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Which features at home make a plant prone to become invasive?

Javier Galán Díaz^{1,2}, Enrique G. de la Riva³, Irene Martín-Forés⁴, Montserrat Vilà^{1,5}

Department of Plant Biology and Ecology, University of Sevilla, Profesor García González Street, 41012 Sevilla, Spain 2 Department of Pharmacology, Pharmacognosy and Botany, Complutense University of Madrid, Ramón y Cajal Square, 28040 Madrid, Spain 3 Department of Biodiversity and Environmental Management, Faculty of Biological and Environmental Sciences, University of León, Campus Vegazana, 24007 León, Spain 4 School of Biological Sciences, The University of Adelaide, Adelaide, South Australia 5005, Australia 5 Doñana Biological Station (EBD-CSIC) – Cartuja TA-10 Edificio I, Américo Vespucio Street, 41092 Sevilla, Spain

Corresponding author: Javier Galán Díaz (javiergalandiaz@gmail.com)

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Abstract

Determining the factors that pre-adapt plant species to successfully establish and spread outside of their native ranges constitutes a powerful approach with great potential for management. While this source-area approach accounts for the bias associated with species' regions of origin, it has been only implemented in pools of species known to be established elsewhere. We argue that, in regions with well-known introduction histories, such as the Mediterranean Biome, the consideration of co-dominant non-introduced species as a control group allows a better understanding of the invasion process. For this purpose, we used occurrence data from GBIF and trait data from previous studies to find predictors of establishment and invasion. We compare the frequency, climatic niche and functional traits of 149 co-dominant plant species in their native region in southern Spain, considering whether they have colonised other Mediterranean-climate regions or not and their level of invasion. We found that large native ranges and diverse climatic niches were the best predictors of species establishment abroad. Moreover, coloniser species had longer bloom periods, higher growth rates and greater resource acquisition, whereas coloniser species becoming invasive had also greater reproductive height and nitrogen use efficiency. This framework has the potential to improve prediction models and management practices to prevent the harmful impacts from species in invaded communities.

Keywords

Climatic niche, exotic plants, functional traits, Mediterranean-climate, source-area approach

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Introduction

Exotic plant species pose an increasing threat to native species and ecosystems conservation (Vilà et al. 2011; Bradley et al. 2019). Identifying predictors of invasion success constitutes a fundamental aim in invasion biology in order to support prevention measures and risk assessments (Pyšek et al. 2020). Key factors that drive successful invasion are high propagule pressure (Cassey et al. 2018) and having competitive traits or general-purpose phenotypes that confer ecological versatility and, therefore, high invasiveness (Drenovsky et al. 2012; Casado et al. 2018). Invasiveness also depends on the interaction with ecological and evolutionary processes occurring in the introduced range (Van Kleunen et al. 2010b); therefore, its determinants are context dependent (Novoa et al. 2020), which emphasises the necessity to identify variables that facilitate invasion under specific environmental constraints.

Most studies interested in identifying factors promoting invasion success frequently focus on understanding the mismatch in functional trait performance between exotic species and their native competitors in the recipient communities (e.g. de la Riva et al. 2019; Galán Díaz et al. 2021a). An alternative approach is to compare functional strategies of species from the same source or geographic region (i.e. source-area approach) to identify whether species' occurrence, traits and climatic niche in the native range allow us to predict their establishment and spread when introduced in other regions. This approach accounts for the bias associated with species region of origin and, potentially, allows us to focus on the role of traits alone (Martín-Forés et al. 2023). In this regard, it has been found that the climatic tolerance and ecological versatility of species in their native range are positively correlated with their capacity to establish and spread in other regions (Pyšek et al. 2009, 2015; Casado et al. 2018). This is probably associated with the display of certain trait attributes (Pyšek and Richardson 2007; Pyšek et al. 2009, 2015) and the fact that many exotic species are not only frequent and abundant in their invaded ranges, but also dominate in the communities of their native range (Firn et al. 2011; Galán Díaz et al. 2021b). Yet, most studies following the source-area approach have only looked at species known to be established in other regions, disregarding the role of co-dominant non-colonisers. We argue that, in regions with well-known introduction histories, the consideration of co-dominant non-introduced species as a control group allow us to broaden our understanding of the predictors of invasion success.

Studies following the source-area approach have mainly explored the importance of life history traits as predictors of invasiveness (Pyšek et al. 2009; Arianoutsou et al. 2013; Casado et al. 2018), whereas the role of functional traits in species native ranges has been frequently overlooked (but see Schlaepfer et al. (2010); Pyšek et al. (2015)). Moreover, the combined consideration of above- and below-ground plant functional traits remains little explored in invasion studies (Fridley et al. 2022). Plant traits might be useful to predict invasion success because, under specific environmental constraints, traits that confer dominance in the native range might be the same that facilitate establishment and spread in the introduced range (Thompson et al. 1995). In this regard, it has been shown that exotic species in Mediterranean regions can be functionally different to other species in their native communities (Galán Díaz et al. 2023) and display phenotypic variation when compared with communities in the introduced range (Martín-Forés et al. 2017, 2018). This might suggest that invasive species could already have intrinsic attributes to establish and thrive in communities with similar abiotic constraints rather than only benefitting from extrinsic ecological and genetic factors (Schlaepfer et al. 2010; Colautti et al. 2014). Therefore, it is important to leverage the performance of plant functional traits within the native range as predictors of the establishment and future stage of the invasion of species in the introduced range. In addition, it is necessary to include measures of phylogenetic relatedness as shared evolutionary histories of species might lead to statistical non-independence of data (Felsenstein 1985; Schlaepfer et al. 2010; Vilà et al. 2015).

Spain is home to many herbaceous species that are naturalised in other Mediterranean-climate regions of the world (Casado et al. 2018). The origin of these introductions can be tracked down to the arrival of the first Europeans settlers into these territories where species were introduced deliberately (i.e. crops, ornamental plants) or accidentally (i.e. weeds introduced with livestock, fodder, wool or cereals) (Barry et al. 2006; Martín-Forés 2017). These species (henceforth coloniser species) co-existed long-term with anthropogenic activities in their native range (Schlaepfer et al. 2010; MacDougall et al. 2018) and benefitted from an initial high propagule pressure. These coloniser species brought novel traits into the recipient communities, such as annual life cycles and efficient resource-use strategies, highly beneficial in a context of farming, intense herbivory, long drought periods and high soil disturbance (Seabloom et al. 2003; Funk and Vitousek 2007; HilleRisLambers et al. 2010; Molinari and D'Antonio 2014). Therefore, Spain communities constitute good candidates to apply the source-area approach.

Here, we compare the occurrence (i.e. frequency), climatic niche and functional traits of co-dominant plant species in their native region in southern Spain considering whether they have colonised other Mediterranean-climate regions or not. Our hypotheses are that: (1) Colonisers are more frequent and show greater climatic tolerances than co-occurring non-coloniser natives. This would reflect the importance of propagule pressure (high association with humans in the native range) and having great ecological versatility; (2) Colonisers are functionally different from non-coloniser species and show traits related to higher resource-acquisition rates and greater competitive ability. This would reflect that coloniser species benefit from niche opportunities or competitive advantages, even in Mediterranean-climate regions where the harsh environmental conditions frequently lead to functional convergence (Galán Díaz et al. 2021b, 2023); (3) Naturalised and invasive coloniser species are functionally distinct in their native range, i.e. certain plant attributes are related to the stage of invasion in other Mediterranean-climate regions.

Material and methods

Grassland surveys

We used trait data from co-dominant grassland species in southern Spain (Andalucía) compiled by Galán Díaz et al. (2022) which is available from Dryad (Galán Díaz et

al. 2022). Dominant species were defined as those whose cumulative cover made up at least 90% of the total community cover (Garnier et al. 2004). We selected as a source species pool all species native to Spain (149 species in total) which were classified as coloniser (98 species) or non-coloniser (51 species), depending on whether they are known to be introduced in other Mediterranean-climate regions of the world or not. We further classified coloniser species according to their stage of invasion or performance in other Mediterranean-climate regions into naturalised (56) and invasive (42) (Arianoutsou et al. 2013; Calflora 2014; Henderson 2020; Pagad et al. 2022). Naturalised colonisers are those species that have established at least in another Mediterranean-climate region; whereas, invasive refers to naturalised species that reproduce and spread fast at least in another Mediterranean-climate region (Richardson et al. 2000; Blackburn et al. 2011). The list of species included in this study can be found in Suppl. material 1: appendix S1.

Occurrence and climate data

Occurrence data of the target species in southern Spain were downloaded via the Global Biodiversity Information Facility (GBIF) using the "rgbif" package (Chamberlain et al. 2022). Although the native range of some species extended beyond this area, we focused on the distribution patterns within the species' native ranges where traits were measured (i.e. autonomous community of Andalusia) because intraspecific variation in species traits can be high across species distribution ranges (Umaña and Swenson 2019). To avoid artefacts related to collection bias and spatial clustering (Larridon et al. 2021), we filtered one observation per species and cell from a raster with a resolution of 30 seconds (0.86 km² at the Equator) which represents species frequency or number of grid cells occupied by the species. For the filtered observations, climate data were obtained from WorldClim at a resolution of 30 seconds (Fick and Hijmans 2017). We used the variables Annual Mean Temperature, Maximum Temperature of Warmest Month, Temperature Annual Range, Annual Precipitation, Precipitation of Driest Month and Precipitation Seasonality which represent average, extreme and seasonal indexes of temperature and precipitation.

Functional traits measurements

We considered eight functional traits that reflect orthogonal axes of plant function related to plant investment in above- and belowground vegetative and reproductive structures and community assembly processes (Table 1; Garnier et al. 2016; Hulme and Bernard-verdier 2018). Traits were measured in 149 species (301 combinations of species \times site). A detailed description of the methodology followed to measure each trait can be found in Galán Díaz et al. (2022). In addition, we retrieved another 13 traits from literature related to life and growth form, reproduction strategies, pollination vectors and dispersal vectors (Table 1; the list of references can be found in Suppl. material 1: appendix S2).

	Trait	Abb.	Units	Significance
	Growth form *		Bulbous/Erect/Graminoid/P	
	Life form *			Therophyte/Geophyte//Hemicryptohpyte/Chamephyte
	Specific leaf area	SLA	cm ² /g	Resource acquisition rate and conservation,
				photosynthetic rate, relative growth rate
af	Leaf dry matter content	LDMC	mg/g	Leaf tissue density, resistance to physical hazards, stress
Le				tolerance
	Ratio C:N	CN	CN Resource allocation	
	Isotopic carbon fraction	$\delta^{13}C$	‰	Integrated water use efficiency
	Specific root length	SRL	cm/mg	Resource acquisition rate and conservation, relative
Root				growth rate
	Root dry matter content	RDMC	mg/g	Root tissue density, resistance to physical hazards,
				drought resistance
	Root diameter	RD	mm	Mycorrhizal association
	Reproductive height		cm	Dispersal capacity
	Seed mass *		g	Seedling survival and establishment
	Onset of flowering *	OFL	months	Reproductive success
	Length of bloom *	LB	months	Reproductive success
ion	Self-compatibility *		1/0	
luct	Pollination mechanism *			Insects/Wind/Selfed
oroc	Dispersal vector *	Agochory	1/0	Humans
Ref		Autochory	1/0	Self-dispersed
		Anemochory	1/0	Wind
		Hydrochory	1/0	Water
		Zoochory	1/0	Animals
	Number of dispersal vectors *	numb_disp	1–5	

Table 1. Traits considered in this study. Traits marked with an asterisk were retrieved from literature (the list of references can be found in Suppl. material 1: appendix S2).

Statistical analyses

First, to estimate species' climatic niches, we performed a Principal Component Analysis (PCA) with the six climatic variables and used the scores of the observations along the first three Principal Components (PCs) to calculate two indexes (Suppl. material 1: appendix S3): (i) climatic niche richness, calculated as the smallest convex hull that encloses all observations of a given species; and (ii) climatic niche diversity, calculated as the mean pairwise distance amongst observations of a given species. These indexes represent two independent facets of species climatic niches. While climatic richness represents the dispersion or range of species climatic niches, climatic diversity indicates how the observations are distributed within the convex hull. The mean pairwise distance is less sensitive to outliers and is better correlated to the number of different habitats occupied by the species in their native range, a known predictor of invasiveness (Pyšek et al. 2015). We used linear models to compare whether the species frequency and climatic niches differ between non-coloniser, naturalised and invasive species.

Second, we compared trait differences between non-coloniser and coloniser species and differences between naturalised and invasive species within non-colonisers. For continuous traits, we used the median value per species. Reproductive height and seed mass were log-transformed prior to analyses. We ran linear models to test for differences in continuous traits and chi-squared tests for categorical data. We ran Wilcoxon ranksum and Kruskal-Wallis tests for onset of flowering, length of the bloom period and number of dispersal mechanisms. To test for the effect of phylogenetic non-independence amongst species (i.e. whether the observed patterns reflect contrasting evolutionary histories), we ran a phylogenetic ANOVA using the aov.phylo function implemented in the "geiger" package (Pennell et al. 2014). For this, we used an existing megaphylogeny to obtain a phylogenetic inference of our study species (Qian and Jin 2016). Species which were missing in the original tree were substituted by congeneric species (de la Riva et al. 2019). The phylogenetic inference is available in Suppl. material 1: appendix S4.

Third, we ran a supervised classification algorithm (random forest) to leverage the relative importance of species occurrence (i.e. frequency), climatic niches and traits as predictors of invasiveness. We removed qualitative traits with missing data and imputed continuous traits using the rfImpute function included in the "randomForest" package. We also included family as a predictor because of the importance of phylogenetic relationships inferred from the phylogenetic ANOVA.

All statistical analyses were performed in R version 4.2.2. To ensure the results of this study are fully reproducible, codes are available from GitHub (https://github.com/galanzse/colonizersathome) and data from the Dryad Digital Repository (Galán Díaz et al. 2022).

Results

Coloniser species were more frequent than non-coloniser species in their shared native range in southern Spain and had greater climatic niche richness and diversity (Fig. 1). When considering the stage of invasion in other Mediterranean-climate regions, naturalised species were more frequent than non-coloniser species; both coloniser groups (i.e. naturalised and invasive species) had similar climatic richness and greater climatic richness than non-colonisers; and invasive species had greater climatic diversity than non-coloniser and naturalised species (Fig. 1).

We found significant functional differences between non-coloniser and coloniser species for four traits: specific leaf area (SLA), specific root length (SRL), length of bloom period and number of propagule dispersal vectors (Fig. 2 and Table 2). Coloniser species had on average 17.68% greater SLA and 15.23% greater SRL than non-coloniser species. The bloom period of coloniser species was one month longer than non-coloniser species. Coloniser species showed more propagule dispersal vectors than non-colonisers.

We found significant differences between groups when considering the stage of invasion of colonisers in other Mediterranean-climate regions (Fig. 3). Naturalised colonisers had on average 23.20% greater SLA than non-colonisers and their bloom periods were one month longer. Invasive colonisers were 11.03% taller and had 20.78%



Figure 1. Species frequency (i.e. number of cells occupied in the native region), climatic niche richness (i.e. smallest convex hull that encloses the observations) and climatic niche diversity (i.e. mean pairwise distance amongst occurrences) of non-coloniser and coloniser species, also considering the stage of invasion of coloniser species (i.e. naturalised or invasive) in other Mediterranean-climate regions.

greater C:N than naturalised colonisers. Both naturalised and invasive coloniser species showed more propagule dispersal vectors than non-colonisers.

The phylogenetic ANOVAs revealed that evolutionary relatedness does not necessarily determine trait differences between non-coloniser and coloniser species, but plays a major role when considering the stage of invasion of colonisers. Functional



븜 non-coloniser 븜 coloniser

Figure 2. Functional differences between non-coloniser and coloniser species. * p-value < 0.05.

differences between non-coloniser, naturalised and invasive species may reflect phylogenetic non-independence amongst groups, mostly due to the large proportion of invasive grasses (Suppl. material 1: appendix S5).

Non-coloniser and coloniser species differed in many qualitative traits (Table 2). Naturalised coloniser were more frequently therophytes, whereas invasive colonisers were more frequently grasses and, therefore, pollinated by wind more than the other groups. More than fifty percent (51.02%) of coloniser species were reported to be self-compatible in contrast to 15.68% of non-coloniser species. Overall, coloniser species presented more dispersal vectors than non-colonisers.

The accuracy of the random forest model was 73.53% when predicting coloniser/ non-coloniser species (Table 3). The most important variables that contributed to this model were richness of the climatic niche, dispersal vectors, agochory, family and zoo-



Figure 3. Functional differences between non-coloniser, naturalised and invasive species. Letters denote statistical differences in post-hoc comparison (p-value < 0.05).

chory (Fig. 4). The inclusion of the stage of invasion decreased the accuracy of the model to 58.82%. The most important variables that contributed to the model specifying the stage of invasion were richness of the climatic niche, dispersal vectors and family.

Discussion

Discerning general invasion syndromes across ecosystems can facilitate the identification of species with greater risks of establishment and support management actions at different stages of the invasion process (Novoa et al. 2020). In this study, we looked at the occurrence, climatic niches and traits of a pool of co-dominant grassland plant

	trait	non-coloniser	coloniser	(n = 98)
		(n = 51)	naturalised (n = 56)	invasive (n = 42)
Life form	therophyte	32	51	28*
	geophyte	2	1	0
	hemicryptophyte	10	4	13
	chamephyte	3	0	1
Growth form	bulbous	3	1	0
	erect	26	28	17*
	graminoid	4	6	17*
	prostrate	13	18	4*
	rosette	2	3	4
Pollination	insects	32	38	18*
	wind	6	9	21*
	self-compatible	8	33	17*
Dispersion	agochory	2	22	23*
	anemochory	12	19	23*
	autochory	4	24	6*
	hydrochory	1	12	11*
	zoochory	13	36	28*

Table 2. Contingency table of qualitative traits of non-coloniser and coloniser species. Coloniser species are separated considering their level of invasion in other Mediterranean-climate regions. * p-value < 0.05.

Table 3. Confusion matrices of random forest models. Rows indicate the actual (true) values for each category and columns indicate predicted values. The classification error corresponds to the proportion of wrongly classified cases, i.e. for a given category, the classification equals to the number false negative predictions divided by the total number of actual cases.

predicted							
la la	Model 1	coloniser	non-	classification error			
	coloniser	79		0.17			
	non-coloniser	20		0.49			
ctui	Model 2	invasive	naturalised	non-coloniser			
a	invasive	18	13	10	0.56		
	naturalised	11	36	7	0.33		
	non-coloniser	6	9	26	0.37		

species in their native range in southern Spain to explore its utility as predictors of invasiveness in other Mediterranean-climate regions of the world.

We found that coloniser species are more widespread (i.e. frequent) in their native region than co-dominant non-coloniser species. This result matches the Casado et al. (2018) positive relationship between the degree of occurrence of herbaceous species in their native range in the Iberian Peninsula and their capacity to successfully occupy other Mediterranean-climate regions. This evidence also adds to previous studies that reported high abundances of coloniser species in their native Mediterranean communities (Firn et al. 2011; Galán Díaz et al. 2021b). This trend, therefore, suggests that the more frequent and dominant species are in their native region, the greater the



Figure 4. Variable importance plot of random forest classification models. Origin indicates whether the species are introduced in other Mediterranean-climate regions of the world (i.e. non-coloniser and coloniser). Invasiveness refers to species' stage of invasion in other Mediterranean-climate regions (i.e. non-coloniser, naturalised and invasive).

probability of coming into contact with humans and the higher the propagule pressure, ultimately facilitating their establishment (Cassey et al. 2018). We also found a positive relationship between the frequencies of coloniser species in their native ranges and their climatic niche richness and diversity, i.e. coloniser species occupy a large proportion of climatically different areas in their native range reflecting their ecological versatility. When considering invasion status, naturalised colonisers were more frequent than non-coloniser species and, whereas we did not find evidence supporting a greater frequency of invasive colonisers than non-colonisers, invasive colonisers showed the greatest diversity in terms of their climatic niche. Similarly, Pyšek et al. (2009, 2015) found that the number of habitats that a species occupies in its native range is positively correlated to the number of regions where it has successfully established abroad. As naturalised and invasive species showed similar climatic niches in terms of richness, this result reflects that colonisers' capacity to fully occupy their climatic and ecological niches in the native range is a good predictor of their capacity to overcome the dispersal and environmental barriers abroad and become invasive (Blackburn et al. 2011).

There were functional differences between non-coloniser and coloniser species. Overall, coloniser species achieve a combination of traits that facilitate rapid growth, regeneration and spread compared to non-coloniser species. That is, colonisers species displayed greater SLA and SRL, which indicates high resource-use efficiency and relative growth-rates (i.e. high C gain and leaf production when resources are abundant; Funk et al. (2017); Fridley et al. (2022)) and higher rates of N uptake (Jo et al. 2015, 2017). Similar trends have been reported across communities of the Mediterranean Biome (Galán Díaz et al. 2021a) and globally (Ordonez and Olff 2013; Fridley et al. 2022). Our findings also indicated that leaf traits of colonisers appear to be coordinated

with root traits, which suggests that synchronisation amongst organs as part of a wholeplant resource uptake strategy is common in Mediterranean plants (de la Riva et al. 2016, 2021). Moreover, we found that coloniser species had longer length bloom periods, which indicates a greater investment in reproductive structures. Hence, coloniser species may benefit from reduced competition via exploiting different temporal niches (Godoy et al. 2009), thereby increasing the chances of producing viable propagules by potentially covering broader seasonal ranges and climatic conditions (Grubb 1977). Coloniser species showed more propagule dispersal vectors (both naturalised and invasive species) than non-coloniser ones. This variety of dispersal vectors provides an advantage when they come into contact with humans in the native region and spread across other regions after establishment (Pyšek and Richardson 2007; Blackburn et al. 2011). Both naturalised and invasive colonisers showed a greater proportion of self-compatible species than non-colonisers. It has been argued that self-compatibility could facilitate the establishment of exotic species but, hinder species of becoming invasive (Pyšek and Richardson 2007). Yet, multiple introductions are frequent and within-population genetic diversity of introduced populations has been found to be comparable to native populations (Bossdorf et al. 2005); therefore, the possibility of self-fertilisation could be an advantage at every stage of the invasion process. This collated evidence suggests that coloniser species could benefit from niche opportunities or competitive advantages in their native region (Galán Díaz et al. 2021b, 2023). These functional differences could present an advantage in anthropogenic habitats globally if they reflect adaptation to agricultural and managed habitats (MacDougall et al. 2018).

As we pointed out, maximising resource uptake and high relative growth rates has been observed as a successful strategy for coloniser species. However, when considering invasion status, the patterns were more nuanced: we did not find significant differences in SRL associated with invasion status and the species displaying the highest SLA and longer bloom periods were naturalised instead of invasive colonisers. Invasive species, in turn, displayed higher values of reproductive height, which is closely correlated to plant stature in grassland species and C:N concentration. Therefore, different traits might be relevant along different stages of the invasion process (Pyšek et al. 2015; Milanović et al. 2020). On the one hand, higher rates of growth and resource acquisition might facilitate plant survival and establishment in seasonal climates with dry seasons such as the Mediterranean (Funk et al. 2016; Galán Díaz et al. 2021a). Additionally, the longer length bloom periods of naturalised species compared to non-colonisers, which were also frequently pollinated by insects, suggests that the potential to participate in native plant-pollinator networks might result in being beneficial (Parra-Tabla and Arceo-Gómez 2021). On the other hand, our results reflect the importance of greater dispersal distance and above-ground competitive hierarchy and competition for light to overcome the dispersal barrier and become invasive (Schlaepfer et al. 2010; Bernard-Verdier et al. 2012). Reproductive height constitutes a well-known driver of invasiveness (Van Kleunen et al. 2010a; Gallagher et al. 2015; Divíšek et al. 2018) and it has been shown that invasive grasses transform grassland native communities by filtering tall native species that can compete for light (Molinari and D'Antonio 2014).

Higher C:N ratio indicates high nitrogen use efficiency in nitrogen-limited communities (Zhang et al. 2020).

The phylogenetic regressions suggest that some observed differences across stages of invasion may be masked by evolutionary relatedness amongst groups: naturalised species were more frequently forbs, whereas invasive colonisers were more frequently grasses. For instance, invasive species not displaying significantly greater SLA than non-colonisers, but showing greater C:N, might reflect greater carbon allocation to leaves in grasses than in forbs (Duffin et al. 2019). In addition, naturalised species were more frequently pollinated by insects, whereas invasive colonisers were more frequently pollinated by wind. The little dependency of invasive species for insect pollination might increase the chances of producing viable propagules. This suggests that trait comparisons expecting competition within the LHS strategy scheme might not be useful to completely understand community assembly processes along different stages of the introduction process (Westoby 1998) and that niche complementarity in terms of life forms, pollination and dispersal vectors are key aspects to consider.

The two most important predictors of the random forest models were climatic richness and number of dispersal vectors. Family was an important variable reflecting the importance of considering evolutionary relatedness in biological invasions to account for unmeasured trait diversity and to correctly interpret the observed differences (Felsenstein 1985; Schlaepfer et al. 2010; Vilà et al. 2015). Agochory (i.e. accidental spread of plants by humans) also contributed to the overall accuracy of the models, suggesting that species with propagules suspected of being dispersed by (and associated with) humans are those with higher probabilities of establishing abroad (MacDougall et al. 2018). However, the first model did not allow us to differentiate non-coloniser species with the capacity to establish in other regions or, conversely, this might suggest that some non-coloniser species could have the climatic tolerance and traits to do so. The second model yielded very low overall performance because of the great overlap between naturalised and invasive colonisers in the distribution of the predictor variables. It is worth noting that functional traits constituted poor predictors of species establishment and invasiveness compared to climatic or ecological tolerance indexes. Therefore, our findings support that, whereas functional traits have the potential to capture community assembly processes (Galán Díaz et al. 2023) or intraregional distribution patterns (Pyšek et al. 2015), traits alone might not directly relate to the stage of invasion in most habitats (Fridley et al. 2022).

Conclusions

We have shown that coloniser species are already pre-adapted to broader climatic niche conditions in their native range, which predisposes them to occupy greater diverse conditions once they are introduced in a new area. In a similar manner, certain traits, especially indicating aided dispersal, high relative growth rate and resource efficiency, are related to successful colonisation; whereas, invasion processes in grasslands are more associated with plants displaying higher reproductive height and nitrogen use efficiency. The source-area approach can be especially useful when comparing regions with shared histories of colonisation and trade where plant introduction histories have been mostly unidirectional as is the case of the Mediterranean Biome. The knowledge derived from such studies may allow us to improve prediction models, identifying key species to monitor; this could, therefore, prevent potential harmful impacts from coloniser species in invaded communities and reduce the investment necessary to target eradication measures.

Author contributions

JGD: Conceptualisation, Methodology, Formal analysis, Investigation, Data curation, Writing - original draft, Writing - review and editing. EGR: Methodology, Supervision, Writing - review and editing. IMF: Investigation, Writing - review and editing. MV: Conceptualisation, Supervision, Funding acquisition, Writing - review and editing.

Data availability statement

The data and codes used in this study are archived in Dryad and Github.

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Supplementary material I

Species list, references accessed during bibliographic research, phylogenetic inference used in the analyses, PCA of climatic variables, and results of linear regressions Authors: Javier Galán Díaz, Enrique G. de la Riva, Irene Martín-Forés, Montserrat Vilà Data type: species, references, phylogenetic, models

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RESEARCH ARTICLE



The relationship between naturalized alien and native plant species: insights from oceanic islands of the south-east Pacific over the last 200 years

Luis Cáceres-Polgrossi¹, Maura Di Rico¹, Diego Parra¹, Hanno Seebens², Stephen D. Galvin³, H. Juergen Boehmer⁴

1 World Ecology Conservation Group, Viale Stazione 2, Levico Terme, Trentino Alto-Adige, Italy 2 Senckenberg Biodiversity and Climate Research Centre, Senckenberganlage 25, 60325 Frankfurt, Germany 3 School of Agriculture, Geography, Environment, Ocean & Natural Sciences, The University of the South Pacific, Suva, Fiji 4 Institute of Geobotany, Leibniz University Hannover, Nienburger Straße 17, 30167 Hannover, Germany

Corresponding author: Luis Cáceres-Polgrossi (cac.polgrossi@gmail.com)

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Abstract

Aim: The relationship between native and naturalized alien species has been widely studied, particularly across large geographic scales. However, our knowledge of the spatial and temporal variations of their relationships is still limited, particularly for remote oceanic islands such as those of the south-east Pacific and across islands and archipelagos. In this study, we aim to assess the relationships between native and naturalized alien species by analyzing their current patterns of species-area relationships at different spatial scales, in addition to temporal variations in species richness, over the last 200 years.

Area: One island (Rapa Nui) and two archipelagos (Juan Fernandez and Desventuradas Islands) comprising a total of 11 oceanic islands of the south-east Pacific (OISEP).

Methods: We assembled the most comprehensive dataset of the vascular flora of the OISEP from currently available island flora checklists and updated with recent publications. Each plant species was classified as being native or naturalized alien. We examined temporal changes by estimating species richness, naturalization rates and naturalized-to-native ratios over time based on the first collection year of each naturalized alien species. Then, we determined the best shape of naturalized alien species richness accumulation over time by contrasting the fit of lineal, exponential, sigmoidal and Weibull regressions. Finally, we analyzed the relationships between native and naturalized species firstly at the inter-archipelagic scale by fitting island species-area relationship models and secondly at the island scale by performing ranged major axis regression analysis on residual values. **Results:** The OISEP flora dataset contained 674 species of which 282 were native and 392 were naturalized alien. Native island species-area relationships were similar to those of the naturalized alien species. Naturalized alien species richness increased notably through time with two clear peaks in 1950 and 2000. A Weibull regression and an exponential shape over time were the most appropriate fits for naturalized alien species richness accumulations at the inter-archipelagic scale, which further emphasizes the notable increase in naturalized alien species richness experienced in the timeframe examined here.

Main conclusions: The relationship between naturalized alien species richness and native species richness was found to be independent of the geographic scale. The number of naturalized alien species clearly exceeded the number of native species on most islands but also for the whole OISEP. The accumulation of newly detected naturalized alien species does not show any sign of saturation and it is likely that new species will arrive in the future. Increased efforts on monitoring, prevention and biosecurity are needed to halt biological invasions on these unique island ecosystems.

Keywords

island flora, islands species-area relationship, naturalized alien species additions

Introduction

Islands have long been of considerable scientific interest for studies in ecology, biogeography and evolution thanks to their well-delimited geographic features and their high levels of biodiversity (Whittaker et al. 2017). In addition, many islands are particularly vulnerable to anthropogenic disturbances (Whittaker and Fernández-Palacios 2007; Keppel et al. 2014), with one of the major drivers of biodiversity loss being the introduction of alien biota and their subsequent naturalization (hereafter, naturalized alien species) (Caujapé-Castells et al. 2010; Leclerc et al. 2018; Fernández-Palacios et al. 2021). In this context, we referred to "naturalized alien species" as plant species deliberately or unintentionally introduced by humans that have, in turn, gone on to form self-sustaining populations - or are in the process of doing so - in an area outside their native range. Such naturalized alien species can be catalysts for biodiversity loss on oceanic islands (Tye 2006; Kueffer et al. 2010). However, the hypothesis that alien plant invasions trigger declines in native plant species populations or, indeed, lead to extinctions, is still debated (Sax et al. 2002; Gurevitch and Padilla 2004; Sax and Gaines 2008). Nevertheless, there is consensus that the number of naturalized alien species has increased distinctly during recent times (Sax et al. 2002; Sax and Gaines 2008; Seebens et al. 2017). This has drastically changed plant species diversities more so on oceanic islands than on continental islands or mainland areas (Sax et al. 2002; Denslow 2003; Sax and Gaines 2006; Castro et al. 2010; Kueffer et al. 2010; van Kleunen et al. 2015).

The combination of steep invasion rates and small island areas suggests that the number of species on oceanic islands might reach saturation as there is, first, a limited number of species that can be supported by the environmental conditions and, second, a strictly defined area within which they can establish reproducing populations. Two possible mechanisms can emerge if an island reaches the saturation point, each of which has different implications for the relationship between naturalized aliens and native species

(Sax and Gaines 2008). The first, called "extinction-based saturation" (Sax and Gaines 2008), predicts that new naturalizations will trigger subsequent species extinctions, in line with the equilibrium theory of island biogeography (MacArthur and Wilson 1963, 1967). The second hypothesis, termed "colonization-based saturation" (Sax and Gaines 2008), predicts that if island species richness remains constant through time, then the colonization would be suppressed without any extinction of native or established species (Tilman 2004). Signs of extinction-based saturation have been found on Alejandro Selkirk island (Juan Fernandez Archipelago; Greimler et al. 2017), while there has been no evidence of colonization-based saturation on any island worldwide (Sax and Gaines 2008; Seebens et al. 2017). In contrast, the observed increases in alien plant naturalizations have been linear on islands worldwide (Esler and Astridge 1987; Wu et al. 2003; Tye 2006; Sax and Gaines 2008). This could be interpreted as an indication of no saturation, whereby the number of naturalized alien species will continue to increase without extinctions (Seebens et al. 2017). Sax et al. (2002) put forward the idea that extinctions of native plant species on oceanic islands were not a consequence of the presence of naturalized alien species. Gaining insights into temporal variation and its relationship with native species richness is highly relevant in understanding current and future patterns of the fate of native species while also helping to define priorities in conservation planning (Tye 2006; Greimler et al. 2017); however, such insights remain limited (Sax and Gaines 2008). In this context, we examined temporal variation of naturalized alien species richness and its relationship to native species diversity at island and inter-archipelagic scales.

Native species richness are also highly correlated after accounting for the area effect (i.e., by means of island species-area residuals; Lonsdale 1999; Sax and Gaines 2008). Even islands rich in native species often also harbor many naturalized alien species (Lonsdale 1999; Rojas-Sandoval et al. 2020). Through the loss of island habitats and increasing propagule pressure of alien plant species, human activity led to increases in naturalized alien species. This, in turn, can negatively influence native species richness - mostly through habitat loss - potentially leading to the extirpation of native species. However, the magnitude of these disturbances is very different across islands triggering different native-naturalized alien species richness scenarios (Caujapé-Castells et al. 2010).

On the other hand, it remains unclear whether naturalized alien species richness increases with area in the same way as native species richness. Here, island species-area relationship models (hereafter, ISAR) have played a central role as their parameters (intercept and slope) can be interpreted with a biogeographic sense (Triantis et al. 2012). ISAR parameters are sensitive to island isolation resulting in more isolated islands having steeper slopes and lower intercepts in comparison to less isolated islands (McArthur and Wilson 1967). In fact, ISAR parameters for islands have produced higher slopes and lower intercepts than for continental areas (Rosenzweig 1995) while oceanic islands showed higher slopes and lower intercepts than continental islands (Triantis et al. 2012; Patiño et al. 2014). It can also be expected that ISAR slopes and intercepts differ between native and naturalized alien species because dispersal barriers have been lowered for naturalized species, potentially resulting in higher colonization rates. Previous studies revealed that the slopes of native and naturalized alien ISAR have shown similar trends on continental

islands (Long et al. 2009) and on islands of mixed origins (Chiarucci et al. 2017). On oceanic islands, the slopes of native and naturalized alien ISAR have shown conflicting patterns in slopes (Burns 2016; Blackburn et al. 2016; Chiarucci et al. 2021). One possible explanation may be that isolation could vary for naturalized alien species that are transported by humans, placing more emphasis on human connectivity over geographical proximity (Russell et al. 2017). Another explanation could be that these three studies have analyzed different area ranges influencing changes on ISAR slopes (Triantis et al. 2012). Thus, naturalized alien ISAR will see lower slopes and higher intercepts as a result of increased human transport, whereby anthropogenic activity facilitates species' arrivals independent of island isolation (McArthur and Wilson 1967; Chiarucci et al. 2021).

Oceanic islands of the south-east Pacific (hereafter, OISEP) include Rapa Nui (also known as Easter Island or Isla de Pascua), which is one of the more anthropogenically impacted islands in the region, while the Juan Fernandez Archipelago has the highest level of endemism per km² for an oceanic archipelago (Caujapé-Castells et al. 2010; Vargas et al. 2014). Although the origins of the naturalized alien plants varied before the arrival of Europeans, today, the dominant source pool for alien plants on OISEP islands is Chile (Castro et al. 2007). This study area is part of the Pacific region, which has, globally, experienced the most rapid increase in instances of naturalized alien plants (van Kleunen et al. 2015). Despite these trends, detailed analyses of naturalization on OISEP are scarce. Most studies focused exclusively on one island (Stuessy et al. 1997; Swenson et al. 1997; Stuessy et al. 1998; Vargas et al. 2011; Greimler et al. 2017; Vargas-Gaete et al. 2018) or a single archipelago (Sanders et al. 1982; Greimler et al. 2002; Danton et al. 2006). A very limited number of studies have focused on the whole island group (Castro et al. 2007, 2010; Castro and Jaksic 2008) albeit only the larger islands. Our study builds upon studies describing the vascular flora of smaller OISEP islands (Danton et al. 2006; Danton and Perrier 2016) and the considerable number of important botanical studies of the OISEP vascular flora (Skottsberg 1937; Sparre 1949; Hoffmann and Marticorena 1987; Hoffmann and Tellier 1991; Zizka 1991; Matthei 1995; Muñoz-Schick 1995; Mueller-Dombois and Fosberg 1998; Cuvertino 2001; Danton et al. 2006; Meyer 2008; Escobar et al. 2011; Finot et al. 2015; Danton and Perrier 2016, 2017). Thus, we aim to test the following hypotheses: (1) naturalized alien species richness has exceeded native species richness at inter-archipelagic and island scales; (2) naturalized alien species richness has linearly increased over time at the inter-archipelagic scale; (3) native and naturalized alien species are not related at island scale, likely due to the aforementioned variations in the history of human colonization; and (4) slopes and intercepts differ between native and naturalized alien ISAR.

Methods

Study Area

We examined 11 oceanic islands and islets in the south-east Pacific, each of which has well-documented native and naturalized alien flora (Fig. 1; see Suppl. material 1:

table S1 in for further details). These islands can be grouped into Desventuradas islands (Fig. 1A), Rapa Nui (Fig. 1B) and Juan Fernandez Archipelago (Figure 1C).

The Desventuradas islands are dominated by two small islands about 890 km off the north coast of Chile and about 810 km north of the Juan Fernandez Archipelago (Fig. 1). The two main islands, San Ambrosio (SA, Fig. 1A) and San Felix (SF, Fig. 1A), are separated by 18.5 km. Gonzalez Islet, at the south-eastern tip of San Felix, was excluded from our analyses because it has no documented flora. The archipelago has an oceanic, subtropical climate with annual precipitation of around 100 mm that falls mainly in winter between May and August (Hajek and Espinoza 1987), while yearly temperatures range between 10 °C and 25 °C (Hoffmann and Tellier 1991). The vegetation in San Felix reflects the arid conditions where plant cover, dominated by bushes, does not exceed 25% of the surface (Hoffmann and Tellier 1991). The more elevated nature of San Ambrosio (479 m in comparison to San Felix's 193 m) facilitates greater vegetation cover thanks to the presence of fog (Johnston 1935; Kuschel 1962) and more developed soils (González-Ferrán 1988). San Ambrosio and San Felix are uninhabited islands, but they are visited occasionally by groups of fishermen (Hoffmann and Tellier 1991).

The Juan Fernandez Archipelago is composed of three islands and multiple islets about 784 km off the coast of Chile (Fig. 1B). The three main islands are Robinson Crusoe (RC), Alejandro Selkirk (AS) and Santa Clara (SC). The archipelago also includes the five islets of Morro Juamango (MJ), Morro Verdugo (MV), Morro Vinilo (Mvi), Morro Sin Nombre (Msn) and Morro Spartan (MS), whose flora has been described by Danton et al. (2006) and Danton and Perrier (2016). The climate is subtropical oceanic with an annual precipitation of around 1100 mm while temperatures range from 15 °C to 25 °C (Hajek and Espinoza 1987). Robinson Crusoe and Alejandro Selkirk islands are home to a greater diversity of vegetation thanks to their larger size (both ~50 km²) and higher elevation (1320 m and 915 m, respectively). Meanwhile, the considerably smaller Santa Clara (2.2 km², 367 m a.s.l.) has predominantly herbaceous vegetation (Hoffmann and Marticorena 1987). Only Robinson Crusoe contains a permanent human settlement with 927 inhabitants, of which 35–50 move to Alejandro Selkirk during the period of increased fishing activity (October-May; Gobierno Regional de Valparaiso, 2016).

Rapa Nui (IP) is the easternmost island of Polynesia, about 3510 km off the north coast of Chile (Fig. 1C). Nearby are the three islets of Motu Iti, Motu Nui and Motu Kao Kao, while Salas y Gomez Island lies about 390 km to the northeast. The flora of these islands has not been documented. The climate is subtropical-oceanic with annual precipitation of 1365 mm (Mueller-Dombois and Fosberg 1998) and yearly temperatures range between 15 °C and 25 °C (Hajek and Espinoza 1987). The vegetation is predominantly herbaceous grassland consisting mainly of introduced grass species (Etienne et al. 1982; Zizka 1991). There are some small, dense forests composed of introduced tree species. The vegetation less impacted by humans is located on inaccessible coastal habitats, the upper parts of Maunga Terevaka and on Rano Kao zones (Zizka 1991). Rapa Nui contains a permanent human settlement with 7750 inhabitants (Instituto Nacional de Estadísticas de Chile 2017).



Figure I. Map of the study area **A** Desventuradas islands, composed of San Felix (SF) and San Ambrosio (SA) **B** Juan Fernandez Archipelago, composed of Robinson Crusoe (RC), Alejandro Selkirk (AS), Santa Clara (SC), Morro Spartan (MS), Morro Sin Nombre (Msn), Morro Verdugo (MV), Morro Juamango (MJ) and Morro Vinilo (Mvi) and **C** Rapa Nui (IP).

Data assembly

We assembled data on the vascular native and naturalized alien flora for the entire OI-SEP (Fig. 1). The many scientific expeditions to the islands over the past two centuries have ensured a comprehensive insight into their flora. We assembled the flora of the Desventuradas islands based on the works of Skottsberg (1937), Sparre (1949), Hoffmann and Marticorena (1987), Hoffmann and Tellier (1991), Muñoz-Schick (1995), Mueller-Dombois and Fosberg (1998), Cuvertino (2001) and Escobar et al. (2011). The flora of the Juan Fernandez Archipelago was gathered using Danton et al. (2006), Danton and Perrier (2016), Danton and Perrier (2017) and Stuessy et al. (2018b). The works of Zizka (1991), Matthei (1995), Meyer (2008) and Finot et al. (2015) provided data for Rapa Nui. Species that have subsequently proved to be misidentified and those for whom there remains reasonable doubt over their identification were excluded (Danton and Perrier 2017). Taxa were standardized according to the Global Biodiversity Information Facility (GBIF) taxonomic backbone using TAXADB package (Norman et al. 2020) of the statistical environment R (R Core Team 2020). Synonyms, heterotypic and homotypic synonyms were changed to the accepted names while the Catalog of the Vascular Plants of Chile (Rodriguez et al. 2018) was used as back-up source of information for more problematic taxa.

The original sources facilitated the classification of the assembled flora into native and naturalized alien species from which the species richness for each island and the whole OISEP was determined. We excluded cultivated or occasional species from the naturalized alien species lists (Tye 2006).

Data analysis

Native and naturalized alien species relationships through time

For the analysis of plant diversity changes over time, we obtained the year of the first record or reference available of each alien plant that became naturalized alien on each island. If multiple first records for one naturalized alien species were provided for different islands (because they have different arrival dates), the earlier first record was selected for the entire study area. On the larger islands of Rapa Nui, Alejandro Selkirk, Robinson Crusoe, Santa Clara, San Ambrosio and San Felix, confidence in the early records is high due the frequent and detailed botany studies carried out throughout time. For the smaller islands of Morro Juamango, Morro Spartan, Morro Sin Nombre, Morro Verdugo, and Morro Vinilo, the first records were gathered during the first expeditions, in 1998 and 2008, respectively (Danton et al. 2006; Danton and Perrier 2016). Altogether, 1410 native and naturalized alien species occurrences and 731 first records were analyzed. This allowed us to investigate the naturalized alien species richness accumulation and the naturalization rate over time at both island and interarchipelagic scales.

We examined how naturalized alien diversity changed over time by applying a regression model using the naturalized alien species richness from 1810 to 2021 for the entire OISEP. This was done by fitting three functions: linear (y = a + bx), exponential ($y = a (exp)^{bx} + c$) and sigmoidal ($y = a (x^b/(x^b + c^b))$). In addition, we fitted a Weibull function ($y = c+(d-c)exp\{-exp[b(log(x)-log(e))]\}$) to test for potential stabilization in the observed naturalized alien richness in recent years. Model fits were compared using Akaike's Information Criterion (AIC), whereby the lowest AIC value was considered to be the best.

Finally, to determine whether and when naturalized alien species richness could have surpassed native species richness, we calculated the naturalized-to-native species ratio over time. This was achieved by examining the naturalized alien species richness at 20-year intervals over the past 200 years at two scales: the individual island level and the entire OISEP. Following that, we obtained the naturalizedto-native species ratio by dividing naturalized alien by native species richness at both scales. Native species richness was assumed to be constant through time as it had not changed notably during the analyzed period (Castro et al. 2007; Sax and Gaines 2008).

Current island native and naturalized alien species relationships

To investigate native and naturalized alien species richness, we used the SARS package (Matthews et al. 2019) of the statistical software environment R to fit two species-area relationship models for the 11 islands studied. To describe the relationship between species richness and area, we employed the commonly-used Arrhenius power function (Arrhenius 1921) in a log-log transformed space:

$$\log_{10}(S) = C + z \log_{10}(A)$$
 (1)

where S is species richness, A is island area and *c* and *z* are two fitted parameters that correspond to the intercept and the slope, respectively. We tested for significant differences between native and naturalized alien ISAR intercepts and slopes using multiple linear regressions. Here, the response variable was species richness (n = 22; 11 native and 11 naturalized alien) and the explanatory variables were area, a categorical variable (entitled status) describing if the response variable corresponds to native or naturalized alien species richness, and the interaction between area and status. Significant differences between intercepts and slopes were verified when the interaction (status*area) and the status variable were, respectively, significant (*p*-value < 0.05) (Gelman and Stern 2006).

To further analyze how species are responding to local island factors such as habitat heterogeneity, productivity, etc. (Stark et al. 2006; Hulme 2008), we extracted the ISAR model residuals, which denote deviations of predicted values from those that were observed. These residuals helped to assess the importance of island area, allowing a comparison of the influence of islands of varying size on species richness (Lonsdale 1999). For this purpose, we extracted naturalized alien and native ISAR residuals and carried out a regression analysis (naturalized alien ISAR residuals against native ISAR residuals) using type II regression (ranged major axis) (Sokal and Rohlf 1995; Legendre and Legendre 2012). In this way, we tested if naturalized alien species richness is influenced by the same island factors that are promoting native species richness. If this is true, then ISAR residuals of both naturalized alien and native species will be strongly correlated with a positive slope of close to 1. The type II regression was run using the LMODEL2 package (Legendre 2018).

Results

Island native and naturalized alien species relationships through time

At the island-scale, 52 alien plant species had already been naturalized on Robinson Crusoe before 1870 (Fig. 2A). The naturalized alien species richness of Robinson Crusoe and Rapa Nui islands increased gradually between 1870 and 1990, surpassing the 1:1 ratio in the late 1980s (Fig. 2A, F). Santa Clara showed two peaks of alien naturalization rates; the first was from 1890 until 1930 (surpassing the 1:1 ratio) and the sec-



Figure 2. Naturalized alien species richness (left y-axis, black solid lines) and naturalization rates (right y-axis, black dashed lines) from <1870 to 2021. Red solid line represents the best adjusted regression (Weibull) naturalized alien species richness over time. The horizontal dashed lines represent the thresholds of the naturalized-to-native ratios.

ond was between 1990 and 2010, where it surpassed the 2:1 ratio (Fig. 2D). The other smaller islands (Morro Spartan, Morro Juamango, Morro Verdugo, Morro Vinilo, San Ambrosio, Morro Sin Nombre and San Felix) showed an increase in naturalized alien species richness from 1990 to 2010 (Fig. 2). The islands of Morro Juamango, Morro Verdugo and Morro Vinilo surpassed the 1:1 ratio (Fig. 2E, G, H), while Morro Sin Nombre and Morro Spartan surpassed the 2:1 and 4:1 ratios, respectively (Fig. 2J, B). At no point did San Ambrosio or San Felix surpass the 1:1 ratio (Fig. 2I, K). The average naturalized-to-native ratio for the islands over the entirety of the timeframe examined is 1.91, while the current ratio for the OISEP is 1.39 (see Suppl. material 1: table S2).

The 200-year dataset showed that, at present, 13% of the total naturalized alien species richness was introduced and naturalized before 1870, the majority of which occurred on Robinson Crusoe. The greatest increase in naturalized alien species descriptions occurred between 1990 and 2010. Thus, 40% of the current naturalized alien species (156 species) was observed in those 20 years. Proportionally, the naturalized alien species richness continued to increase through time, culminating in the entire OI-SEP surpassing the 1:1 ratio in 2000 (Fig. 2L). The most notable increases in naturalized alien species richness – overall for the OISEP and on most islands – were observed after 1990 (Fig. 2; see Suppl. material 1: table S2 for further details). Fig. 2L shows the best fit Weibull distribution for the increase in naturalized alien species (AIC = 843.9),

followed by the exponential, sigmoidal and linear regression curves with increasing AIC values (848.5, 858.1 and 1076.7, respectively) (see Suppl. material 1: tables S3–S6 for details of each model). The alien naturalization rate was very variable over time on the OISEP, showing two peaks: the first in 1920 and the second in 2000 (Fig. 2L).

Current plant biodiversity in the OISEP

Analyses of the OISEP dataset revealed 1410 species occurrences of a total of 674 species, of which 392 were naturalized aliens and 282 were native (Table 1). In absolute terms, Robinson Crusoe island contained the largest number of native species (147), representing 52% of all OISEP species. The next most populous islands in terms of native species were Alejandro Selkirk with 127 species (45%) and Rapa Nui with 50 species (18%) (Table 1). Meanwhile, Robinson Crusoe was also home to the majority of naturalized alien species (282), representing 72% of the total recorded on the OISEP. This was followed by Rapa Nui (157, 40%) and Alejandro Selkirk (136, 35%), while the smaller islands were host to considerably fewer naturalized alien species (Table 1).

Assemblages of native and naturalized alien species varied notably at both interarchipelagic and island scales (see Suppl. material 1: tables S7A, B for details). Juan Fernandez and all OISEP produced the highest Sorensen's index values (native = 0.86; naturalized alien = 0.86). Of the Juan Fernandez Archipelago, Robinson Crusoe islands and all OISEP produced the most dominant index value (native = 0.68; naturalized = 0.84; see Suppl. material 1: tables S7A, B for details). On the other hand, the Desventuradas islands and the OISEP produced the lowest Sorensen's similarity index values (native = 0.14; naturalized alien = 0.05). The Desventuradas islands also produced the lowest Sorensen similarity index with Rapa Nui Island (natives = 0; naturalized = 0.04; see Suppl. material 1: tables S7A, B for details).

There is an uneven distribution of species across the islands with 67% of the OI-SEP native species restricted to just one island. Of those, Robinson Crusoe is home to 24.5%, 22.7% are on Alejandro Selkirk, 14.9% are on Rapa Nui, 3.9% are on San Ambrosio, while San Felix and Santa Clara are each home to 0.35% (Table 1). In comparison, 57.9% of the naturalized alien species are restricted to just one of four islands: 32.4% are on Robinson Crusoe, 22.5% on Rapa Nui, 2.5% on Alejandro Selkirk and 0.5% on San Felix (Table 1).

Current island native and naturalized alien species relationships

The ISAR for native species had a better fit and lower *p*-values for its adjusted parameters than those for the naturalized alien species (adj. $R^2 = 0.7$ and 0.32; intercept *p*-values = $10^{-8} \times 4.5$ and $10^{-6} \times 2.1$, respectively; slopes *p*-values = $10^{-4} \times 7.7$ and $10^{-2} \times 4.1$ respectively). ISAR parameter comparisons revealed no significant differences for parameters *c* and *z* between native and naturalized alien ISARs (*p*-value = 0.303 and 0.697, respectively; Fig. 3A).

Native and naturalized alien residuals were significantly correlated (r = 0.64; *p*-value < 0.05). The regression analysis for ISAR residuals for native and naturalized

Table 1. Native and naturalized alien species richness and their island exclusivity. Iotal SR indicates
the total species richness (native + naturalized alien species); % Natives and % Naturalized aliens are the
proportions of island native or naturalized alien species richness; Ex-Natives and Ex-Natu represent the
amount of native or naturalized alien species exclusively present; % Ex-Natives and % Ex-Natu are the
proportions of native or naturalized alien species exclusively present.

Island	Natives	Naturalized	Total SR	%	%	Ex-	% Ex-	Ex-	% Ex-
		aliens		Natives	Naturalized	Natives	Natives	Natu	Natu
					aliens				
Alejandro	127	136	263	45.0	34.7	64	22.70	10	2.55
Selkirk									
Rapa Nui	50	157	207	17.7	40.1	42	14.89	88	22.45
Morro	13	17	30	4.6	4.3	0	0	0	0
Juamango									
Morro Spartan	6	26	32	2.1	6.6	0	0	0	0
Morro Sin	6	14	20	2.1	3.6	0	0	0	0
Nombre									
Morro Verdugo	11	14	25	3.9	3.6	0	0	0	0
Morro Vinilo	9	16	25	3.2	4.1	0	0	0	0
Robinson	147	282	429	52.1	71.9	69	24.47	127	32.40
Crusoe									
San Ambrosio	21	5	26	7.4	1.3	11	3.90	0	0
Santa Clara	15	42	57	5.3	10.7	1	0.35	0	0
San Felix	11	8	19	3.9	2.0	1	0.35	2	0.51
Total	282	392	674	100	100	188	66.67	227	57.91



Figure 3. Island species-area and its residuals for native and naturalized alien species **A** ISAR fitted for both native (black circles; solid line; dark gray bands represent the 95% confidence interval) and naturalized alien species (white circles; dashed line; light gray bands represent the 95% confidence interval); SE: Standard error. Significance levels are denoted by * (0.01), ** (0.001) and *** (< 0.0001). **B** Type II regression of native and naturalized alien ISAR residuals (solid red line). Dashed line represents the perfect regression with intercept = 0 and the slope = 1; dark-grey band represents the 95% confidence interval.

alien species yielded a slope parameter not significantly different to 1 (estimated slope = 1.71; 0.54–4.97, 2.5%–95% confidence interval; *p*-value = 0.015, Fig. 3B). As Fig. 3B shows, four different island scenarios could be identified: a) islands with a high naturalized alien ISAR residual and a low native ISAR residual (Rapa Nui, Santa Clara and Morro Spartan islands); b) islands with similar naturalized alien and native species residuals (Morro Juamango, Morro Verdugo, Morro Vinilo and Morro Sin Nombre islands); c) islands with high naturalized alien and native ISAR residuals (Robinson Crusoe and Alejandro Selkirk islands); and d) islands with low native and naturalized alien ISAR residuals (San Felix and San Ambrosio islands).

Discussion

Island native and naturalized alien species relationships through time

We can accept our first hypothesis based on the evidence that naturalized alien flora achieved greater species richness than the native flora on OISEP. These results indirectly reflect the history of the whole OISEP area, including anthropogenic disturbances and the pressure placed upon native species richness by invasive alien plant species, domestic herbivores, habitat loss, etc. (Gurevitch and Padilla 2004; McKinney 2004; Sax and Gaines 2008; van der Wal et al. 2008; Caujapé-Castells et al. 2010; Wohlwend et al. 2021). Our results provide evidence of an accelerated level of alien plant naturalization when compared with Sax and Gaines's (2008) estimation that the naturalized-to-native ratio for oceanic islands was 1:1 and that the predicted ratio for 2060 will be 3:2. Considering the rapid increases in naturalized alien species numbers, the already high naturalized-to-native ratios – particularly for Morro Spartan, Robinson Crusoe and Rapa Nui – and the high propagule pressure from non-established plants (Castro and Jaksic 2008) in Robinson Crusoe and Rapa Nui (Zizka 1991; Meyer 2008; Finot et al. 2015; Danton et al. 2006), we can expect a much higher ratio in the future.

The difficulty associated with accessing San Felix and San Ambrosio means that they have been subjected to fewer human impacts when compared to other islands. Instead, only fishers and shellfish gatherers landed sporadically from Robinson Crusoe island (Bahamonde 1987; Hoffman and Teillier 1991; Castro and Jaksic 2008). This provides a plausible explanation for the lower naturalized-to-native ratios in contrast to the rest of the OISEP. However, Aguirre et al. (2009) noted a lack of concern for terrestrial conservation on Desventuradas islands. They reported that the San Ambrosio forests – hosts to a diverse collection of endemic plants (Kuschel 1962) – have disappeared due to the presence of goats. Therefore, more up-to-date inventories for San Felix and San Ambrosio may record higher naturalized alien species numbers.

Our study reveals a notable increase in naturalized alien species richness and diversity overall through time for the OISEP. This increase was better described using a Weibull function as opposed to an exponential function, likely due to the decline in naturalization rate from 1940–1960 and 2010–2021 in conjunction with the ab-

sence of flora descriptions for the same time period. Therefore, due to the fact that the Weibull fit (and the second best fit) show that the number of naturalized alien species is increasing exponentially, we can reject the idea that a saturation point has been reached (Sax and Gaines 2008). Although some other studies identified similar patterns (see Tye 2006; Seebens et al. 2017), we must interpret this result with caution due, for example, to the absence of more recent flora descriptions and the limited knowledge of the flora's temporal variation on smaller islands in Juan Fernandez Archipelago (cf. Tye 2006).

Current native and naturalized alien species relationships

Native and naturalized alien species richness in the OISEP region are positively correlated. This result is in line with other studies that have been interpreted as evidence that native species are not better competitors than naturalized alien species (Lonsdale 1999; Sax et al. 2002; Rojas-Sandoval et al. 2020). Moreover, the resulting type II regressions suggest rejecting our third hypothesis. Here, both naturalized alien and native species richness are responding in a similar way at the island scale (Lonsdale 1999; Stark et al. 2006; Hulme 2008) with at least four island scenarios identifiable. The first (scenario labelled "a" in the results) could be defined as islands that have been considerably disturbed by humans through fire, wood exploitation and introduced fauna such as rabbits, goats and horses, but still retain a rich native species pool. In this context, islands such as Robinson Crusoe and Alejandro Selkirk are exclusively home to the majority of plant biodiversity in the OISEP. The second island scenario ("b") categorizes the smaller islands that surround Robinson Crusoe (Morro Juamango, Morro Verdugo, Morro Vinilo and Morro Sin Nombre islands). Their proximity to Robinson Crusoe has seen these islands suffer from the influence of human activity, with naturalized alien species arriving by means of anemochory (mainly Asteraceae species) and zoochory (mainly Poaceae species). This, in turn, increased the naturalized alien plant species richness in the area (Danton et al 2006; Danton and Perrier 2016). However, these islands have kept their expected native species richness, with the islands of Morro Juamango, Morro Verdugo and Morro Sin Nombre having native standardized residuals near to 0. In comparison, rabbits introduced to Morro Vinilo island mean there is a limited number of native species found there (Danton and Perrier 2016).

The third island scenario ("c") applies to islands that have an impoverished native species pool. This is due to their geographic features in combination with a lower naturalized alien species pool as a result of recent anthropogenic disturbances, such as on San Felix and San Ambrosio islands (Hoffman and Marticorena 1987). Finally, the fourth scenario ("d") is not in line with our general resulting pattern, whereby native and naturalized alien species richness are correlated and respond in a similar way at the island scale. While islands such as Rapa Nui, Santa Clara and Morro Spartan have suffered notable anthropogenic disturbances (scenario "a"), they have also experienced a decrease in their native plant diversity (Zizka 1991; Danton et al 2006; Danton and Perrier 2016). For islands such as Santa Clara and Morro Spartan, this is likely to be due to extirpation, while extinction of possibly seven species has been recorded on Rapa Nui (Zizka 1991).

At the inter-archipelagic scale, that is, the entire OISEP, we showed that native and naturalized alien ISARs do not significantly differ in their fitted parameters leading to a rejection of our fourth hypothesis. Overall, our results follow the same trends identified by others for continental islands (Nichols and Nichols 2008; Long et al. 2009; Burns 2016; Chiarucci et al. 2017) and oceanic islands (Burns 2016) as well as Baiser and Li's (2018) more general assessment of plants for mixed origins. In comparison, our results differed to those revealed for Aeolian Islands (Chiarucci et al. 2021) as well a more global-scale analysis (Blackburn et al. 2016). A potential explanation for the observed differences might be our low sample size (n = 11). A different native and naturalized alien ISAR, as is in line with the findings of Blackburn et al. (2016), Chiarucci et al. (2021; when these ISARs are log-log transformed) and Burns (2016) (i.e., higher slope for native ISAR compared to naturalized alien ones) would support the hypothesis that naturalized alien species have reduced barriers to their dispersal relative to natives (Patiño et al. 2014). However, a higher sample size is required to test this more robustly.

Although there were no differences between the c and z parameters, the fit of each model did differ. The native ISAR fit well (adj. $R^2 = 0.7$), which indicates that native species richness follows the typical dynamics reported in other studies; that is, species richness can be explained to a large extent by island area as the species in question have had time to adapt to and establish permanent communities in the diverse island habitats (Long et al. 2009; Sax and Gaines 2006; Burns 2016; Chiarucci et al 2021). On the other hand, naturalized alien ISAR had a poorer model fit than that of native species. As mentioned previously, this may be because islands such as San Felix, San Ambrosio and Santa Clara have similar sizes and native species richness, but have different island contexts in terms of naturalized alien species richness (D'Antraccoli et al. 2019). Thus, the dynamics for naturalized alien plants differ in comparison to native species; the entire naturalized alien species pool is not well distributed across the diverse island habitats in the OISEP. Exceptions to this are species such as Hypochaeris radicata, Rumex acetosella, Briza minor and Plantago lanceolata. However, although the low number of sample units - that is, OISEPs - available to examine is a factor that is likely to have limited our results, our study still helps to address the notable scarcity of empirical evidence available to investigate and assess naturalized alien and native SARs on oceanic islands.

Ecological and biogeographic implications

This study revealed a dramatic increase in naturalized alien species richness on OI-SEP, which has major implications for both island ecology and biogeography. Overall, oceanic island species richness has increased more than has been identified elsewhere on continental islands and mainland areas (Sax and Gaines. 2006; Castro et al. 2010; Kueffer et al. 2010; van Kleunen et al. 2015). This is due to the many alien plant species that have become naturalized, while few native species have become extinct (Sax et al. 2002; Sax and Gaines 2006). Whereas studies by Sax et al. (2002) and Sax and Gaines (2006) have estimated that species richness increased by ~106.5% on oceanic islands, our study of OISEPs showed that there was an increase of, on average, 84.5%

on islands and an increase of 32.1% for the entire OISEP. Proportionally, other oceanic islands and archipelagos with a similar area to the OISEP (268.7 km²) harbor a lower species richness (that is < 674 natives and naturalized alien species); for example, El Hierro island (268.7 km², Canary islands) has ~550 species (Stierstorfer and von Gaisberg 2006), Tristan da Cunha (207 km², in the Tristan da Cunha archipelago) has ~124 species (Sax et al. 2002) while Lana`i island (364 km² in the Hawaii archipelago) has ~787 species (Wagner et al. 2005). When compared to continental areas, our study site has higher species richness than Weddell island – the third largest continental island of the Falklands islands – where there are ~155 species in an area of 265.8 km² (Upson 2012), while the estimated species richness for Futangue National Park on mainland Chile is ~400 species in 125 km² (Moreno et al. 2013).

Although this study has highlighted distinct richness of species in the study sites, many of these native species across the OISEP have become threatened (from the total, 18.8% are critically endangered, 30.4% are endangered and 10.6% are vulnerable; Danton et al. 2006; Stuessy et al. 2018a; MMA 2023). Due to time lags in the extinction of species, it is likely that the number of threatened species will increase further even without further alien species naturalizations (Tilman et al. 1994; Sax and Gaines 2008; Greimler et al. 2017).

Therefore, it is of the utmost importance to both prevent the introduction of alien plant species and control the most impactful naturalized alien plant species on islands such as Rapa Nui, Santa Clara, Robinson Crusoe and Alejandro Selkirk (Danton et al. 2006; Lenz et al. 2022). The existing procedures to prevent the entry of alien plant species to, for example, Rapa Nui are limited only to safeguard the forest and agricultural productive sector (COCEI 2014). More recently, formal procedures to control and prevent the movement of alien plant species between islands in the Juan Fernandez Archipelago have been established; however, controls from continental South America remain voluntary (MMA 2017). It is also important to control anthropogenic disturbances, including the introduction of herbivorous fauna on islands such as Desventuradas islands where there is low naturalized alien species richness (Wohlwend et al. 2021). A further positive move would be to restore heavily disturbed islands in the study region, in particular Santa Clara, Morro Spartan, Robinson Crusoe, Alejandro Selkirk, Rapa Nui and Morro Vinilo. This could improve the conservation status of endangered plants and maintain focus on the conservation of native plant species across the OISEP (Stuessy et al. 2018a). Additionally, it is necessary to assess the effects of native plant species restoration on the extinction debt process and generate novel evidence on plant conservation research (Downey and Richardson 2016).

Conclusions

By assembling an updated dataset for 11 oceanic islands of the south-east Pacific (OISEP), our study reveals that there has been a dramatic increase of naturalized alien plant species richness in the last 200 years, and that naturalized alien species richness

has become dominant over native plant species richness on most of the islands. Native and naturalized alien species richness, ISAR residuals and ISAR shapes are very much related and, by consequence, independent of the geographic scale. Relevant ecological and biogeographic implications for native and naturalized alien plant species diversity by means of different temporal and spatial scale patterns include similar levels of species richness between island and continental systems. There could be a possible increment of the extinction debt as there are currently no signs that alien plant invasion is reaching a saturation point soon.

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Supplementary material I

Tables with general information

Authors: Luis Cáceres-Polgrossi, Maura Di Rico, Diego Parra, Hanno Seebens, Stephen D. Galvin, H. Juergen Boehmer

Data type: tables (.docx file)

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RESEARCH ARTICLE



HELLAS-ALIENS. The invasive alien species of Greece: time trends, origin and pathways

Margarita Arianoutsou¹, Chloe Adamopoulou², Pavlos Andriopoulos¹, Ioannis Bazos¹, Anastasia Christopoulou^{1,3}, Alexandros Galanidis^{1,4}, Eleni Kalogianni⁵, Paraskevi K. Karachle⁵, Yannis Kokkoris¹, Angeliki F. Martinou⁶, Argyro Zenetos⁵, Andreas Zikos¹

I Department of Ecology and Systematics, Faculty of Biology, National and Kapodistrian University of Athens, Athens, Greece 2 Department of Zoology – Marine Biology, Faculty of Biology, National and Kapodistrian University of Athens, Athens, Greece 3 Centre for Research and Conservation of Cultural Heritage, Faculty of Fine Arts, Nicolaus Copernicus University, Toruń, Poland 4 Department of Environment, Biodiversity Conservation Laboratory, University of the Aegean, Mytilene, Greece 5 Institute of Marine Biological Resources and Inland Waters, Hellenic Centre for Marine Research, Athens, Greece 6 Climate and Atmosphere Research Centre / CARE-C, The Cyprus Institute, Athalassa Campus, 20 Konstantinou Kavafi Street, 2121 Aglantzia, Nicosia, Cyprus

Corresponding author: Margarita Arianoutsou (marianou@biol.uoa.gr)

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Abstract

The current paper presents the first effort to organize a comprehensive review of the Invasive Alien Species (IAS) of Greece. For this purpose, a database was developed with fields of information on the taxonomy, origin, ecology and pathways of introduction of terrestrial, freshwater and marine species. Our database includes a) taxa in the Union's list that are present in Greece, b) taxa already present in Greece and considered to be invasive, and c) taxa highly likely to enter Greece in the next 10 years and become invasive. The Database served as the starting point for the compilation of the National List of Alien Invasive Species (HELLAS-ALIENS) in compliance with the EU Regulation 1143/2014. Overall, the HELLAS-ALIENS comprises 126 species, i.e. 32 terrestrial and freshwater plant species, 14 terrestrial invertebrates, 28 terrestrial vertebrates, 30 freshwater fishes and invertebrates and 22 marine species. Terrestrial invertebrates, birds and mammals are mainly of Asiatic origin. Most of the terrestrial plants have their native geographical distribution in the Americas (North and South). Most of the freshwater invertebrates and fishes are of North American origin, while the majority of the marine species are of Indo-Pacific origin. The first records of IAS concern terrestrial plant species, and date back to the 19th century, while those in freshwater

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ter and marine ecosystems seem to have been systematically recorded some decades later. Regarding the pathways of introduction, most of the taxa arrived in Greece or are expected to arrive through escape from confinement and unaided. The majority of the terrestrial, freshwater and marine species have been evaluated as of High-risk for the indigenous biodiversity and only 3% of the species listed have been evaluated of Low-risk. Our results provide an important baseline for management and action plans, as required by the priorities set by the European Union through the Biodiversity Strategy for 2030.

Keywords

European Union, Invasive Alien Species Regulation, pathways of introduction, risk assessments, temporal trends

Introduction

Biological invasions are a major threat to biodiversity, ecosystem services, the economy and human health (Millennium Ecosystem Assessment 2005; Díaz et al. 2019). Invasive alien species (IAS) pose a significant threat to the receiving environment (Simberloff et al. 2013) impacting species' habitats, synthesis of communities and ecosystem functioning (Hulme 2015; Bellard et al. 2016).

New introductions of alien species have been accelerated in recent decades by the rapid globalization, urbanization and intensification of human activities (Seebens et al. 2017). For example, at a Pan-European scale, a trends' indicator for marine alien species, based on the annual rate of introductions at 6-year cycles, has revealed an increase in new alien species from 6 in the period 1970-75 to 21 new alien species per year in the period 2012-17 (Zenetos et al. 2022). Moreover, climate change and the increase in temperature can further induce the introduction and successful establishment of marine species and fishes in particular (Karachle et al. 2022). A similar increase has been documented for groups of terrestrial species invasions. For instance, the number of terrestrial plants first recorded in the wild as alien to Europe exhibited a remarkable increase in the 20th and 21st centuries, with a constant increase between 1951 and 2010 (Arianoutsou et al. 2021). However, opposite trends have also been reported, i.e., in the new introduction events of the 16 invasive mammals of Union concern in Europe from the 1960s onwards (Tedeschi et al. 2021). In addition, the impacts of IAS may range from changes in the abiotic environment increasing the risk of disturbances, to contributing to the decline of native biodiversity (Ehrenfeld 2010; Schirmel et al. 2016; Catford et al. 2018; Essl et al. 2020; Pyšek et al. 2020) and even to extirpations, and in extreme cases to local extinctions, especially when the competition for resources is high (Gallardo et al. 2019).

Databases are important for gathering, sharing and disseminating information on alien species, fundamental for management, scientific and educational purposes (Dyer et al. 2017). At the European level, the project Delivering Alien Species Inventories for Europe (DAISIE 2009) was a milestone in creating a European database of alien species. Similar initiatives were undertaken at a regional scale, such as the NOBANIS European Network on Invasive Alien Species (NOBANIS 2021) for North and Central Europe, and the East and South European Network for Invasive Alien Species (ESENIAS 2020). An important step towards this goal is the European Alien Species Information Network (EASIN 2020) which has been developed by the European Commission's Joint Research Centre (https://easin.jrc.ec.europa.eu). EASIN acts as a focal point for sharing and disseminating information, where available knowledge on alien species from various data sources is standardized, harmonized and integrated (Katsanevakis et al. 2015). Global datasets, such as the Global Biodiversity Information Facility (GBIF 2020) and the CABI-Invasive Species Compendium (CABI 2020), which also include records of alien species in Europe, should be also mentioned.

At the country scale, the ELNAIS network and database (Zenetos et al. 2015) were established to record and monitor the introductions and spread of aquatic IAS (freshwater and marine species) in Greece. Concerning the alien plant species of Greece, a web-based database was created (https://www.alienplants.gr/) as a by-product of the compilation of the Flora of Greece project (Dimopoulos et al. 2020). There are other databases based mainly on information collected from citizen scientists e.g. the Alientoma database for alien insects of Greece (Kalaentzis et al. 2021).

The European Regulation 1143/2014 encompasses the list of IAS of Union Concern. The EU Regulation (hereafter referred to as the IAS Regulation) requires EU Member States to compile their national lists of IAS and carry out a comprehensive analysis and prioritization of the pathways of introduction and spread of IAS of Union concern. Greece initiated its alignment with the Regulation in February 2021 after an open call for tenders which rendered a project to the research group comprised of the authors of the current work. It was soon realized that any effort to compile a list of IAS should be supported by a database, with all important information on species origin, traits, status, habitat, pathways of introduction, potential impacts and geographical distribution.

The current work reports on the compilation of the Greek national list of IAS (HELLAS-ALIENS), along with their time trends, origin, principal pathways of introduction, and assessment of the risk they might impose.

Material and method

Compilation of the national list of IAS of Greece (hereafter HELLAS-ALIENS) was based on the following criteria:

i. Taxa already present in Greece that are included in the List of Invasive Alien Species of Union concern (hereafter mentioned as EU list) or were proposed to be included in the third update of the list entered into force on 2 August 2022.

ii. Taxa established in the wild and considered invasive (Arianoutsou et al. 2010; Barbieri et al. 2015; Zenetos et al. 2020, experts' opinion).

iii. Taxa not currently present in Greece but highly likely to be introduced within the next 10 years, assessed during a Horizon Scanning (HS) exercise that took place within this project, following the methodology suggested by Roy et al. (2014, 2015, 2019) and implemented by Peyton et al. (2019, 2020), Lucy et al. (2020) among others. For this, five groups of experts corresponding to the five groups of organisms studied were formed. Each expert scored each species based on their likelihood of i) arrival, (ii) establishment, (iii) spread, and (iv) magnitude of the potential negative impact on biodiversity within Greece for the next 10 years. Each group of experts had sequential exhaustive meetings where discussions were held on the final scoring of each species. Finally, a general workshop was held jointly with all experts where a consensus on the first 29 species that had the highest score was reached, and consequently these taxa were included in the HELLAS-ALIENS.

Taxa considered to be included in HELLAS-ALIENS were plants of the terrestrial environment (those of freshwater included), terrestrial vertebrates and invertebrates, freshwater fishes and invertebrates and marine organisms. Cryptogenic species were not considered.

For the selected taxa, contextual/relative information (available until November 2021) was collected and inserted in an exhaustive database, supporting and complementing the HELLAS-ALIENS. The structure of the database is given in Table 1.

For the classification of species with respect to their pathways of introduction into a new area, the Convention on Biological Diversity scheme (CBD 2014) was adopted, which is also used by EASIN (see for example Arianoutsou et al. 2021). This classification scheme follows the six main categories of pathways proposed by Hulme et al. (2008). In the pathways' data analysis, we included information concerning taxa that are already present in Greece, but also taxa that are very likely to arrive within the next ten years based on the HS procedure. The category "Unknown" has been excluded.

For filling the fields of the database various sources have been used: extensive literature reviews and peer-reviewed publications, existing databases [e.g. FishBase (Froese and Pauly 2022), ELNAIS], personal and citizen-scientists observations, such as iNaturalist, GBIF, or eBird (Sullivan et al. 2009), gray literature (i.e. reports, conference proceedings, theses), and occasionally personal communication with experts.

Category of information	Information			
Taxonomy	Scientific name of species, genus, family, order, class			
Alien status	Invasive, potentially invasive, established, casual, unknown			
Origin	(non-exhaustive) Asian, American, Australian (for terrestrial and fresh water taxa),			
	Circumtropical, Western Indo-Pacific (for marine taxa)			
Year of first observation in the wild	When available			
Pathway	Based on the CBD (2014) classification scheme			
Impact	Health, Economy, Natural Ecosystems, other ecosystem services (e.g., fisheries, tourism)			
Geolocation	Coordinates (WGS84), Region, Sea, Locality, Natura 2000 site, Island, Mountain			
Taxa specific traits	(non-exhaustive) in plants: Growth form, life form, pollination mode, flowering period, fruit			
	type, dispersal mode			
	(non-exhaustive) in birds: General guilds (e.g. birds of prey, landbirds, parakeets etc.), nest type, diet			
Habitat	EUNIS, when available till level 2 (Davies et al. 2004)			
References	Full reference of the bibliographic sources used for the compilation of information			
Comments	When applicable			

Table 1. General Structure of HELLAS-ALIENS database.

For species' nomenclature, the most updated and widely accepted sources were used. In particular, the terrestrial plants' nomenclature followed mostly the World Flora Online (2022), except for Pontederia crassipes and Elodea densa, for which the names Eichornia crassipes and Egeria densa, as listed in the EU list, have been retained. The terrestrial vertebrates' nomenclature followed the IUCN Red List approach (IUCN 2022), except for two mammal species, the small Indian mongoose (treated as Herpestes javanicus in the EU list and as Herpestes auropunctatus in the IUCN Red List) and the Siberian chipmunk (treated as Tamias sibiricus in the EU list and as Eutamias sibiricus in the IUCN Red List), which have been treated according to the EU list approach. For the bird taxa, the IUCN Red List approach based on version 5 of the HandBook of the Birds of the World and BirdLife International (2020) has been followed. For terrestrial invertebrates, the CABI Compendium has been consulted regarding species nomenclature (CABI 2020). For the freshwater species, we consulted the World Register for Marine Species (WoRMS Editorial Board 2022), the National Biodiversity Atlas (NBN), FishBase and Barbieri et al. (2015). Finally, for marine species' nomenclature, we followed the World Register of Marine Species (WoRMS Editorial Board 2022).

For the risk assessments (RAs) of taxa a mixed approach, based on the EU risk assessment framework that is compiled with the EU Regulation 1143/2014 and was developed under the "Study on Invasive Alien Species – Development of risk assessments to tackle priority species and enhance prevention" (European Commission 2021), was adopted. Two different versions, adjusted to the Greek bioclimatic conditions, were built: i) an Adapted RA, for the EU list taxa that are already present in the country, which focuses mainly on the impacts of these species (19 taxa in total), and ii) a Summary RA, for the remaining IAS included in the HELLAS-ALIENS and are already present in the country or were shortlisted through the HS procedure, that focuses on impacts and their potential for introduction, entry, establishment and spread (107 taxa in total). Taxa were classified as Low, Medium or High-risk according to the likelihood and consequences of their introduction, establishment, spread, and impact potential.

Results

Overall, the HELLAS-ALIENS comprises 126 species, allocated in five general groups corresponding to terrestrial and freshwater plants (32 species), terrestrial invertebrates (14 species), terrestrial vertebrates (28 species), freshwater fishes and invertebrates (30 species) and marine species (22 species) (see Species List in Suppl. material 1).

General information

Terrestrial – Freshwater plants

Of the 32 plant species of the HELLAS-ALIENS, 18 are considered invasive in Greece (Acacia saligna, Acer negundo, Ailanthus altissima, Azolla filiculoides, Bidens frondosa, Carpobrotus edulis, Cotula coronopifolia, Datura stramonium, Heliotropium curassavicum,

Ludwigia grandiflora, Ludwigia peploides, Nicotiana glauca, Opuntia ficus-indica, Oxalis pes-caprae, Paspalum distichum, Phytolacca americana, Robinia pseudoacacia and Solanum elaeagnifolium) (Arianoutsou et al. 2010; Dimopoulos et al. 2020) and ten were added to the list following the HS procedure. Twelve species are in the EU list. Among them, four (*Acacia saligna, Ailanthus altissima, Ludwigia grandiflora* and *L. peploides*) are already established in Greece, one (*Pennisetum setaceum*) has been observed as a casual escape from cultivation, six (*Eichhornia crassipes, Egeria densa, Elodea nuttallii, Hydrocotyle ranunculoides, Myriophyllum aquaticum* and *M. heterophyllum*) are known as either cultivated or added through the HS procedure, while the presence of *Impatiens glandulifera* in a single locality in northern Greece needs confirmation. One more species *Pistia stratiotes* (cultivated, added after the HS), has been recently included in the EU list with entry force in 2024. *Egeria densa, Fallopia baldschuanica, Reynoutria japonica* and *R. × bohemica* are included in the list of IAS of the European and Mediterranean Plant Protection Organization (EPPO).

Terrestrial invertebrates

Twelve out of the 14 terrestrial invertebrate species included in the HELLAS-ALIENS are present in the country. These are ten insects (*Aedes albopictus, Cydalima perspectalis, Halyomorpha halys, Harmonia axyridis, Linepithema humile, Paysandisia archon, Rhyn-chophorus ferrugineus, Solenopsis geminata, Xylotrechus chinensis, Xylotrechus stebbingi*), one acari (*Tetranychus evansi*), and one platyhelminth (*Caenoplana bicolor*). Two species considered during the HS process as highly likely to arrive in the country were also included in the list, namely *Bursaphelenchus xylophilus* (the pine wood nematode or pine wilt nematode) and *Megachile sculpturalis* (the giant resin bee). One of the terrestrial invertebrate species of the HELLAS-ALIENS, *Solenopsis geminata* (fire ant) was included in the latest version of the EU list.

Terrestrial vertebrates

Terrestrial vertebrate species of the HELLAS-ALIENS included 28 species of amphibians, reptiles, birds, and mammals.

Amphibians

Three amphibians have been included: *Lithobates catesbeianus*, (American bullfrog), included in the EU list and well established in Crete, *Xenopus laevis*, (African clawed frog), a recent addition in the EU list that has casual occurrences in urban parks and *Triturus carnifex*, (Italian crested newt), that is highly likely to invade the country within the next ten years.

Reptiles

HELLAS-ALIENS includes five reptile species. *Trachemys scripta*, (pond slider), a species of Union concern and *Podarcis siculus*, (Italian wall lizard) are already established

in the country. The Italian wall lizard is native to some parts of Europe, but it is considered invasive in others, with potentially significant impacts on the native herpetofauna (Scalera 2019). The remaining three reptile species have not yet been recorded in the wild but are present in the country, in captivity, as pets. Among them, *Lampropeltis getula*, the common kingsnake, one of the most popular pets among herpers, has been recently added to the EU list.

Birds

Twelve bird taxa are included in the HELLAS-ALIENS. Three bird species with casual presence status in Greece have been included in the catalogue because they are EU-listed (*Acridotheres tristis, Alopochen aegyptiaca* and *Threskiornis aethiopicus*). Four bird taxa already established in Greece have been considered and included in the list, as they are threatening biodiversity (*Alectoris rufa, Branta canadensis, Phasianus colchicus* [non subsp. *colchicus*] and *Psittacula krameri*). The species *Myiopsitta monachus* (Monk Parakeet), well established in Attica, was also selected for the HELLAS-ALIENS following the recommended management approach (White et al. 2019) and as a potential disease vector (Kalodimos 2013; Postigo et al. 2019). Four bird species, selected through the HS exercise (*Corvus albus, Pycnonotus cafer, Pycnonotus jocosus* and *Pycnonotus leucotis*) were also included.

Mammals

In total, eight species of mammals were included in the HELLAS-ALIENS. Of those, seven are also included in the EU list. Two of them, the coypu, *Myocastor coypus*, and the racoon, *Procyon lotor*, are already established in Greece; three species (*Ondatra zibethicus*, *Nyctereutes procyonoides*, and *Tamias sibiricus*) have casual occurrences in the country; *Herpestes javanicus* has not yet arrived in Greece but was selected through the HS exercise. The species *Callosciurus finlaysonii* is present in the country only as a pet. Finally, the American mink, *Neovison vison*, though not of Union concern, is well established in Northwest Greece with already recorded impacts on native biodiversity (Galanaki and Kominos 2022).

Freshwater species

The freshwater species of the HELLAS-ALIENS include 16 invertebrates and 14 fish species. With respect to the invertebrates, 12 species are well-established invasive or potentially invasive, while four more, i.e., *Dreissena polymorpha* (Zebra mussel), *Pomacea maculata* (Giant applesnail), *Procambarus clarkii* (the Red swamp crayfish) and *Procambarus virginalis* (Marmorkrebs) were added to the list following the HS procedure. Three freshwater invertebrate species, the established *Pacifastacus leniusculus* (American signal crayfish), and the crayfish species *P. clarkii* and *P. virginalis* currently not present in the wild, are included in the EU list.

As far as freshwater fishes are concerned, 12 species are currently present in the wild, while two more, *Perccottus glenii* (Chinese sleeper) and *Ameiurus melas* (the Black

bullhead), were added to the list following the HS procedure as they are expected to invade Greek freshwater ecosystems. *Lepomis gibbosus* (Pumpkinseed) and *Pseudorasbora parva* (Stone moroko), established in Greece, are included in the EU List, while the also established and widespread Eastern mosquitofish *Gambusia holbrooki* was included in the EU list as recently as July 2022. Of the two species that are likely to arrive and invade, *P. glenii* is included in the EU list, while *A. melas* was included in the EU list in July 2022.

Marine species

With respect to the marine species of the HELLAS-ALIENS, five are plants, nine are invertebrates and eight are fishes. Currently, the only marine species in the EU list are the *Plotosus lineatus* (striped catfish) and *Rugulopteryx okamurae* (brown seaweed). Although several marine species were proposed and risk assessed, none was approved for entering the EU list. Among the proposed ones it is worth mentioning two fishes, namely the silver-cheeked toadfish *Lagocephalus sceleratus* and the lionfish *Pterois miles* as well as the blue crab *Callinectes sapidus* and the rapa whelk *Rapana venosa*. The three former species are well established, with a wide distribution in the Greek seas whereas *R. venosa* has been sporadically reported in North Greece (Zenetos et al. 2015; ELNAIS 2022).

Origin of species

The origin of all taxa is presented in Fig. 1A–C.

Most of the plants have their native range in the Americas (North and South), followed by those of Asian and African origin (Fig. 1A). The Asian origin prevails in terrestrial invertebrates, birds and mammals (Fig. 1A). Amphibians originate from one continent each: America, Africa, Europe, and most reptiles are natives of North America. Species native to Europe include one amphibian (*Triturus carnifex*), one reptile (*Podarcis siculus*) and one bird (*Alectoris rufa*).

Most of the freshwater species, both invertebrates (88%, 14 taxa) and fishes (72%, 10 taxa), are of North American and, secondarily, of Asian origin (Fig. 1B). Two invertebrate species are of South American and Oceanian origin respectively, while one fish species is of European and three of Eurasiatic origin.

As far as the marine species are concerned, the vast majority of all taxa are of Indo-Pacific origin (Fig. 1C). Fishes exclusively originate from the Indo-Pacific, whereas plants are also primarily of Indo-Pacific origin, but their introduction is not related to corridors, but to shipping. Finally, concerning the invertebrates, one species (the foraminiferan *Amphiste ginalobifera*) has a circumtropical distribution and two others (the shrimp *Penaeus aztecus* and the blue crab *Callinectes sapidus*) are native to the West Atlantic including the Tropical Atlantic.

Trends of "introductions" in time

The year of the first record in the wild has been detected for all 100 taxa currently present in the country. Data is available for 54 terrestrial species, 24 freshwater spe-



Figure 1. Treemap graphical representation of HELLAS-ALIENS taxa origin. Colours of tiles are consistent within each group of organisms. **A** terrestrial taxa **B** freshwater taxa **C** marine taxa. C-IP: Central Indo-Pacific; W-IP: Western Indo-Pacific; CT: Circumtropical; T-NP: Temperate Northern Pacific; T-NWP: Temperate Northern Western Atlantic; TR-A: Tropical Atlantic; T-AA: Temperate Australo-Asia.

cies and 22 marine species. The rate of introduction of new IAS records shows a rapid increase during the last two decades (Fig. 2), with the highest number of new records originating from terrestrial environments (Fig. 3). The first records of IAS in the country concerned terrestrial plant species and date back to the 19th century while IAS in freshwater and marine ecosystems seem to have been systematically recorded some decades later (Fig. 3).

Pathways

The pathways followed by the IAS of the HELLAS-ALIENS per environment are shown in Fig. 4. Several taxa were linked to more than one introduction pathway. Pathways are given both for species already present in the country, but also for species that are likely to arrive within the next ten years based on the HS procedure followed. The majority of the taxa arrived in Greece or are expected to arrive through escape from confinement, and unaided.

Most of the terrestrial and freshwater plant taxa (27 taxa) have entered, or are expected to enter, Greece through escape from confinement (See Suppl. material 2: fig. S1). Nine taxa were released in the wild for human-use purposes, and eight taxa contaminated unintentionally transferred commodities. Seven taxa have dispersed unaided from adjacent areas where they were already present, and six taxa moved through artificial corridors (mainly canals) and enter the country. Four plant taxa (*Amorpha fruticosa, Impatiens glandulifera, Ludwigia grandiflora* and *Ludwigia peploides*) use only one main pathway. *Solanum elaeagnifolium* used two principal pathways related to commodities or vectors and in total six sub-categories as a contaminant or stowaway. *Robinia pseudoacacia* also used multiple pathways (two principal), mostly connected to its utilization in forestry, horticulture and erosion control, as well as for ornamental and landscape "improvement" purposes.

Most of the invasive terrestrial vertebrates in Greece have escaped from confinement and this pathway seems to apply also to the species that are expected to enter the country in the next 10 years. Only 17% of the vertebrates enter the country through natural dispersal across borders (Suppl. material 2: fig. S1). *Phasianus colchicus* [non subsp. *colchicus*] (Ring-necked Pheasant) and *Alectoris rufa* (Red-legged Partridge) are the animals released in nature on purpose, as game.

The majority of the terrestrial invertebrates (67%) have arrived as contaminants in transport pathways such as *Xylotrechus chinensis*, followed by transport-stowaway (17%) e.g., *Aedes albopictus* (Suppl. material 2: fig. S1).

Six freshwater invasive invertebrates out of the 16 included in the HELLAS-ALIENS have been introduced through the transport – contaminant pathway (37.5%), six species (37.5%) have entered or are expected to enter unaided, while four species (25%) have escaped or are expected to escape from confinement. Seven freshwater invasive fishes (50%) have entered or are expected to enter the inland water ecosystems of the country unaided. Three species (21.4%) have been un-



Figure 2. Number of new invasive alien species reported during the 1830–2021 period from Greece (blue) and cumulative number of species (red).



Figure 3. Number of new invasive alien species reported per decade and environment. T: terrestrial; F: freshwater; M: marine taxa.



Figure 4. CBD principal introduction pathways for invasive species of Greece per environment. T: terrestrial; F: freshwater; and M: marine taxa.

intentionally introduced as transport-contaminants during commercial fish stockings, two species (14.3%) have escaped from confinement from aquaculture units and two species (14.3%) have been released in nature for sport fishing (*Oncorhynchus mykiss*) and biological control of mosquitoes (*Gambusia holbrooki*) respectively (Suppl. material 3: fig. S2).

Regarding the IAS of the marine environment, all fish species (100%) have arrived unaided (Suppl. material 4: fig. S3). The introduction of marine invertebrate species was facilitated by a more diverse set of sub-pathways to enter or disperse in Greece: 67% have arrived unaided and 17% through transport-stowaway (Suppl. material 4: fig. S3). The majority of the marine plant species (60%) has arrived through transport-stowaway, while 40% have arrived unaided (Suppl. material 4: fig. S3).

Risk assessments and pathways

Out of the 126 taxa, 63% (79 taxa) were evaluated as of High-risk, 34% (43 taxa) as of Medium-risk and only 3% (4 taxa) as of Low-risk. High-risk taxa form the majority in all three environments (terrestrial, freshwater, and marine), with 65%, 60%, and



Figure 5. Grouped bar chart representing percentage of taxa per Risk Assessment category across different environments.

59% of taxa respectively (Fig. 5). The highest percentages of High-risk assessed taxa were found specifically for marine plants (100%), birds (92%), terrestrial invertebrates (86%), mammals (75%), freshwater fishes (71%), and reptiles (60%). Most of the High-risk taxa (84%) are already present in the country either in the wild or in cultivation/captivity.

In the High-risk RA category, 37 taxa have entered or are expected to enter Greece through escape from confinement, while 29 taxa have arrived or are expected to arrive in Greece unaided. In the Medium-risk RA category, 18 taxa entered, or are expected to enter, Greece through escape from confinement, 14 taxa have reached or are expected to reach Greece unaided, and 13 taxa have contaminated, or are expected to contaminate unintentionally, transferred commodities. All taxa using corridors as a pathway category (exclusively terrestrial plants) are of High-risk (Fig. 6). Details on the numbers of taxa per pathway of introduction and environment can be found in the Suppl. material (Suppl. material 5: fig. S4).



Figure 6. Alluvial diagram showing the distribution of introduction pathways across impact categories for all taxa. Nodes on the left represent different CBD principal pathways and nodes on the right the classification of taxa by Risk Assessment categories. Same colour between pathway and risk assessment nodes indicates that all taxa using the specific pathway are exclusively classified in the particular impact category.

Discussion

The scope of the EU 1143/2014 Regulation is to prevent new arrivals and the establishment of IAS in the member states. Consequently, the compilation of national lists and prioritization of their pathways of introduction are of high importance for managing biological invasions. The current study provides a solid scientific base to meet these requirements.

The rate of introductions varied over time, with the number of new IAS arrivals increasing after 1970. Similarly, the introduction rate of species follows a sharp increase after the same period. Records for terrestrial taxa seem to predominate. This could reflect the emphasis placed on monitoring the terrestrial environment, the fact of more frequent introductions in this environment, or the fact that the effects of invasions are more easily detected. Unfortunately, studies on biological invasions in both aquatic and terrestrial environments are rather sparse, so there is not much comparison possible within this field. Seebens et al. (2017), showed that the annual rate of first records worldwide has increased during the last 200 years, with 37% of all first records reported recently (1970–2014). As previously mentioned, terrestrial plants were the first invasive species to be recorded, with some records dating back to the first half of the 19th century. *Phytolacca americana* (A. Strid, pers. comm. 2022) and *Datura stramonium* (Bory de Saint-Vincent and Chaubard 1832-33) were the alien species first observed in the wild (ca. 1830). Similar to other studies (e.g., Nikolić et al. 2013; Sirbu et al. 2022) the accumulation rate of invasive plant species occurrences shows an increasing tendency after the 1950s. The highest number of new introductions per decade is recorded for the periods 1960–1969 and 1970–1979, a fact that could potentially be attributed to more intense field studies. Although the number of alien plant species deliberately introduced for ornamental reasons has generally increased, alien plants' records in the wild have been decreasing during the last two decades, probably due to the raised awareness about the risk of using non-native species, at least for landscape restoration practice.

All terrestrial vertebrates of the HELLAS-ALIENS were introduced into the wild after 1960, except for the Ring-necked Pheasant, which has been intensively reproduced and released as game during the 20th century all over Greece; yet there is no information on the date and place of its first introduction in the wild (Handrinos and Akriotis 1997). There seems to be a constant rate of one terrestrial vertebrate introduction in the wild per decade, which concerns solely animals farmed for food and fur (e.g., the American Bullfrog and the Coypu, respectively) or released intentionally to the wild as game (e.g., Red-legged Partridge). Our data suggest that until the 1990s introductions were attributed predominantly to farmed animals imported into Greece for economic production, while onwards, and especially after 2000, the high increase in introduction rate is mainly attributed to introductions of animals used for human companionship. These pet species were mostly mammals or amphibians and reptiles imported directly into Greece. The European Wild Bird Trade Ban may have reduced bird invasion risks in the recent 15 years (Carrete and Tella 2008; Cardador et al. 2019), a period when there is only one record of invasive pet-bird introduction to the wild in HELLAS-ALIENS, the Common Myna observed in Rhodos Island in 2017, a case that may have to be treated as an unaided spread to Greece from Turkey.

Regarding the twelve terrestrial invertebrates already present in Greece, all first records are after 2003 with the exceptions of the harlequin ladybird *Harmonia axyridis* which was introduced intentionally in the early 1990s (Angelidou et al. 2022) and *Solenopsis geminata* that the only record dates back in 1993 (Salata et al. 2019). The giant resin bee *Megachile sculpturalis* and the pine wood nematode *Bursaphelenchus xylophilus* have not been recorded yet in the country. In Greece, recording terrestrial invertebrates, and insects in particular, has sparked more interest in the early 2020s through citizen science platforms such as the iNaturalist and social media. It is anticipated that this interest will produce more reports and first records in the coming years.

As for the new records of alien freshwater organisms, they seem to have peaked in the period 2000–2010 and, to a lesser degree, in 2010–2020, probably reflecting the increasing negative impacts of globalization on native freshwater biodiversity (Reid et al. 2019). At the same time, they are also correlated to the application of more efficient sampling techniques (e.g., electrofishing for freshwater fishes), wider scale field surveys of lotic and lentic freshwater ecosystems, as well as dedicated efforts to compile anno-

tated lists of the Greek freshwater fauna (Economou et al. 2007; Zenetos et al. 2009; Koutsikos et al. 2012; Barbieri et al. 2015; Vardakas et al. 2022).

The highest number of new introductions for the marine environment of Greece dates back to the 1990s. While only five IAS had entered the Greek marine waters by 1970, and none in the 1970–1980 period, the trend of new introductions appears to be increasing and culminates in the 1990-2000 period with seven new marine IAS. In the last two studied periods, the number of IAS ranges from four to five per decade. This trend in marine waters follows the pattern observed in the Mediterranean Sea for all new alien species introductions (not only invasive ones). Zenetos et al. (2022) documented that the rate of new introductions (excluding parasites, pathogens, and microalgae) on an annual basis, has increased in the Mediterranean since the late 1990's reaching 14 species per year in the period 2012-2017. The increased trend of marine aliens observed in the 1990s (seven IAS) can be attributed either to the increased sampling effort following the interest of the scientific community (Shirley and Kark 2006) or to climate change as documented in Raitsos et al. (2010). The relevant lower number of IAS in the following decades could be an artifact as some of the alien species already introduced in Greek waters might turn out to be invasive. Nevertheless, it is expected that in addition to the time-lapse in reporting IAS (Zenetos et al. 2019), future studies of old data sets, including museum collections, will reveal IAS is already present but neglected to date (Oliver 2015).

Temporal trends within taxonomic groups, which constitute the sum for each environment, are observed and can be explained by the different pathways of introductions of species that differ in their ecology. We must note here that the species included in our analysis are in their majority established species that have been evaluated as invasive.

Terrestrial and freshwater plants constitute a large portion of the species comprising the national list of Greece. This is probably because plant species are easier to be studied but also to the fact that plant species are widely used for ornamental purposes, combined with the fact of easily escaping from confinement. The use of exotic plants in landscape improvement and reforestation used also to be a very common practice; hence, these plants could easily escape and expand their distribution and finally become invasive. The current list comprises 32 terrestrial and freshwater plant taxa of which 84% have escaped from confinement. This is in agreement with relevant studies (Essl et al. 2015; Pergl et al. 2017, 2020; Saul et al. 2017; McGrannachan et al. 2021; Sandvik et al. 2022), which report that plants are the most prominent taxonomic group among those invading an area. Several studies (Essl et al. 2015; Pergl et al. 2017, 2020; Saul et al. 2017; McGrannachan et al. 2021; Sandvik et al. 2022; Sirbu et al. 2022) also agree on the finding that alien plant species are predominantly introduced by means of escape from confinement, as they are mainly used for ornamental purposes. Ornamental horticulture is recognized as an important pathway for introducing and dispersing alien species (Drew et al. 2010). At the European level, Hulme et al. (2008) point to escape from confinement as the most frequent pathway for the introduction of alien species.

Fifteen plant taxa were classified as of High-risk and 16 as of Medium-risk, while only one species (*Matricaria discoidea*) was classified as of Low-risk. *M. discoidea* has been present in Greece since 1994 and, although it is considered an invasive species, its

populations are spatially limited to specific mountains where they are found mainly at high altitudes, in stony/gravelly places (Greuter and Raus 2008; Greuter and von Raab-Straube 2008; Dimopoulos et al. 2013). Therefore, the risk of its future expansion is low if the secondary introduction pathways are properly controlled. Similarly to our findings, most of the plant taxa included in relevant works are classified as of High-risk (Sandvik et al. 2022). Twelve of the 15 High-risk plant species (80%) are already present in the country (in the wild or in cultivation), seven out of the 15 are present in the wild (47%), seven are hydrophytes (47%), while 70% of the hydrophytes are of High-risk.

Most alien invasive plants in Greece originate from the Americas followed by Asian and African species. This pattern is similar to that observed for all alien plants recorded in Greece (Arianoutsou et al. 2010) and it is in accordance with findings for other Mediterranean countries (see for example Celesti-Grapow et al. 2009). This is most probably linked to their pathways of introduction, as the majority of plants have been introduced through escape from confinement. The alien established plant species represent 4.5% of the Greek flora (including archaeophytes and established aliens) while the ratio of established alien to native plant species is 1:12.7 or 0.079. Invasive alien plant taxa account for 12.1% of the established alien plant species.

A published consolidated list of alien terrestrial vertebrates in Greece is missing. According to the HELLAS-ALIENS list, invasive terrestrial vertebrates already present in the wild add approximately 8%, 3%, 2% and 6% to the native amphibians, reptiles, birds and mammals, respectively.

HELLAS-ALIENS contains three terrestrial vertebrate IAS that are native to other parts of Europe and thus cannot be considered for the EU list: Alectoris rufa, Podarcis siculus, and Triturus carnifex. The latter is highly likely to invade the country within the next 10 years as the Horizon exercise performed has shown. Alectoris rufa, has been introduced in the wild as game since at least 1979 (Handrinos and Akriotis 1997) and until 2009, when the intentional release of exotic species as game was prohibited; yet, the genetic pollution of Alectoris graeca, through hybridization was already evident (Barilani et al. 2007). Podarcis siculus, has conquered several new areas inside and outside the EU arriving as a stowaway on cargo and nursery trade (Silva-Rocha et al. 2014; Scalera 2019) which seems to be the case for the Greek colony as well (Adamopoulou 2015). It has exhibited negative impacts on native species mostly through competitive exclusion (e.g., displacement of the critically endangered P. raffonei, see Capula et al. 2002) and hybridization with native Podarcis (Capula 1993, 2002). An unfortunate but probable consequence of its accidental entry in the Aegean islands is that it may threaten island endemic lizards that for the most part have evolved without the presence of competitors, and some are already endangered (Lymberakis et al. 2018).

Another vertebrate worth mentioning in the HELLAS-ALLIENS is *Neovison vison*, (American mink) which is already established in Northwest Greece (Adamopoulou and Legakis 2016) and is expanding (Galanaki and Kominos 2022). It is an IAS with significant adverse impacts on European biodiversity (Bouros et al. 2016), affecting 47 native species (Genovesi et al. 2012). However, it is not listed in the EU list due to the consideration of costs and socioeconomic aspects; concerned Member States could address such species through national measures (European Commission 2021).

Importation of pets followed by either their deliberate release or escape from confinement seems to be an important pathway for several terrestrial vertebrates in accordance with the general pattern in Europe (Roy et al. 2019; Tedeschi et al. 2021). Apart from one, all reptile species in the HELLAS-ALIENS are pet trade species. Among mammal species, escape from confinement is the major pathway, as many of them are kept as pets in private or public collections or bred for their fur. Only *Nyctereutes procyonoides* (the racoon dog) and *Ondatra zibethicus*, (muskrat), seem to enter the country through natural dispersal across Greece's northern borders. Both species have confirmed occurrences in the Balkans (Ćirović 2006; Popova and Zlatanova 2017) and their few verified records are currently restricted to North Greece (Catsadorakis and Bousbouras 2010; Adamopoulou and Legakis 2016).

Twenty-one terrestrial vertebrate species have been assessed as of High-risk, five as of Medium-risk and two of Low-risk for the native biodiversity. High-risk species include, among others, the well-established in Crete *Lithobates catesbeianus*, (the American bullfrog), a carrier of the lethal chytrid fungus that threatens amphibian populations worldwide (Miaud et al. 2016). This species threatens local subpopulations of the endemic, declining Cretan frog, *Pelophylax cretensis*, which is recently assessed as Vulnerable since it occurs in ten or fewer threat-defined locations (IUCN SSC Amphibian Specialist Group 2020).

Most of the terrestrial invertebrates on HELLAS-ALIENS are likely to have detrimental impacts to economic sectors such as agriculture, forestry, the tourism industry and human health (IUCN 2000; Mazza and Tricarico 2018; Haubrock et al. 2021). Unlike plant taxa, most terrestrial invertebrates are unintentionally introduced (Saul et al. 2017; Riera et al. 2021). Most of the terrestrial invertebrates on HELLAS-ALIENS are of Asian origin. Knowing the origin of the non-native terrestrial invertebrates is important during the establishment of early warning systems at points of entry and border controls, however, for terrestrial insects, it was shown that it is generally unknown whether their introduction to Greece is the result of a primary introduction event from their area of origin or a secondary translocation from an already invaded country that either shares borders with Greece or is a major trading partner, e.g. Italy or Germany (Demetriou et al. 2021). Deciphering the biological invasion history, distribution, impacts and species interactions of non-native terrestrial invertebrates by utilising classical methods, citizen science and molecular tools will help us understand better their impacts on ecosystems and native biodiversity and it has been described as a desirable strategy in other Mediterranean countries such as Cyprus (Demetriou et al. 2021).

Updated, relatively recent compilations available for freshwater fishes indicate that alien freshwater fish species of the HELLAS-ALIENS list add approximately 17% to the native freshwater ichthyofauna of Greece (Barbieri et al. 2015). Freshwater invertebrates and fishes also constitute a large part of the national list of invasive species of Greece. This is in agreement with recent studies, focusing on the more well-studied freshwater fishes of Greece (as opposed to invertebrates) and of the Balkans that report a high percentage of alien species in freshwater ecosystems (15%–23%, for Greece, see Barbieri et al. 2015; for all Balkans, see Piria et al. 2018, also for Bulgaria, North

Macedonia and Serbia, see e.g., Simonović et al. 2013; for Croatia and Slovenia, see Piria et al. 2016). Most of the freshwater species of the list are of North American origin, and in this, the list mirrors the dominant origin of introduction of alien fish species also in the Balkans (Piria et al. 2018). Natural dispersal occurs through the several transboundary rivers and lakes shared with neighboring Balkan countries, such as the Prespa lake, the Kerkini lake (Strymon river basin), and the Evros river (Barbieri et al. 2015; for recent invasions see Erőss et al. 2005; Zogaris and Apostolou 2011; Petriki et al. 2014; Karaouzas et al. 2020) is the main pathway of freshwater species invasion in Greece. Other pathways include, for invertebrates, transport contaminants on plants for Botanical gardens/greenhouses or commercial crops (Vinarski 2017; Cianfanelli et al. 2007; Beran and Glöer 2006), as well as the aquarium pet trade (Marrone et al. 2011). In contrast, most fish species introduced as transport contaminants, entered Greek freshwaters accidentally during fish stockings with carp, mostly in lake ecosystems (Perdikaris et al. 2012; Piria et al. 2018). Finally, there are also fish escapes in Greece from aquaculture, the dominant pathway of alien fish introductions in other Balkan countries (Barbieri et al. 2015; Economou et al. 2007; Piria et al. 2018) and, importantly, potential escapes of two highly invasive cravfish species (Procambarus clarkii and Procambarus virginalis) from the aquarium trade (Papavlasopoulou et al. 2014) the major pathway for new non-indigenous crayfish species introductions into Europe as well (Chucholl 2013).

Invasion by alien species constitutes a leading cause of the rapid global freshwater biodiversity loss (Reid et al. 2019); similarly invasive species are a major driver of the geographic range reduction and population decline of the endemic, threatened freshwater fauna of Greece (Perdikaris et al. 2010, 2016; Barbieri et al. 2015; Kalogianni et al. 2019, 2022). Thus, it is not surprising that High-risk species dominate the freshwater taxa of the current list (18 species, including all six species expected to invade Greek freshwaters in the next ten years), with six species in the EU list (such as the highly invasive fish *Lepomis gibbosus* and *Pseudorasbora parva*, widespread in Greece, and the crayfish *Pacifastacus leniusculus*) and conversely, no Low-risk species present.

The origin of the vast majority of marine IAS included in the HELLAS-ALIENS was the Indo-Pacific and in particular the west Indo-Pacific. Most marine IAS have entered Greek waters via the Suez Canal, but not directly. Indeed, the impact of the Suez Canal in the introduction of marine aliens has been previously documented (e.g., Zenetos et al. 2012; Galil et al. 2017; Tsiamis et al. 2018) and accounts for more than half of Mediterranean aliens, and the vast majority of fishes (e.g., Zenetos et al. 2012). However, corridor is not the main pathway of most IAS in the Greek Seas. Although marine species in the HELLAS-ALIENS have progressively entered the eastern Mediterranean via the Suez, they were first established in the Levantine sea from where they invaded the Greek Seas unaided or with vessels (Transport-Stowaway) (Zenetos et al. 2020). In a recent analysis of biological traits that could potentially favor the introduction and establishment of alien fishes in the Mediterranean, Karachle et al. (2022) show that temperature is the most important factor. This finding, combined with the abrupt rising temperature since the end of the 1990s that has modified the potential

thermal habitat available for warm-water species and facilitating their settlement at an unexpectedly rapid rate (Raitsos et al. 2010), further explains the participation of Indo-Pacific taxa in the HELLAS-ALIENS. In particular, Transport – Stowaway - Machinery/equipment is the main vector of macrophytes introduction whether of Indo-Pacific origin e.g., Womerslevella setacea or of NE Pacific or Tropical Atlantic e.g., Codium fragile, Asparagopsis taxiformis. In the case of marine plants, although many are also of Indo-Pacific origin, their introduction is related to shipping and not corridors. The Indo-Pacific origin does not imply an unaided introduction for all invertebrates introduced to the Greek Sea. For example, Transport-Stowaway is suspected to be the mode of introduction of the bivalve mollusc Fulvia fragilis (Crocetta et al. 2017). On the other hand, the blue crab Callinectes sapidus native to the western Atlantic has invaded the Aegean Sea either via ballast waters (Transport-Stowaway) or Unaided from the neighboring Turkish waters. Finally, another species that is worth mentioning is the Atlantic northern shrimp Penaeus aztecus. The pathway of its introduction in the Mediterranean is not very clear, with the aquaculture release/escape prevailing as the most likely pathway (Galil et al. 2016; Karachle et al. 2017). This is also true for the Greek Seas, as the species is considered to enter Greece either unaided from neighboring countries (i.e. Turkey) and/or as an escape from confinement.

For the marine environment, ten (45% of taxa) and seven (32% of taxa) of High and Medium-risk taxa respectively have arrived unaided. It is worth noting that *Penaeus aztecus*, the only taxon that has potentially escaped from confinement, is of High-risk, while the pearl oyster *Pinctada radiata* which has been intentionally released, is of Medium-risk. All marine plants are of High risk. Finally, alien marine taxa add approximately 7% to the native marine biota (Simboura et al. 2019, UNEP/MAP-SPA/RAC 2021).

Conclusions

The present study provides a thorough analysis of the IAS of Greece. Our results based on the systematic review of existing literature reveal that a considerably high number of terrestrial plants and freshwater organisms are threatening local biodiversity and may also pose serious problems in the economy and society, as is the case of marine species (Oliver 2015; Zenetos et al. 2019). One of the most important findings of the study focuses on the pathways of introduction of IAS indicating that escape from confinement is the most frequent pathway of terrestrial taxa. This has serious implications for decisions on the importation of horticultural and ornamental plants as well as on pets and their subsequent accidental (or not) release in the wild. As biological invasions are a dynamic field, surveillance and management of pathways can provide an efficient method to prevent the arrival of new IAS (McGeoch et al. 2016). However, monitoring the pet and aquarium trade (on line trading also included) is rather challenging since it requires detailed knowledge of the species imports (numbers, taxa) through legal or illegal trade or data such as the number of pets kept in captivity and/or sold, which are usually absent. Natural dispersal is the dominant pathway of aquatic taxa, both freshwater and marine, indicating that monitoring of freshwater transboundary waterways and marine corridors and vessels respectively should be a priority. Our work sets the basis for management plans. National and international experts in invasive species could address specific objectives such as assessing the feasibility of eradicating established invasive alien species either countrywide or from the islands which are high in endemic species. Ranking established invasive alien species based on the threat they pose to locations across the Greek mainland, islands and seas, where they are not currently established, should also be a priority. Raising awareness programs to competent authorities, schools and members of the public should take place highlighting the importance of biosecurity to better protect the native biodiversity in the Greek mainland and the islands from invasive alien species should also be a priority.

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Supplementary material I

List of HELLAS-ALIENS species

Authors: Margarita Arianoutsou, Chloe Adamopoulou, Pavlos Andriopoulos, Ioannis Bazos, Anastasia Christopoulou, Alexandros Galanidis, Eleni Kalogianni, Paraskevi K. Karachle, Yannis Kokkoris, Angeliki F. Martinou, Argyro Zenetos, Andreas Zikos Data type: excel file with a list of species

Explanation note: The file contains the full list of alien invasive species of Greece.

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Link: https://doi.org/10.3897/neobiota.86.101778.suppl1

Supplementary material 2

CBD principal introduction pathways for terrestrial invasive alien species of Greece per different categories

Authors: Margarita Arianoutsou, Chloe Adamopoulou, Pavlos Andriopoulos, Ioannis Bazos, Anastasia Christopoulou, Alexandros Galanidis, Eleni Kalogianni, Paraskevi K. Karachle, Yannis Kokkoris, Angeliki F. Martinou, Argyro Zenetos, Andreas Zikos Data type: figure

- Explanation note: fig. S1: CBD principal introduction pathways for terrestrial invasive alien species of Greece per different categories. The category vertebrates includes amphibians, reptiles, birds and mammals.
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Link: https://doi.org/10.3897/neobiota.86.101778.suppl2

Supplementary material 3

CBD principal introduction pathways for freshwater invasive alien species of Greece per different categories

Authors: Margarita Arianoutsou, Chloe Adamopoulou, Pavlos Andriopoulos, Ioannis Bazos, Anastasia Christopoulou, Alexandros Galanidis, Eleni Kalogianni, Paraskevi K. Karachle, Yannis Kokkoris, Angeliki F. Martinou, Argyro Zenetos, Andreas Zikos Data type: figure

- Explanation note: fig. S2: CBD principal introduction pathways for freshwater invasive alien species of Greece per different categories. The category vertebrates corresponds to fishes.
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Link: https://doi.org/10.3897/neobiota.86.101778.suppl3

Supplementary material 4

CBD principal introduction pathways for marine invasive alien species of Greece per different categories

Authors: Margarita Arianoutsou, Chloe Adamopoulou, Pavlos Andriopoulos, Ioannis Bazos, Anastasia Christopoulou, Alexandros Galanidis, Eleni Kalogianni, Paraskevi K. Karachle, Yannis Kokkoris, Angeliki F. Martinou, Argyro Zenetos, Andreas Zikos Data type: figure

- Explanation note: fig. S3: CBD principal introduction pathways for marine invasive alien species of Greece per different categories. The category vertebrates corresponds to fishes.
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Link: https://doi.org/10.3897/neobiota.86.101778.suppl4

Supplementary material 5

Alluvial diagram showing the distribution of introduction pathways across impact categories

Authors: Margarita Arianoutsou, Chloe Adamopoulou, Pavlos Andriopoulos, Ioannis Bazos, Anastasia Christopoulou, Alexandros Galanidis, Eleni Kalogianni, Paraskevi K. Karachle, Yannis Kokkoris, Angeliki F. Martinou, Argyro Zenetos, Andreas Zikos Data type: figure

- Explanation note: fig. S4: Alluvial diagram showing the distribution of introduction pathways across impact categories. Nodes on the left represent different CBD main pathways and nodes on the right the classification of taxa by Risk Assessment categories. Same colour between pathway and risk assessment nodes indicates that all taxa using the specific pathway are exclusively classified in the particular impact category. A: terrestrial; B: freshwater; C: marine taxa.
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- Link: https://doi.org/10.3897/neobiota.86.101778.suppl5

REVIEW ARTICLE



Alien ants (Hymenoptera, Formicidae) on a quest to conquer Greece: a review including an updated species checklist and guidance for future research

Jakovos Demetriou^{1,2}, Christos Georgiadis^{3,4}, Evangelos Koutsoukos^{2,3}, Lech Borowiec⁵, Sebastian Salata⁵

 Joint Services Health Unit Cyprus, BFC RAF Akrotiri BFPO 57, Akrotiri, Cyprus 2 Department of Ecology and Systematics, Faculty of Biology, National and Kapodistrian University of Athens, 15784 Athens, Greece
Museum of Zoology, National and Kapodistrian University of Athens, 15784 Athens, Greece 4 Section of Zoology and Marine Biology, Department of Biology, National and Kapodistrian University of Athens, 15784 Athens, Greece 5 University of Wrocław, Department of Biodiversity and Evolutionary Taxonomy, Myrmecological Laboratory, Przybyszewskiego 65, 51-148 Wrocław, Poland

Corresponding author: Sebastian Salata (sebastian.salata@uwr.edu.pl)

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Abstract

Biological invasions represent one of the main drivers of biodiversity loss with adverse impacts on human societies, economies and public health. More than 500 ant species have been transported outside their native range with the help of humans, while the majority of them have managed to establish viable populations in the wild. Nevertheless, data from the Mediterranean region suggest that most alien ants occupy anthropogenic habitats with little spread in semi-natural and natural habitats. Research on biological invasions of ants in Greece had previously identified a total of 15 alien ant species. In this article, an extensive literature investigation and material examination provide a revised checklist of the alien myrmecofauna of Greece. Although the number of alien ant species remains the same, the checklist's composition is largely altered to provide an up-to-date overview of the country's alien myrmecofauna in order to enhance management decisions and future research. The presence and distribution of alien ants within Greek administrative divisions, NATURA 2000 sites and Corine Land Cover types are analysed and presented. In particular, the species richness of alien ants seems to be highest in the Aegean Archipelago (Crete and Southern Aegean Islands) probably due to uneven collecting efforts and increased climatic suitability. Alien ant species are mostly associated with anthropogenic habitats including urban and agricultural areas, although

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a significant percentage has managed to spread into forest and semi-natural areas, including protected NATURA 2000 sites. Future research directions enhancing the monitoring of alien ants and their impacts are indicated to safeguard native ant biodiversity and conservation efforts of rare and endemic taxa.

Keywords

alien species, biological invasions, *Cardiocondyla obscurior*, first record, invasive alien species, social insects, tramp species

Introduction

The main drivers of global change such as invasive alien species, climate change, landuse change and pollution have been found to synergistically exacerbate global biodiversity loss, both directly and indirectly (Butchart et al. 2010; IPBES 2019). Scientists around the world have warned about the adverse impacts of invasive alien species towards native biodiversity and ecosystem functioning, biogeographic patterns and species' extinction rates, as well as impacts on public health and socio-economic parameters, calling for international cooperation and stronger biosecurity regulations to mitigate their impacts (Bacher et al. 2018; Mazza and Tricarico 2018; Pyšek et al. 2020). Approximately 14,000 alien species have been identified in Europe, with a large proportion of them being insects (EASIN 2022). Alien terrestrial invertebrates are mostly synanthropic, predominantly invading man-made habitats such as parks and gardens, buildings, agricultural land and greenhouses (Lopez-Vaamonde et al. 2010). Although protected areas have been characterised as more resilient to biological invasions, established populations of alien species can be found lurking in their boundaries (Gallardo et al. 2017; Liu et al. 2020).

More than 500 species of ants have been transferred outside their native range and successfully bypassed biosecurity controls, with almost two thirds of them managing to establish populations in the wild (Wong et al. 2023). The global costs of invasive ants have been recently estimated at around 51.93 billion USD annually, however, these numbers are perceived as severely underestimated and there is a call for improved cost reporting (Angulo et al. 2022). Although 17 ant species have been identified as harmful towards native biodiversity and ecosystem function (Wong et al. 2023), more than 80% of worldwide invasion costs correspond to only two species [i.e. *Solenopsis invicta* Buren, 1972 and *Wasmannia auropunctata* (Roger, 1863)] (Angulo et al. 2022). Recent studies addressing alien ants in the Mediterranean have identified around 40 species, mostly invading anthropogenic habitats although the extent of natural and introduced range of some species [e.g. *Cardiocondyla mauritanica* Forel, 1890, *Monomorium subopacum* (Smith, F., 1858)] is somewhat problematic (Schifani 2019). The European Alien Species Information Network (EASIN) currently lists 65 species of ants as alien to or within Europe (EASIN 2022).

The first lists of alien ants in Greece were published by Salata et al. (2019) and Schifani (2019), including 15 and 14 species, respectively. Out of the 14 species

mentioned in Schifani (2019), Salata et al. (2019) had excluded *Aphaenogaster splendida* (Roger, 1859) and *Monomorium monomorium* Bolton, 1987 [previously reported as alien to Greece by Salata and Borowiec (2018), although questionable according to Schifani (2019)], while also adding records of *Nylanderia vividula* (Nylander, 1846), *M. subopacum* and *S. geminata*. Furthermore, Salata et al. (2019) questioned records of *Anoplolepis gracilipes* (Smith, 1857) (Radchenko 2007) and *Pheidole megacephala* (Fabricius, 1793) (Borowiec and Salata 2012). Later, Demetriou et al. (2021) revised the checklist of alien insects inhabiting Greece, listing a total of 15 ant species, strongly resembling that of Salata et al. (2019), although excluding *Hypoponera eduardi* (Forel, 1894) and adding *Lasius neglectus* van Loon, Boomsma & Andrásfalvy, 1990 (Salata and Borowiec 2019b).

In this publication, the checklist of alien ants of Greece is revised including notes on their distribution and providing reasons on why some species were excluded. Literature and distribution maps are presented for each species. Additionally, georeferenced records are analysed in the context of their presence within the NATURA 2000 network and land cover. Lastly, future research directions are discussed.

Materials and methods

Data collection and specimen identification

Records of alien ant species reported from Greece were searched through AntMaps (Janicki et al. 2016; Guénard et al. 2017), available scientific literature (Forel 1886, 1910; Collingwood 1993; Seifert 2003, 2020; Bolton and Fischer 2011; Borowiec and Salata 2012, 2013, 2014, 2017, 2018a, b, d, 2021a; Seifert et al. 2017a, b; Wagner et al. 2017; Salata and Borowiec 2018, 2019a, b; Salata et al. 2019, 2020; Tseng et al. 2019; Borowiec et al. 2021, 2022) and were subsequently catalogued. In addition, samples in the collections of L. Borowiec and S. Salata (Department of Biodiversity and Evolutionary Taxonomy, University of Wrocław, Poland – DBET), and Ch. Georgiadis (Museum of Zoology of the University of Athens, Greece – ZMUA) including both published and unpublished material were included. Identifications were based on the largest collection of Balkan ants preserved in the Museum of Natural History, University of Wroclaw, Poland - MNHW, knowledge resulting from studies on this collection in the last 12 years, comparative studies on types of European ants and several earlier regional works on European ants such as Agosti and Collingwood (1987), Czechowski et al. (2012), Seifert (2018), and recent revisions for genera and species complexes/groups e.g. Wagner et al. (2017) for the Tetramorium caespitum group, Seifert (2003) for the genus Cardiocondyla, Seifert et al. (2017a) for the Tapinoma nigerrimum group, and Seifert (2020) for the genus Lasius.

The native range of species was assessed based on available scientific literature, although in some cases their native range has been characterized as "questionable" or even "unknown" e.g. that of *A. splendida* (Schifani 2019) or *L. neglectus* (Stukalyuk et

al. 2020). Assessment criteria in Essl et al. (2018) were used to evaluate whether a species could be regarded as native or alien to Greece. In cases where a species was previously characterized as alien (i.e. *H. eduardi*, *M. monomorium* and *M. subopacum*) but failed to demonstratively have crossed a biogeographic barrier to enter the country via human activities, this was regarded as native to the country. In addition, the habitats occupied by the assessed species were also taken into consideration with species such as *H. eduardi* that can be found in natural habitats under specific habitat requirements being considered as native.

According to their establishment status, alien ants were catalogued as Established i.e. "non-native species records with established populations in the wild" or Indoors introduced i.e. "non-native species records without established populations in the wild (e.g. in buildings, greenhouses, airport, quarantine surveys)", as per AntMaps categories: exotic and indoors introduced (Janicki et al. 2016; Guénard et al. 2017). Lastly, the establishment status of data-deficient species is regarded as "Unknown". Species excluded from the checklist are discussed.

Data analysis and visualisation

The distribution of alien ant species within the 14 Greek administrative divisions (Kallikratis Programme) was analysed and mapped, calculating their area of occupancy (AOO) in a 2×2 km² grid, the number of occupied administrative divisions as well as the year of first published official record for each alien ant species reported from Greece. A total of 191 georeferenced observations (Suppl. material 1) were pooled in QGIS Version 3.18.2 free and open source Geographic Information System (https:// ggis.org/en/site/) and were assigned to their respective land cover and presence within the NATURA2000 network. Boundaries and habitat types were based on the European layers of Corine Land Cover (CLC) project version CLC2018 and NATURA2000 sites, downloaded from Copernicus Land Monitoring Service and the European Environmental Agency, respectively. According to the Copernicus Land Monitoring Service, records within the following land-cover types were mapped: artificial surfaces, agricultural areas, forest and semi-natural areas, wetlands and water bodies as well as their respective sub-categories (https://land.copernicus.eu/user-corner/technical-library/corine-land-cover-nomenclature-guidelines/html). Since CLC2018 files had an accuracy of 100 m, georeferenced records with only two decimal digits or less in latitude and/ or longitude fields, were excluded from CLC and NATURA 2000 analyses to retain a higher accuracy. Thus, a total of 169 georeferenced records were assigned to their corresponding CLC types and mapped for presence within the NATURA 2000 network.

Specimen photography

Photographs of specimens, unless stated otherwise, were taken by Prof. Lech Borowiec using Nikon SMZ18 and Nikon SMZ 1500 stereomicroscopes, Nikon D5200 camera and Helicon Focus software.

Results

Biodiversity and distribution

The revised checklist of the alien myrmecofauna of Greece currently includes fifteen (15) species distributed in four (4) subfamilies (Table 1). A total of eight (8) species regarded as alien in Greece were excluded from previous publications as they represent misidentifications or proved to be native to the country. In greater detail, following Salata et al. (2019) and Schifani (2019), *Anoplolepis gracilipes, Aphaenogaster splendida, Monomorium monomorium, Nylanderia vividula, Pheidole megacephala,* and *Solenopsis geminata* are removed from previous checklists as dubious records while *Hypononera eduardi* and *Monomorium subopacum* were proved to be native. *Cardiocondyla obscurior* Wheeler, 1929, is presented for the first time for Greece.

The majority of the species have been detected in Southern Greece and its islands, with the South Aegean Islands and Crete hosting a total of 11 and 10 alien ant species, respectively (Fig. 1). North Aegean Islands follow with six species while the Ionian Islands and the Peloponnese each hold five species. In the remaining regions, fewer than four species have been identified whereas Mount Athos and Western Macedonia hold no records of alien ants (Fig. 1).

Tetramorium immigrans seems to be widely distributed, inhabiting ten out of 14 administrative divisions of Greece (Table 2). Nylanderia jaegerskioeldi, Pheidole indica and Cardiocondyla mauritanica follow occupying seven, six and five administrative divisions in Southern Greece and Greek islands, respectively. Alien species found in just one administrative division include C. obscurior and

No.	Subfamily	Tribe	Species	Origin	Establishment status
1	Dolichoderinae	Leptomyrmecini	Linepithema humile (Mayr, 1868)	Neotropics	Established
2		Tapinomini	Tapinoma magnum Mayr, 1861	W. Mediterranean	Established
3	Formicinae	Lasiini	Lasius neglectus Van Loon, Boomsma &	C. Asia	Established
			Andrasfalvy, 1990		
4			Paratrechina longicornis (Latreille, 1802)	Indomalaya	Established
5			Nylanderia jaegerskioeldi (Mayr, 1904)	Africa	Established
6		Plagiolepidini	Lepisiota syriaca (André, 1881)	Near East	Established
7	Myrmicinae	Attini	Pheidole indica Mayr, 1879	Indomalaya	Established
8			Strumigenys membranifera (Emery, 1869)	Sub-Saharan Africa	Unknown
9		Crematogastrini	Cardiocondyla mauritanica Forel, 1890	Palearctic – N. Africa	Established
10			Cardiocondyla obscurior Wheeler, 1929	Indomalaya	Unknown
11			Tetramorium bicarinatum (Nylander, 1846)	Indomalaya	Established
12			Tetramorium immigrans Santschi, 1927	Anatolia and Caucasus	Established
13		Solenopsidini	Monomorium bicolor Emery, 1887	Africa	Established
14			Monomorium pharaonis (Linnaeus, 1758)	Africa	Indoors introduced
15	Ponerinae	Ponerini	Hypoponera punctatissima (Roger, 1859)	Sub-Saharan Africa	Established

Table 1. Updated checklist of the alien myrmecofauna of Greece, including their origin and establishment status.



Figure 1. Number of alien ant species in each Greek administrative division.

Table 2. Area of occupancy (AOO), number of occupied administrative divisions and year of first published official record for each alien ant species reported from Greece.

Species	AOO (km ²)	Number of adm. divisions occupied	Year of first official record (published)
Cardiocondyla mauritanica	60	5	2003
Cardiocondyla obscurior	4	1	2023
Hypoponera punctatissima	4	2	1987
Lasius neglectus	92	4	2016
Lespisiota syriaca	16	3	1928
Linepithema humile	16	4	1967
Monomorium bicolor	68	2	1928
Monomorium pharaonis	N/A	3	1928
Nylanderia jaegerskioeldi	128	7	1932
Paratrechina longicornis	20	1	1988
Pheidole indica	104	6	1910
Strumigenys membranifera	N/A	1	1987
Tapinoma magnum	20	3	2022
Tetramorium bicarinatum	8	1	2019
Tetramorium immigrans	144	10	2017

Paratrechina longicornis in South Aegean, *S. membranifera* collected from Epirus (Salata and Borowiec 2018) and *Tetramorium bicarinatum* known only from the island of Crete (Salata et al. 2020).

Land-use and presence in protected areas

The presence of nine alien ant species within the NATURA 2000 network was detected in 34 sites (Suppl. material 2). These included 11 sites located in South Aegean Islands, seven in Crete, five in Eastern Macedonia and Thrace, four in Central Macedonia and North Aegean Islands (respectively), two in Thessaly and one site in the Ionian Islands. No more than two species were identified from each site. *Lasius neglectus* and *T. immigrans* were each found in 10 NATURA 2000 sites. *Monomorium bicolor* and *P. indica* follow being present in six and four sites, respectively. *Nylanderia jaegerskioeldi* was found in only three sites situated in the South Aegean. *Cardiocondyla mauritanica* and *Hypoponera punctatissima* have been collected from two overlapping protected sites in Crete (GR4330003, GR4330007). Finally, *Tapinoma magnum* and *Tetramorium bicarinatum* have been collected from one protected site in South Aegean (Serifos Island) and Crete, respectively (Suppl. material 2).

Regarding the distribution of ants within different CLC types (Fig. 2), the majority of alien ants (48%) have been collected from artificial surfaces, including urban fabric (continuous and discontinuous) and artificial, non-agricultural vegetated areas such as green urban areas and sport and leisure facilities (Suppl. material 1). Furthermore, 28% of specimens have been collected from agricultural areas (mostly heterogeneous) including permanent crops and arable land. Around one fifth (21%) of records have penetrated forests and semi-natural areas with scrub and/or herbaceous vegetation associations being most common. Lastly, only two records of *T. immigrans* were found in wetlands, specifically within salt-marshes and three coastal records were classified by the analysis as within water bodies.



Figure 2. Corine Land Cover types occupied by alien ant species in Greece.

Discussion

Annotated checklist with comments on biology and distribution

Dolichoderinae

Linepithema humile (Mayr, 1868)

Fig. 3

Literature records. Bernard (1967) (Greece); Radchenko (2007) (Crete); Salata et al. (2019) (Attica, Corfu, Crete, Peloponnese); Salata et al. (2020) (Crete); Borowiec and Salata (2013) (Peloponnese), (2021a) (Corfu).

Georeferenced records. Suppl. material 1.

Invaded administrative divisions. Attica, Crete, Ionian Islands, Peloponnese (4). Notes. An alien species classified as one of the world's 100 worst invasive alien species (GISD 2022), with severe ecological impacts on native biodiversity recorded around the world (Wetterer et al. 2009). In Europe, L. humile has been reported to harm native vertebrate and invertebrate species (Cammell et al. 1996; Carpintero 2003; Carpintero et al. 2005; Wetterer et al. 2006; Alvarez-Blanco et al. 2017; Centorame et al. 2017; Zina et al. 2020) as well as reported as a household pest, infesting disturbed agricultural, urban areas and some natural habitats (Espadaler and Gómez 2003; Carpintero et al. 2004; Wetterer et al. 2009; López-Collar and Cabrero-Sañudo 2021). Such environments may act as "reservoirs" enhancing the survival and further spread of the species to natural habitats, protected areas and climatically non-optimal regions in higher latitudes (Carpintero et al. 2004; Roura-Pascual et al. 2004; López-Collar and Cabrero-Sañudo 2021), as already predicted for other alien Hymenoptera such as Sceliphron curvatum (F. Smith, 1870) in Europe (Polidori et al. 2021). In Greece, it has been collected from only a handful of urban and agricultural localities (Salata et al. 2019; present study). Nevertheless, given its invasion potential and recorded impact on native biodiversity further monitoring and studies on impacts are necessary.

Tapinoma magnum Mayr, 1861

Fig. 4

Literature records. Borowiec et al. (2022) (Thasos).

Georeferenced records. Suppl. material 1.

Invaded administrative divisions. Central Macedonia, Eastern Macedonia and Thrace, South Aegean (3).

Notes. A recently discovered alien ant, native to the Western Mediterranean, that has managed to invade urban disturbed areas in Belgium, France, Germany, the Netherlands, Slovenia and Switzerland through human activities (i.e. through ports and plant nurseries) (Seifert et al. 2017b; Seifert 2018; Bračko 2019). In Greece, it has been detected from the Cyclades, Central Macedonia and Thassos Island in Eastern Macedonia and Thrace (Borowiec et al. 2022). So far, its presence has had no impact on the



Figure 3. Habitus of *Linepithema humile* (Mayr, 1868) in lateral view above and its known distribution in Greece below.

native fauna of occupied Greek sites. According to Seifert et al. (2017b), *T. magnum* in the Mediterranean can be mostly found in "open unstable or degraded areas with significant to very strong anthropogenic influence and a weakly developed tree layer". In Greece, despite the small number of collection sites, the species was collected from artificial surfaces such as parks and one agricultural area (path in meadow with walnut and fruit trees in Thassos) (Suppl. material 1) (Borowiec et al. 2022).



Figure 4. Habitus of *Tapinoma magnum* Mayr, 1861 in lateral view above and its known distribution in Greece below.

Formicinae

Lasius neglectus Van Loon, Boomsma & Andrasfalvy, 1990 Fig. 5

Literature records. Bračko et al. (2016) (Thrace), Borowiec and Salata (2017) (Peloponnese) [as *Lasius neglectus/turcicus* complex]; Seifert (2020) (Rhodes).

Georeferenced records. Suppl. material 1.

Invaded administrative divisions. Eastern Macedonia and Thrace, North Aegean, Peloponnese, South Aegean (4).



Figure 5. Habitus of *Lasius neglectus* Van Loon, Boomsma & Andrasfalvy, 1990 in lateral view above and its known distribution in Greece below.

Notes. The radiation centre of *L. neglectus* is probably situated in Asia Minor (Seifert 2015, 2020) or Central Asia (Turkmenistan and Uzbekistan) (Stukalyuk et al. 2020; AntWiki 2022). Records from Greece have been re-evaluated upon previously reported indistinct records of the *Lasius neglectus/turcicus* complex. Sporadic records have been obtained from the Aegean Islands, and the Peloponnese, and noticeably more populations in Eastern Macedonia and Thrace region. *Lasius neglectus* appears

in both urban and agricultural areas (Fig. 2), although according to our analysis it has managed to spread to forest and semi-natural areas including mixed, broad-leaved forests and natural grasslands of Eastern Macedonia and Thrace and the Aegean Archipelago (Suppl. material 1). Nevertheless, human-induced habitat modifications have been observed in all localities from which the species has been collected, in contrast to localities of native *Lasius turcicus* Santschi, 1921.

Paratrechina longicornis (Latreille, 1802)

Fig. 6

Literature records. Kugler (1988) (Greece); Tseng et al. (2019) (Rhodes); Borowiec et al. (2021) (Rhodes, Kalymnos).

Georeferenced records. Suppl. material 1.

Invaded administrative divisions. South Aegean (1).

Notes. A synanthropic species, collected from only two South Aegean Islands (Kalymnos and Rhodes) within the Dodecanese Archipelago. Despite its expected presence in urban and agricultural sites, a population was collected by Tseng et al. (2019) from a site classified as a natural grassland during the CLC analysis. This site corresponds to an archaeological site in Lindos (Rhodes), which shows that despite reaching more natural habitats the species still exhibits synanthropic behaviour and has not managed to spread to purely undisturbed habitats.

Nylanderia jaegerskioeldi (Mayr, 1904)

Fig. 7

Literature records. Menozzi (1932) (Rhodes); Collingwood (1993) (Karpathos); Borowiec and Salata (2012) (Peloponnese), (2014) (Kefalonia), (2018b) (Euboea), (2018d) (Zakynthos); Salata et al. (2019) (Attica, Crete, Karpathos, Kos, Rhodes); Salata et al. (2020) (Crete).

Georeferenced records. Suppl. material 1.

Invaded administrative divisions. Attica, Central Greece, Crete, Ionian Islands, North Aegean, Peloponnese, South Aegean (7).

Notes. One of the most widespread alien ants in Greece (Table 2; Fig. 7). Its range currently encompasses the Aegean Islands, Southern Greece and the Ionian Archipelago. Most collection sites correspond to urban and agricultural areas (Fig. 2). Nevertheless, two semi-natural areas have been invaded, including a natural grassland in Kefalonia Island (Ionian Archipelago) and sclerophyllous vegetation in Karpathos Island (Aegean Archipelago) (Suppl. material 1). Given its invasion potential further monitoring and studies on impacts are necessary.

Lepisiota syriaca (André, 1881)

Fig. 8

Literature records. Stitz (1928) (Crete); Salata et al. (2019) (Attica, Leros, Telendos).



Figure 6. Habitus of *Paratrechina longicornis* (Latreille, 1802) in lateral view above and its known distribution in Greece below.

Georeferenced records. Suppl. material 1.

Invaded administrative divisions. Attica, Crete, South Aegean (3).

Notes. The alien status of the species in Greece is problematic, while the taxonomic identity of the whole *Lepisiota fraudenfeldi* group is also unclear. Thus, specimens



Figure 7. Habitus of *Nylanderia jaegerskioeldi* (Mayr, 1904) in lateral view above and its known distribution in Greece below.

identified as *Lepisiota* cf. *syriaca* sp. 1 (Borowiec and Salata 2012), were excluded. *Lepisiota syriaca* is regarded as native to the Near East and it is known only from Anatolia in neighbouring Turkey (Kiran and Karaman 2020). Its absence from Aegean Turkey,



Figure 8. Habitus of *Lepisiota syriaca* (André, 1881) in lateral view above and its known distribution in Greece below.

combined with its peridomestic lifestyle in Greece, may suggest its man-mediated introduction to the country. Thus, the species is maintained in the checklist of alien ants of Greece awaiting further investigations.

Myrmicinae

Pheidole indica Mayr, 1879

Fig. 9

Literature records. Forel (1910) (Sporades); Finzi (1939) (Milos); Collingwood (1993) (Chios, Karpathos, Santorini, Zakynthos); Legakis (2011) (Crete, Cyclades, Dodecanese, Eastern Aegean, Ionian Islands); Borowiec and Salata (2012) (Crete, Rhodes), (2013, 2017) (Peloponnese); Salata et al. (2019) (Crete, Naxos, Karpathos, Kos, Rhodes), (2020) (Crete); Borowiec et al. (2021) (Kalymnos, Karpathos, Kos, Patmos, Rhodes, Tilos); Scupola (2021) (Peloponnese).



Figure 9. A Habitus of *Pheidole indica* Mayr, 1879 major and **B** minor worker in lateral view **C** known distribution in Greece.

Georeferenced records. Suppl. material 1.

Invaded administrative divisions. Crete, Ionian Islands, North Aegean, Peloponnese, South Aegean, Thessaly (6).

Notes. A widespread alien ant species collected from Greek islands and coastal areas of the Peloponnese (Fig. 9). It is predicted to occupy most of Southern Greece including Attica and Euboea Island in Central Greece. According to Sarnat et al. (2015), it is not considered to negatively affect native biodiversity or agriculture although its extensive spread and presence in a variety of habitats (Fig. 2; Suppl. material 1) dictates the necessity for further studies to assess its possible adverse impacts.

Strumigenys membranifera (Emery, 1869)

Fig. 10

Literature records. Agosti and Collingwood (1987) (Greece); Salata and Borowiec (2018) (Epirus).

Georeferenced records. None.

Invaded administrative divisions. Epirus (1).

Notes. Only one record from Greece (Arta-Metsovo) confirms the previous literature record of Agosti and Collingwood (1987) (Fig. 10). Further studies regarding its spread and impacts are necessary.

Cardiocondyla mauritanica Forel, 1890

Fig. 11

Literature records. Seifert (2003) (Crete, Paros); Borowiec and Salata (2012) (Crete, Rhodes); Salata et al. (2019) (Crete, Kos), (2020) (Crete); Borowiec et al. (2021) (Kalymnos, Kos, Rhodes).

Georeferenced records. Suppl. material 1.

Invaded administrative divisions. Attica, Crete, Ionian Islands, North Aegean, South Aegean (5).

Notes. Presumably native to Northern Africa, *C. mauritanica* is a xerothermophilous species found both in natural and man-made habitats (Seifert 2003; Wetterer 2014; Carpintero and Reyes-López 2014; Schifani and Alicata 2018; present study). In Greece, it has been collected from artificial, agricultural, semi- and natural habitats including protected areas (Suppl. materials 1, 2), although no negative impacts on native ants have been observed as in Spain, where it is not considered invasive (Carpintero and Reyes-López 2014). Its habitat preferences seem to overlap those of alien invasive *L. humile*, with which it has been found to co-exist (Ward 2005; Gulmahamad 1997; Gómez and Espadaler 2006; Heinze et al. 2006; Wetterer 2014). Wetterer (2012), mentioned that dominant invasive ant species such as *P. megacephala* and *L. humile* may benefit alien *Cardiocondyla* spp. through the exclusion of competing species.



Figure 10. Habitus of *Strumigenys membranifera* (Emery, 1869) in lateral view above [photographed by April Nobile, from www.antweb.org (AntWeb CASENT0173252)] and its known distribution in Greece below.

Cardiocondyla obscurior Wheeler, 1929 Fig. 12

Georeferenced records. Suppl. material 1. Invaded administrative divisions. South Aegean (1).



Figure 11. Habitus of *Cardiocondyla mauritanica* Forel, 1890 in lateral view above and its known distribution in Greece below.

Notes. A cosmopolitan tramp species presumed native to Indomalaya (Wetterer 2015), being known from Egypt and countries of the Levantine coast in the Eastern Mediterranean (Donisthorpe 1930; Mohamed et al. 2001; Seifert 2003; Janicki et al. 2016). A single specimen of this species was collected from a table at a restaurant in the Old Town of Rhodes city (Fig. 12). In Europe, its outdoor locations are strictly restricted to urban sites (Espadaler and Ortiz de Zugasti 2019). *Cardiocondyla obscurior*



Figure 12. Habitus of *Cardiocondyla obscurior* Wheeler, 1929 in lateral view above and its known distribution in Greece below.

is considered an arboreal species nesting in tree cavities and plant structures above ground (Espadaler and Ortiz de Zugasti 2019).

Tetramorium bicarinatum (Nylander, 1846)

Fig. 13

Literature records. Salata et al. (2019, 2020) (Crete). Georeferenced records. Suppl. material 1.



Figure 13. Habitus of *Tetramorium bicarinatum* (Nylander, 1846) in lateral view above and its known distribution in Greece below.

Invaded administrative divisions. Crete (1).

Notes. The species has been collected only once from an urban site on Crete island (Heraklion). A recent citizen-science record from an agricultural area of Chania (Crete),

spotted on iNaturalist (2022) (https://www.inaturalist.org/observations/126973273) reinforces a hypothesis of widespread, established populations on the island in anthropogenic habitats.

Tetramorium immigrans Santschi, 1927

Fig. 14

Literature records. Wagner et al. (2017) (Central Macedonia, Crete, Peloponnese, Samos, Thasos); Borowiec and Salata (2018d) (Zakynthos), (2021a) (Corfu); Salata and Borowiec (2019a) (Corfu, Crete, Central Macedonia, Eastern Macedonia and Thrace, Peloponnese, Rhodes, Thessaly), (2019b) (Zakynthos); Salata et al. (2020) (Crete); Borowiec et al. (2021) (Patmos, Rhodes).

Georeferenced records. Suppl. material 1.

Invaded administrative divisions. Central Greece, Central Macedonia, Crete, Eastern Macedonia and Thrace, Ionian Islands, North Aegean, Peloponnese, South Aegean, Thessaly, Western Greece (10).

Notes. The most widespread alien ant in Greece extending its occurrence in 10 out of 14 Greek administrative divisions (Table 2; Fig. 14) (although its presence throughout the country should be expected). Until recently the taxonomic status of cryptic species within the *Tetramorium caespitum* complex was problematic. Wagner et al. (2017) unveiled the extended spread of this alien species, probably native to Anatolia and Caucasus region, in most of Europe invading not only anthropogenic but also natural habitats. Among its adverse ecological impacts, it can hybridise with the native to Greece *Tetramorium caespitum* (Linnaeus, 1758) (Wagner et al. 2017) and has been recently observed employing soil dropping to compete against native ants in Sicily (Schifani et al. 2022). Nevertheless, its impacts on native biodiversity and human activities have been characterised as mild and its potential "ability to displace native ant species is understudied but questionable" (Moss et al. 2022). Further studies are needed to assess the environmental impacts of this alien ant on native biodiversity given its collection from both man-made and natural habitats (Fig. 2).

Monomorium bicolor Emery, 1887

Fig. 15

Literature records. Menozzi (1928) (Karpathos), (1936) (Alimia, Kalymnos, Karpathos, Kasos, Kos, Rhodes, Telendos); Agosti and Collingwood (1987) (Greece); Collingwood (1993) (Karpathos); Salata et al. (2019) (Crete, Karpathos), (2020) (Crete); Borowiec et al. (2021) (Astypalaia, Karpathos, Ofidousa, Thira).

Georeferenced records. Suppl. material 1.

Invaded administrative divisions. Crete, South Aegean (2).

Notes. Records of Legakis (2011) were excluded upon examination of material and its identification as *M. subopacum* (Salata et al. 2019). The current known distribution of *M. bicolor* includes Crete and South Aegean Islands (Fig. 15). It is a thermophilous, synanthropic species inhabiting arid regions and disturbed habitats, although



Figure 14. Habitus of *Tetramorium immigrans* Santschi, 1927 in lateral view above and its known distribution in Greece below.

many populations have been collected from forest and semi-natural areas particularly scrub and/or herbaceous vegetation associations such as natural grasslands and sclero-phyllous vegetation (Fig. 2).



Figure 15. Habitus of *Monomorium bicolor* Emery, 1887 in lateral view above and its known distribution in Greece below.

Monomorium pharaonis (Linnaeus, 1758) Fig. 16

Literature records. Menozzi (1928) (Rhodes); Bolton (1987) (Central Macedonia, Crete). Georeferenced records. None.



Figure 16. Habitus of *Monomorium pharaonis* (Linnaeus, 1758) in lateral view above and its known distribution in Greece below.

Invaded administrative divisions. Central Macedonia, Crete, South Aegean (3). **Notes.** A synanthropic indoors introduced species. Since Bolton (1987), there is no recent available data on the species distribution in Greece. Further research on its presence, distribution and household impacts is necessary. Citizen-science initiatives looking into ants in buildings and households could potentially help detection and management efforts. Further studies could also investigate the potential occurrence of the cryptic *Monomorium sahlbergi* Emery, 1898 (Boer et al. 2020).

Ponerinae

Hypoponera punctatissima (Roger, 1859)

Fig. 17

Literature records. Agosti and Collingwood (1987) (Greece); Legakis (2011) (Eastern Aegean).

Georeferenced records. Suppl. material 1.

Invaded administrative divisions. Crete, North Aegean (2).

Notes. Native to the Afrotropics, *H. punctatissima* has been deemed as the most accomplished alien ant species due to its worldwide spread (Bolton and Fischer 2011). The species inhabits both urban (gardens, crop fields) and natural habitats such as forests, where it has been collected from rotten wood and topsoil (Bolton and Fischer 2011). In Greece two specimens have been collected from a sandy beach area in Herakleion (Crete) and a deciduous forest in Rethymnon (Crete) (classified as natural grasslands by the CLC analysis in Fig. 2 and Suppl. material 1) (Fig. 17), although further research is needed to assess its distribution and impacts. Further studies could also investigate the potential occurrence of the cryptic *Hypoponera ergatandria* (Forel, 1893) (Seifert 2013).

Species excluded, previously reported as alien to Greece or records designated as dubious

Formicinae

Anoplolepis gracilipes (Smith F., 1857)

Notes. The species has been reported as present in Greece only by Radchenko (2007) in the Fauna Europaea (FE) website. Nevertheless, due to the absence of available material and bibliographic sources the species is not regarded as present in Greece (Salata et al. 2019). Its mention in FE is most probably erroneous as indicated in the case of other ant species in the database such as those indicated by Schifani and Alicata (2018) regarding Sicily.

Nylanderia vividula (Nylander, 1846)

Notes. The species has been reported only once from Rhodes Island (Dodecanese) (Forel 1888), while all European records have been reported from indoor localities (Trager 1984). Additionally, it was reported from Greece before the description of *N. jaegerskioeldi*, a



Figure 17. Habitus of *Hypoponera punctatissima* (Roger, 1859) in lateral view above and its known distribution in Greece below.

tramp species common in outdoors anthropogenic sites in this country. Given the absence of available material for examination we tentatively suggest that *N. vividula* is not present in Greece and Forel's record should be assigned to *N. jaegerskioeldi*.

Myrmicinae

Aphaenogaster splendida (Roger, 1859)

Notes. A recently published review indicated that *Aphaenogaster splendida* is rare in Greece and its known distribution is limited to anthropogenic sites (Salata et al. 2021). Thus, it could also be an introduced species in this region. However, until this case is resolved based on molecular analyses we decided to treat it as native to Greece. According to Schifani (2019) "the definition of its native range remains unclear".

Monomorium monomorium Bolton, 1987

Notes. A widespread species previously reported as alien to Greece (Salata and Borowiec 2018), which has been collected both from urban and natural habitats (Borowiec and Salata 2021b). Its extended distribution in Southern Europe, where the species is believed to be native, suggests that the species could be also native to Greece. Due to the perplexed taxonomy of the *M. monomorium* species group (Bolton 1987), further research is necessary to fully assess its native or alien status in the Mediterranean region.

Monomorium subopacum (Smith, 1858)

Notes. Bolton (1987) assumed that it could be native to the Mediterranean where it is "very widely distributed but appears originally to have been a circum-Mediterranean species which has subsequently been spread by commercial activity". Upon reconsideration, the species should be regarded as native to Greece as considered to other Mediterranean countries (AntWiki 2022).

Pheidole megacephala (Fabricius, 1793)

Notes. Specimens of *P. megacephala* collected from Greece have been deemed erroneous upon re-examination (Sarnat et al. 2015; Salata et al. 2019; Salata and Fisher 2022). A thorough investigation of numerous *Pheidole* specimens at the ZMUA collected from various points around Greece has provided no evidence of the presence of this species.

Solenopsis geminata (Fabricius, 1804)

Notes. The sole record of the species in Greece dates back to 1993 when it was collected from Zakynthos Island in the Ionian Archipelago (Collingwood 1993). Since then, no specimens of this invasive alien species have been collected from the island, despite of additional sampling (Borowiec and Salata 2018d), nor from Greece in general. Due to the high polymorphism evidenced in the worker caste (Wetterer 2011) we hypothesize that records of *S. geminata* are dubious i.e. misidentifications of na-
tive species. Although the severe adverse environmental (competition and elimination of native ant communities from invaded habitats), economic (agricultural pest) and human-health impacts (stinging) associated with the species (Wetterer 2011) necessitate further research into its presence in Greece, we assume that almost thirty years after its initial detection, *S. geminata* should have further spread and its impacts would not go unnoticed. Alternatively, the species may have indeed reached the island of Zakynthos but did not manage to establish. In the absence of examined material from Collingwood's collection and its absence from Zakynthos during more recent collecting events (Borowiec and Salata 2018d), the species is removed from the checklist of alien ants of Greece.

Ponerinae

Hypoponera eduardi (Forel, 1894)

Notes. Although reported as alien to Greece (Salata et al. 2019), *H. eduardi* may indeed be native to the country, as indicated by Bolton and Fischer (2011) by its continuous distribution in the Palaearctic across the Mediterranean. In addition, the species seems to occupy both urban and natural habitats. In the latter, it has been commonly found in well-irrigated and shaded areas, rich in organic matter e.g. deciduous forests and streams (Borowiec and Salata 2017, 2018c, 2021a, 2022; Salata et al. 2019). Thus, we tentatively suggest its removal from the checklist of alien ants inhabiting Greece.

Spread throughout Greek administrative divisions

The number of alien ant species seems to increase from North to South (Fig. 1). Two hypotheses, not mutually exclusive, are suggested. On the one hand, the tropical and subtropical origin of the majority of alien ants (Table 1), may render climatic conditions more optimal in the Southern regions rather than the Northern administrative divisions, with the majority of alien ant species being collected from Southern Greece, especially from the Aegean Archipelago (Fig. 1). Indeed, as evidence shows, the island locations, as well as areas around the Peloponnese, are scoring higher on TDI (Thom's discomfort index), which in essence represents a higher air temperature and higher humidity level envelope (Kambezidis et al. 2021). This seems to be even the trend for the near future based on climate change scenaria assessments (Tzanis et al. 2019). According to our second hypothesis, this can be partly attributed to sampling biases with more myrmecological studies carried out on Greek Islands compared to the mainland. Nevertheless, these observations are in accordance with biogeographic analyses showing that islands are generally more species rich in alien species than the mainland, and that outside tropical regions the number of alien species decreases with latitude (Sax 2001; Pyšek and Richardson 2006). With islands being hotspots of established alien species (Dawson et al. 2017) and given the adverse impacts of biological invasions to island communities (Cole et al. 1992; O'Dowd et al. 2003; Wetterer and Porter 2003;

Abbott 2005; Wetterer et al. 2006; Reaser et al. 2007; Plentovich et al. 2009; Russell et al. 2017; Castro-Cobo et al. 2021) it is important to monitor spatiotemporal patterns of alien species and investigate their possible impacts on endemic island species. Additionally, the alien species richness of administrative divisions such as Attica and Central Macedonia may be significantly underestimated due to reduced collecting effort. After all, the number of established alien species has been shown to increase with GDP per capita, human population density and area (Dawson et al. 2017), with the two administrative divisions accounting for the highest numbers of inhabitants (five and one million, respectively) and GDP per capita. As such, the number of alien ant species in the aforementioned administrative divisions could be higher. However, it is important to add that these parameters cause a steeper rate of increase for alien species richness in the case of islands rather than mainland regions (Dawson et al. 2017).

Alien ants and land-use in Greece

Three quarters of the presented georeferenced records (76%) fall within urban and agricultural sites (Fig. 2). This indicates that alien ants in Greece can be mostly found in degraded, urbanised sites with intense human activity. This does not come as a surprise since the majority of alien terrestrial invertebrates have been found to inhabit human-made habitats, specifically parks and gardens, buildings and houses as well as agricultural and horticultural lands (Lopez-Vaamonde et al. 2010; Pyšek et al. 2010). Similarly, in the case of ants, the majority of recorded alien species has been found to inhabit urban sites (Espadaler and Bernal 2003; Schifani 2019; López-Collar and Cabrero-Sañudo 2021; Rosas-Mejía et al. 2021; present study), with large numbers of alien species collected from points of entry such as airports and ports, agricultural premises (e.g. greenhouses) as well as tourist facilities including botanical gardens and zoos (Boer and Vierbergen 2008; Jucker et al. 2009; Harada et al. 2014, 2016; Gochnour et al. 2019). Such anthropogenic habitats should be intensively surveyed throughout Greece in hopes of detecting novel alien ant species, deciphering their introduction pathways and further supplementing their known distribution. The lack of studies addressing both the socio-economic impacts of alien ants in man-made habitats and their ecological impacts in natural habitats and protected areas, constitute an impediment towards designing management strategies, effectively minimising their spread and mitigating their impacts.

Invasiveness, conservation and future research

Regarding the distribution of individual species (Table 2), the spread of *T. immigrans* and *N. jaegerskioeldi* to most of Greece is worrying given both their observed adverse impacts on native ant biodiversity (Wagner et al. 2017; Salata et al. 2019; Schifani et al. 2022) and occurrence within the NATURA 2000 network (Suppl. material 2). The resilience of protected areas against biological invasions has been recently assessed by Gallardo et al. (2017) and Liu et al. (2020), showing fewer established alien species in protected areas despite their habitat suitability, while generally established populations

of alien species can be found 10-100 km from their boundaries. Overall, nine alien ant species have managed to penetrate 34 NATURA 2000 sites in Greece (Suppl. material 2). Around one third of these sites are situated in Northern Greece (Thessaly, Central Macedonia, and Eastern Macedonia and Thrace = 11 sites), being invaded by *L. neglectus* and *T. immigrans*. The remaining species and further records of *L. neglectus* were collected from protected areas in Southern Greece (Aegean region), where the majority of alien ant species are distributed (Table 1). Although restricted to a few urban areas, *L. humile* also represents a worrying case for the myrmecofauna of Greece and requires further monitoring. A quantitative assessment, including the use of bait traps and structured pitfall sampling, could potentially shed light on their impacts on native ant community assemblages. Such studies could be extended to assess all alien ant species of Greece in both urban and natural sites, including protected areas and their environs.

In addition, citizen-science initiatives could be integrated into the study of alien ants. Despite their small body size and need of expert knowledge for their robust identification, which both constitute impediments to the application of citizen-science approaches (Caley et al. 2020), high-quality photographic material of alien ants such as the presented record of *T. bicarinatum* from Crete or citizen-science records of morphologically discrete species (e.g. *A. gracilipes* and *L. humile*) can supplement the distribution of invasive ant species, especially within urban habitats (Ward 2014; López-Collar and Cabrero-Sañudo 2021; Vásquez-Bolaños and Wetterer 2021). Furthermore, the collection of ant specimens by the public, in the context of organised BioBlitz events or structured citizen-science projects, could further enhance detection efforts, raise public awareness on biological invasions of ants and minimise taxonomic biases (Castracani et al. 2020; Silva-Rocha et al. 2020; Meeus et al. 2021).

Conclusions

In total, 15 alien ant species are currently distributed in Greece (Table 1). Based on historical records, eight additional species have been reported, although their records are deemed dubious or these species have been proved to be native. *Cardiocondyla obscurior* is presented for the first time for Greece. Nevertheless, the presence of widely distributed alien species such as *Trichomyrmex destructor* (Jerdon, 1851) (Wetterer 2009a), *Tapinoma melanocephalum* (Fabricius, 1793) (Wetterer 2009b), as well as the invasive *Brachyponera chinensis* (Emery, 1895) (Menchetti et al. 2022), and *W. auropunctata* gradually spreading throughout the Mediterranean (Vonshak and Ionescu-Hirsch 2009; Vonshak et al. 2009, 2010; Espadaler et al. 2018, 2020; Demetriou et al. 2022), should be further investigated. This updated, commented checklist and analyses aim to provide an overview of the alien ants of Greece in order to enhance any necessary monitoring and strategic planning against invasive alien species, while simultaneously indicating future research needs.

The species richness of alien ants seems to be higher as we move from North to South; alien ants also seem to prefer anthropogenic habitats although some species have managed to penetrate natural and protected areas. Further research is needed to address the adverse environmental and socioeconomic impacts of alien ants in Greece, especially in sensitive island habitats and protected areas.

Dichotomous, online identification tools and educational material for protected areas' officials as well as customs control officers could potentially enhance rapid response and early warning systems, thus preventing new arrivals and further spread of alien ants. Such tools would be particularly important for invasive alien species with the potential to harm native biodiversity, socioeconomic parameters and humanhealth, yet to be found from Greece. For example, *S. geminata, S. invicta* Buren, 1972, *S. richteri* Forel, 1909 and *W. auropunctata*, which have been recently added to the list of invasive alien species of EU concern (EU2022/1203) (Rabitsch 2022a, b). Molecular analyses assessing the genetic diversity of alien ants inhabiting Greece could shed light on their invasion history and introduction pathways.

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Supplementary material I

Georeferenced records of alien ants in Greece

Authors: Jakovos Demetriou, Christos Georgiadis, Evangelos Koutsoukos, Lech Borowiec, Sebastian Salata

Data type: occurences

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Link: https://doi.org/10.3897/neobiota.86.98157.suppl1

Supplementary material 2

Distribution of alien ants in NATURA 2000 sites

Authors: Jakovos Demetriou, Christos Georgiadis, Evangelos Koutsoukos, Lech Borowiec, Sebastian Salata

Data type: occurences

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REVIEW ARTICLE



The use of species traits in invasive seaweed research: a systematic review

Abigail L. Mabey^{1,2}, Marc Rius^{3,4}, Dan A. Smale⁵, Jane A. Catford^{2,6}

I School of Ocean and Earth Science, University of Southampton, National Oceanography Centre, European Way, Southampton, SO14 3ZH, UK 2 Biological Sciences, University of Southampton, Southampton, UK 3 Centre for Advanced Studies of Blanes (CEAB, CSIC), Accés a la Cala Sant Francesc, Blanes, Spain 4 Department of Zoology, Centre for Ecological Genomics and Wildlife Conservation, University of Johannesburg, Auckland Park, 2006, Johannesburg, South Africa 5 Marine Biological Association of the United Kingdom, The Laboratory, Citadel Hill, PL1 2PB, Plymouth, UK 6 Department of Geography, King's College London, Aldwych, WC2B 4BG, London, UK

Corresponding author: Abigail L. Mabey (a.l.mabey@soton.ac.uk)

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Abstract

Species traits have been used extensively in invasion science, providing common metrics across taxa and ecosystems that enable comparisons based on the functional responses and effects of biota. However, most work on traits in invasion science has focused on terrestrial plants, despite the vulnerability of aquatic ecosystems to invasive species, such as invasive seaweeds. Research that focuses on individual species of invasive seaweeds has intensified in recent years, yet few studies have synthesised the information learned on species traits to identify commonalities or knowledge gaps in invasion science. Through a systematic review of 322 papers that investigate the traits of seaweed species from across the globe, here we ask - what are the trends and gaps in research that investigates traits of invasive seaweeds? To address this question, we aimed to: (1) identify publication rates and characteristics of the studies examining traits of invasive seaweeds; (2) clarify which and how many species have been investigated; and (3) assess which traits have been measured and how those traits have been used. Our review revealed that study regions for research on invasive seaweed traits were concentrated in Europe and North America. In addition, we found a total of 158 species that have been investigated, with a large proportion of studies (35%) focusing on just two species, Sargassum muticum and Undaria pinnatifida. Our study revealed that the most researched traits were morphological, which were used to address a wide range of research questions. Key research gaps included relatively few studies from Africa, Asia and South America, a lack of papers researching more than one species and a lack of measurements of biomechanical traits. Altogether, this review provides a

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thorough overview of research progress on species traits of invasive seaweeds and highlights the existing knowledge gaps that may lead to new ways in which the traits of invasive seaweeds can be used to answer important ecological questions.

Keywords

Characteristics, functional traits, macroalgae, non-indigenous, non-native

Introduction

Species traits can be defined as measurable features of an organism that potentially affect performance or fitness and that can be measured at the individual level (Cadotte et al. 2011; Dawson et al. 2021). Traits provide a common metric, comparable across taxa and systems, that allow ecologists to move from taxonomic assessments and comparisons to studies based on functional responses and effects (Funk et al. 2017). Species traits have been widely used across a variety of disciplines, including community ecology, evolutionary biology and biogeography (Díaz and Cabido 2001; McGill et al. 2006; Suding and Goldstein 2008; Violle et al. 2014; Cadotte et al. 2015), within the context of (amongst other objectives) predicting responses to environmental change, understanding ecological processes and predicting species interactions (Matteodo et al. 2013; Funk et al. 2017; Birks 2020; Schleuning et al. 2020). They have become an especially valuable tool in invasion science and biosecurity (Palma et al. 2021a).

Non-native species are those that are transported to areas beyond their native range through accidental or intentional human mediated transport of species (Pimentel et al. 2005; Hewitt et al. 2007; Aguiar and Ferreira 2013). Some of these non-native species may become invasive through dispersing from their point of introduction and increasing their population and range sizes (Blackburn et al. 2011). Species displaying similar behaviour may also be considered invasive even within their own native range (Valéry et al. 2009). Invasive species have been recognised as one of the leading causes of biodiversity loss and can have significant economic impacts (IPBES 2019; Zenni et al. 2021). Identifying traits common to invasive species has proven to be a useful tool to prevent the intentional introduction of species that may become problematic, for example, via the Weed Risk assessment in Australia (Pheloung et al. 1999) or to predict which non-native species should be prioritised for monitoring and management (Grewell et al. 2016). Whilst the use of traits to predict invasive species began with terrestrial plants (Baker 1965), it has been increasingly applied to other taxa and ecosystems (Nyberg and Wallentinus 2005; Jarošík et al. 2015; McKnight et al. 2017; Dalla Vecchia et al. 2020; Tobias et al. 2022). Indeed, a systematic review undertaken by Dalla Vecchia et al. (2020) on functional traits in aquatic plants found an increasing trend in the number of published papers investigating functional traits of macrophytes over time, with invasiveness being the third most investigated topic.

Seaweeds (i.e. marine macroalgae) are important primary producers broadly distributed across the ocean biome and have significant ecological, economic and cultural value (Smit 2004; Delaney et al. 2016; Nurjanah et al. 2016; Mouritsen et al. 2018). Often through human activity, such as aquaculture (Naylor et al. 2001), seaweeds have been transported outside of their native range and have subsequently become established in recipient ecosystems across the globe (Langar et al. 2002; Chandrasekaran et al. 2008; Nejrup and Pedersen 2010; Primo et al. 2010; Lapointe and Bedford 2011; Vasconcelos et al. 2011). The rate of marine introductions is expected to rise in future, due to expanding global shipping (Seebens et al. 2016; Sardain et al. 2019), increases in invasive species rafting on plastics and anthropogenic debris (Carlton et al. 2017), continued rapid expansion of aquaculture (Ahmed and Thompson 2019) and ocean warming facilitating the spread of invasive species (Bellard et al. 2013; McKnight et al. 2021). Despite this, seaweeds are generally under-researched relative to terrestrial plants (Lowry et al. 2013). More information on the processes and mechanisms underpinning seaweed invasiveness is needed to prevent and monitor current and future seaweed invasions.

One of the largest investigations of traits of invasive seaweeds was carried out by Nyberg and Wallentinus (2005), who examined 13 categorical traits of 113 invasive and non-native seaweed species in Europe. Nyberg and Wallentinus (2005) successfully used these traits to predict which species were most likely to become invasive, finding commonalities amongst them, such as tolerance to pollutants and a high likelihood of transportation. The continued increase in research investigating traits of invasive seaweeds, combined with the growing availability of seaweed trait data shared via databases (Mauffrey et al. 2020; Vranken et al. 2022), suggests that there is great potential for the use of seaweed traits to address ecological questions. Therefore, it is timely to undertake a detailed review of the ways in which traits have been used to investigate invasive seaweeds, to identify trends and gaps and to help prioritise future research efforts.

Here, we present a global review of papers that investigate traits of invasive seaweeds. To the best of our knowledge, this is the first systematic review that examines the use of traits in invasive seaweed research. Using a systematic and reproducible methodology (based upon the principles outlined in Moher et al. (2009)), we screened the scientific literature to find relevant papers to address the research question 'what are the trends and gaps in research that investigates traits of invasive seaweeds'? Our study had three main aims: (1) to identify the rate of publications and characteristics of the studies examining the traits of invasive seaweeds, (2) to clarify which and how many species have been investigated and (3) to assess which traits have been measured and how they have been used. This systematic review aims to provide an overview of this subject. This will include providing insights into how rapidly this field is expanding, what species are being investigated the most and which traits are being studied. We conclude by highlighting research gaps and providing recommendations for further work.

Methodology

The databases Web of Science (Core Collection and BIOSIS Citation Index), Scopus and EBSCO*host* Greenfile were searched for records on 21 January 2021 using the following search string:

(trait* OR character* OR growth* OR life* OR phenotyp* OR morpholo* OR attribute*) AND

(invas* OR nonnative* OR native* OR nonindigenous* OR indigenous* OR alien* OR casual* OR exotic* OR foreign* OR naturali* OR introduc* OR allochthonous*)

AND

(seaweed* OR macroalga* OR alga* OR chlorophyta* OR rhodophyta* OR phaeophyceae* OR hydrophyt* OR macrophyt*)

Search results were selected to include articles only and to include results from the maximum number of years possible for each database (Web of Science: 1950–2021, Scopus: All years to present and EBSCO*host* Greenfile: 1973–2021). Irrelevant categories were removed from the Web of Science search (Suppl. material 1: table S1) and, in total, 19,954 records were downloaded from all three databases (Suppl. material 1: fig. S1). Duplicates were removed using the duplicated() function (R Core Team 2021), leaving 15,001 original records.

All of these records were screened by title using the R package 'metagear' (Lajeunesse 2016). Titles were accepted if they mentioned a seaweed, an unspecified invasive or non-native species (or a synonym of) or an unspecified aquatic macrophyte or hydrophyte. From this, 3,067 records were accepted and were screened by abstract (also using the R package 'metagear') and were included where the abstract referenced an invasive or non-native (or a synonym of) seaweed or an unspecified invasive or nonnative species. Records which did not include abstracts were automatically accepted to be screened by full paper. A total of 1,272 records were accepted and searched by full paper and were included in the final review if they measured traits of an invasive or non-native seaweed. Papers that recorded morphological measurements purely for taxonomic classifications or as first records of species in a new area were not included, as characteristics were chosen for taxonomic reasons, not ecological ones. Review papers were only included if they described how the papers were selected, to ensure that the traits included were representative and chosen systematically. Whilst this will have resulted in some apparent duplicates, we are interested in how traits are used to answer questions, so where the same traits may be used to answer different questions is within the scope of this systematic review. At each stage of screening, records were only accepted if they were published in English. This resulted in 322 papers being included in the analysis (Suppl. material 1: fig. S1).

For each paper included in this review, 15 categories were used to collect data, similar to those adopted by Dalla Vecchia et al. (2020) in a systematic review of the use of functional traits in macrophyte studies. Each category contributed to the three

main aims of the systematic review. The first aim (1) to identify the rate of publications and characteristics of the studies examining traits of invasive seaweeds, was investigated by collecting the year and journal of publication, the geographic area of first author, the geographic area of study, the method of data collection, the type of study and the habitat from which the invasive species were collected. The second aim (2) to clarify which and how many species have been investigated was met by collecting data on the taxonomic classification of the invasive species, the name of the invasive species, whether a criteria for invasiveness was included, the number of invasive species in the study and whether the study included a comparison to a baseline [a native species or native population of the invasive species – see van Kleunen et al. (2010)]. Finally, to investigate the third aim (3) to assess which traits have been measured and how they have been used, we recorded the trait category, the environmental variables measured and the main aim of each individual study.

The geographic area of first author was recorded as the country or countries of the associated institutions of the first author. Each country was sorted by continent for ease of comparison and analysis. The geographic area of study was recorded as the continent from where the population of the invasive species was collected. When the geographic area of study was greater than a single continent, the reported larger geographic area was recorded instead (e.g. global or Northern Hemisphere). Multiple geographic areas were recorded for both first author location and the geographic area of study, but this was more common for the latter group.

The method of data collection recorded whether traits were measured from individuals grown under natural conditions (observational) or from individuals grown under manipulated conditions (experimental). The type of study recorded whether the data were collected from species grown in the field or the laboratory or whether the study was a review or modelling paper. The habitat type was recorded as the environment from which the invasive species was collected. Artificial included anthropogenic habitats, such as harbours or breakwaters. Rocky habitats included any natural rocky substrata, including reefs and rocky shores. Sandy/sedimentary habitats included beaches, estuaries and lagoons. Vegetated habitats included seagrass meadows, marshes and algal mats. Any habitats not included in the previous categories were recorded as other and studies which did not record any habitat were included as unknown.

The taxonomic classification of the invasive species was recorded, either as Phaeophyceae, Chlorophyta or Rhodophyta following the classification found in the World Register of Marine Species (Ahyong et al. 2023). The name of the invasive species in the study was recorded and to ensure that the current taxonomic name was included in this review, all species names were checked on AlgaeBase (Guiry and Guiry 2022) and the currently-accepted name was used. The way in which a species is classified as invasive has been proven to affect which traits are determined as important (Palma et al. 2021b). To investigate whether studies accounted for this, we recorded if criteria for invasiveness were noted in the paper and, if so, what criteria were used. We found that the criteria used in the studies corresponded with the four demographic dimensions of invasiveness, which were previously identified by Catford et al. (2016). These were local abundance, geographic range size, environmental range size and spread rate, which can be combined to give 15 forms of invasiveness. We accordingly recorded what combination of the four demographic dimensions each study used. The number of invasive species in the study was recorded and, for ease of analysis, were grouped into three categories, either one species, between two and five species or more than six species. Whether the study included a baseline was recorded as yes if the study also measured traits from either native species or native populations of the invasive species. We chose to note this aspect of a study because some studies may just examine traits of invasive species in isolation, whereas others have used comparisons between invasive species and native species (here referred to as a baseline) to investigate whether invasive species have different traits from those of non-invasive species (van Kleunen et al. 2010).

For ease of analysis and comparisons, trait categories were used to group measured traits into seven comparable groups. Morphology included measures of size or branching diameter. Biochemical included the elemental composition of tissues. Productivity included fresh and dry weight and measures of growth rate. Physiology included physiological processes, such as photosynthesis, nutrient uptake rates, respiration and pigment content. Biomechanics measured mechanical strength and related features. Reproduction included traits related to reproduction and dispersal. Other included any traits not covered by the previous categories.

The environmental variables measured alongside traits were grouped into ten categories. Water included physical or chemical measures of the water column, including temperature, salinity or nutrient content. Sediment/substrate included differences or characteristics of the sediments or substrate. Climate included meteorological variables, such as air temperature. Anthropogenic included environmental conditions caused by human activities, such as nutrient pollution, climate change or control methods. Depth/light included measures of the depth in the water column and variations in light. Hydrology/topology included information on the hydrological regime, often through differences amongst sites. Biotic included interactions or changes of the natural community, including measures of natural enemies, biotic resistance or microbial communities. Season/time included studies which measured how traits changed over time, including both short time-periods (days) or long time-periods (months or years). None is where no environmental variables were measured and other included any environmental variables not included in the categories above.

Finally, the main aim of the paper was recorded to characterise the purpose of the research and, therefore, the reason for measuring traits. Environmental gradients measured how traits varied along environmental gradients, often to investigate the invasive potential of species in different environmental conditions. Competition included papers that measured how traits related to competition, which may have been inter- or intra-specific. Natural enemies measured how traits related to herbivores or pathogens. Anthropogenic investigated the effects of human-induced pressures such as pollution, climate change or management. Impact investigated the effects of invasive species on the surrounding community. Invasive process included papers that investigated how traits changed with the invasive process, such as propagule pressure or differences between native and invasive populations. Other included any main aims that were not included in the previous categories. Several papers had more than one main aim, but no paper had more than two. The bar charts and chord diagrams were created in RStudio using R 4.1.2, using packages 'ggplot2' and 'Rcolorbrewer' for the bar charts (Neuwirth 2014; Wickham 2016, respectively) and 'circlize' for the chord diagrams (Gu et al. 2014).

Given our focus on trends in literature, we re-ran the search on 6 November 2022 in Web of Science and EBSCO*host* Greenfile to estimate how many new papers may have been excluded from our systematic review. Since our initial search date of 21 January 2021, we estimate that approximately 31 additional papers could be included if we had used a November 2022 search date. This accounts for < 10% of the 322 papers used in our review and is, thus, not expected to significantly change the results presented here (Suppl. material 1: appendix 1).

Data availability

All data generated or analysed during this study are included in this published article and its Suppl. materials 1, 2.

Results

(1) To identify the rate of publications and characteristics of the studies examining traits of invasive seaweeds

The first paper investigating traits of invasive seaweeds found in this review was published in 1975 in the journal Botanica Marina. Since then, the number of papers investigating this research area has risen, as 39% of the 322 papers included in this review were published between 2014 and 2021. This reflects trends in the wider literature, as the number of publications that mention ecology, invasive species and traits in the title, abstract or keywords has also increased since 1985 (Fig. 1a; Suppl. material 1: appendix 2, fig. S2a). The papers included in this review were published in a wide range of journals (Suppl. material 1: table S2), with the journal Botanica Marina being the most common (35% of papers in this review) (Fig. 1b; Suppl. material 1: fig. S2b).

First authors were mostly based in Europe (54% of papers), followed by North America (23%). Africa (2%) and Asia (2%) had the lowest number of first author affiliations. The geographic study area followed a similar trend, with the majority of studies sampling European and North American populations (57% and 25%, respectively), with Africa and Asia being the least studied (2% and 2%) (Fig. 2a). Of the study type, many studies investigated seaweeds grown in the field (56% of all papers). Most field studies were observational (grown in unmanipulated conditions) (80% of field studies, 45% of all papers), whereas experimental studies largely took place in laboratory conditions (94% of laboratory studies, 26% of all papers) and fewer papers combined



Figure 1. a The proportion of invasion science papers published on species traits (see Suppl. material 1: appendix 2) over time, alongside the number of papers that met the criteria to be included in this review and **b** stacked bars showing the proportion of papers included in this review published over time, showing the five most common journals where the papers were published.



Figure 2. The **a** geographic area of first author affiliation and the study area (where the invasive species were sampled from) (two papers had a global study area and two had a study area of the Northern Hemisphere which are not shown). Multiple geographic areas were recorded for both first author and study locations, but more so for the latter. The number of papers which **b** used field, lab, review or modelling to collect data or draw conclusions, with the structure of the study shown in stacked bars (Exp. = experimental, Obs. = Observational, N/A = study did not include experiments or observational data) and **c** the habitat type from where the invasive species were collected.

lab and field studies (12% of all papers) (Fig. 2b). Whilst many papers did not record the habitat type from where seaweed samples were collected (n = 111, 34%), for those which did, the majority were taken from rocky habitats (31%) (Fig. 2c).

(2) To clarify which and how many species have been investigated

The 322 papers included in this review measured traits of 158 seaweed species. Of these, the most investigated taxonomic classification was Rhodophyta (65% of all species) and Chlorophyta was the least studied (11%) (Fig. 3a), following broader trends in both the number of orders and the proportion of orders that include a non-native species (Schaffelke et al. 2006) (Fig. 3c). However, the most investigated seaweed species (*Sargassum muticum* and *Undaria pinnatifida*) both belong to the Phaeophyceae (Fig. 3b). Eight papers (2%) included species classified as invasive within their native range.





Figure 3. The number of **a** invasive species in each taxonomic group investigated across all papers in this review [two papers each investigated one charophyte species, (see Nyberg and Wallentinus (2005); Sahlin et al. (2011)) which are not shown], **b** the number of papers that investigated the ten most studied invasive species found in this review and **c** the total number of orders for each taxonomic group and the number of orders which contain non-native species with data taken from Schaffelke et al. (2006). Drawings are courtesy of Tracey Saxby and the Integration and Application Network (ian.umces.edu/symbols/).

15 forms of invasiveness

Combinations of the four dimensions of invasiveness



Figure 4. Proportion of 322 trait-based studies that classify invasive seaweed species into 15 forms of invasiveness, based on the dimensions of invasiveness (local abundance, geographic range size, environmental range size and spread rate) and their combinations, as described in Catford et al. (2016). The black portion of each pie chart indicates the proportion of the 322 studies that explicitly used the corresponding criteria to classify the species as invasive, as represented by the letters (where *G* = geographic range size, *E* = environmental range size, *A* = local abundance and *S* = maximum spread rate). For example, *EGS* indicates that the dimensions' environmental range size, geographic range size and maximum spread rate were explicitly used as criteria for invasiveness. None represents studies in which none of the four dimensions of invasiveness were explicitly used as criteria for invasiveness. Figure modified from Catford et al. (2016).

All 15 forms of invasiveness were represented amongst the 322 studies, i.e. all possible combinations of the four demographic dimensions were used to define invasive species, with geographic range size (15%) and spread rate (10%) being the most frequently used criteria (Fig. 4). However, 20% of papers did not describe the criteria used for classifying species as invasive.

We found that the majority of papers did not include comparisons to a baseline of native species or populations (61% of all papers), suggesting that they are not



Figure 5. The number of papers which **a** compared the invasive species to a baseline (either a native species or a native population of the invasive species) and the number of papers which **b** studied one, two-five or more than six invasive species within the same paper. Stacked bars show the years of publication.

investigating differences between invasive species and native species or populations of the invasive species in its home (native) and invaded (non-native) range (Fig. 5a). Papers published between 1975 and 1983 did not compare the invasive species to a baseline (either a native species or a native population of the invasive species) (Suppl. material 1: fig. S3a). Most papers investigated one invasive species (91%) and 1% investigated more than six (Fig. 5b). All papers published between 1975 and 1983 included in this systematic review investigated a single invasive species (Suppl. material 1: fig. S3b).

(3) To assess which traits have been measured and how they have been used

Morphological traits were the most investigated (49% of all papers), followed by productivity (42%), reproduction (30%) and biochemical (29%) traits (Fig. 6a). Biomechanical traits were the least investigated (3%). The most measured environmental variables related to season/time (39%) and physical and chemical parameters of the water column (33%). Depth/light, hydrology/topology and biotic environmental variables were also regularly investigated (24%, 19% and 22%, respectively) (Fig. 6b). Environmental gradients were the primary main aim investigated by a large margin (31%). Papers which investigated environmental gradients were published in all five time-frames (from 1975 to 2021) (Suppl. material 1: fig. S4c). Commercial application was the least investigated (8%); however, most of these studies were published between 2014 and 2021 (Fig. 6c). Regarding the purpose of the research and, therefore, the reason for measuring traits, the majority of papers investigated one main aim (83%) (Suppl. material 1: fig. S5).

There were no clear trends in which traits were used to investigate certain environmental variables (Fig. 7a) or certain main aims (Fig. 7b). In general, nearly all trait categories were used to investigate all other aims, except for commercial application, which was exclusively investigated using biochemical traits.



Figure 6. Number of papers which measured **a** categories of traits and **b** environmental variables to reach the **c** main aims of the paper, out of a possible 322 papers.



Figure 7. The proportion of papers in which trait categories were investigated **a** alongside environmental variables or **b** how the traits have been used. For clarity, links with less than five connections are not shown in this figure.

Discussion

In this systematic review of 322 papers, we identified several key trends in how studies have investigated traits of invasive seaweeds. These included an increase in publications over time (although this increase did not exceed the background publication rate) and a higher research effort in Europe and North America. We also found a research focus on two brown seaweeds, *Sargassum muticum* and *Undaria pinnatifida*. Finally, morphological and productivity traits were the most investigated and biomechanical traits the least. These results have addressed the three aims of this review, as explained below.

(1) To identify the rate of publications and characteristics of the studies examining traits of invasive seaweeds

The increase of publications over time is in keeping with wider trends in the invasion science literature (Rius et al. 2015), where more papers are being published in ecology generally and for the specific subjects of both traits and invasive species (including when they are considered separately) (McCallen et al. 2019; Anderson et al. 2021). We find that, over time, papers included in this review made up a smaller proportion of the invasion science trait literature (Fig. 1a). The increasing number of papers suggests that traits of invasive seaweeds will continue to be used to answer ecological questions in marine ecosystems; however, we do not find evidence that this increase in publications over time exceeds the background publication rate.

The papers included in this systematic review were published in a wide range of journals, but the five journals in which these were most frequently published were Botanica Marina, Marine Ecology Progress Series, Journal of Experimental Marine Biology and Ecology, Marine Ecology and Biological Invasions. Although papers in these journals investigated an invasive species, only one of these top-5 journals specifically focuses on invasion science. This indicates that, for the topic of invasive seaweed traits, a large body of work may be associated with marine biology and ecology topics, rather than exclusively invasion science.

The most studied geographic areas were in Europe, North America and Oceania, with Africa and Asia being extremely under-represented in the papers included in this review. A similar geographical bias was also apparent in the greater research output in Europe and North America which has also been noted in conservation and invasion science literature previously (Pyšek et al. 2006; Lowry et al. 2013; Di Marco et al. 2017; Watkins et al. 2021). This pattern is also reflected in the location of the first author's affiliation, with the majority located within Europe and North America. This consistent trend may reflect the greater amount of funding available, number of researchers and policy-makers' priorities in these areas, amongst other factors, including language. Papers in this review were only included if they were in published English. This may have influenced the geographic distribution observed particularly for under-represented regions, as studies from those regions may have been published in languages other than English and, therefore, be excluded from our review. Based on our search terms, only 3% of the records screened by full paper were excluded because

they were not written in English, so we do not expect the results to be substantially affected. However, a recent study that explicitly examined the effect of language choice on invasive species research findings showed that 83% of documents that met particular search criteria were published in English and 17% were published in one of 15 other languages (Angulo et al. 2021). It is, thus, important to acknowledge that this systematic review and the conclusions drawn from it, are based on English-language publications only.

(2) To clarify which and how many species have been investigated

Species belonging to Rhodophyta were the most researched, which was to be expected given that this group contains both the highest number of species and the highest proportion of non-native orders (compared to Phaeophyceae and Chlorophyta) (Schaffelke et al. 2006; Guiry 2012) (Fig. 3c). Despite this, the most investigated species were not Rhodophyta, but were Phaeophyceae, specifically the fucoid Sargassum muticum and the kelp Undaria pinnatifida. These species may have been investigated more because they are widespread invaders (Engelen et al. 2015; Epstein and Smale 2017), are of commercial interest (Yamanaka and Akiyama 1993; Silva et al. 2019), their individuals are relatively large in size and they can become abundant and drive ecological change in native communities (Harries et al. 2007; Salvaterra et al. 2013; Heiser et al. 2014; McLaughlan et al. 2014; Epstein et al. 2019). Therefore, these species may be more likely to be noticed, may be easier to collect and measure for functional traits and, therefore, be prioritised for research. In contrast, invasive species that are undetected or are misidentified as a native species or another invasive species [known as cryptic invaders (Morais and Reichard 2018)] are less-well researched. Some of the least investigated species in this review included known cryptic invaders, such as Polysiphonia morrowii (Geoffroy et al. 2012) and Ulva ohnoi (Flagella et al. 2010). Advances in technology have made genetic analysis more frequent in ecological studies (Diepeveen and Salzburger 2012; Anderson et al. 2021), which can be used to identify cryptic species, potentially making it easier to identify and study them.

Most papers investigated only one invasive species (Fig. 5b), likely due to limitations in the logistics of collecting trait data from many species, especially where experimental conditions need to be maintained. The increasing availability of trait databases may facilitate trait-based studies across more species, between invasive species and native species and invasive species and their native populations. Trait databases are currently dominated by terrestrial plants (Kleyer et al. 2008; Paula et al. 2009; Fraser 2020), but databases for seaweed species are increasing, including the recentlypublished dataset of 12 traits across 95 species in the UK (Mauffrey et al. 2020) and a larger pan-European database of 21 traits spanning 1745 species (Vranken et al. 2022). Whilst these datasets are not specific to invasive seaweeds, the availability of seaweed trait data may facilitate studies across a wider number of species, including invasive species and their native populations.

Many papers did not explicitly provide criteria for why species were considered invasive and papers often used non-native and invasive as interchangeable terms. Given the wide remit of invasion science research, it is not practical that a single universal definition of invasiveness could be used across all papers and, indeed, would be impractical and inappropriate to do so across different taxa. However, going forward, it is vital that papers explicitly state the criteria they use to define a species as invasive or non-native. This transparency would facilitate appropriate comparisons across taxa (Catford et al. 2016; Fristoe et al. 2021; Palma et al. 2021b). We, therefore, recommend that papers investigating invasive species provide clear definitions of why a species is considered invasive (such as high abundance or fast spread rate). If the species is not considered invasive, then authors should clarify that the species is at an earlier stage of the invasion process and refer to it as non-invasive (or a synonym of). Explicit use of clear definitions will enable more meaningful and appropriate comparisons across studies, thus helping to reduce the prevalence of apparent context dependence that can stem from comparing studies that differ in methodological approach, including study metrics (Catford et al. 2022).

(3) To assess which traits have been measured and how they have been used

The most measured traits were those relating to morphology and productivity. These are often referred to as 'soft traits', as they are relatively easy to measure, can be measured *in situ* and are generally inexpensive as they do not require specialist equipment and are useful for measuring traits from a large number of species or over a long period of time (Hodgson et al. 1999; Cornelissen et al. 2003). However, soft traits do not generally provide a direct mechanistic link with a species' ecology or ecophysiology, but are usually correlated with and, thus, broadly indicative of, hard traits [traits which capture a precise function (Belluau and Shipley 2018)]. Consequently, soft traits are often correlated with multiple aspects of a species' life history (Lavorel and Garnier 2002; Westoby et al. 2002) and can provide less predictive power than more expensive-to-measure hard traits (Belluau and Shipley 2018).

Both morphological and productivity trait categories were measured in papers that also recorded changes over seasons and years. These temporal studies addressed a range of aims, including how changes in traits over time affected the impact of an invasive seaweed on the native community (Veiga et al. 2014; Najdek et al. 2020), whether the season affected the invasive potential of a seaweed under climate change scenarios (Atkinson et al. 2020) and reproductive phenology to predict future range shifts (Chefaoui et al. 2019). Dalla Vecchia et al. (2020) also found that both morphological and productivity trait categories were the most studied for freshwater and marine aquatic plants, suggesting that these trait categories are easily applicable across taxa.

Despite the importance of biomechanical traits in determining the hydrodynamic conditions in which seaweeds can survive (Demes et al. 2013), very few papers examined these traits. Of those that did, biomechanical traits were linked to differences

in ploidy (Lees et al. 2018), dispersal potential (Watanabe et al. 2009; Oróstica et al. 2012) and recruitment to different sediments (Scheibling and Melady 2008). This represents a clear knowledge gap and further research examining these traits is needed.

The most researched main aim related to environmental gradients, where the study investigated environmental variables (such as light, nutrient availability and temperature) and measured how traits changed along these gradients. All trait categories were used in papers that investigated environmental gradients and were used for a variety of purposes, including investigating the realised niches of species (Koerich et al. 2020) and how this changed throughout the invasion process (Sotka et al. 2018), potential ranges of invasive species (Desmond et al. 2019) and conditions required for bloom formation (Bermejo et al. 2020). Measuring how traits vary along environmental gradients may investigate how invasive species adapt to novel environmental conditions (Weinberger et al. 2008) or phenotypic plasticity (Zanolla et al. 2015). Understanding relationships between species traits and environmental gradients is clearly a key research objective. Overall, each trait group was used to measure all the main aim categories and were measured alongside all the environmental variables. The only exception was the main aim of commercial application, which was exclusively investigated using biochemical traits, such as identifying bioactive compounds for use in biofouling materials (Pinteus et al. 2020, 2021). The broad application to different aims reflects the benefit of a trait-based approach and how these measurements can be applied to a wide range of questions.

In recent years (2014–2021), most papers focused on examining seaweed traits related to anthropogenic pressures and commercial applications. This suggests that there is increasing interest in researching how invasive species respond to human-induced stressors, such as climate change and pollution, for which previous studies have shown a link (Lapointe and Bedford 2011; Dijkstra et al. 2019). This trend may also be due to the use of non-native species to fulfil anthropogenic needs. For example, the invasive species S. muticum has been identified as having several commercial uses, including agricultural applications (e.g. fertiliser) or in a pharmaceutical capacity using bioactive compounds isolated from the seaweed (Milledge et al. 2016). Both of these commercial applications were found as main aims for the papers within our review (Balboa et al. 2016; Sanjeewa et al. 2019; Thompson et al. 2020). We also found papers that focused on the use of invasive seaweed compounds in cosmetics and anti-fouling (Félix et al. 2020; Flórez-Fernández et al. 2021; Pinteus et al. 2021). This reflects the wide range of commercial uses to which seaweeds can be applied and may be of use for managing invasive seaweeds (Milledge et al. 2016). As pressures such as climate change, pollution and habitat degradation increase, these research areas may become more important to understand the relationships between anthropogenic pressures and invasive seaweeds and their potential uses in industry.

Concluding remarks and future directions

The use of traits to investigate invasive seaweeds is a growing research area and this trend is likely to continue given the expected increase in the rate of marine introductions. By quantifying the methods, species and aims used in investigations of traits of invasive seaweeds, we provided an overview of the main trends in this review. Through this, we have identified several research gaps and so propose these recommendations for future research:

i) More research is urgently required in under-studied regions, especially Africa, Asia and South America. It will be impossible to understand how global scale stressors (i.e. increased shipping, climate change) will mediate seaweed invasions without information from these areas.

ii) The terms non-native and invasive should not be used interchangeably and explicit definitions and criteria should be included in the paper where species are considered invasive. This will be more challenging for species that have not been researched extensively, but providing a definition of invasiveness will still help maintain consistency across papers and, therefore, facilitate meaningful inter-study comparisons (Catford et al. 2022).

iii) One of the benefits of a trait-based approach is that comparisons can be made across species and functional groups. However, most of the 322 papers investigated only one invasive species and did not compare it to a native species or with the same species in its native range. Whilst it can be more time intensive and expensive to measure traits from multiple species, doing so will facilitate the general conclusions that can be drawn from trait studies. Additionally, investigating a broader range of species will also facilitate these comparisons, as there is currently a strong research bias towards only a few species (e.g. *S. muticum* and *U. pinnatifida*).

iv) Morphological and productivity trait categories are used to investigate a range of aims. In contrast, biomechanical traits are understudied, even though the ability of seaweeds to physically withstand hydrodynamic forces is an important driver of survival and distribution. The reason for this research gap is unclear, but we recommend that these traits are prioritised for future research as they may be important attributes which influence species distributions.

This systematic review provided an overview of the ways in which traits are used to investigate invasive seaweeds. As pressures on the environment continue to increase, using a functional approach to understand invasiveness of seaweeds will allow for generalisations across taxa and ecosystems, which will be useful for conservation and policy decisions. By providing a concise summary of the research so far, this review has identified knowledge gaps and future research directions for invasive seaweed research.

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Supplementary material I

Supplementary information

Authors: Abigail L. Mabey, Marc Rius, Dan A. Smale, Jane A. Catford Data type: NA (PDF file)

Explanation note: Supplementary information referenced throughout the paper.

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Link: https://doi.org/10.3897/neobiota.86.97392.suppl1

Supplementary material 2

Associated data

Authors: Abigail L. Mabey, Marc Rius, Dan A. Smale, Jane A. Catford

Data type: Categorical data collected from published papers (excel document)

- Explanation note: Data collected from 322 papers included in this review, and the relevant bibliographic information.
- 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 freedom for others, provided that the original source and author(s) are credited.

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R PACKAGE



lydemapr: an R package to track the spread of the invasive spotted lanternfly (Lycorma delicatula, White 1845) (Hemiptera, Fulgoridae) in the United States

Sebastiano De Bona¹, Lawrence Barringer², Paul Kurtz³, Jay Losiewicz⁴, Gregory R. Parra⁵, Matthew R. Helmus¹

Integrative Ecology Lab, Center for Biodiversity, Department of Biology, Temple University, 1925 N 12 Street, Philadelphia, PA, USA 2 Pennsylvania Department of Agriculture, Entomology Department, Bureau of Plant Industry, 2301 N Cameron Street, Harrisburg PA 17110, USA 3 New Jersey Department of Agriculture, Division of Plant Industry, PO Box 330, Trenton, NJ 08625, USA 4 Pennsylvania Department of Agriculture, Communications Office, 2301 N Cameron Street, Harrisburg PA 17110, USA 5 USDA APHIS PPQ Science and Technology, 920 Main Campus Drive, Raleigh, NC 27606, USA

Corresponding author: Sebastiano De Bona (sebastiano.debona@gmail.com)

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Abstract

A crucial asset in the management of invasive species is the open-access sharing of data on the range of invaders and the progression of their spread. Such data should be current, comprehensive, consistent and standardised, to support reproducible and comparable forecasting efforts amongst multiple researchers and managers. Here, we present the lydemapr R package containing spatiotemporal data and mapping functions to visualise the current spread of the spotted lanternfly (Lycorma delicatula, White 1841) in the Western Hemisphere. The spotted lanternfly is a forest and agricultural pest in the eastern Mid-Atlantic Region of the U.S., where it was first discovered in 2014. As of 2023, it has been found in 14 states according to State and Federal Departments of Agriculture. However, the lack of easily accessible, finescale data on its spread hampers research and management efforts. We obtained multiple memorandaof-understanding from several agencies and citizen-science projects, gaining access to their internal data on spotted lanternfly point observations. We then cleaned, harmonised, anonymised and combined the individual data sources into a single comprehensive dataset. The resulting dataset contains spatial data gridded at the 1 km² resolution, with yearly information on the presence/absence of spotted lanternflies, establishment status and population density across 658,390 observations. The lydemapr package will aid researchers, managers and the public in their understanding, modelling and managing of the spread of this invasive pest.

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Keywords

Biological invasions, crop pest, data science, forecasting, *Lycorma delicatula*, management, open access data, reproducibility, spread modelling

Introduction

Due to the globalisation of trade and the homogenisation of urban and suburban habitats, the accidental introduction and establishment of invasive species is ever more likely (Hulme 2009). When establishment goes undetected and eradication becomes less viable, the goal should be to mitigate the negative effects generated by invasive species (Diagne et al. 2020; Fantle-Lepczyk et al. 2022; Leroy et al. 2022). In doing so, one of the main challenges is tracking the spread of established invasive alien species so that control measures to slow spread, reduce impact and conserve biodiversity can be effectively enacted (Robertson et al. 2020). High quality data on past and present spread of invasives are key to model invasive spread accurately enough to provide robust forecasts on which to base management decisions.

A multitude of modelling techniques to forecast spread is available to researchers (Fisher 1937; Skellam 1951; Higgins and Richardson 1996; Kot et al. 1996; Neubert et al. 2000; Travis and Dytham 2002; Clark et al. 2003; Jongejans et al. 2011; Rodrigues and Johnstone 2014; Hudgins et al. 2017). Despite different assumptions and approaches to the modelling itself, fitting and validating models rely on longitudinal, spatially-explicit data on the occurrence or density of the spreading invasive species. Different models need to be built upon the same standardised data for comparisons between models to reflect genuine differences in model assumptions (e.g. Norberg et al. 2019). Comparing models with standardised data highlights which biological aspects of spread coded in each model are crucial to manage (Sakai et al. 2001). In addition, building models on the same data provides a more solid ground to combine them into ensemble models, which offer a higher degree of reliability compared to a single model (Araújo and New 2007). However, there are three hurdles that must be overcome before such standardised data for modelling be made available.

The first hurdle that must be overcome when developing a standardised dataset on invasive spread is to develop relationships with the agencies, institutions and citizen-science projects collecting data on the invasive of interest. For pests with negative impact on agricultural activity or forest habitats, local agencies, state departments and research institutions associated with the species first discovery are likely to operate data collection. If the pest is spreading across geopolitical boundaries, multiple organisations with different jurisdictions and areas of operation are likely to collect field data. In addition, easy-to-identify pests are likely to attract public attention and involvement, fostering the collection of citizen-science data (Dickinson et al. 2010; Catlin-Groves 2012; Sullivan et al. 2014; Kobori et al. 2016; Johnson et al. 2020; Norman-Burgdolf and Rieske 2021; Santaoja 2022). Obtaining access to the data often requires directly contacting the maintainer of the dataset in the relevant institution and obtaining memoranda-of-

understanding to use the data once shared. Each agency will follow unique data sharing agreements, which need to be discussed in-depth at this stage.

Once the data are obtained, the heterogeneity of the data collection protocols adopted by different agencies requires several additional steps to harmonise the survey results before they can be combined into a single dataset (Kelling et al. 2009). This second hurdle is often the most time-consuming and requires a high degree of eco-informatic skill in data handling and management (Michener and Jones 2012). Non-standardised data collection demands an in-depth understanding of the collection protocols used in order to match the information collected across different surveys (Hampton et al. 2013). For this reason, harmonisation often demands an active collaboration with the agencies that collected the data, to ensure the data are interpreted correctly, especially when surveys lack metadata (Jones et al. 2019).

The third hurdle is essential, yet not often acknowledged: data anonymisation. Calls to make scientific knowledge more accessible and transparent have pushed ecological data to be published alongside many scientific papers (Reichman et al. 2011). This process is paramount to improve collaboration and repeatability of scientific studies, although some limitations need to occur to ensure sharing open access data is done safely (Lindenmayer and Scheele 2017; Lunghi et al. 2019). One such limitation concerns data at high spatial resolution, the publication of which could infringe upon individual privacy and personal interests (Zipper et al. 2019). Due to this, invasive spread data need to be carefully and fully anonymised to ensure stakeholders are protected and served. This is especially true when knowledge on the infested state of a property could cause its value to decrease or the value of the goods produced to be affected (Zhang and Boyle 2010; Kovacs et al. 2011). Anonymisation practices include the removal of personal information, as well as data handling that reduces the spatial resolution to an optimal compromise between conveying relevant information and safeguarding privacy.

The spotted lanternfly (*Lycorma delicatula*, White 1845; often referred to as SLF in literature) was first discovered in the United States in Berks County, Pennsylvania, in 2014 (Barringer et al. 2015; Dara et al. 2015) and, by 2023, spread to 14 states across the Northeastern, South-Atlantic and Midwestern United States (Urban et al. 2021; NYIPM 2023). This phloem-feeding planthopper is native to China and was likely introduced accidentally via a shipment of landscaping materials. The spotted lanternfly is known to feed on over 100 species of plants (Barringer and Ciafré 2020; Murman et al. 2022; Huron and Helmus 2022) and poses a major economic burden on viticulture as it feeds on grapevines reducing total yield and plant vigour (Urban 2020). There is a high risk of spotted lanternfly impacting the global wine market by spreading to areas like California and Europe (Huron et al. 2022).

State agencies and the United States Department of Agriculture (USDA) have collected large amounts of data on spotted lanternfly spread through field surveys. In addition, given the species is easily recognised and hard to misidentify, an extensive campaign to educate the public has promoted the collection of citizen-science data. Data are collected through individual use of well-established applications such as iNaturalist, which allow for users to record geo-referenced observations of wildlife sightings, as well as through the use of applications developed *ad hoc* by State Departments of Agriculture to collect data on the spotted lanternfly. Given the variety of sources and the refinement of protocols for data collection, the data on this species are heavily heterogeneous. Currently, any research team analysing the spread of the pest has to invest a significant amount of time processing the data before using them in model construction and validation (Wakie et al. 2020; Cook et al. 2021; Huron et al. 2022; Jones et al. 2022; Ramirez et al. 2023).

Here, we describe the R package **lydemapr** (*Lycorma delicatula* **map**ping in **R**), containing an up-to-date, fully anonymised and regularly refined, longitudinal, spatially-explicit dataset of spotted lanternfly records throughout the United States since its first discovery. The dataset includes information derived from field surveys and citizen-science observations and reports observed presence/absence of this invasive species in surveyed areas, as well as the presence of established populations and estimates of population density. In addition, the package contains tools to visualise the data by mapping them and to obtain summary tables of the dataset. The goal of this package is to provide a baseline for future modelling efforts to forecast the spread of the spotted lanternfly and to foster more effective collaboration between agencies and researchers. The **lydemapr** package was fully developed in R (R Core Team 2021) and is available as an online repository at https://github.com/ieco-lab/lydemapr.

Data and metadata

The dataset contained in the package represents an anonymised and condensed comprehensive record of data collected by several federal agencies, state agencies and citizen-science projects on the presence, establishment and population density of the spotted lanternfly in the United States (Fig. 1). Sources include the Departments of Agriculture for the States of Pennsylvania, Delaware, Indiana, Maryland and New Jersey; the New York State Department of Agriculture and Markets; the Virginia Department of Agriculture and Consumer Services; the Virginia Polytechnic Institute and State University; the United States Department of Agriculture; and public reporting from iNaturalist. The field data were collected through a variety of methods, including surveys aiming to estimate establishment status and spotted lanternfly population density, control actions to manage population through egg mass destruction and trapping of nymphs and adults and citizen-science observations collected through self-reporting or direct involvement through research projects. Self-reporting tools include two separate platforms developed by the Pennsylvania Department of Agriculture (PDA) in association with Penn State University (PSU) and the New Jersey Department of Agriculture (NJDA). In addition, we included data collected through an independent citizen-science projects of limited duration run by the Virginia Polytechnic Institute and State University and the Virginia Cooperative Extension.

At the date of this publication, the aggregated and anonymised dataset contained 658,390 individual observations pertaining to 61,715 point-locations throughout the United States collected between 2014 and 2021. These 61,715 point-locations represent centroids of a 1 km² grid at which the geospatial data were aggregated for



Figure 1. Conceptual graph describing the process leading to the distribution of the R package **lydem-apr**. Data are collected by individual sources through multiple surveying processes. The datasets compiled this way are gathered from the sources and individually processed, then combined into a single comprehensive dataset. This is anonymised through both a censoring step and a spatial transformation to reduce spatial resolution. For the spatial transformation, latitude and longitude of individual survey points are rounded to the centroids of a 1-km² resolution grid. The aggregated and anonymised dataset is distributed through the package, together with functions to visualise the spread of the invasion through time.

anonymisation. The exact latitude and longitude of each survey contained in the geospatial data collected by the sources were rounded to the coordinates of the centroids. This approach, while removing the ability to derive property-level information from the dataset, allowed us to distribute survey-level information the data users can summarise as it best fits their needs. All variables containing traceable information regarding personal names, business names, contact information and comments were also removed from the dataset. The choice of 1 km² was agreed upon by all data contributing agencies to represent a compromise that provides high-resolution spatial data to enable precise spatial forecasting modelling while preserving privacy of the distributed data.

The individual observations recorded in the dataset derive from surveys and individual reporting conducted in 25 states across 8 years. The data points organised by year and state are summarised in Table 1. The distribution of data points by state is greatly skewed towards highly-impacted states. While Pennsylvania and the neighbouring states of Delaware, Maryland, New Jersey, New York and Virginia account for over 95% of data points (630,688 out of 658,390), other states in the western part of the country only account for a handful of surveys, mostly as a result of anecdotal reporting. Across time, it is easy to appreciate how surveying effort has increased, likely due to both the spread of lanternfly and to a higher investment of resources.

About 40% of the total data points were obtained through citizen-science projects; the well-established PDA and NJDA public reporting tools provided over 250,000 individual data points since 2019, while iNaturalist added just over 10,000 points. While management and surveying efforts led by state and federal agencies often focus on the leading edge of the invasion, where control actions are more effective, public reporting provides a constant and consistent source of data at the core. This helps the monitoring of these areas to be consistent and protracted in time, without subtracting important resources and work hours from managing the edge. In addition, iNaturalist provides constant, yet scattered, observations in areas where the surveying effort is not focused, as they are far from the invasion range. Those observations can then be confirmed by specialists during spatially-targeted surveys. The reliability of individually-reported records might vary with the experience and knowledge of the reporter. For this reason, in the dataset, records collected through citizen-science efforts are clearly distinct from records collected through expert-led surveys through the use of different categories under the variable "collection_method". This allows users of the data to only focus on records deriving from management and control actions, if necessary.

Data sets collection and processing

The goal for **lydemapr** is to update the dataset as new data become available and funding for the package is sustained. The plan is to request individual datasets periodically from federal and state sources, often coinciding with the termination of the biological season for spotted lanternfly (late spring, after eggs from the previous season are detected) or the temporary suspension of field operations (autumn-winter). Openly-available data (iNaturalist) are downloaded directly from the source at any time. To ensure we consider only agreed-upon, research-grade entries, the data are downloaded using the following query: "search_on=names&quality_grade=research&identifications=most_ agree&captive=false&place_id=1&taxon_id=324726".

Individual datasets pertaining to one-off collection efforts (e.g. the citizen-science project run by the Virginia Polytechnic Institute and State University) were obtained by contacting directly the data maintainer and are not updated unless the project itself is conducted again.

Individual datasets were processed in batches according to the data source. Each source had unique data collection methods which were generally consistent within a source although they did vary between years and across different data collection types (e.g. between visual surveys, control actions and trapping). Processing the data in batches first allowed us to harmonise individual datasets that shared similar, yet not identical, data structures, producing intermediate data tables that then were combined seamlessly into the final comprehensive dataset provided with **lydemapr**. There were five batches, corresponding to the five categories of the variable "source" (see section "Variables included"): PDA data, State data (consisting of data collected before 2020 from Delaware, Indiana, Maryland, New York and Virginia), public-reporting tool data, iNaturalist data and USDA data. Within each batch, the first step was to homogenise shared variables. This entailed the following steps:

State	2014	2015	2016	2017	2018	2019	2020	2021
AZ	-	-	-	-	-	10	139	100
CT	-	-	-	-	-	3	2081	1269
DC	-	-	-	-	8	21	10	4
DE	-	-	-	-	1075	2207	4545	5354
IN	-	-	1	-	79	101	102	352
KS	-	-	-	-	-	-	-	21
KY	-	-	-	-	-	3	2	18
MA	-	-	-	-	-	-	893	1835
MD	-	-	-	-	39	2404	17408	4600
ME	-	-	-	-	-	-	-	20
MI	-	-	-	-	-	-	1	133
МО	-	-	-	-	-	15	18	-
NC	-	-	-	-	-	14067	5	86
NJ	-	-	-	-	2443	9528	13066	83132
NM	-	-	-	-	-	-	10	28
NY	-	-	-	-	18474	27046	18255	4033
OH	-	-	-	-	-	-	731	406
OR	-	-	-	-	-	-	92	15
PA	370	7677	9269	9229	77047	150109	90390	61802
RI	-	-	-	-	-	-	45	18
SC	-	-	-	-	-	2	7	33
UT	-	-	-	-	-	-	1	-
VA	-	-	-	2	1523	4353	4099	1209
VT	-	-	-	-	-	-	-	2
WV	-	-	-	-	3	995	2367	1550

Table 1. Data points by biological year and state (abbreviated).

• ensuring coordinates are collected using the same projection or transforming them accordingly;

• homogenising date formats for all date variables;

• extracting year information and transforming it into "bio_year" (see the section "Variables included");

• tracking the source agency when merging individual datasets in batches;

• aggregating count data (where present), separately for eggs and nymphs/adult (necessary for a more accurate estimation of density);

• combining variables containing information on detection results (where present) and the aggregated count data into three final variables: "lyde_present", "lyde_established", "lyde_density". These variables define whether any sign of spotted lanternfly was detected, whether an established population was found and what the estimated population density at the site was, respectively (see the section "Variables included" for details on these variables). Some datasets (e.g. iNaturalist) only allow for the extraction of the presence of spotted lanternfly, omitting an assessment of establishment status and population density.

Once the shared variables were homogenised, they were renamed as they appear in the final version of the comprehensive dataset. We then generated an intermediate dataset from each batch, that contained only the shared variables (latitude, longitude, year, biological year, source agency, presence of spotted lanternfly, establishment status, population density), thus excluding all variables relating traceable information (personal names, business names, comments, addresses). Intermediate datasets were then combined together. During this step, the source was tracked through the appropriate variable. In addition, state information was added by intersecting point coordinates for each survey with state polygons (obtained through the package **tigris**) (Walker and Rudis 2023).

During a final cleaning step, we removed all data points not associated with a precise geolocation, a collection date (at least year) or a reference to the presence of the spotted lanternfly. After this, we shared the results as a high-resolution map with agency collaborators for a final check before distribution. Through this process, we were warned directly by the data providing agencies of potential mistakes, conflicts or suspicious data points. These problematic data points were vetted and corrected or removed.

The final step was the anonymisation process, where the precise location was summarised at a coarser 1 km² scale. This was done by creating a 1 km² grid over the spatial extent of the contiguous United States and intersecting this grid with the precise geolocation of each data point in the dataset. The coordinates of each point were replaced with the coordinates of the centroid of the 1 km² grid cell the point fell under. The process was repeated with an even coarser 10 km² grid, producing two additional variables added to the combined dataset, "rounded_latitude_10k" and "rounded_longitude_10k", which can be used to summarise and rarefy the dataset, if necessary, when visualising the data. After the anonymisation step, the resulting dataset **lyde** was saved and stored within the package.

Variables included

• **source:** character variable defining in broad terms the source of the data. "inat" for data obtained from iNaturalist, "PA" from data originating from the Pennsylvania

Dept. of Agriculture's surveying and management effort, "prt" for data collected through public reporting platforms, "states" for data collected by state-level agencies other than PDA, "USDA" for data provided by the United States Dept. of Agriculture. Note: the data originating from the Pennsylvania Dept. of Agriculture are kept separate from data collected by other states, as Pennsylvania was the state where the first introduction was detected. As a result of this, initial surveying efforts were led by this state, which collected the largest share of data early on;

• **source_agency:** character variable refining the definition of the source by indicating the agency/institution/project from which the data point was obtained: possible values are "iNaturalist", "PDA" (Pennsylvania Dept. of Agriculture), "NJDA_Public_reporting" (New Jersey Dept. of Agriculture's Public Reporting tool), "PDA_Public_reporting" (Pennsylvania Dept. of Agriculture's Public Reporting tool), "DDA" (Delaware Dept. of Agriculture), "ISDA" (Indiana State Dept. of Agriculture), "MDA" (Maryland Dept. of Agriculture), "NYSDAM" (New York State Dept. of Agriculture and Markets), "VDA" (Virginia Department of Agriculture and Consumer Services), "VA_Tech_Coop_Ext" (Virginia Polythecnic and State University/Cooperative Extension), "USDA";

• **collection_method:** character string defining the method used to collect data: "individual_reporting" for data collected through iNaturalist and public reporting tools and "field_survey/management" for data collected by agencies in the field. The accuracy and reliability of self-reporting data might be lower than that collected by field surveyors.

• year: integer value defining the calendar year when the information was collected;

• **bio_year:** integer defining the biological year when the information was collected. The biological year follows the species' development schedule and starts around the time of the emergence of first–instar nymphs (1 May–30 April);

• **latitude:** expressed in decimal degrees (WSG84 coordinate system);

• **longitude:** expressed in decimal degrees (WSG84 coordinate system);

• **state:** character defining the state where the data was collected (two-letter abbreviation, https://www.faa.gov/air_traffic/publications/atpubs/cnt_html/appendix_a.html);

• **lyde_present:** logical value defining whether records are present for spotted lanternfly at the site at the time of survey. These might include regulatory incidents where a single live individual or a small number of dead individuals were observed at the site, but no signs of established population could be detected;

• **lyde_established:** logical value defining whether signs of an established population are present at the site at the time of survey. These include a minimum of two alive individuals or the presence of an egg mass as per the working definition of establishment provided by the USDA;

• **lyde_density:** ordinal variable defining the population density of spotted lanternfly at the site, estimated directly as an ordinal category by the data collector or derived from count data. The categories include: "Unpopulated", indicating the absence of an established population at the site (but not excluding the presence of spotted lanternfly in the form of regulatory incidents); "Low", indicating an established population is present, but at low densities, reflecting at most about 30 individuals or a single egg mass; "Medium", indicating the population is established and at higher densities, but still at low enough population size to allow for a counting of the individuals during

a survey visit (a few hundred at most); "High", indicating the population is established and thriving and the area is generally infested, to a degree where a count of individuals would be unfeasible within a survey visit;

• **pointID:** character string uniquely identifying each data point;

• **rounded_longitude_10k:** longitude of the centroid of the closest 10 km² grid cell, expressed in decimal degrees (WSG84 coordinate system), used to rarefy the dataset at a coarser resolution;

• **rounded_latitude_10k:** longitude of the centroid of the closest 10 km² grid cell, expressed in decimal degrees (WSG84 coordinate system), used to rarefy the dataset at a coarser resolution.

Package installation and data access

The **lydemapr** package can be installed in two different ways. The public repository allows the user to install the package directly from GitHub, by executing the following command in a local R or RStudio instance: **devtools::install_github("ieco-lab/lydemapr", build_vignette = TRUE)**. This requires the package **devtools** (Wickham et al. 2022) and its dependencies to be installed locally. Alternatively, the package can be obtained by cloning the repository from the GitHub page https://github.com/ieco-lab/lydemapr. The package can then be installed locally by opening the file **lydemapr.Rproj** in RStudio and clicking "Install package" in the Build tab (or by executing the command **devtools::install()**). Once the package is installed, the user has access to the complete dataset, which can be loaded by typing **lydemapr::lyde** in the R console. In addition, the package contains a rarefied and summarised version of the same dataset at a lower spatial resolution (10 km²), which can be accessed by typing **lydemapr::lyde_10k** instead. All information concerning package installation and data access is also available at the front page of the GitHub repository.

The R package structure allows us to update the dataset regularly as more data become available and if funding is obtained to support this initiative. In addition, a live GitHub repository grants us the ability to add functionalities and to improve the visualisation and summary tools included.

If the user is only interested in accessing the data without using the R package or is unfamiliar with R, all datasets contained in **lydemapr** are available for download through Zenodo (DOI: 10.5281/zenodo.7976229), where the user can download the data (in .csv format) and Metadata associated with it.

Package functions

For a summary overview of the data, the function **lyde_summary()** provides a breakdown of the dataset, showing the number of data points collected each year in each state where data have been collected (Table 1). The package contains two customisable functions that can be used to visualise the data spatially. The function **map_spread()** provides an up-to-date map displaying the progression of the established invasion range through time, in addition to the locations of surveys which did not detect established populations (Fig. 2). Function arguments allow the user to select the spatial resolution at which the data should be mapped (choosing between 1 and 10 km²) and the spatial extent of the figure produced. A second function included in the package, **map_yearly()** maps the findings of the survey efforts in terms of the species' population density. The visualisation is broken down by the year the surveys were conducted (Fig. 3). Through this visual depiction, it is possible to observe where survey efforts have been focusing on each year, as the invasion front progressed.

Conclusion

The dataset we provide on the spread of the spotted lanternfly, a high-impact forest and grapevine pest, will be useful in a variety of current and future efforts. Several models have been developed to forecast the future spread and establishment potential of spotted lanternfly in the United States and globally (Jung et al. 2017; Wakie et al. 2020; Huron et al. 2022; Jones et al. 2022; Lewkiewicz et al. 2022; Maino et al. 2022). Statistical forecasting models (e.g. Wakie et al. 2020; Huron et al. 2022; Jones et al. 2022) heavily rely on high resolution spatial data to derive future predictions. Leveraging this big data-set will allow new models to be developed and current ones to be refined and improved. On the other hand, mechanistic mathematical models (Lewkiewicz et al. 2022; Maino et al. 2022), despite building their predictions through a bottom-up approach that involves a deeper understanding of the species' own biology and ecology, require spatial data for validation and model tuning. To ensure future models can be compared and combined through ensemble procedures, these models should be based on the same historic and present spread data of spotted lanternfly, reaffirming the importance of a unified and readily available dataset.

From a management standpoint, a comprehensive data-set can provide additional information on population trends through time in specific areas, allowing for the expansion of current studies (Cook et al. 2021), as well as offering insight on the efficacy of control actions over time. In addition, our openly-accessible and comprehensive dataset has broad applications in education, to promote citizen-science initiatives in undersurveyed areas, but also to provide an opportunity for data science projects for students. As the issues related to the spread of invasive species are often issues students experience first-hand, working on this dataset can represent an engaging learning opportunity.

There were two unexpected challenges to creating the **lydemapr** dataset. One of the main challenges we encountered was the heterogeneity in the data collection methods. This challenge greatly inflated the time, effort and eco-informatic data-coding skills required to aggregate the data. The heterogeneity was greater in the first few years (until about 2019), when more and more agencies were becoming involved, but the coordination between them was low. To solve conflicts encounters when harmonising



Figure 2. Map produced through the package function **map_spread()**. The map shows the year of first discovery of established populations of the spotted lanternfly (coloured points) in 1-km² grid cells across the eastern United States, as well as the location of negative survey records for the establishment of the species (grey crosses).

the data, which occurred, in particular, when combining different methods to score population density of spotted lanternfly, we contacted directly the maintainers of the individual datasets for insight. An additional challenge we faced was reaching a compromise between safeguarding the privacy of stakeholders while providing a highresolution dataset to allow accurate forecasting and management planning. Protecting individual interests while allowing data to be shared openly is a topic of current relevance (Zipper et al. 2019). The resolution of 1 km² used in our dataset was reached after thorough discussions with the agencies involved, to ensure no breach of privacy



Figure 3. Map produced through the package function **map_yearly**(), showing the population density of spotted lanternfly assessed yearly in 10-km² grid cells across the eastern United States (red tiles).

occurred. Paramount to overcome both challenges was a tight collaboration with the agencies. We contacted data maintainers soon after a new agency was becoming involved in data collection, to start developing a relationship of trust and cooperation. This created an open line of communication with the agencies collecting the data from the field and curating the individual datasets and produced a feedback loop that we believe strengthens the quality and reliability of our dataset.

Author's contribution

SDB and MRH conceived the paper, gathered the data, produced the comprehensive dataset and wrote the code for the package. LB, PK, JL and GRP provided survey data and helped harmonise it across sources. All authors contributed with the writing of the manuscript.

Data availability

The package, containing the open access data, is stored as a public repository at https://github.com/ieco-lab/lydemapr. Additionally, versions of the 1 km² and 10 km² datasets are stored on Zenodo DOI: 10.5281/zenodo.7976229.

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RESEARCH ARTICLE



Assessing the risk of invasion by a vineyard moth pest guild

Hector Zumbado-Ulate¹, Tyler E. Schartel², Gregory S. Simmons³, Matthew P. Daugherty¹

I Department of Entomology, University of California, Riverside, CA 92521, USA 2 Prairie Research Institute, Illinois Natural History Survey, University of Illinois at Urbana/Champaign, 1816 South Oak Street, Champaign, IL 61820, USA 3 United States Department of Agriculture, Animal Plant Health Inspection Service, Plant Protection and Quarantine, Science and Technology, Salinas, CA 93905, USA

Corresponding author: Hector Zumbado-Ulate (zumbadohector@gmail.com)

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Abstract

Biological invasions are most effectively managed when identified in their early stages, which often hinges on robust surveillance programs. The recent invasion of the European grapevine moth (Lobesia botrana) in California suggests that viticultural areas in the western United States may face severe economic consequences from this and other Tortricid and Pyralid moth species if they were to establish. To gain insights into the risk these grapevine pests pose, we used occurrence records for L. botrana and four other moths native to Europe or the eastern United States and selected environmental variables to predict the extent of climatically suitable areas and potential pest co-occurrence along the West Coast of the United States. A suite of models was generated using MaxEnt with species-specific tuning of model settings. Overall, the results confirmed high suitability for L. botrana to establish across much of the study region, driven largely by high monthly variability in precipitation and low elevation. Two species were predicted to have intermediate suitability to establish over the study region (i.e., grape tortrix moth, Argyrotaenia ljungiana; grape berry moth, Paralobesia viteana), while two others had low suitability (i.e., European grape berry moth, Eupoecilia ambiguella; Christmas berry webworm, Cryptoblabes gnidiella). The highest predicted potential for co-occurrence was between L. botrana and P. viteana, accounting for 19% of the total viticulture area, followed by L. botrana and A. ljungiana for 11% of the study area. These results may help with the optimization of surveillance efforts by indicating which species or areas should be prioritized for the deployment of invasive pest detection programs with pheromone traps. Indeed, given the apparent potential for co-occurrence of multiple moth pests in certain areas, our results may inform where single or multi-lure traps should be deployed as a more cost-efficient monitoring tool.

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Keywords

detection trapping, invasion risk, pest surveillance, species distribution model

Introduction

Invasive species are a significant threat to global biodiversity (Richardson et al. 2000; Gurevitch and Padilla 2004) that can have detrimental effects on other species and economic productivity (Meyerson et al. 2019; Shackleton et al. 2020). Human-mediated mechanisms of pest invasions, which include the introduction of pest species into new environments, naturalization, and further spread disturb many native species through predation, competition for limited resources, transmission of pathogens, and disruption of behavioral processes (Pyšek and Richardson 2010; Hoffmann and Courchamp 2016). For agroecosystems, invasive species may precipitate increased costs and substantial production and revenue losses (Paini et al. 2016; Savary et al. 2019). As a result, government agencies and industry groups devote enormous resources to identifying and eradicating established invasive species. However, invasive species management is most efficiently achieved during the initial stages of an invasion, when invader abundance is low (Simberloff et al. 2013; Bradley et al. 2019). Further research is needed to expedite robust responses to invasive species arrival (Leung et al. 2002).

Biological invasions in the United States cost more than \$100 billion annually and are increasing in frequency (Pimentel et al. 2005; Simberloff et al. 2013; Meyerson et al. 2019; Crystal-Ornelas et al. 2021). According to the United States Animal and Plant Health Inspection Service (APHIS; https://www.aphis.usda.gov/), invasive insects have caused significant losses to the US environment and economy, particularly with respect to native forests and a wide range of annual and perennial crops. Such effects may be pronounced in states with large agricultural enterprises, such as California. Between 1990 to 2010, it is estimated that approximately 10 exotic arthropod species were introduced into California each year, 20% of which became significant pests (Dowell et al. 2016). This represents a 62% increase in introductions compared to 1970–1989 despite more rigorous border controls and monitoring programs, reinforcing the need for additional research to anticipate the arrival and ultimate impact of invasive species.

A recent invader of particular importance to California's wine, raisin, and table grape industry is the European grapevine moth (EGVM), *Lobesia botrana* (Lepidoptera: Tortricidae) [Denis & Schiffermüller]; one of several Lepidopteran agricultural pests that have proven capable of rapid geographic range expansion (Suckling et al. 2017). This phytophagous species uses multiple plant species but particularly cultivated grapevines, where its larvae feed on flowers and grape berries, causing direct damage and introducing fungal rots, which can dramatically reduce yields (Delbac and Thiéry 2016). Although the native range of EGVM includes much of Europe, it has successfully invaded other regions, such as western and northern Africa (Ioriatti et al. 2012;

Lucchi and Scaramozzino 2022) and grape-growing regions in the Americas, including Chile, Argentina, and the United States (Varela et al. 2010; Gilligan et al. 2011).

In the United States, EGVM was first detected in California in late 2009 (Gilligan et al. 2011). Following initial detections in select areas of Napa County, more extensive monitoring showed it had spread to several surrounding areas. In 2010, more than 100,000 male moths were caught on nearly 4,000 pheromone traps. EGVM was ultimately recorded in 11 counties in Northern and Central California, up to approximately 300 km from where it was initially detected (Simmons et al. 2021). In response, an eradication program was established that included state-wide monitoring with pheromone traps, insecticide treatments, mating disruption, and a regulatory control program. Subsequently, sharp declines in EGVM captures were seen over the next few years to the point that it was declared eradicated in 2016, following two years without any detections (Schartel et al. 2019; Simmons et al. 2021).

As part of a larger study evaluating the factors that contributed to the successful eradication of EGVM in California, Schartel et al. (2019) used occurrence records from the state-wide monitoring program to develop a suite of habitat suitability models for EGVM in Napa County. The results showed select climatic, landscape, and anthropogenic variables explained observed patterns in EGVM occurrence, but generated uncertainty regarding EGVM suitability estimates during an eradication program (Schartel et al. 2019). Moreover, occurrence records from the program data were insufficient to evaluate suitability for EGVM in other areas of California, let alone for viticultural areas in neighboring states along the West Coast. Thus, while EGVM is considered a threat should it be reintroduced into the region, questions remain about the magnitude of that risk and the specific locations most likely to be affected.

EGVM is only one of several moth pests of grapevines with the potential to be highly destructive. Other species in the families Tortricidae and Pyralidae have proven to be significant pests in other viticultural regions (Ioriatti et al. 2012; Isaacs et al. 2012), and are considered high risk by the California grape industry (Napa County California 2022) or have been included as priority targets by the national Cooperative Agricultural Pest Survey (2022). These species may threaten vineyards along the West Coast of the United States should they be introduced: grape tortrix moth (GTM); Argyrotaenia ljungiana (Lepidoptera: Tortricidae) [Thunberg]), grape berry moth (GBM); Paralobesia viteana (Lepidoptera: Tortricidae) [Clemens]), European grape berry moth (EGBM); Eupoecilia ambiguella (Lepidoptera: Tortricidae) [Hübner]), and Christmas berry webworm (CBW); Cryptoblabes gnidiella (Lepidoptera: Pyralidae) [Millière]). EGBM, GTM and CBW occur naturally in Europe (similar to EGVM) but have invaded portions of Asia, Africa and Oceania (Ostrauskas et al. 2008; Ioriatti et al. 2012). Meanwhile, GBM is native to central and eastern United States, where it shows high fidelity to wild and cultivated grapes, causing significant yield losses (Botero-Garcés and Isaacs 2003; Isaacs et al. 2012). Damage to grapevines varies among species but is generally a function of larval infestation levels that are themselves influenced by characteristics of the grapevine (e.g., cultivar) and climatic conditions that influence moth

phenology and voltinism (Ioriatti et al. 2012). Direct damage from larval feeding can result in minor to extensive reduction in fruit yields, and can facilitate fungal infections or secondary pest infestations (Moschos 2006; Ioriatti et al. 2012; Isaacs et al. 2012).

Monitoring using pheromone-baited traps is commonly employed for pest management, and for early detection of invasive insects (McNeil 1991; Vacas et al. 2011). Maintaining long-term surveillance programs for high-risk pests is costly, but the costs of missing the detection of a newly arrived pest may quickly exceed surveillance costs if the new pest is allowed to spread beyond a point where eradication is feasible (Chase et al. 2018). Hence, there is a need to prioritize the placement of traps in areas that are most conducive to pest establishment so that the limited resources available for pest detection are optimized. Yet, current knowledge gaps regarding the invasive potential of EGVM and these other grape pest moths hamper optimization of those surveillance programs.

We gathered occurrence records from the native and invaded ranges of five highrisk lepidopteran pests of grapevines and selected a number of environmental variables to quantify invasion risk along the West Coast of the United States (Cooperative Agricultural Pest Survey 2022; Napa County California 2022) (Suppl. material 1: fig. S1). The goals of these analyses were to a) estimate the overall invasive potential of each species throughout viticultural areas in the Western United States, b) identify those locations most at risk to the establishment of each species and the environmental conditions that underlie them, and c) identify areas where multiple moth species are likely to co-occur if introduced. Although none of these species currently occur in the region, the threats posed by their introduction, and the potential for multiple species to establish in the same region, warrant further investigation to inform implementation of early detection and surveillance efforts (Cooper et al. 2014; Simmons et al. 2021).

Methods

Study region and focal species

We focused on the invasive potential of five grapevine pests (EGBM, EGVM, GBM, GTM, and CBW) in grape-growing regions along the West Coast of the United States, in portions of California, Oregon, and Washington (5–40°N, 70–118°W; Suppl. material 1: fig. S1). Overall, the study region represents a substantial portion of the high-value grape acreage in the United States and is the only region where one of these moth pests has successfully invaded (Gilligan et al. 2011). Moreover, states along the West Coast include many pathways that could contribute to pest arrival and spread (Dowell et al. 2016). The West Coast covers approximately 835,905 km² and has a wide variety of physiographic characteristics. The climate varies across the study region, but overall, the region receives most precipitation during the winter months (Neiman et al. 2008). Most grape-growing regions have been officially classified into American Viticulture Areas (AVAs), which are established by the Alcohol and Tobacco Tax and Trade Bureau under the US Department of the Treasury. Shapefiles of AVAs were obtained from the

American Viticultural Area Project at the University of California-Davis (https://github. com/UCDavisLibrary). We supplemented California AVAs boundaries with California Department of Water Resources (DWR) polygons depicting 2016 wine-grape growing vineyards (https://gis.water.ca.gov), which included wine, raisin and table grapes areas. The boundaries of DWR polygons were dissolved and a 10 km radius buffer was added to grape-growing locations to capture newly established vineyards (since 2016) in the immediate vicinity. Then, these supplemental vineyards were joined with the AVAs boundary polygons to create a final GIS-referenced shapefile of viticultural areas in the study region, which encompassed 21.4% (178,922 km²) of the West Coast of the United States. All study analyses were conducted with the R statistical language V 4.2.2 (R Core Team 2022) and ArcGIS Pro 3.0.1 (ESRI Redlands, CA, USA). Country-level shapefiles were obtained from the Database of Global Administrative Areas (https://gadm.org).

Occurrence datasets and predictor variables

Risk assessments based on extrapolations of species distribution model (SDM) predictions to regions and periods different from the conditions used to calibrate the model (i.e., model transferability) are effective for pest management and species conservation planning (Heikkinen et al. 2012; Barbet-Massin et al. 2018). It is recommended that species occurrences in both native and non-native ranges be used when developing SDMs to assess invasion risk in newly invaded or at-risk regions (Jiménez-Valverde et al. 2011; Peterson 2011; Jarnevich et al. 2022).

We downloaded occurrence data for all five pest species in their native and other invaded ranges from 1960 to the present date from the Global Biodiversity Information Facility (GBIF; www.gbif.org; Suppl. material 1: figs S2–S6). For EGVM occurrences we also included records from its invasion into Napa County (Schartel et al. 2019). Regarding GBIF records, we only considered those provided by 1) official institutions and biological collections and 2) data citizen science platforms only when the species ID was previously confirmed by specialists. Then, occurrence datasets were cleaned by checking for typos, removing unreferenced records, cross-checking geographic coordinates, and removing coordinates with a geographic inaccuracy > 10000 m. A collection of background points to specific areas was generated by buffering known occurrences in pest native and non-native ranges with a 50 km radius buffer (i.e., calibration areas). The final number of background points differed among species because of the different sizes of the calibration areas and corrections for sampling bias. To reduce the effect of spatial autocorrelation in both occurrence and background datasets, we excluded points that were separated by a distance < 1 km. Final presence-only datasets consisted of 467 occurrence records for EGBM, 459 for EGVM, 54 for GBM, 644 for GTM, and 121 for CBW. Final background datasets consisted of 12331 background points for EGBM, 6741, for EGVM, 3125 for GBM, 14991 for GTM, and 1784 for CBW.

All 19 BIOCLIM variables (Booth et al. 2014) and the global elevation layer were downloaded from WorldClim 2.1 (Fick and Hijmans 2017; https://www.worldclim. org/), along with 12 of the 14 environmental raster layers from ENVIREM (Title

and Bemmels 2018; https://envirem.github.io/). All raster layers were downloaded at 5 min spatial resolution (Suppl. material 1: table S1). Multicollinearity among predictors at moth occurrence and background locations was assessed by estimating the variance inflation factor (VIF) with the R package 'usdm' 1.1–18 (Naimi 2015) . Specifically, we excluded from our analysis highly correlated variables using a VIF threshold of 0.7.

Species distribution modeling

Here, we provide an overview of our climatic suitability modeling methodology following the ODMAP (Overview, Data, Model, Assessment, and Prediction) protocol for species distribution models (Zurell et al. 2020). Specific methodological details for all ODMAP sections are presented as supplementary material (Suppl. material 1: table S2). We used the MaxEnt algorithm (Phillips et al. 2006) with species-specific tuning of model settings implemented through the R package 'ENMeval' 2.03 (Kass et al. 2021) to generate continuous predictions of climatic suitability across the native and invaded range (e.g., Zeng et al. 2016; Zumbado-Ulate et al. 2022). The following settings were used to parametrize and generate 16 candidate models for each species: algorithm = maxent.jar; partition method = block; regularization of multiplier values = 1-4 with increments of 1; feature classes = L, H, Q, LQH; where L = Linear, H = Hinge, Q = Quadratic, Clamping = True.

Model selection was conducted using the highest average of the area under the curve of the receiver-operating characteristic ('AUC mean'), the standardized true skill statistic (sTSS), and the average of the 10-percentile training omission rate ('10.or.pt mean'). For selected models, we estimated the percent contribution of each selected abiotic predictor and generated response curves by comparing the probability of each pest species' presence relative to each abiotic predictor (Elith et al. 2006; Syfert et al. 2013). The Boyce index (Boyce et al. 2002), and the slope of the regression of the response variable on the logit of predicted probabilities according to Miller's calibration statistics (Miller et al. 1991) were estimated to evaluate how much model predictions differed from the random distribution of the observed presences across the prediction gradients and extrapolation of our predictions outside the training data.

Species co-occurrence

To identify areas that may be susceptible to the establishment of multiple moth species, we used two alternative thresholds to generate binary predictions (raster absence-presence maps) of the potential range of each species across the study region. Binary predictions were transformed into polygons to quantify the extent of climatically suitable areas (ESH; Brooks et al. 2019) of each species in square kilometers (km²). Specifically, we used the 10-percentile lowest omission rate logistic threshold (10.or.pt; Radosavljevic and Anderson 2014), which excludes those occurrence points with suitability in the lowest 10 percentile, and the maximum training sensitivity plus specificity logistic threshold (maxSS), which performs an overall true occurrence prediction (Liu et al. 2005). This

approach allowed us to quantify ESH across the study region under two scenarios with different degrees of conservativeness: 1) removing only the 10 percent of the localities having the lowest predicted values of climatic suitability, or 2) maximizing the true positive prediction, resulting in a more restricted definition of climatically suitable areas.

To identify areas of co-occurrence, binary predictions were combined into a single raster. Because the binary predictions only had values of zero and one, the resulting cumulative raster displayed values between zero (no pest species predicted to occur in a pixel) and five. Then, this cumulative raster was transformed into a polygon to estimate the potential co-occurrence of multiple species, from two to five species. To calculate ESH we transformed the projected coordinate system of binary predictions and AVAs from WGS84 to NAD 1983 Albers contiguous USA (ESRI 102003).

Finally, a principal component analysis (PCA) was generated to visualize the environmental space where multiple pest species are predicted to overlap. For this, we selected the ten predictors with highest contributions to the SDMs (Table 1) and simulated 1000 pseudo-occurrences for each study species across the environmental space by generating 1000 random points throughout their climatically suitable areas based on the binary predictions built with the 10.or.pt threshold. All pseudo-occurrences were spatially filtered using a distance of 10 km. Remaining pseudo-occurrences were transformed into cell centroids in grids of 10 km² resolution. This method allowed us to generate a weighted sample size for each pest species according to their ESH and full environmental space.

Results

One preferred model was identified for each species (Suppl. material 1: table S3) from the total set of candidate models (5 species, 80 total models). Selected models varied in feature classes (L, Q, and LHQ), and four of them scored the highest AUC with the regularization multiplier at 1. Overall, both independent and dependent threshold evaluation metrics (Suppl. material 1: table S3) showed that the most robust model for each species exhibited a good fit and performed better than random models: AUC mean values between 0.71 and 0.89, sTSS values between 0.66 and 0.82, and low omission rates (10.0r.pt mean values between 0.01 and 0.1). Similarly, the Boyce Index values (between 0.90 and 0.98), and the slope of Miller Calibration statistics (between 0.6 and 1) showed that model predictions were consistent with the distribution of presences in the evaluation dataset and transferred efficiently into a new geographic area.

Sixteen abiotic predictors were retained among the five models selected (Table 1). Elevation was the only predictor featured in all five species models, but mean diurnal range, precipitation seasonality, precipitation of the warmest quarter, minimum temperature of the warmest month, mean monthly potential evapotranspiration of driest quarter, and monthly variability in potential evapotranspiration appeared in four of the selected models. In general, the percent contribution of each selected abiotic predictor matched the percent of permutation importance of each selected abiotic predictor, but with some inconsistencies that may be attributable to modest multicollinearity (Table 1).

Table 1. Percent contribution (% C) and permutation importance (% P) of selected abiotic predictors in species-specific climatic suitability models (EGBM = European grape berry moth, *Eupoecilia ambiguella*; EGVM = European grapevine moth, *Lobesia botrana*; GBM = Grape berry moth, *Paralobesia viteana*; GTM = Grape tortrix moth, *Argyrotaenia ljungiana*; CBW = Christmas berry webworm, *Cryptoblabes gnidiella*). The two predictors with the highest contributions are in bold.

Predictor	EGBM	EGVM	GBM	GTM	CBW
	% C (% P)				
BIO2; Mean diurnal range (°C)	2.7 (0.5)	-	10.5 (25.6)	32.2 (47)	69.5 (20.1)
BIO3; Isothermality (°C)	7.7 (6.8)	6.1 (5.3)	-	35.5 (35.6)	-
BIO7; Temperature annual range (°C)	-	11.4 (13.9)	-	-	-
BIO8; Mean temperature of wettest quarter (°C)	6 (7.8)	3.9 (5.3)	-	0 (0)	-
BIO13; Precipitation of wettest month (mm)	7.1 (14.7)	6.1 (7.2)	-	-	-
BIO14; Precipitation of driest month (mm)	-	-	0 (0)	-	0.7 (7.4)
BIO15; Precipitation seasonality (mm)	2.2 (5.9)	57.6 (42.1)	-	13.5 (2.4)	0.5 (3.7)
BIO18; Precipitation of warmest quarter (mm)	-	0 (0)	27.1 (41.2)	0.2 (0.4)	0 (0.2)
BIO19; Precipitation of coldest quarter (mm)	3.8 (0)	-	-	-	1.2 (0.1)
Elevation (m)	57.6 (57.6)	12.6 (10)	0 (0)	14.4 (1.6)	7.9 (6.1)
EPQ; Emberger's pluviothermic quotient	-	-	-	0.3 (2.1)	-
gDD5; growingDegDays5 (°C)1	4.4 (5.1)	-	-	-	-
mTW; Minimum temperature of warmest month (°C)	-	0.3 (1.3)	56.5 (23)	3.8 (10.5)	12 (0)
PETDQ; PET of driest quarter (mm) ²	-	1.4 (14.1)	3.7 (2.7)	0.1 (0.4)	3.4 (42.1)
PETS; PET seasonality (mm) ²	8.5 (1.6)	0.6 (0.9)	2.2 (7.4)	-	4 (18.2)
PETWQ; PET of wettest quarter (mm) ²	-	-	_	-	0.9 (2.1)

¹sum of mean monthly temperature for months with mean temperature greater than 5 °C multiplied by the number of days. ²potential evapotranspiration.

Of the five focal species evaluated, the area estimated to be moderate to highly climatically suitable for establishment was highest for EGVM, especially along the coastline, in western and central areas of Washington and Oregon, and central regions of California (Fig. 1A, B). The two abiotic predictors with the strongest contribution to EGVM model predictions (Table 1) were seasonal precipitation (58%) and elevation (13%). The highest predicted suitability (0.9) occurred in areas with the high monthly variability in precipitation, and climatic suitability decreased rapidly as elevation increased from a maximum of 0.4 near sea level (Suppl. material 1: fig. S7). The ESH varied between 36 and 65% of the total viticultural area in the study region, depending on which threshold was considered (Table 2).

Climatic suitability was relatively moderate throughout the study region for two pest species. For GBM, the most climatically suitable regions occurred in small patches across viticulture areas in Washington and Oregon, and very small portions along the coast of California (Fig. 2A, B). The minimum temperature during the warmest month (57%) and precipitation during the warmest quarter (27%) had the highest contributions to GBM model predictions (Table 1). Estimated climatic suitability increased gradually as temperature increased, reaching a maximum of 0.8 at approximately 25 °C (Suppl. material 1: fig. S8a). Conversely, estimated climatic suitability decreased rapidly for locations with higher precipitation during the warmest quarter, from a maximum of 0.8 between 0- and 200-mm precipitation to 0.3 at approximately 500 mm (Suppl. material 1: fig. S8b). The ESH predicted for GBM represented between 0%



Figure 1. Climatic suitability map for the European grapevine moth (EGVM), *Lobesia botrana*, in viticultural regions along the West Coast of the United States **A** continuous climatic suitability estimates **B** binary predictions of climatically suitable areas based on the 10-percentile lowest omission rate threshold.

and 21% of the total viticulture area (Table 2). For GTM, only the viticulture areas in far northern Washington and small portions of central and southern California were climatically suitable for establishment (Fig. 2C, D). The two abiotic predictors with the highest contribution to the model predictions (Table 1) were isothermality (36%) and mean diurnal range (32%). Estimated climatic suitability across the native and invaded range of the GTM increased as the ratio of diurnal variation to annual variation in temperatures increased, reaching maximum suitability of 0.8 near 50 °C, and decreased for locations where the mean differences between maximum and minimum temperatures were the greatest (Suppl. material 1: fig. S9). The ESH of the GTM represented between 0.1 and 13% of the viticulture areas (Table 2).

Finally, the vast majority of the study region was projected to have relatively low climatic suitability for two focal species. For EGBM, the most climatically suitable

Table 2. Extent of climatically suitable areas (ESH) and corresponding percent of the total area of viticul-
ture regions (% VR) for five moth species (EGBM = European grape berry moth, Eupoecilia ambiguella;
EGVM = European grapevine moth, Lobesia botrana; GBM = grape berry moth, Paralobesia viteana;
GTM = grape tortrix moth, Argyrotaenia ljungiana; CBW = Christmas berry webworm, Cryptoblabes gni-
diella) using two binary thresholds for suitability: 10-percentile lowest omission rate threshold (10.or.pt)
and the maximum training sensitivity plus specificity threshold (maxSS).

Species	Threshold						
-	10.or.pt		maxSS				
-	ESH (km ²)	% VR	ESH (km ²)	% VR			
EGBM	21640	12.1	1134.1	0.6			
EGVM	115605	64.6	64894.6	36.3			
GBM	36940	20.6	64.8	0.0			
GTM	22776	12.7	109.6	0.1			
CBW	1074	0.6	123.0	0.1			
Number of species ¹	ESH (km ²)	% VR	ESH (km ²)	% VR			
0	37917.8	21.2	113329.8	63.3			
1	95758.2	53.5	65396.1	36.6			
2	34154.6	19.1	115.5	0.1			
3	9586.5	5.4	79.6	0.0			
4	1402.6	0.8	0.0	0.0			
5	101.3	0.1	0.0	0.0			

¹number of the five moth species predicted to co-occur in an area.

regions for establishment occurred in central Washington and far northern Oregon (Fig. 2E, F). The two abiotic predictors with the highest contribution to EGBM model predictions were elevation (58%) and monthly variability in potential evapotranspiration (9%; Table 1). Climatic suitability was predicted to be highest (0.8) near sea level and decreased at higher elevations as well as increased over a gradient of increasing precipitation (Suppl. material 1: fig. S10). The ESH represented between approximately 1 and 12% of all viticulture area (Table 2). For CBW, most of the study region was predicted to be climatically unsuitable (Fig. 2G, H). The mean diurnal range and the minimum temperature of the warmest month had the highest contributions to model predictions (Table 1). Estimated climatic suitability gradually decreased as the mean difference between maximum and minimum temperatures increased. Estimated climatic suitability also increased at higher temperatures (Suppl. material 1: fig. S11). The predicted ESH ranged between just 0.1 and 0.7% of the total viticulture area (Table 2).

Implementing the 10.or.pt binary threshold revealed that approximately 25% of the overall area of viticulture regions was predicted to be climatically suitable for pest co-occurrence (Fig. 3A). Less than 7% was climatically suitable for the co-occurrence of three or more species (Table 2). The highest predicted potential for co-occurrence based on this threshold occurred between EGVM and GBM, accounting for 19% of the total viticulture area, followed by EGVM and GTM for 11% of the area (Fig. 3B, Suppl. material 1: table S4). All remaining pairs of focal species were predicted to co-occur in between 0.1 and 6% of areas. Results based on the more restrictive maxSS threshold, suggested that just 0.1% of the total viticultural area is climatically suitable for co-occurrence of multiple species, and never for more than two-species (Table 2, Suppl. material 1:



Figure 2. Climatic suitability estimates and binary predictions based on the 10-percential lowest omission rate threshold for four moth species **A**, **B** grape berry moth, *Paralobesia viteana* **C**, **D** grape tortrix moth (GTM), *Argyrotaenia ljungiana* **E**, **F** European grape berry moth (EGBM), *Eupoecilia ambiguella* **G**, **H** Christmas berry webworm (CBW), *Cryptoblabes gnidiella*.

table S4). A PCA (Fig. 3C) was used to visualize clustering of species pseudo-occurrences relative to PCA loadings to assess qualitatively the environmental conditions underlying areas of predicted moth species co-occurrence. The results indicated: 1) an overlap in the environmental envelopes of EGBM and GBM (top left quadrant), driven mostly by annual temperature range; 2) overlapping environmental envelopes for EGVM and GTM (top right quadrant) based on mean diurnal range and minimum temperature during the warmest month; 3) an environmental envelope with less apparent multispecies overlap (i.e., more diffuse spread of pseudo-occurrences; bottom right quadrant), and 4) an environmental envelope where between three (most often EGVM, GBM, GTM) and five species may coexist (bottom left quadrant), which is driven by precipitation of the warmest quarter and to a lesser degree by precipitation during the wettest month.



Figure 3. Regions predicted to be climatically suitable for multiple species **A** occurrence or co-occurrence of up to five of the moth species based on 10-percentile lowest omission rate thresholds **B** regions of potential co-occurrence of the three species with the highest overall suitability in the study region: European green vine moth (EGVM) *Lobesia botrana*, grape berry moth (GBM), *Paralobesia viteana*, and grape tortrix moth (GTM), *Argyrotaenia ljungiana* **C** principal component analysis depicting climatic envelopes and environmental predictors (Table 1) associated with climatically suitable areas for multispecies co-occurrence.
Discussion

Traditionally, researchers have concentrated on understanding biological invasions at large scales (Hoffmann and Courchamp 2016; Lewis et al. 2016). This approach provides fundamental knowledge of the biology of invasive species, but may offer limited predictive power at finer spatial scales (Novoa et al. 2020). Other studies have focused on the combination of pathways, invasive species traits, and characteristics of the invaded environments that underlie dynamics at finer scales, which can be used to apply specific management at regional and species levels (Kueffer et al. 2013). Identifying the environments that are most susceptible to invasion, pathways, routes, and other mechanisms that allow invasive species to establish and spread can help limit their damage (Simberloff et al. 2013; Novoa et al. 2020).

Once invasive species settle, effective management becomes difficult and costly to carry out, especially in regions affected by multiple pest species (Navia et al. 2013). Here, we focused on assessing the risk of invasion of multiple species considered to be high risk to grape-growing areas of the world, where they have caused large losses to industry (Ioriatti et al. 2012; Isaacs et al. 2012). Our analyses drew upon a comprehensive and updated collection of occurrences and utilized robust methods and strict criteria to reduce impacts of unbalanced sampling, spatial autocorrelation, and multicollinearity, to improve prediction accuracy. Our study is applicable to different invasive taxa for which the objective is to guide early detection efforts to mitigate their potential impacts (Lennox et al. 2015; N'Guyen et al. 2016).

Scientists have linked successful invasive species to high abundance, wide distribution in their native ranges, and distinct traits that ease establishment and spread (e.g., Williamson and Fitter 1996). Although all five focal species may fulfill these criteria to varying degrees, our results suggested that EGVM poses the greatest risk of establishing if reintroduced into the study region. Previous studies have shown EGVM to be highly damaging for the grape industry across its native distribution in Europe (Thiéry and Moreau 2005; Ioriatti et al. 2012; Delbac and Thiéry 2016). Our results indicate that a large portion of the study region is likely to be climatically suitable for EGVM establishment. Predicted climatically suitable areas include most viticultural areas of California, Oregon, and western Washington; particularly locations with relatively low elevations, and dry and warm seasonal conditions. Most areas of eastern Washington, where most of the grape wines are grown, were found to be climatically unsuitable for EGVM.

Our results are consistent with those of a prior global analysis of EGVM suitability (Rank et al. 2020) and a physiologically-based demographic model (Gutierrez et al. 2012, 2018), which showed high suitability for EGVM in dry and warm seasonal habitats. Our predictions also coincided in most of our study region with a new large-scale, physiologically-based demographic model developed by the Spatial Analytic Framework for Advanced Risk Information Systems (SAFARIS) for EGVM (SAFARIS 2022). Overall, the major differences in predicted climatic suitability observed between our model and the models described above can be attributed to different approaches used to generate models (correlative vs process-based), the spatial scale, as well as the selected environmental predictors. Given that management strategies derived from predictive models are scale dependent, our model can serve as a precise framework for grape-growing regions across the West Coast of the United States. For the small set of regions that showed conflicting values of suitability among suitability maps, combined prevention strategies can be applied to prevent pest establishment. Given limited resources, higher risk areas can be prioritized for surveillance as an aid to decision making. Finally, we expect it may be important to consider horticultural practices or other management activities within specific grape-growing regions. For example, irrigation, a widespread strategy in vineyards across the Western United States, may affect suitability at very fine spatial scales, but potential effects would depend on local factors such as the frequency and quantity dependent on weather, soil type and variety. Future monitoring of environmental predictors at the site level, development of fine-scale models (e.g., remote sensing derived models), and identification of potential pathways for pest introduction and spreading would complement our analyses.

The prior invasion of EGVM in California, and its ultimate eradication, may yield important lessons for future responses to invasive insects (Schartel et al. 2019). A retrospective analysis suggested that the success of the program was attributable to a combination of efficient transfer of knowledge gained from research conducted in EGVM's native range, appropriate implementation of regulatory and control strategies, and coordinated responses among researchers, cooperative extension personnel, regulatory agencies, members of industry, and the general public (Zalom et al. 2013; Schartel et al. 2019; Simmons et al. 2021). Habitat suitability modeling using occurrence records from the most heavily invaded area, in Napa County, showed certain locations to be highly suitable for EGVM contingent on a combination of climatic conditions, attributes of the surrounding landscape, and anthropogenic variables (e.g., proximity to transportation corridors). Yet, the persistence of statistical hotspots in EGVM occurrences over time was not strongly tied to habitat suitability (Schartel et al. 2019). This pair of apparently contradictory results left open questions regarding the true suitability of the region for EGVM establishment, perhaps reflecting underlying challenges with drawing inferences in the midst of an active eradication program. Fortunately, the present study provides some clarity on this issue. Specifically, the climatic suitability predictions for EGVM indicated that not only is it well suited to those areas most heavily affected in the prior invasion, but a substantial fraction of vineyard acreage in other areas of California, Oregon, and Washington are likely at risk of EGVM establishment should it be reintroduced.

We found that in addition to EGVM, two other moth species, GBM and GTM, might find moderate expanses of climatically suitable areas. Since the expansion of grapegrowing regions in North America, GBM has increased in abundance and distribution, but it has not been observed in the western United States. However, viticulture regions in Washington and Oregon seem to offer suitable conditions, as this species performs well in temperatures in seasonal humid environments (Botero-Garcés and Isaacs 2003; Isaacs et al. 2012). On the other hand, climatically suitable areas for GTM mostly occurs in Central and Southern California, specifically in dry regions with more stable temperatures across the year, which coincides with the habitats described for this species in its native and invaded range throughout the Palearctic (Ioriatti et al. 2012). Although our results showed that much of the study region is unlikely to be climatically suitable for EGBM and CBW establishment, their inclusion in this assessment is substantiated due to their high invasiveness and similar ecology to EGVM. While EGBM has been highly successful invading mainland and islands in Asia, CBW has been reported in Asia, Africa, the Americas, and New Zealand (Ioriatti et al. 2012). Based on occurrence records, EGBM and CBW overlap and potentially interact with EGVM, at least historically, in most of their native range in Europe. Similar studies have assessed the potential distribution of invasive pathogens (Lötters et al. 2009; Turbill and Welbergen 2020), and pests (Narouei-Khandan et al. 2016) and illustrate the utility of SDMs to inform the location and timing of monitoring for potentially invasive species (Srivastava et al. 2019).

An additional benefit of this work was to model multiple species' pest risk establishment probabilities which can also aid efforts to develop tools, such as multi-lure pheromone traps, that can simultaneously monitor multiple species while reducing the costs and time-intensive nature of monitoring efforts (Epanchin-Niell et al. 2014). Ongoing research (A. Lucchi, personal communication; G. Simmons, unpublished data) is evaluating the effectiveness of pheromone traps for each moth species alone and in multilure combinations, given that interference between certain pheromones may influence multi-lure traps' ability to attract and detect focal species (Brockerhoff et al. 2013; Chase et al. 2018; Rowley et al. 2018). Further developments concerning the efficacy of multi-lure traps, coupled with the results of the PCA that complement the climatic suitability maps of our study species and identify variables associated with the potential suitable habitat for multispecies co-occurrence across the West Coast of the U.S., may lead to more targeted, and ultimately effective, multi-pest monitoring programs.

Although a growing number of studies have modeled the distribution of multiple species or assessed co-occurrence of multiple species through joint SDMs or occupancy models (Pollock et al. 2014; Norberg et al. 2019), the use of SDMs to assess the distribution and co-occurrence of multiple pest species remains unexplored (e.g., Briscoe Runquist et al. 2021). The accurate prediction of species co-occurrence has methodological limitations and effectiveness relies on exploratory analyses and robust methods of data collection and cleaning (Dormann et al. 2018). Previous studies have shown overlapping distributions and apparent coexistence of EGVM, EGBM, GTM, and CBW (Ioriatti et al. 2012). Similarly, the ecology and habitat characteristics of the North American GBM suggest this species might successfully invade grape-growing regions where it could potentially co-occur with other moth pests (Ioriatti et al. 2012; Isaacs et al. 2012). For invasive agricultural pests, there are always limitations on the amount of funding available to mount bio-surveillance efforts. Pest risk analysis resources and tools such as the Cooperative Agricultural Pest Survey (2022) and the climate suitability model in SAFARIS (2022), have been designed to aid decision makers to choose which pests, and in which parts of the country, to mount detection programs in order to effectively dedicate funding. While these tools are valuable to make decisions on which states may be at risk of pest establishment, the models presented here refine which grape production areas have the highest relative risk of pest establishment for several key pests to allow optimal use of scarce resources to design pest surveys. Adding information about invasion pathways would further refine efforts to optimize detection efforts in areas of the highest risk of pest arrival and establishment.

Conclusions

Detection and surveillance efforts are important components of early pest management strategies but are often costly and time-intensive (Blackburn et al. 2017). The still-substantial cost and potentially reduced efficacy of multi-lure traps means that informed decisions must be made about where to implement these efforts in at-risk regions. To this end, predictive methods such as SDM may guide pest monitoring efforts. This suggests predictive methods will still be of practical value in guiding early detection and surveillance efforts for entire pest complexes. Results of this work can be used to make preventive management more effective by identifying high and moderate risk areas for pest invasion and potential pathways of pest introduction and spread. Furthermore, this study can be used as a reference for the assessment of other pest complexes.

Our findings suggest that most resources should be used to avoid a secondary spread of EGVM in the viticulture regions of the West Coast of the United States. Additionally, given the apparent potential for coexistence of the European species in some areas (Ioriatti et al. 2012), traps embedded with multiple species' pheromones may offer a logistically easier and more cost-effective way to monitor for multiple species (Chase et al. 2018). Ongoing studies with different combinations of lures are evaluating the potential virtue of these multi-lure traps in grape moth pest monitoring programs (A. Lucchi, Personal Communication; G. Simmons, unpublished data). The results of this work can be integrated with important management tools, such as the USDA Office of Pest Management Policy (OPMP) that serve as valuable inputs into setting pest control strategies.

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Supplementary material I

Assessing the risk of invasion by a vineyard moth pest guild

Authors: Hector Zumbado-Ulate, Tyler E. Schartel, Gregory S. Simmons, Matthew P. Daugherty

Data type: figures and tables (word document)

- Explanation note: table S1. 34 environmental variables considered during the development of species distribution models for five lepidopteran grapevine pests. table S2. Climatic suitability modeling methods as organized by the ODMAP framework (Zurell et al. 2020). table S3. Fit metrics for the most robust model of the extent of climatically suitable habitat for each of five individual moth species. table S4. Estimates of the extent of climatically suitable habitat in km² (and percent of total viticultural regions) shared by pairs of five moth pest species across viticulture regions of the West Coast of the United States. figure S1. Study region with purple polygons denoting the location of viticulture regions within the West Coast of the United States, specifically in California, Oregon, and Washington. figure S2. Known occurrences (orange dots) and climatic suitability estimates for the European grape berry moth, Eupoecilia am*biguella*, across its native range in Europe. **figure S3.** Known occurrences (orange dots) and climatic suitability estimates for the European grapevine moth, Lobesia botrana, across its native range in Europe. figure S4. Known occurrences (orange dots) and climatic suitability estimates for the Grape berry moth, Paralobesia viteana, across its range in North America. figure S5. Known occurrences (orange dots) and climatic suitability estimates for the Grape tortrix moth, Argyrotaenia ljungiana, across its native and invaded range in Europe. figure S6. Known occurrences (orange dots) and climatic suitability estimates for the Christmas berry webworm, Cryptoblabes gnidiella, across its native range in Europe and Northern Africa. figure S7. Response curves of the two environmental predictors with the highest contributions to the model predictions for the European grapevine moth, Lobesia botrana, across its native and invaded range. figure S8. Response curves of the two environmental predictors with the highest contributions to the model predictions for the grape berry moth, Paralobesia viteana, across its native and invaded range. figure S9. Response curves of the two environmental predictors with the highest contributions to the model predictions for the grape tortrix moth, Argyrotaenia ljungiana, across its native and invaded range. figure S10. Response curves of the two environmental predictors with the highest contributions to the model predictions for the European grape berry moth, Eupoecilia ambiguella, across its native and invaded range. figure S11. Response curves of the two environmental predictors with the highest contributions to the model predictions for the Christmas berry webworm, Cryptoblabes gnidiella, across its native and invaded range.
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RESEARCH ARTICLE



High abundance but low diversity of floral visitors on invasive Heracleum mantegazzianum (Apiaceae)

Petr Bogusch¹, Terezie Vojtová^{1,2}, Jiří Hadrava³

University of Hradec Králové, Faculty of Science, Department of Biology, Rokitanského 62, CZ-500 03 Hradec Králové, Czech Republic 2 Research and Breeding Fruit Institute, Holovousy 129, 508 01 Holovousy, Czech Republic 3 Charles University, Faculty of Science, Viničná 7, 128 44 Prague, Czech Republic

Corresponding author: Petr Bogusch (bogusch.petr@gmail.com)

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Abstract

Currently, plant invasions affect native ecosystems across the Earth. Although much attention has already been paid to their effect on local communities, we still lack basic information on the associations between alien and local species. Here, we present the results of our survey of pollinators of the invasive plant Heracleum mantegazzianum (Apiaceae) in central Europe. At 20 sites within the westernmost part of the Czech Republic, which is strongly affected by the invasion of H. mantegazzianum, pollinators on the flowers of *H. mantegazzianum* were examined and compared to the species composition of pollinators on native vegetation in the surrounding area. While the flowers of H. mantegazzianum were frequently visited by high abundance of insects, the communities of H. mantegazzianum pollinators were relatively species poor, and the proportion of abundances of *H. mantegazzianum* pollinators was very uneven, with few species of generalist Diptera and the honey bee (Apis mellifera) dominating over all other flower visitors. Significantly larger species of the family Syrphidae visited flowers of giant hogweed than of other plants. Thus, giant hogweed is not a necessary part of flower communities for flower visiting insects, and it should be eradicated because of its negative effects on other plants, landscape and humans. Our results highlight the need for more detailed studies on direct interactions between alien plant species and native pollinator communities as well as indirect interactions between alien plants and native plants through competition for pollinators.

Keywords

Czech Republic, honeybee, hoverflies, plant invasion, plant-pollinator interactions

Introduction

Invasive or alien plants represent, among the number of non-natives, the most dangerous species, with a certain negative effect on native species, ecosystems, landscapes and often human beings. They usually have a very high ability to overgrow large areas in the landscape of their new area of occurrence and often can destroy or inhibit native communities and species of plants (Randall and Marinelli 1996; Müller-Schärer et al. 2004; Hejda et al. 2009). Therefore, a lot of attention has been paid to this dangerous behaviour of invasive species, and the results of these surveys are used in the elimination of invasive plants. Continental or regional Black, Grey and Watch lists provide information on the most important species and their potential threats (Blackburn et al. 2014; Pergl et al. 2016). Regarding Socio-economic Impact Classification of Alien Taxa (SEICAT), the measuring tool for the potential dangerousness of invasive species of plants and animals, many plant species are marked to bring massive concern for humans (Bacher et al. 2017). Among these plants, the giant hogweed (*Heracleum mantegazzianum*) is, in most of Europe, one of the best known and most discussed invasive plants (Rijal et al. 2015).

The giant hogweed is a perennial herb of the family Apiaceae, with the original area of occurrence in the western Caucasus. This plant is very conspicuous, 2-5 metres tall, and produces umbelliferous inflorescences with a diameter of approximately 30-50 cm (Pyšek and Pyšek 1995). Most likely, the plant was introduced to Europe in the 19th century as an ornamental plant because of its conspicuous inflorescences (Nielsen et al. 2005). Shortly after its introduction, the plant started to spread in Western and Northern Europe, and in the 20th century, it started to form a very strong population and overgrow large areas of various characteristics (Pyšek and Pyšek 1995; Nielsen et al. 2005). Currently, this species has become highly invasive, especially in cooler and humid regions and causes many problems there. The main negative effect is that this plant reproduces very rapidly, produces hundreds to thousands of diaspores every year, and rapidly overgrows large areas supplanting the native vegetation very fast (Nielsen et al. 2005; Pyšek et al. 2010). Giant hogweed is also dangerous for humans because of its metabolites, which cause strong allergic reactions upon contact with human skin. Thus, policies of countries fund specialized programmes focused on the destruction of this plant species to avoid large invasions in large areas, which were caused several times in the past (Thiele et al. 2007; Pyšek et al. 2010).

Because of its large white compound inflorescences with open and easily reachable flowers as well as due to its extraordinary height, it is likely that giant hogweed can be attractive for pollinators like other plants of similar size and with large flowers (Ohashi and Yahara 2001). However, only a few studies on this topic have been done to date, and the most comprehensive by Zumkier (2012) remains unpublished. The first study by Grace and Nelson (1981) compared pollinator diversities and the pollen carried by them on *H. mantegazzianum* and the native *H. sphondylium*. The authors reported similar number of species and individuals of pollinators on both plants but the species spectra differed. Nielsen et al. (2005) studied marginally pollinators of *H. mantegazzianum* and Zumkier (2012) examined the competition for pollinators between the native *Heracleum sphondylium* and invasive *H. mantegazzianum* in Germany. Insects, especially honey bees, visited flowers of the larger giant hogweed much more frequently. Diptera were very numerous, while the genus *Lucilia* (Calliphoridae) overwhelmed other groups of this order. Larger pollinators, hover flies (Diptera, Syrphidae), wasps (Hymenoptera, Vespidae) and beetles (Coleoptera), were much more numerous in plots with invasive vegetation led by giant hogweed. However, most of these studies were focused on one group of insects and/or insects were not identified to a species level, so a comprehensive list of species associated with flowers of giant hogweed is still missing. In addition, a comparison with abundances and diversities of insects of the same groups at the same localities is still missing.

We decided to fill the gaps in the knowledge of insects associated with giant hogweed. We studied all insects searching for pollen and/or nectar on flowers of giant hogweed in the region of the Czech Republic where this plant is the most numerous and where it forms homogeneous vegetation. The main aim of our study was to determine whether giant hogweed is attractive for insects and whether specialized pollinators or red-listed species visit the flowers of this invasive plant at higher abundances. The composition of flower visitors on growths of giant hogweed was compared to the composition of flower visitors collected on native plants in nearby vegetation in order to show which part of the flower-visiting insect community could exploit floras' sources from giant hogweed as well. We also focused on trying to evaluate whether the large compound inflorescences of giant hogweed are visited by larger insects than is the case with flowers of other, smaller plant species (such as the studied example of Syrphidae). Based on the results, we would like to evaluate whether overgrowths of giant hogweed are valuable or dangerous for communities of flower visiting insects.

Methods

Insects on flowers of giant hogweed (*Heracleum mantegazzianum*) were studied near the town of Mariánské Lázně in the western part of the Czech Republic (Central Europe) in July 2020. This region suffers from the largest invasion of this plant in the country for decades, and thus, the strongest populations of giant hogweed in the whole country occur there (Pyšek and Pyšek 1995; Dostál et al. 2013). Out of the sites with the highest densities of flowering *H. mantegazzianum*, 20 sites at a distance of at least two kilometres from each other were selected for the survey. Most of the sites were located in relatively humid stream valleys (12 localities), on meadows (8), two locations were field ruderals. The size of the site ranged between 15 935 and 182 137 m² but most of the sites were smaller (mean 59 995 \pm SD 9 158 m², median 48 744 m²). The characteristics of the localities are in Suppl. material 1: table S1. The map of the Mariánské Lázně region with all localities is shown in Fig. 1.

At each site, we swept all insects from the flowering parts of all *H. mantegazzianum* plants using an entomological net, and additionally, we swept all insects visiting



Figure 1. A map of central Europe with the region of Mariánské Lázně (Czech Republic) emphasized **B** map of the studied region with the localities. Green circles – studied localities, red circles – localities not visited, blue circles – localities with absence of *Heracleum mantegazzianum*, empty circles – localities, which were very near to other localities. Light green area is the area of Slavkovský les Protected Landscape Area.

other flowering plants at each site. We swept all flowers at each site (one person giant hogweeds, second other flowering plants in nearby native vegetation), while each flower was swept only once. In most localities, we had to sweep all flowers of giant hogweed and other plants; in larger localities we swept a linear transect of the length 150-200 m. Each locality was sampled once, at the time of the year when the giant hogweed was in flower. We did the field work in the warmer part of the day (between 11 a.m. and 4 p.m.) and only on days when the weather was warm (temperature above 20 °C) and sunny with no rain. At each locality, we mapped other flowering plants at a distance not more than 10 m from the nearest giant hogweed methodologically similarly to Braun-Blanquet's phytosociological relevées (following the methodology of Kaplan (2012)) to illustrate the species spectra of flowering plants. The species spectra of flowering plants quite highly overlapped (see Suppl. material 1: table S2). All captured insects were immediately transferred into 75% ethyl alcohol using a plastic dish. Captured insects were sorted into orders in the laboratory. Although insects of many orders were captured, we studied only those that were associated with flowers, nectar and pollen: Diptera, Hymenoptera, Coleoptera, and Lepidoptera. All captured members of these four orders were identified to the species level if possible; taxonomically problematic groups of Diptera and Coleoptera were sorted to morphospecies only.

Since the family Syrphidae was the most numerous in individuals and species of all families both on giant hogweed and other plants, we compared the overall lengths of species, while the mean and median were determined, and Mann-Whitney test for comparison was performed. We measured the body lengths of 751 specimens from giant hogweed and 701 specimens from flowers of other plants using the measuring tool

of the microscope Keyence VHX 100. The body length was described as the distance between the mouthparts and topapex of abdomen. Then, we used the software PAST 2.14 (Hammer et al. 2001) to make the box plots, count medians and means and to perform Mann-Whitney test to compare the body lengths.

For all studied groups together and for each group separately, we performed rarefaction curves to show the diversities of studied groups. To estimate their species richness, we calculated the Chao-1 estimator, corrected for unseen species and by plotting the rarefaction curves. To compare the species richness of the analysed datasets, we calculated the Sørensen, Morisita-Horn and the combined Chao's Sørensen raw (uncorrected for unseen species) abundance-based similarity (Colwell and Coddington 1994) indices. We also calculated the total numbers of species and individuals found and the basic diversity indices, including dominance (D = 1 - Simpson index), equitability, Fisher's alpha and Berger-Parker dominance indices. Pearson and Spearman correlation coefficients and their significance were calculated when indicated. All these indexes were performed to show the species richness, diversities and dominances both on flowers of giant hogweed and other plants at the localities, and to compare them. The conservation value of the analysed species was assessed according to the most recent version of the national Red List (Hejda et al. 2017), and in the case of Diptera, which were not assessed in the most recent version of the national Red List, a previous version was used (Farkač et al. 2005). The species included in the Czech Red List were termed "threatened" throughout the text and included species known as vulnerable (VU) or near threatened (NT). All the calculations were performed in SigmaPlot 12.0 and PAST 2.14 (Hammer et al. 2001). Data are shown as the mean \pm standard deviation (SD) unless stated otherwise.

Results

Species recorded

In total, we captured 2,611 individuals of 141 species or morphospecies of insects on flowers of giant hogweed (Suppl. material 1: table S1), of which Diptera was the most numerous group in terms of both species (64) and individuals (1,983). Hymenoptera, with 53 species, was the second most numerous group, but the number of individuals was only 387. We recorded only 236 individuals of 20 species of Coleoptera and five individuals of four species of Lepidoptera. On flowers of other plants, the numbers of species were slightly higher but with a lower number of individuals in Diptera (1,238 individuals of 73 species) and Hymenoptera (296 individuals of 58 species). Coleoptera (588 individuals of 45 species) and Lepidoptera (59 individuals of 18 species) were much more numerous both in individuals and species (Table 1).

Among Diptera, the datasets from giant hogweed showed dominances of several species, while most other species were recorded only in small numbers of individuals. The most numerous flower visitors of *Heracleum* were *Eristalis pertinax* (Diptera, Syrphidae) with 371 individuals, *Gonia ornata* (Diptera, Tachinidae) with 316 individuals,

	All groups		Diptera		Hymenoptera		Coleoptera		Lepidoptera	
	GH	Other	GH	Other	GH	Other	GH	Other	GH	Other
Species	141	194	64	73	53	58	20	45	4	18
Individuals	2611	2181	1983	1238	387	296	236	588	5	59
Chao-1	205	287	77	90	91	103	24	66	6	21
Dominance_D	0.06	0.06	0.09	0.13	0.21	0.26	0.33	0.17	0.28	0.09
Simpson_1-D	0.94	0.94	0.91	0.87	0.79	0.74	0.67	0.83	0.72	0.91
Shannon_H	3.53	3.73	3.00	2.90	2.54	2.44	1.69	2.36	1.33	2.61
Equitability_J	0.71	0.71	0.72	0.68	0.64	0.60	0.56	0.62	0.96	0.90
Fisher_alpha	31.93	51.46	12.64	16.96	16.61	21.56	5.22	11.34	9.28	8.83
Berger-Parker	0.14	0.18	0.19	0.32	0.43	0.49	0.54	0.32	0.40	0.15
Sørensen	0.484	-	0.642	-	0.432	-	0.338	-	0.182	-

Table 1. Diversity indices for all studied groups together and for Diptera, Hymenoptera, Coleoptera and Lepidoptera separately. GH – giant hogweed, other – other plants at the locality.

Sarcophaga sp. with 155, and *Phorocera obscura* (Diptera, Tachinidae) with 149 individuals. Seven other species were recorded in more than 50 individuals, and an additional 14 species were recorded with more than 10 individuals. On flowers of other plants, *Sphaerophoria scripta* (Diptera, Syrphidae), with 392 individuals, was the most numerous, followed by *Dexia rustica* (Diptera, Tachinidae), with 129 individuals, and a small unidentified species of Muscidae (109 individuals). Only one additional species (*Melanostoma mellinum*, Syrphidae, 77 individuals) was recorded in larger number than 50 and 11 others in larger numbers than 10 individuals.

The honey bee *Apis mellifera* was the most numerous species among Hymenoptera in both datasets (168 individuals on giant hogweed and 146 on flowers of other plants), while other species were recorded in much lower numbers of individuals. On giant hogweed, *Dolichovespula sylvestris* (Hymenoptera, Vespidae) was recorded in 31 individuals, and *Lasioglossum fulvicorne* and *Lasioglossum pauxillum* (Hymenoptera, Halictidae) were both recorded in 24 individuals; only two other species were recorded in more than 10 individuals. On flowers of other plants, *L. pauxillum*, with 27 individuals, was the second most numerous species, and only two other species were recorded in more than 10 individuals.

Among Coleoptera, *Rhagonycha fulva* (Coleoptera, Cantharidae) comprised 127 individuals recorded on flowers of giant hogweed, more than half of all recorded individuals of this order. It was followed by *Oedemera femorata* (Coleoptera, Oedemeridae) with 32 individuals, *Oxythyrea funesta* (Scarabaeidae) with 26 individuals and *Stenurella melanura* (Coleoptera, Cerambycidae) with 17 individuals. Surprisingly, the two most numerous beetles on giant hogweed were also the most numerous on other plants, with 191 and 128 individuals, respectively. *S. melanura* was the third most numerous, with 63 individuals, and only five other species were recorded in 10 or more individuals.

All species of Lepidoptera represented only small numbers of individuals both on flowers of giant hogweed and other flowering plants, with *Aphanthopus hyperanthus* and *Maniola jurtina* (both Satyridae) being the most numerous on other plants, both recorded in nine specimens.

Rare and red-listed species

Regarding the Red lists (Hejda et al. 2017 and Farkač et al. 2005), we recorded mostly common and numerous species. Only 16 Red-listed species were recorded, all of them with one or a few individuals (Chrysogaster coemiteriorum, Diptera, Syrphidae, with 14 individuals being the most numerous). Two critically endangered species (CR) were recorded: the crabronid wasp Gorytes quadrifasciatus (Hymenoptera, Crabronidae) and the lepidopteran Zygaena osterodensis (Lepidoptera, Zygaenidae), but both were only on flowers of native plants, not on giant hogweed. The endangered (EN) solitary wasp Symmorphus murarius (Hymenoptera, Vespidae) was recorded on giant hogweed, and the chrysomelid beetle Galeruca dahlii (Coleoptera, Chrysomelidae) was recorded on flowers of native plants. Of seven vulnerable (VU) species, hover flies (Diptera, Syrphidae), Parhelophilus frutetorum, Chrysogaster coemiteriorum, and Xylota tarda, and the crabronid wasp (Hymenoptera, Crabronidae), Gorytes quinquecinctus, occurred both on flowers of giant hogweed and other plants, while the hover fly Parhelophilus versicolor (Diptera, Syrphidae), sweat bee Lasioglossum tricinctum (Hymenoptera, Halictidae) and eusocial wasp Dolichovespula norwegica (Hymenoptera, Vespidae) were recorded only on flowers of giant hogweed. The near threatened (NT) solitary bee Andrena pandellei (Hymenoptera, Andrenidae) and butterfly Melitaea athalia (Lepidoptera, Nymphalidae) were recorded on flowers of native plants, while the butterfly Satyrium *w-album* (Lepidoptera, Lycaenidae) was recorded on flowers of giant hogweed.

Species diversities

The Chao-1 estimator of species richness was 205 ± 20 species (95% CI) for *H. mantegazzianum* and 287 ± 26 species (95% CI) for other plants. The value of the Simpson index showing heterogeneity was 0.94 for *H. mantegazzianum*, which means that several species were numerous and dominant. A similar result was obtained from the Shannon-Wiener index (value 3.529). More surprisingly, the values of both indices were similar for other plants (Simpson index 0.94, Shannon-Wiener index 3.73). Eighty-one species were shared, and the value of the Sørensen similarity index between *H. mantegazzianum* and other plants was 0.48. The rarefaction curve shows the mean of sorting of repeatedly mixed taxa. We can see that more individuals but fewer taxa were recorded on the flowers of *H. mantegazzianum* (Fig. 2). The diversity of insects was larger on other plants, while several species dominated in high numbers on the flowers of *H. mantegazzianum* (Table 1).

Regarding the groups, the estimated diversity on other plants is always slightly higher (Diptera and Hymenoptera) or much higher (Coleoptera) than the estimated diversity on flowers of *H. mantegazzianum* (Table 1). This is also supported by rarefaction curves for all four insect orders (Fig. 3). Especially in Diptera and Hymenoptera, the diversity is higher on other plants, although numerous individuals of several species over-dominated in numbers on flowers of *H. mantegazzianum*. For Coleoptera and Lepidoptera, both the abundances and diversities were much higher on other plants than on *H. mantegazzianum*.



Figure 2. Individual rarefaction for all studied groups A insects of flowers of *Heracleum mantegazzianum*B insects on flowers of other plants at the locality.



Figure 3. Individual rarefaction for the studied groups separately **A** insects of flowers of *Heracleum mantegazzianum* **B** insects on flowers of other plants at the locality.

Regarding the diversity indices, both the Simpson index and Shannon-Wiener index showed that the distribution of species of Diptera was very similar both on *H. mantegazzianum* and on other plants, several species were very numerous, and the distribution of individuals was different among the species, with several species dominating. In Hymenoptera, the situation is similar; only the species distribution shows lower differences than in Diptera. In Coleoptera, the distribution of individuals was equal on *H. mantegazzianum* but unequal on other flowers, with slight dominance of several species. For Lepidoptera, the number of species and individuals recorded was very small, and thus, we cannot make any conclusions.

The Sørensen similarity index is the highest in Diptera, where more than half of the species are shared between *H. mantegazzianum* and other plants. In Hymenoptera, the value is lower than 0.5; in Coleoptera, the value is less than 0.33, and the lowest is in Lepidoptera, which may be due to the low number of recorded species and individuals on the flowers of *H. mantegazzianum*.

The median total length of hover flies found on *H. mantegazzianum* was 12.35 mm, the same for hover flies found on other plants was 9.60 mm (Fig. 4). When compared, we found that flowers of *H. mantegazzianum* were visited by significantly larger species (p < 0.001).



Figure 4. Box plot with the comparison of total lengths of 751 individuals of hover flies recorded on *Heracleum mantegazzianum* (**A**) and 705 individuals on other plants (**B**).

Discussion

The numbers of species recorded in our study are much higher than in all previous surveys, partly because a very large portion of species were identified to a species level, contrary to previous studies (Nielsen et al. 2005; Zumkier 2012). Thus, our study can

serve as the first comprehensive information on insect species associated with flowers of giant hogweed compared to flower visitor communities on nearby native vegetation, and as a starting point for further studies on related topics. Despite the high numbers of individuals recorded, the total number of species recorded on composite flowers of giant hogweed was not very high; the high densities of flower visitors on this plant are driven mostly by a few very numerous species. Thus, the honey bee represented 46% of all individuals of Hymenoptera and common larger hover flies (i.e., Eristalis pertinax) represented 48% of all individuals of Diptera. Except for the Apiaceae specialist Rhagonycha fulva, only a few species of beetles and butterflies were recorded on flowers of giant hogweed, contrary to many more species and specimens recorded on flowers of native plants at the studied sites. Our results thus correspond with those of Zumkier (2012), who recorded that composite flowers of giant hogweed hosted high numbers of individuals of common and usually unspecialized species. The fact that we have not recorded any specialists bound on this plant also supports the results of both abovementioned studies. Interestingly, during the field work, we did not record any bee species collecting pollen from giant hogweed, which is in contrast with the study of Grace and Nelson (1981).

In contrast with previous authors (Grace and Nelson 1981; Nielsen et al. 2005; Zumkier 2012), we didn't compare the flower visitors' spectra between native *Heracleum sphondylium* and the invasive *H. mantegazzianum*. The native *H. sphondylium* flowers about a month later than giant hogweed and the differences of insects visiting the flowers of both species can thus result from the phenology, not only from the preferences of insect species visiting the inflorescences of each plant (see Pyšek and Pyšek 1995). Further, *H. sphondylium* is not very numerous in the studied region and forms usually weak populations. Significantly, *H. sphondylium* is one of the favourite nectar sources for the Gasteruptiidae family (Parslow et al. 2020; Bogusch 2021) but Grace and Nelson (1981) did not record any species of this family and neither did we.

In addition, we cannot compare our results with other studies in detail because most previous studies did not identify the collected material to species level, but only to higher taxonomic levels; (Zumkier 2012) recorded a much lower number of species or dealt with phytophagous species, not pollinators. Zumkier (2012) reported that honeybees were also the most numerous species of Hymenoptera in his studies, as well as larger species of hover flies. The results are contrary to our unpublished records from studies of Canadian goldenrod (*Solidago canadensis*) and hartleaf oxeye (*Telekia speciosa*), which both hosted rich communities of Hymenoptera and many species of bees. Furthermore, females of both polylectic and Asteraceae oligolectic bees were recorded in high numbers collecting pollen, while no bee female collecting pollen was recorded on flowers of giant hogweed. Interestingly, there are ten bee species specialised to pollen from the family Apiaceae recorded in the Czech Republic and several of these species are quite common and widespread and certainly occur in the studied region (Bogusch et al. 2020). However, none of them has been recorded on giant hogweed. In contrast with some other invasive plants, giant hogweed does not seem to be that important for insects as a source of pollen, and the results copy those of studies in which invasive and native plant species were compared (Seitz et al. 2020; Abdallah et al. 2021; Parra-Tabla and Arceo-Gómez 2021). Most species use large composite flowers of this plant only or predominantly as a source of nectar, and larger and numerous species can be found on composite flowers of this plant in very high numbers. However, we think that the negative effects of giant hogweed on other plants, landscapes and people (for details, see Pyšek et al. 2010; Nentwig et al. 2014) outweigh its potential benefit as a nectar source.

Klečka et al. (2018) showed that while representatives of Hymenoptera visit mainly flowers with the same height as surrounding vegetation, many representatives of Diptera prefer highly placed flowers to less laid flowers. We suppose that this difference between both taxa could have affected the composition of flower visitors of *Heracleum* compared to other plants as *Heracleum* is usually much higher than the surrounding herbal vegetation, attracting several representatives of Diptera very effectively. For other taxa, however, such as Hymenoptera, giant hogweed is not as attractive in comparison with other plant species. This effect could thus lead to the observed flower visitation pattern. Consequently, due to the extraordinary height of *H. mantegazzianum*, this invasive species could negatively affect the native plants that are pollinated by Diptera by competition for pollinators, while its effect on plants pollinated by Hymenoptera could be lower. However, further research will be needed to test this hypothesis.

Among hover flies, the majority of rare and endangered species recorded on *Heracleum* as well as other plants were those with saprophagous semiaquatic larvae, associated predominantly with wetlands and oligotrophic fens (Speight 2020). The presence of these rare species is thus driven by the conditions of the surrounding habitats rather than the species composition of flowering plants. It is also necessary to study the interactions among species, bringing more comprehensive information on the ecology, diversity and landscape, than to study only one species (Jordano 2016).

Despite its high population densities and distinctive inflorescences, the giant hogweed hosts only limited spectrum of flower visitors compared to the local species pool of flower visitors recorded on native vegetation. Giant hogweed may represent a good and rich source of nectar for some larger insects (honey bee, social wasps, golden beetles and larger syrphids) but is probably not useful for the majority of insects. We think that its role as a nectar supplier is not as important as its negative and harmful effects on native vegetation, landscape, and humans. It is good to eradicate this plant in areas where it behaves invasively (Dodd et al. 1994; Pyšek and Pyšek 1995; Nielsen et al. 2005; Pyšek et al. 2010; Dostál et al. 2013). The management of habitats connected with the destruction of giant hogweed is thus necessary (Pyšek et al. 2010). We can also support this fact with our observations – giant hogweed was completely absent or present in 1–3 plants in many localities, which local botanists recommended, but it was very simple to find new unmanaged sites with many plants of this species, where nearly nothing else grew under and around giant hogweeds (Fig. 5).



Figure 5. Photo of giant hogweeds at locality 36.

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List of localities

Authors: Petr Bogusch, Terezie Vojtová, Jiří Hadrava

Data type: Occurences (Excel spreadsheet)

- Explanation note: table S1: List of localities of total 39 localities, several were not sampled because no giant hogweeds were present there or the localities were to near to another locality and composed one locality together.
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Link: https://doi.org/10.3897/neobiota.86.100625.suppl1

Supplementary material 2

List of all species

Authors: Petr Bogusch, Terezie Vojtová, Jiří Hadrava

Data type: Occurences (Excel spreadsheet)

- Explanation note: table S2: Lists of all species in all localities occurrences of all four studied groups.
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Link: https://doi.org/10.3897/neobiota.86.100625.suppl2

Supplementary material 3

Other flowering plants in the localities

Authors: Petr Bogusch, Terezie Vojtová, Jiří Hadrava

Data type: Occurences (Excel spreadsheet)

- Explanation note: table S3: Other flowering plant species at all localities with dominances measured in Braun-Blanquet scale.
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