions of hectares of wattle plantations in south-east Asia over the last few decades (e.g. 6% of Vietnam's land area in the last 20 years). Given this recent Acacia boom in south-east Asia it is perhaps a pity that no chapter focused specifically on the history and status of introductions in that region was included alongside the other regional syntheses. Nonetheless, this minor criticism does not detract from the overall global panorama that stands out in this book. This panorama demonstrates that, in addition to comparative biological and biogeographical data, wattle introductions and invasions also present a valuable comparative time series that can provide further potent insights into invasions more generally.

This book presents an outstanding global synthesis of the biology, ecology, biogeography and management of one of the most important groups of tree invaders globally. It is essential reading not just for those with a specific interest in wattles, but to everyone working on the biology and ecology of species invasions more generally.

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Additional information

Conflict of interest

The author has declared that no competing interests exist.

Ethical statement

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Author contributions

The author solely contributed to this work.

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Data availability

All of the data that support the findings of this study are available in the main text.



Research Article

Impacts of native and alien plant dominants at different spatial scales

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Abstract

Plant invasion science has made a substantial progress in documenting the impacts of aliens, but comparisons with the impacts of native dominants are still rare. Further, the impacts on larger spatial scales remain poorly understood. We recorded the impacts of 10 native and nine invasive dominant plants in the Czech Republic on species richness and Shannon diversity by comparing communities with high vs. low cover of the dominant species. To estimate the impacts at the (i) population level and (ii) between-population level, we compared the Jaccard dissimilarity, nestedness and turnover of high- and low-dominance plots. Further, we calculated the Jaccard dissimilarity, nestedness and turnover between the high- and low-dominance plots within each population to express the impacts on species composition. We tested whether (i) native and invasive dominants affect the populationand between population levels of diversity by making the vegetation more homogenous; (ii) whether these effects differ between the native and alien dominants; and (iii) whether the impacts at different spatial levels are related. At the population level, high-dominance plots (with both native and alien dominants) showed higher nestedness and lower turnover compared to the low-dominance plots. Further, all plots with native dominants, both with high- and low dominance, showed higher similarity but lower nestedness than plots with alien dominants. Most importantly, high-dominance plots with native dominants were more similar to each other but showed marginally significantly lower nestedness compared to high-dominance plots with alien dominants. At the between-population level, high-dominance plots with native dominants showed a marginally significantly lower turnover compared to high-dominance plots with alien dominants. The differences in Jaccard dissimilarity, nestedness and turnover between the low- and high-dominance plots at the population level showed strong positive relations to low- and high-dominance differences at the between-populations level. Further, compositional impacts, expressed as the dissimilarity between high- vs. low-dominance plots, positively related to the plot-level impacts on Shannon diversity. Our results show that (i) both native and invasive dominants tend to reduce the diversity over larger areas and that the effect of native dominants may be even stronger, and (ii) the effects on plot-level richness and diversity cannot be easily extrapolated to larger scales but the impacts at the population- and between-populations levels are positively related.

Key words: Alien dominants, beta diversity, impacts, native dominants, spatial scale



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Introduction

In the last decades, progress has been made toward documenting the community-level impacts of invasive plants (e.g. Hejda et al. 2009; Vilá et al. 2011; Pyšek et al. 2020), which includes comparisons between the impacts of native vs. alien dominants (Paolucci et al. 2013; Buckley and Catford 2016; Hejda et al. 2017, 2019; Pergl et al. 2023). However, the impacts of native dominants on the species richness and diversity are still rarely studied (but see Pivello et al. 2018; Hejda et al. 2021), even though it can be presumed that their impacts are comparable to that of invasive dominants, given their aggressive spread and high-levels of dominance (e.g. Hejda et al. 2021). In this sense, many natives behave like so-called "superdominants" (Pivello et al. 2018), with expected strong impacts on species richness, diversity and composition. The association between high levels of dominance and lower species richness has long been established (e.g. Able and Noon 1976) and, at the same time, shifts in dominance are usually apparent earlier than the reduction in species richness, which makes dominance an important indicator of the global change (Chapin et al. 2000). Further, dominant aliens can not only change species richness but also the proportional representation of individual species in the community (Hillebrand et al. 2008). However, how these community-level impacts scale up to larger areas remains mostly unexplored, with the few results so far being rather contradictory (see, e.g. Martin and Wilsey 2015; Dyderski and Jagodzinski 2021). Similarly, previous studies comparing the effects of alien and native dominants have focused on changes in species richness (alpha diversity, e.g. Czarniecka-Wiera et al. 2019), whereas changes in species composition (beta diversity) remain less explored.

There are several ways to define diversity at different spatial scales. A plot-level diversity generally refers to alpha diversity, as it usually represents species richness or diversity measured at scales ranging from 1 m² to a few hundred m². The scale of alpha diversity also represents an important issue, as the number of species sampled increases non-linearly with increasing spatial scale (Gotelli and Colwell 2001), which can lead to different shapes of species-accumulation curves. The scale of wegetation can have very different shapes of species-accumulation curves (Gotelli and Colwell 2001; Roswell et al. 2021). Further, there is a question on how to define beta diversity or a large -scale diversity in general. A common definition of beta diversity is the variation in species composition amongst distinct sites in a particular geographical location (Whittaker 1960). One approach is to partition the regional gamma diversity into within-alpha diversity and between-beta diversity components.

It is evident that when measuring the effects on alpha diversity, the small-scale (plot-level) effects cannot be easily extrapolated to larger scales (Chase et al. 2018). Further, the changes in plot-level richness (or alpha diversity) provide only a limited view of the changes in diversity, and it is necessary to include information on the spatial changes in species composition (Chase et al. 2018, 2019). For example, changes in composition can happen even without changes in the number of species (e.g. species replacement whilst the total number of species remains equal).

A theoretical paper by Socolar et al. (2016) suggests four basic mechanisms for how beta-diversity may be enlarged or reduced: (i) additive heterogenization, when locally specific species are added; (ii) additive homogenization, when common and spatially unspecific species are added; (iii) subtractive heterogenization, when common species disappear, become rare or locally specific; and (iv) subtractive homogenization, when rare or locally specific species disappear. It is most likely the interplay of all these effects that drive changes in large-scale diversity patterns. However, it can be presumed that the mechanism of "subtractive homogenization" plays a major role, as the dominant plants are documented to reduce local species richness and diversity (e.g. Hejda et al. 2021).

The case studies focused on the role of dominant species provide contradictory results and show that native dominant species can result in stronger biotic homogenization than aliens (Dyderski and Jagodziński 2021). Schlegel and Riesen (2021) reported that the native dominant Pteridium aquilinum suppressed the alpha diversity and eliminated the Red-Listed species of Orthoptera but, at the same time, increased beta diversity over large scales. On the contrary, Fukami et al. (2013) documented that alien dominants prevented the vegetation from diverging during succession, reducing riparian vegetation's beta diversity. Martin and Wilsey (2015) showed that the diversity of native- vs. alien-dominated grasslands differed along a north-south gradient (from Minnesota to Texas, USA) with regard to the spatial scale. The local diversity was consistently higher in native-dominated grasslands, and regional diversity was higher in the native-dominated grasslands in the north of the area studied, while alien-dominated grasslands had higher diversity in the south, and the diversity of the alien-dominated grassland was generally greater across the whole area. The authors suggested several mechanisms to interpret this somewhat surprising pattern, including present and past patchiness and inter-patch connectivity, disturbance history, or present and past management (Martin and Wilsey 2015).

This paper aims to address these issues by analysing plant community data sampled across the Czech Republic, central Europe. In particular, we aim to test the following questions: (i) Do the local, plot-level impacts of native and alien dominants on species richness and diversity scale up to the within- and across-population levels (ii) Do these effects differ between the native and invasive alien dominants? (iii) Are the effects of dominants recorded at different spatial scales related or independent?

Methods

Sampling design

We sampled populations of 10 native (*Calamagrostis epigejos, Cirsium arvense, Cirsium heterophyllum, Cirsium oleraceum, Filipendula ulmaria, Petasites hybridus, Phalaris arundinacea, Rubus idaeus, Tanacetum vulgare,* and *Urtica dioica*) and nine invasive dominant plants (*Aster novi-belgii* agg., *Heracleum mantegazzianum, Impatiens glandulifera, Lupinus polyphyllus, Reynoutria japonica, Reynoutria × bohemica, Rumex alpinus, Solidago canadensis,* and *Telekia speciosa*; Suppl. material 1). We sampled plots of 4×4 m in size located within populations of studied species across the Czech Republic (Suppl. material 2) that ranged from hundreds to thousands of m² in size (see Hejda et al. 2021 for details on the sampling scheme); the populations were selected so as to include stands with high and low dominance of the target dominant species. Low dominance referred to 0–25% cover of the target species, and these low-cover plots were used as controls. On the contrary,

high dominance encompassed >50% of the dominant species cover (see Hejda et al. 2021 for details). We then estimated the local impacts of these dominant species on species richness and Shannon diversity index of invaded communities, as well as on species composition.

Diversity measure

To detect the changes in species composition associated with the dominant species, we calculated the Jaccard dissimilarity index, which is based on incidence data (Jaccard 1900) and regarded as robust to taxonomic error as well as both numerical and geographical undersampling (Schroeder and Jenkins 2018).

We calculated the Jaccard dissimilarity index (β_{jac}) at the (i) population-level (= dissimilarity of plots within populations); and (ii) between-population level (= dissimilarity of plots between populations), using the beta.pair function (index. family="jaccard") of the betapart package (Baselga 2013; R Core Team 2022). The values of the index range from 0 (maximum similarity or lowest dissimilarity) to 1 (minimum similarity or highest dissimilarity). The following formula was used:

$$\beta_{jac} = \frac{b+c}{a+b+c}$$

where *a* is the number of species in common between two sites, *b* is the number of species unique to the site with the lowest number of species, and *c* the number of species unique to the site with the largest number of species.

Total Jaccard can be partitioned into turnover (β_{jtu}) and nestedness component (β_{inc}) :

$$\beta_{\rm jac} = \beta_{\rm jtu} + \beta_{\rm jne} = \frac{2b}{(2b+a)} + \left(\frac{c-b}{a+b+c}\right) \left(\frac{a}{2b+a}\right)$$

Nestedness refers to changes in species richness, in which the site with the lowest richness represents a subset of species of the richest site, and turnover, which refers to species replacement from site to site (Baselga and Orme 2012) (see Fig. 1 for a schematic representation of turnover and nestedness).

We estimated the population- and between-population level impacts as differences in similarity between the plots with low vs. high dominance of the selected dominants, assuming that this represents the homogenizing effect of the dominant species (see Fig. 2 for a schematic representation of our sampling design and how the diversity metrics were calculated at distinct spatial scales).

At the population level, we calculated Jaccard, turnover and nestedness amongst all high-dominance plots and amongst all low-dominance plots to each population of each species. We then recorded the median value in each population with high-dominance plots and compared them with the corresponding median values of the low-dominance plots.

Further, we compared the total Jaccard, nestedness and turnover of high-dominance plots with native vs. alien dominants to compare their homogenizing effect. In the case of the population-level impacts, we also calculated the Jaccard dissimilarity, nestedness and turnover between the high- and low-dominance plots within each population to express the population-level impact on species composition, assuming that the lower similarity between the low and high dominance plots (within populations) shows a larger impact on species composition. Here, to tackle the challenge of



Figure 1. Schematic representation of the partitioning of the Jaccard dissimilarity index into turnover and nestedness components (see text for the formula and more information). Turnover refers to the gain and loss of species (species replacement) between the areas (e.g. high dominance plots of a particular dominant species), whereas nestedness refers to the cases where the plot with the lowest number of species represents a subgroup of species of the richest plot/site. In the scheme, the species in blue are unique to plots A and C, the species in black are shared between both plots and the species in orange are unique to plot B.



Figure 2. Scheme of our sampling design and how the impacts were estimated. The plot level is marked with blue arrows, the population level is marked with dashed green arrows, and the between-population level with the dashed orange arrows. In each population, the median value across all high-dominance plots and the median value across all low-dominance plots were computed; these median values of high and low-dominance plots were then compared in the analyses.

comparing different numbers of high and low dominance plots, given that the high vs low combination itself is substantially higher than high vs. high and low vs. low, we combined all high-dominance plots of a population as a single "high dominance plot", and similarly for a single "low dominance plot". Thus, in each population of each species, we recorded a single direct dissimilarity distance of high vs. low-dominance plots.

To express the plot-level impacts, we used LMM regression models to relate the plot-level species richness and Shannon diversity to the cover of selected dominants, accounting for the identity of dominant species and their populations (nested in "dominants") by setting these as random effects. We quantified the plot-level impacts as the slope/intercept ratios of the corresponding LMM regression models, accounting for the a priori different species richness and diversity of different types of vegetation (see Hejda et al. 2021 for details on data processing and analyses).

Further, we used LMM models to compare the similarity, nestedness and turnover of low- vs. high-dominance plots at the population- and between-population levels and the effects of native vs. alien invasive dominants. Further, we used parametric and non-parametric correlations to test the relationships between the effects at different spatial levels.

Results

Impacts at the population level

At the population level, high-dominance plots with both native and alien dominants taken together showed higher nestedness and lower turnover compared to all low-dominance plots (p = 0.018 and p = 0.002, resp.). In other words, sites with high dominance were linked to a higher degree of nestedness (which in turn is related to species losses), consistently for both alien and native dominants (see Table 1).

Considering all plots with native dominants (high and low dominance plots taken together) vs. all plots with alien dominants, we found that the former were more similar to each other but also had a lower nestedness than plots with alien dominants (p = 0.039 and p = 0.043, respectively, Table 2, see also Suppl. material 3 for the details on statistical tests).

Comparing high-dominance plots with native and alien dominants, we found that the former showed lower Jaccard dissimilarity (i.e., were more similar), whereas the latter had marginally significantly higher nestedness (p = 0.045 and p = 0.072, resp). In other words, plots with a high native dominance had more species in common than plots with a high dominance of aliens, where the species loss was stronger.

Considering the low-dominance plots, no significant differences in Jaccard, nestedness or turnover were detected between native and alien dominants. At the population level, no significant differences between the effects of native vs. alien dominants (defined as differences in dissimilarity, nestedness and turnover between the low- and high-dominance plots) were found (Table 1).

Impacts at the between-population level

High-dominance plots with alien dominants showed higher species turnover compared to high-dominance plots with native dominants, but this difference is only marginally significant (p = 0.051, Table 2). Comparing high and low-dominance plots within the same origin of dominants, native dominants show lower levels

| Origin of the dominant species | plot dominance | Jaccard dissimilarity | S.D. | nestedness | S.D. | turnover | S.D. |
|--------------------------------|----------------|-----------------------|-------|------------|-------|----------|-------|
| native and alien | high | 0.306 | 0.233 | 0.048 | 0.07 | 0.213 | 0.205 |
| native and alien | low | 0.347 | 0.261 | 0.029 | 0.04 | 0.302 | 0.241 |
| native | high and low | 0.284 | 0.233 | 0.034 | 0.05 | 0.227 | 0.214 |
| alien | high and low | 0.374 | 0.255 | 0.045 | 0.065 | 0.291 | 0.238 |
| native | high | 0.267 | 0.216 | 0.04 | 0.06 | 0.19 | 0.192 |
| alien | high | 0.35 | 0.244 | 0.058 | 0.079 | 0.238 | 0.217 |
| native | low | 0.299 | 0.25 | 0.027 | 0.035 | 0.261 | 0.229 |
| alien | low | 0.399 | 0.266 | 0.031 | 0.044 | 0.344 | 0.248 |
| native | low v high | 0.033 | 0.34 | -0.013 | 0.072 | 0.073 | 0.316 |
| alien | low v high | 0.049 | 0.386 | -0.027 | 0.081 | 0.106 | 0.344 |

Table 1. Jaccard dissimilarity, nestedness and turnover values as recorded at the population level. Each consecutive line represents the comparison being made (e.g. high and low plot dominance of all dominants taken together). Values differing significantly are in **bold** (p<0.05), values differing marginally significantly are in *italics* (p<0.1). Please see the Suppl. material 3 for more details on statistical models.

Table 2. Jaccard dissimilarity, nestedness and turnover values as recorded at the between-population-level. Values differing marginally significantly are in *italics*. Please see the Suppl. material 3 for more details on statistical models.

| Origin of the dominant species | plot dominance | Jaccard dissimilarity | S.D. | nestedness | S.D. | turnover | S.D. |
|--------------------------------|----------------|-----------------------|-------|------------|-------|----------|-------|
| native and alien | high | 0.296 | 0.126 | 0.032 | 0.035 | 0.194 | 0.114 |
| native and alien | low | 0.357 | 0.146 | 0.015 | 0.011 | 0.311 | 0.153 |
| native | high and low | 0.287 | 0.083 | 0.022 | 0.033 | 0.21 | 0.123 |
| alien | high and low | 0.371 | 0.172 | 0.025 | 0.02 | 0.299 | 0.159 |
| native | high | 0.263 | 0.035 | 0.03 | 0.045 | 0.146 | 0.082 |
| alien | high | 0.333 | 0.177 | 0.034 | 0.024 | 0.247 | 0.125 |
| native | low | 0.311 | 0.11 | 0.015 | 0.012 | 0.275 | 0.126 |
| alien | low | 0.408 | 0.169 | 0.016 | 0.01 | 0.35 | 0.178 |
| native | low v high | -0.049 | 0.111 | 0.014 | 0.047 | -0.129 | 0.186 |
| alien | low v high | -0.074 | 0.334 | 0.019 | 0.024 | -0.103 | 0.286 |

of turnover in high-dominance plots compared to low-dominance plots, whereas alien dominants show higher levels of nestedness in high-dominance plots compared to low-dominance plots (Fig. 3). Similarly to the population level, no differences in the effects of native vs. invasive dominants, defined as the dissimilarity differences between the low- and high-dominance plots, were detected at the between-population level (Table 2).

Relations between the impacts at different spatial scales

No significant relationships between the impacts recorded at the plot- and either population- or between-population levels were detected (Table 3). On the contrary, strong positive relationships between the population- and between-population level impacts were found for Jaccard dissimilarity, nestedness and turnover (Table 3). These strongly significant positive relationships were identified using both parametric (Pearson) and non-parametric correlations (Spearman, Kendall; see Suppl. material 3 for the results of non-parametric correlations).

| spatial level I | spatial level II | measure I | measure II | Pearson correlation | p-value |
|-----------------|--------------------|-----------------------|-----------------------|---------------------|---------|
| plot | population | species richness | Jaccard dissimilarity | 0.283 | 0.24 |
| plot | population | Shannon diversity | Jaccard dissimilarity | 0.123 | 0.616 |
| plot | population | species richness | nestedness | 0.03 | 0.904 |
| plot | population | Shannon diversity | nestedness | -0.052 | 0.833 |
| plot | population | species richness | turnover | -0.259 | 0.285 |
| plot | population | Shannon diversity | turnover | -0.093 | 0.704 |
| plot | between-population | species richness | Jaccard dissimilarity | -0.172 | 0.483 |
| plot | between-population | Shannon diversity | Jaccard dissimilarity | -0.085 | 0.73 |
| plot | between-population | species richness | nestedness | 0.074 | 0.763 |
| plot | between-population | Shannon diversity | nestedness | 0.092 | 0.707 |
| plot | between-population | species richness | turnover | -0.171 | 0.483 |
| plot | between-population | Shannon diversity | turnover | -0.075 | 0.761 |
| population | between-population | Jaccard dissimilarity | Jaccard dissimilarity | 0.963 | p<0.001 |
| population | between-population | nestedness | nestedness | 0.777 | p<0.001 |
| population | between-population | turnover | turnover | 0.911 | p<0.001 |

Table 3. Relations between the impacts at different spatial levels for alien and native dominants taken together. The impacts at the plot-level are defined as the slope/intercept ratios of regression models relating the plot-level richness or Shannon diversity to the cover of the target dominant. The impacts at the population and between-population levels are defined as differences in dissimilarity between the high- and low-dominance plots. Significant relations are in bold. Please see the Suppl. material 3 for more details on statistical models.



Figure 3. Between-population level results for all species. Each dot represents the median value across all sites of the same species at a certain dominance category (high or low); each line connects the dominance category of a species. Alien dominants (a-c) show higher levels of nestedness in high-dominance plots compared to low-dominance plots, whereas native dominants (d-f) show lower levels of turnover in high-dominance plots compared to low-dominance plots. Alien species: An: *Aster novi-belgii* agg., Hm: *Heracleum mantegazzianum*, Ig: *Impatiens glandulifera*, Lp: *Lupinus polyphyllus*, Rj: *Reynoutria japonica*, Rb: *Reynoutria ×bohemica*, Ra: *Rumex alpinus*, Sc: *Solidago canadensis*, Ts: *Telekia speciosa*; native species: Ce: *Calamagrostis epigejos*, Ca: *Cirsium arvense*, Ch: *Cirsium heterophyllum*, Co: *Cirsium oleraceum*, Fu: *Filipendula ulmaria*, Ph: *Petasites hybridus*, Pa: *Phalaris arundinacea*, Ri: *Rubus idaeus*, Tv: *Tanacetum vulgare*, Ud: Urtica dioica.
We found strong positive relationships between the plot-level impacts on Shannon diversity and population-level impacts on species composition, expressed as the similarity between the low- and high-dominance plots within each population (Table 4). We also detected a strong negative relation between the turnover at the population level (the turnover component of the population-level compositional impacts) and the impacts on the turnover of species at the between-population level (expressed as the differences in turnover between the low- and high-dominance plots). Similarly to the previous finding, the relationship between the turnover component of the population-level compositional impacts and the turnover component of the between-population-level impacts was significant when both parametric (Pearson correlation) and non-parametric methods (Spearman and Kendal correlation; see Suppl. material 3) were used.

Discussion

Impacts at the population level

At the population level, high-dominance plots show higher nestedness and lower turnover than low-dominance plots. In other words, taking alien and native species together, the high-dominance plots lose more species in a nested pattern, and the species replacement is lower than in the low-dominance plots. However,

Table 4. Relations between impacts at the plot-, population- and between-population-levels and compositional impacts at the population-level. These refer to the direct low v. high dominance comparison. The impacts at the plot-level are defined as the slope/intercept ratios of regression models relating the plot-level richness or Shannon diversity to the cover of the target dominant. The impacts at the population and between-population levels are defined as differences in dissimilarity between the high- and low-dominance plots. Compositional impacts at the population level are defined as the dissimilarity between the low- and high-dominance plots within each population. Please see the Suppl. material 3 for more details on statistical models.

| Comparison group | level I | level II | impact I | impact II | Correlation |
|---------------------|------------------|--------------------------------|--|--|-------------------|
| А | population-level | plot-level (species richness) | low-high dissimilarity (Jaccard dissimilarity) | slope/intercept ratios | 0.45 (p = 0.053) |
| А | population-level | plot-level (species richness) | low-high dissimilarity (nestedness) | slope/intercept ratios | |
| А | population-level | plot-level (species richness) | low-high dissimilarity (turnover) | slope/intercept ratios | |
| А | population-level | plot-level (Shannon diversity) | low-high dissimilarity (Jaccard dissimilarity) | slope/intercept ratios | 0.586 (p = 0.008) |
| А | population-level | plot-level (Shannon diversity) | low-high dissimilarity (nestedness) | slope/intercept ratios | |
| А | population-level | plot-level (Shannon diversity) | low-high dissimilarity (turnover) | slope/intercept ratios | |
| В | population-level | population-level | low-high dissimilarity (Jaccard dissimilarity) | low-high differences (Jaccard dissimilarity) | |
| В | population-level | population-level | low-high dissimilarity (nestedness) | low-high differences (nestedness) | |
| В | population-level | population-level | low-high dissimilarity (turnover) | low-high differences (turnover) | |
| С | population-level | between-population-level | low-high dissimilarity (Jaccard dissimilarity) | low-high differences (Jaccard dissimilarity) | |
| С | population-level | between-population-level | low-high dissimilarity (nestedness) | low-high differences (nestedness) | |
| С | population-level | between-population-level | low-high dissimilarity (turnover) | low-high differences (turnover) | -0.530 (p = 0.02) |

no significant difference in Jaccard dissimilarity between the low- and high-dominance plots was recorded at the population level, suggesting that the high-dominance plots are not necessarily less diverse and more homogenous than the adjacent low-dominance plots. Apparently, distinctive dominants can lower the local, plot-level (alpha) diversity without affecting the large-scale diversity expressed by the beta diversity indices. However, Kortz and Magurran (2019) found a contrasting pattern: the presence of aliens was associated with an increase in the local diversity, as areas with more aliens tend to have more species, but decreased the large-scale (beta) diversity, by making the vegetation more homogenous due to adding commonly shared aliens amongst the areas. A similar pattern was detected by Nobis et al. (2016): the local richness of native and alien species was positively related. However, the richness of alien species was negatively related to native beta and gamma diversity, which especially concerned red-listed species. Importantly, the fact that aliens contribute to plot-level diversity precludes the competitive exclusion of native species by dominant aliens.

The homogenizing effect of alien dominants was described for some aliens, such as the amphibious *Althernanthera philoxeroides* (Wu et al. 2022). The large-scale impacts of this species were context-dependent, being stronger in invaded terrestrial rather than aquatic habitats and in the northern part of the invaded range in China. In other cases, the effects of invasive aliens on native diversity were detected to be consistently negative across different spatial scales. For example, Stotz et al. (2019) detected a consistently negative effect of the invasive *Bromus inermis* both within and across individual grasslands in Alberta, Canada, and Boscutti et al. (2020) detected a spatially consistent negative effect of the invasive *Amorpha fruticosa* in northern Italy. Interestingly, Bando et al. (2022) detected a negative effect of the invasive *Urochloa arrecta* on both spatial and temporal beta-diversity in Brazil.

We did not find studies comparing the large-scale effects of multiple invasive and native dominants, even though there are studies comparing the large-scale impacts of invasive aliens in their native and invaded ranges – see for example Lolis et al. (2019), who detected a negative effect of the invasive *Eichhornia crassipes* on both alpha and beta diversity in the invaded range, China, but not in its native range, Brazil.

When comparing plots with high dominance of native species with those of aliens, the former were more similar (i.e., showed lower dissimilarity), pointing to their stronger homogenizing effect. At the same time, high-dominance plots with native dominants also showed marginally lower nestedness than their alien counterparts. The same pattern was detected for all plots merged regardless of the degree of dominance: those with native dominants are more similar but show lower nestedness than plots with alien dominants.

Impacts at the between-population level

It needs to be stressed that the tests on the differences between high- and low-dominance plots, as well as between the native vs. alien dominants at the between-population level, are weak due to the high residual variability. This is because the data include samples with different dominants, both native and alien, and with different types of vegetation, both within- and across dominants. Inevitably, this introduces a lot of residual variability that remains unexplained by our models. No significant differences between the low- and high-dominance plots and between the native and alien dominants were recorded at the between-population level, except that high-dominance plots with native dominants showed a marginally significantly lower species turnover. This again suggests a slightly stronger homogenizing effect of native dominants, similar to that recorded at the population level. This is also in line with recent evidence that areas across the globe with alien plants have higher levels of species replacement than areas with native species only (Kortz et al. 2023).

Relationship between the impacts of dominant species recorded at different spatial scales

When the population and between-population-level impacts were defined as differences in Jaccard similarity, nestedness, and turnover between the low- and high-dominance plots, no significant relationships between the impacts recorded at the plot level and those measured at either the population or between-population levels were revealed. However, we recorded strong positive relationships between the impacts at the population- and between-population levels, and this holds for all three indices used, i.e., Jaccard dissimilarity, nestedness and turnover. This clearly shows that the impacts at the population- and between-population levels are strongly related; however, it also confirms that plot-level impacts cannot be easily extrapolated to higher spatial scales.

On the contrary, we recorded strong positive relations between the plot-level impacts on Shannon diversity and the population-level impacts on species composition. This indicates that changes in the plot-level alpha diversity are strongly associated with compositional changes. Further, the turnover component of the population-level compositional impacts was strongly negatively related to the turnover component of the between-population-level impacts, defined as the differences between the low- and high-dominance plots.

Conclusions

Our results suggest that the homogenizing effects of native dominants are equal to or even stronger than those of the invasive alien dominants, which concerns the impacts recorded at the population- and partially also at the between-population levels.

Our results also support the assertion that the plot-level impacts on neither species richness nor Shannon diversity can be easily extrapolated to higher spatial levels. However, the plot-level impacts on Shannon diversity relate to the compositional impacts recorded at the population level, and the impacts recorded at the population- and between-population levels are also positively associated.

These results suggest that conservation efforts aiming at the maintenance of the diversity of communities and landscapes should target not only invasive aliens but also native expansive species with dominant tendencies. This is especially true in Eurasia or the Old World in general, with an array of native synanthropic dominants with expansive tendencies. However, the situation may be completely different in areas without a long tradition of a strong human impact (New World, distant islands, and archipelagos), which may be, therefore, presumed to lack native dominants with synanthropic tendencies.

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

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Data availability

All of the data that support the findings of this study are available in the main text or Supplementary Information.

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Supplementary material 1

The selected native and invasive dominants

Authors: Alessandra Kortz, Martin Hejda, Jan Pergl, Jiří Sádlo, Josef Kutlvašr, Petr Petřík, Martin Vojík, Michaela Vítková, Petr Pyšek

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Supplementary material 2

Map with populations of the selected native and alien dominants

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Supplementary material 3

Primary data, details on the statistical models and summary of the results

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Research Article

Variation in root traits and phenotypic plasticity between native and introduced populations of the invasive plant *Chromolaena odorata*

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Abstract

Understanding intraspecific trait variations, particularly for invasive species that occupy large geographic areas with different resource conditions, can enhance our understanding of plant responses to changes in environmental resources. However, most related studies have focused on aboveground traits, while variations in root traits and responses to changes in resources during biological invasion have not been clarified. To fill this knowledge gap, we compared the root traits of Chromolaena odorata from 10 introduced populations in Southeast Asia and 12 native populations in North and Central America under different soil nutrients. The introduced populations of the invader exhibited greater resource-acquisitive root traits, characterized by reduced fine root diameter but increased proportions of absorbing root length and specific root length, compared to the native populations. Although nutrient addition significantly affected root traits, the introduced populations showed greater phenotypic plasticity in four traits (root / shoot ratio, specific root length, absorbing root length proportion, and branching intensity) than the native populations. Different root trait syndromes were observed between the introduced and native populations. These results indicate that after introduction, C. odorata may shift towards a more soil resource-acquisitive strategy and thus respond more positively to increased soils nutrients, thereby showing better performance in high-resource environments. This study provides a better understanding of how species respond to environment changes and reveals the factors underlying exotic plant invasion success.

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Copyright: © Yang-Ping Li et al. This is an open access article distributed under terms of the Creative Commons Attribution License (Attribution 4.0 International – CC BY 4.0). **Key words:** *Chromolaena odorata*, covariation, invasive species, phenotypic plasticity, root traits, soil nutrients

Introduction

Invasive species encounter diverse abiotic and biotic environmental conditions across their native and introduced ranges (Richardson and Pyšek 2006). The variation of traits within invasive species is constrained by both genetic differentiation and phenotypic plasticity, which reflects the evolutionary history and adaptation of these species to environmental conditions (Díaz and Cabido 2001). Understanding the extent of intraspecific trait variations along ecological gradients is essential for unraveling species' responses to environment conditions within the current global change context (e.g., nitrogen deposition) (Weemstra et al. 2022; Gao et al. 2023). Various studies have explored intraspecific variations in aboveground functional traits (Feng et al. 2011; Zhao et al. 2020). However, few studies have investigated intraspecific variations in root traits despite their importance for the absorption of water and nutrients (Bardgett et al. 2014).

Fine roots (< 2 mm in diameter) represent the interface between plants and soil and thus have received increasing attention (Bergmann et al. 2020; Wang et al. 2021; Gao et al. 2023). Similar to the leaf economic spectrum, the suite of associated fine root traits may also reflect the resource acquisition strategy of a plant (Reich 2014; Weemstra et al. 2016). For example, root diameter, specific root length (root length per unit root dry mass), and specific root area (root area per unit root dry mass) are key traits for measuring plant resource investment in nutrient uptake (Makita et al. 2009). High specific root length, low root diameter, and low dry matter content are considered resource acquisitive traits that are generally associated with fast plant growth and reduced dependence on mycorrhizal fungi for nutrient uptake (Kong et al. 2014; Chen et al. 2016; Ma et al. 2018; Kong et al. 2019). In contrast, thick root diameter, low specific root length, and high root tissue density (root dry mass per unit root volume, reflecting root longevity) are considered resource-conservative root traits that are often associated with slow growth and increased dependence on mycorrhizal fungi for nutrient uptake (Eissenstat et al. 2015; McCormack and Iversen 2019; Bergmann et al. 2020). Soil environmental conditions (e.g., water content and soil nutrients) can affect root trait variation. For instance, in unfavorable environments (e.g., infertile and dry conditions), plants often show high root tissue density to increase root longevity (Ryser 1996; Eissenstat 2000). Intraspecific variations in root traits along an elevational gradient have been observed for 11 species; however, these patterns were species-specific (Weemstra et al. 2020).

Invasive species may encounter distinct selection pressures in their introduced habitats compared to those in their native ranges, potentially leading to variations in fitness-related traits (Keane and Crawley 2002; Joshi and Vrieling 2005; Schrieber et al. 2017). Some studies have found that invasive species shift toward a fast growth strategy (higher photosynthetic rate, specific leaf area, and leaf nitrogen) compared to their conspecifics from their native ranges (Mozdzer and Zieman 2010; Feng et al. 2011; Leishman et al. 2014; Heberling et al. 2016). Additionally, the introduction of invasive plants may also lead to changes in multiple co-varying traits known as "syndromes" (Kueffer et al. 2013; Tewes and Müller 2018; Liu et al. 2021). For example, Tewes and Müller (2018) discovered that Bunias orientalis from introduced populations with high silicle counts displayed increased leaf numbers and higher values in reproduction-related growth traits, whereas this syndrome was not particularly evident for conspecifics from native populations. In terms of belowground trait, Dawson (2015) hypothesized that a suite of root traits related to soil resource uptake ability may exhibit similar dynamics as leaf traits in invasive plants, potentially shifting toward roots with higher resource uptake strategy such as higher specific root length and lower diameter than those of their native conspecifics due to novel selection pressures encountered in introduced ranges. However, limited attention has been given to the variation and covariation of root traits among introduced and native populations of invasive species.

Phenotypic plasticity is often cited as a mechanism that facilitates invasion (Richardson and Pyšek 2006; Davidson et al. 2011). Alien plant species frequently

exhibit limited genetic variation due to their small population sizes upon introduction, and plasticity for important functional trait can facilitate the success of invasive plants across heterogeneous environmental gradients after introduction (Ghalambor et al. 2007; Liao et al. 2016). Bossdorf et al. (2008) found that invasive populations of Senecio inaequidens exhibited greater plasticity in root / shoot ratios compared to native populations when responding to nutrient addition, which may enhance their ability to efficiently utilize increased resource availability. Chun (2011) indicated that the invasive plant Lythrum salicaria showed significantly higher phenotypic plasticity for aboveground biomass in response to changing nutrient levels compared to the native conspecifics. Caño et al. (2008) also found that invasive plants Senecio pterophorus from introduced ranges demonstrated higher survival in disturbed environment than their conspecifics from native ranges, attributed to lower specific leaf area and better water content regulation of invasive populations under drought conditions. As a vital organ responsible for nutrient and water uptake from the soil, plastic responses of root traits can optimize nutrient acquisition and enhance plant performance (Larson and Funk 2016; Chen et al. 2023). However, most previous studies mainly focused on aboveground traits. Understanding the plasticity in root traits among invasive species populations could provide additional insights into how belowground resource strategies influence plant invasion under changing environmental conditions.

Chromolaena odorata (L.) R. M. King and H. Robinson (Asteraceae) is native to Central and South America, but it has become a noxious invasive shrub in Asia, Oceania, and Africa (Muniappan et al. 2005). It can invade different habitats across a wide environmental gradient (Kriticos et al. 2005). Studies have indicated that introduced C. odorata populations are better competitors than native populations (Zheng et al. 2015; Li et al. 2020), and exhibit faster growth economic traits such as higher photosynthetic capacity in introduced ranges compared to the native populations (Li et al. 2022). Molecular analysis revealed a low genetic variation among introduced populations of C. odorata (Yu et al. 2014), which is expected due to phenotypic plasticity facilitating their invasion across diverse environments. Liao et al. (2019) compared plasticity in aboveground traits of C. odorata among populations under different light treatments and found that the introduced populations had higher phenotypic plasticity for height, biomass, and total leaf area compared to their native counterparts but not for root / shoot ratio. Other studies showed that under high-nutrient conditions, invasive populations of C. odorata exhibited higher biomass (Li et al. 2020) or were more competitive (Qin et al. 2013) than their native populations, suggesting a more positive response by introduced populations to increased nutrient availability. These results provide insights into how aboveground traits vary among the invader populations and in their response to nutrient and light conditions. However, it remains unclear how root traits vary among introduced and native populations of the invader and how they respond to different nutrient conditions. Thus, we compared nine root traits of C. odorata from 10 introduced populations in Asia and 12 native populations in Central and South America under two nutrient levels. The following problems were addressed: (1) Do introduced populations shift towards more resource-acquisitive root traits (i.e., low diameter, high specific root length, and high branching intensity) when compared with the native populations? (2) How do root traits respond to soil nutrients? Do the introduced populations also exhibit greater phenotypic plasticity in response to high nutrient levels, similar to aboveground traits, compared to native populations?

Methods

Study site and materials

This study was conducted at the Xishuangbanna Tropical Botanical Garden (XTBG) (21°560'N, 101°150'E; 570 m elevation) of the Chinese Academy of Sciences, located in Mengla County, Yunnan Province, Southwest China. The Botanical Garden is located in the northern part of China's tropics. The mean annual temperature in this region is 21.7 °C, and the mean annual precipitation is 1557 mm, with a dry period from November to April (Feng et al. 2002).

In this study, 12 native and 10 introduced populations of the invader were compared (Table 1). Seeds of *C. odorata* were collected, germinated and grown in July 2010 at XTBG. For each population, the seeds were collected from 10–12 individuals from December 2019 to February 2020.

Experiment design

Chromolaena can invade habitats with different nutrient conditions, such as low-nutrient roadsides with topsoil removed or high-resource wasteland due to disturbance or fertilization. We collected field soil from roadsides near the invader monoculture located in the XTBG and then simulated high-resource habitats by adding nutrients. The seeds were cleansed with 5% NaClO for surface sterilization for 10 min and sown in seedling trays with sand- and humus-rich soil (1:1) in March 2020 in a shade house

| Code | Country/Region | GPS Coordinates | Elevation (m) | | | | | |
|----------------------|-----------------------|-------------------|---------------|--|--|--|--|--|
| Invasive populations | | | | | | | | |
| BK | Thailand | 14°25'N, 101°23'E | 739 | | | | | |
| JD | Yunnan, China | 24°17'N, 100°50'E | 1263 | | | | | |
| ML | Yunnan, China | 21°56'N, 101°15'E | 544 | | | | | |
| MY | Melaka, Malaysia | 2°22'N, 102°21'E | 50 | | | | | |
| PH | Iligan, Philippines | 8°10'N, 124°10'E | 107 | | | | | |
| SL | Kegalle, Sri Lanka | 7°11'N, 80°25'E | 451 | | | | | |
| SM | Yunnan, China | 22°46'N, 100°56'E | 1380 | | | | | |
| SY | Hainan, China | 18°19'N, 109°12'E | 23 | | | | | |
| WX | Vientiane, Laos | 17°58'N, 102°37'E | 170 | | | | | |
| YNS | Southern Vietnam | 11°20'N, 107°24'E | 125 | | | | | |
| Native popula | ations | | | | | | | |
| MCD | Tamaulipas, Mexico | 23°40'N, 99°11'W | 600 | | | | | |
| МСҮ | Chiapas, Mexico | 16°44'N, 93°09'W | 640 | | | | | |
| CUB | Pinar del Rio, Cuba | 22°45'N, 82°50'W | 565 | | | | | |
| FAK | Collier, Florida, USA | 25°52'N, 80°29'W | 1324 | | | | | |
| FBRO | Broward, Florida, USA | 26°08'N, 80°06'W | 3 | | | | | |
| FMAR | Martin, Florida, USA | 27°06'N, 80°15'W | 3 | | | | | |
| FMD | Miami, Florida, USA | 25°38'N, 80°20'W | 3 | | | | | |
| MIC | Michoacan, Mexico | 18°51'N, 103°37'W | 950 | | | | | |
| PM | Manati, Puerto Rico | 18°12'N, 67°06'W | 103 | | | | | |
| PP | Ponce, Puerto Rico | 18°12'N, 67°06'W | 103 | | | | | |
| T1 | Mamoral, Trinidad | 10°27'N, 61°17'W | 63 | | | | | |
| T2 | Felicity, Trinidad | 10°31'N, 61°25'W | 10 | | | | | |

Table 1. Information about the sampled *Chromolaena odorata* populations.

with 30% transmittance. Seedlings were transplanted into 2 L pots (one seedling per pot) when they were ~10 cm in height. The pots contained 40% sand and 60% field soil (total nitrogen (N): 2090 mg Kg⁻¹; available N: 7.79 mg Kg⁻¹; available phosphorus (P): 8.17 mg Kg⁻¹; available potassium (K): 281.48 mg Kg⁻¹). The seedlings were divided into two groups. One group was treated with compound fertilizer (Shanxi Shima Fertilizer Co., Ltd, Shanxi, China) at a rate of 100 mg available N + 100 mg available P + 100 mg available K Kg⁻¹ dry soil. The required amount of fertilizer was weighed, dissolved in 20 mL tap water, and poured carefully into each pot in April and May. The other group of the seedlings was treated with 20 mL tap water as the control. Five replicates were performed for each treatment. In total, we grew 220 seedlings [(10 invasive + 12 native populations) × 2 treatments per population × 5 seedlings per treatment].

The seedlings were randomly placed at an open site with full sunshine, irrigated daily after transplantation, and weeded when necessary. Two months later, all plants were harvested. The shoots of each plant were collected from the soil surface, dried in an oven at 60 °C for 48 h, and weighed. The roots of each plant were carefully washed using tap water in a 1 mm sieve and then further washed in a tray to remove the remaining soil particles.

Root trait measurement

The fine roots (< 2 mm in diameter) of each individual were clipped, disentangled to prevent overlap, and hierarchically dissected into branch orders according to the protocol described by Pregitzer et al. (2002). Absorptive roots (first- and second-order roots) and other fine roots were scanned using a V700 scanner (EPSON Co., Ltd. Japan) at 1200 DPI as 16-bit grayscale images. The RhizoVision Explorer software was used to analyze root images (Seethepalli et al. 2021). The following morphological traits were assessed for absorptive and other fine roots: total length, surface area, diameter, branching intensity (number of branches per root length), and volume. The proportion of absorbing root length (ratio of absorbing root length to total fine root length) was also calculated. The fine root fresh weight was recorded; then, the fine roots were dried in an oven at 60 °C for 48 h and weighed to determine fine root dry matter content, specific root length, specific root area, and root tissue density. Thick roots were also dried in an oven at 60 °C for 48 h and weighed to determine the root / shoot ratio (ratio of total root dry mass to shoot dry mass).

Statistical analyses

Principal component analysis (PCA) of the population mean trait values was performed to explore the associations among traits in the sampled populations. Mixed linear models were used to evaluate the effects of nutrients, ranges (introduced vs. native range), and their interactions on each variable, with nutrient treatments and ranges as fixed factors and populations nested within the range and q-scores as random factors. The population mean STRUCTURE q-scores were added as a random effect to account for the demographic history of the patterns of trait divergence in the mixed models (Li et al. 2022). The least significant difference (LSD) test was used to analyze the differences among groups. Furthermore, we calculated the root trait plasticity index using the following formula:

$$(T_1 - T_2) / T_2$$
 × 100 (Fort et al. 2015),

where T_a and T_c are the mean response values of each population after the nutrition addition and control treatments, respectively. One-way ANOVA was used to test the effect of range on plasticity index.

Pearson's correlation analysis was conducted for the data from each nutrient level and range to test the pairwise correlations among fine root traits. Before the analyses, we tested the normality and homogeneity of variance of each variable and transformed each variable if the assumption was not met. All analyses were performed using IBM SPSS Statistics for Windows 25.0 (IBM Corp. Armonk, New York, USA).

Results

Trait variation between ranges

PCA results showed distinct clustering patterns among populations of *C. odorata* according to their geographical origins and nutrient treatments, with significant overlap observed between the introduced and native populations across both nutrient levels along the first two principal components (Fig. 1). Notably, a substantial proportion of the variation was explained by the first and second axes (PC1 = 49.7%; PC2 = 21.5%). Furthermore, under different nutrient condition, populations exhibited separation primarily along the first principal component, which was mainly correlated with the specific root area, specific root length, root tissue density, fine root diameter, root / shoot ratio, and fine root dry matter content. Additionally, differentiation between populations in absorbing root length proportions, branching intensity, and fine root biomass along the second principal component.



Figure 1. Biplot of principal component analysis (PCA) for the nine traits of 10 introduced (I, circles in orange) and 12 native (N, circles in blue) populations of *Chromolaena odorata* grown in soil with (AN, filled circles) and without (NN, open circles) nutrient addition. RS, root / shoot ratio; FRBM, fine root biomass; RDMC, fine root dry matter content; ARLP, absorbing root length proportions; SRL, specific root length; SRA, specific root area; RTD, root tissue density; BI, branching intensity; D, fine root diameter.

The range (introduced vs. native range) significantly influenced five out of the nine root traits (Table 2). The introduced populations showed higher root dry matter content but lower fine root diameters than the native populations under both soil nutrient levels (Fig. 2c, d). However, the biogeographical differences in the root / shoot ratio, absorbing root length proportions, and specific root length depended on soil nutrient levels (Table 2, Fig. 2a, d, e).

Effect of soil nutrients on root traits

Soil nutrients significantly affected root traits (Table 2). Nutrient addition resulted in a decrease in the fine root dry matter content, specific root length, and specific root area, while it led to an increase in the root / shoot ratio, fine root biomass, root

Table 2. Effects of soil nutrients (n = 2), ranges (n = 2), and their interaction on nine root traits of *Chromolaena odorata*.

| Variable | Nutrient (N) | Range (R) | $\mathbf{N} \times \mathbf{R}$ | |
|--|--------------|-----------|--------------------------------|--|
| Root / shoot ratio | 192.79*** | 10.25** | 10.96** | |
| Biomass of fine root (g) | 93.18*** | 3.96 | 1.24 | |
| Root dry matter content (%) | 113.17*** | 7.16* | 1.88 | |
| Branching intensity (mm ⁻¹) | 3.14 | 0.50 | 11.51** | |
| Absorbing root length proportion (%) | 14.78*** | 22.26*** | 7.70** | |
| Specific root length (m g ⁻¹) | 554.73*** | 8.24** | 6.74* | |
| Specific root area (mm ² mg ⁻¹) | 285.08*** | 0.50 | 2.515 | |
| Root tissue density (g cm ⁻³) | 112.88*** | 0.04 | 0.41 | |
| Diameter (mm) | 513.79*** | 24.22*** | 3.41 | |

, ", and "" refer to P < 0.05, P < 0.01, and P < 0.001, respectively. Populations nested within ranges and q-values were used as random f actors.



Figure 2. Root traits of *Chromolaena odorata* from the introduced and native populations in soil with (black bar) and without (white bar) nutrient addition **a** differences in the root / shoot ratio **b** fine root biomass **c** fine root dry matter content (RDMC) **d** absorbing root length proportions (ARLP) **e** specific root length (SRL) **f** specific root area (SRA) **g** root tissue density (RTD) **h** branching intensity (BI), and **i** fine root diameter.

tissue density, and fine root diameter of both introduced and native populations (Fig. 2). There were significant interactions between nutrient addition and range for plants from different ranges (as shown in Table 2), indicating distinct pheno-typic plasticities between the introduced and native ranges (refer to Fig. 3). In soil with nutrient addition, the introduced populations exhibited higher proportions of absorbing root length and branching intensities compared to those without nutrient addition; however, no significant differences were observed for those traits among the native populations (Fig. 2d, h, Table 2). Furthermore, compared to the native populations, the introduced populations demonstrated higher plasticity in terms of root / shoot ratio and specific root length (Fig. 3a, e).

Trait covariation

Trait covariation pattern differed among ranges and soil nutrient treatments. In the native populations, plants with increased root tissue density exhibited reduced specific root lengths and specific root areas in both soil nutrient level. Conversely, in the introduced populations, plants with increased fine root dry matter content showed reduced specific root areas only in soil without nutrient addition (Fig. 4). Within the introduced populations, increases in specific root length and specific root area were associated with enhanced branching intensity in soil without nutrient addition, while an increase in specific root length was linked to higher proportions of absorbing root length in soil with nutrient addition. A significant negative correlation between root diameter and absorbing root length proportion was observed for the introduced populations under both soil nutrient levels. More-



Figure 3. Plasticity index for root traits of *Chromolaena odorata* from the introduced (grey bar) and native (white bar) populations under two nutrient treatments **a** differences in the root / shoot ratio **b** fine root biomass **c** fine root dry matter content (RDMC) **d** absorbing root length proportions (ARLP) **e** specific root length (SRL) **f** specific root area (SRA) **g** root tissue density (RTD) **h** branching intensity (BI), and **i** fine root diameter.



Figure 4. Pearson's correlation coefficient matrix for the seven root traits in the 10 introduced (I, open circles in blue and red) and 12 native (N, full circles in green and orange) populations of *Chromolaena odorata* grown in soil with (AN, circles in blue and green) and without (NN, circles in red and orange) nutrient addition. RDMC, fine root dry matter content; ARLP, absorbing root length proportions; SRL, specific root length; SRA, specific root area; RTD, root tissue density; BI, branching intensity; D, fine root diameter.

over, for the introduced populations, there was a negative correlation between root dry matter content and branching intensity in soil without nutrient addition but a positive correlation for the native populations in soil with nutrient addition.

Discussion

To understand how root traits of invasive plants change in response to variable soil nutrient conditions during biological invasion, we compared the root traits of *C. odorata* from 10 introduced populations in Asia with those of 12 native populations from Central and South America under two nutrient levels. Our study provided the first evidence for divergence in root trait between introduced and native populations of an invasive species, while further elucidating the differential patterns of response exhibited by these root traits under varying nutrient levels between introduced and native populations.

Variation in root traits between ranges

Our results provide support for Dawson's (2015) hypothesis that invasive species exhibit a shift in root traits towards resource-acquisitive roots, characterized by decreased root diameter and increased specific root length, in their introduced ranges owing to release from belowground specialist enemies. Specifically, the introduced populations of *C. odorata* displayed thinner roots and higher proportions of absorbing root length and specific root lengths (under low nutrient only) than the native populations across different soil nutrient levels. This indicates that a shift in root traits towards more resource-acquisitive roots may enhance soil resources' uptake and confer competitive advantage to the invaders over their new neighbors in introduced ranges. The study of Guan et al. (2023) on *Solidago canadensis* also demonstrated its ability to adjust nitrogen uptake strategy based on the contents and proportions of different forms of soil nitrogen, thereby promoting growth through enhanced nitrogen acquisition. Furthermore, many invasive plant species have been found to exhibit higher nitrogen and nutrient contents compared to their native counterparts (Huang et al. 2020; Liu et al. 2022).

A shift towards more resource-acquisitive roots may decrease enemy defense due to increased physical exposure to soil enemies and the trade-off between resource uptake and defense (Bauerle et al. 2007; Endara and Coley 2011; Rasmann et al. 2011). However, our results did not provide evidence for this prediction. Root toughness provides a direct physical barrier against herbivores (Johnson et al. 2010). The increased fine root dry matter content in the introduced populations may lead to an increase in resistance against soil enemies by enhancing root toughness. In this study, both nutrient conditions resulted in higher fine root dry matter content in introduced populations of C. odorata compared to native populations suggesting higher enemy resistance. One possible explanation is that invasive species may also exhibit defenses against generalist enemies in their introduced ranges, despite escaping from native specialists. Indeed, the rhizosphere soil of C. odorata from its introduced range in India showed an accumulation of local soil-borne pathogens, which are believed to have more negative effects on native species (Mangla and Callaway 2008). Consistent with these findings, Zheng et al. (2015) demonstrated that C. odorata plants from the introduced ranges show better resistance to natural enemies in the soil than those from the native ranges. These results indicate that the root strategy involving enhanced efficient resource uptake and stronger defense mechanisms contribute to the successful invasion of C. odorata.

Response to soil nutrients

The introduced populations of *C. odorata* exhibited a greater diversity and higher plasticity in root traits in response to nutrient addition compared to the native populations. Following nutrient addition, the introduced populations exhibited an increase in both absorption root length proportion and branching intensities, leading to enhanced exploitation intensity under nutrient enrichment conditions. Conversely, these changes were not observed in the native populations. Moreover, the introduced populations also displayed greater plasticity for specific root length, indicating a more positive response to nutrient addition. These plastic responses may enhance the adaptability of the introduced population of *C. odorata* by maximizing their ability to exploit increased nutrient availability and thereby facilitating

aboveground growth. These findings provide an explanation for previous studies conducted by Qin et al. (2013) and Li et al. (2020), which reported that introduction populations of *C. odorata* demonstrated higher plastic in aboveground performance compared to native populations. The results are consistent with the hypothesis posited by Richards et al. (2006), proposing that successful establishment of invasive species can be attributed to their ability to enhance fitness through phenotypic plasticity in response to increased resource availability. The outcomes highlight the significance of phenotypic plasticity in root traits as a pivotal mechanism facilitating invasion of exotic species under changing environmental condition.

Our results also demonstrated that nutrient addition increased fine root biomass and induced changes in the morphological traits of fine roots. High specific root length, small diameter, and low root tissue density are often indicative of enhanced metabolic activity and an increased capacity for nutrient uptake (Eissenstat 2000; Roumet et al. 2016). However, our results revealed a significant decrease in specific root length and an increase in both diameter and root tissue density of fine roots under nutrient addition, suggesting a shift toward higher investment in structural support and reduced allocation to soil resource acquisition as a response to nutrient availability. This could be attributed to the fact that nutrient addition reduces the need for plants to allocate resources towards fine root for efficient nutrient absorption (Taylor et al. 2014). Conversely, the alterations observed in specific root length and root tissue density can be attributed to the increase in fine root biomass resulting from nutrient addition. The augmentation of fine root biomass has the potential to modify plant species' response regarding their ability to uptake additional available nutrients through modifications in their root surface area. This is supported by the functional balance hypothesis which suggests that plants must maintain a stable ratio between aboveground and belowground biomass resources for optimal overall plant performance (Thornley 1991). Du et al. (2020) demonstrated that nitrogen deposition promotes even further accumulation of root biomass within grassland ecosystems with nitrogen limitations. In conclusion, C. odorata responds to increased nutrient availability primarily through an augmentation of its fine root biomass rather than altering its fine root length.

Changes in trait syndromes between ranges

Our study revealed significant correlations among the root traits; however, the patterns of trait covariation differed across ranges and soil nutrient levels. Principal Component Analysis (PCA) results indicated that the specific root area, specific root length, root tissue density, fine root dry matter content, and fine root diameter were subject to selection pressure by the nutrient conditions, while fine root dry matter content, branching intensity, and absorbing root length proportion were influenced by the different ranges. These findings suggest that distinct selection pressures can lead to diverse trait syndromes. Furthermore, novel environmental conditions in the introduced ranges may result in altered pattern of trait coordination (Messier et al. 2018). Trait syndrome reflects the adaptive strategies of plant species to different environmental conditions (Kueffer et al. 2013; Tewes and Müller 2018; Liu et al. 2021). In introduced population, plants with high specific root length and specific root area displayed increased branching intensity in soils without nutrient addition. This root syndrome indicates that plants from the introduced populations may enhance resource acquisition under low-resource conditions by increasing investments in the length of thinner roots and root networks. However, in native populations, plants with high root tissue density exhibited lower specific root lengths and specific root areas in soil with and without nutrition, suggesting a trade-off between resource-acquisitive and resource-conservative strategies for *C. odorata* within its native ranges characterized by high natural enemy pressure. Similar trade-offs were observed in the introduced populations grown in soil with nutrient addition. The distinct root trait syndromes between introduced and native populations imply the involvement of different adaptive strategies across different environments.

Conclusion

The root traits of invasive populations of *C. odorata* exhibited enhanced capacity for soil resource uptake ability and superior adaptability to increasing soil resources compared to those of its native conspecifics. These findings suggest that belowground resource acquisition strategies play a pivotal role in the invasions' success of exotic plants, thereby enhancing our understanding of the mechanisms underlying invasive species.

Additional information

Conflict of interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Ethical statement

No ethical statement was reported.

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Author contributions

Yang-Ping Li: Designed and performed the experiments, analyzed the results, and wrote the paper. Wei-Tao Li: Analysis of the results and writing and review of the paper. Yan-Fen Niu: Performed the experiments. Yu-Long Feng: Writing and review of the paper.

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Data availability

All of the data that support the findings of this study are available in the main text.

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Research Article

Towards integrating and harmonising information on plant invasions across Australia

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Abstract

Terminology for the invasion status of alien species has typically relied either on ecological- or policy-based criteria, with the former emphasising species' ability to overcome ecological barriers and the latter on species' impacts. There remains no universal consensus about definitions of invasion. Without an agreement on definitions, it is difficult to combine data that comes from a range of sources. In Australia, information on plant invasions is provided by a collection of independent jurisdictions. This has led to inconsistencies in terminology used to describe species invasion status at the national level, impeding efficient management. In this paper, we review and discuss the steps taken to harmonise the different terminologies used across Australia's states and territories. We identified mismatches in definitions and records of invasion status for vascular plant taxa across different jurisdictions and propose prioritisation procedures to tackle these mismatches and to integrate information into a harmonised workflow at the national scale. This integration has made possible the creation of a standardised dataset at the Australian national scale (the Alien Flora of Australia). In Australia, having an integrated workflow for referring to and monitoring alien flora will aid early warning and prevent species introduction, facilitate decision-making and aid biosecurity measures.

Key words: Alien flora, biological invasions, biosecurity, invasion status, plant census, standardised dataset, terminology

Introduction

The importance of having high quality, easy-to-access, standardised and unified data sources is widely recognised among researchers and practitioners working with species invasions (Latombe et al. 2017). Having standardised datasets at large spatial scales allows tracking biological invasions, making future predictions and prioritising invasion-based management actions (Hulme et al. 2009; Le Roux et



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Copyright: © Irene Martín-Forés et al. This is an open access article distributed under terms of the Creative Commons Attribution License (Attribution 4.0 International – CC BY 4.0). al. 2020). Ongoing debates include discussions about the taxonomy of biological invasions (Pyšek et al. 2013), the terminology and definitions related to invasion (Colautti and Richardson 2009; Young and Larson 2011; Catford et al. 2016), the determinants of invasion success (Fristoe et al. 2021; Daly et al. 2023) and the significance of impacts (Simberloff et al. 2013), as well as how to delimit and define native range (Guiaşu 2016). Hence, inconsistencies have arisen, subsequently impacting the accuracy of classifying plant species into native and alien and the derived implications of these classifications (Guiaşu 2016).

There are many terms to refer to 'species occurring in ecosystems to which they are not indigenous', including non-indigenous, non-native, exotic, and alien. The term 'alien' was introduced by the Convention on Biological Diversity (CBD) in Nairobi in 1992 without providing any specific definition (United Nations 1992). To alleviate the confusion around plant invasion terminology, Richardson et al. (2000) proposed the concept of the introduction-naturalisation-invasion continuum, by which a species introduced into a new area received different names according to the barriers it overcame. As such, casual aliens are those that have been transported beyond the limits of their native range but do not establish populations; only a fraction of casual aliens become naturalised, that is, forming self-sustaining populations in the invaded range; and only a fraction of those naturalised become invasive, overcoming local dispersal barriers and spreading in the new region. According to Richardson et al. (2000), the subset of invasive species able to impact the nature of the environment were called 'transformers', whereas 'weed' was a common term for undesired species (classically used for plants interfering with crop production) regardless of their native or alien origin (Fig. 1a).

The same year, the International Union for Conservation of Nature (IUCN) incorporated the concept of negative impact into the definition of invasive species as "alien species which becomes established in natural or semi-natural ecosystems or habitats, and are an agent of change, threatening native biological diversity" (IUCN, 2000). Two years later, in 2002, the CBD recognised invasive alien species (IAS) as "species introduced outside their native range that have become successfully established and cause substantial impacts on the environment" (Fig. 1b). In 2006, the IUCN Invasive Species Specialist Group (ISSG) developed the Global Register for Introduced and Invasive Species (GRIIS) as a concept and prototype to be subsequently reviewed before implementation across several countries globally. The methods underpinning GRIIS, and associated guidelines for the checklists of alien species to be implemented by individual countries, were not published until 2018 (Pagad et al. 2018) and only implemented in subsequent years. In 2022, a collation of GRIIS data across 196 countries was published into the country compendium of GRIIS (Pagad et al. 2022). GRIIS follows the impact-based notion of invasive species, to refer to those having a harmful impact on native biodiversity (Fig. 1b).

In 2011, a decade after the definitions for invasive species were proposed by Richardson et al. (2000) and the CBD (2002), Blackburn et al. (2011) published a unified framework on biological invasions to address terminological inconsistencies. The framework is very comprehensive and integrative, and successfully reconciles different synonyms to refer to similar invasion stages along the introduction-naturalisation-invasion continuum (Fig. 1c). It also reconciles terminology, concepts and definitions across different taxonomic groups (e.g., animals and plants), which had largely been addressed separately hitherto in the scientific literature. According to Blackburn et al. (2011), invasive species are alien species

that have been introduced in a new area, have naturalised and have successfully undergone dispersal and spread. The question of invasion impacts falls outside this framework as Blackburn et al. (2011) recognised that certain introduced species can have impacts in a novel environment even if their populations are not naturalised. Other prominent invasion status frameworks also exist, such as Darwin Core (Darwin Core Maintenance Group 2021a). Proposed by the Biodiversity Information Standards (TDWG), Darwin Core is a vocabulary standard and includes a glossary of terms intended to facilitate the sharing of information about biological diversity. Darwin Core published concepts to refer to biological invasions in 2020 based on Blackburn et al. (2011) and classifies species regardless of their impact but adds a dimension of complexity. According to Darwin Core, the vocabulary standard is split into two terms: establishment means (Darwin Core Maintenance Group 2021b), which refers to species origin (i.e., native, introduced or uncertain) and degree of establishment (Darwin Core Maintenance Group, 2021c), which refers to the position along the introduction-naturalisation-invasion continuum. What Blackburn et al. (2011) had simplified and unified, Darwin Core divided into more specific categories introducing new stages such as 'reproducing', 'colonising', or 'widespread invasive' (Fig. 1d).

Despite several attempts to harmonise different concepts and ideas, the terminology to refer to further invasion stages within the continuum has not become consistent over time. This is mainly caused by the scientific community and international regulations proposed by policymakers adhering to two different frameworks, Blackburn's and IUCN's, respectively (however, note that within the scientific community there are also discrepancies with the use of 'invasive'). More recent attempts to clarify definitions, with and without intrinsically including impact, proposed to refer to invasive species with negative impact as 'harmful invasive' (Essl et al. 2020).

In federally managed countries, biosecurity regulations involve a complex interplay between different scales of jurisdiction, including federal, state/territory/



Figure 1. Frameworks on biological invasions adopted by **a** Richardson et al. (2000) **b** CBD and IUCN **c** Blackburn et al. (2011) and **d** Darwin Core. Terminology marked with * in Darwin Core varies according to specific details within the considered barrier; therefore, the terms are not interchangeable. N/A refers to stages that have not been considered in the respective framework.

province, and local levels. The distribution of powers and responsibilities is influenced by the country's federal structure, which allocates certain authorities to the national government and others to the provinces. This division of responsibilities is often based on the principles of subsidiarity, where decisions are made at the most local level possible. Although this idiosyncrasy can lead to a complex and sometimes confusing regulatory landscape, it is intended to allow for tailored responses to local conditions while maintaining a coordinated national approach to tackle biological invasions. The rationale behind having both federal and state-level scoring of species introduction status often stems from the need to address invasive species management comprehensively while acknowledging the diversity of ecosystems and environmental conditions within a large country.

Australia is a clear example of inconsistencies among plant censuses data sources, making the integration of the recorded information on plant invasion an arduous task. Australia is the sixth largest country in the world, with an overall surface comparable to the European continent. It is a biodiversity hotspot and has one of the highest levels of endemism (Gallagher et al. 2021). Despite having one of the strongest biosecurity systems in the world, it does not have unified nation-wide data on alien species, and the number of taxa introduced in Australia increases steadily over time (CSIRO 2020).

Australia's jurisdictions comprise six independent states (New South Wales -NSW; Queensland - QLD; South Australia - SA; Tasmania - TAS; Victoria -VIC; and Western Australia - WA) and two main territories (the Australian Capital Territory - ACT; and the Northern Territory - NT), hereafter referred to as 'states' for simplicity. Australia's plant censuses, including information on whether a species is native or introduced, have been developed at a jurisdictional level by government environment departments, therefore there are currently eight independent plant censuses at the state level. In addition, there are plant censuses for the external territories, which are offshore islands under Australian sovereignty. At the national level, there is one existing plant census for vascular plants that provides information for the whole of Australia, the Australian Plant Census (APC) (Australian Plant Census 2022), endorsed by the Council of Heads of Australasian Herbaria (CHAH). The APC provides authoritative data for names and published taxon concepts for native and naturalised taxa in Australia. Despite being federally managed, the APC provides information on a state-by-state basis, without combining the information into a national status.

In addition, the Global Register of Introduced and Invasive Species (GRIIS) v1.9 was recently published for Australia (Randall et al. 2022), classifying, among taxa from other kingdoms, the alien flora of Australia into introduced and invasive. However, the criteria for species' inclusion and status are based on impact (Pagad et al. 2018).

In summary, different data sources (ten in total) following different criteria resulted in inconsistencies at the Australian national level (Martín-Forés et al. 2023a, b). Similarly, weed lists and management strategies developed at the state level might become inefficient and ineffective if not shared with adjacent states. For example, certain species of brome grass (*Bromus* sp.) are naturalised in most of Australia, and identified as posing harmful impacts; despite this, adjacent states adopting different classification schemes may follow different control strategies, constituting a clear example of ineffective management at the national scale. To overcome mismatches caused by jurisdictional boundaries and enable efficient management and biosecurity of biological invasions by the Australian federal government, a consensus on clearer definitions, concepts and classifications across Australia is much needed.

To harmonise the different criteria followed by independent jurisdictions, here we: i) propose an adapted workflow to refer to plant invasions in Australia, resulting from the combination of all different frameworks used in the data sources; ii) cross-reference the information between different data sources at the state level and combine it at the national level to identify mismatches at both scales, iii) propose a prioritisation procedure to address mismatches at the state and national level in order to harmonise contrasting invasion statuses, iv) provide up-to-date information on the alien flora in Australia.

We developed harmonisation steps as an integration exercise to develop a much-needed automated system able to cross-reference and integrate all the existing datasets across Australia. We only combined information and did not coin any new terms, nor did we reclassify any taxon from its status as recorded in Australian plant censuses. As a result, we recently published the Alien Flora of Australia (AFA) (Martín-Forés et al. 2023a, b), a unified and standardised dataset including invasion status for the Australian flora at the national scale. We hope that both the harmonised workflow proposed here, and the standardised dataset we have created in parallel, will provide a strong evidence-base for planning and informing actions for prevention and to mitigate risks at the Australian national scale. Similarly, this integration exercise can be adapted and extrapolated to any other federally managed country to help bridge the gap between federal and state biosecurity initiatives.

Methodology

The terminology used in Australian plant censuses

Regarding taxonomic differences across Australian plant censuses, we followed the taxonomy and nomenclature adopted by the APC (Australian Plant Census 2022) when taxonomic resolution was needed (see Martín-Forés et al. 2023a, b for details). The APC provides authoritative data for names and published taxon concepts for native and naturalised vascular flora in Australia and is the most recognised authority for the Australian vascular flora at the national level. The APC is one of the taxonomic resources of the Australian National Species List (auNSL; https://biodiversity.org.au/nsl/) and is endorsed by the Council of Heads of Australian Herbaria (CHAH).

The APC displays information on taxon distribution and invasion status for vascular flora contributed by different jurisdictions. It is mostly based on the terminology used by Blackburn et al. (2011) (Fig. 1c) and it classifies taxa as native, naturalised, or with uncertain origin. It follows a system of Boolean flags displayed in a consecutive way for each state and main territory. Therefore, in some instances, more than one status is displayed for a taxon in each territory. For example, a taxon recorded in one state as 'native and naturalised and uncertain origin' is a taxon native to that state, naturalised in other areas within the same state where it was not originally considered native, and appearing in other areas where there is no consensus on its 'nativeness'. Deliberately introduced alien species for gardening and ornamental purposes that have not established outside of cultivation are not listed on the APC and therefore not considered in our workflow and not reported here. The Australian GRIIS (Randall et al. 2022) follows the impact-based definition of 'invasive' (Fig. 1b), therefore classifying alien species as introduced or invasive to Australia, without providing specific information for states and territories. This definition of 'invasive' is based on expert consultation regarding evidence of negative impacts caused by species that are known to be an agent of change and threaten biodiversity (Pagad et al. 2015, 2018). Thus, 'invasive' on GRIIS should not include native species within the country (although see native-alien category in Pagad et al. (2018)).

Regarding plant censuses at the state level, we obtained them from the Australian Capital Territory (Lepschi et al. 2019), the Northern Territory (Northern Territory Herbarium 2015), New South Wales (PlantNET 2022), Queensland (Laidlaw 2022), South Australia (Department for Environment and Water 2022), Tasmania (de Salas and Baker 2022), Victoria (VicFlora 2023) and Western Australia (Western Australian Herbarium 2022). Plant censuses from different states use different terms to refer to alien species and differ in the extent to which they categorise species according to impact or barriers overcome (Suppl. material 1: table S1).

Terminology integration

We use the concept of the introduction-naturalisation-invasion continuum in the harmonised workflow presented here. Therefore, we kept and selected terms based on an adaptation from the Blackburn et al. (2011) framework. We made this decision because we wanted to follow a standard terminology that was not impact-based, and Blackburn et al.'s (2011) framework is the most recognised internationally, and the most directly comparable with the terminology employed in the APC. Impact of alien taxa should be assessed following specific guidelines (Hawkins et al. 2015; Bacher et al. 2018); thus, to acknowledge that the GRIIS' definition of 'invasive' explicitly incorporates negative impacts, we replaced the 'invasive' records on the Australian GRIIS (Randall et al. 2022) with 'harmful invasive', according to the definitions presented by Essl et al. (2020).

Hence, we proposed an adapted workflow (Fig. 2), by which information about presence (present/extinct), origin (native/introduced/uncertain) and invasion status along the continuum (casual/naturalised/invasive) are provided in a combined manner for all data sources. Accordingly, we use 'introduced' where information on an alien taxon status along the continuum had not been provided in a given Australian data source (therefore it can refer to casual aliens or in cases where no information on naturalisation is available, e.g., in the case of binary censuses like the South Australian one). In the harmonised workflow presented here, we did not include 'casual' or 'invasive', because most of the censuses lacked detailed information on the spread and dispersal within the introduced range. In addition, for native taxa that are also recorded as naturalised or doubtfully naturalised within the same jurisdiction, we used 'native colonising' and 'native potentially colonising' acknowledging a mere reflection of dispersal but not impact. Finally, for taxa no longer present in a given state we used 'presumed extinct' for native taxa and 'formerly introduced' for alien taxa (Fig. 2). Our proposed workflow therefore includes the following terms: native (also native potentially colonising and native colonising), introduced (also doubtfully or formerly),



Harmonised terminology proposed for Australia

Figure 2. Harmonised workflow to unify terminology on biological invasions across Australian data sources. The unified terminology is based on Blackburn et al. (2011) but incorporating the notion of impact to account for the species recorded as invasive in the Australian Global Register for Introduced and Invasive Species (GRIIS) following the IUCN's guidelines. The term 'introduced' marked with $\frac{1}{2}$ in our proposed workflow does not refer strictly to 'casual' alien species but has been used instead when information on naturalisation was not available in a specific census. The terms 'casual' and 'invasive' appear in grey as there is currently not available information across the Australian data sources to categorise species within these categories.

naturalised (also doubtfully or formerly), harmful invasive, presumed extinct, and uncertain origin. Certain categories (e.g. doubtfully naturalised, formerly naturalised) specified on the APC, and therefore appearing in this workflow and the Alien Flora of Australia (AFA), do not have a direct translation into other frameworks (e.g., impact-based ones and Darwin Core). For this reason, and to accommodate Australian states like Victoria, where its census follows the Darwin Core standard, we provide equivalences to Darwin Core for the harmonised terminologies used here. We have provided a glossary with specific meanings for each term at both scales and according to different sources of vocabulary for invasion ecology (Table 1).

Identification of mismatches on invasion status

We used the workflow, and developed an associated script, to create a unified and standardised dataset of alien flora in Australia, the Alien Flora of Australia (AFA) (Martín-Forés et al. 2023a, b). The script is available on github (https://github. com/MartinFores/AFA) and Figshare (doi: 10.6084/m9.figshare.23513478). The script curates all the data sources and converts the terms used in each of them to the ones we proposed in the harmonised workflow explained above. Subsequently, the script detects mismatches at the jurisdictional level by comparing the information on invasion status recorded for each taxon on each of the plant censuses and the taxonomic distribution and invasion status provided on the APC for each of the states. The result of the comparison between the state plant censuses and the distribution information recorded on the APC is displayed in the state-by-state datasets comprising the AFA.

| Number | of records nationally | 26,692 | 0 | 104 | 18 | 0 | 40 | 3,026 | 326 |
|-------------|--------------------------------------|--|--|---|--|---|---|---|---|
| | Definition at the national level | Native to at least one Australian state regardless of being introduced or naturalised into other states | NA | Native to at least one Australian state in which it is also naturalised regardless of being introduced or naturalised into other states | Species that is not native to any Australian state and is introduced in at least one state. There is not specific information of its naturalisation in the combined data sources, therefore it is not possible to know. | NA | Species that is not native to any Australian state and neither introduced or naturalised nor doubtfully introduced and doubtfully naturalised in any other state. It could be presumed to have been eradicated although it is likely to still be a casual alien (there are currently 44 species under this category at national scale). | Species that is not native to any Australian state and is naturalised in at least one state. | Species that is not native to any Australian state and is doubtfully naturalised in at least one state, without being known to be naturalised in any state. |
| | Definition at the state level | Native to a given Australian state without being naturalised in other areas of such state | Native to a given Australian state being potentially naturalised in other areas of such state | Native to a given Australian state although being also naturalised in other areas of such state | Species that is an alien and is recorded as introduced into a given state. [7,8] | Species for which it is uncertain if it is introduced in a given state. | Species that was known to have been introduced in the past into a given state. Although it could be presumed to have been eradicated, it would most likely still be a casual alien. | Fraction of introduced species that have been able to form unassisted self-sustaining populations [7,8]. The only species that was recorded as 'reproducing' [12] in one of the states has been grouped under this caregory | Species that despite being introduced, it is unknown if it can form self-sustaining populations. In other sources, sometimes referred to as adventive. |
| | GRIIS | N/A | Native-alien | Native-alien | Alien | NA | Alien | Alien | Alien |
| | APC | Native | Native and doubtfully naturalised | Native and naturalised | NA | NA | Formerly naturalised | Naturalised | Doubtfully naturalised |
| Darwin Core | [10] degree of establishment [12] | Native | Native | Native | -Casual -Introduced (Not enough information) | NA | NA | -Reproducing -Established | NA (unofficially referred to as adventive) |
| Darwin Core | establishment means [11] | Native | Native | Native | Introduced | NA (we assumed it would still be introduced as casual) | NA (we assumed it would still be introduced in a casual form) | Introduced | Introduced |
| F | lerm used in the AFA | Native | Native potentially colonising | Native colonising | Introduced | Doubtfully introduced | Formerly naturalised | Naturalised | Doubtfully naturalised |
| | | Native (any) (any) (any) (any) (any) | | | | | | (any) | |
| | | Alien | | | | | | | |

| Number of records nationally | NA | 77 | 11 | 21 | - | |
|---|--|--|--|---|---|--|
| Definition at the national level | in the invaded range at a significant distance from the act within the invaded community [7,8,12]. | tive impact within the invaded range and/or to pose a GRIIS referred to as invasive [32–34]. | Species of unknown origin that occurs in at least one state. | Species that is now presumed to be extinct in at least one Australian state and is not recorded to be present in any other form any other Australian state. | Species alien to Australia that has now been eradicated or is extinct in at least one Australian state and is not recorded to be present in any other Australian state. | |
| Definition at the state level | Naturalised species that have dispersed and spread introduction point, regardless of its imp | Invasive alien species that is known to have a nega threat to native biodiversity [7]. In | Species for which its origin is not known to be native or introduced to a given state | Species that was native to a given Australian state although is now presumed to be extinct | Species that was known to have been introduced in the past into a given state, but there is no longer present. It could be presumed extinct or have been eradicated. | |
| GRIIS | Alien | Invasive | Cryptogenic Uncertain | NA | N/A | |
| APC | NA | NA | Uncertain origin | | | |
| Darwin Core [10] degree of establishment [12] | -Colonising -Invasive -Widespread invasive | NA | NA | NA | NA | |
| Darwin Core establishment means [11] | Introduced | Introduced | Uncertain | NA | NA | |
| Term used in the AFA | Invasive | Harmful invasive | Uncertain origin | Presumed extinct | Formerly introduced | |
| | Invasive (any) Uncertain Other categories | | | | | |
| | Alien | | | | | |

Irene Martín-Forés et al.: Integration and harmonisation of information on plant invasions across Australia

In a subsequent step, the script combines the information provided at the state level into a national invasion status and compares it with that provided in GRIIS. The script then detects mismatches at the national level and subsequently address them by combining contrasting statuses into a unified national status (see next sections for details); see Martín-Forés et al. 2023a,b for details on the script designed to detect mismatches in invasion status at the state and territory levels in Australia.

Prioritisation procedure to unify invasion status at the Australian state level

We developed a prioritisation procedure to address mismatches on invasion status at the state level in Australia. When a species was not listed on the APC or was recorded on the APC as not present in a given state, we kept the invasion status recorded in the state plant census. For species that appeared in both state and APC sources but these sources displayed a mismatch in the invasion status, we developed a prioritisation procedure following the precautionary principle. Our system prioritises, for each taxon in each state, the recorded invasion status that has advanced the furthest along the invasion continuum. Naturalised, followed by doubtfully naturalised, are prioritised over introduced, formerly naturalised, doubtfully introduced and formerly introduced. Any invasion status recorded within an alien category for a taxon is prioritised over uncertain origin, and those over native statuses, which include, in order of priority, native colonising, native potentially colonising, native, and finally presumed extinct (Fig. 3). In all component datasets developed at the state level as part of the AFA, we incorporated a new column with the unified status for each taxon in each state (See Martín-Forés et al. 2023a, b to access all the standardised regional datasets for all Australian states).



Figure 3. Prioritisation procedure to assign the most conservative invasion status for a given species in a given Australian state after comparing the records in the corresponding state census and in the Australian Plant Census (APC). The status 'naturalised' refers to introduced species that form unassisted self-sustaining populations. *Indicates that in some cases there is not enough information in the state censuses to respond to these questions; therefore, we have assumed that the answer would be no. Darwin Core equivalences with regards to establishment means (native, introduced and uncertain) are also included.

Prioritisation procedure to combine invasion statuses at the Australian national level

The prioritisation procedure used to assign national status differed from the one used at state level (above) as follows: if a taxon was native to at least one state, it was considered native to Australia (Fig. 4). If it was not 'native' to any state, but native colonising (or native potentially colonising), it was considered native colonising at the national scale; and if it was not native in any possible form to any state but recorded with uncertain origin in at least one state, we kept 'uncertain origin'. If the taxon had not been recorded as native or having uncertain origin in any of the states, then the recorded invasion status that had advanced the furthest along the continuum was prioritised as a precautionary measure for addressing potential invasion. Only if the species was not present in any state was it then recorded as presumed extinct at the national scale (Fig. 4).

For the species that were alien (in any form) to Australia at the national scale according to our workflow and that appeared recorded as 'invasive' according to GRIIS, we changed their invasion status to 'harmful invasive' at the national scale, because GRIIS classification is impact-based. When other mismatches were identified (e.g., species that are native to at least one Australian state but appeared recorded as introduced or invasive (i.e. harmful invasive) in GRIIS), we kept the information obtained via our script.

Results

The Australian native and alien flora in numbers

According to the AFA, at the national level, there are 30,527 vascular flora species in Australia, including native species and alien species that are established outside of cultivation. However, because some of these species are only present in



Figure 4. Prioritisation procedure to assign the national status for a given species after merging the most conservative statuses across all the Australian states. The status 'naturalised' refers to introduced species that form unassisted self-sustaining populations. The status 'harmful invasive' was only assigned for the species that, being introduced at the national level, appeared recorded as invasive in the Australian GRIIS. *Indicates that in some cases there is not enough information in the state censuses to respond to these questions, therefore we have assumed that the answer would be no. Darwin Core equivalences with regards to establishment means (native, introduced and uncertain) are also included.

external territories and nine species did not have any distribution information, there are currently a total of 30,287 species listed, from which 3,487 records correspond to alien species that have not been deliberately introduced for gardening and ornamental purposes (11.4% of the total number of species). From these alien species, 58 species are recorded as introduced (not known to have formed self-sustaining populations to date), 3,352 species are recorded as naturalised (able to form self-sustaining populations) and 77 as harmful invasive (which accounts for 2.2% of the total of alien plants reported here). As mentioned above, there is not enough information in the combined data sources to classify Australian taxa as 'casual' or 'invasive' *per se* (sensu Blackburn et al. 2011). There are currently 11 species whose origin is uncertain at the national scale, while 21 species were native and have become extinct (presumed extinct) or were introduced and are presumed to have been extinct or eradicated (formerly introduced) (Table 2; Suppl. material 1: fig. S1).

The number of alien species across Australian states ranged from 564 in the Northern Territory to more than 1,900 in each of New South Wales, Queensland and Victoria. However, the percentage of alien species across Australian states, ranged from 10% in the Northern Territory and Western Australia to over 38% in the Australian Capital Territory (Table 2; Suppl. material 1: fig. S1). Within the alien species in each state, the percentage of harmful invasive species for which there is evidence of negative impact according to GRIIS, ranged from 2% in Tasmania to 4.4% in the Northern Territory (Table 2; Suppl. material 1: fig. S1). Beyond state and federal use, these data can also be used to report on the global status of Australian biodiversity and to provide indicators of biological invasions.

Table 2. Summary showing the number of species within each group (i.e. native, alien, uncertain origin and other categories), and percentage where indicated, regarding invasion status at national and state scales. Alien species at national scale are those for which origin is not Australian, whereas at the state level, alien species refer to those that could be native to other Australian territories. For alien species, the invasion status (e.g. introduced, naturalised and harmful invasive) has also been specified when known. To facilitate understanding, native (any) includes native, native colonising and native potentially colonising; naturalised (any) includes naturalised and doubtfully naturalised; introduced (any) includes introduced, doubtfully introduced, and formerly naturalised, assuming that, most likely, there is still an introduced individual of such species; other categories include species that are presumed extinct and species that were formerly introduced; harmful invasive refers to alien species known to have a negative impact in the native biota. States and main territories have been abbreviated (the Australian Capital Territory, ACT; New South Wales, NSW; the Northern Territory, NT; Queensland, QLD; South Australia, SA; Tasmania, TAS; Victoria, VIC; Western Australia, WA).

| Scale | Region | Total | Native total | Alien total (% of total) | Uncertain origin | Other categories | Alien species | | |
|----------------|-----------|--------|--------------|-----------------------------|---------------------|---------------------|---------------|-------------|----------------------------------|
| | | | | | | | Introduced | Naturalised | Harmful invasive (% of alien) |
| National* | Australia | 30,557 | 26,796 | 3,487 (11.4) | 11 | 22 | 58 | 3,352 | 77 (2.2) |
| Main territory | ACT | 2,034 | 1,245 | 785 (38.6) | 4 | 0 | 120 | 643 | 22 (2.8) |
| State | NSW | 9,248 | 7,296 | 1,952 (21.1) | 0 | 0 | 114 | 1,777 | 61 (3.1) |
| Main territory | NT | 5,600 | 5,032 | 564 (10.1) | 4 | 0 | 63 | 476 | 25 (4.4) |
| State | QLD | 11,812 | 9,904 | 1,904 (16.1) | 0 | 4 | 76 | 1,769 | 59 (3.1) |
| State | SA | 5,686 | 3,940 | 1,739 (30.6) | 3 | 4 | 203 | 1,487 | 49 (2.8) |
| State | TAS | 3,167 | 2,181 | 970 (30.6) | 2 | 14 | 105 | 847 | 18 (1.9) |
| State | VIC | 6,018 | 3,932 | 1,989 (33.1) | 80 | 17 | 121 | 1,819 | 49 (2.5) |
| State | WA | 15,001 | 13,484 | 1,505 (10) | 0 | 12 | 1 | 1,504 | 51 (3.3) |

*There are 29 species that are included in the database because of appearing on the Australian Plant Census (APC) but they are not recorded in any state or external territory. There are also 211 species that are included in the database but only appear in external territories.
Mismatches across Australian alien flora data sources

To report the mismatches here, we grouped invasion status into higher classes. As such, native (any) includes all native, native potentially colonising and native colonising taxa; while alien (any) includes all introduced species regardless of their invasion status; introduced (any) includes all doubtfully introduced, introduced, and formerly naturalised taxa; and naturalised (any) includes all doubtfully naturalised and naturalised taxa. Subsequently, we grouped the mismatches into several classes as follow: mismatches within groups, across alien groups (when they differ in the invasion status or the degree of establishment reported), and across different groups (native vs. alien).

We also identified mismatches related to either taxa presence or origin uncertainty. Finally, the category 'other mismatches' referred to taxa that were either not listed or were an excluded taxon on the APC, taxa recorded as not present in a given state or lacking information about invasion status, and taxa that were pro-parte or pro-parte misapplied and therefore no accurate equivalence of taxonomy and status could be assigned (Fig. 5).

The degree of mismatches at the national scale between the data obtained by our script integrating unified statuses across Australian states and GRIIS showed that, for all alien species, only four had similar statuses recorded in both data sources. This is due to most of the mismatches found (64%) taking place across alien groups (i.e., GRIIS does not include records stating naturalised, therefore over 2,000 species that are naturalised in the AFA appear recorded as introduced in GRIIS). Also, around 30% of the mismatches were due to certain species not being listed on GRIIS. There were 66 species (2% of the national mismatches) that were recorded as introduced according to GRIIS despite being native to at least one Australian state (see Suppl. material 1: tables S2, S3 for details). The case of *Phragmites australis* (Cav.) Trin.



Figure 5. Percentage of similarity and mismatch between the national and the state scales. States and main territories have been abbreviated (the Australian Capital Territory, ACT; New South Wales, NSW; the Northern Territory, NT; Queensland, QLD; South Australia, SA; Tasmania, TAS; Victoria, VIC; Western Australia, WA). Records were grouped in seven categories of mismatch. Similar: no mismatch between data sources. Across groups: mismatches across groups (native vs. alien); Across alien categories: mismatches across alien groups that differ in the invasion status or the degree of establishment reported; Within groups: mismatches within groups (e.g. naturalised vs. doubtfully naturalised); Presence-related: mismatches because of the taxon not present in one of the data sources; Uncertain-related: mismatches because a taxon has uncertain origin in one of the data sources; Not listed, not recorded as present or with misapplied taxonomy refers to mismatches when that is the case in one of the data sources.

Ex Steud. was especially curious as it is native to all Australian states except Western Australia but appeared recorded as invasive (harmful invasive) on GRIIS v1.9.

At the state scale, the mismatches detected ranged from 10% in Queensland to over 40% for South Australia (Fig. 5; Suppl. material 1: table S2). The fact that Queensland had less mismatches is most likely due to the Queensland Herbarium using the same terminology as the APC and therefore species falling within similar categories. By contrast, the highest percentage was detected in South Australia, a state that did not provide precise information about the position along the continuum, and therefore most species could only be assigned to 'introduced'. However, the highest number of severe mismatches (i.e. those across native and alien groups) were detected in Victoria and Tasmania, with 281 and 115 mismatches falling in this category (Fig. 5; Suppl. material 1: table S2).

Discussion

There are currently more than 13,000 vascular plant species naturalised outside their native range in the world (van Kleunen et al. 2015, 2019). While the number of high-quality, freely accessible online databases for alien flora at regional scales have increased in recent decades, their ultimate value for management actions depends on the feasibility of integrating the information they contain at larger spatial scales (Luo et al. 2011; Latombe et al. 2017). Integration is especially important when the data sources follow different criteria and has been previously proposed by merging global databases (Seebens et al. 2020).

We have created the first harmonised workflow and standardised dataset on alien flora in Australia, to assess the inconsistencies among current data sources, and to provide an updated state-of-the-art checklist of non-deliberate plant invasions across Australia. Having a free, easy-to-update Alien Flora of Australia (AFA) standardised dataset at the national scale that combines all up-to-date Australian state and national vascular plant censuses, offers a valuable research infrastructure. This national infrastructure creates cost-effective new opportunities to study biological invasions at the continental scale at a speed and performance appropriate for a broad range of stakeholders ranging from state and national government entities in Australia, both the national and international scientific community, to biosecurity committees, land managers, and society in general.

We would like to clarify that this integration exercise provides a reflection of the diverse information existing in Australia. We have developed tools to be able to combine contrasting information, but we have not classified taxa differently to those in the original records on Australian plant censuses. From our point of view, mismatches on invasion statuses within alien groups (e.g. naturalised vs. doubtfully naturalised) are unlikely to be very problematic for management purposes. Nevertheless, mismatches across groups (e.g. introduced vs. naturalised) fail to provide accurate information along the invasion continuum, thereby hampering development of biosecurity strategies and prioritisation for invasion management or eradication. Finally, mismatches across different groups (e.g. native vs. naturalised) provide contradictory information and pose the highest risk to management and conservation because an alien species could be considered as native and managed as such or vice versa.

Due to the high percentage of mismatches detected regarding terminology and classification, we encourage Australian herbaria to adopt a unified scheme in the way they provide information in the state plant censuses. Ideally, the scheme they adopt should provide information on the stage of the plant taxon along the introduction-naturalisation-invasion continuum based on overcoming ecological barriers. We recommend herbaria to follow Blackburn et al. (2011) when classifying plant taxa because it splits the classification along the continuum in easily recognisable stages. Schemes with intermediate stages such as Darwin Core can be risky to implement, due to the time lag existing between a species moving along consecutive phases of the "continuum" and human detection (e.g. a plant could have been detected as reproducing when it is already naturalised). Too many intermediate phases in the "continuum" can jeopardise the certainty of a taxon being correctly classified in one stage but not in the next one (Essl et al. 2011; Rouget et al. 2016).

We also advise limiting the use of the term 'invasive' to refer to naturalised species that spread and reproduce at multiple sites (e.g. Blackburn et al. 2011; Fig. 1c) and use instead 'harmful invasive' to refer to invasive taxa with negative impacts (Essl et al. 2020). We understand the terminology proposed here differs from international regulations such as CBD or IUCN; hence, we invite international bodies to realign their terminology by replacing the term 'invasive' with 'harmful invasive' when harmful impact is implied. In line with this, if impact status was required to be reported for a given application, complementary steps in future could include assessing the environmental and socioeconomic impacts of alien taxa; Hawkins et al. 2015) and SEICAT (Socio-economic impact classification of alien taxa; Bacher et al. 2018) frameworks, respectively. These frameworks have been adopted by the IUCN to rank introduced species by the magnitude of their potential impacts (Wallingford et al. 2020) and could be used to inform and address impact in Australia (see Box 1 for further discussion regarding the use of 'invasive').

At the end of the present study, we engaged with GRIIS to discuss potential causes and consequences of mismatches in the respective databases. We shared our dataset and findings so that the species lists reported in the Suppl. material 1 could be assessed prior to the release of the new GRIIS version. In the upcoming GRIIS

Box 1. Further discussion on the definition and use of the term 'invasive'.

Invasion frameworks such as Blackburn's (Blackburn et al. 2011), where the definition of invasive is proposed from a perspective of the barriers that a species has overcome, are more of a theoretical concept. However, application of this approach can pose practical difficulties in determining when a naturalised species has reached 'a significant distance' away from the introduction point to be considered invasive.

By contrast, frameworks such as IUCN and CBD, do not illustrate the barriers overcome by alien species and classify them as 'invasive' when impact is evident.

In this sense, we would like to highlight that not all naturalised and invasive species *sensu* Blackburn et al. (2011) have harmful impacts. There are invasive species for which there is no evidence to consider them harmful. Indeed, an alternative framework to the EICAT (Environmental impact classification for alien taxa; Hawkins et al. 2015), namely EICAT+ (Vimercati et al. 2022) has been created in order to assess beneficial impacts of alien taxa.

It is not our intention to discourage the use of 'invasive'; on the contrary, we use the term here to refer to the spread and dispersal of alien taxa within the introduced range, as proposed by Blackburn et al. (2011). However, as there is currently no information regarding spread available on the Australian censuses, we could not classify the species as simply 'invasive'. Due to this limitation, we changed the terminology to 'harmful invasive' as suggested by Essl et al. (2020), to consider for both frameworks, Blackburn's and the IUCN's.

Perhaps 'harmful alien' would be a more accurate term than 'harmful invasive', to avoid any automatic association between species impact and invasiveness, as it is known that small casual populations can still exert a negative impact. The question of impact (negative or positive) could therefore be scored on its own axis, independently from population size and spread.

We hope that the mismatches in definitions and records of invasion status for vascular plants highlighted here help in reaching a consensus in the terminology used both within the scientific community and by policy makers. Towards this end, after the new version of GRIIS is released and after conducting a workshop with relevant Australian authorities in invasion and biosecurity, we would review our own terminology used in the Alien Flora of Australia (AFA; Martín-Forés et al. 2023a,b) and provide new details on any consensus reached in the metadata.

version (to be released soon), a classification category labelled 'native-alien' will be included to refer to species native to a certain area but naturalised somewhere else. Species classified as 'native-alien' could therefore be simultaneously tagged as harmful invasive to refer to impact in the areas in which are introduced. Classification for certain species appearing on GRIIS v1.9 will therefore be modified in the new GRIIS version. In this sense, we will keep combining efforts and collaborating with GRIIS to deliver harmonised information across Australia. As part of this, once the new GRIIS is publicly available, we will adapt our script and publish an updated version of the AFA dataset. Hence, we encourage users to check for updates on Figshare (Martín-Forés et al. 2023b; doi: 10.6084/m9.figshare.23513478) and always use the latest available versions of the script and dataset.

Implications and applications of the AFA

One of the strengths of the AFA, is that the information for each plant species is easily comparable among all Australian states and at the national scale, with new opportunities arising from its use. While the division between federal and state levels makes sense in terms of local adaptability and expertise, effective communication and collaboration between the two policy levels are crucial. National strategies and policies can help ensure a coordinated and cohesive approach to invasive species management, addressing both local and broader concerns. At the same time, a decentralised system allows for adaptability and the opportunity for state agencies to create additional regulations and trigger rapid responses to emerging or pressing threats. In this sense, this harmonised dataset at the national scale is robust, as it allows developing federal strategies whilst simultaneously maintaining the information relevant for each jurisdiction.

As a result of the division in biosecurity legislation between federal and state levels, there are complicated cases of species being native to certain areas of Australia but introduced in others where they cause known negative impact and are therefore listed as weeds. For example, Pittosporum undulatum, or sweet pittosporum, is native to coastal areas of southern Queensland, New South Wales and certain regions of Victoria. However, it is a declared weed in South Australia, and listed as a common environmental weed in Tasmania and Western Australia. Due to expansion in its area of distribution, P. undulatum has been labelled as an environmental weed outside its natural range in Victoria and New South Wales, which gave rise to debate due to potential undesired associated effects (Howell 2003). Cases like this can benefit from overarching federal legislation and coordinated efforts among state agencies to ensure successful outcomes in every jurisdiction. A more notorious example is the case of Bromus diandrus, species original to Mediterranean Europe which is naturalised in all Australian states (doubtfully naturalised in the Northern Territory). Bromus diandrus poses a serious concern as a widespread grass weed having a detrimental impact on crop yield in Western Australia, where it is a declared weed being managed. South Australia, the adjacent state, shares a Mediterranean-type climate with Western Australia. Despite B. diandrus also being naturalised in South Australia, the species has not been declared as a weed in this state. This could potentially contribute to further dispersion into Western Australia, therefore hindering management efforts currently taking place in Western Australia. Cases like brome grass (Bromus sp.) that have successfully naturalised in almost the totality of continental Australia could benefit from a unified national strategy.

To date, only 32 plant species that are likely to become harmful invaders have been incorporated into the Weeds of National Significance (WoNS) (Thorp and Lynch 2000). Once an alien plant species is declared as a WoNS, a national management plan outlining strategies for controlling and managing its spread is developed, typically involving federal and state governments and local authorities. Therefore, to date, National Environmental Biosecurity Response Agreements (NEBRA 2021) have only been developed for these 32 WoNS. We hope that the AFA resulting from this integration exercise assists predicting invasions trends and identifying alien plant species introduced to Australia that are already naturalised in several states. For example, there are 77 alien species that are recorded as naturalised in all Australian states (see Suppl. material 1: table S4); of which, only Lycium ferocissimum Miers is currently considered a WoNS and is included on GRIIS as a harmful invasive. Even though distribution across several states can be a result of multiple introduction events (Koontz et al. 2018), we could expect a species that is already naturalised across multiple regions in Australia to potentially become problematic. Species that are already recorded as naturalised in several states and that are known to have had negative impacts in other areas worldwide should be rapidly assessed for inclusion in both GRIIS and WoNS.

In a similar manner, alien plant species that are currently doubtfully introduced or introduced in only one state, could be the target of eradication efforts (Rejmánek and Pitcairn 2002), with funding allocated to the relevant state, to prevent further naturalisation and potential expansion into other Australian states.

Native plant species that are naturalised in other areas within the state to which they are native (i.e., recorded in the AFA at national scale as native colonising or native potentially colonising), could be associated with effects not only within their own region of origin but also in other states in which they might appear as introduced or naturalised. These range-expanding native species require specific attention (Essl et al. 2019). There are currently 103 species in the category of native colonising; from these, 41 species are also introduced or naturalised in other Australian states (see Suppl. material 1: table S5 for details). This information should be an important consideration for land managers, and when designing conservation strategies. Monitoring those 41 species could also be implemented as part of internal biosecurity procedures in Australia to ensure that these species, despite being native, do not pose any harm to other Australian biodiversity (Wallingford et al. 2020) or international invasion risks if material is exported. It would be especially useful to monitor and model trends for those species under climate change (Hulme 2017). For those species expected to shift ranges under increasing temperatures or rainfall redistribution, this information would be crucial to apply pre-emptive management procedures. In a similar manner, the AFA can help identifying potential native species for which their spread into new areas through climate tracking may not be undesirable if it prevents them from being at risk of extinction.

In closing, we highlight that the information provided here on plant invasions in Australia can be easily updated in the future with upcoming releases of the APC and state censuses. The script we created to develop the AFA (Martín-Forés et al. 2023a, b; https://github.com/MartinFores/AFA) can be used at any time to automatise this process in the future. Such updates may be especially useful when combined with occurrence data in order to monitor alien flora across Australia under global change, as certain alien taxa are predicted to expand (Dullinger et al. 2017) or contract (Pouteau et al. 2021) their distribution ranges, whereas others can shift their distribution to track optimal environmental conditions in contiguous states.

Our script and approach can be adapted and applied to similar situations in other federally managed countries in which idiosyncrasies in the classification of alien species arise among jurisdictions. To do so, the appropriate data curation steps would need to be adapted to the way information is displayed in each of the data sources of a given country. Taxonomy matching could be easily done via the Global Biodiversity Information Facility (GBIF) taxonomic backbone and World Flora Online, with both options currently included within our script. Afterwards, prioritisation procedures can be implemented with the same functions we created.

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

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Author contributions

I.M.F conceived the idea; I.M.F and D.L. contacted the corresponding state authorities to obtain up-to-date censuses and clarify classifications in each state and discussed the validation with the HIS-COM members; I.M.F. analysed the trends from the Alien Flora of Australia (AFA) dataset; I.M.F. led the writing of the manuscript. All coauthors provided insightful advice, valuable feedback on the manuscript and agreed to submit the final version of the manuscript.

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Data availability

The data underpinning the analysis reported in this paper are deposited in the Figshare Data Repository at doi: 10.6084/m9.figshare.23513478. Similarly, the R scripts underpinning the analysis reported in this paper are deposited on GitHub at https://github.com/MartinFores/AFA.

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Supplementary material 1

Supplementary information

Authors: Irene Martín-Forés, Greg R. Guerin, Donna Lewis, Rachael V. Gallagher, Montserrat Vilà, Jane A. Catford, Aníbal Pauchard, Ben Sparrow

Data type: docx

Explanation note: fig. S1. Summary of the records of the alien flora of Australia (AFA) at both the national and state scales with regards to (top) origin (native, alien, uncertain or other categories), and (bottom) within the alien flora, grouped by invasion status (introduced, naturalised and harmful invasive). table S1. Terms, codes, and conversion procedure followed to harmonised terminology on invasions statuses across Australian states to make them comparable. table S2. Mismatches of the status assigned to species between different sources at the national scale (Alien Flora of Australia, AFA, vs. Global Register of Introduced and Invasive Species, GRIIS) and state scale. table S3. Scientific name according to the Australian Plant Census (APC) of the species that are introduced according to the Global Register of Introduced and Invasive Species (GRIIS) despite being native to at least one Australian state according to the Alien Flora of Australia (AFA). table S4. Scientific name according to the Australian Plant Census (APC) of the alien species not originally from Australia that are naturalised in all Australian states. table S5. Scientific name of the native colonising (i.e. those also naturalised in other areas of the state to which they are native). Copyright notice: This dataset is made available under the Open Database License (http://opendatacommons.org/licenses/odbl/1.0/). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same

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Research Article

Introduced species infiltrate recent stages of succession after glacial retreat on sub-Antarctic South Georgia

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Abstract

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Biological invasions are one of the main drivers of global biodiversity decline. At the same time, glacial retreat induced by climate warming is occurring at an alarming rate across the globe, threatening unique taxa and ecosystems. However, we know little about how introduced species contribute to the dynamics of colonisation in newly-deglaciated forelands. To answer this question, detailed inventories of plant and invertebrate communities were undertaken during two summer field seasons in the forelands of three tidewater and three inland glaciers that are retreating on the sub-Antarctic Island of South Georgia. The vascular plant communities present included a large proportion of South Georgia's native flora. As expected, plant richness and cover increased with time since deglaciation along a deglaciation chronosequence. Introduced plants were well represented in the study sites and two species (Poa annua and Cerastium fontanum) were amongst the earliest and most frequent colonisers of recently-deglaciated areas (occurring on more than 75% of transects surveyed). Introduced arthropods were also present around tidewater glaciers, including an important predatory species (Merizodus soledadinus) with known detrimental impacts on native invertebrate communities. Our study provides a rare and detailed picture of developing novel communities along a deglaciation chronosequence in the sub-Antarctic. Introduced species are able to track glacial retreat on South Georgia, indicating that further local colonisation and spread are inevitable as the region's climate continues to warm.

Key words: Biological invasion, *Cerastium fontanum*, chronosequence, climate change, conservation, glacial foreland, glacier-associated communities, *Merizodus soledadinus*, non-native species, *Poa annua*, sub-polar ecosystems

Introduction

Species introduced through human activities (commonly referred to as introduced, alien, non-native, exotic) are considered invasive when they establish and have negative impacts on native biodiversity and ecosystems (Colautti and MacIsaac 2004). Biological invasions are a key component of global environmental change and represent a major threat to biodiversity across the globe (Pyšek et al. 2020; Roy et al. 2023), especially on islands (Moser et al. 2018), and this threat is likely to grow unless effective biosecurity measures are put in place (Seebens et al. 2021). Sub-polar, polar and mountain biomes are increasingly exposed to the cumulative threat of invasive species and global warming (Thorarinsdottir et al. 2014; Alexander et al. 2016; Rew et al. 2020). Although remote sub-Antarctic islands are expected to be particularly vulnerable, data on introduced species are limited and little is known about future invasion trajectories in the face of climate change (Frenot et al. 2005; Leihy et al. 2023).

In most cold biomes across the globe, glaciers have been rapidly retreating over recent decades (Zemp et al. 2019) and, even in the least extreme scenarios of global warming, the majority of the world's mid- and low latitude glaciers are likely to be lost by 2100 (Rounce et al. 2023). This alarming phenomenon impacts biodiversity across multiple spatial and temporal scales, ranging from the loss of specialised communities in the immediate vicinity of retreating glaciers (Hotaling et al. 2017; Wilkes et al. 2023) to regional impacts on water regimes and sea level (Barnett et al. 2005; Zemp et al. 2019). When glaciers melt, new communities are built and an ecological succession becomes apparent from the filtering gradient of environmental conditions along the deglaciation chronosequence (Ficetola et al. 2021; Pothula and Adams 2022). Some specialised taxa may lose their habitat, while others may benefit from colonisation opportunities provided by the newly-deglaciated areas (Cauvy-Fraunié and Dangles 2019; Bosson et al. 2023). To protect these highly vulnerable ecosystems, it is key to describe and understand the processes of ecological succession following glacial retreat (Jacobsen et al. 2012).

To date, biological invasions in glacier-associated communities have received very little research attention. This is surprising, given that invasive species can fundamentally alter the speed and trajectory of ecological succession in other ecosystems (Kuebbing et al. 2014; Bellingham et al. 2016; Gallego-Tévar et al. 2020). In proglacial streams and fjords, it has been suggested that introduced species may arrive late in the succession process following glacial retreat, but clear evidence for this is lacking (Cauvy-Fraunié and Dangles 2019).

To start to understand interactive effects between biological invasions and glacial retreat, we assessed when and to what extent introduced species infiltrate the early successional sequence of proglacial communities. We surveyed pioneer communities of plants (with a focus on vascular plants and key lichens and bryophytes) and invertebrate species (with a focus on macroinvertebrates and Collembola) colonising glacial forelands around three tidewater and three inland glaciers on the sub-Antarctic Island of South Georgia. South Georgia is an important location to investigate how introduced species enter the sequence of colonisation in newly-deglaciated areas, because it harbours multiple introduced plant and invertebrate species (Frenot et al. 2005; Convey et al. 2010; Black 2022). In parallel, most of South Georgia's glaciers have been rapidly receding for decades and are predicted to continue to do so (Gordon et al. 2008; Cook et al. 2010; Rounce et al. 2023), creating large areas of habitat suitable for colonisation by both native and introduced species.

Materials and methods

Study area

The Island of South Georgia is about 170 km long and up to 40 km wide and is located in the South Atlantic, between 54°S-54°55'S and 35°50'W-38°W, about 1000 km north-east of the Antarctic Peninsula. Despite its geographical isolation and relatively harsh sub-Antarctic climate, South Georgia currently hosts species of plants and invertebrates that were introduced by sealing – and later shore-based whaling - industries between the late 18th and mid-20th centuries (Convey and Lebouvier 2009; Convey et al. 2011; Black 2022) with new introductions occurring up to the present day (Convey et al. 2010; Tichit et al. 2023). Some introduced species have negative impacts on native communities (Ernsting et al. 1995; Houghton et al. 2019) and the island's terrestrial ecosystems may be particularly vulnerable to introductions due to the presence of vacant niches that are readily available to new competitive invasive taxa (Convey and Lebouvier 2009; Houghton et al. 2019). To tackle this issue, the Government of South Georgia & the South Sandwich Islands (GSGSSI) has implemented rigorous biosecurity measures and invasive mammals have been successfully eradicated from the Island (GSGSSI 2013; Martin and Richardson 2019). However, some plant species such as the dandelion Taraxacum officinale agg. and the meadowgrass Poa annua and invertebrates such as the carabid beetles Trechisibus antarcticus and Merizodus soledadinus may now be too widespread for any realistic possibility of eradication (GSGSSI 2021).

To assess the ability of established introduced species to colonise deglaciated areas, we surveyed six glacial foreland sites during the austral summer on the north coast of South Georgia (Fig. 1). Three sites, investigated in April 2022, were located in the vicinity of the following tidewater glaciers at low elevation (46 ± 40 m a.s.l.): the Nordenskjöld Glacier between Barff and Greene Peninsulas, the Harker Glacier between Greene and Thatcher Peninsulas and the Lyell Glacier that defines the western limit of Thatcher Peninsula. In January and February 2023, the surroundings of three extant or recently-extinct inland circue glaciers at higher elevation (378 ± 122 m a.s.l.) were surveyed: Hodges and Col Glacier son Thatcher Peninsula and an unnamed icecap west of Husvik on Busen Peninsula (locally known as Husvik Glacier). Of these three sites, only Col Glacier currently persists as an ice remnant approximately 30×100 m in size. Hodges Glacier rapidly receded after 1970 and was lost in 2008 (Bakke et al. 2021), while Husvik Glacier was lost by the late 1950s ("Map of Falkland Island Dependencies: South Georgia" 1958).

To assess the dynamics of foreland colonisation by terrestrial communities, locations with contrasting times since deglaciation (*tsd*) were sampled at each foreland. For tidewater glaciers, detailed maps of glacial front changes were available (Cook et al. 2010; South Georgia GIS, accessed February 2022), enabling us to sample locations positioned with precision along former glacial fronts with *tsd* between five and 30 years. Depending on site accessibility and logistical constraints associated with fieldwork, we were able to sample one to three replicates uniformly distributed and at least 80 m apart on the retreat line for two to four values of *tsd* at the foreland of each tidewater glacier (Suppl. material 1). As no map or record of deglaciation dynamics was available for the inland glaciers, an area with recent *tsd* was identified closest to the current (Col Glacier) or last known position (Hodges and Husvik Glaciers, "Map of Falkland Island Dependencies: South Georgia" 1958) of the ice remnant (Suppl. material 1). For comparison, a second area with Pierre Tichit et al.: Introduced species infiltrate recent stages of succession after glacial retreat on sub-Antarctic South Georgia



Figure 1. Maps and overview of the six glacier sites on the north coast of South Georgia. Plant and invertebrate communities at three tidewater glacial forelands (1–3 purple) and three inland deglaciated sites (4–6 blue) were surveyed. Centre-right: example of transects (black dots) along former deglaciation fronts (from 1993 to 2017, light to dark purple) in the vicinity of Nordenskjöld Glacier.

older *tsd* was determined at a distance of approximately 200 m in the flow direction of the glacier. The validity of this approach relies on the unverifiable assumption that the retreat rate was similar across the three inland glaciers and over their deglaciation history. For both recent and older *tsd*, three approximately equidistant replicate locations were sampled.

Sampling

At each sampled location, plant communities were surveyed along a 30 m transect. All vascular plants present within six adjacent quadrats $(5 \times 5 \text{ m})$ either side of the transect line were recorded (yielding 12 records of plant presence/absence per transect), while the cumulative number of bryophyte and lichen morpho-species (photographs provided as Suppl. materials) across two quadrats at opposite ends of the transect was recorded. For the tidewater glacier sites, the cover of plants and lichens was measured through a point-contact sampling procedure using a frame with 10 equidistant pins (length = 50 cm), placed every 2 m along the transect (yielding 15 records of plant cover per transect). The vegetation at inland glacier

sites was too sparse to achieve representative point-contact sampling; we therefore used a Braun-Blanquet scale to estimate the cover of plants and lichens in each 5 m quadrat (Suppl. material 2; yielding 12 records of plant cover per transect).

Several invertebrate sampling methodologies were applied in order to achieve the most comprehensive description of the communities present. Ground-dwelling (and secondarily flying) arthropods were sampled using pitfall traps (n = 3) consisting of 250-ml beakers half-filled with a water/washing detergent solution and buried to ground-level at the start, middle and end of each transect. Traps were retrieved after being deployed for approximately 48 h. Macro-invertebrates were extracted from approximately 200 ml of substrate obtained at the same three positions along the transect, using Tullgren extractions for 8 h. Micro-invertebrates were sampled on an opportunistic basis from soaked aliquots of the same substrate. Invertebrates sampled using this non-quantitative method were not included in statistical analyses. Finally, ground-dwelling invertebrates under stones and debris were recorded and sampled during hand searches of 8 min and flying insects were captured using sweep nets along a span of 5 m either side of the transect. All sampled invertebrates were rapidly transferred to ethanol for preservation.

Sample identification

All vascular plants were readily identifiable to species level in the field, based on published description and nomenclature (Burton and Croxall 2012b; POWO 2023) with the exception of the native lesser rush, *Juncus inconspicuus* that was considered to be a synonym of the native greater rush *Juncus scheuchzerioides* Gaudich (Kirschner 2002). Observations of the hybrid between the native greater and lesser burnet *Acaena magellanica* × *tenera* were merged with the data for *A. magellanica*. The introduced species aggregate *Taraxacum officinale* may contain several micro-species and so was reported as *Taraxacum officinale* agg.

While some macroinvertebrates could be identified to species level in the field (Burton and Croxall 2012a), most specimens required detailed assessment of anatomical features under stereo- or light microscopy, with reference to the available literature (Enderlein 1912; Hendel 1937; Gressitt 1970; Convey et al. 1999; Kits 2011). Identification confidence for each taxon was categorised as 'possible', 'probable' or 'certain'. All macro-invertebrates and springtails were identified to species-level. All Sminthuridae were reported as *Sminthurinus jonesi*, since there were no consistent taxonomic features supporting the presence of other species, contrary to what was suggested by Convey et al. (1999). Mites and other micro-invertebrates were categorised into morphotaxa.

Statistical analyses

All statistical analyses were performed in *R* (R Core Team 2022). To assess if the observed presence data reflected the true presence of organisms in the glacial foreland communities (Buddle et al. 2005), we plotted species accumulation curves for each transect with the function *specaccum* from the package '*vegan*' (Oksanen et al. 2007). Visual inspection of these curves indicated if the encounter rate of new species across samples taken was sufficient to compute representative diversity metrics.

To visualise the taxonomic composition of vascular plant communities across *tsd* and glacier site, we performed an ordination on a Jaccard dissimilarity matrix of

the presence/absence data at the transect level, using non-metric multidimensional scaling (nMDS) with the function *metaMDS* in '*vegan*' (Oksanen et al. 2007). The score of each species was displayed on the ordination plot.

The presence data were modelled as a function of *tsd* and glacier site through an ordination with the function *cca* from the package '*vegan*' (Oksanen et al. 2007). ANOVA-like permutation tests (n = 999 permutations) for constrained correspondence analysis with the function *anova.cca* were used to test whether community composition was significantly constrained by *tsd*, glacier site and their interaction.

To investigate the effects of deglaciation time on the richness of communities and the presence or cover of species, we employed multivariate models using Bayesian Inference with the package brms (Bürkner 2017), treating the glacier site and tsd as the main explanatory variables. Tidewater and inland glaciers were modelled separately. As the response of communities may depend on glacier sites, we ran a model with a simple interaction between glacier site and *tsd*. For tidewater glaciers, we ran a model with a quadratic term for *tsd* to reflect non-linear responses, as well as a model with both interaction and quadratic terms. We selected the simplest and most informative model using pairwise comparisons of the expected log pointwise predictive density (ELPD) with function loo (Vehtari et al. 2017, Suppl. material 3). The variable *tsd* was a categorical variable for inland glacier sites (recent or old), but continuous and scaled to zero mean and unit variance for tidewater glacier sites. As the availability of mapped former glacial fronts in the period 1993-2018 varied between tidewater glaciers (Cook et al. 2010), the sampling of tsd was heterogeneous and not synchronised across glaciers, which prevented the use of a categorical variable to model *tsd*. When the sampling unit (pitfall traps, pin frame or 5 m quadrat) was nested within a transect, transect identity was included as a random effect. Response variables were observed for species richness, plant cover (at species level or higher) and species presence/absence and were modelled using Poisson, zero-inflated binomial and Bernoulli distributions, respectively. Weakly-informative priors determined by a Gaussian distribution (mean $\mu = 0$, standard deviation $\sigma = 10$) were used to model the effects of predictors. Random effects were drawn from a Student's *t*-distribution (df = 3, mean $\mu = 0$, standard deviation $\sigma =$ 10). Models were run using four chains for 5000 iterations (including 2500 burnin iterations). Traces of the sampling behaviour of each predictor were scrutinised (Suppl. material 4) and the R-hat convergence diagnostic (Vehtari et al. 2021) was computed (Suppl. material 5) to verify that the models converged towards reliable predictions. A posterior predictive check was used to compare modelled and observed data and evaluate the quality of the models (Suppl. material 4). The significance of each effect being positive or negative was assessed using Bayesian 95% credible intervals (CI_{05}).

Results

Taxonomic inventory

Eighteen native species of vascular plant were found at tidewater glacier sites (Suppl. material 6), representing 78% of the native species known from South Georgia. At inland glaciers, only seven native species were observed (30%). Four introduced species occurred on both types of glacier sites: *Poa pratensis, Taraxa-cum officinale* agg., *Cerastium fontanum* and *Poa annua* (Suppl. materials 7, 8).



Figure 2. Frequency of occurrence across transects of the 10 most common vascular plants around tidewater glaciers (\mathbf{a} , n = 21 transects), inland glaciers (\mathbf{b} , n = 18 transects) and most frequent invertebrates around tidewater glaciers (\mathbf{c} , n = 21 transects). Introduced species are highlighted in red.

At tidewater glaciers, *C. fontanum* was the second and *P. annua* was the seventh most frequent species (Fig. 2a). On forelands of inland glaciers, *P. annua* was the second, *C. fontanum* the fourth and *T. officinale* agg. the eighth most frequent species (Fig. 2b).

Sixteen native species of terrestrial invertebrates were identified with high confidence at tidewater glacier sites (Suppl. material 6), representing 48% of the native species on South Georgia. At inland glacier sites, only five native species were present, representing 15% of known native species. Five introduced species were found at the tidewater glacier sites and none at the inland sites (Suppl. material 7): *Merizodus soledadinus* (Coleoptera), *Hypogastrura viatica* (Collembola), *Apterothrips secticornis* (Thysanoptera), *Mycomya* sp. (Diptera) and *Trichocera regelationis* (Diptera). *Merizodus soledadinus* and *H. viatica* were the fourth and tenth most frequent invertebrate species, respectively, at tidewater glacier sites (Fig. 2c).

Sampling quality

Accumulation curves of vascular plant species were close to saturation for most of the sampled transects (n = 39, Suppl. material 9), indicating that samples were largely representative of the communities present. However, accumulation curves of invertebrate species did not reach a plateau or were not possible to produce when transects were the smallest replication unit. In the following analyses, we thus calculated diversity metrics only for plants, for which an assumption of near-complete detection was reasonable. We investigated drivers of presence for a subset of the ten most frequently encountered invertebrate species, assuming that detection – though likely incomplete – remained equally probable across sampling sites.

Community-wide effects of time since deglaciation and glacier site

The structure of vascular plant communities was significantly constrained by *tsd*, glacier site and marginally by their interaction in forelands of both tidewater and inland glaciers (Table 1, Fig. 3).

Around tidewater glaciers, the number of bryophyte morpho-species increased linearly with *tsd*, while the number of vascular plant species initially increased and then reached a plateau (Fig. 4, Suppl. material 5). Bryophytes seemed to be more abundant at intermediate *tsd* and there was no clear effect of *tsd* on the cover of vascular plants, but the cover of lichens was higher in areas exposed for longer (Suppl. materials 5, 10). Compared to Harker Glacier, Lyell Glacier hosted a lower number of vascular plant species and a higher number of bryophyte morphospecies, while Nordensköld Glacier was associated with a higher cover of bryophytes (Suppl. materials 5, 10).

Table 1. Summary of results from ANOVA-like permutation tests (n = 999 permutations) for constrained correspondence testing whether community composition was significantly constrained by *tsd*, glacier site and their interaction.

| | Tidewater glaciers | | | Inland glaciers | | |
|--|--------------------|----|-------|-----------------|----|-------|
| Variable | F | df | p | F | df | Р |
| Time since deglaciation (<i>tsd</i>) | 3.23 | 1 | 0.001 | 3.45 | 1 | 0.007 |
| Glacier site | 3.06 | 2 | 0.001 | 4.86 | 2 | 0.001 |
| Interaction <i>tsd</i> : Glacier site | 1.41 | 2 | 0.068 | 2.28 | 1 | 0.046 |



Figure 3. Taxonomic composition of vascular plant communities across time since deglaciation (*tsd* in years) at tidewater (**a**) and inland (**b**) glacier sites. The two first components of a non-metric multidimensional scaling (NMDS) from an ordination on the presence data at the transect level are mapped. Each circle, rectangle or triangle corresponds to a transect from a given site and deglaciation time (black to red). Small crosses represent the score of the ten most frequent species on the ordination plots.



Figure 4. Effect of time since deglaciation (*tsd* in years) on the number of vascular plant species and bryophyte morpho-species at tidewater (**a**, **b**) and inland (**c**, **d**) glacier sites modelled with Bayesian Inference. Transparent points represent the original data. Lines (**a**, **b**) or points (**c**, **d**) are the estimated mean effects of *tsd*. Purple, turquoise and yellow areas (**a**, **b**, Harker: purple, Lyell: turquoise, Nordenskjöld: yellow) or intervals (**c**, **d**, Husvik: purple, Col: turquoise, Hodges: yellow) represent the Bayesian 95% credible intervals, respectively.

At inland glacier sites, there were significantly more vascular plant species in older than in recently-deglaciated areas (Fig. 4, Suppl. material 5), as well as a higher cover of vascular plants and bryophytes (Suppl. materials 5, 10). Compared to Husvik Glacier, Col Glacier hosted a lower number of vascular plant species and reduced cover of vascular plants and of bryophytes (Suppl. materials 5, 10). Hodges Glacier did not differ from Husvik Glacier in terms of community-level metrics.

Species-level effects of time since deglaciation and glacier site

At tidewater glacier sites, the introduced *Cerastium fontanum* and *Poa annua* were most likely to occur across a broad range of intermediate *tsd* (Fig. 5a, Suppl. materials 5, 10), which was also the case for the native species *Deschampsia antarctica* and *Colobanthus quitensis*. The probability of occurrence of the native *Phleum alpinum* initially increased and then reached a plateau with increasing *tsd*. The native *Festuca contracta, Acaena tenera, A. magellanica, Rostkovia magellanica* and



Figure 5. Scaled effect of time since deglaciation (*tsd* in years) on plant presence (**a**), vascular plant cover (**b**) and invertebrate presence (**c**) at tidewater glaciers modelled using Bayesian Inference. Effects on introduced and native species are represented in red and blue, respectively. Points are the mean effects of *tsd* on the logit scale. Intervals represent the Bayesian 95% credible intervals. The vertical dotted lines correspond to the null hypothesis (effect is zero).

Galium antarcticum were more frequent at older deglaciated sites. Similarly, the two lichens *Stereocaulon* sp. and *Pseudocyphellaria* sp. and the mosses *Syntrichia robusta* and *Polytrichum* sp. were more likely to occur in older deglaciated areas, while the presence of the liverwort *Marchantia berteroana* was not affected by *tsd*. The cover of *C. fontanum* decreased with increasing *tsd* (Fig. 5b, Suppl. materials 5, 10), while the cover of *P. annua* showed no evidence of change. Amongst native vascular plants, the cover of *C. quitensis* showed no evidence of change with *tsd*, *D. antarctica* and *P. alpinum* were most abundant at intermediate *tsd* and *F. contracta* had higher cover in older deglaciated areas. Amongst bryophytes and lichens, the cover of *Stereocaulon* sp., *Pseudocyphellaria* sp. and *Marchantia berteroana* showed no evidence of change with *tsd*, while *Polytrichum* sp. was most abundant at intermediate *tsd* and *Syntrichia robusta* increased in cover with *tsd*.

At inland glacier sites, the occurrence of the invasive *Taraxacum officinale* agg. did not differ between old and recent areas of deglaciation (Fig. 6a, Suppl. materi-



Figure 6. Effect of time since deglaciation (*tsd*) on vascular plant presence (**a**) and vascular plant cover (**b**) at inland glaciers modelled using Bayesian Inference. Effects on introduced and native species are represented in red and blue, respectively. Points are the mean effects of *tsd* on the logit scale. Intervals represent the Bayesian 95% credible intervals. The vertical dotted lines correspond to the null hypothesis (effect is zero).

als 5, 10), while the invasive *P. annua* and *C. fontanum* were more frequent in older deglaciated locations. The native *D. antarctica*, *A. magellanica* and *Polystichum mohrioides* did not significantly differ between *tsd*, while all other native plants became more frequent in older deglaciated areas. The cover of all plants (with the possible exception of *D. antarctica* and *P. alpinum*) was higher in old deglaciated areas (Fig. 6b, Suppl. materials 5, 10).

At tidewater glacier sites, the native spider *Micromaso flavus* seemed more frequent at older deglaciated sites, but there was no clear effect of *tsd* on the presence of other reliably sampled invertebrates (Fig. 5c, Suppl. materials 5, 10).

For both inland and tidewater glaciers, there were notable differences between sites in the presence and cover of species (Suppl. materials 5, 10). The invasive *C. fontanum* was scarce at Lyell Glacier and abundant at Nordenskjöld Glacier, where the introduced springtail *Hypogastrura viatica* was also more common, while *P. annua* was more frequent at Harker Glacier. At inland sites, *T. officinale* agg. was more frequent at Hodges Glacier, while *P. annua* was less abundant at Col Glacier.

Discussion

Colonisation by introduced species

Introduced vascular plants and invertebrates were well represented in the recent stages of community assembly after glacial retreat on South Georgia. Four introduced vascular plants were found on glacial forelands, with *Cerastium fontanum* and Poa annua being very frequent, while Taraxacum officinale agg. and P. pratensis were rarely observed. Around tidewater glaciers, C. fontanum and P. annua occurred across a broad range of *tsd* and *C. fontanum* was more abundant in recently rather than in older deglaciated sites, indicating that these species are effective pioneers on glacial forelands along South Georgia's coast. Notably, flowering specimens of C. fontanum were found in areas deglaciated less than five years prior to the survey, approximately 50 m from the terminus of Lyell Glacier. Both species originate from temperate regions of the Northern Hemisphere (POWO 2023, Suppl. material 7), are widespread on South Georgia (Black 2022) and have successfully invaded most islands in the sub-Antarctic (Frenot et al. 2005). Poa annua is invasive on the maritime Antarctic South Shetland Islands (Molina-Montenegro et al. 2012; Hughes et al. 2015) and both species are also early colonisers of newly-deglaciated areas on a glacier foreland on the sub-Antarctic Kerguelen Islands (Frenot et al. 1998). At tidewater glaciers on South Georgia, the rapid colonisation by C. fontanum and P. annua outpaced that of most native vascular plants, with the possible exceptions of Deschampsia antarctica and Colobanthus quitensis, with these invasive plants effectively short-cutting the successional sequence following glacial retreat. At inland sites, C. fontanum and P. annua were less common in more recently-deglaciated areas, but direct comparisons with tidewater glaciers are not possible due to methodological differences. In contrast, the dandelion T. officinale agg. appeared equally capable of colonising old and recently-deglaciated areas inland, which likely results from its seeds being wind-dispersed over large distances.

We also documented the presence of five introduced invertebrate species on recently-deglaciated forelands, indicating an ability to disperse and survive in challenging environments. This capacity to track glacial retreat is particularly remarkable for three of these invertebrates that are flightless and suggests high mobility through passive dispersal (Hågvar et al. 2020) or active locomotion, as previously reported for the carabid beetle *Merizodus soledadinus* (Convey et al. 2011; Renault 2011; Laparie et al. 2013; Lebouvier et al. 2020). The invasive springtail *Hypogastrura viatica* was frequent on coastal forelands (in particular at Nordenskjöld Glacier), which underlines the high dispersal capacity of this species that is also introduced on other sub-Antarctic islands and in parts of the South Shetland Islands (Frenot et al. 2005; Greenslade and Convey 2012).

What characteristics of introduced plants and invertebrates make them capable of infiltrating the dynamics of colonisation on glacial forelands? The isolation and harsh environment of sub-Antarctic islands generate environmental filters that may provide opportunities for invaders with a mixture of typical invasive traits that guarantee high resource acquisition and efficient dispersal (Laparie et al. 2013; Liao et al. 2021) and pioneer traits such as low plant height and resistance to abiotic stress (Laparie et al. 2012; Mathakutha et al. 2019; Bazzichetto et al. 2021). Both *P. annua* and *C. fontanum* are small annual plants with shallow roots (although *P. annua* can adopt a perennial life cycle and develop into swards), investing heavily in rapid growth and early reproduction and lack the vegetative and longer-lived tissues typical of the perennial native species that allow multi-year survival under stressful abiotic conditions (Frenot and Gloaguen 1994; Frenot et al. 1998; Chwedorzewska et al. 2015; Johner 2020). It is possible that ruderal traits act as pre-adaptations that provide a colonisation advantage as communities develop around receding glaciers.

Possible impacts of introduced species

Although native plants seem to co-occur with the two invasive pioneers C. fontanum and P. annua, these invasive plants may have impacts on native communities in glacial forelands. During competition experiments in the field in the South Shetland Islands, P. annua reduced the biomass and photosynthetic abilities of C. quitensis and D. antarctica (Molina-Montenegro et al. 2012). On South Georgia, C. quitensis and D. antarctica might also be the native plants most likely to experience direct competition with C. fontanum and P. annua, given their similar early position in the succession on glacial forelands. Competitive interactions between invasive and native taxa are likely to change with ongoing environmental changes and climate warming, possibly to the advantage of introduced species that generally originate from more temperate regions (Molina-Montenegro et al. 2019; March-Salas and Pertierra 2020; Convey and Hughes 2022; Daly et al. 2023). However, our data also show that C. fontanum declines in abundance, while P. annua remains equally common in post-glacial plant communities as they are eventually colonised by native perennial plants, suggesting that native plants can be stronger competitors than some invasive annuals. Despite this, the two invasive plants remain a component of plant communities at least 30 years after deglaciation both in inland and coastal forelands and these taxa are now so widespread on South Georgia that large-scale control is not feasible (Black 2022).

Current and future impacts of introduced species will likely vary between glacier locations. For instance, we found that Nordenskjöld Glacier had higher plant cover, but was also more invaded by introduced plants and invertebrates than the two other tidewater sites. Whether these local differences are due to contrasting topography, microclimate, soil quality or disturbance by macrofauna or human activities is still to be investigated, but they deserve consideration when assessing impacts of biological invasions on glacier-associated communities and developing conservation strategies.

Introduced invertebrates may also have impacts on the terrestrial ecosystems of sub-Antarctic islands (Convey et al. 2010; Houghton et al. 2019). In our study, they were restricted to coastal sites, suggesting that inland sites might provide refuges for native taxa (but see Lebouvier et al. (2020) who note that M. soledadinus is now invading inland and higher altitude locations on the Kerguelen Islands). However, with very limited representative survey data available away from coastal locations on South Georgia, it is also unclear whether inland areas would be suitable for many/most native taxa given their high degree of isolation, inhospitable conditions and low diversity of habitats. The presence of the predatory M. soledadinus is of great concern for the native invertebrate diversity as it can locally drive prey species to extinction, impact the life cycle of co-existing species and fundamentally reshape invertebrate communities (Convey et al. 2011; Lebouvier et al. 2020). The introduced springtail, H. viatica, might act as a food source to the introduced predator, as well as competing directly or indirectly with native species, such as Cryptopygus antarcticus (Convey et al. 1999). Our results suggest that communities in newly-deglaciated areas may not be exempt from the negative effects of invasive invertebrates that may alter the trajectory of invertebrate community succession compared to when they are absent.

The early expansion of introduced species likely modifies soil characteristics, provides biomass and generates biotic interactions in newly-deglaciated areas

(Badenhausser et al. 2022), which might have consequences for the entire succession process following glacial retreat. In other systems, biological invasions can alter the speed (Gallego-Tévar et al. 2020) and trajectory of primary successions (Flory and Clay 2010), but little is known in the context of glacier-associated communities. Moreover, the impacts of invasive species in glacial forelands may not be exclusively negative (Walther et al. 2009), as some native taxa might benefit from a modified succession. Our study highlights the need for future research to understand if and how introduced taxa can alter the trajectory and speed of colonisation dynamics following glacial retreat.

Community changes and underlying mechanisms along the deglaciation chronosequence

Overall, we found an increase in the cover and diversity of plants along the chronosequences in glacial forelands. This is consistent with the basic process of primary succession following glacial retreat (Jones and Henry 2003; Flø and Hågvar 2013; Vater and Matthews 2015; Glausen and Tanner 2019; Gwiazdowicz et al. 2020; Pothula and Adams 2022) and we can presume that a similar trend would have been found with invertebrate communities if sampling quality had allowed. Although our study did not include sites deglaciated more than 30 years previously, we found evidence that the rate of accumulation of vascular plant species decreased along the chronosequence, which contrasts with proglacial successions across the world (Jones and Henry 2003; Pothula and Adams 2022), eventually reaching a plateau representing a high proportion of the native flora of South Georgia. Contrasting with other regions globally where glacier-associated taxa represent a very small proportion of the overall biodiversity, these differences may relate to the specificity of the flora on sub-Antarctic islands, that typically consists of species with higher dispersal ability and adaptations enabling survival in harsh abiotic conditions (Convey 1996).

There were interspecific differences in the colonisation speed of native plants that may help to disentangle the mechanisms underpinning the deglaciation chronosequence. Deschampsia antarctica and Colobanthus quitensis were the first native species to colonise tidewater glacier sites alongside two genera of lichen (Stereocaulon and Pseudocyphellaria), followed by Phleum alpinum and, subsequently, Acaena magellanica, A. tenera, Festuca contracta, Rostkovia magellanica, Galium antarcticum and three bryophyte taxa. Interestingly, D. antarctica and C. quitensis are the only two native angiosperms in the more extreme maritime Antarctic and are known for their high degree of tolerance to adverse conditions (Cavieres et al. 2016; Clemente-Moreno et al. 2020), which may contribute to their ability to colonise very recently-deglaciated sites on South Georgia. The pattern of primary succession following deglaciation on the sub-Antarctic Kerguélen Islands showed some differences to South Georgia, as cushion-forming Colobanthus species and tussock-forming Poa kerguelensis, but not D. antarctica, were amongst the first colonisers (Frenot et al. 1998). The early succession on South Georgia resembles proglacial communities of glaciers at high latitudes and altitudes where lichens, mosses and some grasses are first to colonise, but later trajectories differ due to the presence of shrubs and trees (Jones and Henry 2003; Nakatsubo et al. 2005; Garibotti et al. 2011; Fickert and Grüninger 2018; Ruka et al. 2023). Regional idiosyncrasies in the successional colonisation of deglaciated areas on sub-Antarctic islands are likely a result of missing species in disharmonious floras which may lead to increased

vulnerability of developing native communities to invasive plants with traits largely absent for the native species pool. Even across glaciers of the same type on South Georgia, community composition was largely determined by glacier identity, which underlines the importance of the local microenvironment and the composition of adjacent communities in shaping successions following glacial retreat (Bayle et al. 2023). Native invertebrate communities around tidewater glaciers primarily consisted of mites, springtails, dwarf Linyphiidae spiders, Promecheilidae beetles and winged dipterans, resembling proglacial arthropod communities across alpine, sub-polar and polar ecosystems (Kaufmann 2001; Hodkinson et al. 2023).

Conclusions

Besides providing an important baseline on the patterns of community assembly along a deglaciation chronosequence in the sub-Antarctic, this study highlights the need for future research that quantifies the impacts of invasive pioneers on the speed and trajectory of ecological succession in glacier-associated ecosystems. While current colonisation dynamics suggest that invasive species infiltrate the sequence without outcompeting native colonisers, further studies are required to determine whether this co-occurrence will persist with ongoing climate change, glacial retreat and habitat transformation. On South Georgia and other sub-Antarctic islands, invasive species will likely track the ongoing and future retreat of glaciers where they are present. Our study illustrates that synergies between the effects of climate change and biological invasions constitute a key research avenue in vulnerable montane, polar and sub-polar ecosystems.

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

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Author contributions

PT, PC, PB, RN and WD designed the study. PT, PC and WD coordinated logistical support. PT collected and analysed the data. PT and WD drafted the manuscript. PT, PC, PB, RN and WD

revised the manuscript. All authors agree to be held accountable for the content of this paper and approve the final version.

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Data availability

The original datasheets containing all species field and laboratory observations and images of surveyed bryophyte and lichen morphospecies can be downloaded as supplementary materials. Samples are stored at the University of Liverpool.

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Supplementary material 1

Positions of all transects (black dots) along former deglaciation fronts (from 1993 to 2017, light to dark purple) in the vicinity of tidewater glaciers or in recent and old deglaciation areas in the vicinity of inland glaciers

Authors: Pierre Tichit, Paul Brickle, Rosemary J. Newton, Peter Convey, Wayne Dawson Data type: pdf

- Explanation note: For the latter, the approximate last known positions of the glacier are highlighted in light purple (Husvik: 1958, Hodges: 1970, Col: 2023).
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Link: https://doi.org/10.3897/neobiota.92.117226.suppl1

Supplementary material 2

Adapted Braun-Blanquet scale used in the study of inland glacier sites

Authors: Pierre Tichit, Paul Brickle, Rosemary J. Newton, Peter Convey, Wayne Dawson Data type: pdf

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Link: https://doi.org/10.3897/neobiota.92.117226.suppl2

Supplementary material 3

Results of model selection, based on the posterior likelihood of models for each variable

Authors: Pierre Tichit, Paul Brickle, Rosemary J. Newton, Peter Convey, Wayne Dawson Data type: pdf

- Explanation note: SE indicates standard error. The simplest model with best predictive performance determined was that using pairwise comparisons of the expected log pointwise predictive density (elpd-diff). Point estimates of the expected log pointwise predictive density (elpd_loo), the effective number of parameters (p_loo) and the loo information criterion looic are also provided.
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Link: https://doi.org/10.3897/neobiota.92.117226.suppl3

Supplementary material 4

Model traces, conditional effects and posterior predictive check of each modelled variable

Authors: Pierre Tichit, Paul Brickle, Rosemary J. Newton, Peter Convey, Wayne Dawson Data type: pdf

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Link: https://doi.org/10.3897/neobiota.92.117226.suppl4

Supplementary material 5

Summary of effects of time since deglaciation for each glacier site on all variables modelled with Bayesian Inference (including quadratic and interaction terms if retained in the best model)

Authors: Pierre Tichit, Paul Brickle, Rosemary J. Newton, Peter Convey, Wayne Dawson

Data type: pdf

- Explanation note: Effects on the presence and cover of taxa are on a logit scale. Effects on unbound count data are on a log scale. The R-hat statistic is provided to assess the convergence of each estimate.
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Link: https://doi.org/10.3897/neobiota.92.117226.suppl5

Supplementary material 6

List of species found at tidewater and inland glacier sites

Authors: Pierre Tichit, Paul Brickle, Rosemary J. Newton, Peter Convey, Wayne Dawson Data type: pdf

- Explanation note: Introduced species in bold. Taxonomical information from up-to-date database (POWO 2023; Bánki et al. 2024).
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Link: https://doi.org/10.3897/neobiota.92.117226.suppl6
Supplementary material 7

Description of the introduced species observed in the survey (n = 9)

Authors: Pierre Tichit, Paul Brickle, Rosemary J. Newton, Peter Convey, Wayne Dawson Data type: pdf

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Link: https://doi.org/10.3897/neobiota.92.117226.suppl7

Supplementary material 8

Average cover (in %) across transects of the 10 most common vascular plants around tidewater glaciers (a, n = 21 transects), inland glaciers (b, n = 18 transects)

Authors: Pierre Tichit, Paul Brickle, Rosemary J. Newton, Peter Convey, Wayne Dawson Data type: pdf

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Supplementary material 9

Species sampling curves for each surveyed transect

Authors: Pierre Tichit, Paul Brickle, Rosemary J. Newton, Peter Convey, Wayne Dawson Data type: pdf

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Supplementary material 10

Effect of time since deglaciation on the presence of plant and invertebrate species at tidewater and inland glacier sites modelled with Bayesian Inference

Authors: Pierre Tichit, Paul Brickle, Rosemary J. Newton, Peter Convey, Wayne Dawson Data type: pdf

- Explanation note: Transparent points represent the original data. Lines (tidewater) or points (inland) are the estimated mean effects of *tsd*. Purple, turquoise and yellow areas (Harker: purple, Lyell: turquoise, Nordenskjöld: yellow) or intervals (Husvik: purple, Col: turquoise, Hodges: yellow) represent the Bayesian 95% credible intervals, respectively.
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Link: https://doi.org/10.3897/neobiota.92.117226.suppl10

Supplementary material 11

Plant and invertebrate inventory on glacial forelands of South Georgia (2022-2023)

Authors: Pierre Tichit, Paul Brickle, Rosemary J. Newton, Peter Convey, Wayne Dawson Data type: zip

- Explanation note: GPS positions, plant and invertebrate inventories made across tidewater (2022) and inland glaciers (2023) on South Georgia.
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Link: https://doi.org/10.3897/neobiota.92.117226.suppl11

Supplementary material 12

Bryophyte and lichen morphospecies observed on glacial forelands of South Georgia (2022–2023)

Authors: Pierre Tichit, Paul Brickle, Rosemary J. Newton, Peter Convey, Wayne Dawson Data type: zip

- Explanation note: Bryophyte and lichen morpho-species were photographed across two 5 × 5 m quadrats at opposite ends of each 30 m transect on forelands of tidewater glaciers. Specimens are recorded in Suppl. material 11.
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Research Article

The 50-year history of anglers' record catches of genus *Carassius*: circumstantial evidence of wiping out the native species by invasive conspecific

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Abstract

Successful invasive non-native fish species can cause enormous damage to native biodiversity. In mainland Europe, the introduction of the gibel carp (*Carassius gibelio*) has led to a decline in populations of the formerly widespread native crucian carp (*C. carassius*). Both invasive and native species develop two phenotypes, namely stunted and deep-bodied, which depend on the intensity of competition and predation in the water body. The deep-bodied phenotype is associated with a more diverse fish community composition, can attain large sizes and is very attractive to recreational anglers. This study analysed trends in the record sizes of native crucian carp and invasive gibel carp (individuals close to the maximum attainable size of the species) reported by recreational anglers over the last 50 years in Czechia, recording the invasion of gibel carp from its beginnings to the fully established population phase. The study provides circumstantial evidence that gibel carp is behind transition from the relative abundance of large crucian carp to near extirpation, while large gibel carp, which is currently classified as critically endangered in the Red List of Czechia, has very limited possibilities to realise its deep-bodied phenotype. It also shows the potential of using data from recreational anglers for mapping invasion processes and as a source of relatively localised information on endangered species.

Graphical abstract



Key words: Aquatic conservation, culturomics, crucian carp, gibel carp, iEcology, Prussian carp



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Introduction

Invasive non-native species can have an enormous impact on freshwater ecosystems, displacing native species or even causing their complete extinction (Gurevitch and Padilla 2004; van der Veer and Nentwig 2015; Šmejkal et al. 2023). Invasive non-native species can threaten native species through predation (Grabowska et al. 2019), competition for food resources and space in the ecosystem (Tapkir et al. 2022), hybridisation (Papoušek et al. 2008) or through disease transmission (Gozlan et al. 2005). The spread of invasive non-native species has been facilitated by intentional or unintentional introductions (Sakai et al. 2001; Blackburn et al. 2011; Almena et al. 2023) and one of the most common routes of introduction for invasive non-native species fish has been through aquaculture and the ornamental fish trade (Naylor et al. 2001; Balon 2004).

Fish of the Cyprinidae family were the first to be spread outside their native waters (Balon 2004). The gibel carp (*Carassius gibelio*) was accidentally introduced to Eastern Europe in the mid-20th century along with other cyprinids from the Amur Basin to be bred in aquaculture (Hensel 1971; Kalous et al. 2012). The migration of the invasive gibel carp in the Danube River was recorded in the 1970s (Tóth 1976) and the first records in Czechia date back to 1975–1976 (Halačka et al. 2003). The gibel carp rapidly invaded most of Western Europe and today reaches as far as the Scandinavian and Iberian Peninsulas (Wouters et al. 2012; Rylková et al. 2013; Ribeiro et al. 2015). The invasion went unnoticed to a certain extent due to the relatively high morphological similarity with the feral form of the goldfish (*Carassius auratus*) already present in Europe (Hensel 1971; Szczerbowski 2002), so that the exact development of the invasion process and the resulting damage to local aquatic ecosystems were not recorded in detail.

Due to limited resources in monitoring the progress of invasive non-native species, it has proven useful to utilise knowledge, photos and video recordings collected by people through approaches such as citizen science, culturomics and iEcology (Ladle et al. 2016; Jarić et al. 2020a, 2021). In addition, meaningful data can be collected by recreational anglers and managed by angling associations (Pinder et al. 2015; Venturelli et al. 2017; Pentyliuk et al. 2023, which, if collected systematically, can provide relatively standardised evidence of the progress of the species' invasion (Vejřík et al. 2019; Lyach 2022; Thomas et al. 2023). In addition, recreational anglers have a particular preference for the individuals of fish that are exceptionally large for the species in question (Wilde and Pope 2004; García-Asorey et al. 2011). These are referred to as "record" or "trophy" catches and are often presented in social media and angling magazines. These exceptional catches have not been particularly recognised by the scientific community in the past (Boon et al. 2024). However, they can be used to examine the status of the population in a particular area (Jarić et al. 2020b) and a decreasing size of catches and maximum length reached in the population can be indicative of overfishing or overall poor population status (Rochet and Trenkel 2003; Shin et al. 2005; Boon et al. 2024).

Despite the great attention paid by recreational anglers to large species and individuals (Beardmore et al. 2015; Birdsong et al. 2021), so-called "coarse fish species" also participate in record catch competitions, especially in countries with a large recreational angling community (Rolfe 2010; Locker 2014). One of these coarse fish species is the crucian carp (*Carassius carassius*), a cyprinid species that has the extraordinary ability to adapt its morphological characteristics to the experienced level of competition and predation (Brönmark and Miner 1992; de Meo et al. 2021, 2022). This adaptation is so extreme that the two phenotypes produced by crucian carp were previously considered to be two different species (Holopainen et al. 1997). In small water bodies, where competition for food is the main driver, a stunted form develops with a usual maximum size of less than 20 cm and an enlarged head compared to the total body size (Holopainen et al. 1997), while in the presence of piscivorous fish, the crucian carp changes its shape to a deep-bodied morph with a relatively small head and can reach a total length of up to 50 cm (Brönmark and Miner 1992; de Meo et al. 2021; Vinterstare et al. 2023). The latter form is prized by recreational anglers for its relative rarity and is, therefore, likely to be entered in record catches.

The crucian carp used to be one of the most abundant species in small European lentic waters; however, it declined due to habitat reduction and the invasion of the gibel carp in Western and Central Europe (Tapkir et al. 2022, 2023; Fedorčák et al. 2023) and due to competition with congener goldfish and common carp (*Cyprinus carpio*) (Copp et al. 2010; Busst and Britton 2015, 2017), as well as due to changes in pond management (Sayer et al. 2011, 2020). The crucian carp, gibel carp and feral goldfish are relatively similar, but the distinguishing characteristics between the crucian carp and the two invasive *Carassius* species allow the crucian carp to be recognised (Szczerbowski 2002; Papoušek et al. 2008).

This study thus attempts to retrospectively map the disappearance of the largesized crucian carp after the invasion of the gibel carp, which was not well documented by the regular monitoring activities of scientists and nature conservation authorities. To this end, recreational angling magazines and websites dedicated to record catches were scrutinised for focal species. In addition to information on fish and catches, recreational anglers also provided photos of their record catches. The study selected evidence of record catches of native crucian carp and invasive gibel carp and used common bream (Abramis brama) and roach (Rutilus rutilus) as a reference dataset. These species were not as severely affected by the invasion of the gibel carp in Czechia as native species in southern latitudes and the gibel carp did not cause a significant decline in the populations of these species in reservoirs and large rivers (Říha et al. 2009; Lusk et al. 2010; Perdikaris et al. 2012). It was hypothesised that: i) the increase of the invasive gibel carp will be accompanied by a decline in reports of large individuals of the native crucian carp over time and ii) the reference datasets of common bream and roach will not show the same trends as those of native crucian carp due to the lower impact of the gibel carp invasion on these species.

Materials and methods

Record catches extraction and verification

The first dataset compiled for the study includes reported catch records of the focal species for which the recreational angling magazines "Rybářství", "Rybář", "Český Rybář", "Sportovní Rybářství", "Kajman" and the recreational angler's website "mrk.cz" were examined for evidence of record fish of the species crucian carp, gibel carp, common bream and roach from the years 1973–2022, resulting in a dataset spanning 50 years. The submitted photos, together with the total length (TL, in cm), weight (kg; W) and angling area code, were first reviewed by a mag-

azine editor-in-chief or an expert (an experienced angler and often an authority from the Czech or Moravian Anglers Union, or from the anglers' community on the mrk.cz website) before being officially admitted to the competition. Selected photos appeared directly in the magazines, while the rest of the record catches were not selected for publication in the magazines and were included in the annual summarised statistics of record catches. Both datasets were extracted in a standardised manner, focusing on the presence of TL, W, species, water type (lentic, lotic) and numerical angling area identifier (code unique to a particular water body or river section, if available in the record). In addition, due to the similarity between crucian carp and gibel carp, the authors' team reviewed all available photos to assess the reliability of the dataset and changed the category from crucian carp to gibel carp (or vice versa) where appropriate. We also extracted the central GPS position of the angling site and the total area in ha and assigned the angling ground to three existing watersheds in Czechia (Elbe, Danube and Odra; Suppl. material 1).

The angling sites are part of the Czech and Moravian Anglers Unions, which are large organisations with around 330,000 members and whose angling grounds cover the catchment areas of the Elbe, Danube (Morava) and Odra Rivers in Czechia. There are 76,000 kilometres of watercourses and 107 reservoirs in Czechia. The area of waters totals 42,000 hectares, both in lotic and lentic ecosystems and is accessible for recreational angling with a licence.

Statistical analyses

To estimate whether the number of record-sized individuals of a given species follows any pattern in the time series, the data were tested with the funtimes package (Lyubchich and Gel 2023) using the local regression-based WAVK test method (Wang et al. 2008; Lyubchich et al. 2013) within the R software (R Core Team 2023). The Sieve bootstrap enhancement to test for a trend (monotonic or non-monotonic) was used with the WAVK function for each species separately (Lyubchich et al. 2013).

In addition, the records of native crucian carp and invasive gibel carp were analysed to determine whether they differ in their maximum recorded length and weight. The crucian carp and gibel carp datasets were tested for normality assumptions using the Shapiro-Wilk normality test. As the data were not normally distributed, the Mann-Whitney U-test was used for all data regardless of the year of capture.

Generalised additive models (GAM) were used to assess trends in fish size during the study period (Wood 2017). To test whether the trend in maximum length and weight changed over the years, two GAMs were created with all species in the first stage, with length and weight as response variables and species, year and angling ground size as explanatory variables. To check the validity of k-value, the gam. check function was used (Augustin et al. 2012; Wood 2017). In addition, a total of eight GAMs were created (for each species separately) with length and weight as response variables and year as an independent variable to assess species-specific trends over the years. The effect of the variable year was modelled using cubic regression splines (bs = "cr"). General additive models were created using the mgcv package (Wood 2001, 2017).

Generalised additive models were used to plot the points of records of all four species for each decade, using the number of reported catches in each period as the response variable and their GPS locations as the explanatory variable, by creating contour plots (Wood 2017). Each line (or contour) represents the number of reported catches in that area within the country. The proximity of the lines indicates the steepness of the gradient. The model check was performed using the gam. check function (Augustin et al. 2012; Wood 2017). The graphical visualisation of the data was created using the ggplot2 and ggmap packages (Kahle and Wickham 2013; Wickham 2016).

Results

In total, the dataset contained 982 records in the period 1973–2022, with 124 records of native crucian carp (mean TL = 39.8 \pm 4.3 cm, mean W = 1.46 \pm 0.43 kg), 248 invasive gibel carp (TL = 44.5 \pm 4.0 cm; W = 1.82 \pm 0.50 kg), 369 common bream (TL = 62.3 \pm 5.7 cm, W = 3.29 \pm 0.87 kg) and 241 roach (TL = 40.8 \pm 3.5 cm, W = 1.09 \pm 0.27 kg). Of the total number of catches, 66.9% of the native crucian carp were caught in lentic waters, while the figures for invasive gibel carp, common bream and roach were 62.9%, 42.5% and 36.5%, respectively. The highest contribution to the dataset was made by the magazine "Rybářství"(700), followed by Kajman (103), mrk.cz (93), Český Rybář (48), Rybář (34) and Sportovní Rybářství (4). When checking the available photos of crucian carp and gibel carp, 27 and 98 photos were obtained, respectively. The reliability of species identification on these photos reached 63% for crucian carp and 100% for gibel carp. All misidentifications were made after 1993, while all 10 crucian carp records with photos were confirmed as crucian carp before that year.

Trend analyses of reported record fishes

The test for any trend on all four species indicated that all species contain a significant trend in their data (WAVK test: crucian carp p < 0.001; gibel carp p < 0.001; common bream < 0.001; roach < 0.05). Trends in number of record crucian carp reported by recreational anglers declined sharply after 2005 and, for these data and the best fit, we used a model with moving window (MW) 7 and a polynomial fit of degree 11 (WAVK test = 34.098, p < 0.001). Reports of invasive gibel carp first appeared in 1985 and were comparable in number to native crucian carp between 1985 and 2000. Since then, reports of invasive gibel carp have become very dominant in terms of record sizes (Fig. 1A). The best fit for the gibel carp was a linear increasing trend (WAVK test = 152.51, MW = 7, p < 0.001). In comparison to this trend, the record size reports for common bream and roach did not show a strong decreasing or increasing trend (Fig. 1B, C). The best fits were a polynomial fit of degree 3 in common bream (WAVK test = 35.996, MW = 9, p < 0.001) and a linear trend in roach (WAVK test = 40.395, MW = 9, p = 0.021).

Trends in species maximum sizes

The reported native crucian carp were, on average, smaller than invasive gibel carp in both length ($39.8 \pm 4.3 \text{ cm vs.} 44.5 \pm 4.0 \text{ cm}$, W = 6167.0, p < 0.001; Fig. 2A) and weight ($1.46 \pm 0.43 \text{ kg vs.} 1.82 \pm 0.50 \text{ kg}$, W = 8282.5, p < 0.001; Fig. 2B). The general additive model for maximum recorded length (M1) and weight (M2) differed significantly between fish species, with the exception of roach length (Table 1), with a positive estimate for gibel carp and common bream and a negative



Figure 1. The number of record catches extracted from angling magazines and websites between 1973 and 2022 for **A** the native crucian carp (*Carassius carassius*), invasive gibel carp (*C. gibelio*) and reference fish species **B** common bream (*Abramis brama*) and **C** roach (*Rutilus rutilus*). The period captures the invasion phase of gibel carp from early invasion phase to fully established, as well as the current impact on the native and critically endangered crucian carp in Czechia.

estimate for roach in terms of weight and, further, with a positive effect of angling ground size (M1: t = 2.36, p = 0.018; M2: t = 2.34, p = 0.020) and a positive effect on weight in the Elbe catchment (M2: t = 2.28, p = 0.023). The effect of year was significant for both models (M1 F = 4.844, p < 0.001; M2: F = 3.936, p < 0.001) and the total explained deviation of the model was 83.4% and 71.8% for M1 and M2, respectively. The trend for the recorded maximum lengths was unimodal for native crucian carp with maximum values around the year 2000 (GAM: F = 15.12, p < 0.001, 33.4% deviance explained), while it gradually increased for invasive gibel carp (GAM: F = 18.84, p < 0.001, 24.1%), was relatively stable for common bream (GAM: F = 0.009, p > 0.05, 0.0%) and showed a fluctuating trend with the maximum around 1990 in roach (GAM: F = 3.841, p < 0.001, 14.7%; Fig. 3). Similarly, the maximum weight was recorded around the year 2000 for crucian carp (GAM: F = 21.93, p < 0.001, 44.7%), while the maximum recorded weight increased gradually in gibel carp (GAM: F = 3.726, p = 0.002, 8.5%) and the fit was linear in common bream (GAM: F = 2.335, p = 0.014, 7.6%) and fluctuating in roach (GAM: F = 10.19, p < 0.001, 16.7%; Fig. 4).

The GAM contour plots showed the concentration of large-sized fish mainly in the area of the lowland rivers and the interconnected oxbows. While common bream and gibel carp were almost ubiquitous, record-sized crucian carp and roach showed a more aggregated distribution with few hotspots in Czechia (Fig. 5).



Figure 2. The comparison of reported record catches size in the 50-year dataset. The maximum attainable size of the invasive gibel carp (*Carassius gibelio*) significantly exceeds the maximum size of the native crucian carp (*C. carassius*) in Czechia in both **A** total length and **B** weight. The boxplot boundaries represent upper and lower quartiles; the thick lines represent medians and the whiskers represent 1.5 times the interquartile range. Violin plots represent kernel density distribution.

Table 1. The parametric coefficient of general additive models for record catches of native crucian carp (*Carassius carassius*), invasive gibel carp (*C. gibelio*), common bream (*Abramis brama*) and roach (*Rutilus rutilus*) with response variable of total length (upper table) and weight (lower table). The significance of smooth term on variable year was < 0.001 for both models and explained deviance was 83.4 and 71.8%, respectively.

| | Estimate | <i>t</i> -value | <i>p</i> -value | | | | |
|---------------------|-----------------------|-----------------|-----------------|--|--|--|--|
| GAM Length | | | | | | | |
| Intercept | 40.174 74.966 | | <0.001 | | | | |
| Species:Roach | 0.383 | 0.709 | NS | | | | |
| Species:Bream | 22.069 | 43.021 | < 0.001 | | | | |
| Species:Gibel | 3.812 | 6.876 | < 0.001 | | | | |
| Angling ground size | 0.001 | 2.369 | 0.0181 | | | | |
| Type: Lotic | -0.088 | -0.267 | NS | | | | |
| Basin: Elbe | 0.298 | 0.840 | NS | | | | |
| Basin: Odra | -0.820 | -1.152 | NS | | | | |
| GAM Weight | | | | | | | |
| Intercept | 1.408 | 19.973 | < 0.001 | | | | |
| Species:Roach | -0.420 | -5.908 | < 0.001 | | | | |
| Species:Bream | 1.810 | 26.838 | < 0.001 | | | | |
| Species:Gibel | 0.314 | 4.305 | < 0.001 | | | | |
| Angling ground size | 7.094e ⁻⁰⁵ | 2.157 | 0.031 | | | | |
| Type: Lotic | 0.001 | 0.198 | NS | | | | |
| Basin: Elbe | 0.107 | 2.280 | 0.029 | | | | |
| Basin: Odra | -0.041 | -0.440 | NS | | | | |



Figure 3. The GAM trend-line of record catches size (total length) in the 50-year dataset. The GAM fit has been computed with the stat_smooth function. The data suggest: **A** unimodal response in the native crucian carp (*Carassius carassius*) with time **B** increase maximum attainable size in the invasive gibel carp (*C. gibelio*) **C** stabilised size limits in common bream (*Abramis brama*) and **D** maximum in 1990 in roach (*Rutilus rutilus*).



Figure 4. The GAM trend-line of record catches size (weight) in the 50-year dataset. The fit has been computed with the smooth function with a value of k = 1 to avoid overfitting. The data suggest **A** unimodal response in the native crucian carp (*Carassius carassius*) with time **B** moderate increase in maximum attainable size in the invasive gibel carp (*C. gibelio*) **C** relatively stabilised size limits in common bream (*Abramis brama*) and **D** fluctuating trend in roach (*Rutilus rutilus*).



Figure 5. Contour plots based on GAMs for **A** native crucian carp (*Carassius carassius*) **B** invasive gibel carp (*C. gibelio*) **C** common bream (*Abramis brama*) and **D** roach (*Rutilus rutilus*) for all study period, where the number of reported record catches in a given area was used as the response variable and their GPS locations as the explanatory variable. Each line (or contour) represents the reported catches in that region within the country. The proximity of the lines indicates the steepness of the gradient. Colours show the abundance of records with red indicating the highest abundance.

Discussion

Given the speed at which invasions are progressing in the aquatic environment, it appears that utilising the information collected from citizens can help combat the problem (Jarić et al. 2020b, 2021; Löki et al. 2023). This study shows circumstantial evidence of declining trend in the distribution of the native large crucian carp in Czechia, as recorded by recreational anglers' catches. This trend in record catches of invasive gibel carp and native crucian carp corresponds well with the status of crucian carp in Czechia, where the first change in species status from "Least Concern" to "Vulnerable" occurred in 2000, i.e. around the same time that catches of gibel carp appeared more frequently in the record statistics than those of crucian carp. The increase in misidentifications in the native crucian carp records after 1993 indicates that the data are likely to include some misidentified gibel carp, so that their dominance in the catches will be likely even more absolute. However, this dataset did not contain all variables that could have accounted for the decline of crucian carp; thus, there is a chance that other biotic (e.g. more intense common carp stocking) or abiotic (e.g. climate change) factors contributed to its decline.

Trends in occurrence and size with relation to species ecology

Both native crucian carp and invasive gibel carp were found more frequently in the lentic waters, which is consistent with their ecology (Holopainen et al. 1997; Tarkan et al. 2023). The size of the angling water and the catchment area of the Elbe had a slight positive influence on fish size in the general model for all species. This result may need to be tested in more detail using a larger dataset, as not much scientific literature has been published on angling for fish of record size and such result may apply only to some species.

While the records of both reference species showed a relatively stable trend around the same average value, both native crucian carp and invasive gibel carp showed GAM trend-lines indicating changes in maximum size. For crucian carp, the unimodal response with a decline in recorded maximum size in recent years suggests either growth limitations or possible confusion with invasive gibel carp or hybrids between crucian carp and gibel carp around 2000. Both options are possible, as the growth restriction may be caused either by increased interspecific competition due to the invasion of the gibel carp (Auwerx et al. 2021; Tapkir et al. 2022) or by the negative effects of increasing average temperature on fish growth (Emmrich et al. 2014). While the prediction of crucian carp via growth parameters suggests that growth increases with temperature (Tarkan et al. 2016), the record-size crucian carp seems to benefit from rather low temperatures and the best lakes are located in northern latitudes and with the presence of piscivorous fish (Rolfe 2010; Vinterstare et al. 2023).

Hybridisation is also a likely explanation, as both species form hybrids under certain circumstances (Papoušek et al. 2008; Knytl et al. 2018) and hybrids also form between the crucian carp and the goldfish (Smartt 2007). Despite the emphasis on hybridisation in *Carassius* studies (Papoušek et al. 2008; Wouters et al. 2012; Knytl et al. 2018, 2022), the results of strong invasive gibel carp suggest that this is competition between native crucian carp and probably the main reason for the decline in crucian carp populations (Tapkir et al. 2022, 2023).

The sequence of gibel carp invasion in Czechia

The gibel carp was accidentally introduced to Hungary together with the commercial Asian fish species (*Hypophthalmichthys molitrix*, *H. nobilis*, *Ctenopharyngodon idella*) in the 1950s (Tóth 1976; Holčík 1980). The westward invasion of the gibel carp started in the Danube catchment, and commercial catches of *Carassius* genus increased from 3% to 15% in the period from 1958 to 1976 in the Danube (Tóth 1976; Holčík 1980) and the first records in Czechia were in the Morava River (Danube watershed) in 1975–1976 (Halačka et al. 2003). Due to inter-basin aquaculture transfers, the first reports of gibel carp in the Elbe River Basin were recorded as early as 1980 (Kubečka 1989) and soon became the dominant taxa within the genus *Carassius* (Halačka et al. 2003; Lusk et al. 2010). The first record in this dataset also comes from the Danube catchment. However, this study focused on fish of record size, so it is likely that several years will pass between the invasion and the record catches.

There are currently three invasive species of the genus *Carassius* living in Czechia, the goldfish (including feral form), *C. langsdorfii* in addition to already mentioned gibel carp (Kalous et al. 2007, 2013; Rylková et al. 2013). These species can hy-

bridise with each other and form viable populations of hybrid origin (Keszte et al. 2021) and are, therefore, considered a species complex in some studies (Rylková et al. 2013; Knytl et al. 2022). All of them are of similar appearance (Hensel 1971), the largest individuals can reach a length of more than 40 cm and, therefore, all can be included in angling statistics under the name of invasive gibel carp. Although it is widely believed that the gibel carp is the most widespread invasive *Carassius* species in Central Europe and the other two species are of lesser importance in terms of competition with native crucian carp (Lusk et al. 2010; Musil et al. 2010; Fedorčák et al. 2023), it might be interesting to investigate the relative proportion of these invasive species in European mainland.

Engaging public in conservation of crucian carp

The passion for enhancing native crucian carp populations was first brought to public attention in England, where Peter Rolfe launched his attempt as a pilot angler to reintroduce the species to Norfolk waters and promote the existence of exceptionally large fish in ponds (Copp and Sayer 2010; Rolfe 2010). The approach has been underpinned by the scientific literature and the presence of European pike (*Esox lucius*) has been embedded in the management of larger ponds to encourage the presence of the deep-bodied phenotype that can reach exceptional sizes that are attractive to recreational anglers (Brönmark and Miner 1992; Brönmark et al. 1995; Pettersson and Bronmark 1997; Rolfe 2010). This concept involves easing the intraspecific competition through predation (i.e. thinning out the carp population in the water body) and the simultaneous production of crucian carp in small ponds and stocking in larger water bodies.

Although the conservation and fisheries management described above is artificial, it has its roots in the life-history strategy of the crucian carp. In the floodplain rivers, the population has a metapopulation structure with a rare deep-bodied phenotype in multi-species community of large water bodies or lowland rivers (Brönmark and Miner 1992; Brönmark et al. 1995; Holopainen et al. 1997). These individuals can colonise pools in the floodplain and lay the foundation to the shallow-bodied phenotype that is formed in a single-species community without the presence of piscivores due to the frequent occurrence of anoxia (Blažka 1958; Holopainen and Hyvärinen 1985; Piironen and Holopainen 1986). These pools are then source populations and provide a surplus of fish in the main river channels during floods, where they can produce deep-bodied and potentially large-sized fish. From the perspective of Czechia, it appears that the deep-bodied phenotype disappeared faster than the shallow-bodied phenotype, as citizen-science projects resulted in finding few tens of sites (Šmejkal et al. 2021). Water Framework Directive monitoring in the Vltava watershed has not detected crucian carp in the last 15 years, while gibel carp are abundant (Bartoň and Šmejkal 2022), so we can assume that the trend presented in the catch records is reliable.

Culturomics role in fish conservation with emphasis on large-size fish

Culturomics in conservation has been shown to be an effective means of raising public understanding, framing conservation issues and engaging people in timely environmental monitoring (Ladle et al. 2016). Recreational angling with catchand-release ethics for each species is a conservation strategy and these contests have

been shown to be effective in raising awareness of species conservation and getting people's attention (Cooke and Suski 2005). The catch data of mahseer (Tor spp.) from the Cauvery River in India is a good example of how organised angling can be used as a tool to monitor species conservation, as it effectively contributes to species conservation and fisheries management measures (Pinder et al. 2015). The appreciation of environmental goods and services is often a part of societal culture and digitised or documented information, such as angler logbooks, helps to understand the behaviour of recreational anglers towards a species (Hutt et al. 2013) and can be used for conservation and management measures via culturomics. Angler's ecological knowledge, which largely depends on the size and frequency of their catches (van den Heuvel and Rönnbäck 2023), can be an effective tool for conservation alongside the cultural influences on their interpretations of environmental change (Thornton and Scheer 2012). There are approximately 226 million recreational anglers worldwide (World Bank 2002; Arlinghaus et al. 2015, 2019) and ~ 3% of the total population of Czechia are registered in angling unions (Boukal et al. 2012), so this angling information, if systematically retrieved and analysed, can provide a good source of information for conservation efforts.

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

This study did not involve handling of animals or personal information.

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Author contributions

Marek Šmejkal: Conceptualisation, Investigation, Data curation, Formal analysis, Writing Original draft, Writing, Review & Editing, Visualisation. Kiran Thomas: Formal analysis, Visualisation, Writing, Review & Editing. Vladimír Kořen: Conceptualisation, Writing, Review & Editing. Jan Kubečka: Conceptualisation, Data curation, Writing, Review & Editing.

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Data availability

Data will be shared by authors upon reasonable request.

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Supplementary material 1

Individual data points

Authors: Marek Šmejkal, Kiran Thomas, Vladimír Kořen, Jan Kubečka Data type: docx

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Research Article

Proximity to forest plantations is associated with presence and abundance of invasive plants in landscapes of south-central Chile

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Abstract

Invasive plant species (IPs) are widespread in forests and cause substantial environmental, economic and social impacts. They occupy native ecological niches, causing local extinctions to the detriment of native biodiversity and disrupting ecosystem services provision. How landscape characteristics may determine the success of IPs remains unclear and, more importantly, how land-use and land-cover changes may result in spatial shifts in the invasion risk. Furthermore, the study of how landscape factors may influence biological invasions has focused on particular species, but not the IPs' community. In this study, we identify and assess landscape variables that influence the presence and distribution of the IPs' community in temperate forests of a global biodiversity hotspot in south-central Chile. We fitted spatially explicit models, combining field-sampling information and landscape variables related to land-use/land-cover, topography, climate, soil characteristics and anthropogenic factors to explain and predict the presence and distribution of the IPs' community. From the whole sampling of plant species, we identified eight plant species classified as IPs: three trees and five shrubs. We used field data from 125 500 × 2 m-transects, in which we registered species richness, abundance and basal area of IPs' community. Distance to forest plantations was the landscape variable with the most substantial influence on IPs' presence and distribution. Richness, abundance and basal area of IPs' trees were higher at shorter distances from forest plantations. The basal area of IPs' trees was the best model explaining the relationship between IPs' community and landscape variables. All descriptors of the IPs' community showed similar spatial patterns: species richness, abundance and tree basal area are higher in more disturbed areas. Our findings contribute to increasing our understanding of the distribution patterns of IPs in forest landscapes. Our models can be suitable tools for designing strategies to prevent, mitigate or make integrated control of the impacts of invasive species in forest landscapes.

Key words: Alien plants, basal area, biological invasions, land cover, landscape dynamics, land use

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Introduction

Biological invasions might be shaped by landscape characteristics, as landscape structure may influence the patterns of the invasive species community. Anthropogenic landscape alteration plays a fundamental role in explaining the patterns and magnitude of invasions by exotic plants (González-Moreno et al. 2015). This association is mainly mediated by an increase in propagule pressure, the degree of disturbance and habitat connectivity favourable to invasion. Likewise, invasions may shape landscapes, as the invasive species can alter its surrounding environment to make conditions more conducive to its presence (Gouws and Shackleton 2019). For instance, according to Bartuszevige et al. (2006), the landscape structure is of primary importance, while some community attributes, such as disturbance history, canopy openness and woody plant composition, are of secondary importance to determine the invasion risks of the alien shrub Lonicera maackii. In this case, the shrub invades from multiple foci (towns) rather than in a frontal advance, independently of the landscape connectivity (i.e. the number of corridors), but depending on edge habitat, probably due to increased propagule pressure. Thus, some of the community attributes associated with L. maackii invasion may be indicators of past disturbances.

Invasive plants (IPs) can be considered a particular component in the succession of the plant community. IPs distributions show wide ecological amplitudes, considering they might adapt to different and novel climatic and geographical zones (Thinley et al. 2020). The IPs' presence may be regulated by mechanisms occurring at global scales, but also at local scales of anthropogenic (e.g. social, economic and political) and biophysical variables (Montti et al. 2017). Thus, IPs' invasion risks would depend on the co-occurrence of specific factors at different spatial scales, from global to local. These factors include suitable environmental and climatic conditions, propagule introduction by humans and a posteriori landscape-scale dispersal. For instance, agricultural lands are usually most susceptible to invasion amongst all other land-use types, irrespective of the species (Thinley et al. 2020).

The land-use type may be crucial for shaping the invasion process (Kueffer 2017). Land-use changes related to political processes can create an invasion debt that causes unexpected linkages amongst the invasive plant, native dispersers, land management and topography that, together, can cause cascading changes in ecosystems (Lenda et al. 2018). For instance, the invasion of the alien walnut Juglans regia in Poland since 1989 has been a multifaceted process (Lenda et al. 2018). Human-related alterations to propagule pressure biotic and abiotic factors have led to the spread of walnuts from abandoned human settlements and fields to forest ecosystems. Moreover, the changes in land-use and land-cover may result in spatial shifts in the invasion risk (Wang et al. 2016). Although some IPs might not be established in dynamic and heterogeneous landscapes (even with favourable climate conditions), the species may establish when a disturbance such as land-use change occurs (Gillson et al. 2008). The landscape permeability increases, allowing IP colonisation; this produces patchily distributed stands of the same age. Many invasive plants perform better in cleared areas; thus, the connectivity of cleared areas and undisturbed habitat results is critical for their successful colonisation (Green et al. 2006).

Several models represent and predict the dispersion of individual IPs' species considering the characteristics of their natural range, including species distribution

models (Elith 2017). However, few studies have considered the IPs' community to elaborate dispersion or distribution models. Amongst these few studies, we find that of Gong et al. (2020), who used an assemblage-niche-model platform to build niche-based species distribution models and project potential distributions of two invasive plant species (Cecropia peltata and Ulex europaeus), changes in their distribution under the scenarios of global changes, as well as the underlying mechanisms or factors driving these changes. To assess the status of fish stocks, multispecies virtual population analysis is an attempt to take species interactions; some models treat them as aggregate (continuous) biomass and capture more realistic biological interactions and processes (Gupta et al. 2019). According to Plagányi et al. (2022), multispecies models can reduce bias in parameters, reference points and projections. Multispecies models that cover a wide range of species in the ecosystem span multiple trophic levels from primary producers to top predators. In the context of connectivity conservation plans, they generally develop considering a single species and are rarely empirically evaluated for their relevance to others, limiting our understanding of how connectivity requirements differ between species (Brennan et al. 2020). These same authors recommend evaluating multispecies connectivity to prioritise areas for conservation that safeguard the connectivity needs of multiple species of conservation concern.

Landscape characteristics were one of the most critical drivers for most plant responses in the research about constraints of restoration outcomes across spatial scales of an invasive plant (Rohal et al. 2019). According to their research, the abiotic and landscape variables combined at a patch scale drive the plant community results. Climatic and land-use variables were good predictors of landscape susceptibility to invasion in the south-eastern U.S. (Lázaro-Lobo et al. 2020), especially distance to settlements. Systems anthropogenically perturbed, i.e. developed areas and barren lands were more prone to be invaded. Homogenisation of landscapes through anthropogenic activities (agriculture, forest plantations, urbanisation) helps biotic homogenisation and is a process attributed primarily to the establishment of exotic species (Lobos et al. 2016). Landscape heterogeneity and corridors for propagule dispersal may also increase the landscape susceptibility to invasion for most species (Lázaro-Lobo et al. 2020). The influence of landscape composition and configuration on invasion risk is species-specific. Thus, to better understand the potential impacts of IPs, it is necessary to know the IPs' habitat and the main variables that may facilitate/impede their presence and abundance.

In Chile, 743 species of alien plants have been reported, a higher proportion (15%) than in other Latin American countries (Fuentes et al. 2013). Of these species, over 100 are considered IPs (Fuentes et al. 2014). There is a high concentration of alien species in the South-central region, where practically all IPs at the national level are present. Amongst the causes of this distribution are multiple colonisation waves, higher levels of anthropogenic disturbance, great agricultural and livestock activity and intensification of forest crops in the mid-20th century (Fuentes et al. 2014). The eight species that form the community of IPs in our study area are considered invasive, according to Herrera et al. (2016). *Acacia dealbata* reduces species richness under its understorey, plant cover and seed density, thus modifying the floristic composition, while increasing the coverage of other alien plant species (Herrera et al. 2016). *Acacia melanoxylon* promotes an increase in water-nitrogen concentration and alterations in litter characteristics in native riparian forests, altering the activity and community structure of microbial

decomposers (Pereira et al. 2021). Eucalyptus globulus causes alterations of networks of interaction between species of the native community, alters the dynamics of leaf litter-fall, can increase the concentration of soil nitrate, delay the growth of undergrowth plant species and decrease fungal biomass in the river ecosystem (Castro-Díez et al. 2004; Medina-Villar 2016). Cytisus striatus is considered a noxious weed in the United States (Ketchum and Rose 2003) and grows aggressively, displacing native species. It increases the risk and intensity of fires and leads the fire to the top of the trees (Fuentes et al. 2014). Rosa rubiginosa forms monospecific stands, so, in advanced stages of the invasion, it can impoverish the species composition and alter the structure of affected plant communities (Herrera et al. 2016). It can alter pollination mutualisms by attracting native and exotic pollinators and reducing the reproductive success of native plants. Rubus ulmifolius proliferates by colonising open sites, where it prevents the regeneration of native plants, resulting in impoverishment in species composition and altering the structure of affected plant communities (Herrera et al. 2016). It forms impenetrable barriers that limit the circulation of animals and make large areas inaccessible. Teline monspessulana creates favourable conditions for fire generation because it tends to form monospecific groupings, it replaces native vegetation, reduces the load capacity of grazing land and increases combustible material (Herrera et al. 2016). Ulex europaeus is one of the 100 of the World's Worst Invasive Alien Species (GISD 2021). It is highly competitive, displaces cultivated and native plants and alters soil conditions by fixing nitrogen and acidifying it. Ulex europaeus creates an extreme fire hazard due to its oily, highly flammable foliage and seeds and abundant dead material.

Our study provides critical information to understand the relationship between the landscape structure and the IPs in forest landscapes in south-central Chile. Specifically, we: (a) identified and assessed the main landscape variables that influence the presence and distribution of the IPs community and, (b) fitted spatially explicit models to predict the areas with higher IPs' invasion risks. Our proposed model could facilitate early detection and control of IPs, delaying their spread and conserving native flora and fauna, especially in natural protected areas. This research will contribute to our understanding of spatial variation in the key to the success of IPs and control them in the global forests.

Materials and methods

Study area

Our study was conducted in four landscapes of La Araucanía Region in south-central Chile (Fig. 1). These landscapes are in three representative areas of the region: Lumaco (38°18'16"S, 73°05'35"W) in the Coastal-Mountain Range, Freire (38°57'18"S, 72°36'46"W) in the Central Valley and Pucón (39°16'54"S, 71°56'35"W) along with Curarrehue (39°21'28"S, 71°34'59"W) in the Andean-Mountain Range. The two latter contain three natural protected areas: Huerquehue National Park, Villarrica National Park and Villarrica National Reserve (CONAF 2011).

The extension and biophysical characteristics are similar in the four landscapes (Appendix 1: Table A1); however, there are some differences in their main land-use and land-cover types (related to their main economic activities). They constitute a gradient of disturbance, from most disturbed landscapes in the Coastal-Mountain



Figure 1. Location of four landscapes in La Araucanía Region, south-central Chile and their main land uses and land covers.

Range (Lumaco) and Central Valley (Freire) to more minor disturbed landscapes near the Andean-Mountains Range (Pucón and Curarrehue) (Altamirano et al. 2020). In Lumaco, forest plantations occupy 64% of the total area, while the remaining native forest only 16% (Fig. 1). In Freire, agricultural lands occupy 62% and native forest only 11%; while in Pucón and Curarrehue, native forests are the primary land use with 71% and 82% of the area, respectively.

The four landscapes are located inside the Chilean hotspot of biodiversity named Chilean Winter Rainfall-Valdivian Forest, which harbours richly endemic flora and fauna (Mittermeier et al. 2011). This hotspot contains 3,893 native vascular plants, of which 1,957 species (50%) are endemic (Arroyo et al. 2006). However, a generalised loss of native forest cover has occurred recently and keeps going, mainly due to conversions to shrublands and exotic forest plantations in some places (Miranda et al. 2017). These forest plantations (exotic species monocultures, mainly *Pinus* and *Eucalyptus*) have dominated large areas of central Chile since the 1990s.

Field sampling

In each landscape, we located 500×2 m transects via a random sampling scheme stratified by their main land cover (i.e. native forest, tree plantation, agriculture and pastures) and accessibility. The total number of transects was 125: 31 in Lumaco, 36 in Freire, 30 in Pucón and 28 in Curarrehue (Fig. 2). We identified all



Figure 2. Distribution of 500×2 m-transects (n = 125) in four landscapes in south-central Chile. Transects are located via a random sampling scheme stratified by land-use types (see Fig. 1).

trees and shrubs higher than 1.4 m in height to species level in each transect. This height is a good standard metric to register the reality of a moment of the sample, but does not consider smaller, usually younger, plants that could be of great abundance and greater importance in the future. Then, we classified them according to their origin (native or alien) and life form (tree or shrub) and measured their height and diameter at breast height (DBH). We estimated the species richness, trees and shrubs abundance and basal area as potential response variables for those plants registered as IPs to monitor their presence and distribution according to the classification done by Fuentes et al. (2014).

Landscape variables

We extracted a set of landscape variables from spatially-explicit data on climate, topography, soil, and anthropogenic characteristics to obtain the explanatory variables for modelling. We used the climate variables which were obtained from the WorldClim database (www.worldclim.org) and included 19 temperature indicators, rainfall and bioclimatic variables. We derived bioclimatic variables from the monthly temperature and rainfall values to be more biologically meaningful. These variables represent annual trends in seasonality and extreme or limiting environmental factors (Hijmans et al. 2005). In addition, we included elevation, aspect,

slope and distance to rivers (SRTM Data) for topographical variables. For soil variables, we extracted for each sample point the dry bulk density (Bden), cation exchange capacity (CEC), soil pH measured in H₂O (SpH), soil organic carbon (SOC) and soil organic carbon content (SCC) from Soilgrids database (www.soil-grids.org), a collection of international soil classes and characteristics of the world, based on modern statistical modelling techniques (Hengl et al. 2014). We also considered soil information from a local database (La Araucanía soil series; Pfeiffer et al. (2019)): erodability (value and range), erosion risk, erosion class and evapotranspiration. For anthropogenic variables, we estimated distance to roads, wild-fires and agricultural burning (IDE, Minagri https://ide.minagri.gob.cl/geoweb/) and distance to urban centres (i.e. cities and towns). We measure proximity to the main land cover by the Euclidean distance to native forests, forest plantations, agricultural land and pasture covers.

Modelling and predicting IPs community presence and distribution

Our models considered the landscape variables as explanatory (predictor) variables and presence and distribution as response variables (i.e. richness, abundance and basal area of IPs' community). We built a correlation matrix between landscape variables and excluded all highly correlated variables (|r| > 0.6) to avoid multicollinearity for model building. We used boosted regression trees (BRT) for statistical modelling, a technique that comprises two algorithms, to link the explanatory variables (landscape variables) to the dependent variables (IPs variables). BRT generates many regression trees combined into one ultimate regression tree model, drastically boosting accuracy and predictive performance (Elith et al. 2008). We generated regression trees using the gbm package in R (Ridgeway 2007). This procedure uses three variables, namely, learning rate (lr), bag fraction (bf) and tree complexity (tc). We built several models using different lr and tc values to obtain the optimal combination (Elith et al. 2008). We reduced the models by removing variables with less relative influence every time we ran them until they had their best performance, represented by a high explained deviance (D²) and low error (rRMSE). Additionally, the most frequently appearing variables had greater consistency and were eventually selected. After training the model, a validation accuracy score estimates the model performance on an independent dataset (20%). When the dataset of observations is divided into k disjoint subsamples (or folds), then a group is taken as a holdout or test dataset and the remaining groups as a training dataset; this procedure is known as K-fold cross-validation. In our study, we adopted the latter procedure (with K = 5) to validate, avoid overfitting and estimate the average classification.

Then, we calculated the performance for each fitted model (percentage explained deviance; D²) (Littke et al. 2014), the relative root-mean-square error (rRMSE) (Aertsen et al. 2010) and the correlation between observed and predicted values. We chose those predictor variables with a strong relationship with the response variable (> 10% of influence in BRT models). The model estimates the relative influence of predictor variables (influence) by the frequency at which a variable is selected for splitting, weighted by the squared model improvement due to each split and averaged over all trees (Elith et al. 2008). The relative influence of each variable was scaled so that the sum resulted in 100, with higher values, indicating a more substantial influence. The boosting process involves an iterative step-wise process

of selecting the model with the maximum deviance and the minimum rRMSE at each stage (Elith et al. 2008). Finally, models were used to build prediction maps of the IPs distribution and identify the areas with higher values of IPs abundance, richness and basal area. These areas would represent the best conditions for potential IPs invasion according to the landscape variables.

Akin-Fajiye and Gurevitch (2018) used a boosted regression tree to model factors associated with species presence, density and change in density of an invasive plant. Boosted regression trees are suitable for this analysis because they do not require any assumptions about the data distribution, do not impose linearity and accommodate missing data using surrogates. Nunez-Mir et al. (2019) also used a boosted regression tree to develop a statistical model to predict with 86% accuracy on average the invasiveness of alien woody plant species found across the United States by comparing 63 invasive and 794 non-invasive exotic woody plant species naturalised. The boosted regression tree model comprises a flexible regression structure with improved predictive performance affected by boosting (Colin et al. 2018). Boosting is an adaptive method combining many simple models to improve predictive performance. In their research, Colin et al. (2018) conclude that boosted regression trees are an appealing method for estimating green vegetation from remotely-sensed images. Boosted regression trees benefit from being robust to the inclusion of irrelevant predictors and the presence of outliers (Forsyth et al. 2018). Boosted regression trees can also model complex non-linear relationships, including step-functions and generally predict better than traditional modelling approaches (Elith et al. 2008).

Results

General patterns of species richness

We recorded in the study area a total of 247 plant species, of which 61 (24.6%) were alien species (Appendix 1: Table A2). The proportion between life forms (i.e. tree and shrub) were similar and balanced (circa 1:1) amongst landscapes. However, this ratio varied when considering native or alien species. For native species, trees and shrubs were relatively balanced (56% and 44%, respectively). Meanwhile, of the 61 alien species, most were trees (67%) and the rest were shrubs (33%).

Total native species richness was higher in Pucón (58) and Curarrehue (52) than in Lumaco (39) and Freire (31) (Fig. 3a). The proportion between native and alien species was different amongst landscapes, being highest in the number of alien species in Freire, with 28 out of 59 (47.5%), but \leq 20% in the other three landscapes. Proportions between life forms (trees and shrubs) were also variable amongst landscapes. We recorded six trees and five shrubs (20%) of alien plants in Lumaco, nine trees and three shrubs (19%) in Curarrehue and seven trees and three shrubs (15%) in Pucón (Fig. 3b).

We found eight invasive species (IPs community) in the study area, meaning 15% of the total alien species in the study area (a total of 61 alien plants) (Fig. 3b): three tree species (*Acacia dealbata, Acacia melanoxylon* and *Eucalyptus globulus*) and five shrubs (*Cytisus striatus, Rosa rubiginosa, Rubus ulmifolius, Teline monspessulana* and *Ulex europaeus*). In Lumaco, 64% of alien plants were invasive species. In Freire, 25% of alien plant species were invasive, while in Pucón and Curarrehue, we found 50% and 33% of invasive plant species, respectively.





Landscape variables influencing the IPs' community

After checking the correlation matrix, the boosted regression tree models and the consistency of explanatory variables of each model (Appendix 1: Table A3), we selected the following variables for the models: 1) distance to forest plantations, 2) distance to towns and populated centres, 3) distance to rivers; 4) the minimum temperature of the coldest month (TMin), 5) cation exchange capacity at 22.5 cm deep (CEC 22.5) and 6) soil organic carbon stock in 15–30 cm depth (SOC). Due to the large number of landscape variables considered, we ran a high number of models (n = 130) with different explanatory variables. Checking for the deviance value and the best performance evaluation allowed us to obtain fewer and better models relying on a few explanatory variables (Table 1). The models with the best performances (best goodness of fit) included the basal area of IPs' trees, IPs' abundance and IPs' richness, respectively.

Table 1. Performance statistics for boosted regression tree models of invasive plants species using three indicators (species richness, abundance and tree basal area). Explained deviance of the fitted model (D²), Pearson's correlation coefficient (corr) and relative root mean square error (rRMSE) are reported. * Values for cross-validation.

| Model | D ² | D ² cv* | Corr | Corr cv* | rRMSE* |
|-----------------|-----------------------|--------------------|------|----------|--------|
| Tree basal area | 0.97 | 0.68 | 0.98 | 0.66 | 9.04 |
| Abundance | 0.57 | 0.35 | 0.71 | 0.59 | 14.88 |
| Richness | 0.49 | 0.32 | 0.72 | 0.57 | 21.01 |

Modelling IPs community distribution

Distance to forest plantations was the primary explanatory variable in all models (Fig. 4). This explanatory variable had the strongest relative influence on species richness, abundance and basal area of invasive trees, overcoming 50% of relative influence and reaching a maximum of 85%. For IPs richness, distance to forest plantations had 57.5% of the relative influence, while soil organic carbon stock and distance to towns were the second and third variables, with 26.5% and 16%, respectively (Fig. 4a). For IPs abundance, distance to forest plantations had 85% of relative influence. In contrast, cation exchange capacity (CEC22.5) distance to populated centres were the second and third variables, with 8% and 7%, respectively (Fig. 4b). For the basal area of IPs trees, distance to forest plantations was 59% relative influence; the minimum temperature of the coldest month (TMin) and the distance to rivers were the second and the third variables, with 22% and 20%, respectively (Fig. 4c).

Partial dependence plots showed that the less distance from the forest plantations, the greater the IPs richness and abundance and basal area of IPs trees (Fig. 5a). All these explanatory variables showed a striking decrease of around 1000 m to forest plantations. Soil organic carbon stock and distance to towns also appeared as explanatory variables in the species richness model. IPs richness kept constant with soil organic carbon stock until it almost attained 60 tonnes per hectare, then it fell abruptly (Fig. 5b). IPs richness also increased along with the distance to towns up to around 10,000 m and decreased gradually. IPs' abundance constantly decreased along with increased cation exchange capacity (CEC 22.5 deep), with a sudden fall when this explanatory variable reached 30 cmolc/kg. IPs also decreased further from cities. The basal area of IPs' trees was higher near forest plantations; the striking decrease occurs before 500 m distance (Fig. 5c). The basal area remained constant with low values of the minimum temperature of the coldest month (TMin), but increased just when this temperature surpasses 3.8 °C. The relationship between the basal area of IPs' trees and distance to rivers was irregular, decreasing the basal area through increased distance to rivers.

Predicting the IPs community distribution

Distribution models predicted higher IPs' richness in Lumaco than in the other landscapes (Fig. 6a), especially in the northern area. In Freire, the highest IPs' richness was predicted alongside the Allipen River (which crosses the territory) and a tree plantation patch. Meanwhile, in Pucón and Curarrehue, models predicted only small patches of higher IPs' richness. Regarding IPs' abundance (Fig. 6b), in Lumaco, landscape variables enhance the highest abundance of IPs in practically





the entire county. In the other landscapes, the highest abundance coincides with the patches observed for the richness model. We found the highest basal area values of invasive trees in Lumaco (Fig. 6c), but basal area varied more than abundance values. There were small patches with high basal area values in the other landscapes. but to a lesser extent than richness and abundance. IPs' richness, abundance and the basal area of trees had similar spatial patterns; therefore, areas of higher IPs' invasion risks in the study area coincided for all models, although they included different explanatory variables. Boosted regression tree model predictions showed that Lumaco is the county with the highest probability of spreading invasive plants, while Curarrehue has the lowest probability.



Figure 5. Partial dependence plots for the three most influential variables on IPs' richness (**a**), abundance (**b**) and basal area of trees (**c**). Y-axes in logit scale and centred on a zero mean over the data distribution. Interior marks show deciles across the Y-axes.

Discussion

Landscape variables influencing the IPs community

Proximity to forest plantations resulted in the primary landscape variable influencing IPs' distribution. Recent reviews have shown that forest plantations are generally related to lower local species richness than native ecosystems (Escobedo et al. 2017; Brazeiro et al. 2018). In some cases, substituting native ecosystems with forest plantations reduced local plant richness by an average of 35% (Brazeiro et al. 2018). Disturbance often drives plant invasion and may modify the community assembly (Escobedo et al. 2017). Disturbance events (e.g. fire, grazing, mowing activity of fossorial mammals and tree plantation conversion) remove plant biomass and create invasive plant species colonisation (Mouillot et al. 2013). IPs' frequently grow faster than natives, have more efficient seed dispersal and higher resource-use efficiency and fecundity than native species (Van Kleunen et al. 2010); thus, they can rapidly colonise and establish disturbed sites.

Changes in land use and land cover may result in spatial shifts in the invasion risk of IPs (Wang et al. 2016). The invasive plant usually establishes when a disturbance such as land-use change occurs. The landscape permeability increases, allowing colonisation by the invasive plant and producing patchily distributed stands of the same



Figure 6. Predictions for IPs' community distribution for species richness (a), abundance (b) and (c) basal area of invasive trees.

age. Many IPs perform better in cleared areas; thus, the connectivity of cleared areas is as critical for colonisation as the connectivity of undisturbed habitats (Green et al. 2006). One rule of thumb in invasion biology mentions "that land use promotes invasions" and might be reversed in many landscapes; for example, land management can form an invasion barrier, whereas land abandonment often enables invasion (Kueffer 2017). For example, high agricultural labour and intense grazing may temporarily "control" tree and shrub invasions (*Rubus ulmifolius, Ulex europaeus, Acacia* spp). However, it does not imply that those species cannot re-invade after land abandonment or if the land is converted to forest plantations. Selective grazing pressure by livestock, whereby the animals selectively seek the more palatable species first or exclusively, can create an environment conducive to IPs (Morokong and Blignaut 2020).

High values of IPs' richness, abundance and tree basal area were recorded near forest plantations. For the implementation of forest plantations, planting, pruning and thinning activities are carried out in the first years with the application of pesticides. These tasks involve the removal of the original vegetation, the alteration

of both the soil structure and water regulation (Granados-Sánchez et al. 2007; Jullian et al. 2018; Gómez 2021). This generates a scenario of opportunities for new spaces for the entry of IPs. Studies indicate that the invasion of species such as Ulex europaeus has been strongly influenced by landscape context and dynamics, particularly in land covers, such as forest plantations (Altamirano et al. 2016). It reinforces findings from studies in Mediterranean landscapes showing that landscape composition (land use/cover) represents by far the most important group of variables associated with invasions of alien plant species (González-Moreno et al. 2015). IPs are taking advantage of niches available in more open and degraded land covers, such as bare land, agriculture and shrublands (Altamirano et al. 2016). Thus, it is expected that alterations and change dynamics constitute ideal scenarios for establishing invasive species, taking advantage of disturbed or deforested areas and over-grazed meadows. It is essential to recognise the role of linear corridors, such as roads, canals and abandoned lots, like reservoirs and conduits for the movement and re-invasion of invasive plants in the landscape. For example, in our study area, these strips usually contain several herbaceous shrubs and tree species that can survive there because disturbance occurs at a much lower frequency than in the agricultural field. In contrast, some areas have fences that reduce domestic grazing.

A higher basal area of invasive trees near rivers might be related to the basic need for water and the reduced competition from native plants due to regular flooding (Čuda et al. 2017). In the first metres, the rocky riverbed prevents the establishment of these plants. Models predicted the highest basal area values of IPs' trees in the most stable and consolidated riverside area. Rivers may act as a source of IPs' propagules (Chytrý et al. 2008; Catford et al. 2011), thus serving as a dispersal pathway for a high species number (rivers are of the most invaded ecosystems globally). The irregular trend found for the relationship between rivers and the basal area of IPs' trees seen could be based on the topographical profile of areas surrounding rivers and anthropogenic interventions such as roads, forest plantations and agricultural land. Finally, we can add landscape fragmentation; in Chile, the Mediterranean ecosystems of the central zone are the areas most affected by habitat loss and fragmentation in the country (Blondel and Fernández 2012), reducing vegetation to patches. The minimum temperature of the coldest month showed a direct relationship with the basal area of invasive trees. Invasive species require moderate temperatures in the coldest month to maintain their productivity. In temperate climates, most invaded areas by alien plants correspond to higher annual average temperatures and low altitudes, making these areas environmentally more favourable (González-Moreno et al. 2015).

Invasive species richness also indicates key ecosystem services such as carbon storage. For instance, values are higher at a range of 38 to 58 tonnes per hectare of soil organic carbon content; under this interval, there are no data. An adequate amount of soil organic carbon content is essential for sustainable agriculture and mitigating C flux to the atmosphere (Yimer et al. 2006). A decline in SOC generally decreases vegetational productivity and alters the soil's capacity to act as a sink for atmospheric CO₂.

Modelling IPs' distribution

The basal area of invasive trees resulted in the best model to predict IPs' community distributions. Distance to forest plantations, minimum temperature of coldest month and distance to rivers were the main explanatory variables of this model. These variables express the disturbance, climatic condition and water availability of the study

area. Tree basal area is frequently used as an indicator of the condition of tree cover and to evaluate the effect of different phenomena and processes, such as climate change, invasion, forest inventories and restoration (Bradford and Bell 2017; Jo et al. 2018; Suganuma et al. 2018; Corona et al. 2019). Tree basal area is also an indicator of forest recovery and it is amongst the structural attributes suggested as a reference for monitoring restoration projects (Suganuma et al. 2013; Altamirano et al. 2019). Structural attributes are measurable even in the early stages of community development, which places them as good indicators for monitoring the evolution of communities. Basal area values may indicate the incorporation of biomass by the species used in the restoration process with the influence of density (dos Reis et al. 2014). Additionally, there is a relationship with habitat quality since basal area shows the highest values in places with adequate climatic, soil and biotic conditions. Tree basal area has a rapid increase when it is favoured by conditions of high availability of light, the proximity of watercourses and nutrients, which is a fundamental feature for its recommendation as a monitoring indicator and reference values as possible targets for restoration. Londe et al. (2020) considered basal area amongst eleven ecological indicators commonly used to evaluate the monitoring and evaluation of restoration forests. These researchers ratify that these indicators are also suitable for monitoring reference ecosystems of different dimensions since the mature fragments did not influence them. The basal area had a significant relationship with the fragment area. However, we also need to consider some limitations of model predictions (Jarnevich et al. 2015). For instance, the number of samples will be usually desirable, being as large as possible, but it also depends on financial resources. Some context variables are unavailable, but can be useful to explain the variation and distribution of IPs (e.g. social variables). Therefore, uncertainty is part of model inference and a important topic to consider. Our approach has limitations, but is a useful tool to guide management decisions to control IPs.

Predicting the IPs' community distribution

Our models represent introduced organisms that managed to naturalise, establish successfully and disperse widely, occupying environments with a wide variety of climatic, topographical, soil qualities and anthropogenic intervention. Therefore, our prediction models would be more accurate to represent reality. Perret et al. (2019) suggested that the distribution modelling of invasive plants focusing solely on the conditions experimented in the range and native region of a species may be misleading. For example, the genus *Pinus* L. has shown an increase in its niche size by 10% in territories that invade worldwide from its niche size in its place of origin (Perret et al. 2019). These species show great physiological capacities to grow in more diverse and extreme climatic conditions than in their original distribution range. Besides, in their new territories, IPs occupy a niche broader than their original one due to the release from some of the constraints in their territory (such as predators, diseases and parasites) (Guisan et al. 2014; Tingley et al. 2014; Perret et al. 2019).

Boosted regression tree model predictions for the basal area of IPs trees showed a significant relationship between a larger basal area of invasive trees and sites where land use is mainly forest plantations and close to rivers, as occurs in Lumaco. As the most disturbed one (i.e. with the most extensive replacement of native vegetation by forest plantations), this county showed the highest probabilities of IPs' invasion risk. Pucón and Curarrehue, on the opposite extreme of the disturbance gradient, showed the lowest probability values.

The predictions of our models, based on local information, can give early detection of the areas with a higher probability of being colonised by invasive plant species. This would allow government agencies and land managers to respond rapidly to prevent invasive plants from thriving in new environments following their introduction (Battini et al. 2019). Species distribution models are widely used to predict the potential distribution of invasive species, providing excellent tools for designing strategies to prevent or mitigate impacts of alien invasive species. Our predictions can also guide management under a global change scenario.

Our models can be suitable tools for designing strategies to prevent, mitigate or make integrated control of the impacts of invasive species. For example, in Pucón and Curarrehue, strategies based on our inferences and predictions would be helpful to prevent invasion of the protected areas: Huerquehue National Park, Villarrica National Park and Villarrica National Reserve (CONAF 2011). Furthermore, knowing the richness, abundance and distribution of alien species provides essential information to design prevention activities, early detection and integrated control of invasive alien species within protected areas. These actions are being considered urgent globally to ensure the conservation of native flora (Kutschker et al. 2015). On the other hand, our models could be used to mitigate the impact of invasive plant species in Lumaco and Freire and they can even be considered in native forest restoration programmes.

Conclusions

Land use is a critical landscape variable influencing the presence and distribution of the community of invasive plants. In particular, proximity to forest plantations was the most influential variable in all models.

Even IPs occupy human-disturbed environments since these types of interventions enhance biological invasion; we do not know the main factors that allow the invasion's success in anthropogenised temperate environments with high accuracy. We hope our findings will help increase knowledge about the landscape characteristics that influence invasion processes, understand what promotes species invasion outside their natural range and predict which ecosystems will be invaded and under what conditions. In this way, decision-makers could act in time to implement prevention, mitigation and restoration measures against invasions of alien plants, especially in high-diversity places, such as protected areas and sites that deliver ecosystem services.

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

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Author contributions

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Data availability

All of the data that support the findings of this study are available in the main text.

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Appendix 1

 Table A1. Biophysical characteristics of study area.

| Municipality | Lumaco | Freire | Pucón | Curarrehue | |
|--|---|---|--|---|--|
| Climate (Ministerio de Agricultura 2015) | Warm temperate rainy with Mediterranean influence | Warm temperate rainy with Mediterranean influence | Warm temperate with Mediterranean influence and to a lesser extent cold rainy temperate with Mediterranean influence and tundra due to | Cold rainy temperate with Mediterranean influence and in lesser medium tundra due to the effect of altitude and warm temperate with | |
| Average annual temperature (°C) (Hijmans et al. 2005) | 10.94 | 12.07 | 8.62 | 7.69 | |
| Mean maximum temperature warmest month (°C) (Hijmans et al. 2005) | 23.7 | 24.66 | 22.63 | 22.11 | |
| Mean minimum temperature coldest month (°C) (Hijmans et al. 2005) | 2.78 | 3.75 | 0.07 | -1.08 | |
| Average rainfall of the wettest month (mm) (Hijmans et al. 2005) | 228.97 | 266.93 | 294.2 | 227.52 | |
| Average rainfall of the driest month (mm) (Hijmans et al. 2005) | 26.66 | 40.98 | 45.27 | 31.35 | |

 Table A2. Plants species in four landscapes of La Araucanía Region, south-central Chile.

| Life form | a | Study area | | | | |
|----------------|---------------------------|------------|--------|-------|------------|--|
| | Species | Lumaco | Freire | Pucón | Curarrehue | |
| Native species | | · · · · | | | | |
| Tree | Araucaria araucana | | | | X | |
| | Austrocedrus chilensis | | | | Х | |
| | Aextoxicon punctatum | Х | Х | Х | X | |
| | Amomyrtus meli | | | Х | | |
| | Amomyrtus luma | Х | | | | |
| | Cryptocarya alba | Х | | | | |
| | Caldcluvia paniculata | | | Х | | |
| | Dasyphyllum diacanthoides | Х | | Х | X | |
| | Drimys winteri | Х | Х | Х | X | |
| | Embothrium coccineum | Х | Х | Х | X | |
| | Eucryphia cordifolia | Х | Х | Х | X | |
| | Gevuina avellana | Х | | Х | X | |
| | Lithraea caustica | Х | | | | |
| | Lomatia hirsuta | X | Х | Х | X | |
| | Luma apiculata | Х | Х | Х | X | |
| | Laureliopsis philippiana | | | Х | X | |
| | Laurelia sempervirens | Х | | Х | X | |
| | Luma chequen | | | Х | | |
| | Myrceugenia planipes | | | Х | | |
| | Maytenus boaria | Х | Х | Х | X | |
| | Myrceugenia exsucca | | Х | Х | X | |
| | Nothofagus alpina | Х | Х | Х | X | |
| | Nothofagus dombeyi | Х | Х | Х | X | |
| | Nothofagus antarctica | | | Х | X | |
| | Nothofagus oblicua | Х | | Х | X | |
| | Nothofagus pumilio | | | Х | X | |
| | Peumus boldus | Х | Х | Х | | |
| | Persea lingue | Х | Х | Х | X | |
| | Podocarpus nubigenus | | | Х | | |
| | Podocarpus saligna | X | | | X | |

| Life form | Species | | Study area | | | | |
|-----------|---|--------|------------|--------|------------|--|--|
| | | Lumaco | Freire | Pucón | Curarrehue | | |
| Tree | Saxegothaea conspicua | | | Х | X | | |
| | Sophora cassioides | | | X | | | |
| | Weinmannia trichosperma | | | Х | X | | |
| Shrub | Aristotelia chilensis | Х | Х | Х | X | | |
| | Azara dentada | X | | X | X | | |
| | Azara lanceolata | | x | X | | | |
| | Azara serrata | X | X | X | x | | |
| | Azara integrifolia | X | X | X | | | |
| | Azara microphylla | | X | X | X | | |
| | Baccharis concava | X | | | | | |
| | Berberis darwini | X | x | X | X | | |
| | Baccharis racemosa | X | | | X | | |
| | Baccharis poeppigiana | X | | | | | |
| | Buddleja alohosa | | | X | X | | |
| | Berberis empetrifolia | | | X | | | |
| | Baccharis linearis | X | | | | | |
| | Berberis microphylla | | | X | X | | |
| | Berberis merophysia Berberis negeriana | | | 11 | X | | |
| | Berberis negeriumi Revberis votundifolia | Y | | | X | | |
| | Berberis trigona | A | | V | X | | |
| | Chusquea culeou | Y | V | X | X | | |
| | Collectia estimore | X V | Λ | X V | N V | | |
| | Conerna spinosa Chargenea guila | X V | v | X V | X V | | |
| | Colliguea quita | Λ | Λ | Λ | N V | | |
| | Coniguaja sancifona | | | v | Λ | | |
| | Cynanchum pachyphyllum | | | | v | | |
| | Drimys analna | | v | Λ | Λ | | |
| | Discaria serratifolia | | Λ | v | v | | |
| | Desjontainia spinosa | v | | Λ | Λ | | |
| | | Λ | V | V | | | |
| | Fuchsia mageuanica | v | X | X | v | | |
| | Gaultheria mucronata | X | X | X | X | | |
| | Gaultheria pumila | | X | A | | | |
| | Greigia sphacelata | | X | | V | | |
| | Loasa acanthifolia | X | X | X | X | | |
| | | Λ | A | X | Å | | |
| | Lomatia ferruginea | | N/ | X | | | |
| | Lapageria rosea | X | X | X | | | |
| | Myrceugenia chrysocarpa | | | N. | X | | |
| | Maytenus disticha | | | X | X | | |
| | Muehlenbeckia hastulata | | X | | | | |
| | Mitraria coccinea | | | X | | | |
| | Maytenus magellanicus | | | X | X | | |
| | Myrceugenia lanceolata | | | X | | | |
| | Myrceugenia parvifolia | | | | X | | |
| | Myrceugenia leptospermoides | X | | | | | |
| | Ovidia andina | X | | | | | |
| | Piper aduncum | | Х | | | | |
| | Psoralea glandulosa | | Х | | | | |
| | Pseudopanax laetevirens | X | | X | X | | |
| | Rhamnus diffusus | Х | | | | | |
| | Ribes magellanicum | X | | Х | X | | |
| | Rhaphithamnus spinosus | Х | Х | X | X | | |
| | Sophora macrocarpa | X | | | | | |
| | Sphacele chamaedryoides | X | | | | | |
| | Ugni molinae | X | Х | Х | | | |
| | Vestia foetida | | | | Х | | |

| Life form | C | Study area | | | | |
|---------------|-------------------------|------------|--------|-------|------------|--|
| | Species | Lumaco | Freire | Pucón | Curarrehue | |
| Alien species | | · · · · | | | | |
| Tree | Acacia dealbata | Х | | Х | | |
| | Acacia melanoxylon | Х | Х | Х | Х | |
| | Acer pseudoplatanus | | Х | | Х | |
| | Betula sp | | Х | | | |
| | Castanea sativa | | | Х | Х | |
| | Corylus avellana | | Х | | Х | |
| | Crataegus monogyna | Х | | | | |
| | Cupressus macrocarpa | Х | Х | Х | | |
| | Eucalyptus delegatensis | | Х | | | |
| | Eucalyptus globulus | Х | Х | | | |
| | Eucalyptus nitens | | Х | | Х | |
| | Laurus nobilis | | Х | | | |
| | Malus domestica | | Х | Х | X | |
| | Pinus radiata | Х | Х | Х | X | |
| | Populus alba | | Х | | | |
| | Prunus cerasus | | Х | | | |
| | Prunus domestica | | Х | | | |
| | Prunus pérsica | | Х | | | |
| | Pseudotsuga menziesii | | Х | Х | Х | |
| | Quercus ilex | | Х | | | |
| | Quercus petraea | | Х | | | |
| | Quercus Rubur | | | | X | |
| | Salix babylonica | | | | X | |
| | Sequoia sempervirens | | Х | | | |
| Shrub | Acacia farnesiana | | Х | Х | | |
| | Cytisus striatus | Х | Х | Х | | |
| | Rosa rubiginosa | Х | Х | Х | Х | |
| | Rubus ulmifolius | Х | Х | Х | Х | |
| | Salix caprea | | Х | Х | | |
| | Salix viminalis | | Х | Х | | |
| | Smilax aspera | | Х | Х | | |
| | Teline monspessulana | Х | | Х | | |
| | Ulex europaeus | Х | Х | Х | | |
| | Vaccinium myrtillus | | X | X | | |

| Response variable | Explanatory variable | Consistence | Frequency | Mean relative influence (%) |
|--------------------------|--------------------------------|-------------|-----------|-----------------------------|
| Richness | Dist. to forest plantations | 1.0 | 12 | 48.9 |
| | Soil organic C stock | 1.0 | 12 | 24.5 |
| | Dist. to towns | 1.0 | 12 | 15.2 |
| | Dist. to agric. land | 0.9 | 11 | 9.7 |
| | Dist. to populated centres | 0.8 | 10 | 7.4 |
| | Dist. to agric. burning | 0.8 | 9 | 7.3 |
| | Temp. annual range | 0.7 | 8 | 6.5 |
| | Dist. to prairies | 0.6 | 7 | 4.9 |
| | Cation exchange capac. (15 cm) | 0.5 | 6 | 4.1 |
| | Soil org. C content (30 cm) | 0.4 | 5 | 3.8 |
| | Bulk density (15 cm) | 0.3 | 4 | 3.3 |
| | Dist. to forests fires | 0.3 | 3 | 2.4 |
| | Aspect | 0.2 | 2 | 1.4 |
| | Mean diurnal range temp. | 0.1 | 1 | 0.9 |
| Abundance | Dist. to forest plantations | 1.0 | 9 | 86.3 |
| | Cation exchange cap. (22.5 cm) | 1.0 | 9 | 7.5 |
| | Dist. to populated centres | 1.0 | 9 | 5.6 |
| | Soil organic C stock | 0.9 | 8 | 4.9 |
| | Dist. to cities | 0.8 | 7 | 4.2 |
| | Dist. to native forest | 0.7 | 6 | 3.9 |
| | Slope | 0.6 | 5 | 3.1 |
| | Bulk density (15 cm) | 0.4 | 4 | 2.6 |
| | Aspect | 0.3 | 3 | 2.7 |
| | Dist. to prairies | 0.2 | 2 | 1.6 |
| | Elevation | 0.1 | 1 | 0.3 |
| Invasive Tree basal Area | Distance to forest plantations | 1.0 | 15 | 53.4 |
| | TMin | 1.0 | 15 | 13.5 |
| | Dist. to rivers | 1.0 | 15 | 11.0 |
| | Dist. to native forest | 0.9 | 14 | 9.3 |
| | Precipitation Seasonality | 0.9 | 13 | 6.7 |
| | Dist. to prairies | 0.8 | 12 | 6.6 |
| | Soil org. C content (30 cm) | 0.7 | 11 | 4.9 |
| | Dist. to populated centres | 0.7 | 10 | 3.8 |
| | Bulk density (15 cm) | 0.6 | 9 | 2.4 |
| | Dist. to roads | 0.5 | 8 | 2.1 |
| | Soil organic C stock | 0.5 | 7 | 1.0 |
| | Soil org. C content (15 cm) | 0.4 | 6 | 0.6 |
| | Dist. to cities | 0.3 | 5 | 0.5 |
| | Dist. to agric. burning | 0.3 | 4 | 0.4 |
| | Soil org. C content (22.5 cm) | 0.2 | 3 | 0.4 |
| | Dist. to forests fires | 0.1 | 2 | 0.3 |
| | Soil pH × 10 in H_2O (30 cm) | 0.1 | 1 | 0.1 |

 Table A3. Consistency and frequency of explanatory variables of each model.



Research Article

Riparian invader: A secondary metabolite of *Impatiens* glandulifera impairs the development of the freshwater invertebrate key species *Chironomus riparius*

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Abstract

Invasive species represent a significant threat to native biodiversity. The Himalayan Balsam Impatiens glandulifera is an annual plant, which is invasive in Europe and often inhabits the riparian zone. It produces several secondary metabolites causing, for example, growth inhibition of terrestrial plants and invertebrates. One of these metabolites is the quinone 2-methoxy-1,4-naphthoquinone (2-MNQ). The compound gets washed out from the above-ground parts of the plant during precipitation and may then leach into nearby waterbodies. Despite some evidence for the allelopathic effect of plant secondary metabolites on terrestrial invertebrates, little is known about how 2-MNQ affects the survival or development of aquatic dipteran larvae, despite the importance of this functional group in European freshwaters. Here, we investigated the effects of 2-MNQ on larvae of the river keystone species Chironomus riparius in acute and chronic scenarios. The toxicity of 2-MNQ towards the first and the fourth larval stage was determined in a 48-hour acute exposure assay. We show that 2-MNQ has a negative impact on the development, growth and survival of C. riparius. The LC₅₀ of 2-MNQ was 3.19 mg/l for the first instar and 2.09 mg/l for the fourth instar. A ten-day chronic exposure experiment, where the water was spiked with 2-MNQ, revealed that 2-MNQ had a significantly negative impact on larval body size, head capsule size, body weight, development and survival. These results demonstrate the negative impact of the secondary metabolite 2-MNQ from the terrestrial plant I. glandulifera on a crucial macroinvertebrate inhabiting the adjacent stream ecosystem in riverine ecosystems. This may lead to a decline in population size, resulting in cascading effects on the food web.

Key words: Allelopathy, benthic macroinvertebrates, ecotoxicity, invasive species, 2-methoxy-1,4-naphthoquinone

Introduction

The riparian zone, the transition zone between terrestrial and freshwater ecosystems, is amongst the most diverse habitats worldwide. The vegetational and structural diversity acts as a refuge for small mammals hiding in shrubs, trees serve as perching and nesting sites for birds and fallen wood debris provides resources for terrestrial as well as aquatic invertebrates (Naiman and Décamps 1997). Hence, it supplies the freshwater system with allochthonous organic and inorganic materials



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(Gregory et al. 1991; Naiman et al. 1993). A major threat to the riparian zone, the adjacent freshwater ecosystems and their biodiversity are invasive alien species (Pyšek 1994). In times of globalisation, the frequency of biological invasions is rising continuously in every type of habitat and taxonomic group (Mills et al. 1993). Species are frequently introduced through the freight or ballast tanks of ships, planes and trucks, whose traffic have risen strongly because of increasing trade (Verling et al. 2005; Hulme 2009).

Invasive plants can impair native species by producing allelopathic metabolites. The Japanese knotweed Fallopia japonica, for example, produces resveratrol, amongst other chemicals, which has been found to have inhibitory effects on seed germination and seedling growth of various plant species, potentially influencing the structure and composition of plant communities in invaded areas (Abgrall et al. 2018). Rhododendron ponticum, another invasive plant species, is known to significantly impact aquatic habitats through multifaceted ecological interactions (Erfmeier and Bruelheide 2010). The colonisation of freshwater ecosystems by R. ponticum leads to alterations in water quality, light availability and nutrient cycling (Vitousek 1990; Urgenson and Reichard 2007). The shading effect induced by its dense canopy significantly impacts algal growth, while the release of leachates from its leaves influences microbial and fungal communities (Hladyz et al. 2011; Monk et al. 2014; Jones et al. 2019). Furthermore, the slower decomposition rates of R. ponticum litter compared to native plants in waterbodies contributes to organic matter accumulation (Jones et al. 2019). Studies on leachates from Senecio jacobaea or Petasites hybridus have demonstrated notable concentrations of phytotoxins, like pyrrolizidine alkaloids (PA), originating from these plants in small streams and seepage water (Kisielius et al. 2020). Additionally, precipitation amplified PA concentrations by a factor of ten in stream water, posing potential challenges for aquatic ecosystems, particularly during the rainy season (Kisielius et al. 2020).

Another well-known example of an invasive alien species in riparian habitats is the Himalayan Balsam Impatiens glandulifera. It belongs to the family of the Balsaminaceae, reaches a height of up to 2.5 m, can disperse up to 2500 seeds per mature plant in a radius of 10 m and achieves up to 90% cover of invaded plots (Beerling and Perrins 1993; Hejda et al. 2009; Chapman and Gray 2012). The pathways of introduction typically include trade with the plant and seed mixture contamination (Millane and Caffrey 2014). Dispersal can also happen through wildlife or waterways, as the seeds are adapted for water dispersal (Pysek and Prach 1995). A reason for its invasive success is the release of allelopathic secondary metabolites like the quinone 2-methoxy-1,4-naphthoquinone (2-MNQ) (Chapelle 1974; Ruckli et al. 2014a; Meyer et al. 2021). 2-MNQ is released from the roots of I. glandulifera into the ground (Lobstein et al. 2001; Ruckli et al. 2014a). As the substance leaches into the ground, it inhibits the growth of seedlings and juveniles of native co-occurring plants, like the stinging nettle Urtica dioica or inhibits the arbuscular mycorrhiza colonisation of sycamore saplings (Ruckli et al. 2014a, b; Bieberich et al. 2018). 2-MNQ is further washed off the leaves during precipitation leading to a pulsed introduction of this allelochemical in high concentrations into adjacent habitats, including waterbodies in riparian habitats (Lobstein et al. 2001; Ruckli et al. 2014a). Run-off of I. glandulifera has been shown to inhibit the growth of the aquatic green algae Acutodesmus obliquus and also affects the mortality, the growth and the reproduction of Daphnia magna, a key species in standing freshwater habitats, building the link between primary producers and

higher trophic levels (Brett and Goldman 1997; Diller et al. 2022). However, it is not known yet if 2-MNQ of the invasive alien species *I. glandulifera* has an impact on riverine arthropods and ecosystems.

Amongst running waters, rivers belong to the most diverse ecosystems, providing the potential for various ecological niches due to the richness of different and heterogeneous habitat patches (Lake 2000). Here, benthic macroinvertebrates inhabit almost every ecological niche and act as links between the input of allochthonous material and higher trophic levels such as fish (Richardson 1993). Chironomidae (non-biting midges) are essential members of the benthic macroinvertebrate fauna in riverine ecosystems, as they frequently represent the most abundant species group (Armitage et al. 1995). They are often used as bioindicators for water quality and play a significant role in assessing the ecological state and health of flowing waters (Hellawell 1986) due to their high susceptibility to anthropogenic pollutants, such as heavy metals (de Bisthoven et al. 1992), pesticides (Tassou and Schulz 2009) or antibiotics (Park and Kwak 2018). In contrast to these pollutants, the effects of 2-MNQ released by *I. glandulifera* have as yet not been tested on this key species of running waters.

This paper, therefore, aimed to examine the effects of the allelopathic secondary metabolite 2-MNQ on the growth, development and survival of *Chironomus riparius*. We performed acute immobilisation tests, as well as low-dose chronic exposure experiments using concentrations that are comparable to those released during rain events in nature (Ruckli et al. 2014a).

Material and methods

Chironomus culture

The starting culture, consisting of 10 egg ropes, was provided by Dr. Philipp Egeler from the ECT Oekotoxikologie GmbH (Flörsheim am Main, Germany). The organisms were then transferred into a self-built breeder (68 cm high × 42 cm wide × 55 cm deep), located in a Rubarth P 850 climate cabinet (Rubarth Apparate GmbH, Laatzen, Germany) with constant conditions of 20 ± 0.1 °C and 12 h light-dark cycle. The breeder consisted of gauze on three of the four sides and an acrylic glass plate on the front side, with two holes for gloves and a smaller hole to fit, for example, conic centrifugal tubes or exchange the medium, so that the cage never had to be opened. Inside the cage, two white bowls were placed, filled with quartz sand (average grain size: 0.16 mm, purchased from Quarzwerke GmbH, Frechen, Germany) and 1.5 litres M4-Medium (Elendt and Bias 1990) (see Suppl. material 1: fig. S1 for the experimental set-up). The larvae were fed *ad libitum*, every 3 days, with Tetramin fish food (Tetra GmbH, Melle, Germany).

Acute immobilisation test

Solid 2-MNQ was purchased from Sigma-Aldrich (Merck KGaA, Darmstadt, Germany), with 98% purity. In order to make it soluble in water, it was solved in 100 μ l DMSO (Dimethylsulphoxide 99.7% purity; Bernd Kraft GmbH, Duisburg, Germany) per litre medium. The tests were conducted according to the OECD guide-lines (OECD Test No. 235, 2011) for the first and adapted for the fourth instar larvae as those rely on sediment, which is not required in the guideline. The tests

were performed in 6-well plates with a volume of 10 ml (Eppendorf AG, Hamburg, Germany). In each well, five first instar larvae were randomly placed. The first instar larvae were exposed to two control treatments (control: pure M4-medium; solvent control: M4-medium with 100 µg/l DMSO) and seven different concentrations of 2-MNQ (2, 3, 4, 5, 6, 7 and 8 mg/l). These values were chosen according to run-off values from Ruckli et al. (2014a) who found that 12.21 mg 2-MNQ/l can, on average, be found in rainwater rinsed from *I. glandulifera*. Every treatment was replicated five times. The well plates were randomly placed on the same shelf in a climate chamber with constant conditions of 20 ± 0.1 °C and 16 h:8 h light:dark cycle and the experiment was conducted for 48 hours. The individuals were not fed during the experiment. At the end of the experiment, mortality was noted for each replicate in each treatment.

The procedure for the acute immobilisation test with the fourth instar larvae was very similar to that of the first instar, with the difference that 3 g of quartz sand (average grain size: 0.16 mm, purchased from Quarzwerke GmbH, Frechen, Germany) were added to every well. Quartz sand was added to avoid any additional stress for the individuals, as fourth-instar larvae require sediment for building their characteristic living- and feeding tubes (Armitage et al. 1995). Sediment was added in advance and subsequently, the respective treatment suspensions (control medium, solvent control and the different concentrations of DEP dissolved in M4-medium with DMSO) were poured over. The individuals were not fed during the experiment. After the tests, the LC_{50} (the lethal concentration that results in a 50% change of response of the tested animals) was calculated to assess the acute toxicity of 2-MNQ.

Chronic exposure experiment

For the chronic test with C. riparius, 50 second instar larvae, as they are the first sediment-dwelling instar, per replicate (five for every treatment) were randomly placed in a 1 litre Weck- beaker (J. WECK GmbH u. Co., KG, Wehr, Germany) that was filled with 800 ml M4-medium and 120 g quartz sand (average grain size: 0.16 mm, purchased from Quarzwerke GmbH, Frechen, Germany). The control, the solvent control for DMSO and three different concentrations of 2-MNQ (1, 2 and 3 mg/l) were each replicated five times. The concentrations were chosen according to the results of the acute immobilisation test (LC_{50} for the first instar: 3.19 mg/l). The 25 beakers were randomly placed in a climate chamber with constant conditions of 20 \pm 0.1 °C and 16 h:8 h light:dark cycle. All beakers were gently aerated through a pump-hose system, with two pumps aerating the beakers through an air distributor (3 × 12-way distributor, 6 mm diameter each, OSAGA Deutschland, Glandorf, Germany). The larvae were fed with 0.5 mg Tetramin fish food per larva per day. The test lasted ten days until the control individuals had reached the fourth instar. Subsequently, the larvae were fixed in 80% ethanol and photographed under a dissecting microscope (Leica M50, Wetzlar, Germany; light: Leica KL 300 LED, Wetzlar, Germany) equipped with a digital image analysis system (camera: OLYMPUS DP26, Hamburg, Germany; cellSens Dimension v.1.11, OLYMPUS, Hamburg, Germany). The mortality in every replicate was recorded at the end of the experiment and the mean of the five replicates was calculated for the whole treatment. One beaker in the 1 mg/l treatment cracked in the middle of the test and became leaky as a result, which is why it was excluded from the analysis.

The body length of surviving preserved larvae was measured with a digital image analysis system using a polygonal line from the posterior end of the head capsule (HC) to the last visible appendage. After the whole larvae were photographed and measured, they were decapitated for further analysis. The width of the HC was measured from the left margin to the right margin at the widest points of the head. Abnormal head capsules were defined as such when the HC was constricted in combination with heavy pigmentation due to difficulties in the moulting process and recorded (yes/no) (Suppl. material 1: fig. S1).

Measurement of dry weight of larvae

To measure the dry weight, decapitated larvae and the respective heads were placed into disposable weighing pans ($41 \times 41 \times 8$ mm, neoLab Migge GmbH, Heidelberg, Germany) and put into a desiccator for three days, to allow the ethanol to evaporate entirely. After three days, the larvae and the pans were weighed on a semi-micro scale in mg to the nearest second decimal (OHAUS Explorer EX225D/AD, OHAUS Europe GmbH, Nänikon, Switzerland, \pm 0.06 mg linearity deviation). Subsequently, the larvae were removed from the pan and the latter was measured without the larvae to determine the dry weight of the total number of larvae per replicate. For comparing the mean dry weight per larva, the total dry weight was divided by the number of larvae that survived until the end of the experimental period.

Instar distribution

The distribution of the larval stages in the treatments was determined following the method of Watts and Pascoe (2000) where the larval stages can be determined by measuring the head width, which provides reliable information about the larval instar, independent of the nutritional stage.

Data analysis

The data were analysed using the statistic programme R Version 4.0.4 (R Core Team 2020). The LC_{50} -value, the plots and the dose-response curves for the acute immobilisation tests for L1 and L4 larvae were calculated with the built-in R package "drc" (Ritz et al. 2015). Residual plots of response variables were used to test for homoscedasticity and normality using the R package DHARMa (Hartig 2022). Generalised linear models (GLMs) with body length, head capsule width and dry weight as response variables and treatment as a covariate were created using the base R glm() function. We employed a Gaussian distribution with a default logit link function in the GLMs to elucidate the impacts of 2-MNQ on both body weight and head capsule width. For the end-points mortality and abnormal head capsules, we employed binomial distributions with logit link functions. F-statistics were calculated with the function Anova() to assess p-values for differences between treatments. To compare treatment effects, we ran pairwise comparisons using the Tukey-HSD post-hoc test with Holm correction using the multcomp package (Hothorn et al. 2008). Head capsule widths, body lengths, dry weight and instar of individuals from the different treatments were plotted using the ggbetweenstats function from the ggstatsplot package (Patil 2021). General differences in larval stage distributions between treatments

were determined using a Pearson's X^2 test and pairwise comparisons of proportions with Bonferroni correction using the pairwise.prop.test() function. Abnormal HCs were analysed using a Bayesian binomial generalised linear model using the "arm" package (Gelman and Su 2023), due to the extremely wide confidence intervals in the regular binomial glm, leading to incorrect output.

Results

Acute immobilisation test

After 48 hours of exposing the first instar larvae, there was no observable mortality in both the control and solvent control medium and the treatment exposed to 2 mg/l 2-MNQ. The animals in the treatment exposed to 3 mg/l 2-MNQ showed 44% mortality and the animals in the 4 mg/l treatment showed already 80% mortality. Mortality reached 100% in the 5 mg/l treatment (Fig. 1A). As the calculated LC_{50} for first instar larvae towards 2-MNQ is 3.19 mg/l, 3 mg/l was set as the highest concentration of 2-MNQ in the chronic exposure experiment.

The 48-hour acute immobilisation test for the fourth instar larvae revealed a calculated LC_{50} of 2.09 mg/l (Fig. 1B). No mortality was recorded in the controls. The individuals exposed to 2 mg/l 2-MNQ showed a mortality of 20%. The mortality of individuals exposed to 3–8 mg/l was 100%.

Chronic exposure experiment

Body length and head capsule width

The body length of the individuals was significantly different between the treatments (one-way ANOVA: $X^2 = 862.23$; df = 4, p < 0.001). The body length of the individuals treated with 2 mg/l 2-MNQ (mean ± SE 8.33 ± 0.05 mm; n = 5) and 3 mg/l 2-MNQ (mean ± SE 7.05 ± 0.38 mm; n = 5) was significantly smaller than the control (mean ± SE 14.04 ± 0.22 mm; n = 5), the solvent control (mean ± SE 14.17 ± 0.18 mm; n = 5) and the individuals exposed to 1 mg/l 2-MNQ (mean ± SE 13.47 ± 0.21 mm; n = 4) (p < 0.001 for all comparisons). The individuals of the 2 mg/l treatment had a significantly larger body length than those of the 3 mg/l treatment (p < 0.001). There was no significant difference between the control and the solvent control (p = 0.996), the control and the 1 mg/l treatment (p = 0.46) and the solvent control and 1 mg/l 2-MNQ (p = 0.26) (Fig. 2A).

The width of the head capsules (HCs) was significantly different between treatments (one-way ANOVA: $X^2 = 30.562$; df = 4, p < 0.001). The HC-width of the individuals treated with 2mg/l 2-MNQ (mean ± SE 424.03 ± 28.60 µm) was significantly smaller than the control (mean ± SE 547.01 ± 3.46 µm) (p = 0.012), the solvent control (mean ± SE 542.55 ± 2.23 µm) (p = 0.02) and the 1 mg/l (mean ± SE 533.88 ± 3.35 µm) treatment (p = 0.03). The HC-width of the individuals treated with 3 mg/l 2-MNQ (mean ± SE 349.45 ± 33.20 µm) was significantly smaller than the HC of the individuals of all other treatments (p < 0.01), except from the individuals of the 2 mg/l treatment (p = 0.15). The HC of the control individuals was significantly larger than the HCs of the 1 mg/l treatment (p = 0.05). There was no significant difference between the control and the solvent control (p = 0.54) and the solvent control and 1 mg/l 2-MNQ (p = 0.71) (Fig. 2B).



Figure 1. Dose-response curves with the fitted regression curve for the effect of 2-MNQ on the mortality of **A** first instar and **B** fourth instar larvae of *C*. *riparius* and the calculated LC_{50} with standard error for both instars.



Figure 2. Body length (**A**) and head capsule width (**B**) of larvae from *C. riparius* exposed to different concentrations of 2-MNQ (mean +/- SE; ANOVA; p < 0.05). Letters indicate significance between treatments. Framed values represent the mean of each group. Only significant differences between treatments and control are indicated.

Abnormal head capsules

Individuals exposed to 2 and 3 mg/l 2-MNQ showed significantly more abnormalities in form of conspicuous constrictions of the head capsule compared to the control (one-way ANOVA of Bayesian binomial regression: $X^2 = 37.711$; df = 4, p < 0.001) (Fig. 3). Of the individuals exposed to 2 mg/l 2-MNQ, 16 (8%) showed abnormal head capsules (p < 0.001 compared to the control) and of the animals exposed to 3 mg/l 2-MNQ, 8 individuals (9%) showed abnormal head capsules (p < 0.001 compared to the control) (Fig. 3).

Dry weight

There was a significant difference between the treatments for the mean dry weight per larva (one-way ANOVA: $X^2 = 238.6$; df = 4; p < 0.001). The animals exposed to 3 mg/l 2-MNQ (mean ± SE 0.17 ± 0.02 mg) showed a significantly lower mean dry weight per larva than the animals of the control treatment (mean ± SE 0.86 ± 0.07 mg) (p < 0.001), the individuals from solvent control (mean ± SE 0.84 ± 0.05 mg) (p < 0.001) and the individuals exposed to 1 mg/l 2-MNQ (mean ± SE 0.67 ± 0.03 mg) (p < 0.001). The animals treated with 2 mg/l 2-MNQ (mean ± SE 0.67 ± 0.01 mg) showed no difference in the dry weight per larva (p = 0.94), compared to the animals exposed to 3 mg/l 2-MNQ. The individuals exposed to



Figure 3. Distribution of abnormal head capsules in larvae of *C. riparius* exposed to different concentrations of 2-MNQ. Letters indicate significance between treatments. Only significant differences between treatments and control are indicated.

2 mg/l 2-MNQ had a significantly lower dry weight per larva than the controls, the solvent controls and the animals exposed to 1 mg/l 2-MNQ (C: p < 0.001; DMSO: p < 0.001; 1 mg/l: p < 0.001). The animals of the control treatment, the animals from the solvent control and those exposed to 1 mg/l 2-MNQ did not differ significantly in dry weight per larva (Fig. 4).

Instar distribution

The distribution of the larval instars differed significantly between the treatments (X^2 (8, N = 960) = 421.91, p < 0.001). The larval instars' distribution showed that 100% of the control individuals reached the fourth instar at the end of the test. In



Figure 4. Dry weight per larvae from *C. riparius* exposed to different concentrations of 2-MNQ (mean +/- SE; ANOVA; p < 0.05). Letters indicate significance between treatments. Framed values represent the mean of each group. Only significant differences between treatments and control are indicated.

the solvent control, 97.6% of the individuals reached the fourth instar, while.1.6% only reached the third instar and 0.8% did not moult and stayed in the second instar. In the 1 mg/l treatment, 4% of the individuals reached the third instar at the end of the test and 96% reached the fourth instar. In the 2 mg/l treatment, 47.4% of the individuals reached the fourth instar, while 50.5% reached instar three and 2.1% stayed in the second instar. In the 3 mg/l treatment, 36% of the individuals reached the fourth instar, 56% reached the third instar and 8% did not moult at all (Fig. 5).

The distribution of larval instars differed significantly between the individuals exposed to the control treatment and all other groups (1 mg/l: p = 0.005; all other comparisons: p < 0.001), except with the solvent control (p = 0.08).

Mortality

The mortality of *C. riparius* in the 10-day chronic exposure test showed a significant difference between the treatments (one-way ANOVA: $X^2 = 285.66$; df = 4; p < 0.001). The animals exposed to 3 mg/l 2-MNQ (mean ± SE 32.6% ± 2.42) showed significantly higher mortality than the animals of the control (mean ± SE 1% ± 0.45) (p < 0.001), the solvent control (mean ± SE 1.2% ± 0.49) (p < 0.001) and the ones exposed to 1 mg/l 2-MNQ (mean ± SE 1% ± 0.41) and2 mg/l 2-MNQ (mean ± SE 11.6% ± 2.58) (p < 0.001). In addition, the animals exposed to 2 mg/l 2-MNQ expressed significantly elevated mortality compared to the control, the DMSO treatment and 1 mg/l 2-MNQ (p < 0.001 for all comparisons). The other treatments showed no significant difference in mortality (Fig. 6).



Figure 5. Distribution of larval instars from *C. riparius* exposed to different concentrations of 2-MNQ. Letters indicate significance between treatments.



Figure 6. Mortality in percent of the *C. riparius* larvae exposed to different concentrations of 2-MNQ (mean +/- SE; ANOVA; p < 0.05). Letters indicate significance between treatments. Framed values represent the mean of each group. Only significant differences between treatments and control were indicated.

Discussion

Our results show that 2-MNQ has the potential to impair the survival and development of *C. riparius* after acute 48 hour and chronic 10-day exposure. We determined the LC_{50} after 48 h for the first instar larvae of *C. riparius* at a 2-MNQ concentration of 3.16 mg/l and 2.09 mg/l for the fourth instar larvae. Larvae of *C. riparius* exposed to a concentration of 2 and 3 mg/l 2-MNQ in the 10-day chronic exposure experiment had significantly increased mortality, reduced body-and head capsule size, as well as reduced body weight. They were further delayed in their development and showed a significantly higher proportion of individuals with deformed and abnormal head capsules.

The doses applied in the acute (max. 8 mg/l) and chronic (max. 3 mg/l) toxicity tests were below the concentration reported to be leached from one single plant after rain events (12.21 mg/l) (Ruckli et al. 2014a). *I. glandulifera* is known to grow densely and crowd out other plant species by forming monocultures along riverbanks (Pattison et al. 2016; Čuda et al. 2017). Consequently, it could be assumed that rain events and subsequent run-off have a substantial impact on the survival and development of freshwater invertebrates when an *I. glandulifera* monoculture surrounds the waterbody. This of course depends on the velocity of the river and the water volume of the waterbody, which are both important factors in terms of the dilution effects of xenobiotics, where a lower dilution increases the bioaccumulation and contamination risk (Keller et al. 2014; Dris et al. 2015). As a result, benthic macroinvertebrates living in small and slowly running waters should be more susceptible to incoming 2-MNQ because of a higher accumulation risk (Logan and Brooker 1983; Clements 1994).

It has already been shown that low concentrations of 1.5 mg/l 2-MNQ can significantly impair the growth and survival of individuals of the freshwater key species *Daphnia magna* (Diller et al. 2023). In comparison, the closely-related compound plumbagin (2-methyl-5-hydroxy-1,4-naphthoquinone) from the roots of *Plumbago zeylanica* shows toxic effects on survival at 1 mg/l towards marine copepods and the synthetic derivate of 2-MNQ, menadione (2-methyl-1,4-naphthoquinone) has an LC₅₀ of 2.3 mg/l against adults of *Dreissena polymorpha* (Sugie et al. 1998; Wright et al. 2006). These results concerning LC values and survival analyses are in concordance with the LC₅₀ we found (2.09-3.19 mg/l) for 2-MNQ and suggest similar toxicity of 1,4-naphthoquinones towards invertebrate organisms. Responsible for the high toxicity of 2-MNQ towards invertebrates could be the high reactivity of quinones, due to electron-withdrawing carbonyl groups and redox properties, with an even higher reactivity of 1,4-naphthoquinones in an aqueous medium (Pereyra et al. 2019). This is due to a nucleophilic substitution and the interaction of non-polar and hydrophobic regions of reactants, causing irreparable damage to DNA by al-kylating nucleophilic sites (Tandon and Maurya 2009; Pereyra et al. 2019).

The requirement of sediment of fourth instar larvae could be a reason for the higher toxicity of 2-MNQ, compared to the first instar. Naphthalene, for example, a structurally related compound to 2-MNQ, is known to be easily oxidised and interact with a SiO₂/air interface (Barbas et al. 1993). This can lead to a higher concentration of 2-MNQ in the sediment than in the water column, resulting in a higher exposure risk (Corpus-Mendoza et al. 2022) as sediment is crucial for the second to the fourth instar larvae of C. riparius. The sediment is required for building tubes out of silk from the salivary glands, used for nutrient acquisition and protection by the larvae (Armitage et al. 1995). However, it has to be further investigated if 2-MNQ is interacting with the SiO₂ surface of quartz sand in an aqueous environment and if that interaction increases or decreases the toxicity of 2-MNQ. Another possible explanation for the higher toxicity of 2-MNQ towards the fourth instar larvae could be that it is the last developmental stage before pupation. This could lead to higher susceptibility towards endocrine-disrupting substances like 2-MNQ, as the last larval stage of homometabolic insects requires the highest titre of ecdysteroids, to shift the larval genome towards pupal pattern formation (Smith 1985; Mitchell et al. 1999; Mitchell et al. 2007). The development of the larvae could further be impaired by 2-MNQ disrupting the function of the cytochrome P450-dependent steroid hydroxylase ecdysone-20-mono-oxygenase, which hydroxylates the inactive ecdysone to the active moulting hormone ecdysterone, which can lead to delayed moulting or in general impaired postembryonic development and inhibition of pupal formation (Smith et al. 1979; Smith 1985; Mitchell et al. 2007). Other 1,4-naphthoquinones seem to have similar effects on insects. Juglone, plumbagin, menadione and lawsone also show toxic effects on the larvae of the saturniid moth Actias lunas, evident by increased mortality and developmental time (Thiboldeaux et al. 1994). Another possible explanation for why 2-MNQ interferes with moulting is that it could inhibit the chitin synthetase of insect larvae, which is crucial for the moulting process, as shown for the naturally-occurring plumbagin (5-hydroxy-2-methyl-1,4-naphthoquinone) originating from Plumbago capensis towards the larvae of Bombyx mori (Kubo et al. 1983). The darker head capsule may be explained by 1,4-naphthoquinones' ability to bind to and modify the colour of chitosan (Muzzarelli et al. 2003). This could also be the case for chitin, the acetylated version of chitosan (Dutta et al. 2004).

Even though some chironomid species are known for their extreme tolerance towards environmental conditions like pH, temperature, oxygen content and even salinity, they are susceptible to anthropogenically induced pollution, drugs and other endocrine-disrupting substances (Vermeulen et al. 2000; Taenzler et al. 2007; Serra et al. 2017). If their biomass is significantly reduced, there could be a severe impact on higher trophic levels, depending on the chironomids as a food source. This could be shown in modelled exposure scenarios of the Chinook salmon (*Oncorhynchus tshawytscha*) and the associated macroinvertebrate prey community, as

some pesticides only affected the growth rates of salmon populations by reducing the availability of prey (Macneale et al. 2014). In addition, also terrestrial predators like bats and birds are highly dependent on emerging chironomids as food sources, leading to a potential food deficiency or at least increased energy demands due to an increased predation radius and time away from the nest when breeding in those organisms (Barclay 1991; Martin et al, 2000; Jackson et al. 2020).

For the assessment of the impact of 2-MNQ on riverine ecosystems, it might be essential to investigate the potentially different sensitivity of various macroinvertebrates, as *C. riparius* is known to display a comparatively greater tolerance towards deteriorating water quality (Pinder 1986; Jiang et al. 2021; Leitner et al. 2021). Understanding these interspecific differences in sensitivity may be crucial for risk assessment and will, therefore, serve as a basis for effective conservation and management strategies.

Conclusion

This study reveals substantial acute and chronic toxicity of 2-MNQ towards the larvae of *C. riparius*. Individuals exposed to concentrations of 2 mg/l upwards showed a significantly reduced body size and head capsule size, a significantly reduced dry weight per larvae, developmental abnormalities and increased mortality compared to unexposed individuals. *I. glandulifera* is spreading extensively around the world, building monocultures across riverine ecotones and even invading forest ecosystems. The exposure risk to 2-MNQ could be highly increased when larger areas are covered by the plants at high densities along riverbanks. This can result in higher amounts of 2-MNQ leaching into aquatic ecosystems after precipitation, ultimately increasing its concentration within the waterbody. Our findings underscore the critical need for monitoring this neophyte, emphasising the imperative to focus on controlling its spread. This attention is vital to safeguard ecosystem functions of flowing waters.

Future research should include how riverine communities adapt to and are influenced by allelopathic substances, addressing also species interactions and resilience of these ecosystems.

Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

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Author contributions

Conceptualization: FH, CL. Data curation: JGPD, FH. Formal analysis: FH. Funding acquisition: CL. Investigation: JGPD, FH. Methodology: FH. Project administration: CL. Resources: CL. Supervision: CL. Visualization: FH. Writing – original draft: FH. Writing – review and editing: JGPD, FH, HF, CL.

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Data availability

All of the data that support the findings of this study are available in the main text or Supplementary Information.

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Supplementary material 1

Supporting information with figures and the R-Script

Authors: Frederic Hüftlein, Jens G. P. Diller, Heike Feldhaar, Christian Laforsch Data type: docx

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Discussion Paper

Integrating social-ecological outcomes into invasive species management: the *Tamarix* case

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Abstract

Incorporating societal considerations into decisions related to invasive species management is desirable, but can be challenging because it requires a solid understanding of the ecological functions and socio-cultural and economic benefits and values of the invaded environment before and after invasion. The ecosystem service (ES) concept was designed to facilitate such decision-making by establishing direct connections between ecosystem properties and human well-being, but its application in invasive species management has not been systematic. In this Discussion paper, we propose the adoption of the ES cascade model as a framework for understanding the environmental effects, costs and benefits associated with controlling an invasive shrub (*Tamarix* spp.) in riparian systems of the western United States. The cascade model has the advantage of explicitly dissecting social-ecological systems into five components: ecosystem structure and processes, ecological functions, ecosystem services, benefits and the economic and socio-cultural valuation of these services and benefits. The first two have received significant attention in the evaluation of *Tamarix* control effectiveness. The last three have long been implicitly acknowledged over decades of *Tamarix* management in the region, but have not been formally accounted for, which we believe would increase the effectiveness, accountability and transparency of management efforts.

Key words: Conceptual framework, ecosystem services, riparian systems, rivers, saltcedar, operationalisation, tamarisk



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Introduction

Over the last two decades, the ecosystem service (ES, or ecosystem services - ESs) concept has emerged as a powerful tool to facilitate decision-making in environmental planning and natural resources management. The greatest contribution of the ES concept to decision-making is that it uncovers the linkages between ecosystem structure and functioning and the constituents of human well-being (Fisher et al. 2009). By explicitly acknowledging and documenting the dependence of humans on ecosystems (La Notte et al. 2017), the ES concept contributes to the increasingly popular concept of social-ecological systems, encompassing not only economic perspectives, but also other various facets of human-nature relationships such as health, social relations, indigenous and local knowledge and culture and perceptions (Anderies et al. 2004; Potschin-Young et al. 2018).

The ES concept has been employed by international organisations such as the IUCN (Neugarten et al. 2018), the European Commission (Maes et al. 2012; EU FP7 OpenNESS 2017), UNEP (UNEP 2014), and the Intergovernmental Platform on Biodiversity and Ecosystem Services (IPBES) to craft policy and management guidelines (Tengö et al. 2017; IPBES 2019). However, its widespread integration into practical decision-making contexts (i.e. "real-world" situations) has proven challenging (e.g. Rozas-Vasquez et al. (2019) for spatial planning) and has seen slower progress in some fields such as invasive species management. While the effects of invasive species on ESs have been extensively studied (Charles and Dukes 2007; Vilà and Hulme 2017; Rai and Singh 2020), the ES concept has been rarely used in the evaluation of outcomes of invasive species management (Funk et al. 2014; Schaffner et al. 2020). This is unfortunate considering the overall importance of socio-cultural values and perceptions in invasive species management and decision-making (Verbrugge et al. 2013). Using the ES concept would address questions related to the typically conflicting positive (services) and negative (disservices) effects of invasive species on socio-economic systems (Dickie et al. 2014) and would be particularly helpful to justify potential economic returns on investment for invasives' control (Funk et al. 2014; Hanley and Roberts 2019).

In this Discussion paper, we invite land managers and scientists to consider employing the ES concept to integrate social-ecological outcomes in the evaluation of control of invasive species. We frame our discussion around the case of invasive shrubs in the genus *Tamarix* (tamarisk, saltcedar) that have extensively invaded western U.S. river systems (Friedman et al. 2005; Nagler et al. 2011). To date, assessments of the effectiveness of *Tamarix* control have mainly focused on biophysical responses of invaded ecosystems (Goetz et al. 2024). We suggest that the 'ES cascade model' (or simply, the 'cascade model'; *sensu* Haines-Young and Potschin (2010)) could serve as a framework to integrate socio-economic aspects with these more traditional ecological assessments.

Brief history of Tamarix invasion and management

The history of non-native *Tamarix* in North America reflects a dynamic interplay of ecosystem services and disservices that *Tamarix* provided to a changing society, as has been the case for many other invasive tree species worldwide (Dickie et al. 2014). *Tamarix* was initially introduced to North America in the 19th century for ornamental purposes. In the first half of the 20th century, *Tamarix* not only escaped cultivation, but was also intentionally planted along riversides and reservoir shorelines to control sediment erosion (Chew 2009). This facilitated its widespread invasion across the western United States (Robinson 1965; Friedman et al. 2005; Nagler et al. 2011).

Control of *Tamarix* did not become common management practice until the second half of the 20th century, when large amounts of local, regional and federal funds were allocated for this purpose. Beliefs that *Tamarix* consumed more water than native vegetation, coupled with the need to increase water yield in arid river systems was the main motivation for control efforts in the 1950s and 1960s ('water salvage', Stromberg et al. (2009) and references therein). Beginning in the 1970s, society's growing recognition of the importance of natural systems and their preservation triggered interest in assessing the value of *Tamarix* as a wildlife habitat (Anderson and Ohmart 1977) and determining its influence on fluvial geomorphologic processes (Everitt 1980). *Tamarix* control was then justified by alterations in ecosystem functions and other disservices that *Tamarix* was purported to cause, such as increased soil salinity, increased fire risk, degradation of cultural significance of riparian forests, replacement of species with higher suitability as livestock feed and, more recently, restricted recreational access to rivers (e.g. rafting, fishing, camping) (Di Tomaso 1998; Chew 2009; Hadley et al. 2018). Scientists and managers devoted considerable attention to evaluating the effectiveness of different control methods in terms of both compliance and ecological effects during these decades (Taylor and McDaniel 1998; O'Meara et al. 2010; Sher and Quigley 2013; González et al. 2017).

The difficulty of controlling the invasion through conventional chemical or mechanical methods prompted the development of a biocontrol programme that culminated in the release of a host-specific defoliating beetle (*Diorhabda*) at the beginning of the 21st century (DeLoach et al. 2003). Biocontrol has been generally successful in reducing *Tamarix* biomass and growth at the continental scale (Nagler et al. 2018). However, the release of the biocontrol agent was temporarily halted after the realisation that a bird species federally listed as endangered, the Southwestern Willow Flycatcher (*Empidonax traillii extimus*), used *Tamarix* habitat and could be negatively affected by the programme (Bean and Dudley 2018).

We believe the identification and valuation of ESs could help to provide information for decisions regarding potential management interventions in areas where *Tamarix* remains a significant component of the riparian plant community. Although biological control beetles have established along rivers across the American West, residual *Tamarix* populations still occur and are sometimes managed by using targeted chemical and mechanical control combined with active introduction of native vegetation. The presence of *Tamarix* is generally accepted within western riparian ecosystems (Raynor et al. 2017; Darrah and van Riper 2018). It has been recognised that *Tamarix* contributes to some ecological functions and ESs (Sogge et al. 2008; Sher and Quigley 2013; Bean and Dudley 2018) in the absence of comprehensive restoration of riparian systems that are degraded by multiple factors (Shafroth et al. 2008; Stella and Bendix 2019; Briggs and Osterkamp 2021). Nevertheless, no attempts have been made to quantify these ESs.

The cascade model as framework to understand social-ecological systems

ES emerged as a concept in 1981 (Ehrlich and Ehrlich 1981) after early discussions by the Club of Rome in the 1970s (Haines-Young and Potschin 2010; Vermaat et al. 2013), but did not gain popularity until the Millennium Ecosystem Assessment (MEA 2005) used ESs to assess the effects of ecosystem degradation on human well-being. The widespread promotion of ESs into market and payment schemes (Gómez-Baggethun et al. 2010) triggered efforts for a better understanding of the ES delivery process and, hence, its quantification and valuation. The cascade model (Haines-Young and Potschin 2010) addressed this need as it formalised a theoretical pathway from ecosystem structure and functioning to human well-being including valuation of ESs. The model consists of a five-step sequence from identifying: 1) biophysical structure and processes and 2) ecological functions of ecosystems that give the 3) potential basis for human well-being (ESs) in terms of 4) realised gains to society (benefits) that can be 5) valued in economic and socio-cultural terms (Fig. 1).

The sequential nature of the cascade model helped to solve the problem of double counting ESs in valuation approaches, by clearly identifying "intermediate" or sup-

Eduardo González-Sargas et al.: The ecosystem service cascade model for invasive Tamarix



Figure 1. Ecosystem service cascade model of Haines-Young and Potschin (2010) adapted to represent a conceptual framework that integrates socio-economic factors into *Tamarix* control monitoring across U.S. Southwestern rivers. Blue boxes represent the five steps of the model. Processes were considered conjointly with functions (step 2) instead of as part of biophysical structure (step 1) as in the original design. Yellow boxes include elements that can be used to develop the model steps for the *Tamarix* case. For an in-depth development of biophysical structure indicators, see Goetz et al. (2024). We have combined the elements associated with ecosystem services (ESs) (step 3) and benefits (step 4), given that they overlap considerably and to simplify the figure. Arrows reflect linkages between ecosystem structure, functions, ecosystem services/benefits, and values, based on our best judgment. Suppl. material 1: appendix S1 provides a list of references studying the functions of water cycling and evapotranspiration and biocontrol-related herbivory (trophic relationships). Suppl. material 1: appendix S2 includes an extended list of ecosystem services and benefits provided by systems dominated by *Tamarix* and replacement vegetation such as native riparian forest and meadow vegetation that follows the CICES v.5.1 classification (Haines-Young and Potschin 2018). Suppl. material 1: appendix S3 describes economic valuation methods.

porting services (processes and functions in the model) that are necessary to produce final services or ESs in the model (Wallace 2007; Costanza 2008; De Groot et al. 2010; Fu et al. 2011). Primary productivity is an example of a supporting service. A second problem that the cascade model tried to address was the scarce knowledge of how ESs are produced, maintained and affected by changes in the structure and functioning of ecosystems (De Groot et al. 2010). By breaking down each step of the cascade into categories and sub-categories, explicit links between the ecological and socio-economic components of social-ecological systems can be created (Haines-Young and Potschin 2010; Vermaat et al. 2013; Vidal-Abarca et al. 2016). However, the model did not solve the problem of limited knowledge. There is a lack of empirical data for biophysical structure, processes and functions of ecosystems, which have typically been replaced by expert knowledge in ESs quantification (e.g. Riis et al. (2020) for riparian systems). The cascade model set up a conceptual framework necessary to address this limitation (Potschin and Haines-Young 2016; Potschin-Young et al. 2018). In the following section, we develop each step of the cascade model in more detail and discuss how the monitoring of *Tamarix* control outcomes has been following this conceptual framework. Additionally, we offer suggestions for implementing the framework in cases where it is not being followed.

Integrating monitoring of *Tamarix* control outcomes within the ecosystem service cascade model

Biophysical structure and processes of ecosystems

The first step of the cascade model is the assessment of the biophysical structure and processes of ecosystems. The biophysical structure of ecosystems includes the species composition, the structural and genetic diversity of flora and fauna and the description of the physical environment that supports life (Fig. 1). In the original definition of the cascade model of Haines-Young and Potschin (2010), processes are simply the precursor of functions and they are the result of the activities and dynamics of each ecosystem component without an explicit consideration of their interactions (e.g. vegetation growth and river channel formation in our case study) (see also De Groot et al. (2010)). The distinction between processes and functions is ambiguous in literature. However, this distinction does not have high relevance in the determination and valuation of ESs (Spangenberg et al. 2014; Baró et al. 2016; Czucz et al. 2020). For this reason, we only discussed here how biophysical structure has been considered in *Tamarix* control studies and treated processes and functions by Potschin-Young et al. (2018) for adapting the ES cascade model to our case study.

Goetz et al. (2024) exhaustively reviewed the outcomes of *Tamarix* control through monitoring using vote count and a meta-analysis of 96 studies published from 1990 to 2020. They provided a list of indicators and ecosystem components that have been monitored and noted an over-representation of vegetation monitoring and a paucity of studies examining the response of other biotic and abiotic ecosystem components, such as fauna, physicochemical properties of water and soil and geomorphic characteristics of fluvial landforms that riparian vegetation occupies. We agree with the conclusions of Goetz et al. (2024) that more research on effects of *Tamarix* control beyond the vegetation component is necessary and essential to provide information for the next steps of the cascade model and achieve an integrative evaluation of riparian social-ecological systems across the American West.

Ecosystem functioning

Describing ecosystem functioning is the second step in the cascade model (Fig. 1). Ecosystem functions are the subset of interactions between the biological and physical structure and processes that govern the flow of matter and energy across ecosystems (Potschin and Haines-Young 2016; Raimundo et al. 2018; Hu et al. 2022). Recommendations for integrating ecosystem functioning into evaluation of management of natural resources, including invasive species management (e.g. International Standards for Ecological Restoration, Gann et al. (2019)), have not been as widely implemented as those related to biophysical structure (see Palmer et al. (2014) in the field of ecological restoration and González et al. (2015) for restoration of riparian vegetation specifically). Ecosystem functioning has been overlooked for multiple reasons. First, structural indicators are usually sufficient to evaluate compliance of

management projects, which is often the only goal of monitoring (Matzek 2018). Second, there is a tendency to remain at the "structural phase" of evaluation because of the common belief that, if the biophysical structure is restored, recovery of processes and functions will follow (the 'Field of Dreams' hypothesis; see Palmer et al. (1997) and Suding (2011)). Finally, ecological functions are harder to conceptualise and monitor, despite efforts to simplify their quantification (e.g. Meyer et al. (2015)). Advances in functional ecology, such as the emergence and application of functional traits and functional diversity to understand ecosystem dynamics, can help to better characterise ecosystem functions (Díaz et al. 2007; Haines-Young and Potschin 2010; Funk et al. 2014). We are aware of only one study that used functional traits and functional diversity to assess the effectiveness of Tamarix control. Henry et al. (2023) used specific leaf area, plant height and seed mass to explore the response of the riparian plant community to Tamarix biocontrol, but their choice of traits was intended to reflect responses to environmental change ("response" traits) instead of to reflect effects on ecosystem functioning ("effect" traits). Effect traits are still underutilised in monitoring outcomes of management interventions (for example, in ecological restoration, see Loureiro et al. (2023)).

A variety of ecosystem functions have been evaluated in the context of Tamarix control; however, many of these functions have been relatively understudied. As increasing water yield (or 'water salvage') was a long-standing management goal for Tamarix control, the ecosystem function that has received most attention in the evaluation of Tamarix control outcomes is water cycling and evapotranspiration (Suppl. material 1: appendix S1). A growing body of literature has also been considering trophic relationships, directly or indirectly, via studies of the effects of the biocontrol beetle on Tamarix defoliation, dieback, plant physiology and cover and on other ecosystem components (biocontrol-related herbivory; Suppl. material 1: appendix S1). However, a paucity of studies reflecting ecosystem functions other than water cycling, evapotranspiration and biocontrol-related herbivory in Tamarix control evaluations has been explicitly acknowledged by the scientific community. For example, in a paper discussing the possible unintended consequences of the Tamarix biocontrol programme that was beginning to unfold by the time of its publication, Hultine et al. (2010) suggested that the decline in Tamarix may lead to reduced carbon storage and sequestration, at least in the short-term, a reduced carbon exchange in the ecosystem and a release of nitrogen through defoliation and downstream export following erosion of unstable landforms. They made a call to the scientific community to test these hypotheses. More than ten years later, however, little has been done to understand the changes in nutrient cycling that U.S. rivers have experienced after the biocontrol programme was put in place or as a result of Tamarix control efforts using other techniques (but see Uselman et al. (2011), Snyder et al. (2012) and Snyder and Scott (2020), in Suppl. material 1: appendix S1). At least two other studies have quantified the response of other ecosystem functions to Tamarix management. Kennedy et al. (2005) studied changes in aquatic food webs after mechanical clearing of Tamarix along a small creek in Nevada. Tredick et al. (2016) examined black bear scat to understand potential changes in bear diet after removal of Tamarix in Canyon de Chelly National Monument, Arizona.

A core function that remains overlooked and supports several ecosystem services is primary productivity (Fig. 1). In general, a more thorough understanding of ecological functions associated with *Tamarix* control evaluations could be achieved with more frequent implementation of the methodologies and experience developed in

the evaluation of invasive species management and other types of restoration approaches in a riparian context. This includes assessing ecological functions other than water cycling and evapotranspiration, trophic relationships and nutrient cycling.

Ecosystem services and benefits

ESs and benefits are two sides of the same coin. ESs reflect what the ecosystem provides to human welfare in biophysical terms, while benefits represent the contributions to aspects of well-being, such as health and safety. As ESs and benefits commonly overlap and their distinction is not critical for the valuation of the latter, we will concentrate here on the definition and description of ESs and will not distinguish between ESs and benefits in the next sections of the article. ESs are distinguished from functions (step 2) in that there is a direct or indirect use of an ecosystem resource or property by ESs beneficiaries, while functions represent the "capacity" or ability of the ecosystem to generate ESs (Czucz et al. 2020). There are several classifications of ESs (e.g. MEA (2005); The Economics of Ecosystems and Biodiversity - TEEB - developed by De Groot et al. (2010); to name two of the most popular). One of the most used is the Common International Classification of Ecosystem Services (CICES, Haines-Young and Potschin (2013)). In its last published version (v.5.1, Haines-Young and Potschin (2018)), 90 "classes" of ESs are detailed and grouped hierarchically into "groups", "divisions" and "sections". At the highest level (sections), services are classed into: "a) the provisioning of material and energy needs, b) regulation and maintenance of the environment for humans or c) the non-material characteristics of ecosystems that affect physical and mental states of people". These are three of the four main categories of ESs that the MEA (2005) originally referred to as "provisioning", "regulating" and "cultural", respectively. A consensus was reached to consider a fourth category "supporting" as intermediate services. Supporting services are integrated in the previous steps of the cascade model as ecosystem structure, processes and functions (Carpenter et al. 2009). This matching with the MEA framework ultimately reflects the intention of the CICES v.5.1 to cross-reference other classifications and facilitate international comparisons (Haines-Young and Potschin 2018).

The CICES v.5.1 classification particularly addressed the complexity in distinguishing between ESs and benefits (Haines-Young and Potschin 2018). The definition of each service is made up of two parts; one describing the biophysical output from the ecosystem (i.e., what the ecosystem delivers) and the other describing the contribution it makes to human well-being (i.e. how that output is used or enjoyed by people in terms of health, good social relations, security, basic needs etc.). While the CICES list is rather exhaustive, it is not practical to include all ESs in actual evaluations (Matzek 2018). Moreover, the contingent nature of the ES concept implies that establishing a universally applicable, final checklist of ecosystem-supported services is an unachievable (and unnecessary) objective. The list of services should be treated more as a "menu" of ESs and benefits themes, with steps one and two of the cascade model serving to examine how particular systems operate and provide information for the choice and quantification of ESs (Haines-Young and Potschin 2010; Potschin and Haines-Young 2016; Potschin-Young et al. 2018). We are unaware of studies evaluating the effectiveness of invasive riparian plant species management under the prism of an ES approach. However, assessments of ESs outcomes of river restoration have generated lists of ESs, based on project and system singularities (e.g. Acuña et al. (2013); Terrado et al. (2016); Vermaat et al. (2013); Gerner et al. (2018)).

We identified the ESs and associated benefits that riparian systems dominated by native species could provide compared to those dominated by *Tamarix*, as replacing *Tamarix* with native vegetation is one of the main goals of *Tamarix* control (Shafroth et al. 2008). We modified the list of ESs and benefits provided by riparian systems in Riis et al. (2020) for four types of dominant vegetation. We present an abbreviated version of the list in Fig. 1 and an annotated, extended version in Suppl. material 1: appendix S2. Dickie et al. (2014) also listed the ESs provided by *Tamarix*, but we chose to use the classification by Riis et al. (2020) because Dickie et al. (2014) did not use vegetation categories or compare between control/impact or before/after *Tamarix* control. Dickie et al. (2014) simply enumerated the ESs provided by *Tamarix* trees: visual amenity/ornamental (cultural ESs); timber, building materials, poles, posts, pulp, crafts and firewood and charcoal (provisioning ESs); habitat for wildlife, protection from predators (supporting ESs); erosion control, including windbreaks and temperature regulation via shading (regulating ESs).

Some have described ESs provided by riparian systems that were affected by Tamarix control (even though virtually none of them used the term "ecosystem service" in their assessments). Dykstra (2010) enumerated the multiple potential uses of Tamarix biomass obtained from removal efforts, including its transformation into composite wood, its use as biofuel in the form of wood pellets, bio oil and charcoal and for artistic creations ("Timber", "Biomass for fuel", "Indirect interaction – artistic", Fig. 1; Suppl. material 1: appendix S2). Bateman et al. (2012) assessed fire regulation by reduction of fuel loads ("Fire regulation", Fig. 1; Suppl. material 1: appendix S2). Wieting et al. (2023) and references therein showed that Tamarix removal promotes erosion ("Erosion control" and "Buffering and attenuation of mass movement", Fig. 1; Suppl. material 1: appendix S2) by reducing the stability of riverbanks and hydraulic roughness. This is typically perceived as a "disservice" by managers (Suppl. material 1: appendix S3). The ES that has received more attention in the context of Tamarix control assessments is "Maintaining populations and habitats" (Fig. 1; Suppl. material 1: appendix S2). Several publications have compared the suitability of Tamarix-dominated and Tamarix-restored sites as habitat for birds (e.g. Shanahan et al. (2011); Darrah and van Riper (2018); Mahoney et al. (2022)) and for herpetofauna (Bateman et al. 2012, 2015; Mosher and Bateman 2016). To our knowledge, there are no other publications that discuss and quantify the other ESs provided by forest patches and/or fluvial features dominated by Tamarix or where Tamarix has been controlled, listed in Fig. 1. We see this as an avenue for further research. A variety of methods for mapping and modelling the supply and demand of ESs were summarised by Harrison et al. (2018).

Ecosystem service values

Once the ESs/benefits have been identified, the final step of the cascade model is to conduct economic and socio-cultural valuations of the ESs/benefits (Fig. 1). Values in general can be defined as the criteria by which we assign importance to something and valuation is the process of expressing or quantifying that value for a particular action or object (Farber et al. 2002; Potschin and Haines-Young 2016; IPBES 2019). Different valuation methods and techniques exist to give an economic, typically monetary value, to ESs/benefits. They are divided into direct market (e.g. production-based, cost-based), indirect market or "revealed preference" (e.g. travel cost modelling, hedonic pricing) and simulated market or "stated
preference" (e.g. contingent valuation, choice experiments or conjoint analysis, participatory mapping) methods. We present definitions and hypothetical examples of their use in the *Tamarix* control context in Suppl. material 1: appendix S3. See Harrison et al. (2018) for an exhaustive list of ESs valuation methods.

Economic valuations are frequently used in cost-effectiveness, cost-benefit analyses and damage assessments. In the context of Tamarix control, cost-effectiveness and cost-benefit analyses could be used to combine monetary valuation of improvements on ecosystem status and ESs, respectively, with the cost of restoration actions (sensu Terrado et al. (2016)), while damage assessments value the loss of ESs (Unsworth and Petersen 1995; NPS 2005) and are more frequently used to investigate the negative effects of invasive species (Marbuah et al. 2014). Cost-effectiveness and cost-benefit analyses are key to assessing economic viability of management interventions and are particularly relevant for invasive species management (Hanley and Roberts 2019). Great Western Research (1989) analysed the economic, environmental and social effects of Tamarix control in the western United States and northern Mexico and estimated annual beneficial effects of \$22 million and \$40-62 million (\$ are not inflation-corrected) for 50% and 90% control, respectively. Economic benefits outweighed adverse economic effects, but the study did not factor in the control programme costs (Barz et al. 2009). Zavaleta (2000) compared the monetary cost of water consumption and sediment retention by Tamarix with removal costs to conclude that the economic gains of potential eradication were considerable. The work by Zavaleta (2000) was frequently used to justify Tamarix control in the region, but her estimates of water consumption by Tamarix have been discredited by some (Stromberg et al. (2009) and references therein). McDaniel and Taylor (2003) estimated the cost of several removal methods and compared them in terms of their cost-effectiveness using Tamarix mortality as an indicator of project compliance. Hart et al. (2005) provided detailed costs of Tamarix removal during 1999-2003 along the Lower Pecos River (Texas), as well as estimates of percent mortality, changes in salinity of the river water, changes in water flow and estimates of water salvage. However, they did not calculate cost-effectiveness ratios. Barz et al. (2009) conducted more explicit cost-benefit analyses of Tamarix control efforts along the Middle Pecos River (New Mexico). They concluded that attempting Tamarix eradication was not worthwhile, based on consideration of different scenarios: direct costs of herbicide spraying, removal and revegetation; indirect costs of increased bank erosion and reservoir sediment accumulation following the eventual reduction of Tamarix; and benefits such as water salvage and associated groundwater recharge. O'Meara et al. (2010) and Bateman et al. (2012) provided detailed estimates of costs of different control methods, but they did not report cost-effectiveness or cost-benefit ratios. More recently, Albers et al. (2018) used bioeconomic modelling to consider the trade-off in terms of costs and positive effects on the ecosystem between controlling invasive Tamarix and restoring habitats with native species. All these examples show that, in the Tamarix control case, indirect and simulated market methods are underutilised and that the ES concept has been rarely, if ever, invoked. We believe a more systematic use of the ES cascade concept in cost-effectiveness, cost-benefit analyses and damage assessments would facilitate the comparison of results across studies.

Not all ESs and related benefits can be valued economically. While conceptual and methodological developments in economic valuation have aimed to cover a broad range of ESs, including cultural ESs, it can be argued that socio-cultural values (symbolic, aesthetic, ethical, relational etc.) cannot be fully captured by economic valuation techniques (Schröter et al. 2014). Socio-cultural values in invasive species management can be represented in more simple terms by the degree of satisfaction of different interested parties. For example, the aesthetic appreciation of the ecological condition of riparian zones by different groups of people has been evaluated with photo-elicitation surveys (e.g. Le Lay et al. (2013); Chin et al. (2014); Arsénio et al. (2020)). Other methods for understanding preferences or social values for ESs, such as deliberative valuation methods, preference ranking methods and multi-criteria analysis methods (Harrison et al. 2018), have been used in the evaluation of invasive species management planning more often than for monitoring outcomes (e.g. Liu et al. (2011); Japelj et al. (2019)). Perceptions and preferences of different interested parties are important because even the perceptions of success by environmentally-informed sectors of the population such as restoration practitioners do not necessarily align with abiotic and biotic parameters measured in the field (Jähnig et al. 2011) and public acceptance of outcomes is key for restoration success (Heldt et al. 2016). There is currently a dearth of studies that describe and quantify public opinion about Tamarix control and what society perceives as successful riparian ecosystem restoration along rivers in the American West. We are unaware of any studies of this kind. Only Sher et al. (2020) have explored how the human component (manager characteristics and decisions) may help explain Tamarix control outcomes in terms of vegetation structure and composition. Clark et al. (2019) previously showed the high degree of collaboration between restoration practitioners and scientists in Tamarix control contexts.

Finally, the value of ecosystems also has an ecological component that may be represented by fundamental properties of ecosystems, such as resilience, stability, health, complexity and integrity (De Groot et al. 2010). These are ecological values (or intrinsic values of nature) that cannot be expressed in economic or socio-cultural terms because they are not based on human preferences or principles, as they go beyond the anthropocentric approach of ESs (Kretsch and Stange 2016; Potschin and Haines-Young 2016). The quantification of these critical ecosystem properties and the subsequent integration into the evaluation of natural resources management, is still in its infancy and is subject to intense debate and study in academic circles (Jaunatre et al. 2013; Moreno-Mateos et al. 2020; Rohwer and Marris 2021; Dakos and Kéfi 2022; Ren and Coffman 2023). No efforts to value such fundamental ecological properties of systems responding to invasive species management, including Tamarix-dominated systems, have been made. Functional traits can be used to value resilience and stability of plant communities through measurable properties, such as functional redundancy, dispersion and response diversity (Laliberté et al. 2010). Other approaches to measure ecological values include ecological networks (Raimundo et al. 2018) and genome sequencing that incorporates eco-evolutionary processes in ecosystem recovery (Moreno-Mateos et al. 2020).

The importance of determining a relevant spatial scale in the application of the cascade model for *Tamarix* control

An important consideration when assessing ESs and associated benefits in the context of *Tamarix* control is the definition of the smallest spatial scale at which ESs will be examined (i.e. the grain of the spatial scale, Turner et al. (1989)). For example, to quantify the contribution of river restoration to ES provision, Vermaat et al. (2013) determined that the grain should be forest patches or fluvial features (e.g. sand or gravel bar, secondary channel, terrace) no larger than 100 m². Cassiano et al. (2013) also used a 100 m² resolution to assess the contribution of remnant riparian forest patches to water-related ESs in an agricultural landscape of south-eastern Brazil. Rather than determining an optimal value for the grain size, Riis et al. (2020) defined ESs provided by riparian systems using study units based on a classification of four different vegetation types. Determining a spatial scale that can discriminate between *Tamarix*- and native species-dominated units, possibly the forest patch or fluvial features (see, for example, Scott et al. (2022) for criteria to determine relevant geomorphic units), will be key for a fair socio-economic valuation of *Tamarix* control projects using an ES approach. It will also be critical to determine the ecosystem biophysical structure, processes and functions of riparian systems (pre- or post-*Tamarix* control) that constitute the first two steps of the cascade model.

Unfortunately, ESs provided by riparian corridors have usually been overlooked precisely because they have been quantified using an inappropriately large grain where ESs are assigned to general land-use categories, such as agricultural, urban and natural (e.g. Felipe-Lucía and Comín (2015)). Lumping natural areas into one category simplifies the heterogeneity of ecosystems and ignores important differences in dominant vegetation, which can strongly influence some attributes of ecosystem structure, such as biodiversity, that ultimately determine supporting functions and final ESs (e.g. wildlife use: Tamarix-dominated, native-dominated and mixed riparian forests can support different avian communities, Van Riper et al. (2008)). For example, the aesthetic appreciation (class service "3.1.1.1" in CICES v.5.1) of a mixed riparian forest dominated by healthy native cottonwoods (Populus spp.) may not be the same as the one provided by a defoliated Tamarix monoculture, even though they both may be designated as "natural forests" when compared to lands occupied by urban sprawl or agricultural fields. Evaluating the steps of the cascade model at the appropriate scales is important so that resource management actions are likewise implemented and monitored at the appropriate scale.

Conclusion

The ES cascade model provides a research framework to define, quantify and value the services that ecosystems provide to society and we suggest it could be a valuable tool for integrating social-ecological outcomes more systematically in the evaluation of invasive species management, including Tamarix control. The ES concept (and, by extension, the cascade model) can be useful for measuring the socio-economic effects of management actions on human well-being as rigorously as the effects on biophysical structure have been measured thus far for Tamarix control (Goetz et al. 2024). This will ultimately increase effectiveness, accountability and transparency of both management and decision-making processes (Funk et al. 2014). However, the use of an ES approach and the linear structure of the cascade model do not necessarily imply that the final purpose of invasive species management must be to make an ESs/benefits valuation, especially in economic terms. This misconception has prevented more studies of ESs in restoration projects (i.e. fear of denaturalising restoration ecology's motivation to restore the Earth's natural capital, Matzek (2018)) and could risk having the same effect on invasive species management (see also Gómez-Baggethun et al. (2010) and Kallis et al. (2013) for criticisms of commodification of ESs). Each step of the cascade

model is intrinsically valuable. The cascade model is intended to help conceptualise all the possible measures and indicators of ecosystem change and how they connect to each other, to provide an implementation framework and to identify knowledge gaps (Potschin-Young et al. 2018).

Implementation of the cascade model in the context of *Tamarix* control will require overcoming some challenges. For example, the current lack of information on responses to *Tamarix* control for most ecosystem components, processes and functions (Goetz et al. 2024) reduces the confidence of economic and socio-cultural valuations. In addition, the paucity of studies on ESs in the *Tamarix* control context indicates that more collaboration between biophysical and social scientists is needed. The comprehensive approach of the cascade model requires participation of multidisciplinary teams, which can be challenging to assemble depending on the capacity and resources of organisations involved. The good news is that there is evidence that land managers and scientists share information and communicate effectively when working on *Tamarix* control efforts (Clark et al. 2019).

With this paper, we hope to have provided clear guidelines and recommendations for how to achieve a comprehensive and holistic assessment of social-ecological outcomes of a prominent invasive species management case: *Tamarix* control in the American West. Further, we hope to stimulate discussion and consideration of applying the cascade model more broadly to invasive species management in a variety of contexts.

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Supplementary material 1

Supplementary data

Authors: Eduardo González-Sargas, Patrick B. Shafroth, Francesc Baró Data type: docx

- Explanation note: appendix S1 provides a list of references studying the functions of water cycling and evapotranspiration and biocontrol-related herbivory (trophic relationships). appendix S2 includes an extended list of ecosystem services and benefits provided by systems dominated by *Tamarix* and replacement vegetation such as native riparian forest and meadow vegetation that follows the CICES v.5.1 classification (Haines-Young and Potschin 2018). appendix S3 describes economic valuation methods.
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Project Description

Three new strategies for improving biosecurity and invasive species management to build resilience in Pacific Islands

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Abstract

The inaugural Pacific Ecological Security Conference (PESC) was held in October 2022, bringing together over 100 island leaders, policy-makers, natural resource managers and global and regional invasive species experts to prioritise the critical issue of invasive species in the Pacific Islands Region. Participants confirmed that invasive species are a major threat to building and maintaining climate resilience and adaptability of Pacific Island ecosystems, as well as food security, biodiversity, sustainable livelihoods and the protection of cultural resources and way of life. Three region-wide strategic action plans were developed to guide interventions focused on the topics of invasive ants, coconut rhinoceros beetle and the use of biological control as a pest and weed management tool. These plans were the major outcome of the PESC and, when implemented, will result in coordinated activities that take a "whole-of-Pacific" approach to invasive species biosecurity and management. Here, we briefly describe the background, planning and engagement process for the three plans, summarise any country- and territory-level data obtained through the process and detail what is planned to occur over the next few years. In addition to the adoption and implementation of the strategies as a result of this inaugural PESC, we anticipate that the PESC will become the premier regional conference aimed at reducing the entry and impacts of invasive species to improve sustainability of environments and peoples of the Pacific.

Key words: Ants, biological invasions, biological control, border security, climate change, coconut rhinoceros beetle, costs, impacts

Introduction

The Islands of the tropical Pacific are made up of 22 countries, territories and the U.S. State of Hawai'i, within three sub-regions of Micronesia, Melanesia and Polynesia. Thousands of high (mountainous, volcanic) and low (atoll, limestone) islands comprise this vast oceanic region where over 14 million inhabitants reside



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on a total land area of approximately 600,000 km² (The World Bank 2022). The Pacific Islands are home to over 1,000 languages and dialects, strong native and indigenous cultural heritage and numerous terrestrial and marine protected areas and biodiversity hotspots (Lynch 1998; Myers et al. 2000).

Islands worldwide are particularly noteworthy for global conservation efforts because they host more than 20% of the world's terrestrial plant and vertebrate species within less than five percent of global terrestrial area (Kier et al. 2009). Given their geographic isolation, high levels of endemism and population centres that are concentrated close to the coast, tropical islands are also uniquely vulnerable to global threats, such as climate change and invasive species (Fordham and Brook 2010; Bellard et al. 2013; Nurse et al. 2014; Taylor and Kumar 2016; IPBES 2019). Pacific Island ecosystems and communities are particularly vulnerable to climate-induced threats to water resources (Keener et al. 2018; Clilverd et al. 2019; Frauendorf et al. 2019), natural or green/blue infrastructure (Kane and Fletcher 2020; Buffington et al. 2021; Reguero et al. 2021), coral reefs and fisheries (Lehodey et al. 2013; McManus et al. 2021) and agricultural and subsistence activities (Kurashima et al. 2019).

Much of the conservation threat on islands, as well as on mainland ecosystems, arises from invasive species, which are considered to be the second largest driver of extinction globally (Bellard et al. 2016). In the tropical Pacific Islands, however, invasive species are much more than just a primary driver of biodiversity loss (IPBES 2019). Invasive plants and animals can completely alter ecosystems and, consequently, the cultural and ecosystem services they provide (Cordell et al. 2009; Holmes et al. 2019). They also threaten food and water security in the region, especially for subsistence farming, through productivity losses and changing hydrological dynamics, especially by increasing water loss (Vargas et al. 2016; Kappes et al. 2021). The negative impacts of invasive species also reduce environmental and human resilience to climate change. Protecting island ecosystems from the effects of invasive species not only alleviates these effects, but is also an important climate resilience strategy (IPCC 2007; Lawler et al. 2010; IPBES 2019).

Given the impacts that invasive species have on Pacific Island ecosystems and nearly every aspect of life in the region, the Pacific has become a leader in regional approaches for their prevention, control and eradication. One of the first Pacific-wide frameworks for national and regional management efforts was the Regional Invasive Species Strategy (RISS), produced in 2000 by the Secretariat of the Pacific Regional Environment Program (SPREP), a regional multilateral organisation representing its member Pacific Island Countries and Territories (PICTs). A review of this strategy resulted in the development in 2004 of the Guidelines for Invasive Species Management in the Pacific. The subsequent establishment of the Pacific Regional Invasive Species Management Support Service (PRISMSS) has further strengthened SPREP's supporting infrastructure for technical assistance and advice. Whereas SPREP focuses primarily on the ecological impacts of invasive species, a fellow Pacific regional organisation, the Pacific Community (SPC; formerly the South Pacific Commission) provides scientific and technical resources for sustainable Pacific Island economies and food systems in the face of the dual threats of invasive species and climate change. International conservation NGOs, such as Island Conservation, Birdlife International Pacific Secretariat and The Nature Conservancy, have substantial invasive species programmes within the region. Other coordinating groups and networks, including the Pacific Invasives Partnership (PIP), the Regional Invasive Species Council for Micronesia (RISC),

the Pacific Regional Invasive Species and Climate Change management network (Pacific RISCC) and the Asian Pacific Forest Invasive Species Network (APFISN) support international planning, research, training, networking and assistance at the regional or sub-regional scales.

The First Pacific ecological security conference

Despite increased awareness of the importance and seriousness of invasive species, there continues to be an urgent need for increased and coordinated action at the local, national and regional levels to address the Pacific's most urgent problems. In response, an international organising committee initiated preparations for the first Pacific-wide invasive species conference in 2020. The inaugural Pacific Ecological Security Conference (PESC) was held in the Republic of Palau, 3–5 October 2022, hosted by the Government of Palau, the East-West Center, SPC and The Nature Conservancy. The PESC convened over 100 island leaders, policy-makers, natural resource managers and global and regional invasive species experts to address the impact of invasive species on critical issues for the Pacific, including ecosystem sustainability, island livelihoods, cultures, food security and resilience to climate change. The conference focused on developing region-wide plans for action for the priority areas of invasive ants, coconut rhinoceros beetle (CRB) and biological control.

As a forum for regional decision-making, strategic planning, knowledge exchange and networking, it was crucial to the success of the PESC to ensure that the PICTs were well-represented to enhance partnerships and coordination with the United States, Australia and New Zealand. Funding provided by conference sponsors (East-West Center, U.S. Office of Insular Affairs, U.S. Forest Service, Australian Embassy to Palau and Sasakawa Peace Foundation) supported participant travel for representatives from 14 PICTs (Fig. 4), including four Minister-level delegations. Additionally, high-level delegations attended from regional organisations (SPREP, SPC) and regional partner countries (the United States, Australia, New Zealand, Japan, Taiwan). Timing for the PESC was opportune as it was held three months after the 51st Pacific Island Forum Leaders Meeting in Fiji, during which the 2050 Strategy for the Blue Pacific Continent (Pacific Islands Forum Secretariat 2022) was endorsed. As the Strategy serves as a blueprint for sustainable development, climate resilience and healthy people and environments amongst the 18 member countries and territories of the Pacific Islands Forum, motivation for regional collective action was high.

To ensure the goals of the conference were both manageable and achievable, the first PESC focused on developing or updating Strategic Action Plans for two of the most significant and rising invasive species issues in the Pacific Islands (invasive ants and CRB), as well as the underutilised use of biological control as a management tool for particularly damaging and widespread pests and weeds. Over two years leading up to the PESC, working groups engaged PICT representatives and subject-matter experts in the process of developing draft plans. As a result, the bulk of the conference was built around multiple breakout sessions in which participants provided input and direction on the three draft plans. These plans were envisaged to be the major outcome of the PESC, increasing coordinated activities that would take a "whole-of-Pacific" approach to invasive species biosecurity and management. Participants also heard stories from Pacific Islanders about the lived, everyday impacts of invasive species and statements by regional organisations and partners that highlighted potential research, capacity-building or funding capabilities. Following, we provide some of the information presented at the PESC detailing the basis of the need for attention of the three topics of invasive ants, CRB and biological control.

Invasive Ants

Amongst globally significant invasive taxa, ants are particularly notable for their many serious environmental, social and economic impacts (Angulo et al. 2022; Gruber et al. 2022) contributing to extinctions (Banko and Banko 1976; Lumsden 2009; Emery et al. 2021), collapse of ecosystem functioning (O'Dowd et al. 2003; Olds 2008), farm abandonment (multiple PESC participant personal communications) and human deaths (Xu et al. 2012). Notably, some species are predicted to have economically unsustainable consequences if allowed to establish in many places globally, especially on islands (Angulo et al. 2022; Gruber et al. 2022). Given the severity of these impacts and the low prospects of eradication if incursions are not discovered and acted upon early (Hoffmann 2011; Hoffmann et al. 2016), ants are increasingly becoming a priority target of biosecurity measures to prevent their arrival (HAG 2001; PIAG 2004; Environment and Invasives Committee 2019).

Despite the knowledge of invasive ant impacts, surprisingly few data are available about ant incursion rates within the PICTs. However, inferences can be derived from some locations with quantified data. Australia, which now has a strong biosecurity system to prevent incursions, found 17 incursions between 2000 and 2021 (0.8 incursions per year) (Fig. 1; Suppl. material 1: table S1). This incursion rate is almost half that of Lord Howe Island (1.4 incursions per year between 2000 and 2012), which, during that timeframe, had few biosecurity protocols to prevent incursions (Hoffmann et al. 2017) and as such could be representative of most islands throughout the Pacific. Hawai'i, which arguably has a less stringent biosecurity system and significantly smaller volumes of trade than Australia, has found 14 new ant species since 2000 (0.6 incursions per year), bringing the total number of exotic ant species established in the State to almost 70 (Krushelnycky et al. 2005).

Few ant eradication programmes exist in the Pacific (Angulo et al. 2022), so the costs of running such programmes must also be inferred. Australia has been attempting to eradicate almost every exotic ant incursion found in the past two decades and, not surprisingly, the cost of attempting to eradicate the Australian mainland incursions is rising as more and more eradication programmes are being conducted simultaneously, despite five already being completed. Excluding the largest eradi-



Figure 1. Cumulative number of exotic ant incursions found in Australia since the year 2000. (Data sourced from Department of Agriculture, Fisheries and Forestry Consultative Committees Secretariat).

cation programme, targeting the red imported fire ant (*Solenopsis invicta*) in southeast Queensland, the cost of all other eradication programmes in 2019 had reached AUD\$14.3 million (Fig. 2a). When the southeast Queensland *S. invicta* programme is included, that cost in 2019 rises to AUD\$53.6 million (Fig. 2b). Given that the average per capita gross domestic product of Pacific nations is approximately one tenth of the developed world (IMF 2020), it is unlikely that PICTs would have the financial capacity to deal with incursions as Australia is attempting. Additionally, local regulations may limit access to and use of pesticides used during eradication efforts and delay rapid response efforts when a new species detection is made. Clearly, preventing such incursions is far more economical than attempting eradication after they arrive (Leung et al. 2002; Muller et al. 2021; Angulo et al. 2022).



Figure 2. Annual cost of exotic ant eradication programmes within Australia since the year 2000 both excluding (**A**) and including (**B**) the costs of the red imported fire ant eradication programme in south east Queensland. Data sourced from the Invacost database (Diagne et al. 2020).

Coconut Rhinoceros beetle

Known regionally as the "tree of life", the coconut palm (*Cocos nucifera*) has vast utility for PICTs. Over thousands of years, voyaging Pacific Islanders brought varieties of *C. nucifera* to various islands where the palms provide income, food, medicine, cultural and household materials, shade for communities and shade-tolerant crops and are an attraction for tourism (Harries 1978; Foale 2003). At the last census in 2020, 61.5 M tonnes of coconuts were harvested commercially worldwide and much of that production and trade occurred within the Pacific (FAOSTAT 2018). The species is ecologically important because of the vast areas that plantations cover and coastal shorelines it inhabits where, in particular, the plants are highly resistant to wind from storms, withstand erosion and may tolerate salinity in the face of rising sea levels (Parrotta 1993; Labouisse et al. 2007).

The CRB is native to the Asian Region, but has spread to many parts of the world including the Pacific where it is a key pest of coconut and oil palm (Bedford 1980). CRB feed on the palms causing damage that reduces palm health and, in severe cases, kills the palms (Fig. 3). These impacts negatively affect all of the utilities provided by the coconut palm and greatly threaten the economy provided



Figure 3. Coconut palms severely damaged by Coconut Rhinoceros Beetle on Guam (Photo courtesy of Laura Brewington).



Figure 4. Map of the Pacific Region with red stars indicating PICTs that were represented at the PESC.

by the coconut trade. The beetle was first reported in the Pacific Region in Samoa in 1909 and the only PICTs that now remain free of CRB are the Cook Islands, French Polynesia, Federated States of Micronesia, Kiribati, Marshall Islands, Nauru, Niue, Pitcairn Islands and Tuvalu (Paudel et al. 2021).

The impacts of CRB within the Pacific are mostly undocumented, despite being visually prominent and are detailed here from personal experience. Coconut death in Guam from CRB damage has been severe such that few tall palms remain, which has greatly detracted the environment for the locals and tourist industry alike. In places within PNG where CRB has established, there are now localised shortages of coconuts for local consumption. In the Solomon Islands, CRB has devastated coconuts and young, replanted oil palm seedlings in plantations along the Guadalcanal plains. The relatively recent incursion into Vanuatu has spread across almost half of Efate inducing very severe damage (> 80% palms killed) in some areas. If uncontrolled, on-going spread of the CRB is projected to cause the loss of more than half of the country's coconut palms. The *Oryctes* nudivirus (OrNV) has been used successfully as a biological control agent against CRB for over 40 years (Bedford 1980; Huger 2005). However, in recent years, control efficacies have apparently been decreasing across CRB's invasive range.

Biological control

Modern classical biological control is the natural regulation of a pest species by re-uniting the pest with a co-evolved and host-specific natural enemy (biological control agent) collected from the native range of the pest species (van Driesche et al. 2016; Mason 2021). To date, all 22 PICTs have intentionally released at least one natural enemy to control arthropod pests, while 17 PICTs have deliberately released at least one weed biological control agent. In fact, more than 900 species of natural enemies have been intentionally released to control over 250 pest arthropod species in the region (Day et al. 2021). Notably absent to date has been the use of natural enemies to control plant diseases. Most importantly, none of the host-specific natural enemies has shifted from their weed or pest host or negatively impacted other species or the environment. Instead, they have remained intricately linked to their invasive species host, thereby confirming the adequacy of modern risk assessments for the safe release of natural enemies in new locations.

The successful and extremely low-risk use of natural enemies to control weeds in the tropical Pacific has a long history (> 100 years), with 66 natural enemies intentionally released to control over 26 weed species (Day and Winston 2016). Surprisingly, given the many success stories of using biological control in the Pacific Islands (e.g. control of the floating weed *Salvinia molesta* in PNG and the herbaceous shrub *Chromolaena odorata* in PNG and Micronesia) and elsewhere, this technique is still an underutilised tool in most PICTs. This is even more surprising given that using biological control agents has produced huge returns on investment, up to \$4,000 USD for every dollar spent (van Wilgen and De Lange 2011) through reduced control costs and increased productivity. For example, the biological control of cactus species to reclaim and protect range lands in Australia delivered a benefit-cost ratio of 300:1 (Page and Lacey 2006) and, in Hawai'i, a biological control agent brought the endemic wiliwili tree (*Erythrina sandwicensis*) back from the brink of extinction by providing ongoing control of invasive gall wasps since 2008. Currently, biological control is the only widely available tool that can control many widespread pests and weeds that are an existential threat to island resilience, ecological security and the perpetuation of island people's livelihoods and cultures.

Strategic action plans

To drive the invasive species agenda, three Strategic Action Plans, focused on the three themes detailed above, were drafted prior to the meeting. The plans were intended to enhance overall coordination amongst the PICTs, regional multilateral entities and research and funding partners around identified gaps and needs at multiple scales (local to regional).

Invasive ant plan

The Biosecurity Plan for Invasive Ants in the Pacific (BPIAP) was an update to the 2004 Pacific Ant Prevention Plan (PAPP) by the Invasive Species Specialist Group of the International Union for the Conservation of Nature (PIAG 2004). The PAPP was endorsed at the 2004 meeting of the Pacific Plant Protection Organization (PPPO) and the SPC agreed to be the lead agency in implementing the plan. Over the subsequent years, some of the PAPP's elements were addressed, but the plan was in need of updating even well before 2022 (Vanderwoude et al. 2021). The PESC was an opportunity to re-invigorate the original plan and align it with the current status and needs in the Pacific. The plan contains biosecurity and management actions at three levels: regional, country and intra-country. The greatest difference from the prior version is that it contained a dedicated science strategy. In addition, it was notable that many actions influence biosecurity generally, not just for ants.

Before, during and immediately after the PESC, attendees and invitees of all PICTs were requested to complete a survey of their completion status, as well as their expertise and financial assistance needs, relative to the highest-priority actions drafted within the updated version of the BPIAP. Responses were received from 14 PICTs (Suppl. material 1: tables S2–S4). Key findings included the following: none of the PICTs had emergency response plans for any invasive ant species, with the exception of Hawai'i, which had a single plan for the red imported fire ant. Approximately half of the PICTs had no awareness activities for invasive ants. Only one third of PICTs indicated that some form of proactive surveillance was being conducted. There were very few completed pest risk analyses or pathway analyses. Most (64%) PICTs that responded stated that they currently do not have professional development opportunities for people responsible for invasive ant biosecurity. More than 82% indicated that expert assistance was needed to conduct actions. Finally, 97% of PICTs indicated that external financial assistance was needed to conduct actions. Notably, the results are just as relevant for both individual PICTs identifying priority actions to progress ant biosecurity and external parties identifying how they can assist PICTs to achieve such progress (Pacific Ecological Security Conference 2022a).

Coconut Rhinoceros beetle plan

Prior to the PESC, researchers and practitioners from throughout the world drafted the Strategic Action Plan for CRB management and containment across PICTs (CRB Plan). The plan focused on biosecurity measures preventing CRB spreading to the few remaining PICTs that remain CRB-free, improving management and limiting spread where CRB is already present and developing a strong research plan supporting these two biosecurity and management objectives. During and immediately after the PESC, attendees and invitees also completed a survey evaluating awareness of CRB and jurisdictional needs to contain and control the pest. PICTs were divided into three groups of incursion status: those having a recent damaging outbreak (Outbreak), those where CRB has been established for a period longer than 50 years (Established) and those yet to be infested by CRB (CRB-Free). Responses were obtained from 23 PICTs and Hawai'i.

The survey found that the countries without CRB are ill-prepared for incursions and that those with high levels of CRB infestation do not have the resources for a sustained response (Suppl. material 1: table S5). Awareness and response capability were also generally higher where CRB was well established. The following three key points were identified from the responses as well as from discussions at the PESC: 1) There is an urgent need for CRB-free PICTs to establish surveillance and response plans to be able to respond quickly and effectively to a CRB incursion; 2) PICTs with CRB need to reduce their populations, especially around ports and transport hubs, to limit further spread of CRB; and 3) Better tools (new strains of biological control agents, improved traps, rapid detection systems) are needed to provide PICTs with the technologies they need to effectively manage or even eradicate CRB (Pacific Ecological Security Conference 2022b).

Pacific Biological control plan

Prior to the PESC, researchers from 16 PICTs and the State of Hawai'i provided input that resulted in the draft Pacific Biological control Strategic Action Plan (PBSAP) which aimed to expand the use of natural enemies for invasive species management in the Pacific at local, country and regional levels. Notably, the plan does not set priorities for specific pests and weeds, rather, it acknowledges that the prioritisation of pest and weed species must be conducted at the local level.

During and immediately after the PESC, attendees and invitees also provided input on their jurisdictional needs for using biological control, especially for filling key local to regional gaps and needs in the areas of communications, policy, capacity and determining the coordination and collaboration mechanisms that will be necessary for sustained effort to implement the plan. Responses were received from 15 PICTs. More than 86% of the PICTs indicated that they still had to, and needed help to, develop internal communication messaging, preparing communications resources and capacity to build internal support for the use of biological control. Only 14% were already developing such protocols. Developing external communication messaging and resources to increase the public support for biological control was a priority for all PICTs that responded. Just 40% indicated that this was already underway and more than 73% stated that they need assistance to complete this activity. None of the PICTs stated that they had the personnel or the capacity to develop internal and external communication resources, although 13% stated that this was underway. More than 73% stated that they needed assistance and 93% stated that they would require funding to achieve this.

Less than half (40%) of the PICTs had regulations in place to conduct biological control projects, while just over half still had to put regulations in place. Half of the PICTs indicated that they would need assistance to develop such regulations. Less than half (40%) had developed a framework for regulatory applications and local

environmental review for planning and conducting biological control projects, while the remaining PICTs still needed to do this and indicated they would need help setting up or implementing regulatory compliance work locally. More than 86% of PICTs indicated that they still needed to develop or gain access to current best practices, risk assessment protocols, pre- and post-release monitoring procedures for conducting biological control projects and that they would need assistance, partners and funding. Eighty percent reported needing assistance and funding to develop policy and regulatory actions (Pacific Ecological Security Conference 2022c).

There are very few existing high security quarantine facilities in the region, with 80% of PICTs indicating that they would need help and funding to assess needs and construct, if necessary. More than 26% of PICTs had Post Entry Quarantine facilities for receiving natural enemies from other high-security quarantine research facilities, with 73% needing assistance and funding to upgrade or construct new facilities. More than 26% had facilities to rearing natural enemies with the remaining PICTs indicating that they needed assistance and funding to expand current facilities or construct new insect-rearing facilities. Nearly all (93%) respondents indicated they needed professional development opportunities for practitioners and that they needed help, funding and partners to make this happen.

Implementing the plans

All three plans are intended for use by all Island Nations, States and jurisdictions within the Pacific Region, including Australia, New Zealand and the United States. Likewise, the plans can also be used to guide investments by funding agencies, donors and development partners. Inherently, there are many actions that can be taken by individual PICTs, but there are also numerous regional biosecurity initiatives that are beyond the remit of individual jurisdictions. These fall within the perceived roles of regional multilateral entities, amongst which the two primary environmental representatives are SPC and SPREP. Specifically, within SPREP is the PRISMSS, with SPC as a founding partner, but which welcomes participation by all parties with the common goal of practical action to prevent and manage invasive species throughout the Pacific. Such multi-dimensional and multi-entity work is not novel in the Pacific. The Pacific Regional Fruit Fly Program, which ran from 1989 for more than a decade is just one example of a highly successful Pacific regional programme (Allwood and Drew 1997).

Notably, the plans can be used in parallel with, or continue on from, other plans and current programmes. The BPIAP can also be used with the only other known equivalent plan in the world, Australia's National Invasive Ant Biosecurity Plan (Environment and Invasives Committee 2019). The Australian plan has an approach agreed to by all Australian States and Territories to enhance Australia's capacity to prevent exotic ants establishing in Australia and reduce the impacts of those already established. Equally to the BPIAP, the Australian plan also includes actions that are to be implemented offshore (preventing ants arriving), at ports-ofentry and post-entry throughout the continent. The CRB plan can extend from the New Zealand Ministry of Foreign Affairs and Trade Aid Programme "Pacific Awareness and Response to the Coconut Rhinoceros Beetle" (PARC) programme, which is coordinated by SPC and currently covers parts of a Melanesia sub-region (PNG, Solomon Islands, Vanuatu). The PARC programme focuses on limiting the spread within established areas through increased awareness and management efforts. One of the first actions for all three plans is to determine which entity will be the administrator for each plan. The mechanism to determine this will be a combination of discussions between the likely entities (i.e. SPC and SPREP), as well as voting by PICTs through the Pacific Plant Protection Officer network. Regardless, anybody or any entity can do any work on these topics anywhere and anytime and funders can also provide money outside of the bounds of these plans. These plans are just guidance documents to help illuminate gaps and needs and aid the prioritisation and impetus for such work. While these administrative details are being determined, the plans can be accessed from the locations detailed with the reference for each plan (Pacific Ecological Security Conference 2022a, 2022b, 2022c). The plans are living documents and are intended to be updated regularly as management technology improves, as local and regional capacity is increased, as key understandings of target species improve or change and as on-ground statuses change thereby changing priorities. Administrators will also be expected to lead the future refinements of these living documents.

Moving beyond the first PESC

Momentum from the PESC quickly translated into legislative and programmatic achievements for the region. At the 2022 Association of Pacific Island Legislatures (APIL) meeting held immediately following the PESC, participants passed Resolution 39-GA-15 to endorse and support invasive species management, control and eradication in Micronesia. The Strategic Action Plan priorities were featured prominently at the 2023 Micronesian Islands Forum meeting in Pohnpei, Federated States of Micronesia, where island leaders committed to implementing recommendations from the PESC and enhancing inter-island biosecurity measures against CRB and the little fire ant. The latest update to the Regional Biosecurity Plan for Micronesia and Hawai'i (United States Department of the Navy 2015), a process that is scheduled for every five years, has also been re-invigorated as a result of the PESC. At the PESC, the U.S. Forest Service committed to providing funding to support a new Micronesia RISC coordinator position that will ensure all jurisdictions in Micronesia and Hawai'i finalise their respective updates to the Plan.

The PESC also called for increased research, capacity building and technical assistance for addressing invasive species in the region, needs that are subsequently being met by multiple partner entities. In late 2023, in response to recommendations in the CRB Strategic Action Plan, the Micronesia Conservation Trust hired a Regional Research Coordinator to assist in CRB preparation and response throughout Micronesia. The Coordinator also joins the Pacific RISCC Core Team, conducting needed research and coordination support to natural resource managers in the Pacific Islands, while strengthening regional partnerships and awareness around the interactions/synergistic effects of invasive species and climate change. The US Indo-Pacific Command committed during the PESC to improving research and development activities for the detection, surveillance, mitigation and eradication of invasive species in the Indo-Pacific Region and hosted an Invasive Species Forum in 2023 that has ultimately provided information for the next generation of financial investments by the U.S. Department of Defense in research and development. Finally, in late 2023, the U.S. Office of Insular Affairs held a multi-island biosecurity training in Guam for all U.S. insular territories, the Freely Associated States and the nation of Kiribati. Nearly 100 frontline biosecurity personnel and government administrators were in attendance at this technical assistance workshop, which was requested by participants at the PESC and featured CRB and fire ant detection, as well as high risk invasive plants.

Subsequent to the PESC, the Convention of the Parties (COP15) in Montreal, Canada adopted the Kunming-Montreal Global Biodiversity Framework (GBF) which has a specific target (target 6) focused on mitigating the spread and impacts of invasive species, especially in priority sites, such as islands (GBF 2022). This achievement was in no small part due to SPREP's high level engagement at COP15 with input and outcome summaries provided by PESC participants. The International Union for Conservation of Nature (IUCN) Invasive Species Specialist Group (ISSG) was further called upon to ensure a global platform for sharing data and information, continuing compiling policy response indicators and calling states, organisations and experts to support the Global Register of Introduced and Invasive Species (GRIIS). In addition to the GBF, COP15 approved a series of related agreements on its implementation, including a resource mobilisation plan and requesting the Global Environment Facility to establish, as soon as possible, a Special Trust Fund (GBF Fund) to support implementation — for which PICTs would be eligible to apply.

Lastly, it was determined at the inaugural PESC that another similarly-themed conference was desired and that two years would be a suitable interval to allow sufficient time for implementing Strategic Action Plans to the extent that they could be reviewed and refreshed. Additionally, it was recognised that rodents are a significant and comparable invasive species issue within the Pacific. As rodents have already received considerable attention over the past few decades, with many successful eradications achieved on islands and subsequent ecological recoveries (Russell and Holmes 2015), as well as other conferences dedicated to rodent management, this topic was not included as a priority for the first conference. However, it is envisaged that future PESCs will incorporate vertebrate biosecurity and management.

There are numerous sustainability issues in the Pacific Region, such as invasive species and climate change, that cannot be effectively dealt with by individual jurisdictions. Indeed, the 2050 Strategy for the Blue Pacific Continent, endorsed by Pacific Island leaders in 2022, specifically reinforced the commitment to working as a regional collective in pursuit of sustainability, resilience and security (Pacific Islands Forum Secretariat 2022). The PESC brought together international and multidisciplinary participants to foster collaborative networks and increase action on invasive species in the region. It is now up to all jurisdictions and interested parties (i.e. funders, researchers, managers) to rise to the challenge and initiate on-the-ground actions and progress that utilise the Strategic Action Plans. Nevertheless, much more work remains to be initiated. We anticipate that the PESC will grow to be the premier regional conference addressing the interplay of invasive species with other critical factors affecting the sustainability of environments and peoples of the Pacific.

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Data availability

The datasets generated during and/or analysed during the current study are available from the corresponding author on reasonable request.

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Supplementary material 1

Supplementary data

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Data type: docx

- Explanation note: **table S1.** Details of exotic ant incursions found within Australia since 2000. Information sourced from Department of Agriculture, Fisheries and Forestry Consultative Committees Secretariat). **table S2.** Number of PICTs in the three Pacific Regions relative to their completion of highest priority Actions for invasive ant biosecurity. **table S3.** Number of PICTs in the three Pacific Regions relative to their need for personnel assistance to complete highest priority Actions for invasive ant biosecurity. **table S4.** Number of PICTs in the three Pacific Regions relative to their need for financial assistance to complete highest priority Actions for invasive ant biosecurity. **table S5.** Mean scores of PICT responses to questions about CRB biosecurity. PICTs were divided into the three categories, being those having a recent damaging CRB outbreak (Outbreak), those where CRB has been established for a long period > 50 years (Established) and those yet to be infested by CRB (CRB-Free). Responses were provided using a five-point scale of increasing knowledge, preparation, resources and/or self-ability: 0 = No/nothing; 1 = almost nothing; 2 = partly; 3 = moderately so; 4 = yes/fully/completed.
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Research Article

The alien conifer *Cupressus arizonica* can outcompete native pines in Mediterranean mixed forests under climate change

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Evotion

Abstract

Exotic species have been introduced in afforestation and reforestation initiatives worldwide. Climate change, including increased aridity and extreme events, can promote the spread of exotic species used in forest plantations while hampering the performance of natives. Evaluating whether climate change may affect the success of biological invasions is key to project dominance shifts in forest ecosystems, yet it requires a comprehensive approach that integrates main demographic rates driving tree population dynamics. Here, we evaluated the performance of co-occurring native pine species (Pinus pinaster, P. nigra and P. sylvestris) and the exotic Cupressus arizonica in mixed forests in Mediterranean mountains by comparing their main demographic rates (regeneration, mortality and growth) and radial growth response to extreme droughts and to climate change scenarios. Overall, the exotic C. arizonica showed less growth dependence to climatic variability, higher growth resilience to drought, lower mortality and higher regeneration capacity than P. sylvestris and P. pinaster. However, P. nigra showed higher regeneration and similar growth response to extreme droughts than C. arizonica. In addition, growth models pointed to better performance of the exotic species under future climate change scenarios than co-occurring natives. Our results suggest that C. arizonica can increase its dominance (relative presence within the forest area), which can enhance its invasive potential and range expansion. Thus, attention is needed to better control the invasive potential of this exotic species in Mediterranean forest ecosystems.

Key words: Biological invasions, climatic scenarios, dendroecology, drought, forest dynamics, global change, invasiveness, resilience

Introduction

Understanding interactive effects between different global change drivers is key to forecast their impacts on ecosystems (IPBES 2019). Biological invasions and climate change are major drivers of global environmental change, threatening biodiversity and ecosystem functions worldwide (Vitousek et al. 1997; Butchart et al. 2010; IPBES 2023; IPCC 2023). However, assessing how climate change affects the success of biological invasions remains challenging (Cosner 2014; Hulme 2017). Ongoing climate change could favour the colonisation, persistence and



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spread of early successional species in disturbed ecosystems, as is the case of many invasive plant species (Dukes and Mooney 1999; Lenoir et al. 2008). Under climate change, invasive plant species may obtain even more advantage from their greater capacity for carbon gain, higher performance over a wide range of resource availabilities and higher phenotypic plasticity than native species (Davidson et al. 2011; Godoy et al. 2011). Thus, climate change might promote the colonisation of these species by increasing their invasiveness while hampering the performance of natives (Dukes and Mooney 1999; Hellmann et al. 2008; Huang et al. 2011). However, several studies reported a wide range of species-specific and context-dependent responses, calling for further investigations on climate change effects on the performance of co-occurring native and invasive species (Diez et al. 2012; González-Muñoz et al. 2014; Medina-Villar et al. 2020).

Plant species are not only experiencing gradual changes in average climate conditions, but also a higher frequency and intensity of extreme climatic events, such as droughts and heat waves that severely impact Mediterranean ecosystems (Spinoni et al. 2018; IPCC 2023; Toreti et al. 2024). Extreme droughts impose severe stressful conditions on native plant species, which, in turn, could reduce their competitive ability and resistance to invasions. This can prompt the establishment and spread of invasive species populations with greater tolerance to new environmental conditions (Stromberg 1998; Kane et al. 2011). In forest ecosystems, extreme droughts can even exceed the ecophysiological tolerance of native canopy-dominant species, triggering widespread tree mortality (Allen et al. 2015), which implies large releases of resources (e.g. light, water) that could favour the establishment of early successional invasive species (Kane et al. 2011; Diez et al. 2012). The duration of the invasion window after a given disturbance (e.g. extreme climatic event) depends not only on the local environmental conditions (e.g. water, temperature) for the germination and growth of the colonising exotic species (Jastrzębowski et al. 2021; Orbán et al. 2021; Klisz et al. 2023), but largely on the resilience capacity of native species (Diez et al. 2012). Therefore, evaluating the resilience capacity to extreme droughts of co-occurring native and exotic tree species could be used to forecast near-future invasions in drought-prone ecosystems, such as those in Mediterranean and semi-arid regions.

Many exotic tree species have been planted throughout the world's forests in plantations or reforestations, some of which have been successfully naturalised and/or become invasive (Richardson and Higgins 1998; Mortenson and Mack 2006; Vítková et al. 2017; Dimitrova et al. 2022; FAO 2022). The invasiveness of these exotic tree species can be increased by improved performance due to beneficial climatic changes (e.g. warming, Scholze et al. (2006)) and/or by reduced competition during extremely adverse climatic conditions because of higher resilience than co-occurring native species (Olano and Palmer 2003; Suarez and Kitzberger 2010). Recent studies using species distribution models (SDMs) have predicted distributional range shifts of exotic tree species under climate change in Europe (Puchałka et al. 2020, 2023). However, studying species-specific responses to climatic trends and extremes, such as drought events, at local scales is crucial to understand acclimatisation responses of native and non-native tree species (Klisz et al. 2023).

Tree growth is one of the main demographic parameters determining population dynamics along with mortality and regeneration capacity, which are critical to evaluate the invasive capacity of a given exotic tree species. The quantification of tree growth through tree ring measurements has been used to assess the performance of co-occurring exotic and native tree species (Mortenson and Mack 2006; Mácová 2008; Vanhellemont et al. 2011; González-Muñoz et al. 2015). Tree ringwidth series allow us to evaluate growth responses to past and current climatic variability and to analyse growth resilience to extreme climatic events (Fritts 1976; Lloret et al. 2011). Further, ring-width series could be used to forecast growth responses to projected climate changes (e.g. González-Muñoz et al. (2014); Matías et al. (2017)). However, few studies have compared the response of co-occurring native and exotic tree species to projected climatic changes (but see: González-Muñoz et al. (2014)). Thus, the analysis of growth responses to current and projected climate in co-occurring native and exotic tree species, coupled with the evaluation of growth resilience to current extreme climatic events, may contribute to assess potential changes in species performance and subsequent shifts in forest species dominance. In addition, regeneration capacity and background mortality of co-occurring native and exotic species could play a critical role in native-exotic species dynamics. To the best of our knowledge, there is a lack of studies that evaluated the performance of co-occurring native and exotic species following such an integrative approach.

In Mediterranean mountains, native pine species are spatially segregated along environmental and altitudinal gradients according to their drought-tolerance (Ruiz-Benito et al. 2012). In some forest areas, native pine species co-occur with the exotic Cupressus arizonica Greene., an evergreen conifer native to North America adapted to dry and cold conditions and widely planted out of its native range (Flora of North America Editorial Committee 1993; CABI 2020). In southern Europe (e.g. Spain, North Macedonia), C. arizonica was used in afforestation/ reforestation and for soil protection since ca. mid-twentieth century (Dimitrova et al. 2022). Although C. arizonica is not currently considered as invasive species in these areas, it was able to escape plantations and become a naturalised species (Sanz Elorza et al. 2004). However, it was reported as an invasive species in other areas, such as in Hawaii (Swearingen and Bargeron 2016). On average, exotic trees introduced to Europe can become invasive after 170 years from introduction (Kowarik 1995). In the case of C. arizonica, this lag time could be reduced under future climate changes, in which drier conditions could favour the performance of this species over that of the native pine species. However, the ability of this exotic species to spread and invade Mediterranean ecosystems has not been explored yet. This information is essential for the management of established exotic species. In fact, the European Regulation 1143/2014 on invasive alien species established the need to identify potential invasive alien species of European concern, i.e. those likely to arrive, establish, spread and have an impact on native biodiversity or associated ecosystem services in Europe.

Therefore, our main objective was to compare tree performance of co-occurring native pines (*P. sylvestris, P. nigra* and *P. pinaster*) and exotic species (*C. arizonica*) along altitudinal vegetation belts in mixed conifer forests of the central Iberian Peninsula. The specific objectives of the present study were: i) to quantify regeneration capacity and mortality of both native and exotic species; ii) to compare growth-climate relationships between co-existing native and exotic species; iii) to compare components of tree growth resilience in response to extreme drought events between native and exotic species; and iv) to forecast species growth throughout the 21st century under different climate change scenarios. Given species-specific tolerances to drought and their biogeographic origin, we expected that the exotic *C. arizonica* will show lower growth sensitivity to water availability, higher growth resilience to extreme droughts and higher regeneration and lower mortality than *P. nigra* and *P. sylvestris*, but similar to *P. pinaster*. Accordingly, we hypothesised more severe growth declines in the next century for *P. nigra* and *P. sylvestris* compared to *C. arizonica* due to projected increased aridity.

Methods

Study area

The study area is located in La Pedriza, a large granite complex located on the south face of the Sierra de Guadarrama National Park in the central Iberian Peninsula (40°44'N, 3°54'W). La Pedriza comprises about 3,200 ha and ranges from 890 to 2,090 m a.s.l. The climate is continental Mediterranean with cold winters and dry summers. Mean annual precipitation and mean annual temperature are 533 mm and 11.7 °C, respectively (period 1974-2018, data from the nearest meteorological station of the Spanish National Agency for Meteorology "Colmenar Viejo", 15 km away from the study area at 1,004 m a.s.l.). Soils are classified as district Cambisol and Leptosol over a granitic substrate (IUSS Working Group WRB 2015). The study area is dominated by pine forests of several species that are distributed at different altitudes. P. pinaster is the dominant tree species at low elevation stands (about 900-1,200 m a.s.l.), whereas mid-high elevation stands are dominated by P. nigra (about 1,100-1,300 m a.s.l.) and P. sylvestris (about 1,100-1,800 m a.s.l.). Most of these forests originated from afforestation/reforestation programmes between 1940 and 1970. Understorey vegetation is mainly composed of Cistus ladanifer L., C. laurifolius L., Juniperus oxycedrus L. and J. thurifera L., amongst others. Quercus ilex L. and Q. pyrenaica Willd. appear as secondary tree species in some areas.

In this area, *Cupressus arizonica* appears in monospecific stands and mixed with pine species between 900 and 1,300 m a.s.l as the result of afforestation programmes for erosion control between 1960 and 1970 (Valdés and Carlos 1996). In its native range, it occurs in a wide range of soil types at elevations between 1,000 and 2,000 m a.s.l., with an annual precipitation between 400 and 600 mm (Flora of North America Editorial Committee 1993).

Sampling design and dendroecological methods

Within the study area, we randomly selected forest stands where *Cupressus arizonica* co-occurred with one of the three study pine species. We selected three stands for each mixed forest type (i.e. species combination): *C. arizonica - Pinus pinaster* (CP), *C. arizonica - P. nigra* (CN) and *C. arizonica - P. sylvestris* (CS). CP stands ranged in altitude between 950 and 1150 m a.s.l, in density between 350 and 500 trees ha⁻¹ and in basal area between 29.3 and 39.7 m² ha⁻¹ (Suppl. material 1: table S1). CN stands were sampled at altitudes between 1090 and 1250 m a.s.l, showed tree density between 333 and 800 trees ha⁻¹ and had basal area between 32.9 and 76.6 m² ha⁻¹. CS stands ranged in altitude between 1130 and 1270 m a.s.l, in density between 400 and 1233 trees ha⁻¹ and in basal area between 69.4 and 70.0 m² ha⁻¹ (Suppl. material 1: table S1). At each stand, we randomly established two independent 30×10 m transects and recorded the diameter at breast height (DBH), species identity and the number of dead trees. To quantify the regeneration capacity of the studied species, we recorded the presence and species identity of tree seedlings (height < 50 cm) in 10 circular plots of 5 m radius randomly distributed at each forest stand.

We randomly selected at each stand five dominant or co-dominant trees of each species for dendroecological analyses, which resulted in 15 trees per species at each mixed forest type. We recorded the DBH of each target tree and sampled two wood cores at breast height using a Pressler increment borer. Wood cores were air-dried, glued on wooden supports and polished using sandpapers of progressively finer grain. Tree growth series were visually cross-dated using pointer years (Yamaguchi 1991). We used mean inter-series correlation (Rbar) and expressed population signal (EPS) to evaluate the strength of the common growth signal amongst sampled trees (Wigley et al. 1984). Rbar and EPS were 0.38 and 0.92, respectively, suggesting a strong common signal of analysed growth series. First order autocorrelation (AR1) was 0.61. Rbar, EPS and AR1 were calculated using dplR (Bunn 2010). Samples were then scanned at 1,200 dpi resolution (EPSON V8 Perfection) and tree ring width was measured to the nearest 0.01 mm using ImageJ (Schneider et al. 2012). Tree annual growth was quantified as basal area increment (BAI, cm²), following Biondi and Qeadan (2008):

$$BAI = \pi (r_t^2 - r_{t-1}^2)$$

where r_t and r_{t-1} are the stem radius at the end and at the beginning of a given annual ring, respectively. Sampled trees of *C. arizonica* and pines showed similar BAI and age at breast height, but *P. pinaster* and *P. nigra* were significantly greater in DBH than *C. arizonica* (Suppl. material 1: table S2). Despite the oldest tree dated to 1939, we selected 1974–2018 as the study period to maximise sample size for statistical analyses and using the threshold value for EPS of 0.85.

Climatic data

Monthly climatic data (mean temperatures and total precipitation) for the study period (1974-2018) were obtained from Colmenar Viejo meteorological station (Spanish Meteorological Agency, 30 km from the study area). Water balance (P-PET) was calculated as the difference between precipitation (P) and potential evapotranspiration (PET). PET was calculated following Thornthwaite (1948). For each year, we calculated annual mean temperature (T), total precipitation (P) and water balance from October of the previous year to September of the target year. Previous autumn and winter precipitations can play an important role in recharging soil water reserves, thereby influencing current year radial growth in conifers (Sánchez-Salguero et al. 2012; Madrigal-González et al. 2018). Mean temperature and total precipitation were also seasonally calculated: mean temperature and total precipitation of the previous autumn (October to December; Tau and Pau, respectively), current winter (January to March; Twi and Pwi, respectively), current spring (April to June; Tsp and Psp, respectively) and current summer (July to September; Tsu and Psu, respectively). The use of seasonal climatic variables instead of monthly ones allowed the creation of more parsimonious growth models, while maintaining a reliable representation of climatic trends (Matías et al. 2017).

Climatic data for the study area during the period 1974–2100 were obtained from the CRU database (Climate Research Unit, University of East Anglia). Climatic data are projected according with the CMIP5 - Coupled Model Intercomparison Project (Taylor et al. 2012) under the RCP2.6 and RCP8.5 forcing scenarios from IPCC (2013). These scenarios are based on stringent mitigation measures and on no additional efforts to constrain emissions, respectively. Climate scenarios project an increase in mean annual temperature of 1.2 and 4.7 °C for RCP2.6 and RCP8.5, respectively, by the end of the 21st century (2080–2100) compared to the study period (1974–2018). Annual precipitation is expected to decrease by 8 and 139 mm for RCP2.6 and RCP8.5, respectively. Projected seasonal mean temperature and precipitation were calculated as for data from the meteorological station. For the study period (1974–2018), the mean temperature and total precipitation from CRU database and the nearest meteorological station to the study area were significantly correlated (P < 0.001; r = 0.88 and r = 0.72, respectively).

Data analysis

Growth-climate relationships

We fitted a growth model for each pine species (P. pinaster, P. nigra and P. sylvestris) and three growth models for C. arizonica, one for each mixed forest type (i.e. CP, CN and CS). Following the procedure by Fajardo and McIntire (2012), we evaluated climate-growth relationships by fitting generalised additive mixed effect models using the gam function in the gamm4 package (Wood and Scheipl 2017). The response variable (i.e. BAI) was log-transformed to achieve homoscedasticity. We considered tree identity nested within forest stands as the random term in the model to account for non-independence amongst observations within the same tree (i.e. repeated measurements) and within the same forest stand. We also used an autoregressive correlation structure to remove the first-order autocorrelation between observations of consecutive years (Pinheiro et al. 2018). We considered as fixed effects tree age as a smooth spline (with default package settings) and the eight seasonal climatic variables (Tau, Twi, Tsp, Tsu, Pau, Pwi, Psp and Psu) as linear effects. Climatic variables were standardised (i.e. the mean was subtracted from each value and divided by the standard deviation) to allow comparisons across model-estimated parameters (Zuur et al. 2009). To identify the best-supported model, we fitted all potential models and selected the one that minimises the Akaike's Information Criterion corrected for small samples (AICc). Potential models were fitted by the Maximum Likelihood method using the *dredge* package (Barton 2018). The parameters of the selected model were obtained by Restricted Maximum Likelihood (Zuur et al. 2009). We evaluated species' BAI trend for the period 1974–2018 by fitting a linear model per mixed forest type and considering the interaction between species and year as fixed effects. All statistical analyses were done in R v.3.5.3. (R Core Team 2019).

Tree growth response to extreme drought events

We identified drought events as those years with annual P-PET below the 15th percentile of the P-PET series (Muñoz-Gálvez et al. 2021). We identified 1991, 1995,
2005 and 2012 years as drought events in the study period. For each drought event, we evaluated growth resistance, recovery and resilience for each sampled tree following Lloret et al. (2011):

Resistance (Rt) = Dr / PreDr Recovery (Rc) = PostDr / Dr Resilience (Rs) = PostDr / PreDr

where *PreDr* was the mean BAI before the drought event; *Dr* was the BAI the year of the drought; and *PostDr* was the mean BAI after the drought. We calculated these indices considering pre- and post-drought periods of three years (Marqués et al. 2016; Andivia et al. 2020).

We used linear mixed models (LMM) to evaluate inter-specific differences in growth resilience to extreme droughts for each mixed forest type. We fitted an LMM for each pair of species and resilience component (i.e. resistance, resilience and recovery) using the R package *nlme* (Pinheiro et al. 2018). Resistance, recovery and resilience indices were log-transformed to achieve homoscedasticity. We considered tree identity nested within forest stands as the random term in the model to account for non-independence amongst observations within the same tree (i.e. repeated measurements due to the evaluation of different drought events) and within the same forest stand. Species identity was considered as a fixed effect in the model. The DBH of the individuals in the year of the drought event was included as a covariate (Andivia et al. 2020). We also considered as covariates the relative intensity of the drought event, expressed as the P-PET value during the drought and the difference in P-PET between the periods considered to the calculation of the growth resilience indices (DeSoto et al. 2020).

Forecasting species growth under different climate change scenarios

To forecast tree growth for the period 2019–2100, we followed the procedure by González-Muñoz et al. (2014) and Matías et al. (2017). The best-supported growth models in section *Growth-climate relationships* were run to forecast the BAI of each species and mixed forest for the periods 2019–2048, 2049–2078 and 2079–2100 under the RCP2.6 and RCP8.5 climatic scenarios. For each period and mixed forest, we simulated the annual BAI of 1000 individuals per species and stand (i.e. three simulations per species for each mixed forest type) with initial ages at breast height randomly distributed between those values that allow the restriction of simulations to the age range of sampled trees (Matías et al. 2017). Finally, we evaluated the predicted species' BAI trend for each simulated period by fitting a linear model per mixed forest type and climatic scenario and considering the interaction between species and year as fixed effects.

Results

Regeneration capacity and tree mortality

Seedling density of all species was rather low, ranging from 0 to 63.7 ± 33.7 ind/ ha. *Cupressus arizonica* showed higher regeneration than co-occurring pines at CP (8.5 ± 4.2 vs. 0 ind/ha, for *C. arizonica* and pine species, respectively) and CS stands (63.7 \pm 33.7 vs. 12.7 \pm 7.4 ind/ha). However, at CN stands, *Pinus nigra* showed higher regeneration than *C. arizonica* (21.2 \pm 11.2 vs. 12.7 \pm 12.7 ind/ha). Native *Juniperus oxycedrus* and *Quercus ilex* seedlings were present in all the sampled stands, showing values between 12.7 \pm 7.4 and 67.9 \pm 11.2 ind/ha for *J. oxycedrus* and between 46.68 \pm 27.8 and 89.1 \pm 32.1 ind/ha for *Q. ilex*. Regarding tree mortality, we found that 8.9% and 10% of the *P. pinaster* and *P. sylvestris* trees in the sampled stands were dead, respectively. *P. nigra* showed lower mortality rate (2.7%), whereas no *C. arizonica* trees were dead.

Growth trend and climate-growth relationships

We found contrasting growth trends between *Cupressus arizonica* and *Pinus pinaster* and *P. sylvestris* (Fig. 1). In CP stands, *C. arizonica* showed a significant positive BAI trend over the study period (i.e. 1974–2018; slope \pm SE, 0.33 \pm 0.03; p < 0.05), whereas *P. pinaster* showed neutral (i.e. non-significant) growth trend (0.01 \pm 0.04). *C. arizonica* and *P. nigra* showed neutral growth trend in CN stands (-0.07 \pm 0.04 and 0.05 \pm 0.04, respectively). In CS stands, *P. sylvestris* showed a significant negative BAI trend (-0.24 \pm 0.03), whereas *C. arizonica* showed a neutral growth trend over the study period (-0.04 \pm 0.04).

Climatic drivers of tree growth were different for *C. arizonica* and co-occurring pine species (Table 1; Suppl. material 1: table S3). Pine species growth was more sensitive to climatic factors than *C. arizonica* (i.e. absolute values of regression coefficients were higher and more climatic variables explained the growth of pines and, thus, were selected in the models, Table 1). In CP stands, the growth of both species was positively related to spring and summer temperatures and to winter and spring precipitations. The growth of *P. pinaster* was also positively related to autumn and winter temperatures and to summer precipitation. In CN stands, the growth of *C. arizonica* only showed a positive response to winter temperatures and summer precipitation, while the growth of *P. nigra* was positively related to winter and spring temperatures and to precipitations from winter to summer (Table 1). In CS stands, the growth of *C. arizonica* was only related to winter temperatures,



Figure 1. Mean observed (\pm SD; light colours) and predicted basal area increment (dark colours) over the period 1974–2018 for each mixed forest type and species. Black lines represent growth trends for the study period. CP: *Cupressus arizonica* and *Pinus pinaster* mixed stands; CN: *C. arizonica* and *P. nigra* mixed stands; CS: *C. arizonica* and *P. sylvestris* mixed stands.

| | CP stands | | CN stands | | CS stands | |
|-----------------------|---------------|---------------|---------------|---------------|---------------|------------------|
| | C. arizonica | P. pinaster | C. arizonica | P. nigra | C. arizonica | P. sylvestris |
| Tau | | 0.08 ± 0.03 | | | | |
| Twi | | 0.12 ± 0.04 | 0.08 ± 0.03 | 0.13 ± 0.03 | 0.11 ± 0.03 | 0.10 ± 0.03 |
| Tsp | 0.16 ± 0.05 | 0.18 ± 0.05 | | 0.08 ± 0.04 | | -0.16 ± 0.03 |
| Tsu | 0.06 ± 0.04 | 0.17 ± 0.03 | | | | |
| Pau | | | | | | |
| Pwi | 0.08 ± 0.04 | 0.18 ± 0.04 | | 0.05 ± 0.03 | | 0.05 ± 0.03 |
| Psp | 0.11 ± 0.04 | 0.16 ± 0.04 | | 0.08 ± 0.03 | | 0.08 ± 0.03 |
| Psu | | 0.13 ± 0.03 | 0.06 ± 0.03 | 0.10 ± 0.02 | | |
| R ² | 0.401 | 0.287 | 0.369 | 0.363 | 0.369 | 0.352 |

Table 1. Regression coefficients (\pm SE) of the selected tree growth model for each mixed forest type and species.

CP: *Cupressus arizonica* and *Pinus pinaster* mixed stands; CN: *C. arizonica* and *P. nigra* mixed stands; CS: *C. arizonica* and *P. sylvestris* mixed stands. T: Mean temperature; P: Total precipitation; Au: Autumn; Wi: Winter; Sp: Spring; Su: Summer. R²: Regression coefficient.

while the growth of *P. sylvestris* was related to winter and spring temperatures and precipitations. Overall, while the growth of pine species was mainly related to precipitations and winter and spring temperatures, the climatic factors controlling *C. arizonica* growth differed between mixed forest types.

Growth stability to drought events

Mean resistance (\pm SE) was 0.841 \pm 0.036 indicating that growth was reduced during the drought event around 15% compared to pre-drought growth with non-significant differences between species (Fig. 2). Even though study species showed significantly higher growth rates after than during the drought event (mean recovery was 1.443 \pm 0.080), not all species recover pre-drought growth levels. In this regard, *P. pinaster* and *P. sylvestris* showed resilience indices lower than 1 (0.962 \pm 0.007 and 0.909 \pm 0.004, Fig. 3). We found a significant species-specific effect on recovery and resilience indices in CS and CP stands, respectively (Suppl. material 1: table S4). *C. arizonica* showed higher recovery than *P. sylvestris* and higher resilience to drought in CN stands (Suppl. material 1: table S4).

Forecast growth trends

Growth models projected contrasting growth trends over the 21st century in response to climate scenarios for studied species (Figs 3, 4, 5). Overall, *C. arizonica* showed positive to neutral (i.e. non-significant slopes) growth trends, while native pine species showed neutral to negative trends over the projected periods (Suppl. material 1: table S5). Differences in growth trends between the exotic and the native species were more evident under the RCP8.5 scenario. In CP stands, *P. pinaster* showed negative growth trends during the second part of the 21st century under the RCP2.6 scenario and during the whole projected period under the RCP8.5 scenario, while *C. arizonica* showed positive and neutral growth trends (Fig. 3). In CN stands, *C. arizonica* and *P. nigra* showed similar growth rates under the



Figure 2. Boxplots of growth resistance, recovery and resilience indices to drought events over the period 1974–2018 for each mixed forest type and species. P-values show significant differences between species. Ca: *Cupressus arizonica*; Pp: *Pinus pinaster*; Pn: *Pinus nigra*; Ps: *Pinus sylvestris*. CP: *Cupressus arizonica* and *Pinus pinaster* mixed stands; CN: *C. arizonica* and *P. nigra* mixed stands; CS: *C. arizonica* and *P. sylvestris* mixed stands.



Figure 3. Mean predicted basal area increment (BAI) (\pm 95% confidence interval) over the projected period (2019–2100) for *C. arizonica* (grey) and *P. pinaster* (green) mixed forest under forcing scenarios RCP2.6 and RCP8.5. Solid and dashed black lines represent growth trends for *C. arizonica* and *P. pinaster*, respectively.



Figure 4. Mean predicted basal area increment (BAI) (\pm 95% confidence interval) over the projected period (2019–2100) for *C. arizonica* (grey) and *P. nigra* (green) mixed forest under forcing scenarios RCP2.6 and RCP8.5. Solid and dashed black lines represent growth trends for *C. arizonica* and *P. nigra*, respectively.



Figure 5. Mean predicted basal area increment (BAI) (\pm 95% confidence interval) over the projected period (2019–2100) for *C. arizonica* (grey) and *P. sylvestris* (green) mixed forest under forcing scenarios RCP2.6 and RCP8.5. Solid and dashed black lines represent growth trends for *C. arizonica* and *P. sylvestris*, respectively.

RCP2.6 scenario, but the native species showed negative trends while the exotic showed neutral ones under the RCP8.5 scenario (Fig. 4). Similarly, in CS stands, *P. sylvestris* showed negative growth trends under the RCP8.5 scenario, while *C. arizonica* showed neutral and positive responses (Fig. 5).

Discussion

Our assessment of tree performance shows that Cupressus arizonica has some advantages in growth, regeneration and survival over co-occurring native pine species. However, these advantages are species- and altitude-specific. Our results suggest that C. arizonica could outcompete drought-prone Pinus sylvestris at high elevations thanks to its lower climate sensitivity (Table 1), better growth adaptation to future climate (Fig. 5), higher growth recovery after extreme droughts (Fig. 2), higher regeneration capacity and lower mortality. At high elevations, however, P. nigra showed higher regeneration and similar growth resistance to extreme droughts than C. arizonica (Fig. 2), but negative growth trend under the RCP8.5 climate change scenario (Fig. 4). At low elevations, P. pinaster showed higher climate sensitivity (Table 1), negative growth responses to future climate (Fig. 3) and lower resilience than C. arizonica (Fig. 2). Thus, native-exotic dynamics at the study site would depend on the balance between different aspects of demographic rates and the magnitude of climate change. Yet, the generally higher performance showed by C. arizonica under different climate scenarios suggests that C. arizonica has the potential to displace native P. sylvestris and P. pinaster at high and low elevations, respectively, which point to the invasive potential of this exotic species.

Exotic species need to overcome different barriers to establish, naturalize and finally invade an ecosystem (Richardson et al. 2000). Our study relies on a wide evaluation of the performance (past, present and future) of the exotic C. arizonica in Mediterranean mountain forests co-occurring with different dominant pine species. The invasive potential of exotic species is usually assessed comparing different features between native and exotic species under common conditions (Richards et al. 2006; Castro-Díez et al. 2014; Leal et al. 2021). Higher growth rate is considered a trait promoting invasiveness, following the ideal weed hypothesis (Catford et al. 2009; Porté et al. 2012). However, the growth of exotic species can be attenuated when co-occurring with native species (Kawaletz et al. 2013). Our results showed no differences in average radial growth between exotic C. arizonica and co-occurring native pines, in contrast to previous studies comparing exotic and native trees (Rojas-Badilla et al. 2017), but in consonance with the lack of differences in growth between phylogenetically close native and introduced pine species in Central Europe (Klisz et al. 2023) and between exotic- and native-dominated stands in Mediterranean Spain (Lázaro-Lobo et al. 2023).

Nevertheless, *C. arizonica* showed some advantages in radial growth over native pine species. *C. arizonica* is considered a species well-adapted to drought (Harrington et al. 2005; Pool et al. 2013), which could favour its future persistence and spread in the study area under increased aridity. Our results support a lower growth sensitivity of the exotic species to climate than in its native counterparts. First, the number of climatic factors affecting growth are less than in native species and, overall, showed lower coefficients in the growth model, reflecting the high environmental tolerance of this exotic species (Rejmánek and Richardson 1996; Goodwin et al. 1999). Tree growth of study pine species increased with winter temperatures and winter and spring precipitation. However, at the dry edge of pine species distribution, warming can reduce tree growth by increasing water stress in late spring and early summer (Camarero et al. 2015; Marqués et al. 2018; Díaz-Martínez et al. 2023). This might be the case of *P. sylvestris*, which is considered the most vulnerable of the study pine species to drought (Galiano et al. 2010; Herrero et al. 2013;

Herrero et al. 2023) and showed a negative growth response to higher spring temperatures in our study area. Second, growth predictions in the worst greenhouse gas scenario favours the growth of the exotic species, with native pines showing negative growth trends. Previous studies comparing radial growth between native and exotic species did not find that future conditions could benefit exotic over the native species under more humid conditions (González-Muñoz et al. 2014), which suggests that differences in species' performance can be aggravated in water-limited ecosystems. In fact, annual precipitation in our study site was higher as compared to that in the native range of *C. arizonica* (e.g. southeast Arizona, Parker (1980a), https://es.climate-data.org). Finally, *C. arizonica* showed higher recovery from extreme droughts than *P. sylvestris* at high elevation and higher resilience than *P. pinaster* at low elevation. Small differences in resilience capacity to extreme droughts could increase the competitive ability of *C. arizonica* due to the expected increases in frequency and severity of extreme climatic events (IPCC 2023).

Besides radial growth, C. arizonica showed some advantages in other demographic variables. In fact, the exotic species showed higher regeneration capacity than P. pinaster at low elevations and P. sylvestris at high ones. This could be due to the higher tolerance of young seedlings to shade and drought compared to native pines (Parker 1980b; Pool et al. 2013). Although C. arizonica regeneration is associated with disturbances that increase light and remove litter, this species can also tolerate shaded conditions of forest understorey for long-time periods (Parker 1980b). This could represent a benefit in comparison to light-demanding pine saplings (Barbéro et al. 1998). C. arizonica could create a soil seed bank and, thus, take advantage of forest gaps created by disturbances. Both species, P. sylvestris and C. arizonica, regenerate well after wildfires (Parker 1980b; Spînu et al. 2020), but we observed massive regeneration of the exotic species in burnt areas within the study site. This could be advantageous for C. arizonica under climate change scenarios, in which a higher risk of wildfire occurrence is expected (Turco et al. 2018; Dupuy et al. 2020), especially in forests with high tree density and low structural heterogeneity (Stephens et al. 2010). In addition, the exotic C. arizonica was the only species showing no mortality in the study area. This could provide an advantage for C. arizonica, not only due to higher survival rate, because also its understorey seedlings could take advantage of forests gaps and release of resources created by dead trees. However, the competitiveness seems to be greater in the case of Mediterranean P. nigra (with higher regeneration capacity than C. arizonica and similar resilience to extreme droughts) than in boreo-alpine P. sylvestris. In addition, other native species, such as Q. ilex and J. communis, showed higher regeneration density in the area, which also suggests that drought tolerant and resprouting species can be favoured in the future.

Considering all the results together, the future displacement of native pines by the exotic *C. arizonica*, which is more tolerant to drought, seems plausible. At present, the exotic *C. arizonica* is considered a naturalised species in the Iberian Peninsula (Sanz Elorza et al. 2004), but it is likely that *C. arizonica* has not completely overcome abiotic and biotic barriers to successfully invade Iberian Mediterranean ecosystems (Richardson et al. 2000). Many studies of invasive plants have suggested that a "lag" time is a common feature in their population dynamics (Crooks 2005). In the study area, *C. arizonica* can be in a lag time, typically defined as a period of several years to several decades between the introduction and establishment of a species and its period of rapid geographic range expansion (invasion) (Kowarik 1995). Changes in the climate that favour *C. arizonica* over the pines could surely break this lag time.

If *C. arizonica* finally outcompetes native pine species, it could increase the size of its populations and increase its distribution area. This could boost its invasive potential and increase the chances of expanding to surrounding areas. If so, the species would move from the lag phase to the log phase or period of exponential population growth, reproduction and expansion, where management actions to reduce populations of the invasive species are less efficient and more expensive. It is important to note that, for exotic trees introduced to Europe, the average lag time is estimated at 170 years (Kowarik 1995) and that *C. arizonica* was used for afforestation in Spain during the mid-20th century. Thus, it is likely that this exotic species will be close to the end of its lag time period by the end of this century, when expected climatic conditions might increase its dominance over native species in the area. In this context, the current implementation of management actions orientated to reduce the populations of this exotic species would play a key role in controlling its invasive potential.

Conclusions

Our results present for the first time an evaluation of the invasive potential of the exotic *C. arizonica* in Mediterranean forests that integrates species' demographic rates and responses to climatic extreme and climate change scenarios. *Cupressus arizonica* showed less growth dependence to climatic variability, lower mortality and more regeneration than native pine species, which favours the naturalisation of the species and increase the probability of invasion in the study area. Climate change can also favour the invasive potential of this species by hindering the development of native ones. Compared to *P. pinaster* and *P. sylvestris*, *C. arizonica* had greater growth recovery and resilience to drought events, which gives the exotic competitive advantages over the pine species in the context of increased aridity. In addition, our forecast models stressed that *C. arizonica* may be more favoured by warmer and drier conditions in the future than native pines, which showed negative growth trends and, thus, higher vulnerability. Therefore, we recommend implementing actions to control this exotic species that can break its lag time and invade Mediterranean forest ecosystems in the near future.

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

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Author contributions

Conceptualisation: EPC, AH and EA; Investigation: EA, AH, NCM and VCA; Formal analysis and visualisation: EA and VCA; Writing – original draft: SMV and EA: Writing – review & editing: all. Funding acquisition: EA and EPC.

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Data availability

The data underpinning the analysis reported in this paper are deposited at https://dx.doi.org/10.6084/m9.figshare.24680160.

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Supplementary material 1

Can exotic tree species outcompete native ones in Mediterranean mixed forests under climate change

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Data type: docx

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Review Article

Lionfish (*Pterois miles*) in the Mediterranean Sea: a review of the available knowledge with an update on the invasion front

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Abstract

Invasive species often severely impact ecosystems and human activities in the areas that they invade. The lionfishes Pterois miles and P. volitans are regarded as the most successful invasive fishes in marine ecosystems. In the last 40 years, these Indo-Pacific predators have established in the tropical western Atlantic Ocean, with well-documented detrimental effects on the local fish communities. Around 10 years ago, a second invasion began in the Mediterranean Sea, which is being colonised by P. miles. Given the invasive potential of P. miles and the fact that the ecology and biodiversity of the temperate/sub-tropical Mediterranean Sea offer a different setting from the tropical western Atlantic, specific knowledge on this second invasion is needed. Here, we: (i) review the scientific knowledge available on the ecology of invasive lionfishes, (ii) discuss such knowledge in the context of invasion ecology and (iii) suggest future research avenues on the P. miles invasion in the Mediterranean Sea. In addition, we offer an update on the spread of *P. miles* in the Mediterranean Sea. While the history and development of the Mediterranean invasion are resolved and some mitigation plans have been implemented locally, the study of the interactions of P. miles with Mediterranean species and their impact on the local biodiversity is in its infancy. Closing this gap will lead to important fundamental insights in invasion ecology and will result in predictions on the impact of P. miles on the ecology and ecosystem services of the Mediterranean Sea. Such information will have practical implications for policy-makers aiming to devise sound and efficient mitigation plans.

Key words: Citizen science, exotic predators, invasion ecology, marine ecology, predation ecology

Introduction

Invasive species are species that establish and spread in a new range at a high rate (Ricciardi 2013), often with detrimental effects on the local ecosystems. Invasive species can cause environmental degradation (Anderson and Rosemond 2007; Ehrenfeld 2010; Villamagna and Murphy 2010), carry and spread parasites (Gozlan et al. 2005; Iglesias et al. 2015) and compete for resources with native species (Bergstrom and Mensinger 2009; Polo-Cavia et al. 2010). Amongst the most severe ecological problems associated with biological invasions is biodiversity loss through local extinction of native species. This is particularly relevant when there is a direct trophic interaction between invader and local species. For example,



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Copyright: © Davide Bottacini et al. This is an open access article distributed under terms of the Creative Commons Attribution License (Attribution 4.0 International – CC BY 4.0) invasive mammalian predators caused the extinction of more than 100 species worldwide (Doherty et al. 2016) and the invasion of Lake Victoria by the Nile perch (*Lates niloticus*) drove almost 200 endemic cichlids to extinction (Witte et al. 1992). Due to their dramatic ecological impacts, invasive species are regarded as one of the most serious environmental problems of our time (Ricciardi 2013).

The lionfishes Pterois miles and P. volitans (hereafter, referred together as 'lionfish') are virtually undistinguishable and show almost identical morphological traits (Kulbicki et al. 2012). They are considered the most invasive fishes in the marine realm; native to the Indo-Pacific Ocean and Red Sea, lionfish reached the western Atlantic Ocean through intentional or accidental releases by aquarists (Kulbicki et al. 2012; Côté and Smith 2018). Lionfish were first detected in Atlantic waters in 1985 and became a common sight at certain locations in the late 1990s (Whitfield et al. 2002; Schofield 2009). Despite considerable control efforts at the local scale (de León et al. 2013; Dahl et al. 2016; Harris et al. 2019, 2020; Goodbody-Gringley et al. 2023), lionfish have spread through the entire tropical western Atlantic and continue to expand their invasive range along the Brazilian coast (Côté and Smith 2018; Soares et al. 2022, 2023). Lionfish are generalist predators (Green et al. 2011, 2014; Green and Côté 2014; D'Agostino et al. 2020) and are having an impact on the ecosystems of the western Atlantic by preying extensively on various local benthic and demersal fishes, including endemics of high conservation value (Albins and Hixon 2008; Green et al. 2012, 2014; Benkwitt 2015; Rocha et al. 2015; Ingeman 2016). Predation by lionfish can reduce recruitment of juveniles and the biomass of local species by up to 65% (Albins and Hixon 2008; Green et al. 2012). Such marked effects on the local biodiversity have been associated with impacts on the stability of coral reef ecosystems and their degradation (Lesser and Slattery 2011). More recently, a second lionfish invasion has begun in the Mediterranean Sea (hereafter, Mediterranean), which is being colonised by P. miles (Kletou et al. 2016; Bariche et al. 2017; Phillips and Kotrschal 2021). This second invasion raises concerns on possible impacts on the biodiversity and ecosystem services of the Mediterranean (Kletou et al. 2016; Savva et al. 2020).

The Mediterranean is a unique ecosystem: it is the largest enclosed sea on Earth and a highly biodiverse basin, home to more than 11000 animal species, some of which are found nowhere else in the world (Coll et al. 2010; Psomadakis et al. 2012). For example, of the approximately 540 native species of Mediterranean fishes, around 9% are endemic (Psomadakis et al. 2012). In addition, the sea provides economically valuable services to approximately 150 million people in the numerous countries on its coasts (Coll et al. 2010). At the same time, the Mediterranean is suffering from many anthropogenic stressors (Bianchi and Morri 2000; Coll et al. 2010) and it is the most invaded sea in the world. This is largely due to the opening of the Suez Canal (Edelist et al. 2013), which was constructed in 1869 to connect the Mediterranean with the Red Sea for commercial purposes (Costello et al. 2021). Initially, there was little scope for invasions due to the small size of the Canal and the presence of bitter lakes creating a hypersaline barrier between the two seas. However, the Suez Canal has been widened multiple times in recent years, increasing its capacity to carry propagules and reducing the salinity of the bitter lakes (Edelist et al. 2013; Galil et al. 2017; Castellanos-Galindo et al. 2020). New species ('Lessepsian species') enter the Mediterranean every year and the Suez Canal is now the source of two thirds of the exotic species present in the Basin (Galil et al. 2014, 2015, 2017; Fortič et al. 2023).

There are important differences between the Mediterranean and the tropical western Atlantic. The Mediterranean is a temperate/sub-tropical sea dominated by rocky reefs, seagrass meadows and sandy patches (Bussotti and Guidetti 2011; La Mesa et al. 2011; Kleitou et al. 2021). By contrast, the tropical western Atlantic is dominated by coral reefs, similarly to the native range of lionfish (Kulbicki et al. 2012; Côté and Smith 2018). The species composition and biodiversity of the Mediterranean are also profoundly different from those found in tropical seas (Kallianiotis et al. 2000; Brokovich et al. 2006; Albins and Hixon 2008; La Mesa et al. 2011). Both invasive lionfish populations were founded by individuals that went through selection processes that might favour the survival of the resulting invasive populations in suboptimal conditions. Lionfish establishing in the Atlantic survived through the multiple stressors encountered in the aquarium trade (e.g. catching, transportation) and P. miles, establishing in the Mediterranean, survived the suboptimal water parameters encountered either in the Suez Canal or in ballast water. It is unknown how strongly these factors selected on invasive lionfish and to what extent the differences between these stressors are affecting the dynamics of the invasions today. Given the invasive potential of P. miles, their different origin from that of lionfish in the Atlantic and the different ecology and biodiversity of the temperate/sub-tropical Mediterranean, specific knowledge on this second invasion is needed. This information will be essential to understand and predict the impact of *P. miles* on the Mediterranean and to design rational and effective mitigation strategies. Here, we review the available information on lionfish ecology, we discuss such knowledge in the context of invasion ecology and highlight major knowledge gaps on the Mediterranean invasion that require future investigation. In addition, we offer an update on the distribution of lionfish in the Mediterranean, where *P. miles* are still spreading.

Lionfish in the Mediterranean

The origin and history of the Mediterranean invasion

The first lionfish ever reported in the Mediterranean was caught by a trawler off the coast of Israel in 1991 and identified as P. miles (Golani and Sonin 1992). From that moment, no more lionfish were reported until 2012, when two specimens were captured in Lebanon (Bariche et al. 2013). Soon after, lionfish were reported in Turkey, Cyprus, Greece and Italy (Turan et al. 2014; Crocetta et al. 2015; Iglésias and Frotté 2015; Oray et al. 2015; Turan and Öztürk 2015; Azzurro et al. 2017). Lionfish were first considered invasive in the Mediterranean in 2016, when they were reported in large groups and numbers in Cyprus (Kletou et al. 2016). Lionfish have now established and successfully spread through a large part of the eastern Mediterranean (Gökoğlu et al. 2017; Turan et al. 2017; Dimitriadis et al. 2020; Ulman et al. 2020; Vavasis et al. 2020) and continue to expand their range westwards (Azzurro et al. 2017; Phillips and Kotrschal 2021). Today, invasive lionfish populations are confined to the eastern part of the Mediterranean (Dimitriadis et al. 2020; Phillips and Kotrschal 2021), with only sporadic sightings elsewhere. The northernmost report of lionfish is that of a single individual found near the island of Vis, in Croatia (Dragičević et al. 2021) while the westernmost lionfish was also a single individual sighted in the Alboran Sea, Spain (Fortič et al. 2023). Since no established populations are present at these locations, the individuals in Croatia

and Spain may be the result of isolated aquarium releases. The northernmost part of the Aegean Sea has also remained free from lionfish, probably due to the colder waters (Dimitriadis et al. 2020; Phillips and Kotrschal 2021).

Genetic studies revealed that lionfish found in the Mediterranean originate from the Red Sea and that they most likely entered their new range during multiple invasion events through the Suez Canal (Bariche et al. 2017). The origin of Mediterranean lionfish is corroborated by the absence of established populations of *P. volitans* in the Basin; while both *P. miles* and *P. volitans* are often sold together in the aquarium trade (Kimball et al. 2004) and, consequently, are found in the invaded western Atlantic, genetic studies showed that only *P. miles* is present in the Red Sea (Hamner et al. 2007; Kulbicki et al. 2012; Wilcox et al. 2018). Thus, the lionfish population of the Mediterranean is considered the result of *P. miles* entering through the Suez Canal and the reports of *P. volitans* in this sea (e.g. Gürlek et al. (2016); Gökoğlu et al. (2017); Ayas et al. (2018)) are most likely the result of misidentifications or descriptions of individuals that came from isolated aquarium releases.

The northern Red Sea is inhabited by another lionfish species that is biologically and ecologically similar to *P. miles*; *Pterois radiata*. *P. miles* and *P. radiata* often occur together on the coral reefs of the northern Red Sea and in comparable abundances (Gavriel and Belmaker 2021). Interestingly, *P. radiata* has never established in the Mediterranean (Kulbicki et al. 2012; Gavriel and Belmaker 2021). It was hypothesised that *P. radiata* may be less invasive than *P. miles* due to its smaller size and slightly higher degree of habitat and diet specialisation (Kulbicki et al. 2012; Gavriel and Belmaker 2021). Comparative studies analysing behavioural, physiological and reproductive traits in a controlled environment may help elucidate what aspects are preventing *P. radiata* from becoming invasive in the Mediterranean Sea.

Tracking an ongoing invasion

P. miles entered the Mediterranean from one of its easternmost locations and continue to expand westwards and northwards (Bariche et al. 2017; Phillips and Kotrschal 2021), calling for continuous updates to pinpoint the location of their current invasion front. Citizen science, defined as the involvement of lay people in data collection, is an effective tool to track the expansion of invasive species (López-Gómez et al. 2014; Larson et al. 2020; Hermoso et al. 2021). This is especially true for species such as *P. miles*; they are appreciated by divers for their attractive morphology and colouration, increasing the chances of lay people spotting and recognising them. P. miles are also difficult to misidentify, especially in the Mediterranean, where closely-related species (i.e. native scorpionfishes) have a markedly different appearance. Finally, the awareness amongst lay people and stakeholders on the invasiveness of lionfish is high (Kleitou et al. 2021), making them attentive and willing to collaborate with scientists. Citizen science is, therefore, particularly suited to monitor the invasive range of lionfish in the Mediterranean, a sea where the diving industry is well established and dive centres are numerous (Phillips and Kotrschal 2021).

As a follow-up to Phillips and Kotrschal (2021), we contacted dive centres on the Mediterranean coast to ask whether they see lionfish during their dives and if they remember the first year that they saw them. We used a list of dive centres on

the Mediterranean coast compiled in 2021 (Phillips and Kotrschal 2021). From this list, we contacted all the dive centres that were still open and reachable via email in April 2023. In most countries, we sent emails in two languages: the first language spoken in the country and English. Translations into local languages were provided by native speakers. We sent emails in two languages to make our survey accessible to those who do not speak English fluently and to foreigners running dive centres in countries of which they do not speak the local language. Dive centres in Egypt, Albania, Montenegro, Malta and Israel were contacted only in English. We sent a reminder to every dive centre that did not respond within a week and we recorded responses for four weeks after the reminder. We used the GPS coordinates of the location of dive centres as an estimation of the point where lionfish are seen as most dives are done in the waters close to a dive centre. Any response that we received in a language different from English were translated through Google translate. When a dive centre reported a range of years as an answer to the date of the first sighting (e.g. 2020-2021), we considered the most recent year in the range as year of first sighting. Data were analysed in R 3.6.2 (R Development Core Team 2019). Maps were produced with the package 'leaflet' (version 2.0.4.1, Cheng et al. (2021)).

Contacting 996 dive centres yielded 326 responses (Fig. 1A). Sightings were reported by 82 dive centres, mostly in the eastern Mediterranean (Fig. 1B). Lionfish were seen by almost every dive centre that responded from Israel, Cyprus, Turkey, Greece and Albania. The lionfish reported at the furthest locations from the Suez Canal were reported in Croatia (42.6513°N, 18.0608°E), Malta (35.9500°N, 14.4063°E) and the Italian islands of Sicily (36.7330°N, 15.1205°E) and Sardinia (40.5699°N, 8.2430°E). When compared with the results by Phillips and Kotrschal (2021) (Fig. 1C), our data show that, in just two years, lionfish have expanded their invasive range in the Mediterranean at two fronts: the northern Aegean Sea and the southern Adriatic Sea. While most of the dive centres reported no lionfish in 2021 in the northern part of the Aegean, they almost all did in 2023; the only two dive centres reporting no lionfish in the northern Aegean were also the ones with the northernmost coordinates. A limited expansion can be seen also in the southern Adriatic, where two dive centres reported lionfish sightings in 2023, while none did in 2021.

The years and locations where lionfish were first seen (Fig. 2) corroborate an expansion of the lionfish invasive range in the Mediterranean. Lionfish were first seen in the northern Aegean, Ionian Sea and southern Adriatic between 2020 and 2022. Individuals in Sicily, Sardinia, Croatia and Malta were also seen only in the most recent year range. This suggests that lionfish found at these locations are probably not just the results of aquarium releases; if that was the case, we could have also expected reports in the past. More likely, these individuals have been transported by strong currents from the eastern Mediterranean, either as larvae or eggs. It is important to note that none of the dive centres reporting lionfish in Malta, Italy and Croatia provided pictures and, therefore, misidentification is still a possibility for these sightings. The dive centres reporting sightings at these locations confirmed that there are no established lionfish populations there.

Our results show that the invasive range of *P. miles* continues to expand rapidly in the Mediterranean. Similar to most coral reef fishes, lionfish eggs hatch into pelagic larvae (Ahrenholz and Morris 2010; Vásquez-Yeomans et al. 2011). Larvae are the life stage with the highest dispersal potential in coral reef fishes (Shanks 2009)



Figure 1. Maps of respondents and lionfish sightings. Panel **A** shows the respondents to our survey in 2023. Each dot represents a dive centre that we contacted, with orange dots representing dive centres that responded and black dots representing dive centres that did not. Panel **B** shows the responses to our survey in 2023. Each dot represents a dive centre that responded to our survey in 2023 with orange dots representing dive centres that reported lionfish sightings and black dots representing dive centres that reported no sightings. Panel **C** shows the responses to the survey in 2021 (Phillips and Kotrschal 2021). Each dot represents a dive centre that responded to the survey in 2021 with orange dots representing dive centres that reported no sightings.

and are arguably the main contributor to the dispersal of lionfish, which are highly site-attached as adults (McCallister et al. 2018; Gavriel et al. 2021; Phillips et al. 2024). The Mediterranean invasion is following a similar course to that of other Lessepsian species, which typically expand in the Mediterranean starting from the Levantine Sea and gradually spread westwards and northwards towards the Aegean and Ionian Sea (Azzurro et al. 2013).

Many Lessepsian species remain confined to the eastern Mediterranean and are rarely found in high numbers elsewhere (Azzurro et al. 2013; Galil et al. 2017). A modelling study (Johnston and Purkis 2014) predicted that lionfish were unlikely to become invasive in the Mediterranean. However, our and others' (Azzurro et al. 2017; Phillips and Kotrschal 2021) empirical evidence suggests that the lionfish population of the Mediterranean is well-established and keeps expanding westwards. One of the reasons for the unpredicted success of lionfish could be that their invasion is developing under a strong effect of climate change.



Figure 2. Map of years of first sighting. Each dot represents a dive centre that reported lionfish sightings, either in 2021 or 2023 and included in their response the year when lionfish were first sighted. The darkness of dots shows the year range when lionfish were first sighted.

When climate change is accounted for (Loya-Cancino et al. 2023), lionfish are predicted to find suitable conditions in the Mediterranean. Another reason could be that Johnston and Purkis (2014) considered that lionfish only spread as larvae under the action of natural currents and, because the Mediterranean is less connected by internal currents than the Atlantic, they concluded that lionfish are unlikely to spread across the whole Mediterranean. Although larvae are probably the phase at which lionfish move over long distances, adults can enter new areas as happened recently in Brazil, where lionfish managed to cross the Amazon-Orinoco plume, most likely by adults moving along deeper mesophotic reefs (Soares et al. 2022, 2023). Additionally, the Mediterranean is highly trafficked and this could allow lionfish larvae or eggs to cross large stretches of sea independently from currents if they enter the ballast water. It will be challenging to disentangle the effects of the factors contributing to the unpredicted success of lionfish in the Mediterranean, as multiple phenomena are at play without possibilities to manipulate them.

Remarkably, several *P. miles* sightings were reported in areas that were considered to have winter surface temperatures that are too cold for this species (< 15 °C) such as the northern Aegean and southern Adriatic (Kimball et al. 2004; Johnston and Purkis 2014; Dimitriadis et al. 2020). Although it is too early to conclude that *P. miles* will establish at these locations, climate change has been predicted to facilitate the expansion of tropical invasive species' ranges in the Mediterranean and other ecosystems (D'Amen and Azzurro 2020). Climate change is resulting in a gradual process of 'tropicalisation' of the Mediterranean; the biological community composition is shifting in favour of Lessepsian species at the cost of native ones (Giorgi 2006; Galil et al. 2017). This has already resulted in Lessepsian fishes outweighing and outnumbering native ones in marine protected areas of the eastern Mediterranean (Giakoumi et al. 2019). Another major difference between the Mediterranean and the Red Sea is the stronger seasonality of the former. It remains unknown how the seasonality of Mediterranean waters affects the dynamics and distribution of lionfish and other invasive species of tropical origin.

Our study shows that citizen science is a fruitful approach to monitor lionfish populations at the large scale in the Mediterranean, where the dive industry is strong and awareness towards lionfish is high. Different approaches are needed to monitor the state of the invasion on the southern coasts of the Mediterranean, where data are lacking and the number of dive centres is extremely low (Fig. 1A). When we contacted members of a Libyan spearfishing association through social media, they reported seeing lionfish relatively frequently on the (eastern) Libyan coast. Moreover, lionfish were reported at several locations on the southern coast of the Mediterranean in the past, including Tunisia (Dailianis et al. 2016; Al Mabruk and Rizgalla 2019). This suggests that, as expected, the lionfish invasion and its expansion are not limited to the northern coast of the Mediterranean.

The evolutionary ecology of invasive lionfish across ranges

Lionfish morphology and habitat use

Lionfish have 18 venomous spines; one on each of the first 13 rays of their dorsal fin, one on each of their pelvic fins and three on their anal fin (Aktaş and Mirasoğlu 2017). They show high site fidelity and often return to the same hiding place over the course of several weeks (McCallister et al. 2018; Gavriel et al. 2021; Phillips et al. 2024), although this can vary significantly at the individual level (Tamburello and Côté 2015; Gavriel et al. 2021). Lionfish are often found, either individually or in small groups, hiding in caves and crevices during the day and swim in the open only at dawn and dusk to hunt for prey (Cure et al. 2012; McCallister et al. 2018; D'Agostino et al. 2020; Gavriel et al. 2021). The eastern Mediterranean offers a markedly different habitat from the coral reefs of the Indo-Pacific and the tropical Atlantic (Kulbicki et al. 2012; Côté and Smith 2018). The Mediterranean is a sub-tropical environment dominated by rocky reefs, seagrass meadows and sandy patches (Bussotti and Guidetti 2011; La Mesa et al. 2011; Kleitou et al. 2021). Despite these habitat differences, P. miles have established well in the Mediterranean and have already reached higher population densities than in their native range (Kulbicki et al. 2012; Phillips et al. 2024). It is perhaps not surprising that *P. miles* are thriving in the eastern Mediterranean as, in the western Atlantic, lionfish have been reported in habitats that are novel for this species, including mangrove forests, river estuaries and seagrass beds (Barbour et al. 2010; Jud et al. 2011; Claydon et al. 2012). Analyses of the population structure and dissections of females indicate that the Mediterranean population of P. miles is reproducing and will remain a stable presence (Savva et al. 2020; Mouchlianitis et al. 2022).

Predation ecology

Fishes make up most of the lionfish diet (Barbour et al. 2010; Harms-Tuohy et al. 2016; Zannaki et al. 2019), although they have been reported to also feed on invertebrates (Valdez-Moreno et al. 2012). Lionfish are stalking, gape-limited predators: they slowly follow their prey, sometimes for several minutes, with flared pectoral fins before striking and swallowing them whole (Green et al. 2011; Green and Côté 2014). They tend to prefer small, shallow-bodied benthic and demersal fishes in the Caribbean (Green and Côté 2014; Ritger et al. 2020) and show a similar prey preference in the Mediterranean, where they also adopt the same hunting strategy (Zannaki et al. 2019; D'Agostino et al. 2020). In their native range and the invaded Atlantic, lionfish are a widespread component of the community of coral reef predators (Lesser and Slattery 2011; Cure et al. 2012; Kulbicki et al. 2012; Côté and Smith 2018). In the Atlantic, *P. volitans* can have strike success rates as high as 85%, the highest reported in animals in the wild (Vermeij 1982; Green et al. 2011).

The high predation effectiveness in their invaded range has been attributed, at least in part, to prey naïveté (Côté and Smith 2018) (but see Cure et al. (2012)). The 'naïve prey hypothesis' (or 'prey naïveté hypothesis') posits that prey that are exposed to an exotic predator are not prepared to recognise or effectively react to it due to a lack of co-evolutionary history (Sih et al. 2010). Numerous studies support the relevance of prey naïveté in the lionfish invasion in the Atlantic. For instance, several prey species do not react to lionfish with the same readiness as they do with native predators (Anton et al. 2016; McCormick and Allan 2016; Haines and Côté 2019, but see Marsh-Hunkin et al. 2013). In the eastern Mediterranean, exotic prey species from the Red Sea, which co-evolved with *P. miles*, are abundant and occur together with Mediterranean prey. Exotic prey show a markedly higher flight initiation distance when a lionfish is approaching them compared to Mediterranean invasion (D'Agostino et al. 2020).

Experiments on prey naïveté in the context of lionfish invasions raise the question of whether the selection pressure posed by this new predator will result in adaptations in local prey. It follows from the definition of prey naïveté that it can be counteracted by evolutionary adaptation: after several generations of co-existence with a novel predator, prey should evolve innate responses (Anton et al. 2020). However, how rapidly can such evolutionary adaptations evolve in prey? This is an unresolved question: some estimates based on data on multiple taxa suggest that hundreds of generations are needed (Anton et al. 2020), while there is evidence showing that 10–30 generations can be enough for predators to drive evolutionary changes in prey (O'Steen et al. 2002; Nunes et al. 2014; Melotto et al. 2020). The great variability in the number of generations needed for local prey to evolve an innate response to predators is probably explained by factors such as the pressure posed by predators and the genetic variability of prey populations (Nunes et al. 2014). The potential for prey to adapt to a new predator such as lionfish is of high scientific relevance, but also has practical implications because it will determine the long-term effects on the local prey communities of the Mediterranean and western Atlantic. In an experiment in the western Atlantic (Kindinger 2015), the antipredator response of damselfish (Stegastes planifrons) to P. volitans was measured and compared to that displayed against a control, native predator. Damselfish were generally naïve to P. volitans, including individuals from populations that had co-existed with lionfish for three and seven years (Kindinger 2015). Local adaptation by prey to P. miles has never been tested in the Mediterranean.

Prey naïveté interferes with innate predator recognition in animals (Sih et al. 2010; Anton et al. 2020). However, this is not the only mechanism resulting in prey reacting to a predator. Individual fishes can learn which species can pose a threat to their survival through associative learning (Kelley and Magurran 2003). Predator recognition can be learned either directly, when a fish escapes an attack from a predator or indirectly when an individual observes predation events or associates the presence of a predator with the presence of danger-related cues (e.g. blood, stress pheromones) from other fishes (Brown 2003). Learned predator recognition is pervasive in fishes (Brown 2003; Kelley and Magurran 2003; Mitchell et al. 2011); prey fishes can learn to associate danger cues with the presence of a predator during a single conditioning event and retain a behavioural response to that predator for extended periods of time (Chivers and Smith 1994, 1995; Mitchell et al. 2011). Could native prey fishes compensate for their lack of innate

responses to lionfish through learned predator recognition? This is an open question for both the Mediterranean and the Atlantic invasion. Specific work on how well prey species learn that lionfish pose a threat to their survival is limited to one study on a species from the native range of lionfish. This study suggests that even prey that co-evolved with lionfish seem to have difficulties associating them with danger, while other predatory fishes can be learned more readily (McCormick and Allan 2016). This has led to the hypothesis that lionfish circumvent learned predator recognition mechanisms in prey (Côté and Smith 2018). Whether Mediterranean or western Atlantic prey can learn to recognise lionfish as predators is currently unknown and more research is needed to test for the relevance of circumvention of learned predator recognition in lionfish prey.

Predator recognition allows prey to mount an appropriate behavioural response to a predator. Therefore, invasive lionfish are predicted to select on traits that make prey better able to recognise them, either innately or through learning. However, predators can also select on prey behavioural traits that make them less likely to be preyed on due to processes that are not related to predator recognition (Blake and Gabor 2014; Belgrad and Griffen 2016). For example, boldness affects the susceptibility of mud crabs (Panopeus herbstii) to be preyed on, creating the potential for predators to select for boldness in this species. Interestingly, boldness has a different effect on susceptibility to predation depending on the predator: toadfish (Opsanus tau) consumed more frequently shy mud crabs, while blue crabs (Callinectes sapidus) consumed more frequently bold mud crabs (Belgrad and Griffen 2016). This is due to major differences in the hunting strategies of the two predators. In the context of lionfish invasions, individuals of small, benthic fishes that are bolder or simply more active at dusk or dawn can be predicted to be at a higher risk of predation. This is because lionfish hunt at twilight and show a preference for benthic and demersal prey (Cure et al. 2012; Green and Côté 2014; McCallister et al. 2018; D'Agostino et al. 2020; Ritger et al. 2020). We can, therefore, expect lionfish to select for prey individuals whose activity peaks do not coincide with peaks in lionfish hunting and that are, overall, less active or hide more in their hiding spots. This could lead to changes in the behaviour of populations of native fishes in the invasive ranges of lionfish. Whether such selection pressure is at play in the context of lionfish invasions and any consequences on prey populations has never been investigated.

Natural enemies

The 'enemy release hypothesis' posits that exotic organisms benefit from reduced top-down control due to a paucity of natural enemies in their newly-invaded ranges (Colautti et al. 2004). The success of lionfish as invaders has been attributed to a lack of natural predators in the areas that they invade (Côté and Smith 2018). However, the natural enemies and source of mortality of lionfish in their native range remain unknown. It seems unlikely that any predator feeds consistently on the venomous and spinous adult lionfish and events of predation remain sporadic and anecdotal, both in their native and invaded ranges (Côté and Smith 2018). The cornetfish *Fistularia commersonii* and the groupers *Epinephelus striatus* and *Mycteroperca tigris* have been reported to feed on lionfish (Bernadsky and Goulet 1991; Maljković et al. 2008). There is also indication that large groupers may act as biological control agents in the Caribbean (Mumby et al. 2011), although large-scale studies suggest that lionfish density does not correlate with that of groupers

(Hackerott et al. 2013). In the Mediterranean, the only convincing example of predation is that of an octopus (*Octopus vulgaris*) filmed while catching and carrying a lionfish in Cyprus (Crocetta et al. 2021). The scarce knowledge on lionfish predators limits any conclusions on the importance of relaxed predation as an explanation for the high invasiveness of lionfish.

There are other factors than reduced predation on adults that could explain the large population sizes that lionfish reach in their invaded ranges. First, parasites, rather than predators, could be limiting the fitness of adults in their native range (Tuttle et al. 2017). This is supported by data from studies that found relatively low numbers of parasites on invasive lionfish in the Atlantic compared to conspecifics in the native Indo-Pacific (Loerch et al. 2015; Sellers et al. 2015; Tuttle et al. 2017). Such comparisons have not yet included Mediterranean lionfish. Second, a main source of mortality for coral reef fishes is predation at or soon after settlement (Carr and Hixon 1995; Webster 2002; Almany and Webster 2006). Predation on larvae and recruits could, therefore, be the main source of mortality for lionfish (Phillips and Kotrschal 2021). Lionfish larvae are pelagic and probably less defended than the adults (Kitchens et al. 2017) and could be prey of plankton feeders before settlement on the reef and small demersal predators at settlement (Phillips and Kotrschal 2021). Relaxed predation on larvae and recruits could explain the lionfish population increase in their invaded ranges if there were a lower abundance of plankton feeders and predators than in their native range. However, there are no studies comparing the mortality of lionfish recruits between their invasive and native ranges and hypotheses involving lionfish at these stages are difficult to test since spawning in *P. miles* and *P. volitans* has never been described (Côté and Smith 2018).

Impact on invaded ecosystems

The high effectiveness of lionfish as predators implies that they are a potential threat to the native fish community of the areas that they are invading. *P. volitans* are, indeed, having a profound impact on the fish community of the western Atlantic, where they prey heavily on numerous species of very high conservation value (Rocha et al. 2015; Ingeman 2016; Côté and Smith 2018). Invasive *P. volitans* can dramatically reduce the biomass of local species in the Atlantic (Albins and Hixon 2008; Green et al. 2012, 2014), with hypothesised effects on the stability of coral reef ecosystems (Lesser and Slattery 2011). The impact of *P. miles* on the Mediterranean biodiversity has received little consideration. Preliminary assessments suggest that lionfish are reducing the abundance of certain native species and are, therefore, altering the community composition of the Mediterranean (Turan and Doğdu 2022). However, experiments directly linking *P. miles* density with the densities of Mediterranean species are currently lacking.

Interactions with humans and control efforts

The high predation rates shown by lionfish raised concerns on their potential effects on economically valuable species and the fishing industry of the Mediterranean (Kleitou et al. 2019a). It is now well-established that *P. miles* do feed on economically valuable species such as blotched picarels (*Spicara spp.*) and Mediterranean parrotfish (*Sparisoma cretense*) (Zannaki et al. 2019; D'Agostino et al. 2020; Savva et al. 2020). However, specific studies on the impact of lionfish on fisheries are completely lacking, both in the western Atlantic and Mediterranean. Such studies are difficult to conduct as they necessitate large areas and fish stocks are simultaneously subject to many other stressors such as overfishing, climate change and invasive species other than lionfish (Coll et al. 2010). In addition, the possibility of estimating the impacts of lionfish on Mediterranean fisheries is limited by the lack of knowledge on large-scale effects of *P. miles* on the Mediterranean biodiversity.

Lionfish are venomous and reach large population sizes in their invaded ranges (Kulbicki et al. 2012; Aktaş and Mirasoğlu 2017). Consequently, an additional concern around their invasions is that they could become a danger for bathing tourists and divers (Kosker and Ayas 2022). However, lionfish cannot actively sting; the direction of the spines on the body of a lionfish (bending backwards when the fish is swimming forward) does not allow them to actively attack and sting as wasps or bees do. Therefore, unless they are touched with sufficient pressure, it is unlikely that lionfish spines can penetrate human tissues. Moreover, lionfish tend to move away when a swimmer approaches them closely underwater (Côté et al. 2014). This is probably why only few events of envenomation have been reported in the wild, both in the Mediterranean and western Atlantic. On the other hand, most of the envenomation cases reported in the United States were the result of aquarists manipulating lionfish or doing aquarium maintenance at a close distance from lionfish spines and touched them accidentally (Kosker and Ayas 2022). Similarly, although there is no systematic analysis on lionfish-related accidents in the Mediterranean, most of the cases reported in Cyprus involve people (usually fishermen) directly manipulating lionfish out of the water (Jimenez 2021, personal communication).

Lionfish are highly sedentary and easy to identify by divers due to their conspicuous appearance. This resulted in the involvement of lay people in initiatives aimed at curbing lionfish populations through spearfishing. In so-called 'culling tournaments' (or 'derbies'), divers are encouraged to hunt for lionfish by means of spear-guns (often simpler Hawaiian slings) while free or SCUBA diving (Kleitou et al. 2021). Fishing for lionfish has been incentivised by attempts to create a market for lionfish-derived products such as meat or jewellery (Kleitou et al. 2019b; Simnitt et al. 2020). While jewellery will probably remain a niche product, lionfish meat is appreciated for its taste and increasingly served in local restaurants in the invasive ranges of lionfish (Morris et al. 2011; Simnitt et al. 2020). Culling initiatives were shown to be an effective way of limiting lionfish populations at small scales in the western Atlantic and have the potential to become a management tool with beneficial effects on the conservation of local species (de León et al. 2013; Green et al. 2014; Dahl et al. 2016).

Culling tournaments were organised in the Mediterranean soon after the start of the invasion (Kleitou et al. 2021). Although culling can be effective at the local scale, eradication of lionfish from their invaded ranges is considered impossible for three reasons. First, the effort of having to actively spear-fish for lionfish is high and limits the areas that can be covered in culling tournaments (de León et al. 2013; Malpica-Cruz et al. 2016; Kleitou et al. 2021). Second, culling initiatives are restricted to relatively shallow waters (0–40 m), while invasive lionfish can live in much deeper waters, with large aggregations spotted even beyond 300 m of depth (de León et al. 2013; Nuttall et al. 2014; Gress et al. 2017; Rocha et al. 2018). Third, lionfish adjust to the hunting pressure posed by spear-fishers by becoming more wary towards approaching divers, decreasing the effectiveness of repeated culling initiatives in the same areas (Côté et al. 2014). Culling should, therefore, be seen as a containment measure, rather than a definitive solution and should be focused on areas of high ecological interest.

Future research avenues

The history and development of the lionfish invasion in the Mediterranean are well-resolved and can be updated promptly through citizen-science initiatives involving the aware and collaborative local dive centres (Phillips and Kotrschal 2021). Our update shows that *P. miles* keep expanding westwards and northwards and are also establishing in waters that were considered too cold for them to live in. Future initiatives should keep monitoring the invasion front as *P. miles* can be expected to continue expanding. Such initiatives should consider approaches that include the southern coast of the Mediterranean. The high awareness of the lay public to the problem of invasive *P. miles* in the Mediterranean resulted in the organisation of successful control initiatives at an early stage of the invasion process (Kleitou et al. 2021). While these initiatives can certainly have beneficial effects at the local scale and contribute to raise awareness towards the major problem of biological invasions, eradication of invasive lionfish is considered impossible.

Studies on the predation ecology of *P. miles* in the Mediterranean remain scant, especially in comparison with the large body of literature available on the Atlantic invasion (Côté and Smith 2018). P. miles are thriving in the eastern Mediterranean and are feeding extensively on local fishes of ecological and commercial value (Zannaki et al. 2019; D'Agostino et al. 2020; Savva et al. 2020). However, the community-level impact of *P. miles* on the local biodiversity remains unknown. This is a major knowledge gap for ecologists and policy-makers alike. While assessing the effect of invasive lionfish on the productivity of local fisheries is challenging due to the large scales needed and many confounding factors, it is possible to experimentally measure community-level effects of predation by lionfish (Albins and Hixon 2008; Green et al. 2012, 2014). This could be done through a long-term field experiment monitoring the fish community of the Mediterranean and how it varies depending on the lionfish density and time of invasion. Such experiment would benefit from a manipulative component, where the lionfish density is controlled in experimental patches through culls and the fish community is monitored before and after removals (Albins and Hixon 2008; Green et al. 2012). A control (i.e. unculled patches) can be used to account for natural variation and changes in community composition due to seasonality in the Mediterranean.

Prey naïveté is a contributor to the success of lionfish in the Atlantic and Mediterranean, where native prey show virtually no response to this new predator (Anton et al. 2016; D'Agostino et al. 2020). This raises the question of how long it will take local prey to adapt to this new predator through evolutionary change. Invasive lionfish offer an opportunity to test for local adaptations in marine ecosystems, where adaptations to new predators are particularly understudied (Anton et al. 2020). While the high connectivity of marine systems was traditionally thought to limit the possibilities of local adaptations in marine fishes, increasing evidence is suggesting that local adaptation is widespread in marine systems (Anton et al. 2020). The ongoing Mediterranean invasion offers the potential to work with prey populations that have co-existed with lionfish for different lengths of time. This is because many Mediterranean fishes are distributed across the whole Basin and lionfish are only present in its eastern part (Phillips and Kotrschal 2021). Individuals from prey populations that co-existed with lionfish for different lengths of time (from 0 to about 10 years) could be studied in a laboratory setting for their reaction towards an approaching lionfish. Individuals from populations that co-existed with lionfish for longer are expected to show stronger behavioural responses to an approaching lionfish. A major limitation is that, because prey can only be wild-caught, it would be impossible to disentangle the relative effects of innate and learned predator recognition in prey reacting to lionfish.

Individual prey fishes have the potential to learn that lionfish are dangerous through associative learning, even in the absence of co-evolutionary history (Brown 2003; Kelley and Magurran 2003). This would give prey an opportunity to rapidly adjust to the presence of a new predator. The only study conducted on learned predator responses to lionfish suggests that it is more difficult for prey to learn that lionfish are dangerous compared to other predators (McCormick and Allan 2016). The alleged ability of lionfish to circumvent learned predator recognition in their prey raises the intriguing question of how they do so. We hypothesise that any difficulty in prey learning that lionfish are dangerous might be linked to their unique morphology. According to the hypothesis of 'prepared fear conditioning', fears are acquired more easily and persist for a longer time if the conditioner is an object that had an impact on the survival of the ancestors of a species (Öhman and Mineka 2001). As lionfish look remarkably different from other fish predators such as snappers, groupers and barracudas (Marshall et al. 2019), prey may be less prepared to associate them with danger. The relevance of this hypothesis in the predation ecology of lionfish could be tested by training naïve (i.e. captive-born) prey to recognise lionfish and other predators as dangerous. This can be done by pairing visual presentations of predators with alarm cues (Brown 2003) and can be followed by similar experiments based on video presentations of real predators and 3D animated models (Johnson and Basolo 2003; Fischer et al. 2014; Scherer et al. 2017; Watve and Taborsky 2019). The use of models shown on screens will allow for changes in the morphology of an approaching lionfish, disentangling which aspects of their morphology and movement contribute the most to their alleged interference with learned predator recognition.

Another major question on the ecology of lionfish, both in their native and invaded ranges, is what their main source of mortality is (Phillips and Kotrschal 2021). This is an important question which could help explain why lionfish reach such high population densities in their invaded ranges. It seems unlikely that any predators feed consistently on adult lionfish because they are well defended by venomous spines and reports of predation events are extremely rare (Côté and Smith 2018). Parasites have been shown to be more abundant on lionfish in their native range compared to the Atlantic, but it is unknown to what extent such parasites exert a control on lionfish population densities (Loerch et al. 2015; Sellers et al. 2015; Tuttle et al. 2017). On the other hand, studies on lionfish parasites in the Mediterranean are entirely lacking. Finally, lionfish could be preyed upon while in their larval or recruit stage, but it is challenging to catch lionfish in high numbers before they are juveniles of a few centimetres in length. This is a critical limitation in the possibilities of directly testing the suitability of lionfish to the diet of plankton feeders (Ahrenholz and Morris 2010; Vásquez-Yeomans et al. 2011). To test any hypotheses on the effects of filter feeders, it would be necessary to have access to lionfish larvae or eggs, which is currently impossible as they have never been observed spawning (Côté and Smith 2018). However, it is possible to investigate the effects of parasites on lionfish with different approaches. A starting point could be a survey on the parasite load of lionfish fished from the Mediterranean Sea. Such data, combined with the available information from other ranges (Loerch et al. 2015; Sellers et al. 2015; Tuttle et al. 2017), would also ensure that any follow-up manipulative experiments are done with realistic parasite loads. Experimental manipulation of parasite load will reveal how parasites impact lionfish behavioural and physiological traits (Timi and Poulin 2020; Hvas and Bui 2022).

Conclusion

While the history and development of the *P. miles* invasion in the Mediterranean are well-resolved and can be easily updated through citizen-science initiatives, the study of the predation ecology of invasive *P. miles* is its infancy, especially at high ecological levels. In addition, the ongoing lionfish invasion in the Mediterranean offers the opportunity to test for major fundamental questions on prey naïveté and learned predator responses. We outlined approaches that could be used to answer these major questions by taking advantage of the ongoing and more recent lionfish invasion in the Mediterranean. Tackling questions such as the community-level impact of lionfish in the Mediterranean and the evolutionary and learned responses in prey will add to the body of knowledge on the best documented invasion in marine ecosystems. This will result in insights into fundamental questions in invasion and predation ecology, but will also be important for policy-makers to estimate the impact of invasive lionfish on human activities.

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

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Author contributions

D.B. and A.K. conceived the study. D.B. collected the data. D.B. analysed the data and wrote the first version of the manuscript. All authors (D.B., B.A.J.P., R.N., P.A.J., M.N. and A.K.) provided feedback on earlier versions of the manuscript and contributed to its final version.

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Data availability

All of the data that support the findings of this study are available in the main text.

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Research Article

Intra-lake origin and rapid expansion of invasive pelagic threespined stickleback in Lake Constance

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Abstract

The rapid expansion of three-spined stickleback (*Gasterosteus aculeatus* Linnaeus, 1758 (Perciformes, Gasterosteida)) in the pelagic zone of Lake Constance, Central Europe, since 2012 contributed to stark ecosystem-wide effects, such as food-web shifts and declines in native biodiversity, including commercially important fish species. Yet, the origin of this invasive pelagic population remains unclear. Using RAD-sequencing of Lake Constance sticklebacks, we show that the pelagic Lake Constance population likely arose recently within the lake, potentially from the littoral population. We did not detect any substantial genome-wide genetic differentiation between individuals from different habitats, supporting a recent origin of the pelagic population and/or ongoing gene flow. This is further supported by minimal differences in meristic and morphometric traits. However, we also identified multiple outlier loci between littoral and pelagic individuals across the genome, potentially suggesting early signs of adaptation despite high connectivity. In this study, we provide an important example of rapid within-lake ecological diversification of an invasive species from standing genetic variation. Ultimately, our findings will have major implications for the management of invasive pelagic stickleback, as they indicate that the stickleback population has to be managed as a whole and that management efforts cannot only focus on the hyper-abundant pelagic population.

Key words: Genomics, invasion, pelagic, RAD-seq, three-spined stickleback

Introduction

The introduction and establishment of non-native species into novel habitats pose a serious threat to endemic biodiversity, ecosystem and human health globally (Bax et al. 2003; Mainka and Howard 2010). Freshwater ecosystems have been particularly affected by the abiotic and biotic effects of invasive species (Darwall et al. 2018), where the rate of species loss has exceeded those observed in terrestrial systems (Ricciardi and Rasmussen 1999; Albert et al. 2021). Invasive species may harm native fauna and ecosystems indirectly by altering habitat conditions (Crooks 2002; Strayer 2010) or directly through biotic interactions that have cascading effects throughout the food web (Gallardo et al. 2016). Significant community-wide consequences might manifest also due to the evolutionary isolated and at times



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species-deprived states of freshwater systems (Cox and Lima 2006), particularly in isolated, oligotrophic pre-alpine lakes where species may be vulnerable due to their lack of adaptation to invaders (Moyle and Light 1996; Ros et al. 2019).

Lake Constance in Central Europe represents such a system; a large pre-alpine, oligotrophic lake, where the introduction of invasive three-spined stickleback (Gasterosteus aculeatus Linnaeus, 1758) has contributed to substantial ecosystem-wide changes (Gugele et al. 2020). While the exact origins of sticklebacks in Lake Constance are still under debate (Marques et al. 2019; Berner 2021; Hudson et al. 2021), this small fish species was likely introduced around 150 years ago either deliberately or unintentionally into adjacent streams and ponds (Muckle 1972). However, sticklebacks were first recorded in Lake Constance itself in the mid-20th century, where they spread throughout the nearshore environment within a few years (Roch et al. 2018) and have been present in moderate abundance ever since. The stickleback distribution drastically changed in late 2012 with a sudden increase in abundance in the pelagic zone of Upper Lake Constance (Alexander et al. 2016; Rösch et al. 2018; Eckmann and Engesser 2019); small fish density in the pelagial increased from about 420 \pm 145 (individuals ha⁻¹, mean \pm standard deviation) between 2009 and 2011, to 2550 \pm 800 in late 2012 and early 2014 and, ultimately, to 5300 \pm 1970 from late 2014 to 2018 (Eckmann and Engesser 2019). Thus, while sticklebacks might have been present in low numbers in the pelagic zone following the colonisation of the Lake, they likely started occupying and expanding into the pelagic zone only around 10 years ago (Hudson et al. 2021). The question of the causes of the sudden invasion and the subsequently stark increase in abundance, has not yet been answered conclusively. Baer et al. (2024) suggested that the decreasing density of the pelagic fish community, which was originally dominated by native whitefish (Coregonus wartmanni Bloch, 1784), led to a decrease in interspecific competition. The high availability of essential fatty acids (EFA) in the pelagic zone, which are limited in the littoral, likely triggered sticklebacks to expand into this opening niche and increase their abundance (Baer et al. 2024). As a result, the pelagic fish community rapidly changed and sticklebacks made up 95% after only two years (Alexander et al. 2016). This was accompanied by a drastic decline in whitefish fisheries yields by 50% in 2015 (Rösch et al. 2018) and a near collapse in 2022 with a more than 90% decline, representing by far the lowest value since the start of records in 1910 (www.ibkf.org). The loss of whitefish biomass is thought to be caused by sticklebacks being strong competitors for food (Bretzel et al. 2021; DeWeber et al. 2022; Ogorelec et al. 2022a, 2022b) and by predation on whitefish eggs and larvae (Roch et al. 2018; Ros et al. 2019; Baer et al. 2021) which appear to lack adaptive predator avoidance compared to other lake species (Ros et al. 2019). The increased pelagic stickleback abundance might cause further cascading effects through the food-web by shifting the species composition of pelagic zooplankton (Ogorelec et al. 2022a) and changing densities and migration patterns of stickleback-feeding birds (Werner et al. 2018). While these circumstances resemble those in the Baltic Sea, where a recent surge in native stickleback abundance has significantly affected the food web and recruitment of native fish species (Bergström et al. 2015; Byström et al. 2015; Eklöf et al. 2020), such hyper-abundance of three-spined sticklebacks in a large oligotrophic lake is rare, even more so in pelagic waters, which represent an unusual habitat for this species (Erickson et al. 2016).

Lake Constance three-spined sticklebacks provide an excellent opportunity to study the processes and ecosystem-wide effects of freshwater invasions and they have long been used as a model system for studying contemporary evolution across ecological niches (Hudson et al. 2021). Littoral and stream stickleback populations have rapidly diverged (Laurentino et al. 2020) and show substantial phenotypic variation in a range of foraging and defensive traits (Arnegard et al. 2014; Lucek et al. 2014; Schmid et al. 2019) and body size (Sharpe and Räsänen 2008). The lakestream divergence might have been facilitated by introgression of ancient Eastern and Western European lineages via secondary contact in the Lake Constance region (Marques et al. 2016, 2019). However, there is no clear evidence for the origin and drivers of the pelagic stickleback expansion in Lake Constance (Baer et al. 2022; Ogorelec et al. 2022a), although deficiencies in essential fatty acids in the littoral habitat might provide a potential explanation (Baer et al. 2024). It remains untested whether the open-water stickleback populations: i) have evolved in sympatry from the littoral population, ii) if littoral and pelagic populations form genetically distinct groups and iii) if there are genetic changes associated with the rapid pelagic expansion.

This study aims to gain a better understanding of the evolutionary origin of the pelagic three-spined stickleback population in Lake Constance. Using Restriction-site Associated DNA (RAD) sequences, we investigated whether pelagic sticklebacks are genetically distinct from the littoral and tributary (here referred to as 'inflow') sticklebacks. Population genetic analyses were complemented by morphological analyses. Overall, this study provides important insights into the potential of an invasive species to rapidly colonise and/or expand into novel habitats, which will directly inform the management of invasive pelagic stickleback in Lake Constance and comparable waterbodies, such as the Eastern Baltic Sea.

Material and methods

Sampling

Sampling took place in Upper Lake Constance, Germany, in spring and summer 2019 using three different methods: trawling in the pelagic zone, gillnetting in the littoral zone and electrofishing in three tributaries of Lake Constance (Fig. 1; Table 1). Details on the respective fishing methods can be found in Gugele et al. (2020). It is important to highlight that the trawling in the pelagic zone was performed along transects covering the entire area of Upper Lake Constance (Gugele et al. 2020) and that individuals for sequencing were randomly selected from individuals caught across the entire transect, thus representing the lake-wide pelagic diversity. A total of 95 sticklebacks were sampled. Fish from trawling and electrofishing were euthanised with clove oil (1 ml/l water, Euro OTC Pharma, Bönen, Germany) and total length was recorded. Each individual was photographed laterally using a digital camera (Pentax K3 II, 18-135 mm lens, fixed focal length). For genetic analysis, a piece of the caudal fin (approx. 0.5 cm^2) was fixed in pure ethanol. The sex was determined by dissection and the fish were stored at -80 °C until further processing. Fish sampling was carried out according to local regulations ("Landesfischereiverordnung Baden-Württemberg", LFischVO).



Figure 1. Overview map showing the position of the individual sampling locations in Lake Constance and locations of outgroup populations (insert) used in the genetic analysis. Population information and geographic coordinates for all samples are provided in Suppl. material 2. Pelagic zone samples were sampled by trawling in transects across Upper Lake Constance and the location in the map is not highlighting the exact location (see Methods). Outgroup samples from the United Kingdom are freshwater and marine samples from the River Tyne, whereas outgroup samples from Norway and Germany are only freshwater samples (lake and stream).

| Sampling site | Sampling date | Sampling method | Habitat | n total | n female | n male |
|---------------|------------------------|-----------------|---------------|---------|----------|--------|
| Pelagic zone | 26.03.2019 | Trawling | Pelagic zone | 32 | 13 | 20 |
| Littoral zone | 04.06.2019/ 05.07.2019 | Gillnets | Littoral zone | 32 | 19 | 13 |
| Alter Rhein | 16.05.2019 | Electrofishing | Inflow | 11 | 7 | 4 |
| Nonnenbach | 08.04.2019/ 17.04.2019 | Electrofishing | Inflow | 10 | 6 | 4 |
| Brunnisach | 10.04.2019/ 17.04.2019 | Electrofishing | Inflow | 10 | 6 | 4 |

Table 1. Summary of individual sampling events and sampling success in Lake Constance. n = number of individuals sampled.

Meristic and morphometric analyses

To determine the number of lateral plates, formalin-fixed sticklebacks were stained with alizarin red according to a protocol modified from Peichel et al. (2001) (see Suppl. material 1: Methods for details). The mean number of lateral plates for both sides of each individual was used for further analysis (Fig. 2A). Individuals were classified into "fully plated" (> 30 lateral plates), "partially plated" (< 34 and > 10 lateral plates, with a gap) and "low plated" (< 10 lateral plates) according to Bell (2001). Differences in lateral plate number between sampling sites were tested using pairwise Steel-Dwass tests and differences in total length were tested using an ANOVA with a Tukey-Kramer HSD *post hoc* test in JMP 16.0.0 (SAS Institute, Cary, USA).

For the morphometric analysis, 18 unique reference points ('landmarks') were placed on digital images using TPSDig v.2.31 (Rohlf, Stony Brook University, New York, USA) (Fig. 2A). Statistical analysis was performed using "geomorph" v.4.0.3 (Baken et al. 2021). A Generalised Procrustes Analysis (GPA) was performed (function: "gpagen") to remove differences in size, position and orientation. Possible errors in landmark placement were identified using the "plotOutliers" function and affected individuals were excluded from further analysis as appropriate. We tested for differences in shape between sites and sexes using a model that included fish size (i.e. allometric effects) as a covariate, sampling site and sex as a fixed factors, as well as the interaction of both fixed factors: coords = log(size) * site + sex + site:sex. A permutation-based Procrustes ANOVA using residual randomisation (function: "procD.lm" and "anova", permutations = 9999; estimation method: ordinary least squares) was used to examine which factors have a statistically significant effect on shape. A pairwise post hoc test of sampling sites was performed with R package "RRPP" V.1.2.3 (Collyer and Adams 2018, 2021) ("pairwise" function), based on the previously developed model and a null model considering only size and sex (permutations = 9999, test type = distance between vectors ("dist"), confidence = 0.95). P-values were Bonferroni-Holm adjusted (Holm 1979). Procrustes shape coordinates for each individual were used for principal coordinate analysis ("gm. prcomp" function; (see Suppl. material 1: Methods for details).

DNA extraction and RAD sequencing

Due to problems with storage of caudal fin tissue samples, brain tissue of the fish stored at -80 °C was dissected and used for DNA extraction. DNA for RAD sequencing was extracted from frozen brain tissue using the PureLink Genomic DNA Mini Kit (Invitrogen, Carlsbad, USA) according to the manufacturer's instructions. Tissue was homogenised using 2.4 mm diameter metal beads (3 s, max. speed; Bead Ruptor 4, OMNI international, Kennesaw, USA), the homogenate digested for three hours at 55 °C (150 RPM) and RNA was removed using a 1h RNAse treatment. DNA was eluted in 50 µl elution buffer (NanoDrop 2000c, Thermo Fisher Scientific, Waltham, USA), sample concentrations checked using fluorometry (Qubit 3, Life Technologies, USA) and DNA quality determined using agarose gel electrophoresis. Non-degraded samples were shipped to Floragenexs (Eugene, Oregon, USA) for RAD library preparation and sequencing. Restriction-site Associated DNA Sequencing (RAD-seq) libraries were generated as detailed in Etter et al. (2011) using the restriction enzyme *SbfI* (New England Biolabs).







Figure 2. Determination of morphometric and meristic traits in sticklebacks and results of the principal component analysis (PCA) using landmarks **A** (Top) Stickleback with stained bony structures (for more details, please refer to the text), allowing the determination of the lateral plate number. (Bottom) Position of 18 unique reference points ("landmarks") on the body for shape analysis. (Right) Description of the individual locations of the landmarks **B** combined boxplot and violin plot to illustrate variation in size (left) and lateral plate number (right) of sticklebacks from different sampling sites. Lower case letters indicate statistically significant differences (size: ANOVA + Tukey-Kramer HSD post hoc test, lateral plate number: pairwise Steel-Dwass test). Box plots defined in the insert panel on the right **C** scatterplot showing the first two principal components (PCs), which explain most of the variance of the data (see axis labelling in percent). Sticklebacks were grouped according to sampling site (lit_zone = littoral zone, pel_zone = pelagic zone, Bru_inflow = Brunnisach inflow, Non_inflow = Nonnenbach inflow, Alt_inflow = Alter Rhein inflow) and sex (m = male, f = female). Wireframe graphs of the shape changes along the first two PCs in the PCA are shown on the right.

Sequencing and SNP calling

FASTQ data files were demultiplexed using GBSX v.1.3 (Herten et al. 2015) and reads were mapped to the *G. aculeatus* reference genome (release 92; Ensembl) using BWA v.0.7.17 (Li and Durbin 2010). Reads with a Phred quality score < 20 were removed before hard-calling genotypes using the Stacks v.2.6 gstacks module (Rochette et al. 2019). The Stacks output was subsequently filtered using VCFtools v.0.1.16 (Danecek et al. 2011) to remove indels (--remove-indels) and SNPs with minor allele frequencies below 0.05 (--maf 0.05), more than 25% missing data (--max-missing 0.75) and genotype quality below 10 (--minGQ 10). Only loci with a minimum read depth of 5 (--minDP 5), a minimum mean depth of 50 (--maxDP 50) and a maximum mean depth of 50 (--min-meanDP 50) were kept.

Population genetic analysis

Geographic structure across all samples was explored using PCA on filtered SNP data (n = 11,184 unlinked SNPs) in ade4 v.1.7-16 (Dray et al. 2007). SNP data (n = 28,194 SNPs) were pruned for linkage disequilibrium (LD) in Plink v.1.9 (Purcell et al. 2007) in 25 SNP windows with a five SNP window shift and an r^2 of 0.5. Chromosome 19 containing sex-determining regions was removed to avoid any sex-based bias (Peichel et al. 2004). Individual ancestry was assessed using Admixture v.1.3.0 (Alexander et al. 2009), using the LD-pruned SNP dataset, assessing between 1 and 7 clusters (K) to determine the optimal number of K using the tenfold cross-validation.

Genetic differentiation between sampling sites was investigated using haplotype-based relative allelic differentiation (F_{ST}') and absolute divergence (D_{xy}') between population pairs (*populations* module in Stacks) for all loci containing filtered SNPs. Haplotype-based estimates have the advantage of accommodating loci with more than two alleles contrary to SNP-based statistics (Bassham et al. 2018). Gene diversity (*Hs*), a haplotype-based equivalent to nucleotide diversity which is corrected for sampling bias originating from sampling small sample sizes, was calculated for each sampling site.

To identify genomic regions potentially under selection between littoral and pelagic sticklebacks, z-transformed F_{ST} and D_{xy} estimates for the pelagic-littoral population comparison were computed. Loci with z-transformed $F_{ST}' \ge 3$ were classified as differentiated outlier loci. Loci with increased absolute divergence, $zD_{y} \geq 3$, potentially highlight the differential sorting of ancient alleles between habitats. A z-transformed value ≥ 3 approximately corresponds to a p-value below 0.01. Outlier loci were further tested for signs of selection by comparing their interpopulation gene diversity differences $(\Delta Hs = Hs_{littoral} - Hs_{pelagic})$ to the genome-wide background. The expectation was that ΔHs would be higher in loci under selection in the pelagic populations compared to the genomic background, driven by reduced Hs in the pelagic population. We compared median ΔHs values for outliers ($\Delta H_{s_{outlier}}$) to the genomic background ($\Delta H_{s_{br}}$) using a non-parametric two-sided Wilcoxon rank sum test and further compared the distributions of values using a Kolmogorov-Smirnov test. Genetic differentiation amongst the remaining populations and outlier loci overlaps amongst all pairwise population comparisons were also estimated.

Furthermore, we performed phylogenetic analyses of Lake Constance together with whole-genome data from outgroup populations from across Europe to confirm that Lake Constance stickleback cluster with the Baltic lineage (see Suppl. material 1: Methods for details) (Marques et al. 2019; Berner 2021).

Genome-wide association analysis

Genetic association mapping using Genome-wide Efficient Mixed Model Association (GEMMA v.2.1; Zhou and Stephens (2012); Zhou et al. (2013)) was conducted to identify genetic association for body shape and mean lateral plate number. Associations with total length were not performed, as fish were sampled at different times of the year and, therefore, differed in age and size. We fitted Bayesian Sparse Linear Mixed Models (BSLMM) for each phenotype, providing the same genotype and relatedness matrix input files. As the BSLMM does not allow covariate files to correct for sex, we corrected sex-biased traits (body shape) using a linear model in R and used the residual body shape PC scores as input for the BSLMM analyses. We fitted five separate BSLMMs for each phenotype, averaged the results across chains and subsequently across runs. The BSLMM also estimates hyperparameters describing the genomic architecture of a trait, such as the proportion of variance in phenotypes explained by all SNPs (PVE), the proportion of variance explained by sparse effect loci (PGE) and the number of variants with major effects (n gamma). We estimated the means, median and 95th confidence interval (CI) for these parameters. Furthermore, we identified SNPs as those with an average posterior inclusion probability (PIP) above 0.01 as "associated" (Comeault et al. 2014) and those with PIP above 0.1 as "strongly associated" with the studied phenotype (Chaves et al. 2016).

We tested if phenotype-associated SNPs were also significant outlier loci or showed increased genetic differentiation between littoral and pelagic sticklebacks, which would suggest potential selection acting on these phenotypes. To test if phenotype-associated SNPs showed increased genetic differentiation and divergence compared to a random genomic background, we performed random resampling of the same number of SNPs from the entire SNP dataset, estimated the mean F_{ST} and D_{xy} for the corresponding haplotype and repeated this 10,000 times to create a null distribution. Subsequently, we compared the means F_{ST} and D_{xy} of the phenotype-associated SNPs and the null distribution using a Wilcoxon test. We did this for each phenotype and for the sex-chromosome and autosomes separately.

Results

Meristic and morphometric traits

Total length of sticklebacks differed between sampling sites (ANOVA: $F_{4,90} = 23.1534$, p < 0.001; Fig. 2B), with pelagic individuals being smaller than all other groups (pelagic = 5.4 ± 0.3 mm, littoral = 6.4 ± 0.5 mm; inflow: Brunnisach = 6.3 ± 0.4 mm, Nonnenbach = 6.0 ± 0.5 mm, Alten Rhein = 5.9 ± 0.3 mm). Lateral plate numbers did not differ between sampling sites (Steel-Dwass test: p > 0.05, Fig. 2B), with 77.9% of sticklebacks being fully plated, 20.0% partially plated and 2.1% low plated.

The morphometric analysis, based on landmarks, showed a significant effect of size on body shape (ANOVA: p < 0.001; Suppl. material 1: table S1), indicating allometric effects. As these effects were unique to all sites (ANOVA: p = 0.019;

Suppl. material 1: table S1), a size correction was not possible. Furthermore, both sex and sampling site had significant effects on shape (ANOVA: sex: p < 0.001, sampling site: p < 0.001; Suppl. material 1: table S1). Pairwise comparison of sampling sites revealed that fish from the littoral zone differed statistically significantly in shape from all other sites, regardless of size and sex (Table 2). The principal component analysis (PCA) generally visualised the results of the ANOVA, showing fish from the littoral zone being isolated from other sites in both sexes (Fig. 2C, Suppl. material 1: table S2). Changes in body shape along the first two principal components were most evident in the head region, the positioning of the pectoral fin and general body contour (Fig. 2C). The utilised broken stick model indicated that the first two principal components are statistically "meaningful".

Table 2. Results of the pairwise comparison of the shape of sticklebacks from different sampling sites (littoral = littoral zone, pelagic= pelagic zone, Inflow = Nonnenbach, Brunnisach, Alten Rhein). Upper triangle: pairwise procrustes distances between means. Lowertriangle: pairwise *p*-values between means.

| | Alten Rhein | Brunnisach | Littoral | Nonnenbach | Pelagic |
|-------------|-------------|------------|------------|------------|------------|
| Alten Rhein | | 0.02370511 | 0.03856235 | 0.01409519 | 0.01461575 |
| Brunnisach | 1.000 | | 0.04817884 | 0.02631996 | 0.02773204 |
| Littoral | 0.001* | 0.005* | | 0.04335706 | 0.03863615 |
| Nonnenbach | 1.000 | 1.000 | 0.001* | | 0.01534973 |
| Pelagic | 1.000 | 1.000 | 0.001* | 1.000 | |

* statistically significant after Holm-Bonferroni correction ($\alpha = 0.05$; Holm (1979)).

Weak population genetic structuring

The admixture analysis suggested that sticklebacks in Lake Constance were highly admixed, as the genetic structure was best explained by 1 cluster (K = 1; Suppl. material 1: fig. S1). Low population structure was supported by the PCA (Fig. 3). PC1 and PC2 only explained negligible variation in genetic structure amongst individuals (1.75% and 1.52%, respectively). Furthermore, genetic differentiation was low between all sampling sites, both in relative divergence (mean $F_{\rm ST}$ = 0.005 \pm 0.002) and absolute divergence (mean D_{xy} = 0.001 \pm 2.61 × 10⁻⁵) (Suppl. material 1: table S3). Differentiation between the pelagic and littoral three-spined sticklebacks was the lowest amongst all pairwise comparisons ($F_{\rm ST}$ ' LIT-PEL = 0.002). We did not detect any structure for the pelagic samples, which were sampled across Upper Lake Constance.

Furthermore, phylogenetic analyses showed that stickleback from Lake Constance clustered with the Baltic Lineage (Eastern European) stickleback (Suppl. material 1: figs S2, S3, table S4), supporting earlier findings that sticklebacks in Lake Constance are derived from the Baltic lineage (Berner 2021).

Genetic differentiation across the genome

We detected 333 loci with $zF_{ST}' \ge 3$, distributed across the entire genome (Fig. 4). Outlier loci showed on average increased absolute divergence (D_{xy}') compared to the genomic background, both on autosomes (Wilcoxon: W = 2993041, p < 0.001) and the sex chromosome (Wilcoxon: W = 6203, p = 0.012) (Fig. 4B). However, only 16 outlier loci showed strongly increased D_{xy}' values ($zD_{xy}' \ge 3$). Comparisons



Figure 3. Population structure. Principal Component Analysis representing individual structuring across Lake Constance populations. Analysis was performed on pruned data excluding the sex chromosome (11,184 SNPs). Colours indicate different sampling sites, while shapes represent habitats – inflow (circle), littoral (square), pelagic (triangle). Smaller, lighter data points show individual variation, while the larger shapes with a black centre indicate population Principal Component centroids, which were calculated as the mean of both the 1st and 2nd axes.



Figure 4. Signatures of selection **A** *Z*-transformed haplotype-based $F_{ST}'(zFst')$ estimates for loci (dots) across all chromosomes (noted on the x-axis). Outlier loci with $zF_{ST}' \ge 3$ are shown in orange **B** absolute divergence (Dxy') between outlier loci (orange) and the genomic background on autosomes and the sex chromosome. Individual dots denote genomic loci and the distribution of values is shown by density plots. The sex chromosome was analysed separately due to lower recombination rates compared to autosomes and, therefore, potentially higher absolute divergence **C** comparison of delta gene diversity (ΔHs) between the genomic background (zFst' < 3; grey), outlier loci (orange) and outlier loci showing increased absolute divergence ($zDxy' \ge 3$; red). Delta gene diversity was estimated by subtracting gene diversity in pelagic individuals from gene diversity in littoral individuals. Positive ΔHs values are indicative of reduced gene diversity in littoral individuals and vice versa. Individual dots denote genomic loci. Box plots defined in Fig. 2B.

between littoral and pelagic populations with inflow populations showed a similar picture (Suppl. material 1: figs S4, S5).

We further tested for signals of divergent selection by comparing gene diversity (Suppl. material 1: fig. S6) between littoral and pelagic populations. While the mean between-population difference in gene diversity of outlier loci ($\Delta Hs_{outlier}$) was not lower than the genomic background (ΔHs_{bg}), outlier loci showed more extreme values than the genomic background (Kolmogorov-Smirnov test: D = 0.1694, p < 0.001) (Fig. 4C). Outlier loci with increased absolute divergence had on average lower gene diversity in littoral sticklebacks (positive ΔHs) (Fig. 4C), suggesting that these highly divergent loci are likely under selection in the littoral population.

Marker associations with phenotypic traits

Genome-wide association analyses for lateral plate number identified 41 associated SNPs (mean PIP > 0.01), with 7 SNPs (17.1%) showing very strong associations (mean PIP > 0.1). These were mainly located on chromosome 4, with one strongly-associated SNP on chromosome 2 (Fig. 4A). For body shape, the BSLMM detected 104 associated SNPs with PIP > 0.01 and one strongly-associated SNP on chromosome 21 with PIP > 0.1. Although body shape values were corrected for sex, a large proportion of associated SNPs (n = 34; 32.7%) were located on sex chromosome 19.

The proportion of variance explained by all loci was similar for lateral plate number ($PVE_{PN} = 88.4\%$) and body shape ($PVE_{BS} = 85.3\%$), but the proportion of PVE explained by sparse effect loci ($PGE_{BS} = 61.5\%$, $PGE_{PN} = 77.8\%$) and the estimated number of sparse effect loci (mean *n gamma*_{BS} = 28; mean *n gamma*_{PN} = 6) were smaller for body shape compared to lateral plate number (Fig. 5B).

Body shape-associated loci were not strongly differentiated (*i.e.* outlier loci), but autosomal loci associated with body shape showed increased genetic differentiation between littoral and pelagic sticklebacks compared to the genomic background (Fig. 5C). Loci associated with lateral plate number and body shape-associated loci on the sex chromosome, did not show increased genetic differentiation compared to the genomic background (Fig. 5C).

Discussion

The aim of this study was to investigate the evolutionary origin of the pelagic three-spined stickleback population in Lake Constance. We found that pelagic sticklebacks in Lake Constance likely originated within the Lake from the already established littoral population without any recent colonisation and/or introgression from external populations. Despite the absence of genome-wide divergence amongst lake habitats, some regions across the genome show increased genetic differentiation. We found that body shape-associated loci, a trait divergent between littoral and pelagic stickleback in Lake Constance, show increased genetic differentiation between littoral and pelagic individuals. Overall, this suggests that the phenotypic difference in pelagic stickleback and its dramatic demographic expansion is best explained by the colonisation of the pelagic zone by stickleback from other lake habitats and the sorting of adaptive standing genetic diversity present within Lake Constance, rather than by recent colonisation. Thus, effective management strategies must focus on the entire stickleback population rather than only on the pelagic population.



Figure 5. Genome-wide association analyses (GWAS) for phenotypic traits **A** posterior Inclusion Probabilities (PIP) from BSLMMs for all SNPs (dots) across the genome are shown, with outliers SNPs passing significance threshold (PIP > 0.01) shown in red. Manhattan plots are shown for GWAS results with mean lateral plate number, body shape PC1-6 and total length **B** hyperparameters from BLSMMs are plotted, as the mean (large dot) and 95% confidence intervals (grey lines), for body shape (BS: yellow) and lateral plate number (PN: blue) **C** the distribution of genetic differentiation (F_{ST}) values for the permuted null distribution is shown as a histogram and mean differentiation for phenotype-associated loci is indicated as a red line. Results are shown for SNPs associated with later plate number (blue) and body shape (yellow), for autosomes and the sex chromosome separately. No trait-associated SNPs were detected for later plate number on the sex chromosome.

Phenotypic divergence of littoral and pelagic stickleback in Lake Constance

Sticklebacks exhibit a high degree of phenotypic diversity between habitats, with some morphological traits having evolved in parallel during their postglacial dispersal into new freshwater habitats (McPhail 1993; Bell and Foster 1994). In particular, the reduction of lateral plate armour in freshwater populations is regularly observed (Hagen and Gilbertson 1972; Bell 2001). Although this process can happen very quickly (Bell et al. 2004), our findings show that sticklebacks in Lake Constance still exhibit largely full armouring. The littoral zone, where sticklebacks were found before the mass abundance in the open waters, is inhabited by several predatory fish species known to prey on sticklebacks (Donadi et al. 2017; Jacobson et al. 2019). Thus, full plating may have remained relevant as effective predator protection even for the pelagic population during the littoral breeding season (Reimchen 1994; Kitano et al. 2008; Rennison et al. 2019).

Littoral and pelagic sticklebacks differed slightly in snout length and body depth, with longer snouts and deeper bodies in littoral fish (Schluter and McPhail 1992; Arnegard et al. 2014). However, body shape was also clearly affected by size and sex of the fish. A pronounced sexual dimorphism is known for sticklebacks, with males having larger heads and mouths (Kitano et al. 2007). The underlying cause of the differences in body shape between habitats is unclear. A recent study was able to show that littoral and pelagic sticklebacks do not strongly differ in trophic position (Gugele et al. 2023). Habitat-specific morphological variation is common in sticklebacks (Gow et al. 2008; Webster et al. 2011), also in sympatric occurring limnetic and benthic populations (Nagel and Schluter 1998). Stable isotope ratios in muscle did not reveal differences in trophic position between sticklebacks from pelagic and littoral habitats in Lake Constance, but rather a mere preference to forage in the pelagic zone (Gugele et al. 2023). However, differences in $\delta 13C$ levels in the liver, which were attributed to habitat shifts (Gugele et al. 2023), suggest that body shape differences are potentially related to differences in habitat usage rather than trophic eco-morphology.

Observed size differences between sticklebacks from the pelagic and littoral zone are likely related to differences in sampling time rather than growth rate, with fish from the pelagic zone having been captured in late March, while fish from the littoral zone were captured in June and July. It can, therefore, be assumed that this is a time-dependent increase in size over the course of the year. Future common garden experiments, temporal sampling throughout the year and more detailed phenotypic and trophic analyses could shed light on the eco-morphological basis of the rapid pelagic invasion of Lake Constance stickleback.

Intralacustrine origin of pelagic stickleback in Lake Constance

To date, it has been unclear whether pelagic stickleback in Lake Constance, which have increased rapidly in abundance since 2012 (Eckmann and Engesser 2019), originated within Lake Constance or are the result of a separate introduction. Our genetic results suggest a recent intralacustrine origin of pelagic stickleback in Lake Constance. Genome-wide patterns of genetic differentiation were overall weak between habitats, suggesting either a very recent expansion into the pelagic zone by sticklebacks and/or ongoing gene flow. A very recent origin and ongoing gene flow are supported by annual hydroacoustic surveys (Eckmann and Engesser 2019) and spatio-temporal sampling (Gugele et al. 2020), respectively. In Lake Constance, analyses of spatio-temporal movement of sticklebacks suggested temporal migration of sticklebacks from the pelagic zone to tributaries ('inflow populations') and back (Gugele et al. 2020), yet genetic analyses did not suggest a closer relationship between inflow and pelagic stickleback. The slightly weaker genetic divergence between littoral and pelagic sticklebacks, compared to inflow populations, suggests that pelagic sticklebacks might have originated from the littoral population and/or that gene flow is higher between the littoral and pelagic zone compared to tributaries (Gugele et al. 2020). These genetic differences are very subtle, though and not sufficient to confirm putative spawning locations of pelagic sticklebacks. Furthermore, the lack of population structure within the pelagic samples, which were sampled from across Upper Lake Constance, suggests that the pelagic population is genetically and spatially homogeneous, which might be expected under rapid expansion into the pelagic zone.

Stickleback from pelagic and littoral habitats were sampled during slightly different times in our study, potentially biasing estimates of genome-wide genetic differentiation between habitats. However, differences in sampling time would likely result in even lower estimates of genetic differentiation (compared to the 'true' differentiation), if pelagic sticklebacks, which were sampled in the spring, move into the littoral zone to spawn in the summer and are caught together with littoral sticklebacks. Thus, we believe that, overall, there is no strong genome-wide differentiation between habitats, in line with a recent expansion under ongoing gene flow.

The phylogenetic clustering of sticklebacks from Lake Constance as sister to Baltic stickleback from northern Germany (Suppl. material 1: fig. S2) is further in line with the theory that Lake Constance was historically colonised by individuals which shared a substantial proportion of ancestry with marine-like sticklebacks that were repeatedly introduced to streams and ponds in the Lake Constance system from catchments south to the Baltic Sea (Muckle 1972; Marques et al. 2019; Berner 2021; Hudson et al. 2021).

Polygenic basis of pelagic colonisation

Despite the likely recent colonisation of the pelagic zone and minimal genome-wide differentiation between habitats, or lack thereof, we detected a polygenic signal of divergence with hundreds of outlier SNPs across the genome showing increased genetic differentiation between individuals from littoral and pelagic habitats. Such polygenic patterns of divergence between benthic and limnetic sticklebacks were also observed in Canadian populations (Härer et al. 2021). While many studies have identified individual large-effect loci associated with rapid local adaptation in different systems (Barrett et al. 2019; Thompson et al. 2020; Schluter et al. 2021), polygenic responses to selection, as observed in our and other studies (Laurentino et al. 2020; Salmón et al. 2021), can also lead to rapid local adaptation despite ongoing gene flow (Jain and Stephan 2017). Polygenic differentiation under gene flow and recent divergence could have two non-mutually exclusive explanations: a) rapid adaptation via sharing and re-assembly of adaptive alleles through selection on standing genetic variation (e.g. Terekhanova et al. 2014; Roesti et al. 2015; Fang et al. 2020); and b) strong divergent selection pressures arising from the differing environments in the pelagic versus littoral zone (Moser et al. 2016), which acts on adaptive phenotypes, such as body shape.

Genetic differentiation can occur without divergent selection, for example, through linked selection in low recombination regions or genetic drift due to population bottlenecks, yet these are unlikely explanations in this system. Firstly, linked selection is less likely to lead to increased differentiation over such short evolutionary timescales (Burri 2017) and patterns of genetic diversity between habitats do not indicate the presence of genetic bottlenecks, which is supported by large observed stickleback populations (Eckmann and Engesser 2019; Gugele et al. 2020). Furthermore, we observed increased absolute divergence in outlier loci, with strong divergence for a small subset of loci, suggesting a contribution of divergent selection in the genetic differentiation between habitats. Absolute divergence takes longer to build up than genetic differentiation, thus suggesting that increased divergence between pelagic and littoral sticklebacks is potentially due to the sorting of ancient adaptive alleles between habitats, which has been shown to play a role in freshwater adaptation in sticklebacks (Nelson and Cresko 2018). Differences in gene diversity at outlier loci between pelagic and littoral populations compared to the genomic background further support that genetic differentiation

is potentially driven by divergent selection rather than variation in genetic diversity across the genome, which would be expected to lead to reduced diversity in both populations (Cruickshank and Hahn 2014; Burri 2017).

Overall, the fact that we observed genetic differentiation of many loci across the genome, despite low levels of genome-wide differentiation, indicates that habitat preferences might be, at least partially, genetically determined and not purely plastic, although a plastic component cannot be excluded.

Targets of selection

Increased differentiation of body shape-associated autosomal loci between pelagic and littoral sticklebacks suggests that body shape, a trait that seems to differ between populations in these habitats, is under divergent selection between habitats. The observed signal is likely not due to chance, as loci associated with lateral plate number, a trait that does not differ between pelagic and littoral sticklebacks, do not show increased differentiation. We also recovered a well-studied lateral plate number associated genomic region on chromosome 4, further suggesting that we had sufficient power to detect large-effect loci. Hence, the genetic differentiation of body shape-associated loci suggests that the observed divergence between littoral and pelagic stickleback is not purely due to phenotypic plasticity, but is at least partly genetically determined. Variation in morphology could ultimately lead to assortative mating and divergence into distinct ecotypes over time (Garduno-Paz et al. 2020).

We did not test for genotype-association with variation in body size in our dataset, as individuals were sampled at slightly different time-points throughout the year. Whilst body size divergence between Lake Constance and stream stick-lebacks has been demonstrated to be plastic and driven by differences in food availability (Moser et al. 2015), divergence in body size is a substantial driver of reproductive isolation in sticklebacks as it affects reproductive behaviour such as mate choice (Moser et al. 2015) and, thus, may facilitate speciation in future generations (Berner et al. 2017).

Conclusion

Our results suggest that pelagic three-spined stickleback in Lake Constance, which already have had ecosystem-wide effects on biodiversity and food-web integrity, likely arose within Lake Constance. Divergence in body shape between littoral and pelagic habitats and potentially other relevant ecological and physiological traits, is potentially reflective of divergent polygenic selection on trait-associated genes.

The limited SNP-density across the genome precludes us from determining the genomic targets of selection and phenotype-associated loci. Furthermore, temporal sampling of stickleback throughout the year will be needed to determine if there are seasonal differences in genetic and phenotypic patterns. Lastly, common garden experiments and temporal sampling in the wild could help to better understand the roles of evolutionary change *versus* plasticity in the rapid invasion of the pelagic zone and identify putatively adaptive phenotypic traits.

A better understanding of the processes facilitating the rapid invasion of the pelagic zone of Lake Constance could aid management of this population and in other systems with rapid pelagic invasions, such as the Baltic Sea. Our results suggest that the observed pelagic colonisation was potentially facilitated by large standing genetic variation and the sorting of potentially adaptive alleles between habitats. The lack of genome-wide differentiation and large amount of standing genetic variation suggest that the entire stickleback population and not only the pelagic sub-population, is potentially capable of colonising the pelagic zone and re-invasions of the pelagic zone from other habitats are a possibility if the pelagic population is removed through control measures. Hence, the entire stickleback population in Lake Constance should be managed as a whole, rather than focusing efforts on the pelagic sub-population.

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

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Author contributions

A.B. conceived the project. Sampling was performed by A.R. and phenotypic analysis was performed by S.R. Genomic analysis was performed by C.D and A.J, with input from K.R.E. C.D. and S.R. wrote the first version of the manuscript with input from A.J. All authors contributed to the final version.

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Data availability

All newly-generated sequence data for this study are available in the NCBI SRA under the BioProject PRJNA1090479 with the following run accessions: SRR28409948–SRR28410042.

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Supplementary material 1

Supplementary methods and results

Authors: Carolin Dahms, Samuel Roch, Kathryn R. Elmer, Albert Ros, Alexander Brinker, Arne Jacobs

Data type: docx

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Supplementary material 2

Sample information

Authors: Carolin Dahms, Samuel Roch, Kathryn R. Elmer, Albert Ros, Alexander Brinker, Arne Jacobs

Data type: xlsx

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Connectivity and climate change drive the global distribution of highly invasive termites

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Abstract

Termites are amongst the most abundant and ecologically-important groups of insects in tropical forests. However, the destructive potential of some species amounts to billions of dollars in damage each year. Despite their economic and ecological impacts, only a limited number of invasive termite species have been studied using distribution modelling and no studies have taken trade, transport and demography variables into account. We used Species Distribution Models (SDMs) to investigate the potential distribution of 10 highly-invasive termites. Our study includes bioclimatic conditions, land-use patterns, elevation and connectivity predictors (i.e. urban areas, human population, accessibility to cities and private vessels), alongside different climatic and socioeconomic change scenarios.

The distribution of the termite species hinges on bioclimatic and connectivity variables, highlighting the significance of these latter factors in invasive species analyses. Our models demonstrate the potential of these invasive termites to thrive in large urbanised and connected areas within tropical and sub-tropical regions and to a lesser extent within temperate regions. As climate changes and urbanisation intensifies, most species' range could expand, particularly under a "fossil fuel-driven development" scenario. Furthermore, while some species may have a slightly reduced range, they could extend their presence into more urbanised and connected areas, increasing the risks and costs associated with termite damages. Our models highlight the anticipated role of growing connectivity and climate change dynamics in facilitating the widespread proliferation of invasive termites in the coming years.

Key words: Biological invasions, climate change, connectivity, invasive species, invasive termites, species distribution models



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Introduction

Invasive species pose a significant threat to not only biodiversity by causing species extinction, but also mankind by spreading vector-borne diseases as well as imposing economic burdens to control invasive species (Seebens et al. 2018; IP-BES 2019). Estimating economic costs of invasive species is a challenging task, requiring international and interdisciplinary expertise (Diagne et al. 2020), but recent papers suggest that the total reported costs exceed US\$1.5 trillion (Angulo et al. 2021; Diagne et al. 2021). Such costs encompass lost product and service values, diminished crop yields, infrastructure damage, altered ecosystem services, medical expenses and costs related to invasive species control (Bradshaw et al. 2016; Hoffmann and Broadhurst 2016; Diagne et al. 2021). Alarmingly, the overall cost of biological invasions – likely underestimated – triples every decade (Diagne et al. 2021).

The number of biological invasions is continuously rising, affecting even the most remote regions of the world (Seebens et al. 2017). In the coming decades, three main drivers - climate change, trade and transport and socioeconomic activities - will further impact biodiversity through biological invasions (Essl et al. 2020). Climate change, characterised by temperature increases, disrupted precipitation patterns and intensified extreme events (Seneviratne et al. 2021), will reshape the distribution of invasive species: some species will experience range expansions or contractions and previously unsuitable environments will become favourable for their establishment (Bellard et al. 2018). Shifts in trade dynamics, such as changes in volume and trade routes, will increase the number and sources of potential new introductions of alien species (Westphal et al. 2008; Humair et al. 2015; Eguíluz et al. 2016; Cope et al. 2019; Sardain et al. 2019; Essl et al. 2020). Despite efforts to strengthen quarantines and controls, alien species closely mirror trends in international trade, steadily growing (Liebhold et al. 2017; Hulme 2021). Moreover, ongoing land-use changes and socioeconomic development, particularly rapid urbanisation, will accelerate the establishment and spread of invasive species. Urban areas, serving as hubs for global material, food and energy flows (Decker et al. 2000), provide ideal entry and expansion points for opportunistic and invasive species (Bellard et al. 2016). Urban areas have already doubled since 1992 (IPBES 2019) and it is projected that up to 60% of the global population will reside in cities by 2030 (UN DESA 2020). This growing urbanisation results in significant biodiversity loss through the conversion of natural habitats to urban land (McDonald et al. 2020) and may create favourable conditions for invasive species.

Of the 3106 described termite species worldwide, 183 are considered pests and 28 are invasive (Oloo et al. 1990; Evans et al. 2013; Krishna et al. 2013). Termites are one of the most abundant and ecologically important groups of insects in tropical forests and play a crucial role as decomposers and ecosystem engineers, feeding on organic matter, including dead wood, leaves and roots (Holt and Lepage 2000; Eggleton and Tayasu 2001; Freymann et al. 2008; Jouquet et al. 2016). Termite pests, however, cause an economic impact of over US\$40 billion annually worldwide (Rust and Su 2012; Evans et al. 2013; Krishna et al. 2013). Invasive termites cause extensive economic damage by infesting and feeding on various structures, including build-ings, wooden furniture, utility poles and agricultural crops (Krishna et al. 2013). Consequently, preventative measures, such as quarantine regulations, early detection systems and integrated management strategies are crucial to prevent the introduction of invasive termites and minimise their spread (Rust and Su 2012; Evans et al. 2013).

Species distribution models (SDMs) can be a useful tool in preventing invasive species by identifying areas at risk of invasion and providing insights into their potential distribution in response to climate change and land-use modifications. While previous studies primarily considered bioclimatic factors to project distribution of invasive termites (e.g. Li et al. (2013); Buczkowski and Bertelsmeier (2017)), these variables oversimplify the complex trajectories associated with their spread in an increasingly interconnected and urbanised world (Essl et al. 2020). To address this limitation, we combined bioclimatic, land-use and elevation data with connectivity variables into SDMs. Connectivity variables are linked to trade, transport and demography and reflect the contemporary modes of termite dispersal. Historically, invasive termites were introduced through cargo and wood ship-

ments (Gay 1969), but strict quarantine inspections now mitigate new invasions (Scheffrahn 2023). However, private vessels like yachts or sailing boats, exempt from strict quarantine inspection, often traverse long distances through regions rich with termite species, posing a significant risk as potential vectors for termite invasions (Scheffrahn and Crowe 2011; Hochmair et al. 2023; Scheffrahn 2023). To our knowledge, our research is the first to consider connectivity variables (i.e. urban areas, human population, accessibility to cities and private vessels) into the framework of termite species distribution modelling. Their use is imposed by the decisive influence of human trade and transport in the spread of termites and by the presence of termites in urban environment and man-made structures (Gay 1969; Evans 2010). Our approach affords insights into the current and future distribution of ten highly-invasive termite species under two potential scenarios of Shared Socioeconomic Pathways (SSP2-4.5 "middle of the road scenario" and SSP5-8.5 "fossil-fuelled scenario") for two future periods (2021-2040 and 2041-2060). By revealing the potential distributions of 10 highly-invasive termite species, we identify, at a global scale, potential high-risk areas in the context of climate change, land-use change and increasing connectivity. Our study not only provides information for preventative strategies, but also furnishes a roadmap to help curtailing introduction and early-stage introductions of invasive termite species.

Methods

Species distribution data

In 2013, Evans et al. reported 28 invasive termite species worldwide. Distribution data for these species were extracted from reliable sources including Global Biodiversity Information Facility (GBIF 2024), Sistema de Informação sobre a Biodiversidade Brasileira (SiBBr 2024) and the University of Florida Termite Collection (UFTC) curated by Scheffrahn (2019). Of the 28 species, six had less than 30 occurrences after curation (removing duplicates, excluding coordinates with low accuracy and coordinates from countries where the species had not been reported in the literature). Detailed information on the remaining 22 species, including their respective families, feeding groups, nesting types, breeding systems, target damage, native and invaded ranges and spread methods are given in Table 1 (see Suppl. material 2 for occurrences of the 22 initial invasive species and GBIF DOIs). From this subset, we narrowed our focus on the 10 most invasive termites, discarding those with limited spread capacity (e.g. those inhabiting rotten wood) or those lacking recent reports. Six of them belong to the Kalotermitidae family (Cryptotermes brevis (Walker, 1853), Cr. domesticus (Haviland, 1898), Cr. dudleyi (Banks, 1918), Cr. havilandi (Sjöstedt, 1900), Incisitermes immigrans (Snyder, 1922) and I. minor (Hagen, 1858)), three to the Rhinotermitidae family (Coptotermes formosanus (Shiraki, 1909), Co. gestroi (Wasmann, 1896) and Reticulitermes flavipes (Kollar, 1837)) and one from the Termitidae family (Nasutitermes corniger (Motschulsky, 1855)). All produce secondary reproductives and consume wood (Evans et al. 2013). All have a life stage in which they nest in a single piece of wood in which the colony is founded. The Kalotermitidae nest within their food source for the entire life of the colony (i.e. single-piece nesting termite; Abe (1987)); the Rhinotermitidae establish their incipient colony inside a piece of wood or at the wood-soil interface before settling in the soil (Ferraz and Cancello 2004; de Lima

et al. 2006); for *Nasutitermes corniger*, the construction of the final carton nest, whether on a tree or on the ground, may follow the establishment of an incipient colony in a piece of wood (Thorne and Haverty 2000). These life-history traits make them particularly good invaders (Evans et al. 2013).

The curation process of our ten species yielded an average of 313 occurrences per species (Table 1). Three sets of 1000 randomly selected pseudo-absence points were generated for each species using Biomod2 version 4.2-4 package (Thuiller et al. 2009) in the software R version 4.2.0 (R Core Team 2022). These pseudo-absence points were chosen with equal weighting for both presence and absence, following the methodology described by Barbet-Massin et al. (2012).

Explanatory variables

Explanatory varisables were standardised to the same resolution (0.25° , the resampling was done using the nearest-neighbour algorithm), dimensions (*nrow* = 600, *ncol* = 1440), extent (*xmin* = -180°, *xmax* = 180°, *ymin* = -60°, *ymax* = 90°) and format (WGS84 EPSG:4326) using the software QGIS (QGIS 2023). For each species, a raster stack was built with explanatory variables using the package raster_3.6-14 (Hijmans et al. 2015).

Climatic variables

To determine the current distribution of species, we obtained 19 bioclimatic variables from Worldclim 2.1 (Fick and Hijmans 2017) at 2.5 min resolution. These variables were then standardised (same resolution, dimensions, extent and format) using QGIS, as described earlier. To select the most influential variables for each species, we assessed variable importance using six different algorithms through Biomod2. The six algorithms were selected out of the ten available algorithms in the package, based on their strength and widespread usage: Flexible Discriminant Analysis (FDA, Hastie et al. (1994)), Random Forests (RF, Breiman, (2001)), Maximum Entropy from the maxnet version 0.1.4 package (MAXNET, Phillips et al. (2004); Phillips et al. (2017)), Generalised Additive Model (GAM, Hastie and Tibshirani (1986)), Generalised Linear Model (GLM, Nelder and Wedderburn (1972)) and Generalised Boosting Model (GBM, Bühlmann and Hothorn (2007)). The mean importance values were calculated and only the top two variables, which exhibited the highest importance and were uncorrelated (with a Pearson correlation coefficient of less than 0.70, Suppl. material 1: S1), were selected for each species to avoid autocorrelation. Details of the selected variables can be found in Suppl. material 1: S2.

For future climate projections, we accessed several global climate models (GCMs) from the sixth Coupled Model Intercomparison Project (CMIP6; Eyring et al. (2016)) through Worldclim 2.1, also at a 2.5 min resolution. Each CMIP6 GCM has its own strengths and limitations due to differences in its structure, parameterisation, initial condition settings and climate representation (Wang et al. 2021). For this reason, we used three different GCMs (EC-Earth3-Veg-LR, Had-GEM3-GC31-LL and MIROC6), based on forcing data availability and representation of the CMIP6. To account for different climate change scenarios and time periods, we selected three combinations. The SSP2-4.5 scenario ("middle of the road": extrapolation of past and current global development into the future; under this scenario, temperatures rise by 2.7 °C by the end of the century) was chosen

for the 2021–2040 (20 years' average) and 2041–2060 time periods. Additionally, we selected the SSP5-8.5 scenario ("fossil-fuelled development": global markets and development, based on fossil fuel resources; under this scenario, current CO_2 emissions levels roughly double by 2050 and warming could reach 4.4 °C in 2100) for the 2041–2060 period to consider a more pessimistic outlook (Riahi et al. 2017). For each scenario and variable, the grid-cell mean was computed amongst the three GCMs to reduce differences between the GCMs. The variables were then standardised (same resolution, dimensions, extent and format) using QGIS, as described earlier. To maintain consistency in the species distribution modelling, we used the same two bioclimatic variables that were chosen for each species' present distribution to model their future distribution.

Land-cover variables

We incorporated land-cover information to capture the habitat preferences of the selected termite species. Land-cover layers were obtained from the Land-Use Harmonization 2 (LUH2) project (Hurtt et al. 2020). This dataset includes 12 layers potentially relevant for termites (See Suppl. material 1: S3 for details). Moreover, each of these layers is available for different years under different shared socioeconomic pathways (SSPs). To align with the bioclimatic variables, we downloaded the 12 layers for four scenarios as similarly as possible: current (SSP2-4.5, year 2023), SSP2.4-5 2021–2040 (SSP2.4-5, year 2040), SSP2.4-5, 2041–2060 (SSP2.4-5, year 2060) and SSP5.8-5 2041-2060 (SSP5.8-5 year, 2060). Like the bioclimatic variables, the land-cover layers were standardised (same resolution, dimensions, extent and format) using QGIS, following the method described earlier. To identify the most influential land-cover variables for each termite species, we applied the variable importance command from the Biomod2 package, using the same set of algorithms as before. The mean importance values were calculated and only the top two variables with a Pearson correlation coefficient of less than 0.70 were selected for each species. This approach ensured that the chosen variables were not strongly correlated with each other, thus avoiding redundancy and maintaining model robustness (Suppl. material 1: S1, S3). For future species distribution modelling, we used the same land-cover layers that were chosen for each species' present distribution.

Connectivity (trade, transport and demography) variables

Socioeconomic variables, such as distance to airports, seaports and human density, are the most significant factors determining the distribution of global invasive species after climatic variables and habitat characteristics (Bellard et al. 2016). Looking ahead, trade and transport, climate change and socioeconomic activities are poised to become the main drivers of biological invasions (Essl et al. 2020). Termites' invasions are typically human-induced, owing to their reliance on wood, a globally-traded commodity. While cargoes and commercial boats containing wood were historically primary vectors for termite invasions (Gay 1969), biosecurity measures have now largely mitigated this risk (Scheffrahn 2023). However, the ten invasive species are likely invading new regions via private vessels such as yachts and sailing boats and, also, in the case of the Kalotermitidae, through the transportation of infested furniture (Scheffrahn 2023; Chouvenc, personal communication, January 2024; Table 1).

| I Intermediate- Yes SF, EF and Yes Buildings, Australia New Guinea From imported logs of | I Intermediate- Yes SF, EF and Yes Buildings, Australia New Guinea From imported logs of | piece MF horticultural Eucalyptus and hardwood and forest trees, and forest trees, logs from Australia in the las plastic plastic mainly through live potted pla | | I Single-piece Yes No Sawn timber, dead trees and living trees Australia From imported second-hand I Single-piece Yes adad trees and living trees New Zealand From imported second-hand I I Inving trees Inving trees Inving trees Inving trees I I Inving trees Inving trees Inving trees I I Inving trees Inving trees | I Single-piece Yes ? No Rotten wood North Hawaii Unknown, as it feeds on rotte America America commodity, low risk | I Single-piece Yes MF No Rotten wood US Japan Unknown, as it feeds on rotte wood which is not a great commodity, low risk | | I Single-piece Yes ? Yes Buildings Coastal S and N America, From furniture, wooden articl Chile, Peru W Africa, Azores, pallets, dunnage, sailboars, shi Australia (Brisbane), Fiji, Pacific and Atlantic islands, Egypt | I Single-piece Yes ? Yes Buildings SE Asia China, Taiwan, Japan, Intercepted in private vessel: Australia, Pacific high risk Ocean, Polynesia |
|--|--|--|----------|---|---|---|---------|--|---|
| Occurrences Fet after (Doi curation et al. | | 50 | | 101 | 690 | 54 | | 467 | 32 |
| and Short (ies name | mitidae | mes Mdar nuis ; 1897) | nopsidae | es Pada (, 1897) | psis Zang Ilis 1858) | psis Znev is 1874) | nitidae | Thes Cbre Valker, | imes Cdom us J, |

Helal and Ali (1982); Scheffrahn et al. (2009); Evans et al. (2013); Haigh et al. (2023)

Scheffrahn and Crowe (2011); Evans et al. (2013)

Scheffrahn and Crowe (2011); Evans et al. (2013)

Intercepted in private vessels, high risk

India, Bangladesh, Indian Ocean, East Africa, Australia, Micronesia, South America

SE Asia

Buildings

Yes

۸.

Yes

Single-piece

г

50

Cdud

Cryptotermes dudleyi (Banks, 1918)

Evans et al. (2013); Yashiro et al. (2018)

References for native and invaded range, and spread methods

Gay (1969); Evans et al. (2013);

Lenz et al. (2013); Chouvenc, personal communication, January 2024 Pearson et al. (2010); Evans et al. (2013); Chouvenc, personal communication, January 2024

Evans et al. (2013)

| References for native and invaded range, and spread methods | Gay (1969); Evans et al. (2013); Chouvenc, personal communication, January 2024 | Evans et al. (2013) | Gay (1969); Evans et al. (2013) | Gay, 1969; Evans et al. (2013); Chouvenc, personal communication, January 2024 | | Miller (1940); Lenz et al. (2013); Evans et al. (2013); Chouvenc, personal communication, January 2024 | Atkinson et al. (1993); Jenkins et al. (2002); Messenger et al. (2002); Evans et al. (2013); Tonini et al. (2014); Chouvenc et al. (2016); Evans et al. (2019), Scheffrahn et al. (2020) | Gay (1969); Evans et al. (2013); Tonini et al. (2014) | Scheffrahn and Crowe (2011); Tonini et al. (2014); Evans et al. (2013); Chiu et al. (2016) | Szalanski et al. (2004); Evans et al. (2013); Carrijo et al. (2020) |
|---|---|--|--|---|-----------------|--|---|--|--|--|
| Spread methods and risk | Probably from wooden rafts or boars from Madagasear long time ago and now probably in boars like other <i>Cryptatermes</i> species, high risk | Very limited spread, low risk | From infested wood from a wrecked schooner in the last centuries and now probably through movement of furniture like <i>I. minor</i> , high risk | From wooden chests, furmiture, and grape boxes from US West Coast and now through movement of furmiture, high risk | | From railroad ties and telephone poles from Australia in the last centuries, but now low risk mainly through live potted plants | From recycled railroad ties, potted plants, furniture and private vessels, high risk | From railroad ties and imported logs from Australia in the last centuries, but now low risk mainly through live potted plants | Intercepted in private vessels, high risk | Probably shipboard infestations in the last centuries and now private vessels, medium risk |
| Invaded range | E Africa, India, S America, West Indies and Indian islands | New Zealand and Fiji | Pacific Ocean, Hawaii, Japan | Eastern US, Canada, China, Pacific Ocean, Japan | | New Zealand | Japan, US, Israel | New Zealand | Taiwan, Pacific Ocean, Micronesia, Mexico, Florida, West Indies, Brazil | US (Florida) |
| Native range | West Africa | Australia | Central and South America | South- western US and northern Mexico | | Australia | China and Taiwan | Australia | SE Asia | Bahamas, Panama, Cuba, Jamaica, Cayman Islands, Panama Colombia |
| Damage targets | Buildings | Non-significant | Buildings | Buildings | | Buildings, orchard trees, rubber trees, oil palms, plastic | Buildings, sugarcane, plastic | Buildings, eucalyptus trees | Buildings, pine trees, plastic | Buildings |
| Important pest (Rust and Su 2012) | Yes | No | No | Yes | | Yes | Yes | Yes | Yes | Ň |
| Breeding system (Vargo 2019) | ~. | <u>.</u> . | ~· | SF, EF and MF | | ۵. | SF and EF | ۵. | ~· | SF, EF and MF |
| Secondary reproductives (Evans et al. 2013) | Yes | Yes | Yes | Yes | | Yes | Yes | Yes | Yes | Yes |
| Nesting type (Abe 1987) | Single-piece | Single-piece | Single-piece | Single-piece | | Intermediate- piece | Intermediate- piece | Intermediate- piece | Intermediate- piece | Intermediate- piece |
| Feeding group (Donovan et al. 2001) | I | Ι | I | Ι | | I | Ι | I | I | П |
| Occurrences after curation | 42 | 55 | 40 | 311 | | 464 | 367 | 132 | 285 | 320 |
| Short name | Chav | Gbre | limm | Imin | 1 | Caci | Cfor | Cfre | Cges | Hcar |
| Family and species | Gryptotermes havilandi (Sjöstedt, 1900) | Glyp totermes brevicornis (Froggatt, 1897) | Incisitermes immigrans (Snyder, 1922) | Incisitermes minor (Hagen, 1858) | Rhinotermitidae | Coptotermes acinaciformis (Froggatt, 1898) | Captotermes formosanus (Shiraki, 1909) | Coptotermes frenchi (Hill, 1932) | Coptotermes gestroi (Wasmann, 1896) | Heterotermes cardini (Snyder, 1924) |

| Family and species | Short name | Occurrences after curation | Feeding group (Donovan et al. 2001) | Nesting type (Abe 1987) | Secondary reproductives (Evans et al. 2013) | Breeding system (Vargo 2019) | Important pest (Rust and Su 2012) | Damage targets | Native range | Invaded range | Spread methods and risk | References for native and invaded range, and spread methods |
|---|---------------|----------------------------------|--|----------------------------|--|---------------------------------------|---|-----------------------------------|--|--|--|---|
| Haterotermes convexinotatus (Snyder, 1924) | Hcon | 460 | н | Intermediate- piece | Yes | SF, EF and MF | Yes | Grops and buildings | Southern Mexico, Nicaragua, northern Colombia, Panama, northern Venezuela | Puerto Rico, Haiti, Antigua, Barbados, Martinique, Guadeloupe, Saint Kitts, Saint Martin, Galapagos | Probably shipboard infestations in the last centuries and now private vessels, medium risk | Szalanski et al. (2004); Evans et al. (2013) |
| Haterotermes teruis (Hagen, 1858) | Hten | 449 | | Intermediate- piece | Yes | SF, EF and MF | Yes | Grops and buildings | Argentina, Brazil, Bolivia, Colombia, Costa Rica, Ecuador, Guianas, Panama, Panama, Perguay, Perul | West indics | Probably shipboard infestations in the last centuries and now private vessels, medium risk | Szalanski et al. (2004); Evans et al. (2013) |
| Reticulitermes flavipes (Kollar, 1837) | Rfla | 812 | Ι | Intermediate- piece | Yes | SF, EF and MF | Yes | Buildings | Eastern US, northern Bahamas | Canada, Europe, South America, Easter Island | From imported timbers and from railroad ties from North America in the last centuries, but now probably through budding in infested furniture, high risk | Gay (1969); Scheffrahn et al. (2006); Evans et al. (2013); Baudouin et al. (2018); Perdereau et al. (2019) |
| Reticulitermes grassei (Clément, 1977) | Rgra | 33 | Ι | Intermediate- piece | Yes | SF, EF and MF | No | Buildings and oak trees | South- western Europe (France and Spain) | Britain, Azores | Very limited spread, medium risk | Evans et al. (2013) |
| Termitidae | | | | | | | | | | | | |
| Nasutitermes corniger (Motschulsky, 1855) | Ncor | 726 | II | Separate- piece | Yes | MF | Yes | Buildings, ornamental trees | Central, S America, West Indies | New Guinea, Florida | Intercepted in private vessels, high risk | Scheffrahn et al. (2002); Scheffrahn et al. (2005); Scheffrahn and Crowe (2011); Evans et al. (2013) |
| Termes hispaniolae (Banks, 1918) | This | 420 | II | Separate- piece | Yes | <u>.</u> . | No | No damage | Coasts of Central and S America | West indies | Intercepted in shipments of firewood in the last century, low risk | Gay (1969); Evans et al. (2013) |
To address these dynamics, we selected three connectivity variables (four if including urban areas): Accessibility to Cities (ATC, trade and transport related, Weiss et al. (2018)), human population (POP, demography related, Jones and O'Neill (2016)) and a leisure vessels variable (LVE, transport related, Cerdeiro et al. (2020)). The LVE variable draws from a comprehensive 6-layer dataset containing various vessel types, such as commercial and fishing ships, as well as recreational vessels (LVE) like yachts and sailboats.

The ATC layer quantifies the time it takes to travel to the nearest urban area through foot, roads, railways and rivers, as of 2015 (Weiss et al. 2018), providing valuable insights into the pathways through which invasive termite species can be introduced. While future projections are not yet available, the ATC layer was used for the current and future projections.

POP gives a more precise representation of densely populated areas compared to the urban variable, as it considers the number of inhabitants rather than solely the footprint of a building (Jones and O'Neill 2016). Both ATC and POP are anticipated to correlate with furniture transportations, as denser and more connected urban centres facilitate increased exchange. Projection of POP into future scenarios align with land-cover variables, employing the same scenarios and years. For the current year, the SSP2 year 2020 was used, as it is the closest to the present.

The LVE variable (downloaded from the Worldbank.org database) delineates leisure vessels density based on AIS (automatic identification system) positions of leisure vessels between January 2015 and February 2021, with higher densities observed in major marinas, influencing model outcomes (Cerdeiro et al. 2020). As these boats frequently linger in marinas for extended periods, reproductive individuals have ample opportunity to emerge and take flight inland towards illuminated areas (Scheffrahn and Crowe 2011; Hochmair et al. 2023; Scheffrahn 2023). Moreover, leisure vessels, particularly yachts, may traverse oceans via specialised transport vessel (DYT Yacht Transport 2024), thereby extending their potential impact on dispersal patterns. Although no future projections are available, the variable was used for both current and future projections.

All three layers (ATC, POP and LVE) were standardised (same resolution, dimensions, extent and format) using QGIS, following the methodology described earlier. The Pearson correlation analysis (refer to Suppl. material 1: S1) did not result in the elimination of any of the three layers, as none had a correlation higher to 0.70. By integrating these three connectivity variables (four if including urban areas) into our modelling framework, we aim to capture the intricate interplay between private vessels, human populations, furniture exchanges and the potential distribution patterns of invasive termite species.

Elevation variable

Termite diversity typically decreases with increasing elevation, primarily due to lower temperatures that result in unsuitable habitats for warm-adapted species (Gathorne-Hardy et al. 2001; Palin et al. 2011; Chiu et al. 2019). However, higher elevations are also associated with lower air pressure, increased solar radiation, steeper slopes and higher wind speeds, all of which can significantly impact terrestrial insects (Hodkinson 2005). Additionally, elevation has been observed to influence the shape of termite nests in certain species (Jamilu Bala Ahmed et al. 2019). Given these findings, elevation holds the potential to be a significant predictor variable for the distribution of invasive termites. Consequently, an elevation (ELE) layer was acquired from earthenv.org at a 1 km resolution and in a median aggregated format (Amatulli et al. 2018). The layer was then standardised (same resolution, dimensions, extent and format) using the same methodology described earlier in QGIS. The elevation variable had no strong correlation (> 0.70) with the other variables (Pearson correlation analyses, refer to Suppl. material 1: S1), validating its inclusion in the models.

Modelling and evaluation

The entire modelling and evaluation process was conducted in R4.2.0 using the Biomod2 4.2-4 package. We performed modelling analyses by integrating bioclimatic, land-use, connectivity and elevation variables into our models. Additionally, we ran models exclusively using bioclimatic variables to assess outcomes and discern any divergences. The same algorithms (FDA, RF, MAXNET, GAM, GLM, GBM) as described earlier were used for all the modelling. For model training, only 75% of the randomly-selected occurrences were utilised, while the remaining 25% were kept for model evaluation. The performance of the models was assessed using two metrics: True Skill Statistic (TSS, Allouche et al. (2006)) and Area Under a Receiver Operating Characteristic (ROC or AUC, Hanley and Mc-Neil (1982)). To validate the models, a 5+1-fold cross-validation was conducted for each species. This resulted in a total of 108 models (six algorithms multiplied by 5+1 cross-validations multiplied by three pseudo-absence samplings) fitted for each species, considering both current and future shared socioeconomic pathways. The importance (i.e. the contribution to the model) of each variable (climatic, land-cover, connectivity and elevation) for each species was evaluated using the variable importance command from Biomod2.

Ensemble modelling, which combines individual forecasts into a consensus projection (Araújo and New 2007), has become a popular technique in species distribution modelling (Hao et al. 2019). However, it may not be always the best approach if all default settings of Biomod2 are chosen, as it can lead to underperforming models compared to well-tuned individual models (Valavi et al. 2022). Therefore, except for MAXNET, FDA and GBM, the default settings of Biomod2 were not used. For RF, downscaled performance is improved by adding the sampsize option and ntrees was set to 1000 as recommended by Valavi et al. (2022). GAM performed best using the GAM_mgcv algorithm, the binomial family (logit) and the REML method (Pedersen et al. 2019). GLM utilised the binomial family (logit) (Hastie et al. 2001). To ensure that only high-performing individual models were included in the ensemble modelling, a threshold of 0.75 was set for the TSS metric. The weighted average method was employed to create the consensus model, as it provides more robust predictions alongside the mean compared to other methods (Marmion et al. 2009). Finally, the same metrics (TSS and ROC) used for the individual models were used to assess the quality of the final consensus model. For ROC, models can be considered poor for values in the range 0.5-0.7, fair in the range 0.7-0.9 and excellent when the value ranges between 0.9 and 1 (Swets 1988). For TSS, models can be considered poor for values ranging from 0.2 to 0.5, useful when ranging from 0.6 to 0.8 and can be considered good to excellent when ranging from 0.8 to 1 (Coetzee et al. 2009).

Evaluating the range shift between the present and the future

To facilitate the visual comparison between present and future scenarios, the range size function from Biomod2 was used instead of relying on multiple maps. This function computes the number of pixels that are lost, stable or gained, along with their relative proportions, when comparing two species distribution models. To perform this analysis, the current and future ensemble models were transformed into binary predictions (absence: 0 or presence: 1) by applying an optimised threshold derived from TSS (Thuiller et al. 2009). This approach allowed us to generate a single map that delineates the regions where each species is contracting, stabilising, expanding or absent. Additionally, using Biomod2, the net increase (percentage of pixels predicted to be gained compared to the number of pixels currently occupied) and decrease (percentage of pixels currently occupied and predicted to be lost) were calculated for each species. This methodology provides a clear representation of the spatial dynamics for each species and quantifies the net changes in terms of percentage for each species, offering valuable insights into the projected shifts in their distributions.

Mapping high-risk invasion area

To delineate potential high-risk invasion areas, the same methodology as outlined in the previous section was used. However, "lost" and "absent" pixels were converted to 0, while "stable" and "increase" pixels were converted to 1. This adjustment enabled the summation of values for each species across all pixels, providing an estimate of the potential number of species in each pixel under the selected scenario.

Results

Models' performance and variables' importance

The evaluation process supports the robustness and accuracy of the models in predicting species distributions. For ROC, all the individual models could be considered excellent (0.900–1), ranging from 0.968 to 1, while all the ensemble models were close to perfect, ranging from 0.986 to 1 with an excellent average of 0.996. For TSS, all the individual models could be considered good to excellent (0.800–1), ranging from 0.819 to 0.999, while all the ensemble models were good to excellent ranging from 0.879 to 0.994 with an excellent average of 0.958 (Suppl. material 1: S4).

The analysis of variable importance revealed that bioclimatic variables were overall the most important predictors, followed by our four connectivity variables. In contrast, the significance of elevation and land-cover variables (excluding urban land) appears comparatively lower than other variables (Fig. 1, Table 2). The combined use of bioclimatic, land-use, connectivity and elevation variables as predictors refine our projections by reducing by an average of 313% the areas suitable to the establishment of all termite species under study (Table 3).

Amongst the top three most important variables, a bioclimatic variable ranked first for six species and urban land for four species. Ranking second in importance, bioclimatic factors held for six species, whereas urban land held for two species. Accessibility to Cities (ATC) and elevation (ELE) held this position for one species. Lastly, the third-rank variable category encompassed bioclimatic factors for four



Figure 1. Number of times each variable was identified as the most important (First), second most important (Second) and third most important (Third) for each species.

species, C4 perennial crops for two species, ATC for two species, leisure vessels (LVE) and elevation for one species (Fig. 1). Our results underscore the prevailing role of bioclimatic variables and the substantial influence of trade, transport and demography factors (i.e. the connectivity variables) in shaping the distribution patterns of invasive termite species. Concerning the land-cover variables (excluding urban land), only one variable, C4 perennial crops, managed to reach the top three positions. In addition to several bioclimatic and most land-cover variables, the population variable (POP) failed to secure a position in the top three average contributions. Amongst the bioclimatic variables, those linked to temperature held a significant presence in the top three, occurring seven times more frequently as variables tied to precipitation (Fig. 1, Table 2, Suppl. material 1: S5 for the response curves).

Potential current habitat suitability

The majority of the ten invasive species demonstrate significant potential for occupying a wide range of habitats for the current climate conditions and socioeconomic development. Although no overarching trends apply to all our species, some preferences can be observed with our models. For instance, species such as *Cryptotermes brevis*, *Cryptotermes domesticus*, *Incisitermes immigrans*, *Incisitermes minor*, *Coptotermes formosanus*, *Coptotermes gestroi* and *Reticulitermes flavipes* all show preference for large and well-connected urban areas, while *Cryptotermes dudleyi*, *Cryptotermes havilandi* and *Nasutitermes corniger* appear to be slightly more restricted to environments resembling their native habitats (Table 3, Suppl. material 1: S6 for all the maps). Below, we will describe the results of the models for each species, focusing solely on their statistical performance without considering their ecological context or the actual conditions of their habitats. For a deeper analysis incorporating these factors, please refer to the Discussion section. **Table 2.** Average contribution of each predictive variable to the model for each species. In total, eight variables (2/19 for bioclimatic and 2/12 for land-use) were chosen for each species (see Suppl. material 1: S2 and S3 for further details). The three highest values are highlighted. The name of the termite species is as follows: *Cryptotermes brevis*, Cbre; *Cryptotermes domesticus*, Cdom; *Cryptotermes dudleyi*, Cdud; *Cryptotermes havilandi*, Chav; *Incisitermes immigrans*, Iimm; *Incisitermes minor*, Imin; *Coptotermes formosanus*, Cfor; *Coptotermes gestroi*, Cges; *Reticulitermes flavipes*, Rfla; and *Nasutitermes corniger*, Ncor.

| Variable | | Kalotermitidae | | | | | Rhinotermitidae | | | Termitidae |
|---|-------|----------------|-------|-------|-------|-------|-----------------|--------|-------|------------|
| | Cbre | Cdom | Cdud | Chav | Iimm | Imin | Cfor | Cges | Rfla | Ncor |
| Bioclimatic | | | | | | | | | | |
| Annual Mean Temperature | | | | | | | 0.159 | | | |
| Mean Diurnal Range | | | 0.218 | | | | | | | |
| Isothermality | | | | | | | | | | |
| Temperature Seasonality | | | 0.407 | | | | | | | |
| Max Temperature of Warmest Month | | | | | | | | | | 0.086 |
| Min Temperature of Coldest Month | | | | | | | | | | |
| Temperature Annual Range | | 0.407 | | 0.572 | 0.662 | | | | 0.090 | 0.484 |
| Mean Temperature of Wettest Quarter | | 0.354 | | 0.311 | | | | | | |
| Mean Temperature of Driest Quarter | | | | | | | | | | |
| Mean Temperature of Warmest Quarter | | | | | | | | | 0.177 | |
| Mean Temperature of Coldest Quarter | 0.203 | | | | | 0.164 | | 0.2853 | | |
| Annual Precipitation | | | | | | | | | | |
| Precipitation of Wettest Month | | | | | 0.088 | | | | | |
| Precipitation of Driest Month | 0.038 | | | | | | | | | |
| Precipitation Seasonality | | | | | | | | | | |
| Precipitation of Wettest Quarter | | | | | | | 0.086 | | | |
| Precipitation of Driest Quarter | | | | | | | | 0.047 | | |
| Precipitation of Warmest Quarter | | | | | | | | | | |
| Precipitation of Coldest Quarter | | | | | | 0.121 | | | | |
| Land-use | | | | | | | | | | |
| C3 annual crops | | | | | 0.097 | | | | | 0.029 |
| C3 nitrogen-fixing crops | | | | | | | | | | |
| C3 perennial crops | | | | | | | | | | |
| C4 annual crops | | | | | | | | | | |
| C4 perennial crops | | | 0.161 | 0.071 | | | | | | 0.057 |
| Managed pasture | | | | | | | | | | |
| Forested primary land | | 0.121 | | | | 0.061 | | | 0.061 | |
| Non-forested primary land | 0.015 | | 0.067 | | | | | 0.025 | | |
| Rangeland | | | | 0.101 | | | 0.024 | | | |
| Potentially forested secondary land | | | | | | | | | | |
| Potentially non-forested secondary land | | | | | | | | | | |
| Connectivity | | | | | | | | | | |
| Urban land | 0.284 | 0.090 | | | 0.252 | 0.543 | 0.468 | 0.233 | 0.360 | |
| Accessibility to cities | 0.119 | 0.263 | 0.111 | 0.010 | 0.152 | 0.065 | 0.014 | 0.159 | 0.073 | 0.095 |
| Population density | 0.020 | 0.116 | 0.077 | 0.057 | 0.079 | 0.025 | 0.011 | 0.045 | 0.028 | 0.012 |
| Leisure vessels | 0.019 | 0.060 | 0.029 | 0.148 | 0.019 | 0.004 | 0.003 | 0.004 | 0.006 | 0.007 |
| Elevation | | | | | | | | | | |
| Elevation | 0.014 | 0.403 | 0.137 | 0.085 | 0.064 | 0.018 | 0.085 | 0.232 | 0.050 | 0.016 |

Kalotermitidae

Cryptotermes brevis, originating from Coastal Chile and Peru, has expanded its distribution to encompass North and South America, western Africa, the Azores, Australia (around Brisbane) and numerous Pacific and Atlantic islands (Table 1). In addition to its native range, model analysis indicates current suitability predominantly in the urban areas of eastern US, as well as in the West Indies, throughout patches of Central and South America and around Lagos, Lake Victoria and Lower Egypt in Africa where it has already established itself. In Europe and Asia, the

Table 3. Summary of the main results. Native range, invaded range, potential current habitat suitability, range shift between our models and our models using only bioclimatic variables, potential lost and new ranges for the most pessimistic scenario and range shift for each scenario according to our models for each species.

| | | | | Differences | Potential lost and new ranges | Range shift between current and: | | |
|----------------------------|---|---|--|--|--|----------------------------------|-----------------------|-----------------------|
| Family and species | Native range | Invaded range | Potential current habitat suitability (See Suppl. material 1: S6 for maps) | between multifactorial modelling and bioclimatic modelling | for SSP5-8.5 2041–2060 compared to potential current habitat (See Suppl. material 1: S6 for maps) | SSP2-4.5 2021-2040 | SSP2-4.5 2041–2060 | SSP5-8.5 2041–2060 |
| Kalotermitida | e | | | | | | | |
| Cryptotermes brevis | Coastal Chile, Peru | S and N America, W Africa, Azores, Australia (Brisbane), Fiji, Pacific and Atlantic islands, Egypt | Mainly cities of eastern US, West Indies, big cities of Central and South America, around Lagos, Lake Victoria and Lower Egypt. Big port towns in Europe, large economic areas of Asia and a few cities of the eastern coast of Australia | 34.79% | New ranges: deeper into the US, Europe, India, China, and Japan, western Australia. Some lost ranges: Central America, Brazil, India, Indonesia | 5.47% | 3.12% | -11.85% |
| Cryptotermes domesticus | SE Asia | China, Taiwan, Japan, Australia, Pacific Ocean, Polynesia | SE Asia, southern coast of China, south-eastern coast of India, Japan, Taiwan, Central America, West Indies, Florida and major cities of the Guinean coasts | -1175.27% | New ranges: deeper into SE Asia, eastern and western coasts of Africa, Florida, Central and South America | -22.66% | 19.15% | 81.21% |
| Cryptotermes dudleyi | SE Asia | India, Bangladesh, Indian Ocean, East Africa, Australia, Micronesia, South America | SE Asia, southern coast of China, India, Japan, Taiwan, Central America, South America, West Indies, Florida and major cities of the Guinean coasts | -47.73% | Lost ranges: mainly in South America, western Africa and India | -37.49% | -60.96% | -29.22% |
| Cryptotermes havilandi | West Africa | E Africa, India, S America, West Indies and Indian islands | Western Africa, West Indies, Central and coastal South America, SE Asia, Sri Lanka, southern tip of India | -120.91% | New ranges: deeper into Central and South America, Africa, India and SE Asia | 16.11% | 47.04% | 105.34% |
| Incisitermes immigrans | Central and S America | Pacific Ocean, Hawaii, Japan | Central and S America, western Africa, SE Asia | -256.91% | New ranges: large urban areas of the US and Australia; deeper into Africa and SE Asia. Lost ranges: in some parts of South America and western Africa | -17.17% | 2.62% | 17.11% |
| Incisitermes minor | South- western US and northern Mexico | Eastern US, Canada, China, Pacific Ocean, Japan | Large cities of North America, Europe, around the Mediterranean Sea and important economic areas of Asia and Australia | -168.78% | New ranges: deeper into the US, Europe, Middle-East, Australia, China | 34.95% | 64.44% | 80.98% |
| Rhinotermitic | lae | | | | | | | |
| Coptotermes formosanus | China and Taiwan | Japan, US, Israel | Large cities of: south-eastern US, south-eastern China, Japan, India, Indonesia, Australia, Brazil, Argentina, Puerto Rico, Israel and Egypt | -1059.63% | New ranges: large urban areas of the US, Europe, western Africa and deeper into China, Japan, India, Indonesia, Australia, Brazil, Argentina, Israel and Egypt. Lost ranges: in a few places between China and Vietnam | 67.88% | 77.68% | 174.70% |
| Coptotermes gestroi | SE Asia | Taiwan, Pacific Ocean, Micronesia, Mexico, Florida, West Indies, Brazil | SE Asia, Brazil, West Indies, Florida as well as large economic areas of: south-eastern China, Japan, India, Australia, western Africa. In a few cities of the US and Europe | -216.41% | New ranges: more urban areas of US and Europe, deeper into Central America, South America, Africa, India, China, Japan, SE Asia and Australia | 38.96% | 54.34% | 28.13% |
| Reticulitermes flavipes | Eastern US, northern Bahamas | Canada, Europe, South America, Easter Island | Eastern and western US, southern South America, most of Europe and the coasts of the Mediterranean Sea, most of eastern China, Korea, Japan and the main cities of Australia | -72.68% | New ranges: deeper into the US, Europe, southern South America and Africa, southern Australia, Japan. Lost ranges: US (Texas, Louisiana, Arkansas, Mississippi), northern Africa, China | 38.26% | 33.23% | 47.25% |
| Termitidae | | | | | | | | |
| Nasutitermes corniger | Central, S America, West Indies | New Guinea, Florida | Central America, South America, West Indies, Florida, tropical Africa and tropical India as well as SE Asia | -46.24% | Lost ranges: mainly South America but also in some parts of Central America and tropical Africa | -21.83% | -54.24% | -34.56% |

model suggests some suitability in large economic hubs such as major port cities in Europe, the Guangdong-Hong Kong-Macao Greater Bay Area in China, Jakarta and Tokyo. In Australia, suitability is limited to a few cities on the eastern coast where *Cr. brevis* is already established (Table 3, Suppl. material 1: S6).

Cryptotermes domesticus, originates from Southeast Asia and has invaded China, Taiwan, Japan, Australia and Pacific islands (Table 1). Modelling shows significant suitability beyond its native range, particularly along the southern coast of China, south-eastern coast of India and major cities in Japan and Taiwan. Some areas show less likely suitability due to the presence of the mutually exclusive *Cr. brevis* (Scheffrahn et al. 2009), such as Central America, the West Indies, Florida and major cities along the Guinean coasts (Table 3, Suppl. material 1: S6).

Cryptotermes dudleyi, also originating from Southeast Asia, has already invaded India, Bangladesh, Indian Ocean islands, eastern Africa, Australia, Micronesia and South America (Table 1). Modelling suggests current suitability similar to *Cr. domesticus*, but with larger coverage, especially in India (Table 3, Suppl. material 1: S6).

Cryptotermes havilandi, originating from western Africa, has spread to eastern Africa, India, South America, Indian Ocean islands and the West Indies (Table 1). Modelling suggests strong suitability in areas where it has already spread, such as the West Indies and coastal South America, as well as Southeast Asia, Sri Lanka and the southern tip of India (Table 3, Suppl. material 1: S6).

Incisitermes immigrans is native to Central and South America and, though not a structural pest, has been introduced to several Pacific islands, such as the Galapagos, Polynesia, Hawaii and Japan (Table 1). Beyond the native range, modelling reveals primarily suitability in other tropical regions like western Africa and south-eastern Asia (Table 3, Suppl. material 1: S6). Japan shows limited suitability according to the models.

Incisitermes minor, native to south-western USA and northern Mexico, has extended its range to eastern USA, Canada, China, Pacific Islands and Japan in part through the transportation of infested furniture (Chouvenc, personal communication, January 2024, Table 1). In addition to its endemic range, modelling indicates potential suitability in major cities of Europe and around the Mediterranean Sea, as well as in key economic areas of Asia (mainly in China and Japan) and Australia. South America and Africa have high suitability in their largest cities (Table 3, Suppl. material 1: S6). Its spread is ensured by the transportation of infested furniture since *I. minor* does not disperse to new localities by imago flights (Scheffrahn, personal communication, March 2024).

Rhinotermitidae

Originating from China and Taiwan, *Coptotermes formosanus* has established populations in the US, Hawaii, Israel and Japan (Table 1). Beyond its native range, modelling suggests suitability patterns consistent with its current distribution, particularly in large cities in south-eastern US, Japan, Israel and Egypt, with additional areas of concern in the less likely humid tropics like India, Indonesia, Australia, Brazil, Argentina and Puerto Rico (Table 3, Suppl. material 1: S6).

Coptotermes gestroi, native to Southeast Asia, has become invasive in Taiwan, Micronesia, Mexico, Florida, the West Indies, Brazil and several Pacific Islands (Table 1). Beyond the native range, the modelling shows suitability in Brazil, the West Indies and Florida, where it is already present, as well as potential suitability

in major economic centres in China, Japan, Australia and western Africa (Table 3, Suppl. material 1: S6).

Reticulitermes flavipes, a native pest of the eastern US and the northern Bahamas, has been introduced to Canada, Europe, South America and Easter Island (Table 1). Beyond the native range, modelling reveals large suitability in regions where other pestiferous *Reticulitermes* species are present, such as western US, southern South America, most of Europe, the coasts of the Mediterranean Sea, eastern China, Korea, Japan and major cities in Australia (Table 3, Suppl. material 1: S6).

Termitidae

Nasutitermes corniger, a pest native to Central and South America and the West Indies, has spread to Florida and New Guinea (Table 1). Modelling suggests potential suitability across most tropical regions outside its native range, in Africa, India and Southeast Asia (Table 3, Suppl. material 1: S6).

Range shift in a changing climate and socioeconomic development

In the short term (2021–2040) and under the SSP2-4.5 scenario, four species are projected to have a significant (> 20%) expanded range: *I. minor* by 35%, *R. flavipes* by 38%, *Co. gestroi* by 39% and *Co. formosanus* by 68%. In contrast, three species are expected to experience a significant decline in their habitat range: *N. corniger* by 22%, *Cr. domesticus* by 23% and *Cr. dudleyi* by 37%. Three species, *Cr. brevis, Cr. havilandi* and *I. immigrans*, are forecast to maintain their current distribution with minimal variations during this period and scenario (Fig. 2, Suppl. material 1: S7).

When considering the long term (2041–2060) under the same SSP2-4.5 scenario, the trend remains consistent, except that one more species, *Cr. havilandi*, is expected to experience a significant range expansion, by 47% instead of the previous 16% observed in the short term (Fig. 2, Suppl. material 1: S7). For most species, the change in range becomes even more pronounced during this later period.

Shifting to a more pessimistic scenario ("fossil-fuelled scenario", SSP5-8.5) reveals a broader impact, with six species significantly increasing their habitat range. *Co. gestroi* is expected to expand by 28%, *R. flavipes* by 47%, *Cr. domesticus and I. minor* by 81%, *Cr. havilandi* by 105% and *Co. formosanus* by 175%. Conversely, *Cr. dudleyi* and *N. corniger* could experience a significant reduction in range, by 29% and 35%, respectively, under this scenario; while *Cr. brevis* could see a slight decrease of 12% (Fig. 2, Suppl. material 1: S7).

Overall, the average range shift is consistently positive for each scenario and increases over time as the combined effects of climate change and socioeconomic developments intensify. Specifically, in the short term (2021–2040 SSP2-4.5), the average range shift is low at 10%. In the long term (2041–2060) under the same scenario, this increases to 19%. In a scenario characterised by higher fossil fuel reliance, the range shift reaches 46% (Suppl. material 1: S7). These percentages represent net changes in terms of pixels and do not offer insights into the specific regions that may be affected in the future. The right side of Fig. 2 addresses precisely this limitation by showing the number of species potentially suitable in each pixel of the map for each scenario. Upon closer examination, regardless of the scenario, it appears clear that major cities and thriving economic hubs are the most at risk, especially in North America, South America, western Africa, Europe



Figure 2. Potential projected range shift (left) and high-risk invasion map (right) for selected periods and socioeconomic-shared pathways.

and the Asia Pacific Region. In these areas, the number of potential species for the worst scenario is between 5 and 10. When focusing on individual countries, several seem to be especially at high risk: the US, Brazil, Nigeria, China, Indonesia, Japan and Australia. These countries could host a substantial number of cities with a high number of invasive species. Nevertheless, all continents have significant areas suitable for more than four species at a time (Fig. 2).

To look at the range shift for each species separately, a comprehensive set of 30 distinct maps providing a visual depiction of the changes for each species, timeframe and shared socioeconomic pathway has been developed (Suppl. material 1: S6). Overall, the trend shows that, under more pessimistic scenarios and over time, species tend to shift towards higher latitudes, both northwards and southwards. Most species are, however, expected to experience a slightly reduced range in lower latitudes (Table 3, Suppl. material 1: S6). For instance, a striking comparison can be made amongst three contrasting species, *Incisitermes minor*, *Reticulitermes flavipes* and *Nasutitermes corniger*. *I. minor*, originating from the south-western US and northern Mexico, has spread likely through the transportation of infested Incisitermes minor: Current vs 2041-2060 SSP5-8.5



Reticulitermes flavipes: Current vs 2041-2060 SSP5-8.5



Nasutitermes corniger: Current vs 2041-2060 SSP5-8.5



Figure 3. Potential projected range shift for *Incisitermes minor*, *Reticulitermes flavipes* and *Nasutitermes corniger* between potential current suitability and the period of 2041–2060 under the SSP5-8.5 scenario.

furniture to eastern US, Canada, China, various islands in the Pacific Ocean and Japan. In a pessimistic scenario (SSP5-8.5 2041–2060), *I. minor* is expected to extend its range across the US, Europe, Japan, China and Australia, particularly in densely urbanised regions (Fig. 3, Table 3). In contrast, according to our models, both *R. flavipes* and *N. corniger* show a lower dependency on urban environments,

especially *N. corniger. R. flavipes* is native to eastern US and northern Bahamas and has been introduced to Canada, Europe, South America and Easter Island. Under similar scenarios, its range potentially expands significantly across the US, Europe, southern Australia, southern Africa and southern South America. However, at the same time, its suitable range could decrease in southern US and in southern parts of China (Fig. 3, Table 3). On the other hand, *N. corniger*, originating from Neotropical Regions (Central and South America, West Indies), has established itself in only a few areas, in Florida and New Guinea. According to our models, *N. corniger* is projected to experience significant declines in its potential suitable tropical range, particularly in Africa and Brazil (Fig. 3, Table 3).

Discussion

The aim of our study was to predict the potential global spread of highly invasive termite species. We expanded the analysis beyond commonly considered bioclimatic and land-cover variables by incorporating elevation and connectivity factors, which encompass trade, transport and demographic patterns. Our objective was to forecast the short-term (2021–2040) and long-term (2041–2060) distribution of these species, considering climate change and socioeconomic development worldwide, under two shared socioeconomic pathways, SSP2-4.5 ("middle of the road") and SSP5-8.5 ("fossil-fuelled development"). Climate change, trade, transport and socioeconomic changes will be the main drivers of biological invasions in the coming decades (Essl et al. 2020). Despite their economic and ecological impact, only a few invasive termite species have been subject to distribution modelling so far (e.g. Li et al. (2013); Guerreiro et al. (2014); Tonini et al. (2014); Buczkowski and Bertelsmeier (2017); Goodman et al. (2022)).

Temperature and precipitation play a crucial role in determining the distribution of termites (Eggleton 2000), thereby explaining the predominant reliance on bioclimatic variables in most termite distribution models (Tonini et al. 2014; Buczkowski and Bertelsmeier 2017; Goodman et al. 2022). However, our study highlighted the importance of considering trade, transport and demographic factors in understanding termite invasions, with a particular emphasis on urbanisation and connectivity. Indeed, the period since the 1960s has witnessed an unprecedented upsurge in global transportation and urban expansion, catalysed by the advent of commercial jet aircraft. This trend highlights the escalating interconnectivity amongst urban hubs globally and its profound implications for termite population dispersal. The impact of propagule pressure on the success of invasions (Lockwood et al. 2005) further accentuates the critical significance of these aforementioned factors.

Our findings reveal that numerous invasive termite species could find suitable habitats in heavily urbanised and connected areas within major economic regions of every continent (excluding Antarctica). This trend is particularly evident as climate change and socioeconomic development intensify, providing more favourable bioclimatic conditions and human infrastructure for many species. Moreover, land-use changes – whether driven by urbanisation or deforestation for agriculture – profoundly shape species distribution (Jung et al. 2019). Our study introduces the use of land-cover variables within various scenarios of socioeconomic development, thereby enhancing the precision and accuracy of our climate and socioeconomic change projections. Our results align with other research studying climate change's impact on termites, showing an expansion of the distribution for several

economically important termite species worldwide (Buczkowski and Bertelsmeier 2017) and in South Korea (Lee et al. 2021). However, our study is more comprehensive, as it encompasses not only bioclimatic and/or elevation variables, but also land-cover and connectivity factors.

Variables' importance

Our study validates the significance of bioclimatic conditions as fundamental variables to understand termite distribution patterns (Eggleton 2000); amongst these factors, temperature emerges as the most influential determinant. We also note the minor influence of precipitation variables compared to temperature; a finding consistent with Guerreiro et al. (2014). It is worth noting, however, that invasive termites tend to establish nests within controlled-temperature human structures (Su and Scheffrahn 1998), highlighting the importance of considering not only bioclimatic factors, but also variables reflecting termite movements through these human structures ("connectivity" in this study). Our analysis highlights the significant role of the connectivity variables, particularly urban cover and Accessibility to Cities (ATC) and, to some extent, leisure vessels (LVE), in explaining the distribution of invasive termites. This echoes previous research showing the substantial predictive power of socioeconomic variables, ranking second only to bioclimatic and habitat variables (Bellard et al. 2016). The significance of human activity in facilitating the establishment of invasive termite populations is notable, given their primary reliance on wood, a ubiquitous commodity found in every household, boat and city worldwide. Regions with higher human activity should be predisposed to facilitating establishment of invasive termite populations. However, our results suggest that the human population (POP) layer contributes relatively little to the predictive capacity of our distribution models. This could be attributed to its high correlation with urban cover (0.53), suggesting potential redundancy with greater efficiency. Notably, areas such as seaports, airports and industrial zones, despite exhibiting lower population densities, exert a more pronounced influence on invasion risk compared to population density itself (Bellard et al. 2016).

Elevation (ELE) was found to play a minor role in predicting the distribution of invasive termites. While Guerreiro et al. (2014) reported a significant contribution of elevation to their model for *Cr. brevis*, our modelling revealed that the distribution of this species is primarily shaped by a combination of bioclimatic (bio11) and connectivity (urban and ATC) factors, with elevation contributing by less than 2%. If Guerreiro et al. (2014) used four variables (three bioclimatic factors and elevation) per species, our approach, utilising a comprehensive set of eight variables per species, likely attributed greater significance to other variables, reducing the prominence of elevation.

A previous study had integrated land-cover variables to project the spatial distribution of two invasive termite species (Tonini et al. 2014), but the extent of their contribution to the models was not reported. Here, excluding urban cover, the impact of land-cover variables – encompassing the cultivation of crops, including C3 perennial and C4 annual varieties, as well as forested, deforested and pasture areas – showed limited influence on the models. These results are expected given that agricultural crops are subject to significant disruption from human activities (e.g. pesticide applications). However, forthcoming environmental regulations and enhanced human health measures could bolster the survival rates of invasive termite species within these ecosystems (Haifig et al. 2008).

Current habitat suitability

Most of the ten invasive termites we studied show the ability to occupy a wide range of habitats, especially urban areas, confirming the global threat posed by invasive termites. Contrary to previous descriptions (Buczkowski and Bertelsmeier 2017), our models portray a more confined distribution, but with a heightened focus on urban and well-connected areas. This result is in line with the biology of invasive termites, often establishing themselves initially in urbanised localities before spreading to natural environments.

We also noted important differences for Cr. brevis, with a narrower suitable range compared to previous reports (Guerreiro et al. 2014; Buczkowski and Bertelsmeier 2017). This species primary inhabits in buildings outside its endemic range (Scheffrahn et al. 2009) and places of similar endemic climate such as Morocco (Najjari et al. 2023). Our modelling accentuated a preference for cities and economically developed regions, especially in the Americas and Africa. Interestingly, Asia and Europe, aside from major cities like Tokyo, Jakarta, Manila, Shanghai and the Guangdong-Hong Kong-Macao Greater Bay Area, showed less suitability, likely due to the presence of other Cryptotermes species in the Asia Pacific habitat (Scheffrahn et al. 2009; Guerreiro et al. 2014). Similarly, our models for Cr. domesticus, Cr. dudleyi, Cr. havilandi and I. immigrans identified limited distribution along the coastlines of tropical countries in Africa and South America, as well as suitability in most of Southeast Asia, especially Indonesia. The suitability is particularly high in major cities of these regions like São Paulo, Rio de Janeiro, Jakarta, Greater Bay Area or Lagos. This contrasts with the broader suitability suggested by Buczkowski and Bertelsmeier (2017) for these four species across tropical regions. These variations might be attributed to our comprehensive integration of land-cover, elevation and connectivity variables: elevation was a significant variable for Cr. domesticus, while C4 perennial crops was for Cr. dudleyi, leisure vessels (LVE) for Cr. havilandi, and both Accessibility to cities and urban land for I. immigrans. A similar divergence emerged for *I. minor* in higher latitudes, highlighting the strong influence of large urbanised and connected areas (e.g. most large US cities, southern California, São Paulo, London, Belgium, Madrid, Greater Bay Area and main cities of eastern Australia).

Our models for Co. formosanus and Co. gestroi also showed a distribution heavily associated with urban areas (see also Li et al. (2013) and Tonini et al. (2014)) both in their native and introduced regions. The use of connectivity variables for both species likely contribute to these results, accounting for 50% and 44% to the models, respectively. On the other hand, we identified suitability for Co. gestroi in European and American cities, such as Paris, London, Madrid or New York, although such suitability is highly improbable due to the species' restriction to tropical regions, necessitating favourable conditions, such as adequate humidity and high temperatures (Li et al. 2013). Nonetheless, our models indicate high suitability for Co. gestroi in more likely regions, such as large economic areas in tropical and subtropical regions like western Africa, Southeast Asia or south-eastern China. Conversely, Coptotermes formosanus, with a warm temperate to subtropical distribution (Cao and Su 2016), presented heightened risk in large cities of south-eastern US and Asia, as well as South America. As the effects of climate change reshape ecosystems globally, disparities between the two species are likely to become more apparent, especially considering instances like Co. formosanus

potentially expanding its range into the Korean Peninsula due to increasing temperatures (Lee et al. 2021).

Regarding *Reticulitermes flavipes*, our models suggest a threat to most cities in temperate and subtropical regions, particularly in its native range in the US, but also in Europe and eastern Asia, with a notable focus on urban areas (the urban layers contribute 36% to the projections). Our results partially disagree with those of Buczkowski and Bertelsmeier (2017) who suggested potential suitability in higher latitudes (e.g. Iceland, Norway, Alaska or Patagonia) and the Tropics (Indonesia, Ecuador, Colombia). Such locations appear unlikely given the current distribution of the species (Evans et al. 2013). Modelling also shows that the distribution of *R. flavipes* does not extend to cold regions, such as the Alps or the Carpathians in Europe, a limitation attributed to the elevation layer.

Finally, our results suggest that *N. corniger* is highly adapted to tropical regions. Our results agree with those of Buczkowski and Bertelsmeier (2017), except that the latter also designate parts of southern Argentina, Chile, Morocco, the Arabian Peninsula and Australia as potentially suitable. This seems unlikely, as this species is strictly restricted to tropical regions, its actual distribution ranging from southern Mexico to southern Brazil and northern Argentina, including most of the West Indies (Scheffrahn et al. 2005).

Key functional traits to invasive success

Facon et al. (2006) proposed three scenarios to understand the relationship between invasive species and their new environments, shedding light on the role of human activities in biological invasions. The first scenario suggests that invasion is limited by the small population size of the invasive propagule (to establish a viable population), but changes in migration patterns, possibly caused by human activity, can trigger the invasion. The second scenario suggests that invasion can proceed if the introduced species finds a suitable match with the environment; this adequacy can be facilitated by changes in the biotic or abiotic environment, changes often influenced by human activities. The third scenario highlights genetic changes in the invader as a factor initiating invasions, including reduced genetic variance, inappropriate range of adaptive variation in the original species and maladaptation due to excessive migration. Invasive termites fit perfectly within this framework. Migration change (e.g. by wood exchanges through furniture or private vessels) and human activities in urban areas offer many opportunities to establish and invade new territories. Evans et al. (2013) identified three characteristics common to all 28 invasive termite species that increase their likelihood of successful propagule. First, invasive termites are all wood feeders (Table 1).

Secondly, nesting in wood is particularly advantageous for invasions given the ubiquitous presence of wood in households worldwide (e.g. Grace et al. 2009). While some species live, eat and nest exclusively in wood (called single-piece nester, here the Kalotermitidae species), others (here the Rhinotermitidae species) begin their colonies within wood or at the soil-wood interface before establishing their colonies underground or in another piece of wood (Ferraz and Cancello 2004; de Lima et al. 2006). The latter are called intermediate-piece nesters and will forage outside their colony after this single-piece stage (Abe 1987). *Nasutitermes corniger*, though typically nesting on trees, poles, walls or directly on the ground (Thorne 1980), can also establish an incipient colony inside small wood pieces (Thorne and

Haverty 2000; Scheffrahn et al. 2014). All ten invasive species can, therefore, use wood as a hidden mean of transport for at least part of their lifecycle.

All ten invasive species share a third characteristic: the ability to produce secondary reproductives, typically through neoteny of nymphs (nymphoid reproductives), workers or pseudergates (ergatoid reproductive) or through the retention of alates (adultoid reproductive) (Myles 1999). In the case of *N. corniger*, ergatoids are produced, rendering any piece of wood with foraging workers a viable propagule at any time of year (Thorne and Noirot 1982). These ergatoids, combined with the fact that they are polygynous, probably allowed *N. corniger* to invade New Guinea 100 years ago via sugar trade shipping from the West Indies, travelling more than 15,000 km (Roisin and Pasteels 1986; Scheffrahn 2013).

Consequently, all ten of our highly-invasive species are capable of nesting in wood, whether in furniture or in boats (Scheffrahn 2023; Chouvenc, personal communication, January 2024), rendering invasions extremely likely, be it from one household to another or from a marina to nearby coastal residences, as exemplified by N. corniger or Coptotermes (Scheffrahn and Crowe 2011; Scheffrahn et al. 2014; Hochmair et al. 2023; Scheffrahn 2023). Flying imagoes are attracted by light poles and illuminated houses near marinas, serving as an initial entry point into the lands (Scheffrahn et al. 2014; Scheffrahn, personal communication, January 2024). However, once arriving in a new environment, invasive species may face new challenges in establishing themselves if the environment differs or is already saturated by other species. To succeed under such conditions, the species may undergo substantial adaptations (Facon et al. 2006). For example, native populations of Reticulitermes *flavipes* consist of colonies headed by monogamous pairs of primary reproductives; in contrast, introduced populations in France exhibit a breeding structure where hundreds of related neotenics reproduce while colonies lose intraspecific aggression and get a propensity to fuse (Perdereau et al. 2013; Perdereau et al. 2015). These changes in colonies composition and organisation confer advantages in terms of resource exploitation and competition, thus facilitating ecological dominance.

Some termite species have biological and/or behavioural characteristics that can help them invade and survive in new territories. For instance, Reticulitermes species are naturally well-adapted to low temperatures and can move the nest to deep underground during the winter (Cabrera and Kamble 2001; Takata et al. 2023). This behavioural trait can prove decisive in extending their range northwards (Cabrera and Kamble 2001; Takata et al. 2023). Additionally, climate change may relax constraints on naturalisation and, hence, increase the hybridisation risk amongst invasive and native populations (e.g, Co. gestroi and Co. formosanus in Florida), further influencing invasion dynamics (Chouvenc et al. 2015; Fournier and Aron 2021). Elevated temperatures also enhance termite foraging activity (Kasseney et al. 2011; Zanne et al. 2022). For example, Co. gestroi and Co. formosanus have a significantly higher wood consumption rate between 22-35 °C than between 10-15 °C (Patel et al. 2019). Finally, biological invasions could also be facilitated by the bridgehead effect (Lombaert et al. 2010). Introduced populations are often the source of other invasions (Yang et al. 2012; Sherpa et al. 2019; Blumenfeld and Vargo 2020). These secondary invasions, therefore, originate from populations that have already succeeded in overcoming all the barriers - geography, survival, reproduction, dispersal, environment - that punctuate from introduction to propagation invasion processes. For instance, native to eastern Asia, Co. formosanus first established populations in Hawaii before invading the US mainland (Blumenfeld et al. 2021).

What to expect in the future: combined effects of global warming, urbanisation and growing connectivity

Urbanisation is an inevitable phenomenon as projected by the United Nations Department of Economic and Social Affairs (UN DESA 2020): up to two-thirds of the global population is expected to reside in urban areas by 2050. Moreover, the number of megacities (with over 10 million inhabitants) is projected to rise from 33 in 2018 to potentially 43 in 2030. Urbanisation and megacities, notably through the urban heat-island effect (Szulkin et al. 2020), will therefore constitute invasion hotspots that may serve as bridgeheads in surrounding natural habitats as temperatures increase due to climate change. Our study demonstrates that most species could thrive in a changing climate and an increasingly urbanised world, particularly under a fossil-fuelled future (SSP5-8.5). This finding aligns with other studies on different and shared species and using different variables, collectively suggesting a consensus that climate change will generally increase the distribution of most invasive or pest termites (e.g. Tonini et al. (2014); Buczkowski and Bertelsmeier (2017); Lee et al. (2021)). While some species might experience localised contractions in their ranges, they are anticipated to make gains in other regions, particularly within densely urbanised areas. This trend is evidenced by our incorporation of connectivity variables, which reveals the potential for more substantial and costly damage. For instance, our modelling shows that Cr. brevis could experience a reduced tropical range, yet extend its distribution into urbanised higher latitude regions. Thus, a contraction in range does not necessarily translate into a reduction in damage costs, especially for termites that predominantly target human structures, such as species from the Kalotermitidae and Rhinotermitidae families. Conversely, other species like Co. formosanus could mainly expand their range, with close to zero reduction compared to their potential current suitable habitat. The Formosan subterranean termite could potentially thrive in higher latitudes in a fossil-fuelled world, placing most American, European and eastern Asian cities at risk. On the other hand, N. corniger will lose significant suitability in a fossil-fuelled world within Brazil and central Africa, probably due to the combined effects of increased deforestation and less favourable bioclimatic conditions.

Overall, most of these ten invasive termites will thrive in a changing climate and a heavily transformed world marked by escalating urbanisation, particularly under a fossil-fuel-dependent trajectory. Even if our models do not consider the full force and speed of future connectivity, the undeniable expansion potential of the ten termite species and, therefore, the damage concomitant with invasions, underscores the urgency of addressing climate change, urbanisation and growing connectivity. These factors will be crucial in contributing to the spread of invasive termites, posing a significant threat not only to the economies of invaded regions, but also, to some extent, to biodiversity and ecosystem functioning.

Conclusion

As our world becomes increasingly interconnected and urbanised, it is imperative to recognise the importance of incorporating connectivity variables – trade, transport and demography – into invasive species distribution modelling, particularly for termites. We have demonstrated that ten highly-invasive termite species could potentially spread to heavily-urbanised and connected areas in tropical, subtropical and, to a lesser extent, temperate regions. This risk is amplified with the combined effects of global warming, urbanisation and growing connectivity. Most species could experience expanded ranges or find suitable habitats in more urbanised and connected areas, resulting in costly damage regardless of range shifts. Major cities, particularly in tropical, subtropical and temperate areas, should swiftly implement rigorous termite control measures and citizen-science initiatives to prevent and detect further invasions before irreversible damage occurs.

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

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Author contributions

Edouard Duquesne: Data curation, Formal analysis, Methodology, Software, Visualisation, Writing – original draft.

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Data availability

All of the data that support the findings of this study are available in the main text or Supplementary Information.

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Supplementary material 1

Supplementary tables and figures (S1 to S7)

Authors: Edouard Duquesne, Denis Fournier

Data type: docx

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Link: https://doi.org/10.3897/neobiota.92.115411.suppl1

Supplementary material 2

Occurrences of the 22 invasive termites as well as their source

Authors: Edouard Duquesne, Denis Fournier

Data type: xlsx

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Research Article

Towards a spectrum of dissent: A content analysis of Hawai'i's invasive species media

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Abstract

Invasive species denialism (ISD) has emerged as a concern in invasion science. While some scholars argue ISD is increasing, others contend science denialism is being confused with broader forms of dissent including disagreement and skepticism. Despite attempts to clearly define ISD, most definitions remain subjective and overly reliant on rhetorical markers, creating uncertainty over how to distinguish science denialism from these other, more valuable, forms of dissent. We propose a conceptual framework which utilizes knowledge and porosity as variables to identify science denialism. In doing so, we highlight science denialism's relationship to broader dissent (i.e., skepticism, disagreement, and unfamiliarity). To validate this framework, we conduct a thematic content analysis of media articles discussing the common coquí (Eleutherodactylus coqui) in Hawai'i from 1980-2022. We find that while invasive species denialism builds from and amplifies other forms of dissent, it is nevertheless distinguishable within our framework. Moreover, our findings suggest that early and appropriate engagement with dissent can inhibit ISD. Beyond countering ISD, engagement with dissent is important to help mitigate challenges related to distrust of invasion science, issue-framing within public perception, and injustices generated from dismissal. Ultimately, we suggest that the Spectrum of Dissent framework can help scientists, managers, and environmental communication specialists build a healthy dialogue with the public, obtain productive feedback, and facilitate the success of invasive species initiatives.

Key words: disagreement, *Eleutherodactylus coqui*, science communication, science denialism, skepticism, unfamiliarity



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Introduction

Invasive species denialism (ISD), broadly defined as a relentless and unsubstantiated refutation of scientific consensus on invasive species, has emerged as a concern in invasion science - an interdisciplinary field concerned with the study, management, and governance of invasive species (Vaz et al. 2017; Ricciardi and Ryan 2018a). Despite definitional ambiguity (Colautti and MacIsaac 2004a; Shackleton et al. 2022), invasive species are typically defined as species anthropogenically introduced to areas beyond their historical range and whose populations spread, resulting in ecological, economic, or social changes (Lockwood et al. 2013). In 2017, Russell and Blackburn (2017b) raised a concern that ISD is rising in academic and public media. Shortly thereafter, Ricciardi and Ryan (2018a) attempted to illustrate the exponential growth of ISD beyond invasion science's peer review spaces (e.g. media and opinion articles in academic journals). In response, Boltovskoy et al. (2018) countered such claims by noting the percentage of legitimate ISD is minute and has not increased since 1990. Regardless, the existence of ISD presents a serious concern as studies within the arena of climate change suggest that even small amounts of science denialism can hamper policy outcomes, decrease public trust of experts, and reduce public perception of scientific consensus (Biddle and Leuschner 2015; Koehler 2016; Ranney and Clark 2016; Stuart et al. 2022).

Despite ongoing debate over the magnitude of the problem, addressing ISD requires a systematic way of identifying it. Russell and Blackburn's (2017b) article about ISD prompted heated debate in invasion science regarding what constitutes ISD (Briggs 2017; Crowley et al. 2017b; Davis and Chew 2017; Tassin et al. 2017). Indeed, some scholars have suggested that disagreement and skepticism in invasion science are being misinterpreted as science denialism (Crowley et al. 2017b; Frank 2021). Others, meanwhile, contend that these disputes may be the result of how different individuals frame ISD (Stratton et al. 2022). Such critiques, expanded on in the subsequent section, are generally grounded in one of two arguments: 1) ISD definitions are inadequate (Crowley et al. 2017b; Frank 2021), and 2) the methods utilized to identify ISD are insufficient (Munro et al. 2019).

Together, these exchanges outline a landscape of uncertainty around how to identify ISD, and what distinguishes it from broader dissent, defined here as objections to scientific consensus grounded in skepticism, unfamiliarity, or disagreement (Frank 2021). Building on this observation, we propose a framework to distinguish science denialism from broader dissent. This is critical because where science denialism may be detrimental in its effects, broader dissent can be incredibly useful for invasion science. Indeed, Stratton et al. (2022) and Frank (2021) both suggest that more nuanced responses are needed to address ISD, strengthen invasion science, and advance management outcomes.

In this article, we engage with the issue of ISD, with a goal to 1) more clearly distinguish it from and 2) outline its relationship to broader dissent on invasive species. Without a clear conceptual mapping of dissent, invasion science scholars/ practitioners risk confusing science denialism with other, more valuable, forms of dissent. This can be problematic given power structures in science that have historically privileged certain forms of knowledge (e.g., Western) while devaluing others (e.g., Indigenous) (Harding 1991; Mignolo 2005; Elk 2016). Attention to power is critical in invasion science (Gonzalez Cruz and Johnson 2022; Shackleton et al. 2023), a field which while making strides to improve, continues to struggle with gender imbalances (Campbell and Simberloff 2022), skewed racial and geographic representation (Kuebbing et al. 2022), and limited engagement with and consideration of alternative worldviews (Wehi et al. 2023).

While a handful of studies have examined ISD (Russell and Blackburn 2017b; Boltovskoy et al. 2018; Ricciardi and Ryan 2018a; Munro et al. 2019; Frank 2021; Stratton et al. 2022), and noted that ISD primarily occurs beyond peer review (Russell and Blackburn 2017b; Ricciardi and Ryan 2018a), few have focused exclusively on its manifestation in the media. We address this gap via an examination of invasive species media in Hawai'i, focusing on *Eleutherodactylus coquí* - hereafter coquí. Hawai'i represents an exemplary microcosm to study invasive species dynamics due to its sociocultural dynamics, immense biodiversity and growing experience with invasive species management (Pejchar et al. 2020). The coquí is a tree frog endemic to Puerto Rico, where it is heralded as a longstanding cultural icon (Joglar 2005). Inadvertently arriving in the 1980s, the coquí became established in Hawai'i. The coquí's spread throughout the Hawaiian archipelago generated substantial contention between the public, policymakers, and scientists both in Puerto Rico and Hawai'i about 1) the extent to which coquí posed a problem/threat to Hawaiian socio-ecological systems, 2) how it should be managed, and 3) whether the management approaches ultimately employed were science-based and/or ethical (Beard and Pitt 2012). We leverage the tension around coquí to conduct a thematic content analysis of media discourse. Our objectives are threefold: 1) present a framework that helps distinguish between ISD and broader dissent; 2) validate our framework; 3) identify obstacles to effective invasion science communication. The proposed framework can inform broader environmental communication discourse on adjacent subjects with growing science denialism (i.e. extinction, and climate change).

In the next section, we provide a brief sketch of the current limitations to identifying ISD, outline a theoretical overview of dissent, highlight the importance of discernment, and situate our discussion within literature on environmental communication. In the third section, we outline our methods. Finally, we share our results within a larger discussion on the precautionary principle, message framing, and stakeholder dismissals. We conclude with a note to guide invasion science's future engagement with ISD, and articulate avenues for prospective research.

ISD and current limitations to identifying it

Scholars within invasion science have grouped several arguments under the umbrellas of contrarianism (Simberloff 2011; Richardson and Ricciardi 2013; Simberloff and Vitule 2014; Kuebbing and Nuñez 2018), and/or, more recently, ISD (Russell and Blackburn 2017b; Ricciardi and Ryan 2018a). For example, Davis et al. (2011) argue that a species' origin should not play a significant role in determining what is/not an invasive species, while Pearce (2015) and Briggs (2017) contend there is little evidence connecting invasive species to major contemporary extinctions. Sagoff (2018) claims that definitions within the field contain tautologies (e.g. biodiversity) and normative dimensions (e.g. harm), while Guerin (2019) asserts that a bias towards the negative impacts of invasive species presents problems for broader generalizations within the field. Others go further, arguing that invasion science is biased, pseudoscientific, and/or an unnecessary subdiscipline within ecology (Davis and Thompson 2002; Theodoropoulos 2003; Valéry et al. 2013). Invasion science scholars have actively responded to criticisms of and within the field, particularly those seen as contrarian or ISD (Simberloff and Vitule 2014; Ricciardi and Ryan 2018b). We allude to these arguments not as an endorsement, nor as a comprehensive review, but rather to illustrate the breadth of arguments currently included under ISD.

While academic attention to ISD is a relatively recent phenomenon (Russell and Blackburn 2017b), science denialism in and of itself is not novel. Science denialism has been observed in the realms of climate change (Rahmstorf 2004; Antilla 2005; Capstick and Pidgeon 2014; Björnberg et al. 2017), extinction (Lees et al. 2020), tobacco smoking (Oreskes and Conway 2011; Proctor 2012), HIV/AIDs (Nattrass 2007, 2012), and, more recently, COVID-19 (Malinverni and Brigagão 2020). This scholarship broadly recognizes science denialism as an extreme form of dissent along a continuum (Dunlap 2013; Corry and Jørgensen 2015; Kumar et al.

2016; Haltinner and Sarathchandra 2021). Researchers have explicitly recognized this continuum in invasion science, underscoring that concepts like skepticism and disagreement should be considered distinct from science denialism (Crowley et al. 2017b; Russell and Blackburn 2017a; Ricciardi and Ryan 2018a; Frank 2021). Despite this recognition, systematic identification of ISD has been hampered by two interrelated challenges: 1) variable definitions of science denialism (Crowley et al. 2017b; Frank 2021; Stratton et al. 2022); and 2) a methodological overreliance on rhetorical markers as confirmation of science denialism (Munro et al. 2019).

With regard to the first challenge, existing literature underscores that the way we define science denialism is important because it carries implications for how we study and come to recognize it. In research with participants from the Great Lakes region, for example, Stratton et al. (2022) find that multiple framings of ISD exist, suggesting that ISD is not universally defined. Indeed, invasion science has utilized multiple, often competing, definitions to engage with science denialism. For example, Russell and Blackburn (2017b) suggest science denialism is "where evidence is disregarded, or motivations are disingenuous" (p. 4) and the "rejection of undisputed scientific facts (p. 4). In their study of science denialism within scholarly journals and the mainstream media, Ricciardi and Ryan (2018a) define ISD as the use of "rhetorical arguments to disregard, misrepresent or reject evidence in an attempt to cast doubt on the scientific consensus that species introductions pose significant risks" and the act of "ignoring or denying scientific facts and making claims that have already been refuted in the peer-reviewed literature" (Ricciardi and Ryan 2018a). Although within seminal texts on ISD, such definitions have been critiqued for assigning motivation (i.e. casting doubt) as a fundamental characteristic of ISD (Frank 2021). This critique arises because motivation is notoriously difficult to ascertain (Frank 2021). Speculation of motivation may be more useful for addressing science denialism, but less so for identifying it. In an attempt to sidestep issues of motivation, Frank defines ISD as "normatively inappropriate dissent" which both violates epistemic norms (e.g. straw-man arguments) and is anticipated to cause harm (e.g. delays necessary management) (2021). This definition, while generative remains problematic because expected harm is similarly difficult to assess and may not be comprehensible until after the harm is done, a shortcoming Frank (2021) recognizes. The definitions presented herein each contain strengths and weaknesses. Thus, we contend that this definitional problem remains.

With regard to the second challenge, Hoofnagle and Hoofnagle (2007) and Diethelm and McKee (2009), from which Ricciardi and Ryan (2018a) and Frank (2021) draw in their definitions, suggest that denialists utilize common rhetorical strategies in lieu of facts to build arguments against scientific consensus and heaps of evidence (Hoofnagle and Hoofnagle 2007). These rhetorical markers were later consolidated into a comprehensive framework entitled FLICC: fake experts, logical fallacies, impossible expectations (e.g. seeking 100% certainty), cherry-picking, and conspiracy theories (Hoofnagle and Hoofnagle 2007; Diethelm and McKee 2009; Cook 2017). While we acknowledge and affirm the value of rhetorical markers, we simultaneously point to the foundational premise of this argument which is that science denialists commonly use such rhetorical techniques, not that such rhetorical techniques are unique to science denialists. This distinction clouds the utility of such rhetorical tactics for distinguishing science denialism from broader forms of dissent, which might also utilize such strategies. Thus, we assert that

current methods which outline FLICC markers as pivotal to the identification of ISD are insufficient for distinguishing it from broader dissent. Munro et al. (2019) similarly suggest that current methods are insufficient, though their claims arise from efforts to replicate Ricciardi and Ryan's (2018a) study of ISD. Overall, these issues make it difficult to develop healthy dialogue regarding ISD and underscore that a more systematic approach to identifying ISD is needed (Guiaşu and Tindale 2018; Frank et al. 2019).

In light of these definitional and methodological problems, we suggest invasion science should be more intentional with its conceptualization of science denialism and its relationship to other forms of dissent. While we identify and build from existing critiques concerning ISD, such challenges are not unique to invasion science. Indeed, climate change denialism literature has seen similar pushes to refine its conceptual language to move away from dichotomies (e.g. denier/believer) and/ or imprecisions (i.e. climate skeptic) (O'Neill and Boykoff 2010; Björnberg et al. 2017), and better differentiate between doubt over science (epistemic and factbased) as opposed to doubt over policy and solutions (value-based) (Capstick and Pidgeon 2014). Ultimately, the ability to systematically identify ISD in invasion science is critical to build a more productive dialogue in a field characterized by areas of both high consensus and polarization (Shackleton et al. 2022).

Theorizing dissent within invasion science

Building on invasion science's acknowledgement of ISD as part of a continuum, we offer a framework which situates science denialism along a spectrum of broader dissent (Fig. 1). In suggesting a move beyond dichotomous vocabularies of non/ denialism in climate change science, Corry and Jorgensen highlight the common thread linking such labels in the literature is information and the underlying claims of validity (2015). As such, we conceptualize dissent as an embodiment of four distinct relationships to information: disagreement, skepticism, unfamiliarity, and denialism.

To limit definitional ambiguity and address the limitations outlined above, we draw from Ricciardi and Ryan (2018b) and Ferkany (2015) to suggest science denialism be defined as- an iterative pattern (1) of espousing unsubstantiated knowledge claims (2), refuting scientific evidence (3), and eluding opportunities to learn or adapt with new/updated information. Together, these characteristics display evidence of a low knowledge base and low porosity to new information, without overly relying on FLICC rhetorical markers and/or motivation. When examining a particular interaction utilizing the spectrum of dissent, an individual or community's position is characterized by their knowledge base (i.e., demonstrated knowledge/understanding about the issue) and their porosity to new information (i.e., indicated probability that additional information would alter one's perspective) (Fig. 1). An individual's knowledge base is determined by the in/accuracy of information presented in or underlying their remarks. Porosity, on the other hand, is determined by expressions of open/closed mindedness - characteristics which Ferkany (2015) utilize to distinguish between naive denial and a more dogmatic denial. Open-mindedness is characterized by things like generative dialogue, regard for other's viewpoints, good-faith questions/curiosity, whereas close-mindedness is characterized by the opposite (e.g., entrenched stance, firm dialogue, disregard).



Figure 1. Spectrum of Dissent. The spectrum demonstrates the relationship between disagreement, skepticism, unfamiliarity, and denialism, which are all types of dissent. The x-axis represents porosity to new information (likelihood that additional information would change one's perspective). The y-axis represents knowledge base (extent an individual or community is knowledgeable about a subject).

Based on this framework, we expect someone who dissents out of disagreement may exhibit knowledge of the subject matter but fundamentally diverge in opinion or interpretation. Similarly, an individual with unfamiliarity, in this framework, may naively deny scientific details but maintain an openness to shifting their position with new information (Ferkany 2015; Mason 2020). Such dissent is distinct from science denialism, which is grounded in denial that actively eludes correction (Ferkany 2015). Invasion science researchers generally recognize science denialism is also distinct from skepticism, an organic component of the scientific process which may question scientific conclusions with substantiated claims, but is ultimately receptive to dialogue and updated information (Russell and Blackburn 2017b; Ricciardi and Ryan 2018a; Frank 2021; Jylhä et al. 2023).

In basing determinations of knowledge base and porosity on displays of behavior, we attempt to remove the (sometimes speculative) consideration of cognitive beliefs and/or motivations. Thus, while some science denialists have deliberately lied, hiding their true (high) knowledge base to gain attention, financial incentives, or other benefits (Diethelm and McKee 2009; Björnberg et al. 2017), their exhibited behaviors were of a low knowledge base and low porosity. The exhibited behaviors are those with which scientists and the public must contend when identifying science denialism, and thus the focus of our framework. Moreover, the spectrum of dissent is intended for use on a case-by-case assessment, and in no way indicates that an individual acting as a science denialist in one instance will do so in every instance. Thinking about ISD in terms of a spectrum of dissent present/represented and thereby facilitate a healthier or more constructive dialogue (Hoffman 2011).

Dissent and power

A conceptual framework that systematically distinguishes between denialism and other forms of dissent is critical because dissent is often recognized as contributing to revo-

lutionary advances in science (Kuhn 2012). Skepticism and disagreement have already proven valuable for invasion science; prior waves of criticism, for example, have demonstrably reduced context bias (Warren II et al. 2017). Longstanding debates around topics like the enemy release hypothesis (Colautti et al. 2004) or the passenger-driver model (MacDougall and Turkington 2005), and recurring critiques about the field's language (i.e. militaristic, colonial, xenophobic) and normative/value-laden dimensions continue to challenge the field (Subramaniam 2001; Colautti and MacIsaac 2004b; Larson 2008; Essl et al. 2017; Reo et al. 2017; Janovsky and Larson 2019). Moreover, in a survey of the field, Shackleton et al. (2022) identify several moderate to highly polarizing topics within invasion science, including questions of whether the field is objective, whether invasive species benefits are understated; if non-native species should be included or excluded in biodiversity counts, what constitutes the definition of invasive species, and what the feasibility of plant eradication is, to name a few.

Yet, due to the field's complexity, its value-laden aspects and the polarization evident in some areas of the field, there is concern that some scholars have leveraged charges of ISD to silence scientific and ethical debates (Crowley et al. 2017b; Frank 2021; Stratton et al. 2022). Recently, Davis (2020) likened some of invasion sciences' responses to dissent as gang science, a practice of scientists banding together to argue against challenged ideas in a way that can be read as intimidation or bullying. Such tense dynamics are especially troubling because although ISD has the potential to greatly impede invasive species scholarship and management, spurious allegations run the risk of dismissing valid concerns, undermining diverse communities and their knowledge, and/or furthering systemic injustices (Frank 2021).

Shackleton et al. (2023) urge attention to dissent and encourage conservationists to "be wary of how consensus and the absence of conflict might sometimes be the product of power relations" (p. 10). Such tensions demand reflection about how consensus forms, especially amidst public dissent. This is particularly important in the context of Hawai'i and Puerto Rico - two archipelagos colonized by the United States. Some Indigenous communities, in Hawai'i and beyond, for example, have exhibited different language and frameworks for thinking about "invasive species", which are at times at odds with "conventional" invasion science (Bach and Larson 2017; Reo and Ogden 2018; Wehi et al. 2023). If "science denialism is the rejection of undisputed scientific facts" as Russell and Blackburn (2017b) contend, the question remains: undisputed by who? (Crowley et al. 2017b). Such definitional bounds may inadvertently devalue stakeholders' voices and superimpose dominant perspectives. We contend that such epistemic injustices (i.e., negating credible knowers) can reproduce the field's current demographic disparities (McConkey 2004; Campbell and Simberloff 2022; Davinack 2022; Kuebbing et al. 2022). For example, a recent study by Kuebbing et al. (2022) suggests that while the current make-up of the editorial board for the journal of "Biological Invasions" is more diverse than it historically has been, it remains largely white (85%), English speaking (70%), male (60%), and US-based (nearly 50%).

This begs the question: How can invasion science foster productive dissent, which helps create a more just discipline and practice, without heightening claims of ISD? We suggest the ability to accurately and analytically identify ISD could enable less fearful or dismissive engagement with wider dissent, which may simultaneously provide opportunities to build trust and facilitate stakeholder engagement around emergent public concerns. Ultimately, such an effort can improve science-society relations while also opening invasion science and management to more diverse approaches.

Science denialism in media

An important area for invasive species communication is media, from contemporary social media (e.g. Youtube, Facebook, etc.) to print media (Davis et al. 2018). Here, we focus on print media. Journalism practice norms play a pivotal role in the development of different forms of dissent. For example, media, in an effort to achieve neutral and balanced reporting, may create an echo chamber wherein denialist thought is disproportionately amplified and promoted, producing an illusion of scientific debate (Elsasser and Dunlap 2013). The allure of sensational or attention-grabbing stories such as conflict tend to draw greater attention to science denialism in media (Brüggemann and Engesser 2017), potentially boosting the reach of misinformation

Given its potential role in amplifying denialism, and the growing interest in ISD, more empirical research on dissent in invasive species media is needed (Russell and Blackburn 2017b; Ricciardi and Ryan 2018a). Invasive species are increasingly covered as a newsworthy topic and thus open to public debate in news stories, editorials, and public letters. Indeed, if invasive species stakeholder engagement is limited and participation does not actively inform decision-making as research suggests (Shackleton et al. 2019), media may currently provide the most approachable (and perhaps democratically effective) means of voicing broader dissent and influencing invasive species outcomes. Furthermore, recent research demonstrates how media's portrayal of invasive species can positively or negatively influence public perception of the species (Geraldi et al. 2019), and/or related policy (Miller et al. 2018).

In a study comparing scientific and media coverage of ecological effects, for instance, Geraldi et al. (2019) found invasive species media cycles to be relatively brief, lasting one to two years. They suggest this is likely due to a temporal reduction in "newsworthiness" and invasive species impacts failing to live up to the media's exaggeration of risks. It is worth noting that such news cycles vary by species, with many species receiving little to no coverage at all (Ballari and Barrios-García 2022). Leppanen et al. (2019) further outline how media obscure or omit uncertainty over, and scientific debate of, invasive species management, including concerns over efficacy and non-target species effects. These studies illustrate a growing interest in invasive species media and provide key findings to guide science communication. Invasive species media thus provides an important, but understudied, empirical avenue for studying ISD.

Hawai'i, the coquí, and dissent

Hawai'i has been embroiled in a public debate over the coquí since its introduction. The coquí quickly spread to all four principle islands (Hawai'i, Maui, O'ahu, and Kaua'i), though it is presently contained to Hawai'i and Maui (Beard et al. 2017). A nocturnal terrestrial frog which undergoes direct development (i.e. no tadpole stage), the coquí is most prominently recognized by its two-tone mating call (Beard et al. 2017). Indeed, its iconic nocturnal call, combined with its status as a charismatic invasive species, has helped generate a heightened public, and thus media response in Hawai'i (Kraus 2009; Jarić et al. 2020b). In contrast, the coquí has a long-standing reverence in Puerto Rico, symbolically represented from pre-colonial Borikén petroglyphs to present day consumer products in Puerto Rico and the wider diaspora, including jewelry, toys, art, music, etc. (Joglar 2005). As a species of great cultural significance to people in one US colony (Puerto Rico), and a subject of eradication in a different US colony (Hawai'i), it is apropos to discussions on power and knowledge.

Methods

Content analysis is a media analysis tool within communication studies that allows researchers to systematically comb through large textual datasets while documenting patterns in the process (Krippendorff 1980). With the capacity to combine qualitative and quantitative techniques, content analysis can yield insights that advance conservation goals (e.g. documenting subjects of attention, effects of communication, dominant voices, etc.) (Krippendorff 1989; Wolch et al. 1997; Muter et al. 2009; Houston et al. 2010; Renz et al. 2018). Following methodologies for media analyses of invasive species (Geraldi et al. 2019; Leppanen et al. 2019; Ballari and Barrios-García 2022; Tateosian et al. 2023) and other conservation contexts (Jacobson et al. 2012; Muter et al. 2012; Unger and Hickman 2020), we constructed a content analysis protocol to 1) guide inclusion/exclusion of media articles, 2) code for the presence/absence of dissent and other descriptive details, and 3) inductively draw out significant dissent themes. While briefly summarized here, the full protocol is included in supplementary materials (Suppl. material 1).

This study built its corpus using the Star Advertiser Archive, which holds a fully searchable subsection of Hawai'i's newspapers dating back to 1840, including the Hawaii Tribune-Herald, Honolulu Advertiser, Honolulu Star-Bulletin, West Hawaii Today, The Polynesian, The Daily Bulletin, The Hawaiian Star, The Evening Bulletin, and the Garden Isle. A search for articles on the coquí using its common name "coquí" was conducted in Spring of 2023, yielding 2,974 pages. Documents collected in the corpus were manually screened to ensure they met the following inclusion criteria: 1) Focus on coquí; 2) discusses species in the context of Hawai'i; 3) relevance (e.g., excludes advertisements); and 4) does not concern species in captivity. Documents that failed the inclusion criteria and duplicates were removed, resulting in a total of 445 documents for analysis. See Suppl. material 2 for a full list of included media.

We coded data across four blocks of content categories: metadata, coquí natural history, dissent, and descriptors and key events. Block one (metadata) included information such as date of publication, title, author(s) name, author(s) affiliation, forum of publication, publication type (e.g. news article, opinion piece, etc.), article valence, and language. Following Golebie and colleagues, article valence (e.g. positive, neutral, negative) was dictated based on the tone of how the coquí was discussed (2022). For example, "negative" framing was assigned to articles which emphasized the need for eradication due to the coquí's "nuisance", "noisy", or "shrill mating call". Terminological language (i.e. pest, non-native, invasive, etc.) utilized to discuss the coquí was also coded. Block two consisted of details related to the coquí's impact and risk, coded as present or absent. We differentiated risk from impact (present or past oriented) by its future orientation. Block three addressed dissent. To distinguish dissenting articles from non-dissenting articles, dissent, as a whole, was characterized by the presence of oppositional statements (i.e.

disagreement, disbelief, and/or skepticism). Block four focused on descriptors and key events to assist with a timeline reconstruction of events. Following Alexander and Quinn (2012), we documented words describing the coquí within media articles to qualitatively explore thematic word clusters. Finally, media interest in the common coquí was quantified by the number of publications per year. Additionally, as part of our literature review, we conducted a Scopus and Web of Science search of coquí research in Hawai'i. This served to contextualize claims made in the media and provide a baseline comparison between scientific and media attention (Geraldi et al. 2019).

The first author was involved in full content analysis and protocol development; additional authors coded a subset of the articles. To assess interrater reliability, a portion of the corpus was selected at random (n=50) and given to each author for independent coding. We used Cohen's Kappa and Gwet's coefficient to measure intercoder reliability (Cohen 1960; Cohen 1968). Strong agreement is indicated by kappa values above 0.75 (Banerjee et al. 1999). Occasionally, a low kappa will result despite high percentage agreement due to the effects of variable prevalence on the determination of chance, a factor known as the paradox of kappa (Gwet 2008). In other words, a high imbalance between the presence/ absence of variables can lead to a greatly lowered kappa value even with few disagreements. To address this fault, we also calculated Gwet's AC, coefficient (Gwet 2002). Kappa values and Gwet's AC_1 coefficient were calculated for each variable using ReCal2 (Freelon 2010) and R Statistical Software version 4.3.1 (v. 4.3.1; R Core Team 2022), as well as the irrCAC R package (Gwet 2019), respectively. Per content analysis best practices (Lacy et al. 2015), variables that did not meet the standard of intercoder reliability were revisited, discussed until coder consensus was reached, and adapted in the codebook to reflect outcomes of discussion. Upon reaching consensus and coder re-training, an additional subset of articles were coded (n=25) and tested for intercoder reliability, yielding high agreement (Table 1). Any variables where reliability was not achieved were dropped (see Suppl. material 1 for more information).

While content analysis allowed for a reliable identification of dissent, thematic analysis provides a methodology to dig deeper into these codes and parse out patterns that would yield insights into science denialism and broader invasive species dissent. Thematic analysis is an iterative qualitative method best utilized to identify patterns or themes within a data set (Boyatzis 1998). Thus, we immersed ourselves in the dissent data, generating descriptive codes as they emerged, which were then further grouped into themes and sub-themes (Javadi and Zarea 2016).

| Intercoder reliability results (n=25) | | | | | | | | |
|---------------------------------------|---|-------------|---------------|--------------------|--|--|--|--|
| Variable | Example | % Agreement | Cohen's Kappa | Gwet's coefficient | | | | |
| Publication Type | Opinion Piece | 96 | 0.935 | 0.942 | | | | |
| Valence | Negative | 100 | 1.000 | 1.000 | | | | |
| IS Language | Pest | 92 | 0.880 | 0.904 | | | | |
| Impact | "We can no longer sleep with windows open due to noise" | 92 | 0.818 | 0.858 | | | | |
| Risk | "I imagine property values will drop" | 96 | 0.919 | 0.921 | | | | |
| Dissent | "It was first stated that they were a threat to our native birds by competing for insect food. A convincing argument has not been made for this" | 88 | 0.603 | 0.830 | | | | |

 Table 1. Intercoder reliability results, including percentage agreement, Cohen's Kappa, and Gwet's Coefficient for each variable, as an example.
Results and discussion

Coquí coverage

Nearly 47.6% of the media were news articles (n=212), while another 40.2% were opinion pieces (n=179) and the remaining 12.1% were feature columns (n=54). The quantity of opinion pieces, in comparison with news media, demonstrates a substantial public interest in coquí issues and highlights the media as an attractive venue for invasive species discussion. This reflects the agenda-setting hypothesis which states that levels of media coverage coincide with public importance of those topics (McCombs and Shaw 1972).

As a contributor to public perception and behavior (de Vreese 2005), valence, or a message's tone, is key to understanding dissent. Akin to Ballari and Barrios-García's (2022) findings on valence in invasive species media, coquí media valence skewed negative (82%), with neutral (11.4%) and positive (6.5%) valence minimally represented. This negative skew is largely due to an emphasis on the coquí as a noise nuisance, and, to a lesser extent, its potential impact on native species. This is reflected in the distribution of descriptor words. Of 268 descriptor words, 45% described the coquí's mating call in terms like "annoying", "deafening", "clamorous", or in metaphoric descriptors – like a "jet engine", "chainsaw", "jackhammer", "alarm clock", and more. While communication of negative aspects is an integral part of invasive species communication, an overly negative valence can also foster feelings of helplessness in some individuals with implications for management outcomes (Golebie et al. 2022).

Coquí impact and risk narratives, emerging in 1999, included ecological, social, and economic effects, though scientific research on these concerns occurred later (Fig. 2). Approximately 61% of media articles (n=271) brought up impacts, while about 44% (n=198) invoked risks attributed directly to, or indirectly to, the coquí. Recall that risk is a potential or future oriented impact and suggests greater uncertainty. Within the 198 pieces of media, 323 individual risk references were made, of which nearly half were ecologically focused (n=159). Almost eight percent of media pieces (n=35) alluded to the risk of invasional meltdown, which stipulates that invasive species facilitate subsequent species invasions (Simberloff and Von Holle 1999; Braga et al. 2018). Economic risks were mentioned in 25.7% of articles (n=59). Of the 271 articles which brought up impacts, 352 individual impact references were made. Approximately 68% (n=242) of these centered social impacts via the coqui's mating call (e.g. sleep disturbance, annoyance, etc.), while economic impacts and ecological impacts were equally referenced about 16% of the time (n=55). The dominant focus on the coquí's social impact is critical to note because iterative exposure to such messages can reinforce or cultivate how people think about a subject matter (Gerbner 1998).

Maximum annual media coverage occurred in 2005 (n=67), aligning with Geraldi et al.'s (2019) observation that this generally occurs six years post initial media coverage (Fig. 3). Overall, the bulk of media was published between 2001 and 2010 (n=354), whereas more than half of scientific publications on coquí in Hawai'i were published after 2010 (n=26), suggesting media interest decreased as scientific publications increased (Fig. 3). Two factors likely contributed to these observations. First, an official narrative concerning coquí impacts/risks emerged in 1999, despite delays in the scientific study of such impacts/risks (Fig. 2). This gap in time between communicated risks/impacts and studied risks/impacts is due, in part, to the slow and Jesann Gonzalez Cruz & McKenzie Johnson: Towards a spectrum of dissent



Figure 2. Timeline of coquí impact and risk. Timeline illustrating when major concerns surfaced in comparison to when they were studied.



Figure 3. Coquí media and scientific publications over time. To accommodate the scalar difference, annual quantities of coquí media are represented in orange while scientific publications, in blue, are a cumulative representation with annual quantities highlighted above each bar.

often extensive nature of invasion species data collection and the common lag in invasive species impact detectability (Simberloff 2010). While acknowledging the complexities of invasion science, we suggest this gap represents a "fragile moment" for invasive species communication and management, wherein dissent is more likely to arise. This observation is bolstered by studies in parakeet management which similarly suggests that time is an important factor in the way management policies are viewed and received by the public (Crowley et al. 2019). Second, over time, group dynamics solidify and peer pressure to conform to broader social consensus heightens such that voicing opposing sentiments/thoughts is increasingly frowned upon. Indeed, research shows that social consensus is critical in shaping belief and behavioral non/acceptance on polarized issues (Goldberg et al. 2020). For example, in the same month as the First International Coquí Conference, someone wrote: "After being all but hung in effigy for objecting to the inhumane genocide of the coquí in my neighborhood, I had promised myself that protecting my pets from possible retaliation was more important than voicing my views. However, thanks to the recent letters from [Redacted Name] of Hilo and [Redacted Name] of Honokaa, I have, again, found my backbone. Several points come to mind: Research has shown that the coquis do, indeed, eat the nasties – cockroaches, ants, centipede larvae and even possibly those Chinese rose beetles mentioned by [Redacted Name] (when available from the scorched earth, our native birds seem fat and healthy in spite of the suggested competition)...."- Individual-A (2008)

Thus, while delays in science represent an organic, and perhaps inevitable component of invasion science, they nonetheless hold implications for dissent formation and proliferation - a point we return to in the section entitled "Skepticism as dissent".

Documenting dissent

Documenting dissent and its focus is another critical step to understanding wider debates around the coquí and whether they represent science denialism. Of the 445 media articles studied, only nineteen percent (85/445) exhibited dissent. This could be attributed to the dominant discourse that emerged after introduction, which characterized the frog as an invasive species with negative impact. While relatively more uncommon, dissent nevertheless emerged immediately - only two weeks after the first media coverage of invasive coquí. Terminological ambiguity (i.e. invasive species, pest, introduced species, among others), a source of debate in the literature (Latombe et al. 2019), did not play a prominent role in dissent formation in the public realm.

Instead, our thematic content analysis revealed that dissent largely concentrated on impact and eradication. These findings support previous observations of invasive species conflict (Crowley et al. 2017a). More specifically, we found that eradication dissent centered on specific practices, the logic or evidence underlying eradication decisions, and whether the coquí should be prioritized for eradication. Impact dissent was attributed to the timing of the underlying science and the experience of invasive species impacts. Yet, impact dissent and eradication dissent are tightly interwoven. This linkage between impact dissent and eradication dissent may be an example of uncertainty transfer, wherein uncertainty in one area influences perceptions of uncertainty in another (Spence et al. 2012).

Skepticism as dissent (high knowledge, high porosity)

To an extent, skepticism emerges naturally in invasion science. Although all invasive species are introduced, not all introduced species become invasive, and, in fact, many are innocuous (Ricciardi and Ryan 2018b). An invasive species that is established and spreading, however, generates concern over potential negative impacts, even if currently unknown (Lockwood et al. 2013). Despite advances, impact forecasting overall remains a challenge for the field (Ricciardi et al. 2021). To prevent the most serious socio-ecological effects from occurring, invasion scientists have adopted a precautionary approach (Shackelford et al. 2013). The precautionary principle for invasion scientists flips the burden of proof such that action is not delayed as a result of insufficient information (Gonzalez-Laxe 2005).





Invasion scientists often cite two major challenges to acquiring relevant data quickly. First, species impacts may remain undetectable for decades or centuries (Simberloff 2010), and waiting until impacts manifest may result in catastrophic and/ or irreversible ecosystem changes. Second, the species and/or ecosystem in question may be data-poor (i.e. species lacks invasion history or ecosystem is understudied such that impact is difficult to discern) (Pyšek et al. 2020). As a result, the rapid dispersal of newly introduced species often prompts eradication (Simberloff and Vitule 2014).

This approach presents a temporal conundrum in the initial stages of the invasion process, wherein the public is invited to engage in eradication practices based on scientific speculation and experience, rather than concrete evidence. For the public, tangible impacts are often a critical contributor to their perception of invasive species (Simberloff et al. 2013). This disciplinary quandary is best characterized by dissenters' calls for "more evidence" or claims of little to "no evidence", as Individual-B (2005) expresses (Fig. 4). Such opposition to the precautionary approach and its underlying justification have been previously linked to invasive species conflict (Crowley et al. 2019).

Individual-B (2005) highlights their attention to coquí news, alluding to high knowledge. Their focus on and desire to see evidence suggests high porosity, despite their conspiratorial suggestion. As conspiracies are a FLICC rhetorical marker for science denialism (Hoofnagle and Hoofnagle 2007), we highlight Individual-B's remark to illustrate FLICC's insufficiency for distinguishing between science denialism and broader dissent under conditions of high uncertainty.

Indeed, coquí dissenters often articulated skepticism of negative risks because they had yet to visibly manifest and science was lacking. The precautionary approach, while critically important in many instances, can nevertheless foster distrust of scientific claims. This dynamic produces a tricky terrain for invasion scientists to navigate as they attempt to reinforce concern. Indeed, upon studies in 2014, scientists learned that coquí did not appear to be in competition with native birds (Smith et al. 2018). As Smith and colleagues suggest, this finding "should not be surprising, because coquís in Hawaii mostly forage in the leaf litter, whereas most extant Hawaiian birds forage on insects in the canopy and understory" (2018). Other studies did find evidence for negative impact, however. Smith and colleagues found that coquí presence increase the abundance of non-native birds (Smith et al. 2018); Choi and Beard (2012) learned that coquí alter invertebrate communities; Hill and colleagues demonstrated that coquí presence is associated with greater abundances of mongoose (Hill et al. 2019); all of which may contribute to future undesirable effects. Thus, there was reason for the precautionary approach but also reason for skepticism.

While falsifying hypotheses is a natural component of scientific investigation (Popper 2005), we highlight how the temporal conundrum presented by the precautionary principle may elicit public skepticism. When knowledge is missing, people rely on trust for decision-making (Siegrist 2021). However, such reliance requires a foundation of trust. Invasive species risk literature suggests that institutional distrust may arise due to prior failures, and general societal dynamics (e.g. "fake news") (Norgaard 2007). As context-specific history shapes the public's (lack of) confidence in invasive species authorities (Crowley et al. 2017a), conspiratorial rhetoric within dissent claims may be indicative of prior conflicts or failures. Low confidence in institutions and scientists have also been observed due to unsafe management practices (Norgaard 2007), perceptions of low efficacy and/or effort in management, and lack of transparency (Wald et al. 2019). Thus, a combination of several factors may have contributed to public distrust in the early stages of coquí management, including 1) safety and pollution concerns of caffeine, the first proposed eradication technique; 2) federal funding challenges stunting the magnitude of early initiatives; 3) the initial limitations in scientific evidence of risks; and/or 4) a historical event or dynamic not observed within this study which nonetheless impacted invasion science-society relationships. Non-dissenters also acknowledged the lack of studies on coquí impacts (Editorial Board 2002b), further suggesting institutional dis/trust plays a role in whether people support expert claims on invasive species sans direct impact evidence. Trust, moreover, is asymmetric in nature such that it is far easier to lose than it is to gain (Slovic 1999).

Disagreement as dissent (high knowledge, low porosity)

Although disagreements arose throughout our sample for varied reasons, including issues related to ethics (i.e., animal rights) and governance (i.e., management infringement on property rights), we highlight message framing as the most prominent obstacle to invasive species support in the case of the coquí. Message framing is critical for its effect on public actionability, or the public's willingness to accept and act on a given issue (Otieno et al. 2014). Indeed, message framing influences interpretations of invasive species impact and risk. Media message framing shapes information salience by emphasizing certain aspects over others (de Vreese 2005). As discussed in the "Coqui coverage" section, media message framing emphasized the coqui's call over all other issue frames. Individual-C (2000) illustrates how this overemphasis can contribute to disagreement. Despite exhibiting high knowledge of recent invasive species developments (Fig. 5), they display a strong difference of opinion related to the coqui's call, and whether the coqui should be prioritized. This situates their comments as disagreement.

| FLICC Rhetorical Markers | Low Porosity They are dismissive in noting their personal experience does not align with the opinion of others | High Knowledge |
|--------------------------------|--|---|
| Anecdote Falso | " <u>Some of us from 4-mile beach in Hilo (Kalanianaole) had the pleasure of visiting the Puna</u> eleutherodactylus coqui (frogs) the other night. We have to disappoint you, [Redacted Name], but the noise | Individual is highly knowledgable |
| Faise Equivalence | level of said frogs in no way compared to what we are subjected to in our neighborhoods on 4-mile. Deafening airplanes flying over the building day and night, and ear/nerve shattering motorcycles continually using Kalanianaole for a drag strip until wee hours of the morning. We | about invasive species current events |
| <u>Ad</u> <u>Hominem*</u> | have been discussing frogs for what, two years now? <u>Hawaii is mostly</u> <u>all talk when it comes to solving problems!</u> Recently the talk has shifted to the brown tree snakes in Maui endangering the local birds existence. The snakes have been hitchhiking to Hawaii from Guam where there are now an estimated one million snakes. What will we be | |
| | talking about next year? How to properly insert earplugs? Or shall we sell umbrellas to tourists in Maui so the snakes don't fall on their heads. Maybe we'll have a new income-producing market for Hawaii. 'Huli-Huli Frog legs?' Enough talk already. Let's do something for once about these problems before they get out of hand." - 9/10/2000, Individual C | |



Individual-C's mention of the brown tree snake's impact on birds, but none of the coqui's ecological impact alludes to how the media's overemphasis on the coquí's call as a social impact overshadows or obscures the species' other potential risks. As people are more likely to support eradication of invasive species with economic and/or ecological impacts (Bremner and Park 2007), this overemphasis on noise likely contributed to heightened dissent around coquí eradication. The media's overemphasis of the coquí problem as a "noise issue", situated coquí impacts in the realm of social negotiation, rather than scientific discussion. Indeed, where the connection between a species and the alleged species' risks is not overtly clear and/ or evident, the decision to eradicate and/or control the species will also seem dubious (Wald et al. 2019). Selective attention to social/economic dimensions can lead to environmental impacts that are discounted or ignored altogether, as Essl et al. (2017) contend in the case of the American mink (Neovison vison). The American mink is known to impact ground-nesting birds, rodents, amphibians, and the endangered European mink (Mustela lutreola) across Europe, yet have also been seen as an important source of revenue for the fur industry in countries like Denmark and Sweden (Bonesi and Palazon 2007). Essl et al. (2017), thus, highlight how normative values and selective attention to different aspects of the issue can create divergent assessments concerning the scale of the issue and what to do about it.

Moreover, the shift in debate from science to social negotiation brings culture, values, and politics to the fore. Individual-C (2000) demonstrates how members of the public may disagree about the severity of immediate social impacts and how they should be addressed, if at all. We agree with the idea that value system disagreements and risk perception are tightly interwoven in invasive species conflicts

(Estévez et al. 2015). Where public support is lacking, or opposition is present, invasive species management initiatives may be stunted (Caceres-Escobar et al. 2019). As a result, disagreement, not grounded in science denialism, may resemble efforts to prevent, stop, or limit invasive species management. Yet, science denialists are often similarly linked to efforts to thwart solutions (Ricciardi and Ryan 2018a; Stuart et al. 2022). Recalling Frank's (2021) emphasis on "normatively inappropriate dissent" in his definition of ISD (see section: "ISD and current limitations to identifying it"), this similarity highlights why invasion science must be intentional with how it conceptualizes science denialism in relation to broader dissent.

Unfamiliarity (low knowledge, high porosity) and Dismissals – a justice concern

Stakeholder engagement in its myriad forms, including through print media, is recognized as a tool for social learning about invasive species (Shackleton and Shackleton 2016). Higher invasive species knowledge tends to be associated with increased education levels and with greater activity in the context of interest/related activities (e.g. boaters have greater knowledge of aquatic invasive species) (Eiswerth et al. 2011). On the other hand, research indicates that low knowledge of invasive species is common among the general public (Colton and Alpert 1998; Randler et al. 2007), which Shackleton and Shackleton (2016) indicate may be attributable to inadequate media coverage (e.g. not targeted enough, flawed messaging). Hence, invasion science scholarship suggests that low stakeholder knowledge of invasive species is indicative of a need to revisit outreach and communication efforts, re-evaluate their effectiveness, and/or broaden their reach (Nanayakkara et al. 2018). Eiswerth et al. (2011) contend this is especially true for more expansive management efforts which require cooperation from a broader constituency. Yet, research on scientist and policy-maker perceptions of stakeholder knowledge illustrate that some scientists perceive stakeholder engagement to be of limited value, due to their association of stakeholder knowledge with misinformation and/or general lack of knowledge (Moon et al. 2015).

The coqui case study illustrates that even stakeholders with limited knowledge of invasive species can carry important contributions for invasive species management and the field. As a long-established cultural symbol of Puerto Rico (Joglar 2005), news of coquí eradication led to some tension between people in Puerto Rico and Hawai'i, as well as the Puerto Rican diaspora in Hawai'i and beyond (e.g., Abbett 2001; Balive 2001; Thompson 2001; Wassman 2001; James 2002). Individual-D (2001) broadly captures these various sentiments (Fig. 6)

In this statement, Individual-D (2001) suggests a desire for healthy dialogue indicative of high porosity. They link eradication ("if you happen to catch one) solely to the coqui's sound, demonstrating a low knowledge of the other reasons underlying coqui eradication and invasive species in general. Nonetheless, they flag a need for increased cultural competency. Indeed, this notion of sending frogs "back home" was stated by multiple individuals within the sample, suggesting a literal desire for alternative solutions beyond eradication. This example illustrates how, even unintentionally, invasive species become coupled with discourses about cultural communities and their histories. This call for cultural competency reflects wider critiques of invasion science's rhetoric (Wolschke-Bulmahn 1997; Subramaniam 2001; Larson 2008; Davis et al. 2011; Warren 2011; Reo et al. 2017). For example, Subramaniam (2001)





outline the rhetorical similarities between immigration discourse and invasive species discourse. Reo et al. (2017) push back on discourse in invasion science which fails to depict Indigenous peoples as innovative and proactive invasive species managers. Multiple studies document invasion science's use of militaristic language and metaphors (Larson 2008; Janovsky and Larson 2019). Together, these studies have reiterated calls for the field to reflect on, revisit, and adapt its rhetoric to remove language associated with painful histories and/or harmful ideas. As a field heavily dependent on public participation for successful prevention and rapid response, invasion science cannot afford to alienate people by dismissing their critiques or concerns. Stakeholder er engagement can ultimately be counter-productive if stakeholder views are automatically dismissed by scientists and decision-makers (Mackenzie and Larson 2010).

Such discourse concerning cultural competency demands care and suggests that invasion science needs deeper reflection on the language practices within its scholarship and its engagement with diverse publics, particularly as these expressions of cultural disagreement were poorly received in Hawai'i, and often dismissed. As one Honolulu Star Bulletin editorial put it, they were "based on ecological ignorance and should not be taken seriously" (Editorial Board 2002a), a sentiment expressed by some scientists as well:

"This is the point at which some people remember that some other species of frogs around the world are dying off for unknown reasons. Eleutherodactylus is in no such danger, [Scientist A] said. 'These frogs are really tough.' Within this one genus are more species than any other backboned animals on earth, he said. These are 'tramp species' traveling the world with humans, he said. 'These things are

similar to rats." - (Thompson 2000)

While dissent as unfamiliarity may lead to dismissal, dismissal is not a problem unique to unfamiliarity as skepticism and disagreement may be similarly dismissed. Dismissal of the concerns of invasive species stakeholders has been previously observed within the invasion science literature (Mackenzie and Larson 2010; Crowley et al. 2019; Stratton et al. 2022). The problem of dismissal is one of recognition, a failure to acknowledge and value another's culture, identity, and/or knowledge, and is an issue which extends beyond ISD to conservation more broadly (Fraser 2008; Guibrunet et al. 2021). Yet, recognitional justice does not mean "anything goes". Rather, it requires consideration and possible modification of power structures and/ or systemic cultures such that people are listened to, respected, empowered to speak, and included in decision-making processes (Shackleton et al. 2019). Who defines the problem and how it is defined has implications for what is considered important versus what is deemed irrelevant (Slovic 1999). Indeed, Tassin and Kull (2015) demonstrate how cultural perspectives are an integral, but insufficiently addressed, component of invasive species research and management. Dismissive approaches, such as those utilized by Scientist A, promote an impasse over a productive debate wherein discussants aim to learn from one another, reach resolution, and/or find middle ground (Hoffman 2011). Indeed, studies show that misinformation is best corrected alongside worldview affirmation (Lewandowsky et al. 2012). Without recognition, dismissal of the public's (cultural) concerns may limit learning, alienate potential participants, foreclose collaboration, exacerbate dissent, and, ultimately, entrench power dynamics (Shackleton et al. 2023). Stratton et al. (2022) further suggest that dismissal can bias public engagement and decision-making processes.

Denialism (low knowledge, low porosity)

Geraldi et al. (2019) suggest that media coverage of invasive species is generally short-term, lasting one to two years, due to decreases in newsworthiness and differences between expected ecological impacts and actual outcomes. Our analysis of coquí media elucidates how dissent may elongate anticipated media coverage well beyond the short-term. The difference dissent makes in media coverage produces a paradoxical trade-off for science communication of invasive species. On the one hand, increased media coverage generates greater issue awareness, a substantial obstacle with invasive species when compared to other environmental issues like climate change (Jarić et al. 2020a). Greater invasive species awareness can facilitate early detection, as well as eradication and control efforts, contributing to invasive species management goals (Novoa et al. 2017; Cordeiro et al. 2020). However, greater dissent can also provide fodder for science denialism.

Here, we illustrate how broader dissent arguments can blur into denialism, specifically as science denialists combine broader dissent discourse into their arguments. We find that ISD is present in Hawai'i public media, though stemming from a small number of individuals. Eighteen cases, about 21% of coquí dissent expressions, could be attributed to a single couple (Individual-E and F). However, even limited quantities of science denialism should not be disregarded, as prior research suggests that science denialism need not be massive to shift public perception of scientific consensus (Koehler 2016).

This couple's larger-than-average expression of dissent points to a pattern of iterative engagement. Like broader dissenters, they utilized several rhetorical techniques to combine various dissent threads and morph these expressions into a larger narrative which attempted to discredit scientific authority, undermine institutional trust, and ultimately foster a counter-narrative (Fig. 7). Beyond rhetoric, the couple launched vigorous campaigns against official mitigation efforts, which included coquí protection efforts and pro-coquí publications. Below, we outline a denialist sample text and highlight the way this approach feeds from broader public dissent (Fig. 7).

| FLICC Rhetorical Markers | Low Porosity MarkersEquates coqui eradication with being wrongDisbelief in scientific expertsDiminishes scientific | Low Knowledge |
|---|--|---|
| <u>Fake Experts</u> Conspiracy Theories | Before you jump to the wrong conclusion about the coquis, you should know that the entire anti-coqui agenda has been a carefully planned smear campaign. Fraudulent and exaggerated claims against the frogs have generated hate and intolerance to justify funding for a frog warWhen the 'experts' claims nothing would kill coqui except caffeine, they did not disclose that the University of Hawaii owns the patent on the caffeine gene, extracted from coffee. This patent was issued in 1999, the same yea the frog 'crisis' began. If the EPA approved the use of caffeine as a pesticide, the value of this would have increased, along with the stock value of Integrated Coffee Technologies, Inc., sole licensee for the use of the | Views invasive species agenda as a smear campaign Many techniques were tested- caffeine |
| Magnified Minority | gene, and run by an ex-dean from the universityTHE FACT is, there is a silent majority of people in Hawaii who like coquis. Why? Coquis are a natural form of pest control. <u>One</u> <u>man told us that he didn't like coquis until he saw one eating a cockroach.</u> Coquis also eat termites stinging caterpillars, and the notorious fire ants. People who live with coquis soon | emerged as the most effective Mosquitos |
| <u>Anecdotal</u> <u>Evidence</u> | notice that mosquito populations are downMany people also love coquis' sound at nightHowever, efforts to control the coqui will be ongoing, since they are virtually impossible to eradicate. And these efforts are dangerous to humans, pets, and plants. Coqui control now involves the experimental use of calcium hydroxide, commonly referred to as hydrated lime, which can cause irreversible eye damage and skin burns, as well as | have not been found in coqui diets At this point, |
| <u>False</u> Equivalence | death from inhalation <u>IT IS ironic that frogs are dying worldwide because of pollution</u> and development, while in Hawaii environmental extremists and exterminators are <u>busy polluting and bulldozing the environment, trying to kill frogs</u> " - 6/7/2005, Individual E | chytrid fungus was contributing to global declines |

Figure 7. Invasive species denialism. Close reading sample text of Individual-E (2005), highlighting FLICC markers as well as the porosity and knowledge characteristics which identify it as invasive species denialism.

In describing coquí impact claims as fraudulent and exaggerated, Individual-E (2005) makes several counter claims, including the claim that coquí eat mosquitos. These claims are unsubstantiated. The complete absence of counterevidence, and a failure to point to any scientific gaps (e.g. missing evidence) differentiates this from skepticism. Their limited engagement with coquí science suggests low knowledge. While the coquí as mosquito-catcher claims could initially be attributed to unfamiliarity (Armstrong 2001), scientists have repeatedly debunked this claim based on a study in Puerto Rico and a 2004 study in Hawai'i (Beard 2007), going as far as informing Individual-E of their misinformation in 2001. The coquí-as-mosquito catcher argument in the sample text, occurring in 2005, illustrates a failure to update their mental model based on new information – a marker of low porosity.

Invasion scientists fear that invasive species benefits such as the coquí-as-mosquito-catcher may be used to offset or understate any negative impacts (Lockwood et al. 2023). Our research suggests this is a valid concern as Individual-E, despite active involvement in past coquí discourse, highlighted only what they perceived to be the coquí's benefits while intentionally omitting any mention of negative impacts. Yet, we see similar benefit claims from other dissent types. Indeed, benefit counter-claims are likely due to the temporal conundrum noted above, and the overall sentiment that invasive species benefits are understated, an idea that is highly polarized within invasion science (Shackleton et al. 2022). In ISD, however, benefit counterclaims may present sticky ideas; that is, they persist, even when repeatedly debunked. As recently as 2019, despite ample reporting and scientific evidence to the contrary, this idea of the coquí-as-mosquito-catcher continues to circulate in Hawai'i (Dey 2019). Research illustrates that misinformation can be incredibly difficult to combat after-the-fact, as corrections may reinforce beliefs and/or fail to reduce them (Cook et al. 2015). This suggests it may be important to consider benefits early and widely, as a form of inoculation, before misinformation stickiness develops, rather than in reaction to dissent.

We note that individual-E's arguments are reflected in other examples throughout. For example, their allusion to the global amphibian crisis is evident in the unfamiliarity expressed in Fig. 6 and the atmosphere of "hate" is evident in the response quoted in Fig. 5. This style of additive argumentation is noted in climate change denialism as well (Poortinga et al. 2011), primarily because, as research suggests, science denialism is seldom about the science itself but rather a result of things like personal interest (Kahan et al. 2012; Stratton et al. 2022). Although there is overlap, close engagement and attention to knowledge/porosity can help better differentiate science denialism from broader dissent. Furthermore, as perceptions of consensus are susceptible to the effects of science denialism (e.g. influence of misinformation) (Koehler 2016; Cook et al. 2017), this allusion to the broader dissent discourse presented within the ISD commentary may act as a gateway into denialism from other types of dissent. Due to factors like confirmation bias and motivation bias, invalid or faulty arguments may appear increasingly convincing to members of the public if there is a common idea to bridge them (Correia 2011). Confirmation bias refers to the tendency to gravitate towards information that affirms your beliefs while ignoring that which doesn't, while motivational bias concerns the influence of an individual's desire and emotion on their critical thinking (Correia 2011). Such susceptibilities raise the importance of addressing dissent early and appropriately, particularly if denialism has yet to reach saturation, as Ricciardi and Ryan suggest (2018b).

Conclusion

Dissent can and should be viewed as growing pains, or friction points that will contribute to the field's long-term development (Shackleton et al. 2019). For example, unfamiliarity may highlight the need for greater reflection on the field's language/word choices and/or a gap in educational initiatives. Rather than merely something to eliminate, unfamiliarity can provide an opportunity for scientists and science communicators to reflect on public engagement, and if merited, the field more broadly. Skepticism and disagreement likewise provide a chance to build trust, revisit foundational theories, and open the field to diverse ways of thinking.

While evident in the coquí media of Hawai'i, ISD constitutes a small but loud problem. For reasons illustrated, utilizing rhetorical techniques and a harm criterion to identify science denialism within invasion science is insufficient for the recognition of ISD. Instead, we propose knowledge base and porosity provide additional benchmarks from which to distinguish science denialism and offer the spectrum of dissent as a starting point to unpacking invasive species dissent. Such an endeavor is fruitful for two principal reasons.

First, appropriately engaging ISD and broader dissent can limit negative repercussions. As denialism mirrors broader dissent, directly addressing or engaging dissent carries the potential to hamper the growth of ISD. Second, carefully distinguishing between ISD and broader dissent allows for invasion science to salvage valuable feedback that can help the field grow and advance. For example, in engaging with dissent throughout this article, we extend the conversation on three inter-related obstacles science communicators must mitigate: 1) the relationship between trust and temporal lags in evidence; 2) the influence of issue framing salience on public perception; and 3) the danger of dismissal. Although these challenges are not new to invasion science, their relationship to the varied forms of dissent has been less clear – a contribution of this article. As Estévez et al. (2015) suggest, "understanding the root of the conflict should allow the identification of more effective management actions and reconcile tensions before they become entrenched, unmanageable, and destructive".

Greater stakeholder engagement may help preempt dissent, including but not limited to, co-creation of evidence (i.e. citizen science), invasive species co-prioritization, multi-structured decision-making, etc. (Shackleton et al. 2019). Moon et al. (2015) indicate barriers to invasive species eradication can be mitigated through initiatives like co-management and knowledge co-production, which emphasize power-sharing and equal partnership. Shrestha et al. (2019) illustrate one way to integrate expert and community priorities in their exploration of community invasive species prioritization wherein they prompt participants to rank problematic invasive plants based on impacts and need for management. While this may not be practical in every case (Larson et al. 2017), moving towards a culture of co-creation and implemented stakeholder engagement can foster better science-society relationships that help accommodate urgent problem-solving amidst high uncertainty. Such initiatives not only serve to educate but democratize and legitimate decision-making in the eyes of the public. For example, in a study of landowner perceptions of rapid response programs to address the invasive emerald ash borer, Mackenzie and Larson (2010) suggest that inclusive processes can foster trust which "help to overcome conflicting values and thereby increase satisfaction with potentially unfavorable outcomes", especially when uncertainties are communicated alongside cost/benefits of available options. This idea, pointing towards outcome improvements upon greater attention to trust and stakeholder engagement processes, is long supported by risk researchers (Slovic 1999).

Ultimately, further research on ISD is merited. Additional work is needed to validate the spectrum of dissent framework at larger scales (e.g., regional, national, global), and within more recent timescales. Similarly, this article focuses on print news media, but more research is needed to determine if any significant differences are evident between news media and social media. Moreover, while numerous studies have offered strategies to address denialism, few have actively tested the efficiency of such approaches (Björnberg et al. 2017), suggesting a productive avenue for interdisciplinary work between scholars in invasion science, environmental communication, and psychology, among others.

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Data availability

All of the data that support the findings of this study are available in the main text or Supplementary Information.

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Supplementary material 1

Coding protocol

Authors: Jesann Gonzalez Cruz, McKenzie Johnson

Data type: pdf

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Supplementary material 2

Included media list

Authors: Jesann Gonzalez Cruz, McKenzie Johnson

Data type: xlsx

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