RESEARCH ARTICLE



Leaf trait differences between 97 pairs of invasive and native plants across China: effects of identities of both the invasive and native species

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Abstract

Many studies have attempted to test whether certain leaf traits are associated with invasive plants, resulting in discrepant conclusions that may be due to species-specificity. However, no effort has been made to test for effects of species identity on invasive-native comparisons. Here, we compared 20 leaf traits between 97 pairs of invasive and native plant species in seven disturbed sites along a southwest-to-northeast transect in China using phylogenetically controlled within-study meta-analyses. The invasive relative to the native species on average had significantly higher leaf nutrients concentrations, photosynthetic rates, photosynthetic nutrients- and energy-use efficiencies, leaf litter decomposition rates, and lower payback time and carbon-to-nitrogen ratios. However, these differences disappeared when comparing weakly invasive species with co-occurring natives and when comparing invasives with co-occurring widespread dominant natives. Furthermore, the magnitudes of the differences in some traits decreased or even reversed when a random subset of strongly to moderately invasive species was excluded from the species pool. Removing rare to common natives produced the same effect, while exclusion of weakly to moderately invasives and dominant to common natives enhanced the differences. Our study indicates that the results of invasivenative comparisons are species-specific, providing a possible explanation for discrepant results in previous

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studies, such that we may be unable to detect general patterns regarding traits promoting exotic plant invasions through multi-species comparisons.

Keywords

Invasive plant species, leaf functional traits, multiple species experimental comparisons, native species, species identity, within-study meta-analysis

Introduction

Thousands of plant species have established wild populations outside their native regions (van Kleunen et al. 2015a), and the number is still increasing (Seebens et al. 2017). Some of these non-native species spread rapidly and can reach abundances much higher than those of most co-occurring native species or their native conspecifics (Inderjit et al. 2011; Zheng et al. 2015; Zhao et al. 2020). The mechanisms underlying such non-native plant invasions have become one of the major topics in biology (Richardson and Pyšek 2006; Feng et al. 2009; van Kleunen et al. 2010; Li et al. 2015; Hulme and Bernard-Verdier 2018). As a group, these invasive non-native (hereafter invasive) species may have distinct traits that allow them to compete with or even outcompete co-occurring native species (van Kleunen et al. 2015; Huang et al. 2020).

In order to disentangle the traits associated with invasive plants, many case studies have compared traits of invasive species with both native and non-invasive exotic species (McDowell 2002; Feng et al. 2007; Feng 2008; Wang et al. 2013; Liu and van Kleunen 2017; Liu et al. 2017). However, the conclusions were inconsistent or even contradictory among these studies, and no general pattern was evident. For example, Feng et al. (2007) found that the invasive plant *Buddleja davidii* has a higher specific leaf area than co-occurring native *Berberis vulgaris* and *Crataegus monogyna*, but similar to native *Cornus sanguinea*, *Sambucus nigra* and *Betula pendula*, and a higher leaf photosynthetic rate than the native plants except *B. pendula*. These results indicate that identities of the focal species strongly determine whether invasive-native differences in leaf functional traits were detectable.

Many researchers have attempted to obtain a conclusion with universal significance for traits associated with invasiveness (Baruch and Goldstein 1999; Leishman et al. 2007; Heberling and Fridley 2013; Divíšek et al. 2018; Huang et al. 2020). Unfortunately, there were still large variations in the conclusions from the above-mentioned multi-species (dozens of or more) comparisons. For example, the differences in seven of the 11 traits (64%) between invasive and native species were inconsistent (even opposite) among multi-species comparisons (Suppl. material 2: Table S1). Besides the multi-species experimental comparisons, five studies summarized the results from published case studies (Daehler 2003; Leishman et al. 2007; Pyšek and Richardson 2007; van Kleunen et al. 2010; Castro-Díez et al. 2014). In total, five traits were compared in more than one of these reviews (Suppl. material 2: Table S1), and differences between invasive and native species in four of the five traits (80%) were inconsistent among these reviews. Combining the multi-species comparisons and the reviews, we found that 14 traits were compared in more than one study, and the conclusions were inconsistent or opposite in nine of the 14 traits (64%) among these studies. The high frequency of the inconsistent results in these comparisons indicates that it is difficult to find general conclusions regarding traits associated with invasive species.

There are many reasons for discrepant conclusions among comparative studies between invasive and native species. For example, conclusions generated from reviews may be confounded by publication biases, which generally overestimate trait advantage of invasive species (Rosenberg et al. 2000; Leimu and Koricheva 2004; Koricheva and Gurevitch 2014). The conclusions of multi-species experimental studies may also be influenced by environmental factors such as disturbance regimes (Leishman et al. 2007). Trait differences between invasive and native species may be environment-dependent (Hulme and Bernard-Verdier 2018). However, the most important and often overlooked influencing factor may be the inherent trait characteristics of the invasive and native species compared. The differences between invasive and native species may vary with the changes in the species compared (McDowell 2002; Feng et al. 2007; Liu et al. 2017). Until now, however, no effort has been made to explicitly test the effect of species identity on invasive-native trait comparisons.

To address this problem, we compared 97 pairs of invasive and co-occurring native plant species at seven sites in six provinces from tropical to mid-temperate zones of China. The invasive species were divided into three categories according to their invasiveness (invasion status) in China, and the native species were also grouped into three categories according to their distribution and abundances in China. We focused on 20 leaf functional traits, which greatly influence plant resource capture ability and use-efficiency, and therefore plant growth and reproduction. We firstly determined the overall differences between the invasive and native species using a within-study meta-analytical approach, and then tested for the effect of species identity on the differences between the invasive and native species. We hypothesize that (1) the differences at least in some traits may be significant when the strongly to moderately invasive species are compared with their cooccurring natives, but not significant when the weakly invasive species are compared with their co-occurring natives. (2) Similarly, the differences may be significant when the rare to common natives are compared with their co-occurring invasives, but not significant when the widespread dominant natives are compared with their co-occurring invasives. (3) The magnitudes of the differences may decrease when we gradually exclude a random subset of strongly to moderately invasive species (also including the natives paired with them) from the species pool (97 pairs), while exclusion of weakly invasive species may enhance the differences. (4) Similarly, the magnitudes of the differences may decrease when we gradually exclude a random subset of rare to common natives from the species pool, while exclusion of widespread dominant natives may enhance the differences. (5) The magnitudes of the differences may be smaller when the invasives are compared with the natives that are invasive elsewhere than with the natives that are non-invasive elsewhere. To the best of our knowledge, no study has addressed the aforementioned issues, although many have compared traits of invasive and native species.

Materials and methods

Study sites and plant species

This study was conducted at seven sites in six provinces along the southwest-to-northeast axis of China. We selected two sites in Heilongjiang Province and one site in each of the other five provinces (Suppl. material 2: Table S2). All sites were disturbed severely and had many invasive plant species. In each site, the vegetation was mainly composed of mixed herbs and shrubs with scattered trees (see Suppl. material 3: Table S3 for the detail habitat of each species pair). The sites spanned 24° in latitude (21°56'– 45°39'N) and 28° in longitude (101°15'–129° 34'E), including tropical, subtropical and temperate zones (Fig. 1). The linear distance between the most southwestern and northeastern sites was ~3600 km.

In each site (at least 2000 m² with irregular shape), we first located as many invasive plant species (5-23) as possible, and then tried to select a taxonomically related (congeneric or confamilial) and/or functionally similar (with the same growth form, e.g. herb vs herb) native species near each invader (< 2 m), forming a comparable species pair (three replicates for each species). Taxonomically related and/ or functionally similar natives may share more similar growth strategies with the invasives, and thus increasing the comparability. For some of the invasive species, however, taxonomically related and/or functionally similar natives were not found, in which case the invasives were compared with their nearby randomly chosen natives, respectively (14 pairs, see Suppl. material 3: Table S3). To reduce confounding effects of phylogenetic distance between the invasive and native species in each species pair on the comparative results, phylogenetic relatedness was controlled when analyzing the differences between the invasive and native species (see statistical analysis section). Environmental heterogeneities within and especially among the sites were large, which inevitably influenced the variances within and between species categories (invasives vs. natives). Thus, we used a paired-species comparison approach (within-study meta-analysis) in order to decrease the confounding effects of environmental heterogeneities on species comparative results.

In total we compared 97 species pairs, including 56 invasives (35 annual herbs, 13 perennial herbs, 2 shrubs, 2 trees and 4 climbers) and 60 natives (23 annual herbs, 24 perennial herbs, 2 shrubs, 6 trees and 5 climbers) (Suppl. material 3: Table S3). The invasives were grouped into three categories according to their degree of invasiveness (distribution and ecological impacts; Ma 2013): 15 species with strong invasiveness, 17 with moderate invasiveness, and 24 with weak invasiveness, which represented 44.1%, 24.6%, and 14.5% of the total species in each category in China, respectively (Suppl. material 3: Table S3). The strongly invasive species were distributed in more than one geographic area, and had caused tremendous ecological and/or economic losses in China (Ma 2013). The moderately invasive species of species were also distributed in more than one geographic area but with less ecological and/or economic losses compared with the former (Ma 2013). The weakly

invasive species were locally distributed and caused minor ecological and/or economic losses in China (Ma 2013). The natives were grouped into three categories according to their abundance and distribution in China: 11 widespread dominants, 10 commons, and 39 rares [Li 1998; Flora of China (http://foc.eflora.cn/)]. This classification was based on the intrinsic characteristics of the natives, and the result of this classification had nothing to do with whether invasive species exist or not. In our study sites, the existing states of the invasive and native species were consistent with above classifications, i.e., strongly invasive plants and widespread natives had higher abundances than weakly invasives and rare natives, respectively. The natives were also separated into two categories according to their invasive elsewhere: 11 invasive elsewhere and 49 non-invasive elsewhere (http://www.griis.org/sources. php; and the references given in Suppl. material 3: Table S3). Some invasives were measured in more than one site.



Figure 1. Sample sites spanning 24° latitudes from tropical to temperate zones in China.

Measurements

For each of the 97 species pairs, we measured six individuals of the invasive and native species (582 individuals in total). Light-saturated photosynthetic rate ($P_{\rm max}$), stomatal conductance ($G_{\rm s}$) and dark respiration rate ($R_{\rm d}$) were measured in the morning on the youngest fully expanded leaves using a Li-6400 Portable Photosynthesis System (Li-Cor, Lincoln, NE, USA). Leaf temperature was set to 30 °C, photosynthetic photon flux density to 2000 µmol m⁻² s⁻¹, and CO₂ concentration in the reference chamber was 380 µmol mol⁻¹. We recorded $P_{\rm max}$ (µmol m⁻² s⁻¹) and $G_{\rm s}$ (mol m⁻² s⁻¹) when their values had become stable, then we switched off the light source and recorded $R_{\rm d}$ (µmol m⁻² s⁻¹) when its value had become stable. All the measurements were done in July and August, when the plants were at the vigorous growth stage.

For each leaf that was used for photosynthesis measurement, we measured its average thickness using a microcalliper at more than 10 points (avoiding veins), and single-side area using a Li-3000C Leaf Area Meter (Li-Cor, Lincoln, NE, USA). Then the leaf was oven-dried at 60 °C to constant weight, and weighed. Specific leaf area (SLA, cm² mg⁻¹) was calculated as the ratio of leaf area to dry mass, and leaf-tissue density (g cm⁻³) as the ratio of leaf mass to volume, i.e., leaf mass / (thickness × area). Mass-based P_{max} (µmol g⁻¹ s⁻¹), G_{s} (mmol g⁻¹ s⁻¹) and R_{d} (µmol g⁻¹ s⁻¹) were calculated from their measured area-based values and SLA.

For measuring leaf-element concentrations, 6 to 30 mature leaves around the leaf used for measuring photosynthesis were also collected from each sample plant. Leaf-carbon $(C_m, \text{mg g}^{-1})$ and nitrogen $(N_m, \text{mg g}^{-1})$ concentrations were determined using an Elementar Vario MAX CN analyser (Elementar Analysensysteme, GmbH, Germany). Leaf-phosphorus $(P_m, \text{mg g}^{-1})$ and potassium $(K_m, \text{mg g}^{-1})$ concentrations were determined using an IRIS advantage-ER inductively coupled plasma atomic-emission spectrometer (ICP-AES, Thermo Jarrell Ash Corp., MA, USA). Due to a limited amount of leaf material, C_m and N_m were not measured for seven of the 97 species pairs, and P_m and K_m were not measured for 17 of the species pairs (Suppl. material 3: Table S3).

Leaf-construction cost (CC, g glucose g⁻¹) was calculated as (5.39 × carbon concentration - 1191) / 1000, following Feng et al. (2007). Photosynthetic nitrogen-use efficiency (PNUE, µmol g⁻¹ s⁻¹), photosynthetic phosphorus-use efficiency (PPUE, µmol g⁻¹ s⁻¹), photosynthetic potassium-use efficiency (PKUE, µmol g⁻¹ s⁻¹), photosynthetic water-use efficiency (PWUE, µmol mol⁻¹), and photosynthetic energy-use efficiencies (PEUE, µmol g⁻¹ s⁻¹) were calculated as the ratios of P_{max} to N_{m} , P_{m} , K_{m} , G_{s} , and CC, respectively. Payback time (PT, d) of leaf-construction costs was calculated as (CC × 10⁶) / [12 × (P_{max} / 2 × 12 × 3600 - R_{d} × 12 × 3600) × 180 / 72], following Feng et al. (2011).

For measuring leaf-decomposition rate, we collected the remaining functional mature leaves of each sample plant and the mature leaves from nearby conspecific plants, which were oven-dried at 60 °C to constant weight and stored in desiccators until used. Enough leaf material for the decomposition experiment was available for 73 of the 97 species pairs. We weighed 1 to 2 g of dry leaves of each sample plant, and put the leaves into 15 × 20 cm nylon mesh bags that had 1 mm holes. In August (rainy season) the decomposition bags (438 in total) were put on the soil surface, after removal of natural litter, under a primary tropical rainforest in the Xishuangbanna Tropical Botanical Garden of the Chinese Academy of Sciences (21°41'N, 101°25'E, a.s.l. 570 m), Yunnan Province, southwest China. The three bags containing the leaves of each invasive species were put adjacent to the ones containing the leaves of its native counterpart species in order to decrease variation due to environmental heterogeneity. The pair-wise bags were placed randomly and at least 20 cm apart from one another. In September, the bags were collected, and the remaining leaves were washed gently, oven-dried at 60 °C to constant weight, and weighed. The concentrations of C and N were determined using an Elementar Vario MAX CN analyser. For 28 of the 73 species pairs, the remaining leaf material was insufficient for determination of C_m and N_m . Mass- (Loss-M; %), carbon-(Loss-C; %), and nitrogen-loss (Loss-N; %) rates of the leaves were calculated as (initial value - final value) / initial value.

In our decomposition experiment, mature leaves instead of leaf litters were used as it was impossible to collect enough leaf litter for these species. Strong disturbance of the study sites, differences in progress of leaf senescence and abscission among the species, and the great distance among the study sites all obstructed leaf-litter collection. Several previous decomposition experiments also used oven-dried mature leaves, and found that decomposition rates are not significantly different between dried green mature leaves and senescent yellow leaves (Leung 1986; Tam et al. 1990). It has been documented that nutrient concentrations in leaf litter are positively correlated with those in mature leaves, and that the latter better explain litter decomposition (Kobe et al. 2005; Cornwell et al. 2008; Bakker et al. 2011). Thus, interspecific differences in decomposition rate of mature leaves are likely to reflect the differences in decomposition rate of naturally senesced leaf litter (Bakker et al. 2011).

Statistical analyses

The overall differences between the invasive and native species in the 20 leaf traits were tested using within-study meta-analyses (van Kleunen et al. 2011; Huang et al. 2020). We firstly calculated the effect size (Hedges'd) and the corresponding sampling variance (v_d) of each trait for each species pair using the *escalc* function in R package metafor (Viechtbauer 2010). Hedges'd was calculated as:

$$d = \frac{\left(\overline{X}_i - \overline{X}_n\right)}{S}J$$

where \overline{X}_i and \overline{X}_n are trait means of the invasive and native species, respectively; *S* is the pooled standard deviation of the invasive and native species; and *J* is a weighting factor based on the number of replicates. *S* and *J* were calculated as:

$$S = \sqrt{\frac{(N_i - 1)(S_i)^2 + (N_n - 1)(S_n)^2}{N_i + N_n - 2}}$$

$$J = 1 - \frac{3}{4(N_i + N_n - 2) - 1}$$

where N_i and N_n are the numbers of the replicates of the invasive and native species (here 3 for all species), respectively; S_i and S_n are the standard deviations of the invasive and native species, respectively. The sampling variance of Hedges'*d* was calculated as:

$$v_d = \frac{N_i + N_n}{N_i N_n} + \frac{d^2}{2(N_i + N_n)}$$

We then calculated the weighted mean effect size (d^{++}) (using reciprocal of v_d) and 95% confidence interval (CI) of each trait for all species pairs using the random-effects model of the *rma.mv* function in R package metafor (Viechtbauer 2010). The overall difference was significant if the 95% CI did not include zero. The value of d > 0 indicates that the invasive species is higher in the trait than its native counterpart in the same species pair.

To determine whether the overall difference between the invasive and native species was affected by other factors besides sampling error, we tested for total heterogeneity in effect size of each trait among all species pairs (Q_T) . If Q_T was significant (P < 0.05) for a trait, we conducted the mixed-effects multivariate models using the *rma.mv* function to test for effects of other factors on the overall difference in this trait. In the mixed-effects models, Q_T was separated into two components: structural model (Q_M) and unexplained heterogeneity (Q_E) , and all were tested using the *Q*-test (Viechtbauer 2010). The factors included invasiveness of the invasive species (strong, moderate, and weak), and abundances (dominant, common, and rare) and invasive elsewhere (invasive and non-invasive elsewhere) of the native species.

To further determine the effects of the identities of both the invasive (invasiveness) and native (abundance) species on their overall differences, we compared invasive and native species separately from many subsets of species pairs. The subsets of species pairs were created by gradually and randomly removing invasives with different invasiveness (or natives with different abundances) from the species pool (4–10 pairs each time according to species number in each category; see Figs 4, 5). To increase the proportion of strongly invasive species in each subset of species pairs (until 100%), we first removed weakly invasive species and then moderately invasive species. Similarly, to increase the proportion of weakly invasive species in each subset of species pairs (until 100%), we first removed strongly invasive species and then moderately invasive species. To increase the proportion of rare natives in each subset of species pairs (until 100%), we first removed widespread dominant natives and then common natives, while removed rare natives and then common natives in order to increase the proportion of dominant natives in each subset of species pairs (until 100%).

Phylogenetic distance between the invasive and native species in each species pair, latitude and altitude of each study site, and the times for which each invasive species was compared with natives were used as random factors in our analyses. To obtain the phylogenetic distance, we constructed a phylogenetic tree using ribosomal DNA internal transcribed spacer (*ITS1* and *ITS2*) from GenBank (https://www.ncbi.nlm.nih.gov/). For 10 of the 116 species, the *ITS* sequences were not found in GenBank, and were substituted by those of their congeners, respectively: *Axonopus compressus* by *A. capillaris, Bidens maximovicziana* by *B. cernua, Buxus megistophylla* by *B. microphylla* subsp. *Sinica, Clinopodium* sp. by *C. gracile, Pistia stratiotes* by *Pinellia ternata* (confamilial), *Plantago asiatica* by *P. major, Polygonum strigosum* by *P. thunbergii* (syn. *Persicaria thunbergii*), *Pueraria edulis* by *P. montana* var. *lobata, Rheum* sp. by *R. altaicum, Rorippa globosa* by *R. indica*). This did not influence the results in such large-scale phylogeny. We first aligned the DNA sequences using MUSCLE in MEGA (version 6.06; Tamura et al. 2013), then constructed a maximum-likelihood tree and tested it with 100 bootstrap replicates. *Podocarpus macrophyllus* var. *maki* (gymnosperm) was used as an outgroup to root the tree (Suppl. material 1: Fig. S1). Finally, we calculated the phylogenetic distance between the invasive and native species in each species pair using *cophenetic* function in the R package ape (Swenson 2014).

All analyses were performed in R 3.5.2 (R Core Team 2018).

Results

Overall differences between the invasive and native species

Based on our phylogenetically controlled within-study meta-analyses, the invasive relative to the native species on average had significantly higher leaf-nitrogen concentrations ($N_{\rm m}$), light-saturated photosynthetic rates ($P_{\rm max}$), photosynthetic energy- (PEUE), nitrogen- (PNUE), phosphorus- (PPUE), and potassium-use (PKUE) efficiencies, leaf carbon- (Loss-C) and nitrogen- (Loss-N) loss rates (Fig. 2). Leaf-phosphorus concentrations ($P_{\rm m}$; 95% CI: -0.016 to 0.623) and stomatal conductance ($G_{\rm s}$; 95% CI: -0.027 to 0.531) were marginally higher for the invasives. In contrast, the invasives had shorter payback times (PT) and lower carbon-to-nitrogen ratios (C:N) than cooccurring natives. The invasive and native species were not significantly different in leaf-construction costs (CC), leaf tissue density (Density), leaf-potassium concentrations ($K_{\rm m}$), leaf mass-loss rates (Loss-M), photosynthetic water-use efficiency (PWUE), dark respiration rates ($R_{\rm a}$), specific leaf area (SLA), and leaf thickness (Thickness).

For all 12 traits that showed significant differences between all invasive and native species, the overall differences were affected by other factors besides sampling error, as showed by the significant heterogeneities in the effect sizes of the 12 traits among the invasive-native species pairs (for Q_{1} , P < 0.05; Suppl. material 2: Table S4). We focused on these 12 traits in the following sections.

Effects of invasiveness of the invasive species

Invasiveness of the invasive species influenced the differences between the invasive and native species in Loss-N ($Q_M = 8.99$, P = 0.011), but not in other 11



Figure 2. Phylogenetically informed mean effect sizes (Hedges'*d*) and their 95% confidence intervals showing the overall differences in 20 leaf functional traits between the invasive and native species. The figures between brackets on the left indicate the number of the invasive species included and the number of species pairs compared, respectively. C:N, leaf-carbon-to-nitrogen ratio; CC, leaf-construction costs (g glucose g⁻¹); Density, leaf tissue density (g cm⁻³); G_s , mass-based leaf stomatal conductance (mmol g⁻¹ s⁻¹); K_m , leaf-potassium concentration (mg g⁻¹); Loss-M, leaf-mass-loss rate (%); Loss-C, leaf-carbon-loss rate (%); Loss-N, leaf-nitrogen-loss rate (%); N_m , leaf-nitrogen concentration (mg g⁻¹); P_m , leaf-phosphorus concentration (mg g⁻¹); P_{max} , mass-based leaf light saturated photosynthetic rate (μ mol g⁻¹ s⁻¹); PEUE, leaf photosynthetic energy-use efficiency (μ mol g⁻¹ s⁻¹); PKUE, photosynthetic potassium-use efficiency (μ mol g⁻¹ s⁻¹); PNUE, photosynthetic nitrogen-use efficiency (μ mol g⁻¹ s⁻¹); PUE, photosynthetic mass-lased leaf rate (μ mol g⁻¹ s⁻¹); PNUE, photosynthetic nitrogen-use efficiency (μ mol g⁻¹ s⁻¹); SLA, specific leaf area (cm² mg⁻¹); Thickness, leaf thickness (mm).

traits (Suppl. material 2: Table S4). As expected, the strongly or moderately invasive species had significantly higher Loss-N than their co-occurring natives, while the difference disappeared when comparing weakly invasive species with their cooccurring natives (Fig. 3A). Also consistent with our expectation, the magnitudes of the differences between the invasive and native species in Loss-N decreased when gradually and randomly excluding strongly to moderately invasive species from the species pool (Fig. 4; see downwards). The difference became not significant when 10 of the strongly invasive species were excluded from the species pool. Furthermore, invasives were even lower in Loss-N than natives (although not significant) when only the weakly (or including four moderately) invasive species were compared with their co-occurring natives (Figs 3A, 4). However, effects of the exclusions of moderately or even weakly invasive species were relatively small (Fig. 4; see upwards).

Invasiveness of the invasive species also influenced the differences in other 11 traits between the invasive and native species (Suppl. material 1: Figs S2, S3), although its effects on these traits were not detected in our mixed-effects models (Suppl. material 2: Table S4). The differences in these traits were not significant when only the weakly (or including few moderately) invasive species were compared with their co-occurring natives. In addition, the magnitudes of the differences in $P_{\rm max}$, PNUE, and Loss-C increased when gradually excluding weakly to moderately invasive species from the species pool.



Figure 3. Effects of invasiveness of the invasive species (**A**) and abundances of the natives (**B**) on differences between invasive and native species, respectively. S, M and W indicate that strongly, moderately and weakly invasive species are compared with their co-occurring natives, respectively. D, C and R indicate that widespread dominant, common and rare natives are compared with their co-occurring invasives, respectively. The traits whose interspecific differences were not affected by those factors were not shown. See Figure 1 for trait abbreviations. The figures between brackets on the left indicate the numbers of species pairs included in the analyses.

Effects of abundances of the native species

Abundances of the natives significantly influenced the differences between the invasive and native species in C:N ($Q_M = 18.66$, P < 0.001), Loss-N ($Q_M = 6.00$, P = 0.049), N_m ($Q_M = 10.13$, P = 0.006), and PKUE ($Q_M = 7.01$, P = 0.030), but not in other eight traits (Suppl. material 2: Table S4). The invasives had similar C:N, Loss-N and N_m , and higher PKUE when compared with co-occurring widespread dominant natives (Fig. 3B). When compared with rare or common natives, the invasives had significantly lower C:N, higher Loss-N (not significant with common natives) and N_m , and similar PKUE. Also consistent with our expectation, the magnitudes of the differences in C:N, Loss-N, and N_m decreased when gradually excluding rare to common natives from the species pool (Fig. 5; see upwards), while increased when gradually excluding dominant to common natives (Fig. 5; see downwards).

We also detected the effects of the abundance of the natives on other eight traits through species exclusion approach (Suppl. material 1: Figs S4, S5), although its effects on these traits were not detected in our mixed-effects models (Suppl. material 2: Table S4). The differences in these traits disappeared when the invasives were compared with their co-occurring dominant and common natives. In addition, the magnitudes of the differences in $P_{\rm max}$, PEUE, and PPUE decreased when gradually excluding rare to common natives from the species pool, while increased when gradually excluding dominant to common natives (Suppl. material 1: Fig. S4).

Effects of invasive elsewhere of the native species

Contrary to our expectation, whether the natives were invasive elsewhere did not influence the differences in the 12 traits between the invasive and native species (Suppl. material 2: Table S4).

Discussion

Overall differences between invasive and native species

Our phylogenetically controlled within-study meta-analyses showed that the invasive relative to the co-occurring native species had significantly higher leaf nutrient concentrations, photosyntheses, photosynthetic nutrients- and energy-use efficiencies, and higher leaf litter decomposition rates, but lower carbon-to-nitrogen ratios and shorter payback time of leaf construction cost (Fig. 2). Our results regarding leaf nitrogen and phosphorus concentrations and leaf carbon to nitrogen ratio were consistent with those from all multi-species comparisons and reviews that compared the three traits (Suppl. material 2: Table S1; Baruch and Goldstein 1999; Leishman et al. 2007; Heberling and Fridley 2013; Huang et al. 2020). Our results regarding photosynthetic energy-use efficiency and payback time of leaf construction cost were also in line with those of Heberling and



Figure 4. Effects of invasiveness of the invasive species on the differences between invasive and native species from a subsets of the species pairs in leaf-litter nitrogen loss rate (Loss-N). "All" on the right indicates that all measured species pairs were included in the analysis. Arrows upwards from "All" indicate that species pairs containing weak and moderately invasive plants were excluded gradually and randomly from the analyses; arrows downwards from "All" indicate that species pairs containing strongly and moderately invasive plants were excluded gradually. "S" indicates that only the strongly invasive plants were compared with their co-occurring natives; "SM" indicates that both strongly and moderately invasive plants were compared with their co-occurring natives; "WM" indicates that both weakly invasive plants were compared with their co-occurring natives; open circles indicate the differences when a random set of species pairs was excluded. The figures between brackets on the left of each panel indicate the numbers of species pairs included in the analyses.

Fridley (2013), which was the only multi-species comparison of these traits between invasive and native species. These traits may contribute more to the invasion success of invasive species than the others (Liu et al. 2017; Huang et al. 2020).

For other traits, however, many multi-species comparisons and reviews reported inconsistent results with ours. For example, Daehler (2003) and Baruch and Goldstein (1999) found similar photosynthesis and photosynthetic nitrogen-use efficiency for invasive and native species, respectively. Higher specific leaf area was found for invasive species in two multi-species comparisons (Baruch and Goldstein 1999; Leishman et al. 2007) and three reviews (Pyšek and Richardson 2007; van Kleunen et al. 2010; Castro-



Figure 5. Effects of abundances of the native species on the differences between invasive and native species from a subset of the species pairs in leaf-carbon-to-nitrogen ratio (C:N), leaf-litter nitrogen loss rate (Loss-N), leaf-nitrogen concentration (N_m) , and photosynthetic potassium-use efficiency (PKUE). "All" on the right of each panel indicates that all measured species pairs were included in the analysis. Arrows upwards from "All" indicate that species pairs containing rare and common natives were excluded gradually and randomly from the analyses; arrows downwards from "All" indicate that species pairs containing widespread dominant and common natives were excluded gradually. "D" indicates that only the widespread dominant natives were compared with their co-occurring invasives; "RC" indicates that both widespread dominant and common natives were compared with their co-occurring invasives; "RC" indicates that both rare and common natives were compared with their co-occurring invasives; open circles indicate the differences when a random set of species pairs was excluded. The figures between brackets on the left of each panel indicate the numbers of species pairs included in the analyses.

Díez et al. 2014), while similar values of this trait were found for invasive and native species in three multi-species comparisons (Heberling and Fridley 2013; Divíšek et al. 2018; Huang et al. 2020) and a review (Leishman et al. 2007). It is hard to know the reasons for the discrepant results of our studies and those of previous ones, because there

are many factors that differ between the studies. Our study controlled phylogenetic relatedness between the invasive and native species, which may increase the objectivity of the results. If we did not control the phylogenetic relatedness, the comparative results would be differences in four traits (C:N, leaf density, stomatal conductance, and phosphorus concentration; Suppl. material 1: Fig. S6). We also controlled other potentially influencing factors such as latitudes and altitudes of sample sites. The identical protocol was applied for all species and in all sites in our study, while different protocols were used in different case studies that were included in the aforementioned reviews. Another advantage of our study over reviews is that our results are not affected by publication biases (Rosenberg et al. 2000; Leimu and Koricheva 2004; Koricheva and Gurevitch 2014). The higher frequency of inconsistent results among reviews relative to experimental studies (in 80% vs 64% of the traits; Suppl. material 2: Table S1) may provide indirect evidence for the confounding effects of publication biases as well as other factors (such as experimental protocols).

Most importantly and interestingly, we found that identities of both the invasive and the native species influenced the differences between the invasive and native species, which may give another explanation for the inconsistencies in the results of previous and current studies.

Effects of identities of the invasive and native species

Our study provided strong evidence that invasiveness of exotic species and abundances of natives influenced the differences between invasive and native species, and showed how they influenced the differences. As expected, strongly or moderately invasive species had higher leaf nitrogen-loss rates than co-occurring natives, while the difference disappeared when comparing weakly invasive species with co-occurring natives (Fig. 3A). In addition, the magnitude of the difference decreased when gradually and randomly removing invasives with strong to moderate invasiveness from the species pool (Fig. 4). Also like expectation, invasives were significantly different from rare or common natives in leaf carbon-to-nitrogen ratios (lower), nitrogen-loss rates (higher) and nitrogen concentrations (higher), while similar with widespread dominant natives (Fig. 3B). The magnitudes of the differences in these traits also increased when removing common to dominant natives from the species pool, while decreased when removing rare to common natives (Fig. 5). Similar patterns to the aforementioned were also found for other traits (Suppl. material 1: Figs S2-S5). Consistent with our results, McDowell (2002) found that invasive Rubus discolor has higher leaf nitrogen concentration than native congener R. leucodermis but not than native R. ursinus, which may be due to the fact that the *R. ursinus* is a ruderal with high abundance in habitats (Caplan and Yeakley 2013). Huang et al. (2020) found that invasives had higher leaf nitrogen concentrations than co-occurring natives, but not higher than cooccurring non-invasive aliens. Recently, Huang (2020) found that invasives had higher leaf nutrient concentrations and photosyntheses than co-occurring natives with low abundances in communities, but not than dominant natives with high abundances. Similarly, species identities also influenced the differences in competitive ability between invasive and native species (Zhang and van Kleunen 2019; Zheng et al. 2020). Our results clearly show the effects of species identities on trait differences between invasive and native species, and give a possible explanation for the discrepant results in references, which compared invasives with different invasiveness and natives with different abundances (Baruch and Goldstein 1999; Daehler 2003; Leishman et al. 2007; Pyšek and Richardson 2007; van Kleunen et al. 2010; Castro-Díez et al. 2014).

Our results indicate that it is most likely to detect significant difference between strongly invasive species and rare natives, and the magnitude of the difference is the greatest among the comparisons of strong to weak invasives and rare to dominant natives. In contrast, it is most unlikely to find trait advantage for invasives when comparing weakly invasive species with widespread dominant natives. In our study, a few strongly and weakly invasive species were occasionally compared with rare and dominant natives (four combinations). By analyzing the invasive-native differences, respectively, we found that strongly invasive species were significantly different to rare natives in a third of the traits, while no significant differences were found when comparing weakly invasive species with either rare or dominant natives, and comparing strongly invasive species with dominant natives (Data not shown). Weakly invasive species (especially for annuals) may not have trait advantages over natives, and their invasions may merely be due to vacant niche in recipient habitats (Rhymer and Simberloff 1996). Significant correlations between leaf functional traits and species abundances have been documented (Zhang et al. 2018; Huang 2020), which indicate that dominant natives may have some trait advantages over rare natives, and thus are more ecologically similar to invasives than to rare natives (Caplan and Yeakley 2013; Zhang and van Kleunen 2019; Huang 2020). Widespread dominant natives may even have trait advantages to compete with or even suppress alien invasives (Canessa et al. 2018).

Our study indicates that results of comparative studies, irrespective of the number of species included, may always be species-specific and environment-dependent. Discrepant results between our current and previous multi-species comparisons and reviews may be at least partially originated from the species-specific effects (Baruch and Goldstein 1999; Daehler 2003; Leishman et al. 2007; Pyšek and Richardson 2007; van Kleunen et al. 2010; Castro-Díez et al. 2014; Huang 2020). Thus, it is difficult to reveal common traits (if any) shared by invasives through multi-species comparisons or meta-analyses of published data. In the future, we would do better to compare functional traits of invasive and native species at both species and community levels in wild communities, rather than compare broadly across many species pairs. We should also account for potential influencing factors such as invasiveness, residence time and invasion stages of invasives; abundances of natives; resource availability, enemy regimes, plant species diversity, functional diversity and phylogenetic diversity in communities. In this way, we may better understand the traits promoting invasion in both species and community levels.

Conclusion

Overall, the invasive plants had significantly higher leaf nutrient concentrations, photosyntheses, photosynthetic nutrients- and energy-use efficiencies, and higher leaf litter decomposition rates, but shorter payback time of leaf construction cost and lower carbon-to-nitrogen ratios than co-occurring natives. More importantly and interestingly, the differences were affected significantly by identities of both the invasive and the native species. Furthermore, the magnitudes of the differences in some traits decreased or even reversed when gradually excluding a random subset of strongly to moderately invasive species from the species pool. Removing rare to common natives produced the same effect, while exclusion of weakly to moderately invasive species and dominant to common natives enhanced the differences. Our results provide a possible explanation for the discrepant results between our current and previous studies, and indicate that it may be unlikely to obtain general leaf traits (if any) for invasives through multi-species comparisons, which are species-specific and environment-dependent. In the future, we should compare invasive and native species at both species and community levels in different habitats, and account for possible influencing factors.

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Supplementary material I

Figure S1–S7

Authors: Ming-Chao Liu, Ting-Fa Dong, Wei-Wei Feng, Bo Qu, De-Liang Kong, Mark van Kleunen, Yu-Long Feng

Data type: docx. file

- Explanation note: Figure S1. Sample sites spanning 24° latitudes from tropical to temperate zones in China. Figure S2. Topology of the maximum likelihood phylogenetic tree for all studied species. Figure S3. Effects of invasiveness of the invasive plants on the differences in $P_{\rm max}$, PEUE, PNUE, PPUE, PT, and Loss-C between invasive and native plants from a subsets of the species pairs. Figure S4. Effects of invasiveness of the invasive plants on the differences in C:N, G_s , N_m , P_m , and PKUE between invasive and native plants from a subsets of the species pairs. Figure S5. Effects of abundances of the native plants on the differences in $P_{\rm max}$, PEUE, PNUE, PT, and Loss-C between invasive and native plants from a subset of the species pairs. Figure S5. Effects of abundances of the native plants on the differences in $P_{\rm max}$, PEUE, PNUE, PT, and Loss-C between invasive and native plants from a subset of the species pairs. Figure S6. Effects of abundances of the native plants from a subset of the species plants on the differences in G_s and P_m between invasive and native plants from a subset of the species pairs. Figure S7. Phylogenetically non-informed mean effect sizes (Hedges'd) and their 95% confidence intervals showing the overall differences in 20 leaf functional traits between the invasive and native species.
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Supplementary material 2

Table S1, S2, S4

Authors: Ming-Chao Liu, Ting-Fa Dong, Wei-Wei Feng, Bo Qu, De-Liang Kong, Mark van Kleunen, and Yu-Long Feng

Data type: docx. file

- Explanation note: Table S1. Differences in leaf functional traits between invasive and native or non-invasive alien plants in references that compared multiple species. Table S2. Background information on the seven sample sites. Table S4. Effects of identities of the invasive and native plants compared on the invasive-native differences.
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Supplementary material 3

Table S3

Authors: Ming-Chao Liu, Ting-Fa Dong, Wei-Wei Feng, Bo Qu, De-Liang Kong, Mark van Kleunen, and Yu-Long Feng

Data type: excel file

- Explanation note: Table S3. Background information on the studied species and the values of 20 leaf functional traits for these species.
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RESEARCH ARTICLE



Plant invasions in riparian areas of the Middle Danube Basin in Serbia

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Abstract

Riparian areas experience strong invasion pressures worldwide and represent important points of spread for invasive alien plants (IAPs) in the European mainland. The Danube Basin is a well-known point of high plant invasion levels. Given that the middle part of the Danube Basin is critically understudied and the general lack of data for Serbia, the study aimed to provide an insight into the spatial patterns of plant invasions in the riparian areas of Serbia (Middle Danube Basin area). A total of 250 field sites, distributed along 39 rivers (nine catchment areas) and six canal sections, were studied during a four-year period (2013-2016) for the presence and abundance of IAPs. At the landscape scale, we studied distribution patterns of IAPs, differences in invasion levels in different catchment areas and between rivers and canals. At the local scale, we investigated how the proximity to roads/railway lines, housing areas, different landuse types (primarily agriculture), and dominant vegetation on site related to invasion patterns. Of the 26 studied IAPs, those with a well-known weedy behavior, long history of cultivation and strong affinity for riparian areas prevailed in the study area. Riparian zones of the Danube catchment exhibited the highest invasion levels in terms of IAPs richness and abundance, followed by the catchment areas of the Timok, Sava and Zapadna Morava rivers. Surprisingly, the Danube-Tisa-Danube canal network had the lowest invasion level. At the local scale, agriculture in proximity of the field site and dominant vegetation on site were observed as significant predictors of the invasion level. On the other hand, proximity to roads/railway

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lines and housing areas was not related to the invasion level. Finally, our study provides the first systematic overview of IAPs' distribution data for riparian areas of the Middle Danube Basin in Serbia, which could provide a basis for long-term monitoring of IAPs and development of future management plans.

Keywords

Alien plants, Danube, Danube-Tisa-Danube hydro-system, invasion corridor, invasive plants, riparian zone, river, waterway

Introduction

Estimates show that over 13,000 vascular plant species, approximately equaling the entire European native flora, have become naturalized outside of their native range (van Kleunen et al. 2015, 2019), with temperate and subtropical mainland regions of the world having the highest numbers of both naturalized and invasive (*sensu* Richardson et al. 2000) alien plant species (Essl et al. 2019). On a regional scale, habitat type is considered to be the best predictor of plant invasion levels (Chytrý et al. 2008a, 2008b; Chytrý et al. 2009; Pyšek et al. 2010), surpassing the importance of propagule pressure and climate (Chytrý et al. 2008a). Riparian areas are among the habitat types containing the highest numbers of invasive alien plants species (IAPs) (Vilà et al. 2007; Chytrý et al. 2008b).

Rivers and riparian areas are important hotspots of native species diversity (Ward et al. 2002), where a mosaic of different vegetation types (Hejda et al. 2015) provides a vast array of important ecosystem services (Pattison et al. 2017). However, these dynamic ecosystems (Naiman and Decamps 1997) are conflict zones (Vicente et al. 2011) exposed to numerous anthropogenic pressures and various disturbances (Tickner et al. 2001). The colonization of invasive alien species (IAS) has strongly affected European riparian areas over the past decades (Pattison et al. 2017). Given that riparian habitats are centers of IAPs diversity, they are consequently important potential sources of their outward spread (Tickner et al. 2001; Säumel and Kowarik 2010; Descombes et al. 2016; Arredondo et al. 2018), which usually starts along the watercourse and could expand further inland (see Burkart 2001).

For the European continent, Chytrý et al. (2009) have predicted that the lower Danube Basin area will be characterized by high levels of invasion and will show, in addition to the basin of the Po river, the highest presence of neophytes in Europe. Additionally, neighboring Hungary is an important invasion hotspot in Europe (Kröel-Dulay et al. 2019). However, there is a critical gap in knowledge about invasion patterns in the Middle Danube Basin – as holds true for the national scale in Serbia, both in studies on regional trends (Lambdon et al. 2008; Chytrý et al. 2009) and global databases on invasive species (EASIN, EPPO, NOBANIS, GRIIS, GLONAF). Meanwhile, various policies on global and European level have decreed goals and targets calling for action on IAS (Genovesi et al. 2014; Essl et al. 2020), including the zero draft of the post-2020 global biodiversity framework (CBD 2020), thus highlighting the need for IAPs distribution mapping and monitoring (Latombe et al. 2017). Given this, our idea was to analyze how rivers of the Middle Danube Basin area have fared in respect to alien plant invasions.

Consequently, the study was designed to assess plant invasions in riparian zones of the Middle Danube Basin in Serbia. We analyzed (i) general invasion patterns, (ii) distribution patterns of dominant IAPs, (iii) differences in invasion levels between river and canal sites, and (iv) how site-specific factors (proximity of roads/railway lines, housing areas, land use in the vicinity of the field site and dominant vegetation on site) relate to invasion patterns. Additionally, analyzed IAPs were grouped, based on their origin and life form, to test how specific groups of IAPs relate to altitude. Finally, distribution data on the 26 IAPs is provided.

Methods

Study area

Serbia lies in the central part of the Balkan peninsula, covering a territory of 88,361 km². Its northern and southeastern parts are characterized by a continental climate, with cold winters and semi-arid summers, while its western parts experience a more humid, temperate climate. The eastern and central parts of Serbia are characterized by a semi-arid temperate-continental/sub-continental climate, with some transitional sub-Mediterranean elements (Stevanović and Šinžar-Sekulić 2009). While its northern low-lying part is a mosaic of hills, alluvial plains, river terraces and loess plateaus along the major rivers (i.e. Danube, Sava, and their left tributaries; Radulović et al. 2011), the southern part is mostly mountainous, except for major river valleys of the Velika Morava, Zapadna Morava, Ibar, Južna Morava, and Nišava rivers (Stevanović and Šinžar-Sekulić 2009).

The total length of all waterways in Serbia is 65,980 km, with a prevalence of small to medium rivers, not longer than 100 m. All rivers in Serbia belong to three main drainage basins. The Danube catchment area, belonging to the Black Sea drainage basin, covers 92.5% of the territory, containing also the longest rivers in Serbia: Danube, Sava, Tisa, Velika Morava, Timok, Mlava, and Pek, with many tributaries. The Adriatic Sea drainage basin occupies 5.4% of the territory, primarily consisting of the basin of the Beli Drim river, located mainly in the Metohija valley. The Aegean Sea drainage basin covers 2.2% of the total area of Serbia, with the Pčinja river being one of its three main rivers, located in the far southeastern part of the country (Gavrilović and Dukić 2014).

The Danube-Tisa-Danube (DTD) canal system is the greatest hydrotechnical complex made in Europe (outside of Russia), built in the period from 1728 to 1957 (Gavrilović and Dukić 2014). It was built in the northern, low-lying part of Serbia (the Vojvodina Province) as a multipurpose solution for flood control, irrigation, water supply for the industry, and various societal values, such as recreation, fishing, and



Figure 1. Distribution of field sites included in the analysis within different catchment areas of Serbia. Original photos of three selected field sites **a** - canal section of the Danube-Tisa-Danube hydro-system, loc. Vlajkovac **b** - river Čemernica, Zapadna Morava catchment area, loc. Konjevići **c** - Pčinja river, Aegean Sea drainage basin, loc. PIO "Dolina Pčinje".

navigation. The total length of all main and side canals in the network is 651.33 km, with 301.13 km located in the western Bačka region and 350.20 km in the eastern Banat region of the Vojvodina Province (Gavrilović and Dukić 2014).

Field research

Field research was carried out at a total of 250 field sites to cover all river catchments and the entire territory of Serbia (Fig. 1), i.e. all eight river catchments of the Black Sea drainage basin (Danube basin), the catchment area of the Pčinja river in the Aegean Sea drainage basin, and the Danube-Tisa-Danube (DTD) canal system (See supplementary file 1), with a total of 39 rivers and six canal sections studied (217 and 33 field sites, respectively). Field sites along rivers and canals were uniformly distributed along the selected watercourses, with the distance between the field sites and their total number depending on the length of the studied watercourse.

Field research was conducted during the peak of the vegetation season (July-September) over four consecutive years (2013–2016). The timing of field research was selected based on the period when the studied plant species are fully developed and in full bloom. Based on preliminary findings from these field studies, 26 IAPs which occurred in at least three of the 250 surveyed field sites were selected for the analysis. We did not include *Portulaca oleracea* L. in this analysis, due to its uncertain geographic origins (but see Anđelković et al. in press for further details). The species selected for analysis are all listed in the preliminary list of invasive species in Serbia (Lazarević et al. 2012) and the Invasive species of Vojvodina database (IASV 2011).

Data collection

Vegetation data was collected on 100 m long longitudinal transects, set up parallel to the watercourse (following Aguiar et al. 2001, 2005), at approximately the same distance to the river. The transects were set up on the river/canal bank (Aguiar and Ferreira 2005) to better reflect the transitional nature of the riparian zone. Each longitudinal transect consisted of five 20 m long plots, aligned along the transect (modified by Aguiar et al. 2001). Cover of the recorded plant species was recorded (in percentage covers) in each plot, and the cover and abundance values were also assigned for each species according to the numerical van der Maarel scale (van der Maarel 1979) on the entire 100 m long vegetation transect. Plants were determined following the relevant literature, with their nomenclature following the Euro+Med PlantBase database (Euro+Med 2006–2020). Field data were georeferenced using the hand-held GPS Garmin eTrex 10 and distribution maps were made using QGIS software (QGIS Development Team 2009).

In order to test which site-specific conditions had a significant effect on the presence and abundance of the studied IAPs, a number of site-specific variables were tested against the total number and cover of IAPs per site. Data on the dominant vegetation type (broadleaf forest, tree plantation, shrub vegetation, herbaceous vegetation, bare land) and data on adjacent land use (housing areas, cropping land - field crops, pastures and meadows, primary natural habitat, industry) in the 500 m radius from the transect were recorded. These data were later verified, and amended if necessary, using original photographs from the field and Google Earth platform. Furthermore, distances to the nearest main road/ railway track and housing area were measured, using the Google Earth platform.

Data analysis

The effects of dominant vegetation on the total number of analyzed IAPs and their total cover (of all target IAPs combined) were tested using one-way ANOVA, with dominant vegetation as a factor variable. To test for differences in invasion levels (expressed as the total number of IAPs recorded on site) between the catchment areas one-way ANOVA was also applied, with catchment area as a factor variable. Results were then compared and separated using Tukey's honest significant difference test, with Levene's test used to ascertain the homogeneity of variance.

To test whether invasion levels were greater in river vs. canal sites, the total number of IAPs and their total cover on site were compared using the Student's *t*-test. The *t*-test was also used to compare invasion levels (expressed as the total number of IAPs recorded and their total cover) between field sites located in proximity (500 m radius) of a road/railway track, housing area and cropping land (field crops), and sites located at a distance over 500 m from these potential sources of propagules. Non-parametric Mann-Whitney U test was used to compare the total IAPs numbers in field sites located in urban zones vs. non-urban field sites.

Linear regression analysis was used to test for correlation between invasion level proxies (the total number of IAPs and their total cover) and altitude. Correlations between the total number of IAPs and their total cover and distances measured between the transect and the nearest road/railway track and housing area were also tested using linear regression analysis.

The database used for multivariate analysis consisted of 26 invasive alien taxa (Table 1). The dataset referring to the percentage covers of the analyzed taxa (averaged across the five plots within the transect), was used in two separate canonical correspondence analyses (CCA), related to altitude and distance from housing areas. Response curves fitted with a generalized additive model (GAM) were used to show how selected species are related to altitude and distance from housing areas.

For further analysis, two groupings of taxa based on percentage covers were done using the "trait averages" option. Taxa were first grouped based on their origin (Table 1), while the second grouping of taxa was done based on the IAPs life form (Table 1). These groups were analyzed in relation to altitude used as a nominal variable, using two separate redundancy analyses (RDA).

Univariate analyses were done using STATISTICA 7.0 and CANOCO (ver. 5.0, ter Braak and Šmilauer 2012) was used for multivariate analysis.

Results

General invasion patterns

A total of 1153 records of the selected IAPs have been documented in riparian areas of the analyzed rivers (Table 1). Of the analyzed IAPs, *Xanthium orientale* subsp. *italicum* was the most frequently documented and widely distributed, recorded on a total of 142 field sites (Fig. 2). The second most widely distributed was *Amorpha fruticosa* (Fig. 2), followed by *Erigeron canadensis* (Fig. 3), *Robinia pseudoacacia* (Fig. 2) and *Echinochloa crus-galli* (Fig. 2).

When the number of invaded rivers is analyzed per taxon, *R. pseudoacacia* and *X. ori*entale subsp. *italicum* stand out, being recorded along the course of 92.3% and 89.7% of

Taxon	code	life	origin	number of records per catchment area										
	in the analyses	form		total number or records	Danube (S1)	Sava (S2)	Kolubara (S3)	Drina (S4)	Velika Morava (S5)	Zapadna Morava (S6)	Južna Morava (S7)	Aegean Sea (S8)	Timok (S9)	DTD system (K)
Abutilon theophrasti Medik.	ABUTH	Т	As	9	6	-	-	-	-	-	1	-	-	2
Acer negundo L.	ACRNE	Р	NAm	27	19	3	-	-	2	1	1	-	1	-
Ailanthus altissima (Mill.) Swingle	AILAL	Р	As	29	7	4	-	-	-	4	6	-	7	1
Amaranthus retroflexus L.	AMARE	Т	NAm	75	34	5	1	4	6	11	8	-	1	5
Ambrosia artemisiifo- lia L.	AMBEL	Т	NAm	85	29	10	12	6	2	8	4	-	1	13
Amorpha fruticosa L.	AMHFR	NP	NAm	108	47	10	1	3	5	6	11	1	10	14
Asclepias syriaca L.	ASCSY	G	NAm	6	2	1	-	-	-	-	-	-	-	3
<i>Broussonetia papyrifera</i> (L.) Vent.	BRNPA	Р	As	6	2	1	-	-	1	-	-	-	-	2
Datura stramonium L.	DATST	Т	C+SAm	14	8	-	2	-	1	1	1	-	-	1
<i>Echinochloa crus-galli</i> (L.) P. Beauv.	ECHCG	Т	As	99	42	7	9	9	5	14	6	2	5	-
<i>Echinocystis lobata</i> (Mi- chx.) Torr. & A. Gray	ECNLO	Т	NAm	79	16	4	8	7	9	12	11	-	10	2
<i>Eleusine indica</i> (L.) Gaertn		Т	mix	4	3	-	-	-	-	-	-	-	-	1
<i>Erigeron annuus</i> (L.) Pers.	ELEIN	Т	NAm	57	25	2	4	2	1	4	4	-	2	13
Erigeron canadensis L.	ERICA	Т	NAm	103	31	4	8	5	6	9	15	1	11	13
<i>Fraxinus pennsylvanica</i> Marshall	FRAPE	Р	NAm	19	1	3	7	-	-	-	6	-	2	-
Helianthus tuberosus L.	HELTU	G	NAm	27	-	1	2	9	-	4	3	1	6	1
Parthenocissus quinquefo- lia (L.) Planch.	PARQU	L	NAm	12	5	1	-	-	2	-	-	-	2	2
Paspalum distichum L.	PASDI	Т	trop	17	10	1	-	1	-	3	-	-	2	-
Phytolacca americana L.	PHYAM	G	NAm	13	3	-	1	-	-	4	3	-	2	-
<i>Reynoutria×bohemica</i> J. Chrtek & A. Chrtkova	REYBO	Н	As**	12	-	3	1	4	-	4	-	-	-	-
Robinia pseudoacacia L.	ROBPS	Р	NAm	102	18	5	10	8	7	17	19	2	9	7
<i>Solidago gigantea</i> Aiton	SOLGI	Н	NAm	8	2	-	-	-	-	-	-	-	-	6
<i>Sorghum halepense</i> (L.) Pers.	SORHA	G	EuAs	47	19	4	2	2	2	8	1	-	-	9
Symphyotrichum spp.	SYMSP	Н	NAm	45	10	2	6	3	6	1	10	-	2	5
<i>Xanthium orientale</i> L. subsp. <i>italicum</i> (Moretti) D. Löve	XANST	Т	C+SAm	142	43	11	13	9	10	18	21	2	11	4
Xanthium spinosum L.	XANSP	Т	SAm	8	2	-	-	-	-	-	-	-	-	6
Total number of IAPs in the catchment area		1153	384	82	87	72	65	129	131	9	84	110		
Total number of field sites in the catchment area		250	74	17	17	18	16	25	34	2	14	33		
Mean number of records per field site in the catchment area		4.61	5.19	4.82	5.12	4.00	4.06	5.16	3.85	4.50	6.00	3.33		

Table 1. Number of records of the studied invasive plant taxa in different catchment areas in Serbia, with data pertaining to their life form and origin.

* T – therophyte; P – phanerophyte; NP – nanophanerophyte; G – geophyte; H – hemicryptophyte; L – scandetophyte; As – Asia; NAm – North America; C+SAm – Central and South America; trop – Tropical; mix – Africa and Asia

** Hybrid species; origin assigned based on the origin of its parental species R. japonica Houtt. and R. sachalinensis (F. Schmidt) Nakai



Figure 2. Xanthium orientale subsp. *italicum*, Amorpha fruticosa, Robinia pseudoacacia and Echinochloa crus-galli occurrences in the studied sites of riparian areas of Serbia. Invasive species distribution points relate to the survey areas shown in Fig. 1.

rivers, respectively. They are closely followed by *E. crus-galli* and *E. canadensis*, both recorded along 71.8%, and *A. fruticosa* in the riparian areas of 64.1% rivers (data not shown).

With regards to their origin, IAPs originating from North America were most frequent in the field, with 766 records (66.4% of total IAPs records; see Suppl. material 3). In terms of life form, therophytes were most frequent, with 692 records, followed by phanerophytes (183) and nanophanerophytes (represented by *A. fruticosa*; 108 records) (see Suppl. material 4).

The total number of IAPs per site was negatively correlated with altitude (r=-0.30, p < 0.001), as was their total cover (r=-0.19, p < 0.01). A generalized additive model revealed



Figure 3. Erigeron canadensis, Amaranthus retroflexus, Ambrosia artemisiifolia and Abutilon theophrasti occurrences in the studied sites of riparian areas of Serbia. Invasive species distribution points relate to the survey areas shown in Fig. 1.

that altitude generally predicted individual IAPs cover on site (F = 7.1, p = 0.002). The abundance of *R. pseudoacacia, Helianthus tuberosus* and *Reynoutria* × *bohemica* was positively correlated with altitude, while the other IAPs' cover exhibited a negative correlation with this parameter (Fig. 4). A redundancy analysis (RDA; F = 2.4, p = 0.024) illustrated the relationship of IAPs grouped by origin and altitude. The results show that while all groups are more frequent at lower elevations (< 200 m a.s.l.), some (tropical, South American and mixed origin IAPs) were exclusively found here (for further details see Fig. 5). Redundancy analysis of IAPs grouped by life-form in relation to altitude (F = 5.0, p = 0.002) showed that while all groups dominated at lower elevations (<200 m a.s.l.), abun-



Figure 4. Response curves of the selected invasive alien plants in relation to altitude in the studied areas of Serbia. Names of taxa are abbreviated, see Table 1 for full names.

dance of geophytes (G), hemicryptophytes (H) and phanerophytes (P) became more pronounced in field sites between 200 and 500 m a.s.l. Phanerophytes (P) were the only group recorded more than others at altitudes between 500 and 800 m a.s.l. (Fig. 6).

Differences in invasion levels

Sites along rivers had significantly more IAPs than sites along canals $(5.35\pm2.49 \text{ vs.} 3.61\pm2.29, \text{ df} = 248, p < 0.001; t-test)$. Similarly, the total cover (in %) of analyzed IAPs was significantly higher at river vs. canal sites $(44.33\pm29.83 \text{ vs.} 24.42\pm21.82, \text{ df} = 248, t = 3.93, p < 0.001; t-test)$.

Catchment area had a highly significant effect on the total number of IAP records per field site (p < 0.001; See Suppl. material 5). The Timok catchment area (Eastern Serbia) had the highest mean number of IAP records per field site (6.14 ± 0.64), followed by the Danube (5.88 ± 0.28) and Sava (5.71 ± 0.58) catchment areas. Meanwhile, the DTD canal system had the lowest mean number of IAP records per field site (3.39 ± 0.42).

Effects of site-specific variables

Site-specific variables were differently related to invasion patterns in the study area. Sites in the proximity of roads or railways (< 500 m) had fewer IAP species, compared to the more distant sites (4.74 ± 2.52 vs. 6.05 ± 2.34 , df = 248, t = 3.93, *p* < 0.001).



Figure 5. Pie chart diagram (RDA) showing the association of selected invasive alien plants grouped by origin with field sites categorized by altitude (a = < 200 m a.s.l.; b = 200 - 500 m a.s.l.; c = 500 - 800 m a.s.l.). Names of groups are abbreviated, please refer to Table 1 for full names.

Thus, an increase in distance from the road/railway track was positively correlated with IAPs number (r = 0.18, p < 0.001).

The proximity of housing areas did not have a significant effect on the total number or total cover of IAPs per site (See Suppl. material 6). Furthermore, distance from housing areas and the IAPs number were not significantly related (p > 0.05). However, the CCA showing distance from housing areas in relation to the cover of individual IAPs was significant (F = 2.0, p < 0.01) and response curves of the selected species are shown in Fig. 7.

Sites located in proximity of agricultural land (< 500 m) had more IAP species, compared to the more distant sites (5.26 ± 2.6 vs. 4.51 ± 2.25 , df = 248, t = 2.03, p < 0.05). On the other hand, contrary to our expectations, there was no significant difference (p > 0.05; Mann-Whitney U test) in the number and cover of IAPs per site between field sites located within an urban zone and those found outside of cities.

The total cover of studied IAPs per site was significantly different (p < 0.01) between sites with different vegetation types (See Suppl. material 5). The lowest cover of IAPs, on average, was found for field sites dominated by bare land (14%) and a mix of broadleaf forest and shrub vegetation (28.8%), while field sites with dominant shrub vegetation had the highest cover of IAPs (49.4%). The dominant vegetation type was not significantly related to the total IAP species number (p > 0.05).



Figure 6. Pie chart diagram (RDA) showing the association of selected invasive alien plants grouped by life form with field sites categorized by altitude (a = < 200 m a.s.l.; b = 200 - 500 m a.s.l.; c = 500 - 800 m a.s.l.). Names of groups are abbreviated, please refer to Table 1 for full names.

Discussion

This study provides the first systematic overview of plant invasion patterns and IAPs distribution data for riparian areas of the Middle Danube Basin in Serbia. General invasion patterns, differences among catchment areas, and among individual invasive species were detected. Additionally, we also show which site-specific variables were related to invasion patterns.

General invasion patterns

Results pertaining to the relevance of species' origin and life form are consistent with those reported for other riparian systems (Schnitzler et al. 2007; Nucci et al. 2012; Liendo et al. 2015; Lapin et al. 2019). Species originating from North America, followed by Asian species, were the most frequent (See Suppl. material 3), as were annual species (therophytes; See Suppl. material 4).

The overall decrease in alien species richness with increasing altitudes is a wellknown phenomenon, recorded worldwide (Pyšek et al. 2005; Chytrý et al. 2009; Liendo et al. 2015; Vorstenbosch et al. 2020). Moreover, the tendency of the majority of studied IAPs to favor lowland riparian sites (Fig. 4, 5 and 6) falls in line with previous studies (Schnitzler et al. 2007; Pattison et al. 2017; Lapin et al. 2019; Giberti et al. 2021). It has been argued that the effect elevation has on IAPs distribution and abundance is linked to the climatic conditions of their native ranges (Chytrý et al. 2005; Schnitzler et al. 2007) and temperature range of the invaded area (Skálová et al. 2015). Furthermore, unlike lowland areas, the mountainous areas are subject to fewer anthropogenic activities and consequently fewer disturbance events and lower propagule pressure, making them less prone to invasion (Nucci et al. 2012; Liendo et al. 2015). These effects are reflected in the abundance of the studied IAPs groups (Fig. 5 and 6). An exception to this general tendency are $R. \times bohemica$ and H. tuberosus (Fig.



Figure 7. Response curves of the selected individual invasive alien plants in relation to the distance to housing areas. Names of taxa are abbreviated, see Table 1 for full names.

4, but also reflected in Fig. 6), and their association with altitudes between 200 and 500 m a.s.l. This association echoes their invasion along rivers in the Drina and Zapadna Morava catchment areas (field obs.). The presence of *R. pseudoacacia* at altitudes between 500 and 800 m a.s.l. reflects its cultivation history since it had been planted there for decades to stabilize the riverbanks (Nicolescu et al. 2020).

Differences in invasion levels across catchment areas

This study has found significant differences in invasion levels between the studied catchment areas, highlighting the catchment areas of the Timok and Danube rivers as the most invaded overall. Such findings are consistent with other studies denoting the Danube as an important plant invasion corridor (Stevanović et al. 2004; Paunović et al. 2015; Anđelković et al. 2016; Wagner et al. 2020). The highly invaded Timok river catchment area, geographically a part of the Carpathian massive, seems to be experiencing a similar increase in invasion levels already observed in the Carpathian Mountains of Ukraine (Simpson and Prots 2013). On the other hand, some field sites were uninvaded thus far, including several in the Južna Morava catchment area (Table 1). In this sense, three invasion-free field sites along the Vlasina river are an important finding, as a large portion of this river is protected under a range of national and international legislature, due to its conservation value (Amidžić et al. 2018).

Surprisingly, results have shown that the canal network of the Danube-Tisa-Danube hydro-system is the least invaded of the analyzed catchment areas. Such invasion levels along the canals are contrary to general expectations, given that field sites along the canal network

are under strong and constant anthropogenic pressure. Additionally, they are found within an entirely agricultural landscape of the Vojvodina Province and consequently experience seasonal nutrient-enrichment, due to N leaching from the surrounding agricultural fields (Hejda and Pyšek 2006). Finally, these results are especially surprising considering the effect agriculture had on invasion levels in the study area (See Suppl. material 6).

The observed invasion tendencies on river vs. canal sites could potentially be explained by the management regime which is being undertaken by the stakeholders in charge of the DTD canal network upkeep. While the banks of the DTD canal system are under a regular management system (mowing), riverbanks are mostly free from this form of anthropogenic control and IAPs are therefore allowed to spread unchecked. Such a situation could suggest that traditional management regimes still being employed along the canal banks control the spread of IAPs along canals. Regardless, all management plans need to take into account those species where management activities such as mowing (R. × *bohemica*; Jones et al. 2020) and coppicing (R. *pseudoacacia* and A. *altissima*; Brundu et al. 2020) are counterproductive, actually encouraging the further spread of IAPs.

Invasion patterns of the dominant IAPs

Our results on the most frequent and most abundant IAPs (Table 1; Figs 2 and 3) concur with other riparian and wetland area studies from Serbia and SE Europe (Török et al. 2003; Oprea and Sîrbu 2006; Čavlović et al. 2011; Krstivojević et al. 2012; Batanjski et al. 2015; Radovanović et al. 2017; Stanković 2017; Tmušić et al. 2019).

Amorpha fruticosa was recorded as the second most frequent IAP (Table 1, Fig. 2), which echoes its presence in other European riparian systems (Zavagno and d'Auria 2001; Dumitrașcu et al. 2013). Similarly, *R. pseudoacacia* was recorded at over 90% of the studied rivers (Fig. 2). The distribution of this species reflects its long-term cultivation history in Europe, and consequently Serbia (see Fig. 1 in Vítková et al. 2017). In fact, this invasive species is still being planted in Serbia, as a forest crop in the Danube River floodplains (Andrašev et al. 2015). Such practices have resulted in an area of over 150,000 ha under *R. pseudoacacia* in Serbia (c.f. Nicolescu et al. 2020), supporting further invasions by this species.

Finally, some of the most frequent IAPs in riparian areas (*X. orientale* subsp. *italicum*, *E. canadensis*, *E. crus-galli*, *Amaranthus retroflexus*, *A. artemisiifolia*) are also widely distributed in ruderal and agricultural areas of the region and spread intensively across the Balkans and SE Europe (Török et al. 2003; Weber and Gut 2005; Šilc et al. 2012; Kröel-Dulay et al. 2019). This could support the invasion of riparian habitats by these species.

The rather constrained distribution of *Asclepias syriaca* in the riparian areas of Serbia was an unexpected result, given that previous research (Vrbničanin et al. 2008b; Popov 2016; Stanković 2017) has revealed it to be widespread, especially in the northern parts of Serbia, with a strong tendency for expansion along watercourses (Popov 2016). Results were similarly surprising regarding the frequency and distribution of *R. × bohemica*, bearing in mind its strong preference for riparian habitats (Bailey and Wisskirchen 2004; Mandák et al. 2004; Bailey et al. 2007) and its current distribution in Serbia (Jovanović et al. 2018). Despite the low number of records observed in this
study, it needs to be pointed out that Jovanović et al. (2018) have shown that in SE Europe, Serbia has the highest number of appropriate habitats (primarily riparian) for further expansion of R. × *bohemica*.

Effects of site-specific conditions

Local site conditions determine the susceptibility of a field site to invasion (Chytrý et al. 2008b). In this sense, certain land use types, particularly agriculture, proximity of transport infrastructure (i.e. roads and railway lines) and degree of urbanization are expected to favor the presence and dominance of IAPs (Chytrý et al. 2008b; González-Moreno et al. 2014; Benedetti and Morelli 2017; Horvitz et al. 2017; Rat et al. 2017).

Agriculture, as land use type observed in the 500 m radius from the studied field site, was an important predictor of IAPs richness (See Suppl. material 6). Such observations echo the effects propagule pressure (originating from agriculture, both field crops and backyard gardens/orchards) and constant influx of vast amounts of nutrients have on the presence and abundance of IAPs. These results align with studies highlighting the role of agriculture in the spread of alien plant species (Osawa et al. 2013; González-Moreno et al. 2014, 2017) and the fact that the majority of alien plant taxa was introduced to this area as contaminants in seed material and nursery saplings (Anačkov et al. 2013). Furthermore, some of the most frequently recorded IAPs in the field are among the most frequent agricultural weeds in SE Europe (Šilc et al. 2012; Follak et al. 2014; Kröel-Dulay et al. 2019), highlighting the importance of agriculture as a source of plant invasions in the Middle Danube Basin area.

Surprisingly, we did not detect a link between the proximity of roads/railway lines and the number of observed IAPs per site. The role of these transport corridors in the spread of invasive plants is generally well-known (Rouifed et al. 2014; Bacaro et al. 2015; Benedetti and Morelli 2017). As roadside spread of alien plants at higher elevations has recently been observed (Vorstenbosch et al. 2020), a similar trend could occur in those riparian areas (> 500 m a.s.l.) in Serbia which are positioned close to main roads.

No effects were observed between the proximity of field sites to housing areas, or their position in urban areas, and the level of invasion. This was unexpected, given the importance of urbanization for plant invasions (Horvitz et al. 2017). Furthermore, Jehlík et al. (2019) and Rat et al. (2017) have also shown that urban areas along rivers harbor high numbers of neophytes.

This study showed that dominant vegetation on site is a significant predictor of the total cover of studied IAPs. Riparian field sites dominated by shrub vegetation had the highest recorded cover of invasive plants, which aligns with other studies showing that riverine scrubs are characterized by the highest proportions of IAPs (Vilà et al. 2007; Chytrý et al. 2008a, b; Stanković et al. 2019). The presence of IAPs on field sites dominated by bare land could have implications for the future and needs close monitoring, as such bare grounds (e.g. river bars or recently disturbed grounds) represent perfect venues for the incursion of invasive plants in riparian systems (see Liendo et al. 2021 and references therein).

Consequently, we can surmize that agriculture and dominant vegetation on site override the importance of proximity of transport infrastructure and housing areas (as human-related factors *sensu* Horvitz et al. 2017) at the local scale. It can also be theorized that, in addition to agriculture, the river-mediated dispersal of propagules (Pyšek and Prach 1993; Richardson et al. 2007) could also be considered as an important source of invasive plants in the study area, which should be tested in future studies.

Conclusion

Our study revealed differences in invasion levels between catchment areas of the Middle Danube Basin area. The Timok and Danube catchment areas were shown to support highest invasion levels. While some catchment areas (e.g. Sava and Zapadna Morava) also had high numbers of IAPs, other were less subjected to invasions. The results presented here have important practical implications and can support the development of future management plans for the control of IAPs in riparian areas of both rivers and canals in the region. Furthermore, we believe that our results, in addition to their local and regional value, will contribute to documenting the invasion trends of IAPs in riparian areas of the Danube Basin and this part of Europe. Finally, this snapshot study, with well-defined survey areas, could serve as a basis for long-term monitoring of IAPs, which is critically needed for supporting the prioritization of management and conservation actions (Pergl et al. 2020).

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Supplementary material I

List of the studied rivers/canal sections and their catchment area affiliation (and code in the analysis)

Authors: Ana A. Anđelković, Danijela M. Pavlović, Dragana P. Marisavljević, Milica M. Živković, Maja Z. Novković, Slađana S. Popović, Dušanka Lj. Cvijanović, Snežana B. Radulović

Data type: List of rivers included in the filed word.

- Explanation note: This file presents a comprehensive list of all the rivers which were included in the analysis. It is included as supplementary data as it provides additional information on the watercourses which were included in the analyses.
- 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.

Supplementary material 2

Geographical distribution data of the studied invasive alien speces

Authors: Ana A. Anđelković, Danijela M. Pavlović, Dragana P. Marisavljević, Milica M. Živković, Maja Z. Novković, Slađana S. Popović, Dušanka Lj. Cvijanović, Snežana B. Radulović

Data type: (measurement/occurrence/multimedia/etc.)

- Explanation note: This file includes 26 tables containing geographical distribution data of the analyzed invasive alien plat taxa. In addition to latitude and londiude, data is also provided on the locality, watercourse along which data was recorded and the catchment area this watercourse belongs to.
- 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.

Link: https://doi.org/10.3897/neobiota.71.69716.suppl2

Supplementary material 3

Figure S3

Authors: Ana A. Anđelković, Danijela M. Pavlović, Dragana P. Marisavljević, Milica M. Živković, Maja Z. Novković, Slađana S. Popović, Dušanka Lj. Cvijanović, Snežana B. Radulović

Data type: Tiff file.

- Explanation note: Origins of the analyzed invasive alien plants in the riparian areas of Serbia (expressed as the percent of records per each group).
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Supplementary material 4

Figure S4

Authors: Ana A. Anđelković, Danijela M. Pavlović, Dragana P. Marisavljević, Milica M. Živković, Maja Z. Novković, Slađana S. Popović, Dušanka Lj. Cvijanović, Snežana B. Radulović

Data type: Tiff file.

- Explanation note: Biological spectrum of the analyzed invasive alien plants in the riparian areas of Serbia (expressed as the percent of records per each group).
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Link: https://doi.org/10.3897/neobiota.71.69716.suppl4

Supplementary material 5

Tables

Authors: Ana A. Anđelković, Danijela M. Pavlović, Dragana P. Marisavljević, Milica M. Živković, Maja Z. Novković, Slađana S. Popović, Dušanka Lj. Cvijanović, Snežana B. Radulović

Data type: Docx file.

- Explanation note: Results of one-way ANOVA analyses, and subsequent Tukey's HSD post hoc tests.
- 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.

Supplementary material 6

Table

Authors: Ana A. Anđelković, Danijela M. Pavlović, Dragana P. Marisavljević, Milica M. Živković, Maja Z. Novković, Slađana S. Popović, Dušanka Lj. Cvijanović, Snežana B. Radulović

Data type: Docx file.

- Explanation note: Mean total numbers of invasive alien plants recorded per site and their total cover values (± SD) in field sites depending on their proximity to main road/railway track, housing and adjacent land use types (cropping land, field crops, pastures and meadows, primary natural habitat, industry).
- 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.

BOOK REVIEW



Foundational text gets a second edition

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Invasion biology, as a discipline, has grown along a trajectory that is commonly observed in biological invasions themselves – an early establishment initiates a lag phase followed much later by exponential growth. As measured by the number of peer-reviewed journal articles, the log-phase of invasion biology begins around 1990 but the lag phase stretches back centuries to observations by Charles Darwin and Alexander von Humbolt (Chew 2011). Along this trajectory there is likely no single contribution that has been more influential to the modern field of invasion biology than Charles Elton's book "The Ecology of Invasions by Animals and Plants" (Elton 1958).

Reprinted in 2000 with a foreword by Daniel Simberloff (Elton 2000), I remember reading The Ecology of Invasions and how much it impacted my early studies as an undergraduate research assistant. More recently, the edited volume "Fifty Years of Invasion Ecology: The Legacy of Charles Elton" (Richardson 2008) updated the stateof-the art in invasion biology, with contributions from leading researchers in invasion biology and related fields.

As a key figure in the much broader fields of animal ecology and conservation biology, it perhaps isn't surprising that many influential ideas in invasion biology were introduced by Elton in 1958 and remain highly relevant to the field today. Despite its status as a foundational scientific text, The Ecology of Invasions reads less like a textbook and more like a David Attenborough narrative on the natural history of invasions. Peppered with fascinating observations of the natural world that demonstrate foundational concepts, the original text remains a 'must read' for students and trainees.

Given its prominence to the field and my personal experience, I was keen to receive a copy of the 2020 "Second Edition" of The Ecology of Invasions. In contrast to the

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reprint (Elton 2000) and the edited volume (Richardson 2008), the Second Edition includes the nine original chapters and Preface to which have been added New Introduction and Conclusion chapters, along with nine new Foreword chapters. Written by Anthony Ricciardi and Daniel Simberloff, the new content draw from Elton's extensive notes while updating the last sixty years of peer-reviewed research in invasion biology.

For students and trainees, the new chapters provide important context and useful updates from modern studies and observations. As a more seasoned reader with almost two decades of research in biological invasions, I enjoyed learning more about the historical context and insights into the cognition of an influential scientist gleaned from a thorough investigation of Elton's notes and marginalia.

If I have a criticism to share it is not with the book itself so much as with our collective tendency to elevate and idolize our scientific pioneers – the giants on whose shoulders we stand. While it is fair to marvel at Elton's prescient contributions to conservation biology, ecology and animal behavior it is perhaps worth recognizing the role that status and privilege play in determining who has opportunities to make such contributions. As ecologists and conservation biologists we should teach students about the history of ideas. As researchers who understand the value of diversity, perhaps we should increase efforts to reverse historical trends of under-representation. Just as stale scientific observations are updated with modern data by Ricciardi and Simberloff, maybe we should equally update pictures of men in suits, both figurative and literal, with contributions from modern researchers and practitioners who represent the diversity of ideas that define modern science.

Of course, it is unfair to place the blame on the authors of this book, which remains perhaps the best introduction to the field of biological invasions. With Charles Elton's death in 1991, this important contribution by Ricciardi and Simberloff is likely as close as we can get to a second edition of the most influential book in the field of invasion biology.

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RESEARCH ARTICLE



Biosecurity and post-arrival pathways in New Zealand: relating alien organism detections to tourism indicators

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Abstract

Between-country tourism is established as a facilitator of the spread of invasive alien species; however, little attention has been paid to the question of whether tourism contributes to the arrival and subsequent dispersal of exotic organisms within national borders. To assess the strength of evidence that tourism is a driver for the accidental introducing and dispersal of exotic organisms, we sourced three national databases covering the years 2011 to 2017, namely international and domestic hotel guest nights and national population counts, along with records of exotic organism detections collected by the Ministry for Primary Industries, New Zealand's government agency that oversees biosecurity. We fitted statistical models to assess the strength of the relationship between monthly exotic organism interception rate, guest nights and population, the latter as a baseline. The analysis showed that levels of incursion detection were significantly related to tourism records reflecting the travel of both international and domestic tourists, even when population was taken into account. There was also a significant positive statistical correlation between the levels of detection of exotic organisms and human population. The core take-home message is that a key indicator of within-country human population movement, namely the number of nights duration spent in specific accommodation, is statistically significantly correlated to the contemporaneous detection of exotic pests. We were unable to distinguish between the effects of international as opposed to domestic tourists. We conclude that this study provides evidence of impact of within-country movement upon the internal spread of exotic species, although important caveats need to be considered.

Keywords

Biosecurity risk, exotic species, forward selection algorithm, invasive alien species, risk assessment, spatial risk

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Introduction

International trade and tourism, while essential to the world's economy, has also been implicated as facilitating the dispersal of exotic species (Early et al. 2016; Seebens et al. 2018). Tourism, in its broadest sense, can provide significant economic gain to a country's GDP, but, if not managed carefully, there are also economic, social, cultural and environmental costs associated with the industry (e.g. Scott et al. 2016; Trivellas et al. 2016; Peeters et al. 2018; Smith et al. 2019). From a biosecurity perspective, the sometimes massive and rapid movement of people associated with international tourism has been implicated in the dispersal of exotic organisms both across and within countries, some of which become invasive (Thuiller et al. 2005; Anderson et al. 2015; Haddaway and Dunn 2015; Early et al. 2016; Hall 2019). Biosecurity failures can have a significant impact on the tourism industry itself, for example, in curtailment of activities once in the country, reducing the value of a country's image to prospective tourists, and a potential reduction in the number of visitors (Blake et al. 2003; Vinson 2013). Exotic species introduced via the tourism pathway can have a direct economic cost, but there are also associated biodiversity losses (Pyšek and Richardson 2010). For countries with a high proportion of endemic biota (such as New Zealand, e.g. McGlone et al. 2001; Lee and Lee 2015), the impacts of exotic species can be significant (Bertram 1999; Barlow et al. 2002; Williams and Timmins 2011).

International tourism has been shown to provide a pathway for the dispersal of many organisms including insects (Russell and Paton 1989; Liebhold et al. 2006), bedbugs (Reinhardt and Siva-Jothy 2007), ticks (Molaei et al. 2019), plant material (Mack and Lonsdale 2001), human diseases (Wilson 1995; Tatem et al. 2006; Khan et al. 2009) and diseased meat products (Pharo 2002). Infested fruit carried by passengers potentially carry unwanted organisms such as fruit fly (Ceratitis and Bactrocera spp.), which could have a significant impact on a country's export fruit industry (SriRamaratnam 1996; Kriticos et al. 2007). Sheridan (1989) found pathogenic fungi on the clothing and baggage of passengers while pockets of clothing have been shown to carry potential risk material including dried and fresh foliage, seeds and feathers (Chirnside et al. 2006). Used tents may carry plant and animal debris, and live insects (Gadgil and Flint 1983). Soiled footwear carried in the luggage of passengers arriving at international airports in New Zealand supported a range of viable bacteria, fungi, seeds and nematodes (McNeill et al. 2011), and included species or strains that were categorized as unwanted organisms under New Zealand's biosecurity regulations. Within a country, contaminated clothing, footwear, camping gear, recreational equipment and vehicles have been shown to provide pathways for dispersing pathogens (Worboys and Gadek 2004; Kidd, et al. 2007), weeds (Whinam et al. 2005; Lloyd et al. 2006; Bouchard et al. 2015) and aquatic organisms (Kilroy and Unwin 2011), into natural and ecologically sensitive environments. Furthermore, the inherent mobility of tourists once within a country's borders (e.g. Forer 2005), also has the potential to facilitate the unintentional

transfer of arthropod pests or pathogens from one location to another (Forer and McNeill 2008).

To understand the value of tourism to New Zealand, and thereby associated biosecurity risk, it is worthwhile summarizing some key facts. In the year ended December 2019 there were 3.9 M international visitor arrivals to New Zealand, a 1% increase from the previous year (Stats 2020a). In addition, a further 3.1 M New Zealandresidents returned from overseas holidays (defined as New Zealand residents arriving in New Zealand after an absence of less than 12 months) (Stats 2020b). In the year ended March 2020, total tourism expenditure (both international and domestic) was NZ\$42 B, an increase of 2.4% from the previous year, and represented 5.5% of the country's gross domestic product (GDP). For New Zealand, which relies heavily on tourism and primary industries for its economic wealth, biosecurity is strategically important in managing tradeoffs between protecting key economic and environmental assets and encouraging tourism and trade (Parliamentary Commissioner for the Environment 2000).

In this respect, the tension between tourism and biosecurity risk is not unique to New Zealand (e.g. Toral-Granda et al.2017; Melly and Hanrahan 2021), but has been brought into focus with the impact of Covid-19 pandemic and a greater awareness the role tourism plays in dispersing exotic organisms. While the Covid-19 pandemic has had a significant impact on international tourism since the beginning of 2020, the expectation is that in a post-Covid world, there will be a recovery in international travel and renewed growth in global tourism.

In New Zealand, biosecurity monitoring and mitigation of risk at arrival points is a well-established strategy targeting both international and returning New Zealandresident travelers (Jay et al. 2003). But identification and removal of biosecurity risk organisms is not absolute, so tourists (international and returning New Zealanders) may pass through border screening inadvertently carrying undetected risk organisms. Travelers can therefore introduce propagules (sensu Lockwood et al. 2005) in or on their luggage, clothing, and footwear. These propagules (plant pathogens, nematodes, insects, seeds, etc.), can then be deposited at any point along the travel route, depending on activities or events they are undertaking. This could happen when removing boots or jackets from luggage for use while visiting a botanic garden or hiking activity. At this point, a propagule can be deposited at a location where the items were removed from the luggage or along the walking route. The ease for subsequent secondary dispersal may then depend on propagule size and the ability for the exotic organism to be vectored. For example, the introduction of didymo (Didymosphenia geminata, (Lyngbye) M. Schmidt), a freshwater diatom into New Zealand, was strongly linked to anglers arriving from overseas carrying contaminated equipment (Kilroy and Unwin 2011). First found in the southern river systems of the South Island, secondary dispersal was strongly related to human activity, particularly by freshwater anglers (Kilroy and Unwin 2011).

Therefore, understanding the links between international tourist flows once in the country and the potential biosecurity risks that these visitors may present is a new and

important area of research. While attempts to visualize tourist movement beyond the port of arrival (either air or sea) within New Zealand, have been made using historical data (e.g. Forer 2005), little is known about subsequent pathways along which international tourists travel. Behavior of tourist flow can differ based on geographical, socioeconomic, demographic, psychographics and behavioral characteristics (Forer 2005; Bigné et al. 2007; Yang et al. 2018). For example, unlike European tourists, Indian and Chinese tourists spend their first few days in Auckland, the main point of arrival into New Zealand before heading elsewhere. In the context of tourism and biosecurity risk, this study sought to address this relationship by using data on (a) New Zealand's monthly hotel guest nights for both international and New Zealand domestic tourists and (b) general population distribution, in relation to biological risk organisms (exotic organisms) detected by New Zealand's biosecurity authority, the Ministry for Primary Industries (MPI). The overall aim was to determine if biosecurity interceptions were best explained by either international or domestic tourist movement within the country, or population density. The broader program would use the results to assist in development of more effective biosecurity risk monitoring and mitigation procedures relating to the different tourist segments. Finally, the information could inform biosecurity authorities on the allocation of resources in relation to other potential pathways (e.g. sea freight).

Materials and methods

We applied a model-comparison approach to assessing the strength of evidence for the competing explanations of the interception patterns. Three data holdings were sourced from the Ministry for Primary Industries (MPI) and Stats NZ Tatauranga Aotearoa (hereafter referred to as Stats NZ). MPI provided the Notification and Investigation Management Application (NIMA) data and Stats NZ, both the monthly hotel domestic and international guest nights data, and annual population data.

Response data (NIMA)

NIMA is the incursion investigation risk identification and reporting framework for notifications to MPI of organisms that may represent a biological risk. The NIMA incursion response data were provided in confidence by MPI and covered the years 2011–2017 (data for earlier years were also provided but not used for the analysis). An incursion is defined by MPI as an exotic organism not previously known to be present in New Zealand, where there is a likelihood that the specimen(s) found is part of a self-sustaining/breeding population. The analysis used the positive records from NIMA as the response variable. A positive also refers to when a risk organism not known to be present in New Zealand is found, but there is no evidence that a selfsustaining / breeding population is present. In this case destroying or treating the risk organism or the risk goods (as the habitat of the organism) removes the threat. The database comprised records of insects, Arachnid spp. (spiders and mites), snails, plants



Figure 1. a map showing Crosby areas and boundaries used by the Ministry for Primary Industries (MPI) for recording detection areas of exotic organisms **b** territorial authorities and **c** region councils from which the annual population datasets were sectioned. New Zealand is divided into 16 regions and 73 territorial authorities. The regions are divided for local government purposes. Territorial authorities are the second tier of local government in New Zealand, below regional councils. Territorial authority districts are not subdivisions of regions, and some of them fall within more than one region. Maps generated using ESRI. ArcGIS Pro. Version 2.7.4. Mar. 6, 2021. https://www.esri.com/en-us/arcgis/products/arcgis-pro/overview



Figure 2. The monthly count of positive NIMA exotic organisms incursion reports. The x-axis year labels indicate the start of each year. Data source: Ministry for Primary Industry (MPI).

(terrestrial and aquatic), nematodes and microbes (bacteria, fungi and viruses) (all referred hereafter as exotic organisms), their location and date of discovery. Locations were based on the Crosby area codes for recording specimen localities in New Zealand (Crosby et al. 1976). The system comprises 29 geographic areas, with boundaries defined by mountain ranges or rivers, State Highways or straight lines between points (Fig. 1a) (Crosby et al. 1976). A monthly count of NIMA incursion reports is provided in Figure 2, which shows a spike just after the start of each year, corresponding to summer, with smaller winter spikes apparent in some years. NIMA data does not include biological material intercepted at the border such as international airports, seaports or quarantine transitional facilities.

Annual population data

The annual population data were provided by Stats NZ and comprise both city-level and regional annual population data (Fig. 1b, c). In terms of population numbers, the city of Auckland has the highest population, followed by the Canterbury district (Figure 3).

Tourism data

The tourism data comprised monthly counts of international and domestic visitor nights for accommodation establishments by district for the 2011–2017 period. The accommodation survey collected data on guests (including country of origin) staying in short-term commercial accommodation such as hotels, motels, backpackers, and holiday parks. Domestic data comprises New Zealanders undertaking tourist activities as well as those who may have been away from home for work, family, medical,



Figure 3. Annual population count either by city (Auckland, Wellington, Dunedin), or district (remaining labels). The x-axis labels indicate the start of each year. Data source: Stat NZ.

education and reasons other than simply 'tourism'. Hosted and private accommodation, such as bed and breakfasts and holiday homes, are not included. These include AirBnB, BookaBach, campervans, and friends and family that provide accommodation to both domestic and international guests. While there was no data for 2011 and 2012, this component of accommodation activity was first estimated by Stats NZ in 2013 as 8,4% of the total accommodation industry, rising to 14,5% in 2017 (Grant 2019). Territorial authorities are defined at the meshblock level and represent district and city councils boundaries (Stats 2017). The boundaries of territorial authorities are defined by the 'community of interest', the relevance of the components of the community to each other, and the capacity of the unit to service the community in an efficient manner (Stats 2017).

Auckland was found to dominate domestic occupations, followed by Canterbury (Fig. 4). Domestic tourist nights are much more sharply focused around the New Year than are the international tourist nights, while the pattern for international occupations is much more regular compared to domestic tourist nights. However, international tourist nights show a considerable winter surge in some regions that is not matched by domestic tourists (e.g., Otago Lakes, in particular Queenstown, Figure 4). The total count of international and domestic guest nights are broadly similar across the 20 unique locations (Figure 4).



Figure 4. Monthly guest nights (thousands) by territorial authority, region, or regional tourism organisation. The x-axis labels indicate the start of each year. Data source: Stats NZ.

Managing the spatiotemporal scale

The data represented processes that had been measured at different spatiotemporal levels: the daily (detection), monthly (tourism), and annual (population) levels, and organized variously within the city and district levels. Our goal was to assess whether there is any statistically detectable correlation between the NIMA incursion data and either or both of annual population and monthly tourism data. We chose to construct the model using data corresponding to monthly time-steps, which pick up any seasonal tourism patterns, and at the district or city level.

To complicate matters, the labelling of cities and districts were not consistent within the Stats NZ tourism and population data, respectively. Furthermore, while the district boundaries used in the NIMA incursion data were not the same as applied in the population and tourism databases, there was general alignment with the territorial boundaries used by Stats NZ to segment the latter databases (Fig. 1a, b). We aggregated the datasets to the lowest possible common level of aggregation, leaving 20 distinct locations.

The NIMA data were aggregated to month, and some districts merged to match the population and tourism data. For example, the NIMA data had distinct values for North Canterbury, Mid Canterbury, and South Canterbury, but this level of detail is not supported in the other datasets, so we created a single 'Canterbury' location. The tourism data are reported by month, so no change is needed to the temporal gradient, but as with the other datasets, some merging of district-level data was needed. The population data are annual, so no time changes are needed, and only modest district merges.

Analysis

We applied a *forward selection* algorithm that starts from a base model and adds (and tests) terms in a curated way. This is because the main alternative, namely *backward elimination*, involves fitting a complete model and doing so was very time-consuming for these data. The process involved several statistical tests that guided the choices between models. These tests were augmented by other model summary statistics. We compared models using two indices, namely (i) the adjusted R², which can be interpreted as the amount of variation in the response variable that statistically aligns with variation in the predictor variables, adjusted (penalized) to reflect the model size, and (ii) Akaike's Information Criterion (AIC).

The response variable was the number of positive reports each month at a location, which is a non-negative integer. We assumed that the response variable was conditionally Poisson, using a generalized linear modeling approach. We did not consider it safe to assume that the relationship between the candidate predictors and the response variable was a straight line. We fitted a model that allows the relationships to be wiggly, but penalizes the wiggle, so overall it would prefer to be straight, namely an additive model using splines (e.g., Wood 2017). Finally, although the dataset was reasonably large,

comprising 1560 monthly observations, it is also highly structured – for example, there are only 20 unique locations (see Figure 1), and the population data are recorded at the year level rather than at the month level. We needed to make the structure of the model match the structure of the data to be confident that the statistical model would discount the data appropriately. We did this by using a mixed-effects model, with year and district random effects. The base model was therefore

$$y_{dm} \sim Poisson(\lambda_{dt})$$

$$\log\left(\lambda_{dt}\right) = \beta_0 + s\left(x_{dt}\right) + \gamma_d + \gamma_t$$

where γ_{dm} is the number of positives in district *d* during month *m*; λ_{dt} is the mean monthly number of positives in district *d* during year *t*; β_0 is the population average (per month, per district); $s(x_{dt})$ is some smooth function *s* of the population in district *d* during year *t*, where *s* is chosen by the fitting algorithm as a trade-off of lack of fit against wiggliness; and γ_d and γ_t are iid Normal random effects for district and year with mean 0 and variances σ_d^2 and σ_t^2 respectively.

We applied the following model-fitting approach.

1. We started with a generalized additive mixed-effects model (gamm) that just uses the noted random effects (namely, year and district).

2. We then added annual population as a fixed-effect predictor to account for various levels of otherwise un-measured risk, e.g. sea cargo arrival rates. This term was not formally tested, although its performance will be discussed. This was the base model (above).

3. Next, a penalized smooth function of the sum of domestic and international nights and the difference between domestic and international nights were added, as fixed-effect predictors. Detailed diagnostic checks were made for each model, including spatial and temporal autocorrelation. Checks included:

a. Examining a scatterplot of residuals against fitted values to check for obvious lack of fit in the mean or variance model;

b. Examining plots of estimated autocorrelation to assess whether the residuals are temporally independent; and

c. Adding a smooth surface (a thin-plate spline) in UTM coordinates to see if there is any signal North–South or East–West, which would express in the original models as spatial autocorrelation.

4. This quartet of models (one from step 2 and three from step 3) were then compared, and the comparison interpreted for the statistical information that it provides as to the predictability of positive reports by population and hotel accommodation guest nights.

Results

Model fit statistics are recorded in Table 1. The second row reports the population effect, the third row reports total tourist nights, and the fourth is whether international tourist nights can be distinguished from domestic tourist nights. Both population and total tourist nights are strongly correlated to the number of NIMA incursion reports. Analysis showed that population effect was always monotonically increasing, and either close to linear or linear, and always statistically significant in the model. The total guest nights effect was always linear and increasing and seemed to modify the population effect only very little. Adding international and domestic guest nights improved the Akaike's Information Criterion (AIC). Finally, the difference between international and domestic guest nights effect was flat, suggesting that there is no significant difference in the model based on these data.

The final model of all terms is summarized in Figure 5, which shows that (i) total nights is strongly and linearly related to the natural log of exotic organism reports even when population is considered, and (ii) there is no evidence of any greater risk from international than from domestic nights. A further note on interpretation is that if

Table 1. Model fit showing the adjusted R² and Akaike's Information Criterion (AIC) in relation to exotic organism interceptions (NIMA reports) in New Zealand. For the AIC values, the lower the number, the better the model fit. The first row reports the base model as defined above; the second is base with (annual) population level added. The third row reports the base model with population and total (monthly) nights of guest nights, and the fourth row includes the previous terms and the difference between international and domestic guest nights. The P-values are generated from the final model in the table (specifically, the full model).

Model description	Adjusted R ²	AIC	P-value
Base	0	2197	-
Adding Population counts	0.551	2189	0.0046
Adding International + Domestic guest nights	0.586	2180	0.00078
Adding International – Domestic guest nights	0.588	2184	0.7611



Figure 5. Estimated model effects of the conditional relationship between (i) population and biosecurity incursion reports, (ii) total nights and incursion reports, and (iii) the difference between domestic and international nights and incursion reports. Dashed lines represent approximate 95% confidence limits.

the dashed lines intersect (such as in the center and right panel) then the fitted line is straight, otherwise (as in the left panel) it has curvature. The y-axis in each case is labelled with a measure of the magnitude of the curvature needed to capture the relationship. If absent, then the requited curvature is 1, signifying a straight line. Our examination of the model assessment graphics revealed no important caveats (not shown here).

Discussion

The following discussion summarizes the performance of the candidate predictor terms across the set of four nested models that we fitted. There is considerable spatial and temporal variation in the NIMA incursion reports, much of which correlates highly to base human population. The model-fitting exercise shows that there is a clear statistical signal that links reported incursion reports with the hotel guest nights (Table 1). However, it is impossible with the current data to distinguish between the variability that correlates to international as opposed to domestic hotel guest nights.

We drew these conclusions using statistical reasoning as follows. Adding the population predictor to the base model greatly enhanced model fit (Table 1). We then added a flexible function of the combined guest nights, that is, the sum of international and domestic guest nights, and found further model improvement, which suggests that variation in guest nights relates to variation in incursion reports that is not otherwise related to population. Finally, we added a flexible function of the subtraction of international from domestic tourist nights. If this term were statistically significant, then this significance would suggest that there is a difference between the effect of domestic as opposed to international tourist nights upon the response variable, and indeed whether the influence of one is greater than the other. No such signal was detected, leading us to conclude that the important apparent relationship is for tourist nights regardless of whether they are international or domestic. The model sketch provided in Figure 5 affirms that both population and total tourist nights are positively correlated to incursion reports, and the model cannot distinguish between the effects of international as opposed to domestic tourist nights. Overall, our analysis showed that tourism, either international or domestic, represents a significant pathway for the introduction and secondary dispersal of biosecurity threats to the extent that this can be established by statistical modeling of an observational study.

We now describe caveats relevant to our interpretation of the model outputs with regards to the underpinning scientific questions. Our goal was to assess the statistical strength of candidate explanatory factors for pest arrival and within-country transport. However, the response variable is the number of exotic organisms detected in the area per month, rather than the number of pests arriving in the area per month. Therefore, we are obliged to assume a tight connection between the arrival of an exotic organism and its detection that amounts to them occurring in the same month. However, this assumption may not always hold; as the research literature shows that a number of historical positives are known to have dispersed undetected, for example emerald ash borer, *Agrilus planipennis*, (Coleoptera: Buprestidae) in the USA (Siegert et al. 2014) and clover root weevil, *Sitona obsoletus* Gmelin (Coleoptera: Curculionidae) in New Zealand (Barker et al. 1996). Conversely, early detection of brown marmorated stink bug *Halyomorpha halys* Stål (Heteroptera: Pentatomidae) in luggage and a hotel room in New Zealand (MPI, unpublished data), exotic fruitfly (*Bactrocera* and *Ceratitis* spp.) in surveillance traps (Quilici and Donner 2012), and granulated ambrosia beetle (*Xylosandrus crassiusculus*, (Motschulsky) (Coleoptera Scolytidae) (Anon 2019), as part of surveillance programs, can improve the probability of determining the pathway for entry as well as improve the probability of eradication if an exotic species were to establish. Positive detection might correlate better with passive surveillance efforts (e.g., citizen science) (Froud et al. 2008; Hester and Cacho 2017) and larger human population centers may have higher probability of detection. We tried to correct for this by including baseline human population in the model, but this assumption could be better tested by a trace-back of each of the reported detections to assess the 'maturity' of the positive at the time of detection. Such an exercise was beyond the remit of our project.

The analysis only considers population count and a measure of within-country tourist activity (monthly number of guest nights). The analysis therefore excludes other potential pathways, including sea freight associated with international trade. The volume of trade imports is generally held to be a more substantial source of biosecurity risk than are international passengers (See Hulme 2009; Sikes et al. 2018). If passenger and freight arrival volumes are correlated, then any potential statistical signal for passengers could be complicated by failing to account for cargo movements. It may be reasonable to believe that arriving freight is correlated with human population concentrations (e.g. Auckland, which is the most populous urban area in New Zealand), however, hitchhiker organisms on freight may have a seasonal pattern that the annual population variable cannot represent. This assumption could be tested by including a candidate predictor that would represent freight activity, for example, monetary value or volumes of imports arriving at both air and sea ports. However, information about subsequent within-country freight movement is not available.

The accommodation survey includes data on short-term commercial accommodation (hotels, motels, backpackers, and holiday parks). Other accommodation types such as 'accommodation-sharing' e.g. AirBnB are not captured, but as noted previously was estimated at c. 8% in 2013 increasing to c. 14% in 2017 of the total accommodation industry (Grant 2019). Therefore, as accommodation-sharing comprised a minor component of the accommodation industry, the biosecurity incursion reports associated with international and domestic visitor nights were highly representative. Within-country tourist accommodation likely comprises a wider variety of activities. For example, some camping grounds and visits to friends and family are not included in the domestic and international guest nights data. Camping trips could make an important difference to the travel statistics, because an unknown proportion will likely involve destinations in more remote or vulnerable areas (see, for example, Runghen at al. 2021). This assumption could be tested by finding further information on campground occupation statistics and recreational vehicle rentals. The analysis ignores a reasonable supposition that the first few nights for arriving passengers are probably the riskiest from the point of view of the movement of exotic organisms. In the analysis, all nights of accommodation are treated equally. However, the locations of the first few nights for international passengers are likely to be concentrated in areas with high population counts, especially for Auckland, which is New Zealand's main international arrivals airport. On the other hand, analysis of the first seven nights for international passengers shows that they disperse quickly once in the country (Wilson et al. 2018).

The analysis was also unable to discern between New Zealand residents who have arrived from international departure points and New Zealand residents whose travel is purely domestic. However, we consider it reasonable to assume that the influence of returning New Zealanders is relatively negligible in distinguishing between the impact of international and domestic tourism on within-country spread.

The analysis also assumes that the true population data do not change appreciably within the year. Conversely, the other candidate predictors (international and domestic guest nights) both show substantial within-year variation. Therefore, it is possible that the true population data could also change within the year, an assumption that could be assessed if finer-scale data were available.

These results generally support the findings of Edney-Browne et al. (2018), who found that the number of international tourist arrivals to New Zealand, was an important component to explain spatial patterns for establishment of exotic organisms. Conversely, a broader modeling analysis of the major drivers to invasion risk for the "100 among the world's worst invasive alien species", found that socioeconomic variables including human population density, distance to the nearest airport or distance to the nearest seaport, were important contributors to explain the distribution of most taxonomic groups in the list (Bellard et al. 2016).

In conclusion, this analysis using population density and accommodation nights found that the number of reported positive interceptions of exotic organism was significantly positively related to population density and at the same time significantly positively related to total guest nights (combining international and domestic guests). There is no evidence of any difference between international and domestic guests in terms of the relationship with interceptions of exotic organisms. Therefore, we suggest that this study provides conditional evidence that international tourism contributes to the introduction of exotic organism, and within-country movement of both international and domestic tourists aids the secondary dispersal of exotic organisms. While the analyses showed a strong relationship between data for exotic organism interceptions and tourist guest nights, it does not allow us to determine if tourists are also the vector for exotic organisms. However, it may be a reasonable assumption to suggest there is a link which could be investigated. Further research that differentiates the respective role of both tourist segments, and their overall contribution to biosecurity risk in relation to other pathways (e.g. sea freight) for the introduction and dispersal of exotic organisms would also seem warranted. This would contribute to the development of more effective biosecurity risk monitoring and mitigation procedures.

The core take-home message is that anthropogenic movements associated with tourism correlate with detection of exotic organisms in New Zealand. The results also reinforce the need for biosecurity authorities to continue to allocate resources to managing the tourism pathway.

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RESEARCH ARTICLE



Mate choice errors may contribute to slow spread of an invasive Eurasian longhorn beetle in North America

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Abstract

Tetropium fuscum (Coleoptera: Cerambycidae) is a Eurasian longhorn beetle and forest pest that first became invasive to Nova Scotia, Canada around 1990. In the time since its introduction, *T. fuscum* has spread only about 150 km from its point of introduction. In its invasive range, *T. fuscum* co-exists with its congener *Tetropium cinnamopterum*. Although they are ecologically similar species, *T. fuscum* tends to infest healthier trees and has a smaller host range than *T. cinnamopterum*. If they successfully interbreed, this could lead to hybrid individuals that are more problematic than either parent species. On the other hand, if *T. fuscum* can make mating errors in the field, but is not producing hybrid offspring, then this waste of mating resources could help explain the slow spread of *T. fuscum* in North America. We conducted nochoice and choice mating experiments between *T. fuscum* and *T. cinnamopterum* males and females and determined that both *T. fuscum* and *T. cinnamopterum* males make mate-choice errors with heterospecific females in a laboratory setting. Our results suggest that mating errors may play a role in the slow spread of *T. fuscum* in North America.

Keywords

Congener, hybridisation, invasion biology, mating behaviour

Introduction

Invasive species are a threat to global biodiversity (Rhymer and Simberloff 1996; Vitousek et al. 1997) and those that successfully establish exploit resources, such as food and shelter, thereby decreasing resources available to native species. They can also act as natural enemies (predators or parasites) for the native species they encounter. Furthermore, depletion of food sources, predation or removal of an important predator by an invasive species can have catastrophic ripple effects in an ecosystem. The rate of invasion by introduced species has been steadily rising due to climate change, habitat modification, international trade (Findley and O'Rourke 2007) and globalisation in transport of unprocessed wood products (Haack 2006), allowing for accidental introductions (Allendorf et al. 2001; Sax et al. 2007; Kelly and Sullivan 2010). Invasive species are now ubiquitous (Seebens et al. 2016) and cause significant ecological and economic impacts around the globe (Vitousek et al. 1996; Pimentel et al. 2000, 2005). Nearly half of the endangered species in the USA are threatened because of competition with and predation by invasive species (Stein and Flack 1996).

Several factors determine whether an introduced species will establish itself and become invasive in a novel habitat (Ehrlich 1986; Williamson and Griffiths 1996). Understanding factors that drive invasiveness could allow us to predict and prevent potential invaders and manage those already present (Pyšek and Richardson 2010). Traits that are predictors of invasiveness across taxa include high dispersal ability (Moyle 1986; O'Connor et al. 1986; Kolar and Lodge 2001), high reproductive rates (Gallagher et al. 2014; Mathakutha et al. 2019), high competitive ability (O'Connor et al. 1986; Newsome and Noble 1986; Moyle 1986), high propagule production (O'Connor et al. 1986; Kolar and Lodge 2001), association with humans (Kolar and Lodge 2001; García-Berthou 2007; Mathakutha et al. 2019), fast growth (Newsome and Noble 1986; Kolar and Lodge 2001), ability to tolerate and adapt to a broad range of conditions (Ehrlich 1986; Moyle 1986), large body size (Ehrlich 1986; Kolar and Lodge 2001; García-Berthou 2007) and a generalist diet (Ehrlich 1986). However, the specific combination of species traits that would allow a species to invade one habitat may not extend to the same species in another habitat or a different species in that same habitat (Lodge 1991) and we still lack a fully predictive understanding of invasions and the multiple factors that can determine invasiveness.

Many species are accidentally introduced but do not establish or experience population growth sufficient to gain pest status (Williamson and Griffiths 1996). Species that successfully establish, but then undergo limited spread, such as the phloemfeeding longhorn beetle, *Tetropium fuscum* Fabricius (Coleoptera: Cerambycidae), are poorly understood and offer an interesting window on traits and ecological factors that determine invasiveness. We examine some factors that may be negatively impacting reproductive rate in *T. fuscum* and, thus, impeding its ability to invade North America.

Tetropium fuscum experienced initial success in establishment and population growth upon its introduction to North America (in or before 1990), but by 2010, it had spread only ~ 80 km from its point of entry in Halifax, Nova Scotia (Canada)
(Rhainds et al. 2011). To date, it has only been identified in one small area in the south-eastern part of the neighbouring Province of New Brunswick (CFIA 2017), an additional 70 km from its point of introduction. *T. fuscum* is native to western Europe and northern Eurasia (Juutinen 1955), including areas with climates very similar to the invasive range in Nova Scotia. It was first discovered in mature red spruce trees in Point Pleasant Park, Halifax, NS, in 1999 (Smith and Hurley 2000), but collections in the Nova Scotia Museum of Natural History indicate that it had been present since at least 1990, having been misidentified as its native counterpart *T. cinnamopterum* Kirby (Sweeney et al. 2004). In its native range, *T. fuscum* attacks predominately stressed or moribund Norway spruce (*Picea abies* (Linnaeus) Karsten) (Juutinen 1955), but in Nova Scotia, it has been observed attacking apparently healthy red spruce (*Picea rubens* Sargent), white spruce (*Picea glauca* Moench (Voss)), black spruce (*Picea mariana* (Miller) Britton, Sterns and Poggenburg) and Norway spruce (Smith and Humble 2000).

Tetropium fuscum is unusual in that the introduced population neither died out, nor saw rapid and successful expansion in North America. T. fuscum has established a stable population in the Halifax area, but its expansion into other parts of North America has been extremely slow (Rhainds et al. 2011). T. fuscum's co-existence with the native congener T. cinnamopterum in the invaded range and their ecological similarities could result in Allee effects that contribute to its slow spread in North America. The two species share many similarities including phenology and preferred host plants. Tetropium *fuscum* and *T. cinnamopterum* both emerge in the spring, beginning in May and their flight period lasts until late August (Juutinen 1955). Although T. fuscum emerges on average 2 weeks earlier than *T. cinnamopterum*, their flight periods overlap significantly (Rhainds et al. 2011). Tetropium fuscum is limited to trees in the genus Picea (spruces), while T. cinnamopterum's somewhat broader host range includes Picea spp. amongst other conifers (Furniss and Carolin 1980), providing plenty of opportunity for interspecific encounters. Notably, the species share the highly conserved male-produced pheromone component S-fuscumol, which synergises attraction of males and females of both species when combined with host (spruce) volatiles (Silk et al. 2007; Rhainds et al. 2010; Sweeney et al. 2010). Thus, pheromone blends emitted by males of one species may attract females of both species, particularly if the male is emitting from a host tree - and this sets the stage for possible mate choice errors. Mate choice also involves more local signalling; however, T. fuscum and T. cinnamopterum males both respond to cuticular hydrocarbons on the surface of females (Silk et al. 2011).

We hypothesised that *Tetropium fuscum* males, where the two species co-occur, make mate choice errors by sometimes mating with *T. cinnamopterum* females rather than with *T. fuscum* females. Such errors might be expected to be particularly common near *T. fuscum*'s range edge. Invasive species populations are often the densest at the epicentre of invasion and become more sparsely distributed closer to the range edge (Udvardy and Papp 1969; Sagarin and Gaines 2002; Sagarin et al. 2006; Mlynarek et al. 2017). Thus, near the edge of their invasive range, *T. fuscum* males are likely to encounter primarily *T. cinnamopterum* females. If such matings produce fewer or no viable, fertile offspring, then wasted mating resources would hinder population growth of *T. fuscum*. Copulation

by *Tetropium* spp. can take several hours to complete and these beetles only live for 1–4 weeks on average (Juutinen 1955). Thus, the time it takes to locate and copulate with even one female is a non-negligible proportion of the entire lifespan of a *Tetropium* male; repeated mating errors would be even more costly. We tested whether mate choice errors occur for *T. fuscum* and *T. cinnamopterum* males in the laboratory, using: 1) choice experiments reflecting mate encounters expected at the centre of the invaded range where both species are common and 2) no-choice experiments reflecting mate encounters expected at range edges where *T. fuscum* will more frequently encounter *T. cinnamopterum*.

Methods

No-choice mating experiment

Source of beetles

We obtained *T. fuscum* from a laboratory colony at the Great Lakes Forestry Centre, in Sault Ste. Marie (Ontario, Canada). We placed them in a fridge at 5 °C, in a containment lab at the Atlantic Forestry Centre, Fredericton, New Brunswick until used in experiments.

We obtained T. cinnamopterum from baited red spruce bolts. In April 2015, we haphazardly chose and felled 10 red spruce trees (*Picea rubens*) with a diameter at breast height of approximately 25 cm at the Acadia Research Forest, Noonan (New Brunswick, Canada; 46°0'2.99"N, 66°20'32.72"W). We cut each bole into six 120 cm long logs and arranged them in pyramid-style decks (three largest logs on the bottom, two on the second layer and one on top) to favour infestation by T. cinnamopterum. We attached three lures including fuscumol, ethanol and a blend of monoterpenes, as outlined by Sweeney et al. (2010), to enhance attraction and increase the likelihood of infestation. In October 2015, we took the top three logs from each deck, cut each into four 30 cm long bolts and held them outdoors in an open, but covered storage shed at the Acadia Research Forest, exposed to ambient temperatures, until late December. We brought bolts to the Atlantic Forestry Centre, 40 at a time and reared them in sealed Plexiglas cages in a quarantine facility at 20-24 °C with constant dehumidification and a 16:8 photoperiod [L:D] to obtain live adult beetles. Once beetles began to emerge (4 weeks on average), we brushed the bolts down twice per day - once in early morning and once in early afternoon - to ensure collection of beetles as close to emergence as possible. These bolts produced only T. cinnamopterum. We sexed the beetles upon collection and placed them immediately in the same fridge as T. fuscum. All beetles were individually placed in 1.5 ml microcentrifuge tubes and labelled with sex, species and emergence date.

No-choice mating protocol

We checked beetles for vigour before using them in matings. Some beetles lived longer than others and thus we held beetles for variable amounts of time; however, most beetles were used within 7 days of collection. We presented beetles with potential mates, without choice, in Petri dishes lined with moistened filter paper. We used four treatments: 1. *T. fuscum* male with *T. fuscum* female; 2. *T. fuscum* male \times *T. cinnamopterum* female; 3. *T. cinnamopterum* male \times *T. cinnamopterum* female; and 4. *T. cinnamopterum* male \times *T. fuscum* female (n = 85, 154, 132 and 91, respectively). We excluded any beetles with obvious deformities and attempted to match males and females by size as much as possible. After 30 minutes, we allowed any pairs that were engaged in copulation to continue to completion.

Mating behaviour

We define a mating attempt as an instance in which a male tries to mount a female and orient their genitalia together. This behaviour includes the male positioning himself dorsally and slightly posterior to the female, extending his aedeagus and attempting to connect it to the female's ovipore. Mating attempts are distinguished from instances when a male simply climbs over a female while walking around the Petri dish. Successful mating attempts are when the male and female connect through the aedeagus and ovipore. When this connection is made, there is a visible transparent tube extending from the posterior end of one beetle to the posterior end of the other. Typically, during successful copulation, female *Tetropium* run around and drag the males behind them by their genitalia.

Statistical analysis

We compared five response variables across treatments: proportion of beetle pairs attempting to mate, proportion mating successfully, time until first mating attempt, time until successful mating and time spent in copula.

As our no-choice mating experiment is essentially two independent no-choice mating experiments, one using *T. cinnamopterum* males and another using *T. fuscum* males, we ran some of the analyses for these two experiments separately. We chose to do this for the proportion of males that attempted and the proportion of males that succeeded because the comparisons we were interested in were treatment 1 (*T. cinnamopterum* male \times *T. cinnamopterum* female) compared to treatment 2 (*T. cinnamopterum* male \times *T. fuscum* female), as well as treatment 3 (*T. fuscum* male \times *T. cinnamopterum* female) compared to treatment be proportion, we tested the prediction that the proportion of mating attempts would be greater with conspecifics than heterospecifics, using a two-sided Fisher's Exact Test. We similarly tested a second prediction, that the proportion of pairs with successful matings would be greater with conspecifics than heterospecifics.

As both *T. fuscum* and *T. cinnamopterum* males respond behaviourally to contact pheromones present in female cuticular hydrocarbons, time until first mating attempt and time until successful mating reflect events, respectively, before and after males contact females and gain information about their identity (Silk et al. 2011). We asked whether there were differences amongst treatments in time until first mating attempt, which would reflect behaviour of *Tetropium* males before they obtain information

about cuticular hydrocarbons. We performed Box-Cox transformation of data for time until first mating attempt, using the R package bestNormalize (v. 3.3.5 2021) (Peterson and Cavanaugh 2019) to determine the most effective transformation within the Box-Cox family. The best lambda values were 0.15 for time until first mating attempt and 0.22 for time until successful mating attempt. We performed a two-way ANOVA on each response variable, using male species and female species as factors, to compare times amongst treatments. We used Tukey's HSD for pairwise comparisons where main effects were significant.

A longer time until a successful mating attempt indicates that the male is reluctant to mate with the female they are interacting with. This longer time to success, coupled with behaviour of *Tetropium* males after touching the females with their antennae prior to copulation, suggests that this reluctance is based on the female's cuticular hydrocarbon composition. Once a male had committed to mating with a particular female, we expected the time spent in copula to be the same whether with a heterospecific or conspecific female. We transformed our time-in-copula data using a hyperbolic arcsine, based on the recommendation of bestNormalize. We then tested the hypothesis with a two-way ANOVA with male species and female species as factors. We performed all statistics in R, using base R version 4.0.4 (R Core Team 2021).

Choice mating experiment

Source of beetles

In April 2016, we felled six red spruce trees (*Picea rubens*) with a mean diameter at breast height of about 25 cm from each of four sites: Acadia (NB) (46°0'2.99"N, 66°20'32.72"W), Sandy Lake (NS) (44°44'42.67"N, 63°40'40.76"W), Antrim (NS) (44°57'59.80"N, 63°22'18.58"W) and Westchester (NS) (45°36'52.86"N, 63°42'25.59"W). We also felled two additional trees of the same criteria from Acadia and transported them to a fifth site in Memramcook (NB) (46°3'8.06"N, 64°34'46.45"W). We arranged the trees into decks and baited them with pheromone as described for the no-choice mating experiment. In November 2016, we cut the top three logs from each deck into four 30 cm bolts and brought the bolts back to the Atlantic Forestry Center in Fredericton, New Brunswick. We cut up all six logs from the two Memramcook decks to increase the number of beetles we got from this site. We placed the bolts into a containment freezer at -2 °C in order to simulate winter conditions. We left the bolts in the freezer until January 2017, when we brought batches of bolts out of the freezer and warmed them up in sealed Plexiglas cages in containment facilities at 20-24 °C with constant dehumidification and a 16:8 photoperiod [L:D] to allow the beetles to develop into adults. We collected and stored the beetles as for the no-choice mating experiment.

Choice mating protocol

We checked beetles for vigour prior to their use in matings, as in the no-choice experiment. Most beetles were used within 10 days of collection. We had two treatments for this experiment: 1. *T. fuscum* male presented with *T. fuscum* female and *T. cinnamopterum* female; and 2. *T. cinnamopterum* male presented with the same choice (n = 42 and 30, respectively). We placed the females together and placed the male directly across a Petri dish lined with moistened filter paper. We gave the males 30 minutes to begin copulating with one of the females. If, at the end of the 30-minute time period, the male was in copula with one female, we removed the other female and left the mating pair in the dish until completion of copulation. If, at the end of the 30-minute time period, the male was not in copula with a female, we removed all three beetles from the Petri dish.

Statistical analysis

We compared four response variables between treatments: time until first mating attempt, species of female first touched by male, species of female that males first attempted to mate with and species of female for successful matings.

As our choice mating experiment is essentially two independent choice mating experiments, one using *T. cinnamopterum* males and another using *T. fuscum* males, we ran some of the analyses for these two experiments separately. We chose to do this for species of first touch female and species of first female attempted because the comparisons that were meaningful to us were *T. cinnamopterum* males with conspecific females compared to heterospecific females and, separately, *T. fuscum* males with conspecific females compared to heterospecific females. For each experiment, we tested for preference of species of first-touch female using an Exact Binomial Test with p set at 0.5. In each case, we used a second Exact Binomial Test with p set at 0.5 to look at preference of species of female first attempted with. We did not do formal statistics on our time until successful mating in this experiment because of the clear-cut pattern for preference of conspecific females and the low sample size of heterospecific matings in both treatments. We calculated 95% confidence intervals for rates of heterospecific matings using a binomial CI calculator (Pezzullo 2009).

We used the R package bestNormalize (v. 3.3.5 2021) (Peterson and Cavanaugh 2019) in order to determine the most effective transformation for the data, leading us to do a logarithmic transformation. We performed a two-way ANOVA, using male species and heterospecific vs. conspecific females as factors, to compare times amongst treatments, followed by a Tukey's HSD for pairwise comparisons of significant main effects. We conducted all statistical analysis in R using base R version 4.0.4 (R Core Team 2021).

Results

No-choice mating experiment

Tetropium cinnamopterum males both attempted ($p < 2 \times 10^{-16}$) and succeeded ($p < 2 \times 10^{-16}$) significantly less with heterospecific females than with conspecific females. We

saw the same pattern with *T. fuscum* male attempts ($p = 5.81 \times 10^{-6}$) and successes (p = 0.02) (Fig. 1).

Neither male ($F_{1.203} = 0.83$; p = 0.36) nor female ($F_{1.203} = 0.58$; p = 0.45) species had a significant effect on time until first mating attempt (Fig. 2), but the interaction of the two was significant ($F_{1.203} = 29.77$; $p = 1.41 \times 10^{-7}$). Tukey's HSD analysis suggests that both *T. cinnamopterum* and *T. fuscum* males take significantly longer to attempt to mate with heterospecific females than conspecific females ($p = 3.03 \times 10^{-5}$, p = 0.02, respectively).



Figure 1. Proportion of *Tetropium fuscum* (TF) and *Tetropium cinnamopterum* (TC) males in a no-choice mating experiment that did not attempt to mate, attempted to mate but failed and succeeded to mate (n = 85, 154, 132, 91).



Figure 2. Time until first mating attempt by *Tetropium fuscum* (TF) and *Tetropium cinnamopterum* (TC) males in a no-choice mating experiment (n = 72, 26, 50, 63, respectively). Lines represent Q1-3, whiskers show +/- $1.5 \times IQR$ and dots represent outliers. Boxes with different letters are significantly different (Tukey's HSD, p < 0.05).

Male species had no effect on time until successful mating attempt (Fig. 3; $F_{1.122} = 0.70$; p = 0.40), nor did female species ($F_{1.122} = 0.17$; p = 0.68), but the interaction of the two was significant ($F_{1.122} = 9.73$; p = 2.27×10^{-3}). *Tetropium cinnamopterum* males took significantly longer to successfully mate with heterospecific females than conspecific (Tukey's HSD; p = 0.02), but *T. fuscum* males did not (Tukey's HSD; p = 0.66).

There was no effect of male species ($F_{1.122} = 0.29$; p = 0.86), female species ($F_{1.122} = 0.61$; p = 0.44) or the interaction of the two ($F_{1.122} = 3.49$; p = 0.06) on time spent in copula (Fig. 4).



Figure 3. Time until successful mating attempt by *Tetropium fuscum* (TF) and *Tetropium cinnamopterum* (TC) males in a no-choice mating experiment (n = 54, 6, 33, 37, respectively). Lines represent Q1-3, whiskers show +/- $1.5 \times$ IQR and dots represent outliers. Boxes with different letters are significantly different (Tukey's HSD, p < 0.05).



Figure 4. Time spent in copula by *Tetropium fuscum* (TF) and *Tetropium cinnamopterum* (TC) males in a no-choice mating experiment (n = 54, 6, 33, 37, respectively). Lines represent Q1-3, whiskers show +/- 1.5 × IQR and dots represent outliers. There were no significant differences amongst treatments.

Choice mating experiment

Species of male had no significant effect on time until first mating attempt ($F_{1.58} = 1.41$; p = 0.24) (Fig. 5). Species of female also had no effect on time until first mating attempt for either *T. fuscum* or *T. cinnamopterum* males ($F_{1.58} = 0.66$; p = 0.42) (Fig. 5).

Species of first touch female for *T. fuscum* males was 25 conspecific and 17 heterospecific. For *T. cinnamopterum*, it was 13 conspecific and 17 heterospecific. Neither *T. cinnamopterum* nor *T. fuscum* males showed any significant preference for conspecific or heterospecific females at first touch (p = 0.58, 0.41, respectively).

Species of female for first mating attempt for *T. fuscum* males was 28 conspecific and five heterospecific. For *T. cinnamopterum*, it was 27 conspecific and two heterospecific. Both *T. cinnamopterum* and *T. fuscum* males showed significant preference for conspecific over heterospecific females at first mating attempt ($p = 1.62 \times 10^{-6}$, 5.65 × 10⁻⁶, respectively).

Of the 42 *T. fuscum* males used in the choice mating experiment, 12 successfully mated. 11 of those 12 matings were conspecific (95% CI 0.2 - 38% heterospecific matings). Of the 30 *T. cinnamopterum* males, 17 mated successfully and all 17 were conspecific (95% CI 0 - 19.5% heterospecific matings). Despite a clear-cut pattern of both species of male preferring conspecific over heterospecific females, we cannot reject quite high rates of heterospecific choice (up to 19% even for *T. cinnamopterum*).

Discussion

We saw evidence of interspecific mating by both *Tetropium fuscum* and *T. cinnam-opterum* males in the no-choice experiment. For both species, males attempted and



Figure 5. Time until first mating attempt by *Tetropium fuscum* (TF) and *Tetropium cinnamopterum* (TC) males in a choice mating experiment (n = 27, 2, 5, 28, respectively). Lines represent Q1-3, whiskers show +/- 1.5 × IQR and dots represent outliers. There were no significant differences amongst treatments.

succeeded significantly less with heterospecific females than with conspecific females. However, rates of heterospecific attempts and successes were both considerable. While both T. fuscum and T. cinnamopterum males took longer to attempt mating with a heterospecific female than a conspecific one, they still mated quite rapidly with heterospecific females. The same was true for time until successful mating. We often observed males touching females with their antennae prior to attempting to copulate, consistent with reports that Tetropium spp. males respond to female cuticular hydrocarbons (Silk et al. 2011), but inconsistent (because heterospecific matings still occurred) with a model in which a cuticular-hydrocarbon "match" is required for mating. Silk et al. (2011) also observed low percentages of heterospecific mating in both T. fuscum and T. cinnamopterum with dead females and suggested this may be due to the presence of a common cuticular hydrocarbon, 11-methylheptacosane, on the elytra of females of both species – although the overall mix of hydrocarbons differs between the species. T. fuscum males attempted and succeeded with heterospecific females more frequently than did T. cinnamopterum males, but we do not know whether this reflects lesser ability to recognise heterospecific partners or looser specificity in accepting them.

Tetropium beetles make mating errors even when they have ample opportunity to avoid them. Under choice conditions, one of twelve *T. fuscum* males mated heterospecifically. While we did not observe any heterospecific matings by *T. cinnamopterum* males in the choice experiment, our sample size was small and we cannot reject an underlying rate as high as 19%. In these choice trials, both *T. fuscum* and *T. cinnamopterum* males made first mating attempts in the same mean amount of time regardless of whether that attempt was on a heterospecific or conspecific female. We considered that perhaps males would simply mate with the first female they bumped into in the Petri dish, but in fact, first-touch female species did not adhere to any significant pattern, while both species of males preferentially made their first mating attempt on conspecific females. This indicates that males have the ability to "choose" conspecific females over heterospecific females – but they do not always do so.

Both *T. fuscum* and *T. cinnamopterum* males spent as much time in copula with heterospecific females as they did with conspecific females. This suggests that *Tetropium* males determine the suitability of a mate (imperfectly), based on the precopulatory act of touching the cuticular hydrocarbons of the female. If the barrier to copulation were something pericopulatory, like a genital lock-and-key mechanism, we would expect to see prematurely terminated copulation in heterospecific pairs. It also suggests that beetles will pay full time and resource costs of heterospecific matings, rather than breaking them off and moving on to other mating opportunities.

Our matings were all conducted in Petri dish arenas and, like any laboratory experiment, may not fully capture insect behaviour in nature. Lab experiments are commonly used to investigate arthropod mating behaviour for a wide range of arthropods including beetles (Nilsson et al 2002; Kumano et al. 2010; Rutledge and Keena 2012), moths (Jiménez-Pérez and Wang 2003; Bento et al. 2006), bed bugs (Reinhardt et al. 2009), predatory bugs (Bonte et al. 2012) and wolf spiders (Vaccaro et al. 2010). Lab experiments are particularly important for invasive species, where field manipulations may be logistically and/or ethically problematic. Experiments under field conditions, perhaps with captive beetles released near the centre of the invasive range where such releases do not threaten to accelerate the invasion, would be worth pursuing.

While mating errors occurred under both choice and no-choice conditions, they were much more frequent in our no-choice experiments. In no-choice situations, *T. fuscum* males were more reluctant to attempt mating and less likely to successfully copulate with heterospecific females than with conspecific females; but given enough time, many of them did. This suggests that *T. fuscum* males may become less choosy the longer they go without locating a mate, a situation that may be most common at range edges. In Nova Scotia, the population density of *T. fuscum* is highest at the range centre and decreases outwards (Heustis et al. 2017; Anderson, unpublished data). At the edges of *T. fuscum*'s invasive range, then, males are more likely to encounter *T. cinnamopterum* females than *T. fuscum* females. If such hybrid matings do not produce fertile offspring, this could reinforce the edge of their range preventing the population from spreading further (Rhainds et al. 2015). Such Allee effects can limit spatial spread of a species even after establishment of a stable population (Keitt et al. 2001).

Of course, it is also possible that heterospecific matings do produce viable and fertile offspring. If so, the encounter between the two *Tetropium* species could pose a different set of challenges to forest managers. Hybrid offspring may exhibit traits intermediate to their parents (Roe et al. 2014; Patterson et al. 2017), hybrid breakdown (McQuillan et al. 2018; Pâques 2019) or hybrid vigour (Shao et al. 2019; Kumar et al. 2020). Tetropium fuscum attacks more vigorous trees than T. cinnamopterum (Smith and Humble 2000), although T. cinnamopterum can attack a broader range of conifers in North America than T. fuscum can (Furniss and Carolin 1980). Hybrid Tetropium might display both traits and, thus, be more threatening to North American forests than either parental species. There are similar concerns in other invasive insects. For instance, the winter moth Operophtera brumata Linnaeus is invasive to north-eastern North America and co-exists with its native congener Operophtera bruceata Hulst (Elkinton et al. 2010; Simmons et al. 2014). As in Tetropium, sex pheromones are highly conserved across the genus and the sex pheromone blend of O. brumata females attracts both O. brumata and O. bruceata males (Khrimian et al. 2010). Unsurprisingly, O. bruceata and O. brumata are known to hybridise (Elkinton et al. 2010) and, in this case, the hybrids are fertile (Havill et al. 2017). In winter moth, hybridisation between the invasive and native congeners may be aiding the spread by alleviating the Allee effects often seen in small founder populations of invasive species (Elkinton et al. 2014). Furthermore, the intermediate traits exhibited by hybrids could confer an invasive and evolutionary advantage to the hybrid offspring (Havill et al. 2017). All this suggests that it will be important to determine whether mating errors in Tetropium produce offspring and, if so, if those offspring are fertile and display hybrid vigour. But do they? Although very few morphologically intermediate Tetropium specimens have been identified in eastern Canada, morphology is not always a reliable predictor of introgression (Rhymer et al. 1994). We are currently surveying wild populations to determine whether hybrid beetles occur where the two *Tetropium* species are sympatric.

Allee effects, arising from mate-choice errors, are not the only mechanism that could be behind the slow range expansion of T. fuscum. Pinned edges of a species' geographical range can result from many things. Dispersal limitation can often slow an invasion, especially for species that are unlikely to be transported by humans. Restrictions on the movement of untreated lumber and firewood (Canadian Food Inspection Agency 2019) may have slowed the *Tetropium* invasion, but are unlikely to be responsible for its near cessation. More interestingly, Darwin's naturalisation hypothesis suggests that, when a species invades an area where a close relative is already established, it will be less likely to successfully establish due to higher competition for resources (Darwin 1859; Jiang et al. 2010; but see Ricciardi and Mottiar 2006; Park and Potter 2013; Sol et al. 2021) and such competition can pin range edges (Heller and Gates 1971; Bull and Possingham 1995; Case and Taper 2000). Tetropium fuscum may be in direct competition for resources with T. cinnamopterum, at least in Picea spp. Indeed, in Nova Scotia, T. fuscum has largely displaced the native T. cinnamopterum in the invaded zone (Dearborn et al. 2016). Furthermore, the two species are exploited by some of the same species of parasitoids, particularly in stressed spruce trees (Flaherty et al. 2011). It is perhaps most likely that a combination of factors is responsible for the apparently pinned range edge of *T. fuscum*, including competition with the native species and shared natural enemies as well as mating errors. Testing this hypothesis directly in wild populations will, unfortunately, be difficult.

Tetropium fuscum is not spreading as rapidly and destructively as other invasive forest pests, such as emerald ash borer (*Agrilus planipennis* Fairmaire). Emerald ash borer was first detected in North America in 2002, making its invasion about as old as *T. fuscum*'s, but it has already killed hundreds of millions of ash (*Fraxinus* spp.) trees in the USA alone (Herms and McCullough 2014), costs tens of billions of dollars for mitigation (Kovacs et al. 2010) and is now spreading in eastern Canada. However, our results do not mean that we should ignore the potential for future *T. fuscum* spread. Many invasive species experience a "lag phase" in which their population size and range do not increase rapidly at the beginning of the invasion (Mack 1981) while the population evolves to be better adapted to the novel environment or until environmental changes allow the species to spread (Crooks and Soulé 1999). It is important to continue the monitoring of *T. fuscum* populations in North America, so that we are not caught off guard should a sudden increase in population size or emergence of introgressed individuals become problematic.

We have demonstrated that *T. fuscum* and *T. cinnamopterum* males make matechoice errors in the lab and we present a logical case that this may also happen in the field, especially near the edges of the invasion zone. This may well play an important role in impeding the North American spread of *T. fuscum*. If so, there are implications beyond *T. fuscum*'s invasion in particular. While some invasive species establish without any close relatives sharing their new habitat, many others, like *Tetropium*, invade alongside native congeners. Adding mate-choice errors to the list of reasons this can matter advances our understanding of why some introductions spread catastrophically, while others fade quietly away.

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RESEARCH ARTICLE



Predatory ability and abundance forecast the ecological impacts of two aquatic invasive species

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Abstract

Characterising interspecific interaction strengths, combined with population abundances of prey and their novel predators, is critical to develop predictive invasion ecology. This is especially true of aquatic invasive species, which can pose a significant threat to the structure and stability of the ecosystems to which they are introduced. Here, we investigated consumer-resource dynamics of two globally-established aquatic invasive species, European green crab (*Carcinus maenas*) and brown trout (*Salmo trutta*). We explored the mediating effect of prey density on predatory impact in these invaders relative to functionally analogous native rock crab (*Cancer irroratus*) and Atlantic salmon (*Salmo salar*), respectively, feeding on shared prey (*Mytilus* sp. and *Tenebrio molitor*, respectively). We subsequently combined feeding rates with each predator's regional abundance to forecast relative ecological impacts. All predators demonstrated potentially destabilising Type II functional responses towards prey, with native rock crab and invasive brown trout exhibiting greater *per capita* impacts relative to their trophic analogues. Functional Response Ratios (attack rates divided by handling times) were higher for both invasive species, reflecting greater overall *per capita* effects predicted severe impacts by European green crabs. However, brown trout, despite possessing higher *per capita* effects than Atlantic salmon, are projected to have low impact owing to currently low abun-

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dances in the sampled watershed. Should brown trout density increase sixfold, we predict it would exert higher impact than Atlantic salmon. Such impact-forecasting metrics and methods are thus vital tools to assist in the determination of current and future adverse impacts associated with aquatic invasive species.

Keywords

Aquatic invasive species, consumption rate, feeding, freshwater, functional response, Functional Response Ratio, impact, invasion, marine, predation, Relative Impact Potential

Introduction

Invasive species exert measurable and often catastrophic changes in recipient communities (Ricciardi et al. 2013; Gallardo et al. 2016; Flood et al. 2020). As invasion rates continue to increase globally (Seebens et al. 2017), understanding and mitigating invasion impacts is pivotal. Freshwater and marine environments support diverse assemblages of non-indigenous species (Strayer 2010). Many such species have had demonstrable impacts on their recipient systems, with approximately one-fifth of the 100 world's worst invasive species found in aquatic habitats (Kulhanek et al. 2011). However, comparative trait analyses between native and non-indigenous species have focused primarily on terrestrial ecosystems (Leffler et al. 2014). Evaluating the impacts of aquatic invasive species is, therefore, paramount to manage their effects (Ojaveer et al. 2015). However, the inherent difficulty associated with quantifying invasive species' ecological impacts requires a more mechanistic approach that can also forecast ecological impacts with readily available data, based on *per capita* effects and abundances of the interacting species (Dick et al. 2014, 2017a).

Analysis of a predator's density-dependent consumption rates [i.e. its functional response (FR)] can provide insights into its *per capita* effect (Holling 1959). In addition, experimentally-derived estimates of invasive species' *per capita* effects relative to those of native analogues are useful tools to forecast the former's potential ecological impact (Dick et al. 2014). Invasive species often demonstrate higher and more efficient resource utilisation relative to ecologically similar native species across taxonomic groups (Dick et al. 2014; Crookes et al. 2019; Dickey et al. 2021). Taking such *per capita* impact prediction one step further, the Functional Response Ratio (FRR) is derived from the FR's constituent parameters (attack rate divided by handling time). By synthesising its parameters into a single metric, the FRR provides greater mechanistic insight into drivers of predator impact on affected prey species than use of either attack rate or handling time variables in isolation (Cuthbert et al. 2019). As the FRR integrates predator effects at both low and high prey densities, it may provide increased predictive power of *per capita* type (i.e. FR) experiments (Cuthbert et al. 2019; Madzivanzira et al. 2021).

While species' resource consumption can provide insights into their projected ecological impacts (Dick et al. 2014), the magnitude of an effect is also determined by the predator's local abundance (Parker et al. 1999). Dick et al. (2017a) thus devised a new metric, the Relative Impact Potential (RIP), that incorporates *per capita* feeding rates and local field abundances as proxies for functional and numerical responses, respectively, to predict the ecological impact of an invasive species versus that of a comparative native species. This method shows promise to screen potential invasive species and perform rapid impact assessments of established (as well as potential) invaders on both prey communities and relative to co-occurring native predators (Hoxha et al. 2018; DeRoy et al. 2020; Dickey et al. 2020a). Indeed, the RIP metric was 100% successful in its ability to predict the actual field impacts of a range of invasives across trophic and taxonomic groups (Dick et al. 2017a).

The objective of our study was to discern whether *per capita* and overall impacts differed between aquatic invasive species and respective native analogues, using two globally-established invasive species. We utilised the aforementioned trio of metrics (i.e. FR, FRR and RIP) to quantify the predatory impacts of two aquatic invasive species – the marine European green crab (*Carcinus maenas*) (hereafter, green crab) and the freshwater brown trout (*Salmo trutta*) – each of which are established in Canada and other regions globally. Both are listed amongst the 100 of the worst invasive species (Lowe et al. 2000), in part due to their strong observed effects on recipient ecosystems. Given that differences in feeding behaviour may influence competitive ability and ecological impact in the field (Dick et al. 2017a), we expected that the outcomes of these experiments would reflect the relative impact of both invasive and native predators.

To accurately direct management efforts of invasive species, researchers must understand their projected effect across and within regions to which the species has spread, relative to native analogues. Such predictions provide essential information to possible management interventions of invasive species.

Methods

Collection and maintenance

Brachyuran crabs

Invasive green crab (*Carcinus maenas*) and native rock crab (*Cancer irroratus*) (N = 30 each) were collected during the summer of 2015 using Fukui traps (baited with herring) from the upper subtidal zone at North Harbour within Placentia Bay, Newfoundland (NL). Green crab was first detected in this region in 2007 (Blakeslee et al. 2010) and has since spread throughout Placentia Bay and Fortune Bay on the NL south coast. In this and other regions, green crab has precipitated cascading, ecosystem-level changes to fish communities and their habitat (Matheson et al. 2016) and has had demonstrable negative effects on indigenous decapods (MacDonald et al. 2007; Rayner and McGaw 2019). Rock crab was selected given that it shares similar habitat and diet with the invasive green crab (Bélair and Miron 2009; Matheson and Gagnon 2012a, b). The former is also an economically and ecologically important species and serves

as the primary prey for American lobster (*Homarus americanus*) (Sainte-Marie and Chabot 2002).

Only male crabs with all appendages intact were selected to avoid potential variation in foraging that could result from morphological or behavioural differences between the sexes (Elner and Hughes 1978; Abello et al. 1994). We also selected only green crab with a green carapace and did not retain those with a slightly orange or red carapace, which can indicate a stronger and thicker carapace and potentially stronger chelae (Reid et al. 1997). Lastly, all crabs were hard-shelled to minimise potential foraging variation that could result from the use of individuals undergoing moulting.

Mytilus sp. mussel prey $(25 \pm 3 \text{ mm})$ – on which both crab species are known to feed (Matheson and Gagnon 2012a) – were collected by hand by divers within Conception Bay, NL. This size of mussels was selected based on previous size selection experiments with rock and green crabs (Matheson and Gagnon 2012a). Understanding the impact on mussel prey is important, given the threat posed by green crab to large-scale commercial shell-fisheries (Grosholz et al. 2011), including that of the blue mussel (*Mytilus edulis*) (DFO 2011; Pickering and Quijón 2011).

Crabs and mussels were transported in containers with seawater to the Northwest Atlantic Fisheries Centre in St. John's, NL. Species were held separately in holding tanks (275 l) equipped with a flow-through seawater system (11.8 \pm 1.5 °C) and fed *ad libitum* mussels and scallops. The photoperiod (13 h light:11 h dark) was kept constant throughout the experiment. Crabs and mussels were allowed to acclimatise to the system and monitored at least one week prior to and post use in FR trials.

Rock crabs were significantly larger [carapace width (notch to notch) \pm SE: rock crab: 104.3 \pm 1.57 mm; green crab: 64.2 \pm 0.62 mm] and heavier (mass: rock crab: 201.4 \pm 7.55 g; green crab: 82.8 \pm 2.45 g) than green crab (Wilcoxon rank sum: W = 0, P < 0.0001). Cheliped size, which can be a proxy for crushing strength, for the rock crab was also larger (22.9 \pm 0.36 mm) than the green crab crusher cheliped (19.1 \pm 0.37 mm) (Wilcoxon rank sum: W = 81, P < 0.0001). This difference resulted from the intentional selection of typical full-sized adult rock and green crabs found in the same habitats, which further allowed comparisons with other studies that used the same approach. Use of both invasive and native adult crabs, therefore, permitted us to discern maximum potential impact of these species.

Salmonids

Experimental trials with invasive brown trout (*Salmo trutta*) (N = 31: mean \pm SE wet weight: 49.4 \pm 2.1 g) and native Atlantic salmon (*Salmo salar*) (N = 18: 91.7 \pm 5.4 g) were conducted at the University of Windsor's Freshwater Restoration Ecology Centre (FREC, LaSalle, ON Canada). Brown trout were purchased from Kolapore Springs Fish Hatchery (Thornbury, ON, Canada) in the summer of 2015 and transported to FREC in insulated tanks with continuously aerated water. Atlantic salmon were reared at FREC.

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We selected brown trout as our focal invader given its cosmopolitan distribution and long invasion history (Klemetsen et al. 2003). Its ecological impacts span multiple trophic levels (reviewed in Well et al. 2017) and affect various ecosystem processes (Townsend and Simon 2006). The species has been deliberately introduced into many regions, including New Zealand (Townsend and Simon 2006) and sub-Saharan Africa (Weyl et al. 2017). However, despite brown trout's ubiquity, impact assessments in invaded habitats are relatively recent (McIntosh et al. 2011). Atlantic salmon was chosen based on its high niche overlap with our focal invader (Armstrong et al. 2003).

All fish were acclimatised for one week during which time they were fed mealworms (*Tenebrio molitor*) *ad libitum*. Animals were housed in climate-controlled facilities prior to and during experiments (15–17 °C air temperature; 10 h light:14 h dark regime). Fish from individual species were held communally in recirculating housing tanks (800 l; 5% turnover per day), in accordance with University of Windsor's Animal Care guidelines.

Experimental trials

Brachyuran crabs

FR trials were run across six circular opaque fibre-glass tanks (275 l; 100 cm diameter and ~ 50 cm water depth) configured in rows of two. Each tank was set up with its own individual light source and inflow to standardise environmental conditions (10.25 °C \pm 0.04; ~ 5–10 l/minute flow rate). All tanks were covered with mesh (1.3 cm opening) to prevent potential escape. A random number generator allotted predators and prey density treatments to individual trial tanks.

Trials were conducted between 7am and 3pm. Individual crabs were selected at random and held in experimental tanks supplied with flow-through seawater 48 hours prior to experimental trial to acclimatise and standardise hunger. To initiate a trial, mussels (free of epibionts) were presented haphazardly throughout the tank at six densities (2, 4, 8, 16, 32 and 64 mussels per tank). Each feeding trial lasted five hours, after which we examined prey capture, defined as any crab-mussel interaction that resulted in the crushing or opening the shells of a mussel. We conducted five replicates at each prey density and one control trial for each prey density in the absence of a predator to quantify background mortality rates. Each crab was only used once. We excluded any trial in which the foraging crab moulted in the week following the experiment to further minimise potential variation in crab behaviour during the feeding trial.

Fisheries and Oceans Canada provided regional abundance estimates (CPUE \pm SE) for both green and rock crab in North Harbour, Placentia Bay, NL. An average multi-year estimate (2015–2019) was used to account for spatiotemporal variability in population densities. Each yearly estimate was based on 12 traps (four lines of three traps set perpendicular to the shore in the shallow subtidal) set during each of five monthly surveys (June through to October). Trapping estimates recorded the number of crabs obtained per trap per day. The soak time during each deployment was approximately 24 hours with traps set at low tide.

Salmonids

Fish were starved for 24 hours to standardise hunger levels and acclimatised to experimental tanks prior to trial onset. Fish were randomly selected and assigned to one of two flow-through 50 l trial tanks (Mean \pm SE: 10.24 °C \pm 0.16, flow rate: 1 l/ minute) containing aquarium water. Species were alternated between trials. Tanks were wrapped in black plastic to mitigate observer influences.

To initiate the start of a trial, mealworms (1 cm, cut using a razor) were introduced to the water surface at one of six prey densities (8, 16, 32, 64, 128 and 175 prey per tank). Due to limited stock of Atlantic salmon, three repetitions were conducted per prey density with no re-use. Five replicates were performed per density for brown trout, with the exception of the prey density of 175, for which six replicates were conducted. Mealworms were launched via a weigh boat from the same point across trials. In this regard, they mimicked drifting invertebrates on which salmonids commonly feed (Bridcut 2000). Following their addition, predators were left to feed for one hour, after which they were removed and we counted the number of prey items remaining. Each predator was only used once. After each trial, we euthanised fish via MS222 (300 mg l⁻¹) and recorded their wet weight. We verified the number of prey items consumed via stomach contents. The use of dried prey precluded use of control trials for prey mortality.

To compute an estimate of the relative impact for our study species, we procured abundance estimates for Atlantic salmon and brown trout within the Credit River watershed (2015–2019) from Credit Valley Conservation Authority. The Credit River watershed is an important system for juvenile salmonids, including Atlantic salmon, of which both naturally and hatchery-reared individuals are present. Atlantic salmon is native to this region and is currently the subject of restoration efforts (Dimond and Smitka 2005). Alongside other non-indigenous salmonids, brown trout has been introduced extensively in this region to meet recreational demand (Stewart and Schaner 2002). Both species are subject to stocking (Ontario Ministry of Natural Resources and Forestry 2016).

Abundance data were obtained using single pass electrofishing [see Credit Valley Conservation Authority (2019) for a detailed overview of their methodology]. Abundance estimates were procured in the summer, several months after stocking. Estimates were calculated as the number of individual fish divided by stream area (m²).

Statistical analyses

Data analyses were performed in R, version 4.0.2 (R Core Team 2020). Data exploration was performed according to Zuur et al. (2010). We verified the appropriateness of GLMs by visually inspecting residuals (package DHARMa, Hartig 2020).

Brachyuran crabs

We tested for effects of species (factor, two levels), prey density (factor, six levels) and their interaction on consumption rate (continuous) using a GLM (glmmTMB,

Brooks et al. 2017) with a negative binomial error distribution with default parameterisation. Crusher cheliped size (continuous) was included as a covariate in the GLM to control for its effects. A negative binomial distribution was selected after fitting candidate distributions to consumption data via maximum likelihood estimation to determine best fit (fitdistrplus, Delignette-Muller and Dutang 2015). We included a dispersion formula for prey density in the GLM to account for heteroscedasticity. Candidate models (with or without an interaction term between factors) were assessed based on Akaike's Information Criterion (AIC) and interpretation of scaled residuals. Model assumptions were verified by plotting residuals versus fitted values and inspecting residuals for goodness-of-fit patterns. We computed coefficients of the best fitting model with analysis of deviance Type III sums of squares, given the presence of the interaction term (car, Fox and Weisberg 2019). Where a term was significant, we used Tukey comparisons via estimated marginal means for pairwise testing (emmeans, Lenth 2020).

We assessed differences in *per capita* feeding rates via FR curves. We fitted both Type II and III FR models to consumption rate data, using maximum likelihood estimation (bbmle, Bolker and R Development Core Team 2016) and compared fit via AIC. To account for prey depletion over the duration of the experiment, we modelled the resultant Type II FRs using Rogers' random predator equation (Rogers 1972):

$$N_{e} = N_{0} \left(1 - exp \left(a \left(N_{h} - T\right)\right)\right)$$
 (Eqn. 1)

where N_e is the number of prey eaten, N_0 is the initial density of prey, *a* is attack constant, *h* is handling time and *T* is the total experimental period (5 hours).

Predator consumption rates – as well as consumer-resource interaction variables, such as search rate, detection distance and handling time on which such rates depend – often vary with individual mass (Kalinkat et al. 2013). In turn, this may implicate changes in *per capita* interaction strength between predators and their prey and the resultant FR. To account for size discrepancies between crabs, FR parameters were allometrically scaled following Kalinkat et al. (2013). We used a fixed allometric-scaling exponent of 0.65 to account for body mass-metabolic rate scaling in brachyuran crabs (Griffen and Sipos 2018), such that attack rate scaled positively with predator body mass:

$$a = a_0 m^{0.65}$$
 (Eqn. 2)

and handling time scaled negatively with predator body mass:

$$h = h_0 m^{-0.65}$$
 (Eqn. 3)

In both Eqns. 2 and 3, a_0 and b_0 are constants and *m* is predator mass (g).

We fitted the allometrically-scaled FR models using all data for a given species to obtain initial parameter estimates for bootstrapping. We then bootstrapped (N = 100) the data to construct 95% confidence intervals around the fitted curves and extract

median values for model parameters. Convergence in FR confidence intervals indicated a lack of significant difference between species' consumption rates.

We computed FRRs (attack rate *a* divided by handling time *h*, i.e. a/h) for each species using median attack rate and handling time parameters. The FRR is a novel metric that has successfully differentiated ecologically-damaging invasive species (Cuthbert et al. 2019). Higher values indicate greater inferred impact, since high values of *a* and low values of *h* both predict high *per capita* effects across the FR curve and, hence, across low and high prey densities (Cuthbert et al. 2019).

Finally, we determined the maximum feeding rate of each predator (1/h) and combined these values with field abundance estimates to derive a Relative Impact Potential (RIP) estimate according to Dick et al. (2017a):

$$RIP = \left(\frac{\text{FRinvader}}{\text{FRnative}}\right) * \left(\frac{\text{ABinvader}}{\text{ABnative}}\right)$$

This allowed us to discern the relative impact of introduced green crab to native rock crab.

Salmonids

Using the same methodology as described above, differences in overall prey consumption amongst species (factor, two levels), prey density (factor, six levels) and wet weight (continuous) were assessed using a GLM with negative binomial error distribution (glmmTMB, Brooks et al. 2017). As there was no interaction found between the main factors, interaction terms were removed to identify the most parsimonious model. We incorporated a dispersion model to account for heteroscedasticity amongst prey densities and between species. We used Type II analysis of deviance to compute overall effects of GLMs (car, Fox and Weisberg 2019) and made post-hoc pairwise comparisons using Tukey's tests [package emmeans (Lenth 2020)].

FR type was confirmed following the protocol outlined above. We subsequently incorporated allometric functions in FR models to account for size discrepancies between salmonids (Kalinkat et al. 2013). On average, metabolic rates in fish conform to a 0.89 power-law scaling of maximum consumption with predator body mass (Jerde et al. 2019). Handling time and attack rate parameters were scaled negatively and positively, respectively, using a fixed allometric exponent of 0.89.

Allometrically-scaled FR models were fitted following the aforementioned methodology to obtain median estimates of attack rate and handling time. We then computed FRRs (a/h) for each species as well as corresponding maximum feeding rates (1/h). We subsequently used both species' maximum feeding rates and abundances to compute the RIP estimate. Stocking effort and abundance were both greater for the native Atlantic salmon. Given field abundance disparities between our focal salmonid predators, we projected impact potential of brown trout in increments of 0.01 ind/ m² to determine the point at which RIP would exceed a value of 1. That is, we determined when brown trout's projected ecological impact may exceed that of native Atlantic salmon.

Results

Brachyuran crabs

In control trials, we experienced no prey mortality and thus ascribed all prey death to predation, which was also directly observed. Predator consumption rates were best described by Type II FRs (Fig. 1).

On average, rock crabs consumed more mussels than green crabs, though the difference was not significant (Wilcoxon: W = 415, P = 0.61). Analysis of species' *per capita* effects revealed more nuanced differences in consumptive impact. Rock crab consumed more mussels than green crab, both with and without correcting for size differences between crab species (Table 1; Suppl. material 1: Table S1). Differences in consumption rates between species was contingent on prey density (species * prey density: $\chi^2 = 29.04$, df = 5, P < 0.0001). Rock crabs out-consumed their invasive analogues at higher prey densities (32 prey: estimate \pm SE: -0.80 \pm 0.24, P = 0.002; 64 prey: -0.44 \pm 0.25, P = 0.09) (Fig. 1). However, species' consumption rates were not significantly different at low prey densities, as evidenced by overlapping confidence intervals (Fig. 1). Cheliped size – here used as a proxy for crushing strength – was significantly and positively associated with consumption rate ($\chi^2 = 6.28$, df = 1, P = 0.01).

Green crab had a higher FRR, reflecting a steeper FR curve at low prey densities (i.e. larger attack rate, *a*) that compensated for a higher handling time (*h*; and, hence, lower maximum feeding rate), indicating European green crab will potentially impact prey populations more than rock crab. Further, green crab abundance (mean \pm *SE*: 29.44 \pm 6.91) was orders of magnitude greater than that of rock crab (0.17 \pm 0.12), driving a large RIP value (Table 1, Fig. 2).



Figure 1. Functional responses of invasive green crab and native rock crab towards mussel prey. Lines represent initial functional response fits from the random predator equation; shaded areas are 95% confidence intervals (n = 100 non-parametric bootstraps).

Table 1. Relative Impact Potential (RIP) and Functional Response Ratio (FRR) scores, as well as mean \pm standard error (SE) estimates of maximum feeding rate, recorded for both invasive-native species pairs. RIP > 1 are predicted to be high impact invaders, those < 1 are low impact relative to native predators.

System	Species	Maximum feeding rate (1/b) (± SE)	RIP	FRR (<i>a/b</i>) (± SE)
Marine	Green crab	0.82 (0.01)	71	0.17 (0.01)
	Rock crab	2.02 (0.19)		0.12 (0.01)
Freshwater	Brown trout	0.48 (0.01)	0.20	0.04 (0.002)
	Atlantic salmon	0.41 (0.02)		0.001 (<0.001)



Figure 2. RIP biplot comparing invasive green crab and rock crab feeding upon native mussel prey. Biplots generated using mean \pm standard error (SE) estimates for FRs (allometrically-scaled maximum feeding rate, prey/5 hour) and field abundances (CPUE). Ecological impact increases from bottom left to top right.

These results corroborate two independent Ecological Impact Scores used by Laverty et al. (2015) and Ricciardi and Cohen (2007). Both Scores are ordinal rankings of impact, where higher scores demonstrate more negative effects. Maximum available scores for each metric are 5 and 7, respectively. Using the regression equations in Figure 2 of Dick et al. (2017a) – the relationship between actual field impact and RIP value – we predict green crab to have serious ecological impacts of 4.05 on the Laverty et al. (2015) scale and 6.05 on the Ricciardi and Cohen (2007) scale.

Salmonids

Both salmonids exhibited Type II FRs (Fig. 3). While Atlantic salmon was significantly heavier than brown trout (Wilcoxon: W = 528.5, P < 0.0001), the latter, on average, consumed significantly more prey both in terms of raw consumption and per unit mass (raw: Wilcoxon: W = 117, P = 0.001; per unit mass: Wilcoxon: W = 74, P < 0.0001).

Consumption rates increased significantly with increasing prey density ($\chi^2 = 32.40$, df = 5, P < 0.0001) and by predator mass ($\chi^2 = 16.60$, df = 1, P < 0.0001). Brown trout was more voracious than Atlantic salmon across all levels of prey availability ($\chi^2 = 46.17$, df = 1, P < 0.0001) (Fig. 3). However, consumption rates were not significantly

different at the highest two prey densities, as evidenced by overlapping confidence intervals. The observed FR relationship was unchanged when correcting for size differences between salmonids (Table 1; Suppl. material 1: Table S1).

Brown trout exhibited a higher maximum feeding rate and FRR relative to Atlantic salmon (Table 1). However, their lower field abundance dampened the resultant RIP (Table 1, Fig. 4). Modelling of projected impact potential suggests that an



Figure 3. Functional responses of invasive brown trout and native Atlantic salmon towards dried mealworm prey. Lines represent initial functional response fits from the random predator equation; shaded areas are 95% confidence intervals (n = 100 non-parametric bootstraps).



Figure 4. RIP biplot comparing invasive brown trout and Atlantic salmon feeding upon mealworm prey. Biplots generated using mean ± standard error (SE) estimates for FRs (allometrically-scaled maximum feeding rate, prey/hour) and field abundances (ind/m²). Ecological impact increases from bottom left to top right.

abundance of 0.06 ind/m² – equivalent to that of Atlantic salmon – would be required to increase the RIP to a level where brown trout would exert a greater impact than Atlantic salmon (Fig. 4).

Discussion

Understanding differences in resource consumption by invasive and native species can provide meaningful insights into potential impacts of invaders in colonised ranges (Dick et al. 2014). When combined with an invasive species' abundance, meaningful understanding of expected ecological impacts may become apparent (Dick et al. 2017a; Ricciardi et al. 2021). Here, we examined *per capita* effects of two notorious invasive species using functional response (FR) methodology and the new Functional Response Ratio (FRR) and, subsequently, examined how these effects were modified by each species' abundance using the Relative Impact Potential (RIP). This combined experimental approach links *per capita* feeding rate with field abundance to provide best estimates of invader impact relative to comparable native species (Dick et al. 2017a; DeRoy et al. 2020).

Our study highlights strong density-dependence of both *per capita* and total estimated population effects. All species demonstrated inverse density-dependent prey mortality and potentially destabilising Type II FRs for prey populations. While invasive species often exhibit higher FR curves relative to functionally analogous native species (Dick et al. 2014), we observed mixed results. FR results suggested a strong *per capita* effect by brown trout and a much more muted one by green crabs, relative to their native analogues. However, the FRR metric, which blends the parameters of attack rate (*a*) and handling time (*h*), was a good predictor of both invasive species having high impact on native prey compared to that of native predators (see Cuthbert et al. 2019). Relative impact incorporating species' numerical responses better captured the full potential of each invader and suggested dominant impacts overall by each of green crab and Atlantic salmon. We expect differences in projected impact reported herein to correlate with field ecological impacts, as corroborated by past research (Dick et al. 2014; Dick et al. 2017a).

Invasive species' impacts are often context-dependent, in part mediated by abundance (but also *per capita* differences; see Howard et al. 2018). Reported abundance of green crab in Placentia Bay exceeds that of the species elsewhere in the Canada's eastern provinces (DFO 2011) as well as in western United States and Canada (Yamada et al. 2020; Ens et al. 2021). Such differences may portend dissimilar ecological impacts. Their high population abundance also highlights potential commercial impacts on bivalve and lobster fisheries. Aquaculture is a growing economic driver for many locations, such as the Atlantic Canadian region, which is highly dependent on eastern oyster (*Crassostrea virginica*) production (Bernier et al. 2020). Actual and potential fisheries impacts of green crab have been well-documented throughout their invaded range (Yamada 2001; Matheson and McKenzie 2014; Rayner and McGaw 2019), with economic losses projected to increase with their range expansion (Grosholz et al. 2011). Such inter-regional differences in ecological and economic impact of green crab need further exploration globally.

The high attack rate of green crab at low prey densities can potentially drive mutual prey species to become increasingly rare or even extinct (Dick et al. 2014) (Fig. 1). These impacts on native prey populations could have negative spill-over implications for native rock crab. Green crab's abundance, in conjunction with their high attack rate, could exclude rock crab from preferred resources like mussels. However, species' prey consumption suggests that rock crab could co-exist with green crab in areas where the latter is present at low abundance or when prey abundance is sufficiently high. As a result, where green crab numbers are high, species' co-existence could be facilitated by numerical control of the invader. However, traditional population suppression is complicated by the life history of green crabs, which demonstrate the potential for density-dependent, stage-specific overcompensation (Grosholz et al. 2021). That is, eradication efforts targeting adult green crabs may inadvertently facilitate enhanced survival and growth of juveniles released from cannibalism (Grosholz et al. 2021). To protect against such a scenario, functional eradication - suppressing populations below the threshold that would cause significant ecological harm and a positive numerical response by juveniles - may prove viable (Green and Grosholz 2021). Findings, presented herein, may provide a useful starting point to understand the species' non-linear population dynamics, on which the aforementioned management strategy is based.

Analysis of freshwater salmonids revealed greater levels of consumption by brown trout across all levels of prey availability, despite their smaller size. These findings are consistent with FRs of other high impact invasive species (Dick et al. 2014) and are in accordance with strong negative effects of brown trout in invaded systems (reviewed in McIntosh et al. 2011). Effects of brown trout may be most significant under resource limitation owing to their high FR and heightened attack rate at low prey densities.

Field abundance provides an estimate or proxy of predator numerical response (Dickey et al. 2020a and 2021) and, when combined with FR data, extends predictive understanding of ecological impacts substantially (Dick et al. 2017a). Widespread stocking of brown trout has traditionally supported its range expansion, often at the expense of native fishes (McKenna Jr et al. 2013). Despite high reported abundances of brown trout throughout its introduced range (for example, in excess of 1 ind/m², McIntosh et al. 2011) – which frequently exceeds that of sympatric natives (Jones and Closs 2011; Al-Chokhachy et al. 2016) – native Atlantic salmon is purported to have a greater ecological impact on prey within the sampled watershed as a consequence of its high relative abundance (Fig. 4). These disparities in abundance are similar elsewhere regionally where the species are sympatric (Larocque et al. 2020).

Abundance discrepancies may dampen the potential for interspecific competition and produce limited, but strong interactions between the two species, as evidenced by their overlapping isotopic niches (Larocque et al. 2020). Furthermore, resource partitioning between Atlantic salmon and resident fish appears to reduce trophic interactions (Larocque et al. 2020), which may further species' co-existence. These results support the need to disentangle density-mediated effects from *per capita* effects to better understand the processes driving impacts of individual invasive species.

The current risk of brown trout appears low, based on analyses of population-level impact. However, numerical estimates of abundance, as reported herein, may not represent abundances of the focal species in other systems. It is possible that brown trout impact could be far more substantial in areas where the numerical difference between these species is lower (and in systems without external manipulation), as corroborated by our model (Fig. 4).

Our findings have important implications. If left unchecked, they suggest that burgeoning brown trout populations are likely to produce significant ecological impacts, potentially to the detriment of both native Atlantic salmon and prey populations. Despite the invader's high *per capita* effect, management interventions can suppress its potential population-level impact on recipient systems by keeping relative densities low. Sustaining native species' populations while ensuring productive fisheries – like that of brown trout – therefore depends on balanced management (Dettmers et al. 2012). It also suggests a need to reconcile the paradox of brown trout as both an important sport fish and a detrimental invader (Cowx et al. 2010).

Future research

Future research should consider the ecological impact of our focal species across a wider variety of prey types in field and laboratory settings. A growing body of literature reinforces the resource-specific nature of invasive species' *per capita* effects (e.g. Chucholl and Chucholl 2021). We encourage subsequent studies to consider ecological impact under varying prey and resource identities to gain a more complete picture of predator-resource dynamics, as differences or similarities in prey preference and related competitive interactions can have cascading influences on overall ecological patterns and impacts.

Additionally, investigation into non-consumptive effects of both green crab and brown trout are needed to ascertain implications for native predators and ultimately consequences to prey. For example, habitat use and depth distribution overlap in shallow waters in areas where our focal crab species co-occur (Tremblay et al. 2005; Matheson and Gagnon 2012a). Green crabs are also highly agonistic and territorially competitive, often outcompeting other crustaceans in foraging and shelter contests (McDonald et al. 2001; MacDonald et al. 2007; but see Jensen et al. 2002). These factors may lead to exploitative and/or interference competition for food or habitat, which may increase as green crab become more numerically dominant. Similarly, brown trout often occupy preferred foraging positions which provide preferential access to food (Alanärä et al. 2001). Brown trout is also a better competitor relative to Atlantic salmon (Van Zwol et al. 2012) and exhibits higher levels of aggression (Scott et al. 2005; Van Zwol et al. 2012; Houde et al. 2015). These traits may hinder the growth, survival and consumption rates of native species like Atlantic salmon (Van Zwol et al. 2012; Houde et al. 2015). In turn, interactions between invasive and native predators may ultimately influence each predator's per capita effects on prey populations. Whether these effects have the potential to subsequently mediate ecological impact remains unclear – and is beyond the scope of this study – but demands further investigation.

Understanding the synergistic influence of co-occurring stressors on invasive species' impacts is a priority area for invasion science (Ricciardi et al. 2021). Future changes in environmental parameters, such as temperature and salinity, have the potential to mediate feeding behaviour (Iacarella et al. 2015; Dickey et al. 2020b), as well as prey availability, and should be incorporated into subsequent impact predictions. This area of research is particularly important for aquatic invasive species, for which research investigating the combined influence of temperature and salinity regimes is scant (Cuthbert and Briski 2021). Physiological tolerances of our focal invasive predators portend increased impacts in light of a changing climate. Green crabs have broad physiological tolerance (Simonik and Henry 2014) and predation rates are positively correlated with temperature (Matheson and Gagnon 2012a, b). Increases in water temperature are similarly likely to favour brown trout at the expense of native salmonids (Al-Chokhachy et al. 2016; Hoxmeier and Dieterman 2019). The potential for variations and potentially higher impact under climate change thus warrants additional studies across taxonomic groups.

Conclusions

Functional and numerical response methodology provides meaningful insights into assessing invader impact and has become especially robust when used in conjunction with the FRR and RIP metrics. These results imply that, if the *per capita* impacts and relative abundance of non-indigenous species are well-known, its potential relative impact can be predicted and appropriate management actions devised, if needed. Our findings further underscore the importance of population suppression to effectively manage invasive species and promote co-existence with native analogues and prey populations. While our results provide novel insights into the implications of our focal predators, further work is required that incorporates environmental change scenarios.

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Supplementary material I

Table S1

Authors: Emma M. DeRoy, Steven Crookes, Kyle Matheson, Ryan Scott, Cynthia H. McKenzie, Mhairi E. Alexander, Jaimie T.A. Dick, Hugh J. MacIsaac

Data type: docx file

- Explanation note: Unscaled mean ± standard error (SE) estimates of maximum feeding rate and Functional Response Ratio (FRR) scores, recorded for both invasivenative species pairs.
- 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.

Link: https://doi.org/10.3897/neobiota.71.75711.suppl1

RESEARCH ARTICLE



Blacklists do not necessarily make people curious about invasive alien species. A case study with Bayesian structural time series and Wikipedia searches about invasive mammals in Italy

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Abstract

Blacklists of invasive alien species (IAS) are a popular tool for managing and preventing biological invasions. Moreover, blacklists also have the potential to make the general public more curious about biological invasions, usually by benefiting from media coverage and providing accessible examples of IAS.

We have tested if the implementation of the first List of IAS of Union concern by the European Union increased visits to Wikipedia pages on invasive alien mammals in Italy. We adopted causal impact analysis to quantify changes in the overall volume of visits to pages about invasive alien mammals that appeared on the list, by using pages about native mammals as a control. Following the publication of the first Union list, there was no increase in the amount of visits to Wikipedia pages on invasive mammals, regardless of their inclusion in the Union list. Rather, visits to Wikipedia were irregular in time, coinciding with media coverage of single, charismatic species. Our results indicate that important policymaking initiatives do not necessarily increase curiosity about biological invasions, even when they are covered by generalist media and are relatively easy to understand. We would therefore emphasise that policymaking initiatives should be coupled with adequate communication campaigns and should adopt communication guidelines for generalist media.

Keywords

Bayesian structural time-series, Europe, invasive mammals, Italy, negative-list, Wikipedia

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Introduction

In recent years, blacklists and accept-lists have become standard policy tools for tackling biological invasions (Genovesi and Shine 2004). Blacklists, also known as "negative lists", identify invasive alien species (IAS) – alien species whose introduction or spread has been found to threaten or have an adverse impact on biodiversity and related ecosystem services (EU 2020) – whose introduction is forbidden and for which trade bans, management initiatives and eradication should be enforced. On the other hand, accept-lists (or "white" or "positive" lists) identify those alien species which carry a low risk of becoming invasive, or impacting, and which are able to be traded, maintained in captivity or present in nature (Kaiser 1999; Perrings 2005). Both blacklists and accept-lists are based on risk assessments: in the former case, the aim is to ban a species from a country or a geographic area; in the latter case, the purpose is to demonstrate its "safety" for the environment and/or human well-being.

While the two approaches have different benefits, limitations and costs, blacklists have become far more common worldwide, with accept-lists being limited to a few countries (e.g. Australia, https://www.environment.gov.au/biodiversity/wildlifetrade/live-import-list and New Zealand, Brenton-Rule et al. 2016). For example, the July 2016 European Regulation on invasive alien species (no. 1143/2014) produced an initial list of 37 IAS of European concern (hereafter "*Union list*"; EU Regulation no. 1141/2016), which was then updated in 2017 (49 species, no. 1263/2017) and in 2019 (66 species, no. 1262/2019). Following these Regulations, 25 EU Member States implemented at least one type of national blacklist, with 4 States (Austria, Croatia, Germany and Spain) also implementing regional blacklists. On the other hand, 5 Member States and another European country (Norway) developed accept-lists, mostly for specific taxa (Eurogroup for Animals 2020; Toland et al. 2020).

To date, blacklists have been evaluated in terms of their effectiveness in preventing introductions (Maceida-Vega et al. 2019) and as blueprints for prioritising control and eradication initiatives (Tollington et al. 2017; Bertolino et al. 2020). However, we are still in the dark as to whether blacklists also increase the curiosity of the general public towards IAS. In principle, they should be capable of doing so: they imply the removal of IAS from the environment or captivity, which can trigger conflicts between stakeholders and institutions (e.g. Crowley et al 2017), and sometimes also benefit from media coverage (Lioy et al. 2019). Furthermore, as blacklists offer concrete examples of IAS, which are sometimes also popular species, laypeople can understand their practical importance, easily incorporating them into networks of pre-existing beliefs about wildlife, animal welfare or the environment. This combination of media echo and ease of understanding can increase the curiosity in some segments of the general public about biological invasions. Similar potential was recognised by the International Union for the Conservation of Nature (IUCN), which set up, in 1999, a list of 100 high-profile invasive species (list of 100 of the world's worst invasive alien species, Lowe et al. 2000) as a communication tool to address this issue. A similar list with 100 of the worst invasive alien species was drawn up in Europe (Vilà et al. 2009) and extended by Nentwig et al. (2018).

If blacklists really do have this impact, this would make them a valuable conservation tool, going far beyond the intention to regulate introduced species. For environmental topics, generating a public debate is often fundamental in order to enter the political agenda (e.g. climate change, Dunlap and McCright 2010) and to achieve long-term endorsement by politicians and by society (Heberlein 2012). Considering that some policies on biological invasions now include blacklists (Outhwaite 2017; Young et al. 2006), measuring whether they increase the curiosity of laypeople towards IAS is fundamental in order to predict whether those policies will be supported in the long-term. In this study, we aim to bridge this gap by estimating the causal effect of the publication of the first List of IAS of Union Concern on the number of Wikipedia searches on invasive alien mammals in Italy.

These days, people regularly seek information online, particularly in those countries with good Internet penetration. Such behaviour is more common for those topics that are also debated in traditional media (Tizzoni et al. 2020) and whose nature is controversial and open to multiple interpretations (Yenikent et al. 2017), such as environmental issues (Anderegg and Goldsmith 2014; Burivalolva et al. 2018; McCallum et al. 2013; Mittermeier et al. 2019). Information retrieval on the Internet occurs across multiple platforms, such as search engines like Google, dedicated websites and social networks. However, it also takes place on Wikipedia, the largest online encyclopaedia (Okoli et al. 2014). An analysis of visits to Wikipedia pages is particularly interesting, for two reasons. Firstly, because Wikipedia contains open data on the daily visits to each page (https://pageviews.toolforge.org/). This information is far more transparent than any such data provided by search engines, such as Google, which do not disclose overall searches but, rather, offer indirect metrics, such as the GoogleTrends index. Moreover, information seeking on the Internet can be regarded as a hierarchical process: once people become curious about a particular topic, they look for it on search engines, check and evaluate outputs, then decide whether or not to access pages, such as Wikipedia, where they can find further information. Of course, some users do not search for in-depth information or access Wikipedia or dedicated websites. Therefore, the analysis of visits to Wikipedia pages on IAS can truly capture changes in the number of persons whose curiosity about the topic is genuine, thus being a more truthful measure of public interest than overall Google searches. Dedicated websites would, of course, be another valuable source of information but the number of daily visits to the same is almost never made public.

The publication of the Union list was announced by the EU (https://ec.europa. eu/environment/efe/news/first-eu-list-invasive-alien-species-2016-08-04_it), as well as by the Italian media (Suppl. material 1). Mammals are, on average, iconic vertebrates, salient even to laypersons: it is reasonable to assume that, once it was announced that a certain mammal had been included in the Union list, some people became curious and searched for information on its dedicated Wikipedia page. Testing for the existence of this dynamic could be important, as it would mean that blacklists also contribute to invasive alien species becoming more well-known, at least superficially, by laypersons. Therefore, we predicted that: (*i*) H_1 : the implementation of the Union list increased the number of Wikipedia searches for invasive mammals included on the list, compared to native species, (*ii*) H_2 : this effect declined rapidly over time, in the absence of a dedicated budget for permanent outreaching initiatives (Turbelin et al. 2017), (*iii*) H_3 : Wikipedia views also increased in August 2017 and 2019, due to Union list updates, (*iv*) H_4 : the implementation of the Union list also increased the number of searches for invasive mammals that were not included, due to the increased interest in IAS in general.

Methods

In this study, in assessing the causal effect of the Union list on visits to Wikipedia pages about invasive mammals, we compared their volume of visits with that of pages on native mammals. The entry into force of the Union list was regarded as a natural experiment, with some time-series (Wikipedia pages on invasive mammals) receiving such treatment, and other time-series (Wikipedia pages on native mammals) being unaffected and able to be used as a control. Native mammals were a suitable synthetic control as, prior to the Union list, visits to their Wikipedia pages correlated well with those of invasive mammals (Pearson's correlation coefficient = 0.63), due to seasonal patterns in human-wildlife interactions and a long-term growth in Internet searches about wildlife caused by increased Internet access. The use of a control group allowed us to rule out the effect of long-term trends in interest towards wildlife, as well as seasonal effects in Wikipedia usage, estimating differences in Wikipedia visits between the two groups that could only be attributed to the Union list.

Indeed, we distinguished between two groups of invasive mammals. The first one (adopted to test for H_1 , H_2 and H_3) included IAS that appeared on the Union list and that were established in Italy in July 2016: the coypu (*Myocastor coypus*), the raccoon (*Procyon lotor*), the Eastern grey squirrel (*Sciurus carolinensis*) and the Siberian chipmunk (*Tamias sibiricus*). The second one (adopted to test for H_4) included IAS that did not appear on the Union list and that were present in Italy in August 2016: the Eastern cottontail (*Sylvilagus floridanus*), the American mink (*Neovison vison*), the Barbary sheep (*Ammotragus lervia*) and Finlayson's squirrel (*Callosciurus finlaysonii*) (Loy et al. 2019).

The control group with native Italian mammals included 81 native species and 4 species that were introduced in historic times, as these are traditionally deemed to be part of Italian fauna by the general public (Table 1). To respect the assumptions of the synthetic control approach, some species were discarded. From the IAS, we excluded Pallas's squirrel (*Callosciurus erythraeus*), which has no page on Italian Wikipedia, as well as the raccoon dog (*Nyctereutes procyonoides*) and the muskrat (*Ondatra zibethicus*), which appeared on the second update of the blacklist. We also excluded the common genet (*Genetta genetta*), which, in 2016, was still present only occasionally in Italy, with few records.

Common name	Scientific name	Wikipedia page					
Common name Scienting name Wikipedia page							
Course	Mussice and species included	https://it.wikipadia.arg/wiki/Muscastor_coupus					
Валана	Niyocastor coypus	nttps://it.wikipedia.org/wiki/Myocastor_coypus					
Faccooli	L'rocyon lolor	https://it.wikipedia.org/wiki/Procyon_lotor					
Eastern gray squirrei	Schurus carolinensis	https://it.wikipedia.org/wiki/Sciurus_carolinensis					
Stbertan chipmunk Iamias sibiricus https://it.wikipedia.org/wiki/lamias_sibiricus							
г	Invasive alien species that were not in	ncluded in the first Union List					
Eastern cottontail	Sylvilagus floridanus	https://it.wikipedia.org/wiki/Sylvilagus_floridanus					
American mink	Neovison vison	https://it.wikipedia.org/wiki/Neovison_vison					
Barbary sheep	Ammotragus lervia	https://it.wikipedia.org/wiki/Ammotragus_lervia					
Finlayson's squirrel	Callosciurus finlaysonii	https://it.wikipedia.org/wiki/Callosciurus_finlaysonii					
Native species							
European hedgehog	Erinaceus europaeus	https://it.wikipedia.org/wiki/Erinaceus_europaeus					
Bicolored shrew	Crocidura leucodon	https://it.wikipedia.org/wiki/Crocidura_leucodon					
North African white-toothed shrew	Crocidura pachyura	https://it.wikipedia.org/wiki/Crocidura_pachyura					
Sicilian shrew	Crocidura sicula	https://it.wikipedia.org/wiki/Crocidura_sicula					
Lesser white-toothed shrew	Crocidura suaveolens	https://it.wikipedia.org/wiki/Crocidura_suaveolens					
Eurasian water shrew	Neomys fodiens	https://it.wikipedia.org/wiki/Neomys_fodiens					
Alpine shrew	Sorex alpinus	https://it.wikipedia.org/wiki/Sorex_alpinus					
Eurasian pygmy shrew	Sorex minutus	https://it.wikipedia.org/wiki/Sorex_minutus					
Apennine shrew	Sorex samniticus	https://it.wikipedia.org/wiki/Sorex_samniticus					
Etruscan shrew	Suncus etruscus	https://it.wikipedia.org/wiki/Suncus_etruscus					
Blind mole	Talpa caeca	https://it.wikipedia.org/wiki/Talpa_caeca					
Roman mole	Talpa romana	https://it.wikipedia.org/wiki/Talpa_romana					
Common bent-wing bat	Miniopterus schreibersii	https://it.wikipedia.org/wiki/Miniopterus_schreibersii					
European free-tailed bats	Tadarida teniotis	https://it.wikipedia.org/wiki/Tadarida_teniotis					
Mediterranean horseshoe bat	Rhinolophus euryale	https://it.wikipedia.org/wiki/Rhinolophus_euryale					
Greater horseshoe bat	Rhinolophus ferrumequinum	https://it.wikipedia.org/wiki/Rhinolophus_ferrumequinum					
Lesser horseshoe bat	Rhinolophus hipposideros	https://it.wikipedia.org/wiki/Rhinolophus_hipposideros					
Mehely's horseshoe bat	Rhinolophus mehelyi	https://it.wikipedia.org/wiki/Rhinolophus_mehelyi					
Western barbastelle	Barbastella barbastellus	https://it.wikipedia.org/wiki/Barbastella_barbastellus					
Northern bat	Eptesicus nilssonii	https://it.wikipedia.org/wiki/Eptesicus_nilssonii					
Serotine bat	Eptesicus serotinus	https://it.wikipedia.org/wiki/Eptesicus_serotinus					
Savi's pipistrelle bat	Hypsugo savii	https://it.wikipedia.org/wiki/Hypsugo_savii					
Alcathoe bat	Myotis alcathoe	https://it.wikipedia.org/wiki/Myotis_alcathoe					
Brown long-eared bat	Myotis bechsteini	https://it.wikipedia.org/wiki/Myotis bechsteini					
Lesser mouse-eared bat	Myotis blythii	https://it.wikipedia.org/wiki/Myotis blythii					
Brandt's bat	Myotis brandtii	https://it.wikipedia.org/wiki/Myotis brandti					
Long-fingered bat	Mvotis capaccinii	https://it.wikipedia.org/wiki/Myotis_capaccinii					
Daubenton's bat	Mvotis daubentonii	https://it.wikipedia.org/wiki/Myotis_daubentonii					
Geoffrov's bat	Mvotis emarginatus	https://it.wikipedia.org/wiki/Myotis_emarginatus					
Mouse-eared bat	Muatis muatis	https://it.wikipedia.org/wiki/Myotis_enalginatas					
Whiskered bat	Myotis mystacinus	https://it.wikipedia.org/wiki/Myotis_mystacinus					
Felten's myotis	Myatis hunicus	https://it.wikipedia.org/wiki/Myotis_pupicus					
Greater poctule bat	Nuctalus laciontarus	https://it.wikipedia.org/wiki/Nyotalus_punicus					
Lessar postulo	Nustalus laislani	https://it.wikipedia.org/wiki/Nyctalus_lasiopterus					
Common noctulo	Nustalus nostala	https://it.wikipedia.org/wiki/Nyctalus_nestula					
Kubl's pipistralla	Dististualles heldii	https://it.wikipedia.org/wiki/Nyctatus_noctula					
Nathurius' ninistralla	Pipistretus kuntt	https://it.wikipedia.org/wiki/Pipistrelius_kullil					
Construction in the literation of the literation							
Common pipistrelle	Pipistreuus pipistreuus	https://it.wikipedia.org/wiki/Pipistrelius_pipistrelius					
Brown big-eared bat	Plecotus duritus	https://it.wikipedia.org/wiki/Plecotus_auritus					
Gray big-eared bat	Plecotus austriacus	https://it.wikipedia.org/wiki/Plecotus_austriacus					
Sardinian long-eared bat	Plecotus sardus	https://it.wikipedia.org/wiki/Plecotus_sardus					
rarti-coloured bat	vespertilio murinus	nttps://it.wikipedia.org/wiki/Vespertilio_murinus					
Golden jackal	Canis aureus	https://it.wikipedia.org/wiki/Canis_aureus					
Ked tox	Vulpes vulpes	https://it.wikipedia.org/wiki/Vulpes_vulpes					
European wildcat	Felis silvestris	https://it.wikipedia.org/wiki/Felis_silvestris					
Eurasian lynx	Lynx lynx	https://it.wikipedia.org/wiki/Lynx_lynx					
Eurasian otter	Lutra lutra	https://it.wikipedia.org/wiki/Lutra_lutra					
Beech marten	Martes foina	https://it.wikipedia.org/wiki/Martes_foina					
Pine marten	Martes martes	https://it.wikipedia.org/wiki/Martes_martes					
Eurasian badger	Meles meles	https://it.wikipedia.org/wiki/Meles_meles					

Table 1. List of invasive and native species of mammals that were considered for data analysis.

Common name	Scientific name	Wikipedia page		
	Native spe	ccies		
Stoat	Mustela erminea	https://it.wikipedia.org/wiki/Mustela_erminea		
Least weasel	Mustela nivalis	https://it.wikipedia.org/wiki/Mustela_nivalis		
European polecat	Mustela putorius	https://it.wikipedia.org/wiki/Mustela_putorius		
Alpine ibex	Capra ibex	https://it.wikipedia.org/wiki/Capra_ibex		
Apennine chamois	Rupicapra pyrenaica ornata	https://it.wikipedia.org/wiki/Rupicapra_pyrenaica_ornata		
Alpine chamois	Rupicapra rupicapra	https://it.wikipedia.org/wiki/Rupicapra_rupicapra		
European roe deer	Capreolus capreolus	https://it.wikipedia.org/wiki/Capreolus_capreolus		
Red deer	Cervus elaphus	https://it.wikipedia.org/wiki/Cervus_elaphus		
Wild boar	Sus scrofa	https://it.wikipedia.org/wiki/Sus_scrofa		
European water vole	Arvicola amphibius	https://it.wikipedia.org/wiki/Arvicola_amphibius		
European snow vole	Chionomys nivalis	https://it.wikipedia.org/wiki/Chionomys_nivalis		
Common vole	Microtus arvalis	https://it.wikipedia.org/wiki/Microtus_arvalis		
Alpine pine vole	Microtus multiplex	https://it.wikipedia.org/wiki/Microtus_multiplex		
Savi's pine vole	Microtus savii	https://it.wikipedia.org/wiki/Microtus_savii		
European pine vole	Microtus subterraneus	https://it.wikipedia.org/wiki/Microtus_subterraneus		
Common red-backed vole	Myodes glareolus	https://it.wikipedia.org/wiki/Myodes_glareolus		
Forest dormouse	Dryomys nitedula	https://it.wikipedia.org/wiki/Dryomys_nitedula		
Garden dormouse	Eliomys quercinus	https://it.wikipedia.org/wiki/Eliomys_quercinus		
Edible dormouse	Glis glis	https://it.wikipedia.org/wiki/Glis_glis		
Hazel dormouse	Muscardinus avellanarius	https://it.wikipedia.org/wiki/Muscardinus_avellanarius		
Striped field mouse	Apodemus agrarius	https://it.wikipedia.org/wiki/Apodemus_agrarius		
Alpine field mouse	Apodemus alpicola	https://it.wikipedia.org/wiki/Apodemus_alpicola		
Yellow-necked field mouse	Apodemus flavicollis	https://it.wikipedia.org/wiki/Apodemus_flavicollis		
Wood mouse	Apodemus sylvaticus	https://it.wikipedia.org/wiki/Apodemus_sylvaticus		
Eurasian harvest mouse	Micromys minutus	https://it.wikipedia.org/wiki/Micromys_minutus		
Alpine marmot	Marmota marmota	https://it.wikipedia.org/wiki/Marmota_marmota		
Cape hare	Lepus capensis	https://it.wikipedia.org/wiki/Lepus_capensis		
Corsican hare	Lepus corsicanus	https://it.wikipedia.org/wiki/Lepus_corsicanus		
European brown hare	Lepus europaeus	https://it.wikipedia.org/wiki/Lepus_europaeus		
Mountain hare	Lepus timidus	https://it.wikipedia.org/wiki/Lepus_timidus		
Species that	at were introduced in historic times (considered altogether with native species)		
Fallow deer	Dama dama	https://it.wikipedia.org/wiki/Dama_dama		
African crested porcupine	Hystrix cristata	https://it.wikipedia.org/wiki/Hystrix_cristata		
House mouse	Mus musculus	https://it.wikipedia.org/wiki/Mus_musculus		
Wild rabbit	Oryctolagus cuniculus	https://it.wikipedia.org/wiki/Oryctolagus_cuniculus		

Among the IAS, we also disregarded the brown rat (*Rattus norvegicus*) and the black rat (*Rattus rattus*), as they are mostly managed by rodent control companies and their search volumes could be ascribable to infestation levels in urban areas. We also excluded the red squirrel (*Sciurus vulgaris*) from the list of native species, as its news coverage was related to the management of *S. carolinensis* (Bertolino et al. 2014; Lioy et al. 2019) and two large carnivores, the grey wolf (*Canis lupus*) and the brown bear (*Urus arctos*), whose news coverage was complex and volatile, due to their interaction with humans and the political debate around their management. We also excluded marine mammals, as they could have stronger seasonal patterns than other mammal species, due to summer tourism and mortality events. Time series were downloaded from 29 June 2015 to 3 February 2020.

We adopted Bayesian structural time series (BSTS, Brodersen et al. 2015) to compare differences in time-series after the Union list. BSTS can estimate the causal effect of an intervention over a single target time-series, by comparing its post-treatment values with a counterfactual constructed from a synthetic control, constituted by untreated time series that were predictive of the target time series in the pre-treatment period. The post-treatment difference between the target time-series and the counterfactual represents the causal effect of the treatment. BSTS are state-space models, whose mathematical structure is rather sophisticated and beyond the scope of this research article. However, we refer to Brodersen et al. (2015) for a comprehensive overview on the underlying mathematics of our approach and for documentation of the "CausalImpact" package, which was adopted to implement causal impact analysis in R (https://google.github.io/CausalImpact/CausalImpact.html). The reproducible software code is available at: https://osf.io/9yb8w/.

Bayesian structural time series for causal impact analysis are suitable only to compare single target time series with one or more control series. Therefore, Wikipedia views were added together in each group (invasive species in the Union list, invasive species not in the Union list, native species). Aggregation also measured interest in invasive species as a whole, rather than interest in specific species. This choice improved the use of Wikipedia as a proxy for public attention on the topic of IAS, as visits to individual pages could have been more prone to fluctuations caused by species-specific factors, which would have masked important post-treatment patterns. Moreover, daily visits were aggregated on a weekly basis, to increase the signal-to-noise ratio (Fig. 1).



Figure 1. Number of visits to Wikipedia pages on invasive alien mammals included in the Union list (a), invasive alien mammals not included in the Union list (b) and native mammals (c). Dashed lines, from left to right, represent the publication of the first blacklist (July 2016), its first update (July 2017), the implementation of the first Italian law on invasive species (February 2018) and the second update of the blacklist (July 2019).

Results

Our findings do not highlight any effect of the implementation of the first Union list over the volume of visits to Wikipedia pages on invasive alien mammals that were included in the list (Fig. 2). The visits did not systematically increase, compared to what would have been expected from our control group containing native species. There were more visits than expected only during some weeks in October/November 2016, as well as in May and August 2018.

Our findings also do not highlight any clear effect of the Union list on invasive mammals that were not included in the list. The visits did not increase, except until early 2017, and there were more visits than expected at irregular times, from 2017 to mid 2018, peaking between December 2018 and February 2019 (Fig. 3).



Figure 2. Causal impact of the first Union list (vertical dashed line) on visits to Wikipedia pages about invasive alien mammals that were included in the list. Upper plot: visits to pages of invasive mammals in the list (solid line) versus the counterfactual, obtained from visits to pages of native mammals (dashed line and highlighted area). Middle plot: estimated causal effect, expressed as the difference between treated and control time series. The causal effect was significant if its 95% credibility interval did not include zero. Lower plot: cumulative causal effect in time, significant only when the 95% credibility interval did not include zero.



Figure 3. Causal impact of the first Union list on visits to Wikipedia pages about invasive alien mammals that were not included in the list. Upper plot: visits to pages of invasive mammals not in the list (solid line) versus the counterfactual, obtained from the visits to pages of native mammals (dashed line and highlighted area). Middle plot: estimated causal effect, expressed as the difference between treated and control time series. The causal effect was significant if its 95% credibility interval did not include zero. Lower plot: cumulative causal effect in time, significant only when the 95% credibility interval did not include zero.

Discussion

To the best of our knowledge, this study constitutes the first attempt to evaluate blacklists as a tool for making the general public more curious about IAS. Although, in Italy, the first Union list included some invasive alien mammals that were relatively wellknown, and although it was covered in the media, it failed to increase the number of visits to the Wikipedia pages on those mammals.

Following the publication of the first Union list, the number of visits to Wikipedia pages on invasive mammals in the two groups, namely those that had been included in and those that had been excluded from the Union list, did not demonstrate any particu-

lar increase, compared to native mammals. For both groups we did not observe any systematic change, but only individual weeks with significantly more views than expected. Those weeks with anomalous volumes of visits to Wikipedia did not coincide with the publication of the first Union list or any of its updates, or with media coverage. As media coverage boosts people's interest in a certain topic in the short-term, with a subsequent decline over time (e.g. pandemics, Bento et al. 2020; wildlife, Fernández-Bellon and Kane 2020), we expected an increase in visits to Wikipedia soon after the publication of the Union list, in July/September 2016, and on some random occasions in the following months. Therefore, we argued that there was no appreciable causal effect of the Union list, and its associated media coverage, and all our hypotheses were rejected.

Rather, individual weeks with anomalous volumes of visits to Wikipedia aligned with news about some particular species unrelated to the Union list. For example, peaks aligned with news about the coypu, the species raising the most serious concerns among public administrations in Italy, due to its effects on the stability of riverbanks. This news item covered the publication of the national management plan for the species (May 2018, Bertolino and Cocchi 2018), an official note from the Lombardy region about the implementation of a regional management plan (July 2018, https://www.regione.lombardia.it/wps/portal/istituzionale/HP/lombardia-notizie/ DettaglioNews/2018/07-luglio/23-29/emergenza-nutrie-rolfi-sindaci), and the publication of a viral video of the species (November 2016, https://www.cremonaoggi. it/2016/11/04/nutria-via-xi-febbraio-paura-curiosita-passanti-catturata/). Similarly, in relation to IAS that had not been included in the Union list, the peak observed between late 2018 and February 2019 was probably caused by news about the release of 4,000 minks (Neovison vison) from a fur factory in Northern Italy in December 2018, an event that attracted considerable attention in the national and regional media (see, for example, https://parma.repubblica.it/cronaca/2018/12/09/news/mille visoni in fuga_raid_animalista_nel_parmense-213849071/; Fig. 4).

It should be noted that we also observed various peaks of visits to the Wikipedia pages of the various species of invasive mammals which did not coincide with any major news that could be found on the Internet. These peaks may have been caused by local outreach initiatives from individual conservation projects about IAS, such as the LIFE ASAP project (https://lifeasap.eu/index.php/it/), or by some media coverage that could not be found on the Internet. Unfortunately, at the time of the study, comprehensive data on television news and newspaper articles in Italy did not exist. There was also no dataset regarding outreaching initiatives from conservation projects on IAS. We believe that such a gap should be addressed in future, to test the effectiveness of local communication initiatives at raising public interest in biological invasions.

Our study also had some intrinsic limitations. The first was our focus on a single measure of public curiosity, Wikipedia. As we explained in the Introduction, people search for information on the Internet on multiple platforms, including search engines, social networks and dedicated websites. We chose Wikipedia as it was the only one to provide open data on visits, and as it is likely to reflect accurately changes in the behaviour of Internet users who are truly interested in a given topic. Moreover,



Figure 4. Number of visits to Wikipedia pages on invasive alien mammals included in the Union list (left column) and invasive alien mammals not included in the list (right column). Dashed lines, from left to right, represent the publication of the first blacklist (July 2016), its first update (July 2017), the implementation of the first Italian law about invasive species (February 2018) and the second update of the blacklist (July 2019).

Wikipedia data could be aggregated into a treatment and control time series, a prerequisite for causal impact analysis, which was not possible using Google Trends. However, this choice excluded dedicated websites, which can be an important source of information about IAS and biological invasions. Combining visits to Wikipedia and dedicated websites can provide a more comprehensive picture on changes in public curiosity and future studies should attempt to access and combine these two sources of information to obtain a more comprehensive metric of public interest that would produce a reliable picture of different social groups and geographical areas.

The second limitation of our study was our decision to focus on invasive alien mammals, which limits the validity of our findings for other taxa. However, compared to invasive alien plants or invertebrates, vertebrates (Jaric et al. 2020), especially mammals, are more salient to people as they can be assimilated to human beings (Manfredo et al. 2020), also based on their evolutionary similarity (Batt 2009). Our decision should therefore have magnified the impact of the Union list on the volume of visits to Wikipedia. We believe that any study replicating our approach to other groups of IAS would reach similar conclusions, at least for Italy, as it will deal with species that are less salient than vertebrates to laypersons.

Interestingly, Cerri et al. (2021) showed that Google searches for general terms about biological invasions, such as "invasive species" or "alien species", increased over time in Italy and even after the entry into force of EU Regulation no. 1143/14 in January 2015. On the other hand, they did not detect any change in visits to three Italian Wikipedia pages about general terms related to IAS. This might indicate that policymaking initiatives about biological invasions can sometimes change the volume of searches on search engines, such as Google, but not on more specialist websites, such as Wikipedia. Moreover, media coverage and outreach initiatives on biological invasions might have different effects on information seeking behaviour, in the case of abstract concepts, such as "invasive alien species" or in the case of practical examples, such as alien species on a blacklist. Future studies, combining in-depth qualitative interviews with manipulative approaches, such as factorial survey experiments, might be useful to ascertain whether these differential patterns exist and how they affect Internet searches.

Finally, this study emphasises the influence that the media have on public interest about IAS and aims to encourage policymakers to exploit media coverage to produce effective communication on biological invasions. Online searches were clearly not affected by news about the Union list, but they peaked in coincidence with sensational news about individual invasive alien mammals, such as viral videos, news about large-scale control initiatives or mass escapes from captivity. Although it is unlikely that traditional media will alter their coverage of these sensational events, we believe that policymakers should exploit them to communicate information on IAS. For example, following the media echo associated with a viral video of an invasive alien mammal in an urban area, environmental agencies could publish a post on their official social media channels, citing the original news, giving information on the characteristics and impacts of the species, together with existing regulations about its management at national and European scale. By doing so, they would exploit the media echo to disseminate knowledge about IAS, their impacts and their management. Moreover, agencies could strengthen their cooperation with traditional media, pushing for the inclusion of expert interviews whenever sensational news about IAS is to be broadcast and adopting established codes of conduct for scientific communication (MacFarlane and Rocha 2020).

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Supplementary material I

Supplementary information

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Data type: pdf. file

- Explanation note: Newspaper and television news related to the publication of the Union list (The list of invasive species of Union concern connected to the European Regulation on invasive alien species no. 1143/2014).
- 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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Horizon scanning for prioritising invasive alien species with potential to threaten agriculture and biodiversity in Ghana

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Abstract

Invasive alien species (IAS) continue to shape the global landscape through their effects on biological diversity and agricultural productivity. The effects are particularly pronounced in Sub-Saharan Africa, which has seen the arrival of many IAS in recent years. This has been attributed to porous borders, weak cross border biosecurity, and inadequate capacity to limit or stop invasions. Prediction and early detection of IAS, as well as mechanisms of containment and eradication, are needed in the fight against this global threat. Horizon scanning is an approach that enables gathering of information on risk and impact that can support IAS management. A study was conducted in Ghana to establish two ranked lists of potential invasive alien plant pest species that could be harmful to agriculture, forestry, and the environment, and to rank them

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according to their potential threat. The ultimate objective was to enable prioritization of actions including pest risk analysis, prevention, surveillance and contingency plans. Prioritisation was carried out using an adapted version of horizon scanning and consensus methods developed for ranking IAS worldwide. Following a horizon scan of invasive alien species not yet officially present in Ghana, a total of 110 arthropod and 64 pathogenic species were assessed through a simplified pest risk assessment. Sixteen species, of which 14 were arthropods and two pathogens, had not been recorded on the African continent at the time of assessment. The species recorded in Africa included 19 arthropod and 46 pathogenic species which were already recorded in the neighbouring countries of Burkina Faso, Côte d'Ivoire, and Togo. The majority of arthropod species were likely to arrive as contaminants on commodities, followed by a sizable number which were likely to arrive as stowaways, while some species were capable of long distance dispersal unaided. The main actions suggested for species that scored highly included full pest risk analyses and, for species recorded in neighbouring countries, surveys to determine their presence in Ghana were recommended.

Keywords

Horizon scanning, invasive arthropods, pathogens, pathway of introduction, pest prioritisation, pest risk analysis

Introduction

The spread of invasive alien species (IAS) has been increasing exponentially over the years, greatly facilitated by international trade and the global transport industry (Perrings et al. 2005; Meyerson and Mooney 2007). The International Union for the Conservation of Nature (IUCN) defines an alien species as a species, subspecies, or lower taxon introduced outside of its natural range and dispersal potential, i.e. outside the range it occupies naturally or could not occupy without intentional or unintentional introduction or care by humans (IUCN 2000). An alien species becomes invasive once it threatens biological diversity, food and economic security, and human health and well-being (Meyerson and Mooney 2007). In particular, IAS can cause significant economic damage through their negative effect on crop harvests and the sustainability of rural economies, thereby threatening livelihoods of hundreds of millions of people, especially in the developing world (Paini et al. 2016; Pratt et al. 2017).

In recent years, Sub-Saharan Africa (SSA), a region dominated by resource-poor farmers, has suffered from an increasing number of invasive plant pests. Eschen et al. (2021) estimated that the annual cost of IAS to agriculture in Africa reaches USD 65.58 Bn per year, with yield losses, reductions in livestock derived income and IAS management costs, mainly labour costs, constituting most of the estimated losses. In their study, the pest causing the highest yield losses (USD 9.4 Bn) was the fall army worm (*Spodoptera frugiperda*). This American pest was first recorded in Africa in 2016 and has since spread to SSA, threatening smallholder maize and sorghum production (De Groote et al. 2020; Tambo et al. 2020). Plant pathogens are also extremely damaging. For example, maize lethal necrosis, a disease caused by co-infection of *Maize chlorotic mottle virus* and *Sugarcane mosaic virus* was first reported in Kenya in 2011 but has since been reported in Democratic Republic of Congo, Ethiopia,

Rwanda, and Tanzania (Mahuku et al. 2015; Mengesha et al. 2019; Kiruwa et al. 2020). The disease has had devastating effects on maize production in SSA (Mahuku et al. 2015; Boddupalli et al. 2020). Other plant pests recently reported in the region with devastating effects include tomato pinworm (*Tuta absoluta*) (Mansour et al. 2018), *Cassava brown streak virus* (Ferris et al. 2020), wheat stem rust (*Puccinia graminis* f. sp. *tritici*) (Fetch et al. 2016) and potato cyst nematodes (*Globodera rostochiensis* and *G. pallida*) (Mwangi et al. 2015; Mburu et al. 2020).

Increased trade between countries and regional blocks on the African continent has resulted in the spread of IAS once they have been reported on the continent (Nagoshi et al. 2018). It should also be noted that not all IAS invade Africa from overseas; some may be native to parts of Africa but are intentionally or unintentionally introduced to some countries or spread across the continent (Gezahgne et al. 2005; Roux and Coetzee 2005; Nakabonge et al. 2006). The spread of IAS from overseas and within the continent can be attributed to porous borders, weak cross border biosecurity, and inadequate capacity to limit or stop invasions (Early et al. 2016; Kansiime et al. 2017; Nagoshi et al. 2018; Graziosi et al. 2020). This exposes Africa both to repeated invasions from novel diseases, invertebrate pests and weeds and to continued spread across the continent once they have arrived (Day et al. 2017). Successful management of IAS involves prevention or early detection of invasions and ensuring effective management in case of arrival (Hulme 2006). Prevention of invasions remains the most cost-effective option of reducing impact of IAS (Wittenberg and Cock 2001; Leung et al. 2002). However, this requires an assessment of the highest risk species to enable the management of pathways of introduction, interception of movements at border points, and assessment of risk for planned imports (Simberloff et al. 2013). Once prevention fails and an IAS enters any jurisdiction, early detection, which allows for costeffective removal, is important to institute eradication and containment interventions (Wittenberg and Cock 2001; Keller et al. 2007).

Horizon scanning for invasive species is an approach that provides countries with opportunities to gather information about IAS likely to head in their direction (Peyton et al. 2019). It involves the systematic search for potential IAS, their impacts on biodiversity, the potential to harm biodiversity, economic activities and human health, and opportunities for impact mitigation (Roy et al. 2014, 2019; Peyton et al. 2019, 2020). It is an important tool that contributes to prevent arrival, early identification and eradication of an IAS and is an essential component of IAS management with demonstrated net economic and ecological benefits (Keller et al. 2007; Caffrey et al. 2014). Horizon scanning has been used to determine the potential arrival, establishment and impact of invasive alien species in Europe (Roy et al. 2014, 2019; Gallardo et al. 2016; Peyton et al. 2019) and provides a practical and affordable option for African countries. The objective of this study was to employ horizon scanning to, firstly, establish a list of potential invasive alien plant pests (arthropods including insects and mites, and pathogens including fungi, bacteria, fungi and nematodes) that are considered not yet present in Ghana but may be harmful to Ghana's agriculture, forestry or environment if introduced. Secondly, to rank these arthropods and pathogens according to their potential threat, which will allow to prioritise actions including pest risk analysis, prevention, surveillance and contingency plans to mitigate the negative effects of introduced species (Peyton et al. 2019; Roy et al. 2019).

Methods

The prioritisation was carried out by a panel of 23 Subject Matter Experts (SMEs) from Ghana research institutions and academia with experience in entomology, bacteriology, mycology, nematology and virology. An adapted version of the consensus method developed for ranking IAS (Sutherland et al. 2011; Roy et al. 2014) was used to derive a ranked list of invertebrates and pathogens harmful to plants and likely to enter Ghana in the near future. The approach involved the following steps:

Step 1. Preliminary horizon scanning

The study started with a first workshop on 24–25th October 2019 in Accra, Ghana, during which the SMEs made a preliminary selection of pests that are not yet officially present in Ghana. This exercise was carried out using the premium version of the horizon scanning tool included in the CABI Crop Protection Compendium (CPC) (CABI 2020a). In this tool, information from the CPC datasheets is used to generate a list of species that are absent from the selected 'area at risk' but present in 'source areas', which may be chosen because they are neighbouring, linked by trade, or share similar climates. The list of species can be filtered using various criteria (e.g. pathways, habitats and taxonomy). The first scan provided the name of 1486 arthropods, nematodes and pathogens qualified as plant pests, present in Africa but absent from Ghana. The list was narrowed by selecting only the species with full datasheets in the CPC (to consider the most important pests) and included in the Invasive Species Compendium (ISC) (CABI 2020b), to eliminate those species in CPC that have not been reported as invasive anywhere and, thus, do not show any characteristics of invasiveness. This search provided 149 species of arthropods and 123 species of pathogens and nematodes, which were further discussed among two thematic groups (entomologists and pathologists/nematologists). During discussions, 63 arthropods and 77 pathogens/nematodes determined to be irrelevant to this exercise were removed, such as those that already occur in Ghana but were not listed as occurring in Ghana in the CPC, or those that were unanimously considered by the SMEs as not important for plants in Ghana, e.g. species that are specific to a plant genus that does not occur in the country. In contrast, 24 arthropod species and 18 pathogens/nematodes were added, in particular species that do not occur yet in Africa but are listed as quarantine pests by the National Plant Protection Organisation (NPPO) or species that had recently spread rapidly across other continents but not yet in Africa. Finally, a shortlist of 110 arthropods and 64 pathogens/nematodes was put forward for further assessment and scoring.

Step 2. Definition of a scoring system

At the same workshop in October 2019, the group of experts defined a scoring system, structured as a simplified Pest Risk Analysis (PRA). The system used by Roy et al. (2019) was modified according to the specificity of the prioritisation and tested, in groups, on some species. The final version of the scoring system is provided in the Suppl. material 1. It included questions on the likelihood of entry; likelihood of establishment; potential socio-economic impact; and potential environmental impact. Each of the four questions was scored from 1 (unlikely to enter or establish; and minimal impact) to 5 (very likely to enter or establish; massive impact). Each score for each question was defined.

The overall score was obtained by the following formula:

Likelihood of entry × likelihood of establishment × (magnitude of socio-economic impact + magnitude of environmental impact)

In addition, the system also asked for information on the likely pathway of arrival (contaminant, stowaway and/or unaided, as defined by Hulme et al. (2008)). It was not possible to provide more detailed levels of pathways assessment because, for many species, the exact pathways of introduction and spread in Africa were not known. A confidence level was attributed to each individual score and the overall score following Blackburn et al., (2014). The likely pathway of arrival and the confidence levels were used to help focus discussions but were not used to build the final scores.

Step 3. Scoring of species

After a group training at the first workshop, the scoring of species was done remotely and independently by at least three assessors per species. The assessors were selected among the SMEs within each thematic group. Each expert assessed at least 20 species. The assessments were sent to the two thematic groups' coordinators who compiled all data and sent them to all assessors before the consensus workshop.

Step 4. Consensus workshop

On 27–28th February 2020, a consensus workshop was organised in Accra with the same experts who were involved in the initial scoring. All species were discussed separately in the two thematic groups. Discrepancies between scores were discussed among the three assessors of the species and the other experts. The assessors had the opportunity to modify their scores according to the opinion of the other experts. At the end, a final risk score was obtained for all assessed species by calculating the median score for all four questions and the final score as above. This score was validated by the group through consensus. In case of disagreement, the single scores were re-discussed. Species were then ranked according to their potential threat for Ghana. Some assessors who could not attend the second workshop were provided the possibility to comment on the scores by email after the workshop.

Step 5. Post workshop adjustments

After the workshop, discussions were carried out among the experts via email to assess, for the species that had scored high, what actions could be taken to mitigate them, e.g. PRA, prevention, surveillance or contingency plans. All experts had the opportunity to review the actions and add comments. In addition, in March 2021, all 174 species were screened again, by searching on the internet and through unpublished reports, to verify that the listed species had not been reported in Ghana since the second workshop.

Results

The full results of the assessments are provided in the Suppl. material 2 while the 40 species with the highest scores are provided in Table 1 and Table 2, which also presents the most suitable actions to be taken against them.

Arthropods

A total of 110 species were assessed, 101 insects and 9 mites. Fourteen species were not yet recorded in Africa at the time of assessment, 19 were already recorded in countries neighbouring Ghana (Burkina Faso, Côte d'Ivoire, and Togo) and 77 elsewhere in Africa. The scores varied from 12 to 160, the four highest scores (Maconellicoccus hirsutus, Aleurothrixus floccosus, Liriomyza trifolii, and Thrips palmi) being reached by species already present in neighbouring countries, thus likely to enter and establish, and known as important plant pests (Table 1 and Suppl. material 2). Only one mite, Brevipalpus phoenicis, was present with 19 insects in the 20 invasive alien arthropods considered to be highest risk. Among these, 11 were Hemiptera, three Diptera, two Thysanoptera, two Coleoptera and one Lepidoptera. The majority of the arthropods (95%) were likely to arrive as contaminants on commodities, i.e. on their host plants, but a sizeable number of them was also likely to arrive as stowaways (23%), whereas some good fliers already present in neighbouring countries could also enter unaided (Suppl. material 2). The most frequent suggestions for the most needed actions against the 20 species with the highest scores were full PRAs and surveys for the presence or introduction of the species in the country (Table 1). There were also a few cases of invasive species that have so far been identified to the genus level, for example Liriomyza spp. and *Thrips* spp., and for which sampling and proper identifications are needed.

Pathogenic organisms

In total, 64 pathogenic species were assessed: 14 bacteria (includes one phytoplasma), 16 fungi, 14 nematodes (Kingdom: Animalia), seven water moulds (Kingdom: Chromista), and 13 viruses (Suppl. material 2). Two of the 64 pathogenic species, *Moniliophthora perniciosa* and *M. roreri*, had not been reported anywhere in Africa

Species	Order	Score	Suggested actions
Maconellicoccus hirsutus	Hemiptera	160	Surveys for its potential presence in Ghana
Green			
Aleurothrixus floccosus	Hemiptera	150	Surveys for its potential presence in Ghana
(Maskell)			
Liriomyza trifolii (Burgess)	Diptera	150	Since only <i>Liriomyza</i> sp. is reported in Ghana, <i>Liriomyza</i> spp. should be sampled in the country for molecular analyses and morphological ID to assess which species is present
<i>Thrips palmi</i> Karny	Thysanoptera	150	Since only <i>Thips</i> sp. Is reported in Ghana, <i>Thrips</i> spp. and related genera should be sampled in the country for molecular analyses and morphological ID to assess which ones are present in Ghana
Aonidiella orientalis (Newstead)	Hemiptera	140	Conduct a full PRA
Unaspis citri (Comstock)	Hemiptera	125	Surveys for its potential presence in Ghana and conduct a full PRA
<i>Spodoptera eridania</i> Stoll	Lepidoptera	120	Surveys with pheromone traps and sampling
Bemisia tabaci (Gennadius) (MEAM1)	Hemiptera	120	Sampling of <i>B. tabaci</i> in Ghana for molecular analyses to assess which sibling species is present
Brevipalpus phoenicis (Geijskes)	Trombidiformes	120	Conduct a full PRA
Callosobruchus chinensis L.	Coeloptera	120	Surveys to check if the species is not in Ghana. Because the other one is abundant
Dialeurodes citri (Ashmead)	Hemiptera	120	Conduct a full PRA
Diaphorina citri Kuwayama	Hemiptera	120	Conduct a full PRA
Dysmicoccus neobrevipes (Beardsley)	Hemiptera	120	A paper suggests that it may present in Uganda (only record in Africa), but the information is not clear. Ask the authors or specialists in Uganda
<i>Icerya purchasi</i> Maskell	Hemiptera	120	Check with Togo if the presence reported in Togo is confirmed. If yes, make surveys in Ghana
<i>Liriomyza huidobrensis</i> (Blanchard)	Diptera	120	Since only <i>Liriomyza</i> sp. is reported in Ghana, sample <i>Liriomyza</i> spp. in the country for molecular analyses and morphological ID to assess which species is present
<i>Liriomyza sativae</i> Blanchard	Diptera	120	Since only <i>Liriomyza</i> sp. is reported in Ghana, sample <i>Liriomyza</i> spp. in the country for molecular analyses and morphological ID to assess which species is present
<i>Scirtothrips</i> dorsalis Hood	Thysanoptera	120	Since only <i>Thips</i> sp. Is reported in Ghana, sample <i>Thrips</i> spp. and related genera for molecular analyses and morphological ID to assess which ones are present in Ghana
Trioza erytreae (Del Guercio)	Hemiptera	120	Conduct a full PRA
Aonidiella citrina (Coquillett)	Hemiptera	120	Check with Côte d'Ivoire if the recorded presence in Côte d'Ivoire is confirmed. If yes, make surveys in Ghana
Rhynchophorus ferrugineus (Olivier)	Coleoptera	112	Conduct a climate matching assessment and possibly a full PRA

Table 1. The twenty Arthropod species with the highest scores in the prioritisation exercise and suggested actions.

at the time of assessment, leaving 62 pathogenic organisms with a presence in Africa. The agaricales *M. perniciosa* and *M. roreri*, which have potential to devastate the cocoa industry in Ghana, were only scored 60 (Suppl. material 2). These two species had a high likelihood of establishment and magnitude of socio-economic

Species	Kingdom	Score	Suggested actions
Xanthomonas oryzae pv. oryzae (Ishiyama) Swings, van	Bacteria	150	Survey for its potential presence in Ghana
den Mooter, Vauterin, Hoste, Gillis, Mew & Kersters			
Armillaria heimii (Pegler)	Fungi	150	Survey for its potential presence in Ghana
Thanatephorus cucumeris (Kühn)	Fungi	150	Survey for its potential presence in Ghana
Meloidogyne enterolobii (Yang & Eisenback)	Animalia	150	Survey for its potential presence in Ghana
Meloidogyne mayaguensis (Rammah & Hirschmann)	Animalia	150	Survey for its potential presence in Ghana
Maize dwarf mosaic virus	Virus	140	Survey for its potential presence in Ghana
Maize lethal necrosis disease	Virus	140	Conduct a full PRA
Clavibacter michiganensis subsp. michiganensis	Bacteria	125	Survey for its potential presence in Ghana
(Smith)			
Xanthomonas oryzae pv. oryzicola (Fang, Ren, Chen,	Bacteria	125	Survey for its potential presence in Ghana
Chu, Faan & Wu) Swings, Mooter, Vauterin, Hoste,			
Gillis, Mew & Kersters			
Tomato spotted wilt virus	Virus	125	Survey for its potential presence in Ghana and conduct full PRA
Banana bunchy top virus	Virus	120	Survey for its potential presence in Ghana and conduct full PRA
Cassava brown streak virus	Virus	120	Conduct a full PRA
Ralstonia solanacearum Race 2 (Smith)	Bacteria	105	Conduct a full PRA
Maize chlorotic mottle virus	Virus	105	Conduct a full PRA
Cocoa yellow mosaic	Virus	105	Survey for its potential presence in Ghana and conduct full PRA
Meloidogyne hapla (Chitwood)	Animalia	100	Survey for its potential presence in Ghana
Xanthomonas campestris pv. musacearum (Yirgou &	Bacteria	90	Conduct a full PRA
Bradbury) Dye			
Maize stripe virus	Virus	90	Survey for its potential presence in Ghana and conduct full PRA
Meloidogyne ethiopica (Whitehead)	Animalia	90	Survey for its potential presence in Ghana
Phytophthora vignae (Purss)	Chromista	84	Survey for its potential presence in Ghana

Table 2. Pathogenic organisms with the highest scores in the prioritisation exercise and suggested actions.

impact but a very low likelihood of entry and magnitude of environmental impact. Of the 62 pathogenic species, 16 had not been reported in countries neighbouring Ghana (Suppl. material 2). The 16 pathogenic species included four bacterial species, *Clavibacter michiganensis* subsp. *michiganensis*, *Leifsonia xyli* subsp. xyli, *Xanthomonas oryzae* pv. *oryzae*, and *Xanthomonas oryzae* pv. *oryzicola*; four fungal species, *Armillaria heimii*, *Olivea tectonae*, *Puccinia agrophila*, and *Thanatephorus cucumeris*; two nematode species, *Meloidogyne hapla*, *Meloidogyne mayaguensis*; four viral species, *Maize dwarf mosaic virus*, *Maize stripe virus*, *Sweet potato feathery mottle virus*, *Tomato potted wilt virus*, and one water mould, *Phytophthora cinnamomi*.

The overall score after considering all parameters ranged from 12, the lowest recorded for *Pseudomonas savastanoi* pv. *savastanoi* and *Ditylenchus dipsaci* to 150, the highest recorded for *Xanthomonas oryzae* pv. *oryzae*, *Armillaria heimii*, *Thanatephorus cucumeris*, *Meloidogyne enterolobii*, and *Meloidogyne mayaguensis* (Table 2; Suppl. material 2). The likely pathways of arrival of the assessed pathogenic species in Ghana were mainly two: as contaminants on commodities and/or as stowaways (Suppl. material 2). The majority (31, 48.4%) of organisms were likely to arrive in Ghana through both as contaminants or stowaways followed by those which could only arrive as contaminants (26, 40.6%) and lastly those which could exclusively arrive as stowaways. All fungi were likely to arrive in Ghana as contaminants on commodities (16), while seven could arrive as stowaways. All the assessed nematodes were likely to arrive as contaminants on commodities while three could also arrive either as stowaways or as contaminants. All the viruses could either arrive as contaminants or stowaways. Five of the bacteria species were likely to arrive as contaminant, five as stowaway and three as contaminants or stowaways. The only phytoplasma assessed was likely to arrive either as contaminants or stowaways. Four of the water moulds could arrive as contaminants or stowaways, while one could arrive as contaminants and two as stowaways, respectively. As for arthropods, in pathogens the most suggested actions for the high scoring species were to survey for their potential presence in Ghana, especially for species recorded in neighbouring countries and full PRAs (Table 2).

Discussion

The prioritization method used in this study was inspired from horizon scanning and prioritization of IAS (Roy et al. 2014, 2017, 2019; Bayón and Vilà 2019) and was used successfully to create two separate ranked lists of alien plant pests according to their potential threat for Ghana and to prioritize actions. The species with the highest scores were mostly those that scored high in the likelihood of entry, i.e. mostly those that were already recorded in neighbouring countries or spreading rapidly in Africa. It is logical that these species are prioritised and immediate actions taken through organising surveillance programmes. Species that were far from the country and were not spreading rapidly had a lower entry score that impacted the overall score, even though they could have serious effects if they arrived in Ghana. Examples of these species scoring low in likelihood of entry but high in impact included two cocoa pathogens, Moniliophthora roreri, the cause of frosty pod rot of cocoa (Phillips-Mora and Wilkinson 2007; Bailey et al. 2018) and *M. perniciosa* which causes "Witches broom disease" in cocoa (Meinhardt et al. 2008; Lisboa et al. 2020). Although M. roreri causes lower losses than some pathogens on a global scale due to its limited range, its economic impact in any epidemic ranks among the major pod pathogens (Ploetz, 2016). It is also ranked among the main yield-limiting factors of cocoa production in tropical America (Bailey et al. 2018). Severe outbreaks of *M. roreri* have resulted in abandonment of cocoa cultivation in extensive areas of Peru, Costa Rica, Colombia and Mexico (Phillips-Mora and Wilkinson 2007). In the 1970s, Moniliophthora perniciosa caused pod losses exceeding 90% in Rondonia, a Brazilian State, causing a significant socio-economic impact on the development of that State (Lisboa et al. 2020). In the State of Bahia, the pathogen was deliberately introduced in what is now considered an act of terrorism ("agro-terrorism"), which caused a reduction in production by almost 70% within 10 years (Saatchi et al. 2001; Caldas and Perz 2013; Lisboa et al. 2020).

The likelihood of establishment played a less important role in the prioritisation because species that are unlikely to establish because of unsuitable climate or absence of host plants were excluded in the preliminary sorting. Thus, most species scored high in the likelihood of establishment. The impact score also played an important role in the overall score, but mostly through their potential economic impact. Few species scored high in environmental impact, probably because most invasive plant pests in tropical regions are rather known for their economic impact and those that cause concern for non-commercial plants attract less attention and may pass under the radar of such horizon scanning. Many invasive arthropods are also known for their environmental impact (Kenis et al. 2009), but most of these are invasive predators such as ants and ladybirds, or pollinators. Nevertheless, some alien herbivorous arthropods and plant pathogens also have huge impacts on biodiversity and ecosystem functions worldwide, in particular those affecting tree species such as emerald ash borer, which has killed tens of millions of ash (Fraxinus spp.) in North America (Herms and McCullough 2014), hemlock woolly adelgid causing the decline of hemlock (Tsuga spp.) in North America (Ellison et al. 2018), box tree moth, which decimates wild box stands (Buxus sempervirens) in Europe (Mitchell et al. 2018), and the pathogens causing chestnut blight (Rigling and Prospero 2018), Dutch elm disease (Harwood et al. 2011), and ash dieback (Mitchell et al. 2014), which have had a dramatic impact on chestnut (Castanea spp.), elm (Ulmus spp.) and ash, respectively, in North America and Europe. Some serious invasive tree pests such as the sirex woodwasp (Sirex noctilio) (Tribe and Cillié 2004), Eucalyptus long-horned borers (Phoracantha semipunctata and P. recurva) (Paini et al. 2016), Cypress aphid (Cinara cupressi) (Watson et al. 1999), Coniothyrium stem canker (Gezahgne et al., 2005) and pink disease caused by Erythricium salmonicolor (Roux and Coetzee 2005) have also been recorded in Africa but mostly concern exotic trees. An exception is Euwallacea fornicatus, a wood-boring beetle from Asia that damages many native trees in South Africa (Paap et al. 2018).

Several alien arthropods and pathogens were identified in neighbouring countries, which suggests that some of these species may already be present in Ghana but have not yet been recorded or identified to the species level. It is essential that these species are sampled and identified using morphological and molecular methods. This could be the case for some species that reached high scores in the assessment. For instance, Maconellicoccus hirsutus is a scale insect that is a serious pest of cocoa (Fornazier et al. 2017), a key crop in Ghana. It is present in all three neighbouring countries, but not yet officially reported in Ghana. Another typical example is that of the leaf mining flies of the genus Liriomyza (Parrella 1987; Lee et al. 2004; Migiro et al. 2010). Three species of this genus, L. trifolii, L. huidobrensis and L. sativae, are notorious for being invasive and all are alien in Africa (Radcliffe and Lagnaoui 2007; Migiro et al. 2010; Akutse et al. 2013; EFSA Panel on Plant Health et al. 2020b). However, so far, only "Liriomyza sp." has been reported in Ghana (Garmonyou et al. 2014) although L. sativae has been intercepted in the European Union on products from Ghana, suggesting that it is present in the country (EFSA Panel on Plant Health et al. 2020b). Similarly, the highly invasive thrips, Thrips palmi (Cannon et al. 2007; EFSA Panel

on Plant Health et al. 2019) is reported from neighbouring countries and it is known that *Thrips* spp. cause serious damage to vegetables in Ghana (Baah et al. 2015), but it is not clear what species are present in the country. The whitefly *Bemisia tabaci* is known to be a complex of many sibling species, several of them being highly invasive worldwide (Perring 2001; Vyskočilová et al. 2018). These species can only be identified using molecular tools (Vyskočilová et al., 2018) and it is not clear to which species of the *Bemisia tabaci* complex the numerous records in Ghana refer.

Species that are most probably not yet present in Ghana but already in neighbouring countries or spreading fast on the continent may require implementation of surveillance programmes, which could either be based on visual surveys or trapping campaigns (Berec et al. 2015; Ward et al. 2016). An example is *Spodoptera eridania*, found in Africa in 2016 and already present in several African countries including Nigeria and Benin (Goergen 2018; EFSA Panel on Plant Health et al. 2020a). There is uncertainty regarding the risk of several species, either because the likelihood of entry and establishment is unclear or because the potential impact is difficult to assess. In such cases, a full PRA would be needed. Pest risk analyses may also be needed for species that are undoubtedly considered as high-risk pests but require quarantine measures that can only be justified based on full PRAs carried out following international standards.

When assessing risks, it is important to supplement the answers with a confidence level, or a level of uncertainty (Holt et al. 2014). Our simplified PRA system asked assessors to provide a confidence level for the answers, both for the single scores and for the overall score. However, the overall confidence level provided by the entomology and pathology groups (Suppl. material 2) were very different, i.e. the pathology group considering that the overall scores for pathogens and nematodes were obtained mostly with high confidence whereas the entomology group was more cautious and provided mostly medium confidence levels for arthropods, although there is no reason to believe that data on arthropods are less reliable than those on pathogens and nematodes. Moreover, the levels of confidence provided by the different assessors for the same questions using the same information sources often differed from high to low, suggesting that, in the future, instructions for the scoring of confidence levels should be more clearly defined.

Conclusion

We have demonstrated that through horizon scanning, a country can identify potential invasive plant pests, both invertebrates and pathogens, and use the information to determine the risk associated with each. This will enable the country to invest the limited resources in priority actions such as preventing arrival and establishment of IAS, PRAs, surveillance and developing contingency plans. This study can serve as a model for future projects on plant pests' prioritisation in Africa and elsewhere. It would be applicable for assessing the risk of invasive plant pests in any country or region, e.g. trade blocks, with minor modifications of the method, particularly in the mini-PRA protocol used to score species.

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Supplementary material I

Guidelines for horizon scanning for plant pests potentially threatening Ghana

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Data type: Guidelines for horizon scanning.

- Explanation note: Guidelines for the horizon scanning method used to score potential invasive alien plat pests in Ghana.
- 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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Supplementary material 2

Risk scores for potential invasive alien plant pests in Ghana

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Explanation note: Risk scores for all species assessed in the horizon scanning of potential alien invasive plant pests in Ghana.

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RESEARCH ARTICLE



Using leaf functional traits to remotely detect Cytisus scoparius (Linnaeus) Link in endangered savannahs

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Abstract

Identification of invasive plant species must be accurate and timely for management practices to be successful. Currently, *Cytisus scoparius* (Scotch broom) is expanding unmonitored across North America's west coast, threatening established ecological processes and altering biodiversity. Remote detection of leaf functional traits presents opportunities to better understand the distribution of *C. scoparius*. This paper demonstrates the capacity for remotely sensed leaf functional traits to differentiate *C. scoparius* from other common plant species found in mixed grassland-woodland ecosystems at the leaf- and canopy-levels. Retrieval of leaf nitrogen percent, specifically, was found to be significantly higher in *C. scoparius* than each of the other 22 species sampled. These findings suggest that it may be possible to accurately detect introduced *C. scoparius* individuals using information collected from leaf and imaging spectroscopy at fine spatial resolutions.

Keywords

Biodiversity, invasive plants, mixed grassland-woodland, partial least squares regression, Scotch broom, spectroscopy

Introduction

The introduction of invasive plant species to an ecosystem can drastically alter diversity and threaten ecosystem processes, such as soil water dynamics and nutrient availability (Shaben and Myers 2010; Albert et al. 2012; Slesak et al. 2016; Carter et al. 2018). In the past 200 years, humans have expanded across the planet and enhanced the capacity of plant species to migrate (Zerega et al. 2004; Olivares et al. 2019). Some species have transited oceans for agricultural production, while others simply provide ornamental value (Hawkes and Francisco-Ortega 1993; Bossard and Rejmanek 1994). *Cytisus scoparius* (L.) Link, or Scotch broom, is one such transplant. A nitrogen-fixing legume introduced to numerous countries around the globe, *C. scoparius* has proven adept at establishing in climatically temperate regions of North America, Australia and New Zealand (Downey and Smith 2000; Richardson et al. 2000; Odom et al. 2003; Slesak et al. 2016). Initially transported from its native range in northern Africa and Europe, *C. scoparius* was a preferred decorative shrub of New World colonists due to its low-maintenance and striking yellow flowers (Fuchs 2001). The nitrogen-rich leaves of nitrogen-fixing species, such as *C. scoparius*, are relatively more productive than non-nitrogen-fixing species and make them adept at invading ecosystems with favourable environmental conditions (McKey 1994; Richardson et al. 2000).

One such ecosystem exists along the west coast of North America. Defined as a mixed grassland-woodland, Garry oak (*Quercus garryana* Douglas ex Hook) savannahs provide habitat for several endangered plant and animal species (Bjorkman and Vellend 2010). In Canada, the footprint of this ecosystem has been reduced by urban and agricultural expansion to less than 5% of its original area (MacDougall et al. 2004). Increased anthropogenic interaction has also introduced a variety of invasive plant species that could destabilize traditional plant assemblages (Fuchs 2001).

C. scoparius presents a variety of challenges to native plant species (Shaben and Myers 2010). As a nitrogen-fixing species, it can alter soil chemistry, an unseen change that has the potential to disturb nutrient cycling (Fogarty and Facelli 1999; Carter et al. 2018). In mixed grassland-woodland ecosystems, the fast-growing nature of *C. scoparius* competes well against native shrubs, forbs and graminoids that maintain relatively slower growth strategies (Shaben and Myers 2010). Over time, this can result in a shift in species diversity and further uproot traditional ecosystem processes (Carter et al. 2018). The dense soil seed bank created by reproducing *C. scoparius* individuals, which begins approximately 4 years post-establishment, virtually ensures perpetual species presence and renders removal of reproducing individuals irrelevant (Downey and Smith 2000).

Despite its damage to natural ecosystems, programs monitoring the spread of this species are not common. Initial analysis of multispectral satellite and airborne imagery has confirmed that large, dense *C. scoparius* patches can be observed during spring bloom; however a more reliable method of year-round identification at finer spatial scales is needed for realistic removal efforts (Odom et al. 2003; Hill et al. 2016). A common issue faced by previous studies relates to the availability of relevant imagery. Odom et al. (2003) used high-spatial resolution airborne imagery and manually delineated *C. scoparius*, which was both cost and time intensive. In contrast, Hill et al. (2016) used satellite imagery with a relatively coarse spatial resolution (Landsat Thematic Mapper, 25m after resampling) and automated classification of reflectance. Unfortunately for mixed grassland-woodland ecosystems, such mapping techniques may only prove relevant upon the large-scale establishment of *C. scoparius*, at which point removal efforts are redundant.

Continuing improvements in both the platforms and sensors used for remote landscape classification present a variety of options for monitoring *C. scoparius* presence. The estimation of foliar functional traits across a site using remote sensing techniques presents an opportunity to identify invasive species, like *C. scoparius*, in mixed grassland-woodland ecosystems and has yielded success in a variety of other ecosystems (Asner et al. 2008; Niphadkar and Nagendra 2016; Große-Stoltenberg et al. 2018). Essentially, spectral information is acquired across several narrow bands and modelled with a measured plant functional trait, such as leaf nitrogen percent (%N), to generate a predicted trait value for each pixel in an image. This methodology has proven successful at remotely identifying unique plant species in both tropical and temperate climates and lends well to analyses conducted at a range of spatial scales (Asner and Martin 2009; Wang et al. 2019). The continued improvement of hyperspectral imaging sensors on remotely piloted aircraft systems (RPAS), or drones, and airplanes presents another opportunity to estimate plant functional traits at relatively small spatial scales over large areas (Asner et al. 2016; Van Cleemput et al. 2018).

Before air- or spaceborne analyses can be conducted, however, significant differences in both foliar functional traits and spectral reflectance between *C. scoparius* and other common mixed grassland-woodland plant species should be demonstrated at the leaf- and canopy-level. The aim of this study is to identify leaf functional traits of *C. scoparius* that are significantly different from other grassland-woodland species at the leaf- and canopy-levels through four hypotheses:

1. The measured value of at least one leaf functional trait of *C. scoparius* is significantly different than that of the 22 other site species sampled (henceforth referred to as 'Site').

2. Significant differences of predicted leaf-level functional trait values remain between *C. scoparius* and Site species.

3. Significant differences of predicted canopy-level functional trait values remain between *C. scoparius* and Site species.

4. Alterations in illumination conditions do not impact the significance of predicted canopy-level trait differences.

Methods and materials

Study site

Leaf material for 23 plant species was collected in and around a mixed grassland – woodland savannah within the Cowichan Garry Oak Preserve (CGOP; 48°48'29.85"N, 123°37'54.34"W) between May 4–19, 2019 (Fig. 1). Located near Duncan, British Columbia, Canada, this site harbours more than 61 plant species and a variety of other wildlife, including the red listed Western Bluebird (*Sialia mexicana*; IUCN Least Concern). The 23-plant species were selected based on a variety of criteria, including widespread abundance, known North American range and interest to local manag-



Figure 1. True color composite Imagery of **a** the Cowichan Garry Oak Preserve (CGOP) and **b** the extent of *Quercus garryana* (Little 1971) and locations of *Cytisus scoparius* (https://doi.org/10.15468/dl.dfdv48) individuals along North America's west coast.

ers. These mixed grassland-woodland ecosystems, often called Garry oak savannahs, are considered endangered in Canada as the percentage of near-natural habitat is less than 5% of its original footprint (MacDougall et al. 2004; Bjorkman and Vellend 2010). Abiotic threats stem mainly from the complete suppression of fire, which has enabled woody plants to establish unabated (Fuchs et al. 2000). Biotic threats include invasive plant species, such as *C. scoparius*, herbivory and the encroachment of Coastal Douglas-fir forests (Fuchs 2001).

Target species

C. scoparius presents a unique challenge to Garry oak ecosystems due to its ecology. Labelled "invasive" due to profuse seed production and capacity for year round growth, this shrub faces limited competition from native plant species and is capable of altering soil chemistry through nitrogen fixation (Shaben and Myers 2010; Slesak et al. 2016). Upon establishment in a non-native environment, the spread of *C. scoparius* can be limited by a lack of compatible pollinators, but in general has shown strong capacity to alter plant diversity through native species exclusion and non-native recruitment (Parker 1997; Carter et al. 2018). Growing quickly and reaching heights exceeding three meters, this invasive shrub faces few barriers upon introduction (Parker 1997).

Leaf trait evaluation

Chemical and spectral measurements

A total of 14 traits were measured across 23 unique plant species and four plant life forms. All leaf samples taken are considered to be from sunlit positions. Chemical evaluation of chlorophyll a + b (Chlab) and carotenoids (Car), as well as leaf dry matter content (LDMC), equivalent water thickness (EWT) and %N were conducted following standards presented by the Canadian Airborne Biodiversity Observatory (CABO) (Laliberté 2018; Ayotte et al. 2019; Girard et al. 2019). Due to a lack of normality in the distribution of measured trait values for multiple species the Mann-Whitney (Wilcoxon) test was used to determine if C. scoparius exhibits significantly different trait values from the other 22 plant species sampled (Milton 1964). Leaf spectroscopy was conducted using a Spectra Vista Corporation (SVC) DC-R/T integrating sphere to measure 6 leaves from each individual plant samples (n = 201), with the number of samples ranging from 3-10 per species, and followed CABO standards (Laliberté and Soffer 2018a, 2018b). Reflectance values from 400 - 2400 nm were used in analyses after undergoing vector normalization and a Savitzky-Golay filter to enhance differences in spectral shape and reduce noise, respectively. All leaf samples underwent spectroscopy within 6 hours of collection and bulk leaf samples were chilled until chemical analyses began.

Modelling functional traits

Individual leaf traits were modelled using partial least squares regression (PLSR), a statistical method well-suited for modelling datasets with high dimensionality, such as those created from spectroscopy. The data was split into training (70%) and test (30%) sets. This methodology models the relationship between spectral reflectance values recorded by leaf spectroscopy and measured leaf chemistry to enable the accurate prediction of leaf functional traits (Haaland and Thomas 1988). PLSR modelling has successfully predicted leaf traits in tropical forests and temperate grasslands from spectroscopy data, highlighting its cross-biome utility and capacity to evaluate large, highly-correlated datasets (Curran 1989; Asner and Martin 2009; Feilhauer et al. 2017). A Shapiro-Wilks test found the leaflevel chemical data to be non-parametric, so an independent 2-group Mann-Whitney test was used to determine if significant differences existed between the leaf functional traits of *C. scoparius* and the 22 Site species evaluated at the measured and predicted leaf-level.

Canopy-level modelling

Radiative transfer models (RTM) are important methods of simulating the spectral reflectance of vegetation (Asner et al. 2011; Féret et al. 2017). There are generally two spatial scales at which models are designed: leaf and canopy. We employed the canopy-level RTM PROSAIL to simulate canopy spectra from an airborne imaging spectrometer using four measured chemical values obtained from 201 plant samples of

all 23 species (Jacquemoud et al. 2009). The PLSR models developed using leaf-level spectra and chemical values were applied to the simulated spectra created by PROSAIL to predict relative trait values at the canopy-level.

The four traits used as input arguments for the PROSAIL algorithm were Chl*ab*, Car, LDMC and EWT. To determine the if canopy-level predicted traits react to changes in illumination geometry, such as different flight dates and latitudes, PROSA-IL simulations were conducted at a variety of solar zenith angles spanning $20 - 70^{\circ}$ at 1-degree intervals. The functional trait models derived from PLSR were then applied to these spectra to generate predicted trait values at the canopy-level. An independent 2-group Mann-Whitney test was used to determine if the predicted trait values of *C. scoparius* were significantly different from predicted trait values of the Site species.

Software

All data manipulation was conducted in R (R Core Team 2021). The package 'spectrolab' was used to organize and manipulate data obtained through leaf spectroscopy (Meireles and Schweiger 2021). The 'pls' package (Liland et al. 2021) was used to conduct partial least squares regression and 'hsdar' (Lehnert 2020) enabled the use of PROSAIL.

Results

An independent 2-group Mann-Whitney test determined that 11 of the 14 measured traits exhibited a significant difference between *C. scoparius* and the 22 Site species (Table 1, Fig. 2). Of these, %N (W = 1908, p-value = 1.08e-07) and carbon-nitrogen ratio (C:N; W = 15, p-value = 1.61e-07) demonstrated the largest differences (Table 1). The mean measured %N value for *C. scoparius* and Site species were 2.93% and 5.37%, respectively. Mean measured C:N values for *C. scoparius* and Site were 8.94 and 16.66, respectively. Due to the overlap in measured C:N values between *C. scoparius* and Site species, as well as the complexities introduced by measuring two traits compared to one, only %N was used in this study (Fig. 2). Leaf-level %N was accurately predicted using PLSR (R² = 0.70, NRMESP = 17%) (Table 2, Fig. 3). This is within the acceptable range of model accuracy presented in the literature and confirms its suitability for analyses (Asner and Martin 2016; Wang et al. 2019).

The use of the %N PLSR model to predict foliar %N from leaf spectral signatures determined that the leaf-level predicted %N values of *C. scoparius* and the 22 Site species were significantly different (W = 1910, p-value = 1.02e-07) (Fig. 4). The significant functional difference displayed by *C. scoparius* at the leaf-level remained at the canopy-level as testing determined that relative %N of *C. scoparius* at the canopy-level was different to that of the 22 Site species (W = 1653, p-value = 1.003e-04) (Fig. 5). Alterations in viewing geometry did not compromise the significant differences found between canopy predicted relative %N of *C. scoparius*

Table 1. Resulting p-values from Mann-Whitney tests comparing measured *Cytisus scoparius* nitrogen percent with the 22 Site species. The difference in %N between *C. scoparius* and each of the 22 other species is significantly different (p < 0.05). The number of individuals sampled per species is included in parentheses under their names.

Species	Nitrogen (%)	Species	Nitrogen (%)
Berberis aquifolium Pursh (10)	1.08E-05	Lomatium utriculatum (Nuttall ex Torrey & A.	1.08E-05
		Gray) J.J. Coulter & Rose (10)	
Bromus sitchensis var. carinatus	1.08E-05	<i>Oemleria cerasiformis</i> (Torrey & A. Gray ex	1.08E-05
(Hooker & Arnott) R.E. Brainerd		Hooker & Arnott) J.W. Landon (10)	
& Otting (10)			
Bromus sterilis Linnaeus (6)	2.50E-04	Plectritis congesta (Lindley) de Candolle (10)	1.08E-05
<i>Camassia leichtlinii</i> (Baker) S.	5.67E-06	Poa pratensis Linnaeus (10)	2.50E-04
Watson (10)		-	
Camassia quamash (Pursh) Greene	1.08E-05	Polystichum munitum (Kaulfuss) C. Presl (7)	1.03E-04
(10)		-	
Claytonia perfoliata Donn ex Will-	1.08E-05	<i>Quercus garryana</i> Douglas ex Hooker (10)	1.08E-05
denow (10)			
Crataegus monogyna Jacquin (10)	2.50E-04	Rosa nutkana C. Presl (10)	1.08E-05
Dactylis glomerata Linnaeus (10)	1.08E-05	Sanicula crassicaulis Poeppig ex de Candolle (10)	1.08E-05
Festuca idahoensis Elmer (6)	2.50E-04	Sericocarpus rigidus Lindley (3)	0.007
Holodiscus discolor (Pursh) Maxi-	1.08E-05	Symphoricarpos albus Poeppig ex de Candolle	1.08E-05
mowicz (10)		(10)	
Lathyrus sphaericus Retzius (6)	2.50E-04	Vicia sativa Linnaeus (10)	4.33E-05



Figure 2. Comparisons of 14 functional traits between *C. scoparius* and Site species. Boxplots depicting the differences between *C. scoparius* (yellow) and 22 other "Site" plants (green) for 14 leaf functional traits using a Mann-Whitney test, 11/14 of which are significantly different. The level of significance is denoted in the banner of each facet (* <= 0.05, ** <= 0.01, *** <= 0.001).

Trait	R ²	RMSEP (NRMSEP)	Components
Chlorophyll a (mg/g)*	.54	3.25 (31%)	7
Chlorophyll <i>b</i> (mg/g)*	.56	1.16 (33%)	8
Carotenoids (mg/g)	.36	0.68 (31%)	4
Nitrogen (%)*	.70	0.5(17%)	4
Carbon (%)	.48	0.99 (2%)	6
C:N*	.71	2.98 (18%)	4
Leaf mass per area (g/m²)*	.67	10.34 (25%)	6
Leaf dry matter content (mg/g)*	.69	48.64 (22%)	7
EWT*	.85	0.002 (16%)	4
Solubles (%)	.41	9.78 (16%)	4
Hemicellulose	.36	6.43 (40%)	4
Cellulose*	.59	3.96 (27%)	4
Lignin	.46	3.64 (55%)	4
Recalcitrants	.28	0.12 (56%)	4

Table 2. Partial Least Squares Regression model evaluation. Functional traits selected for hypothesis testing and their associated model performance metrics (R², Root mean squared error of the predictor (RMSEP), normalized-RMSEP (NRMSEP) and the number of components, or latent variables).

*accepted trait





Figure 3. PLSR prediction plot. Comparison of the measured and predicted leaf nitrogen percent (%N) for 23 plant species at the Cowichan Garry Oak Preserve.



Figure 4.Measured and predicted leaf %N. Comparison of measured and predicted leaf N% of *C. scoparius* (yellow) and 22 Site species of various lifeforms (Site; green) sampled at CGOP.



Figure 5. Measured leaf %N and predicted canopy N%. Comparison of the measured leaf-level and predicted canopy-level %N for *C. scoparius* (yellow) and 22 other plant species (Site; green) sampled at the CGOP in May 2019. Note that the y-axis scale varies, with the relative %N values predicted by PROSAIL being negative. This occurs as a result of using the relatively lower reflectance values generated by PROSAIL with a PLSR model developed using leaf-level spectra.



Figure 6. Predicted relative %N compared between *C. scoparius* and Site species using various solar zeniths. Boxplots demonstrating the difference between the PROSAIL predicted relative %N for *C. scoparius* (yellow) and Site species (green) using different solar zeniths (20 degrees, 45 degrees and 70 degrees).

and Site species (20°: W = 1653, p-value = 0.0001; 45°: W = 1653, p-value = .0001; 70°: W = 1652, p-value = .0001026) (Fig. 6).

Discussion

Mapping the spatial extent of invasive plant species is a key component of managing biodiversity at any scale. In North America, the invasion of *C. scoparius* populations is destabilizing the traditional species composition of plant communities, especially in mixed grassland-woodland ecosystems (Fuchs 2001; Shaben and Myers 2010). Previous monitoring efforts have mapped *C. scoparius* through observing yellow inflorescence from multi-spectral satellite imagery and, although effective at mapping well established populations, precludes removal efforts of young, unestablished individuals (Odom et al. 2003; Hill et al. 2016).

This paper demonstrated that *C. scoparius* is distinguishable from other common grassland-woodland plants based on leaf functional traits, rather than bloom color. Multiple *C. scoparius* leaf traits were significantly different from those of 22 other plant species evaluated, with %N proving the most different. This is unsurprising as *C. scoparius* is a nitrogen-fixing legume and is likely to have leaves that are relatively nitrogen-rich (McKey 1994; Große-Stoltenberg et al. 2018). Such differences can lead to competitive advantages in photosynthetic capacity for nitrogen-fixers, which may in part explain the success *C. scoparius* has experienced at establishing beyond its traditional range in the Mediterranean (Shaben and Myers 2010; Große-Stoltenberg et al. 2018). These findings are consistent with research in tropical and dune ecosystems, and strengthen the idea of using leaf %N to detect invasive plant species in a variety of environments (Asner et al. 2008; Große-Stoltenberg et al. 2018). It should be noted, however, that the use of leaf %N to map nitrogen-fixers is dependent on the absence of other nitrogen-fixing species that present similar leaf %N to the target species.

The leaf-level PLSR model used to predict leaf %N explained 70% of the total variance between measured and predicted values while demonstrating a normalized error of 17%. The use of only four components suggests that this model is well fitted. Differences in measured and predicted leaf %N between *C. scoparius* and Site species promoted testing whether leaf %N was scalable from the leaf- to canopy-level. It is interesting to note that similar differences existed for C:N, suggesting that this trait could potentially be used to differentiate *C. scoparius* from Site species. This would, however, require the measurement of two traits, rather than one.

The RTM canopy model PROSAIL was used to simulate canopy reflectance of C. scoparius and Site species, and determined that significant differences in %N scale from the leaf to canopy. This scalability suggests that this method could be used for the detection of individuals that have recently been introduced. There are currently no civilian satellite programs capable of providing this type of data at the required spectral and spatial resolution, meaning that the imagery must be acquired from airborne sensors. Some studies have demonstrated that imagery collected from drone-based sensors can accurately map shrubland vegetation (Prošek and Šímová 2019) or predict functional traits in the arctic (Thomson et al. 2021), but questions remain surrounding the capacity of these methods to differentiate small individuals in species-rich ecosystems (>20 species per 1 m²), such as mixed woodland-grasslands. It may be possible, however, to generate a new nitrogen-index by selecting only bands common in multi-spectral sensors (Heim et al. 2019) or correlate pre-existing multispectral remote sensing indices with the measured leaf %N values, eliminating the need for hyperspectral data collection and reducing the cost of both data acquisition and processing.

Conclusion

The significant differences in measured and predicted leaf %N between *C. scoparius* and 22 other plant species common in Canadian mixed woodland-grassland savannahs suggest that remote detection of *C. scoparius* is possible. This concept is supported by the up-scaling of leaf traits using the radiative transfer model PROSAIL, which dem-

onstrated the aforementioned differences in leaf %N scale from the leaf- to the canopylevel. Successful scaling, in turn, proves that *C. scoparius* could be detected based on its relatively high leaf %N, given that remote sensing technologies have the required spectral and spatial resolutions to identify small, individual plants.

Technological advances have made RPAS more affordable, allowing them to become a common platform used for the collection of imagery with fine spatial resolution in a variety of ecosystems (Sankey et al. 2018; Arroyo-Mora et al. 2019). The recent development of RPAS-based imaging spectrometers compliments the findings of this study and suggests that land managers could deploy these sensors prior to the bloom period of *C. scoparius* across a mixed grassland-woodland ecosystems in order to identify areas that may contain young individuals. Considering the capacity for *C. scoparius* to alter soil chemistry, encourage establishment of other invasive plant species and outcompete native species, the ability to detect unestablished populations through leaf functional traits presents an interesting monitoring opportunity that could prove effective in a variety of ecosystems across the globe.

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RESEARCH ARTICLE



A review of invasive species reporting apps for citizen science and opportunities for innovation

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Abstract

Smartphone apps have enhanced the potential for monitoring of invasive alien species (IAS) through citizen science. They now have the capacity to massively increase the volume and spatiotemporal coverage of IAS occurrence data accrued in centralised databases. While more reporting apps are developed each year, innovation across diverse functionalities and data management in this field are occurring separately and simultaneously amongst numerous research groups with little attention to trends, priorities and opportunities for improvement. This creates the risk of duplication of effort and missed opportunities for implementing new and existing functionalities that would directly benefit IAS research and management. Using a literature search of Early Detection and Rapid Response implementation, smartphone app development and invasive species reporting apps, we developed a rubric for quantitatively assessing the functionality of IAS reporting apps and applied this rubric to 41 free, English-language IAS reporting apps, available via major mobile app stores in North America. The five highest performing apps achieved scores of 61.90% to 66.35% relative to a hypothetical maximum score, indicating that many app features and functionalities, acknowledged to be useful for IAS reporting in literature, are not present in sampled apps. This suggests that current IAS reporting apps do not make use of all available and known functionalities that could maximise their efficacy. Major implementation gaps, highlighted by this rubric analysis, included limited implementation in user engagement (particularly gamification elements and social media compatibility), ancillary information on search effort, detection method, the ability to report absences and local habitat characteristics. The greatest advancement in IAS early detection would likely result from app gamification. This would make IAS reporting more engaging for a growing community of non-professional contributors and encourage frequent and prolonged participation. We discuss these implementation gaps in relation to

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the increasingly urgent need for Early Detection and Rapid Response frameworks. We also recommend future innovations in IAS reporting app development to help slow the spread of IAS and curb the global economic and biodiversity extinction crises. We also suggest that further funding and investment in this and other implementation gaps could greatly increase the efficacy of current IAS reporting apps and increase their contributions to addressing the contemporary biological invasion threat.

Keywords

biosurveillance, citizen science, early detection and rapid response, invasive species, mobile device, species occurrence, wildlife technology

Introduction

Invasive alien species (IAS) are a leading contributor to biodiversity loss (Bellard et al. 2013; Simberloff et al. 2013; IPBES 2019) and cause annual economic damage in the order of hundreds of billions of US dollars in each of many countries around the world (Pimentel et al. 2005; Bradshaw et al. 2016; Sepulveda et al. 2020). The rate of new introductions shows no sign of saturation across time (Seebens et al. 2017) and the impacts and spread of IAS are expected to increase under climate change (Rahel and Olden 2008; Jourdan et al. 2018). The prevailing paradigm for IAS research, monitoring and management is Early Detection and Rapid Response (EDRR; Crall et al. 2012; Reaser et al. 2020a), which calls for coordinated, standardised and verifiable occurrence data across large spatial scales to support monitoring, biosurveillance and risk assessment (Martinez et al. 2020; Reaser et al. 2020a; Wallace et al. 2020).

Reports from volunteers (commonly called community or citizen scientists) make growing contributions to meeting these monitoring data needs, from providing first detections of new invasions (Vendetti et al. 2018; Eritja et al. 2019) to providing additional data that improves species distribution models (e.g. Roy-Dufresne et al. 2019; Zhang et al. 2020). The advent and rapid growth of mobile technology and smartphone software applications (hereafter apps) have greatly enhanced the potential for IAS reporting and the collection of crowdsourced (i.e. derived from many contributions) IAS occurrence data at unprecedented scales (Silvertown 2009; Teacher et al. 2013; Adriaens et al. 2015; Marchante et al. 2017). The integration of mobile apps with centralised databases is a major technological innovation contributing to the potential increase in available community science data for meeting the data demands of EDRR (Andrachuk et al. 2019; Wallace et al. 2020).

However, there are concerns that the current use of IAS mobile reporting apps is not maximising the potential of this powerful new technology for upscaling EDRR implementation needed to combat the worsening invasive species crisis (Martinez et al. 2020). The rapid growth, development and increasing proliferation of IAS apps has occurred quickly and with little coordination and communication amongst developers. This poses a major risk of development in apps that duplicate effort, result in errors (bugs) and is done in an in isolated environment where developers are unaware of the learning experiences and best practices proposed by others (Luna et al. 2018; Johnson et al. 2020). Martinez et al. (2020) suggested that the current technological toolbox to deal with IAS is still incomplete and inadequate and mobile apps constitute a major opportunity to address the needs of the field through technology.

There are a growing number of published articles describing IAS reporting apps (e.g. LaForest et al. 2011; Goëau et al. 2013; Scanlon et al. 2014; Wallace et al. 2016; Barre et al. 2017; Schade et al. 2019; Mäder et al. 2021), necessitating a solid conceptual framework for assessing how effectively existing and future apps can contribute to the broader vision of EDRR and global-scale invasion research and monitoring. Adriaens et al. (2015) provided a valuable review of IAS reporting apps in Europe, but many of these no longer exist (Schade et al. 2019) and mobile technology has made substantial strides in the last six to seven years, with the advent of 5G networks and a rapidly growing user-base now in excess 2.8 billion people (Alavi and Buttlar 2019).

We synthesised existing literature across the disciplines of invasion biology, citizen science and mobile app development to design a comprehensive rubric for assessing IAS app functionalities that could greatly improve the contribution of reporting apps to ongoing EDRR efforts (Martinez et al. 2020; Reaser et al. 2020a). Rubrics have been used to evaluate apps from other disciplines, especially education and healthcare (Lee and Cherner 2015; Stoyanov et al. 2015; Robinson et al. 2020) and can serve as a tool to assess the functionality of individual apps and the existing app corpus with respect to disciplinary and user needs. We applied this rubric to all free English-language apps available through the Apple App Store and Google Play in North America. We highlight trends and implementation gaps amongst reviewed apps and suggest key pathways for future innovation using existing technology. This review and the resulting rubric are intended to guide future IAS reporting app development and help address the demand for high-quality mobile platforms for collecting IAS occurrence data and while making the best use of the technological resources available to developers.

Methods

We modelled our rubric format after Lee and Cherner (2015), who divided rubrics into thematic units called domains, which contain any number of dimensions corresponding to particular elements, features or functionalities of mobile apps. We compiled information on app features and functionalities from our literature search (see Fig. 1) into four domains: Data Collection, Identification, Reporting, and User Engagement (Fig. 1). These domains were established a priori, based on recent EDRR literature referencing the proposed framework and the integration of mobile technology for reporting IAS (e.g. Martinez et al. 2020; Meyers et al. 2020; Morisette et al. 2020; Reaser et al. 2020; Wallace et al. 2020, Fig. 1).

The Data Collection domain includes app functionalities pertaining to the type, method, geographic scale and taxonomic scope of data that an app can collect, while the Reporting domain focuses on how user-submitted data are input, collected and managed. The Identification domain pertains to features that aid in taxonomic identification, with features like built-in field guides or machine learning for image recognition. Finally, the User Engagement domain entails all participant-focused features, including options for guidance, help and feedback, ease of use and features to promote participation and sustained use, such as games and social networking elements.

We then conducted targeted searches on the Web of Science (WOS) and Google Scholar to identify the dimensions for our rubric (Fig. 1). We compiled a list of 498 papers which were distributed between two of the authors to determine relevance and extract app features described as potential dimensions for the rubric. To determine relevance, the abstracts and introductions of each paper were first visually scanned for references to smartphone or mobile apps, invasive species research, citizen science or other similar terms (Suppl. material 1: Table S1). The 91 relevant publications (Suppl. material 1: Table S1) were then examined more closely to identify pertinent dimensions which were added to a running list (Table 1). Due to the use of multiple terms within different sources for similar dimensions, we consolidated similar functionalities into single rubric dimensions. For example, games, contests and rewards were grouped together as gamification.

Our final rubric consisted of 35 dimensions which are listed by domain along with definitions and source information in Table 1. Most dimensions were scored by the presence (3 points) or absence (0 points) of key functionalities, although some used a scale including 1, 2 and 3 points for dimensions with multiple levels (e.g. different geographical scales, wherein local scales received a score of 0, state or province scales, a score of 1, regional scales, a score of 2 and national or international, a scale of 3; Table 1).



Figure 1. App review workflow. Each box header displays the workflow stage, examples of search terms used, and the number of papers used for that stage. The top-left box shows the search terms used for identifying rubric domains. These papers were reviewed to identify broad categories into which smartphone features could be organized for the rubric. The bottom left panel depicts the search string used to identify app dimensions within these domains (N = 498 papers, see also Table 1 for a detailed list of dimensions). In the central bottom panel, these dimensions are grouped by domain.

Table 1. App dimensions organized by the four rubric domains with source information (relevant literature) and rubric scoring scale used to rank smartphone mobile apps. Domains are indicated by superscript prefix as follows: DC = Data Collection; ID = Identification; Rep = Reporting; Eng = User Engagement. Letters within the parentheses following each dimension name correspond to that dimension in Figure 3.

Dimension	Definition	Rubric Scoring Scale	Relevant Literature
^{DC} Absence Data (A)	Users can submit negative reports or the absence of a specific IAS.	0 = not present; 3 = present.	Wallace et al. 2016.
^{DC} Abundance/ Area (B)	Users can enter the number of individuals, abundance, or area covered by the observed IAS.	0 = not present; 3 = present.	Schade et al. 2019; Wallace et al. 2016.
^{DC} Catch Per Unit Feature/ Time Spent for Observation (C)	User can include information on time spent looking for IAS. This can be used to calculate catch per unit effort and potentially estimate abundance.	0 = not present; 3 = present.	Bannerot, S. P., and Austin, C. B. 1983
^{DC} Climate/ Habitat Data (D)	Reporting interface includes climate and habitat/site context-related metadata fields (i.e., temperature, water flow rate, substrate, etc.)	0 = not present; 3 = present.	Adriaens et al. 2015; Andrachuk et al. 2019; Reaney et al. 2019.
^{DC} External Sensors (E)	Users can sync external devices that collect data or detect IAS and/or the app allows upload of additional data types (sound recordings, rapid genetic identification results from biofouling or propagule analysis, eDNA/PCR/ddPCR results).	0 = not present; 3 = present.	Adriaens et al. 2015; Andrachuk et al. 2019; Brick et al. 2020; Joseph et al. 2020; Kamolov and Park 2019; Liew et al. 2020; Martinez et al. 2020; Pastick et al. 2020; Rowley et al. 2019; Shao et al. 2020.
^{DC} Internal Sensors (F)	App has access to utilize smartphone's thermometer, gyroscope, air humidity sensor, internal clock, barometer, and GPS to gather background data for sighting.	0 = not present; 1 = one internal sensor used; 2 = two internal sensors used; 3 = three or more internal sensors used	Andrachuk et al. 2019; Adriaens et al. 2015; Bergquist et al. 2020; Hu et al. 2019; Kvapilova et al. 2019; Reaney et al. 2019; Schade et al. 2019; Schneider 2014; Wallace et al. 2016; Wu et al. 2019.
^{DC} Large Geographical Range (G)	Data collection is not limited by the spatial focus of the app.	0 = local; 1 = state/ province wide; 2 = regional; 3 = national or international	Adriaens et al. 2015; Schade et al. 2019.
^{DC} Manual Notes/ Data Entry (H)	Allows users to input manual notes to capture observation/situational data that is not part of the formatted reporting form.	0 = not present; 3 = present.	Scott et al. 2020.
^{DC} Sighting Type/ Status Documentation (Alive/Dead and/or LifeStage) (I)	User can document the life stage, infestation stage or condition of the species observed (alive vs dead).	0 = not present; 3 = present.	Pochon et al., 2017
^{DC} Sampling Method Documentation (J)	User can indicate type of sampling method (i.e., visual observation, hook and line, snorkeling, trail camera, etc.)	0 = not present; 3 = present.	Shuster et al., 2005
^{DC} Taxonomic Range (K)	Data collection is not limited by the taxonomic focus of the app. Data can be recorded for all types of IAS.	0 = single species; 1 = single taxonomic group (eg, genus, family) ; 2= multiple, non-nested taxonomic groups; 3 = any species or taxon	Adriaens et al. 2015; Wallace et al. 2016.
^{DC} Tracks Target Over Time (L)	Allows monitoring specific target or location over time to track spread and changes to abundance or area covered by an IAS. Prompts follow up searches or reporting over time. App allows the user to report follow up visits or allows the second user/visit to validate sightings through comments on existing record	0 = not present; 3 = present.	Adriaens et al. 2015; Liew et al. 2020; Lin et al. 2020; Wallace et al. 2016.
^{ID} AI/Photo ID (M)	App identifies taxa or returns results based on photo and machine learning or uses machine learning to train algorithms to gather data.	0 = not present; 3 = present.	Hosseinpour et al. 2019; Veenhof et al. 2019.

Dimension	Definition	Rubric Scoring Scale	Relevant Literature
^{1D} IAS List/ Field Guide (N)	App includes a list of known and common invasives with pictures and information or the app includes an interactive key that allows users to choose from IAS morphological attributes and the app makes suggestions to assist with identification.	0 = not present; 3 = present.	Adriaens et al. 2015; Schade et al. 2019; Wallace et al. 2016.
^{ID} Map w/ Observations (O)	App has a map screen with points for verified IAS sightings. Ideally, this map is interactive allowing the user to access observational data by tapping the point.	0 = not present; 3 = present.	Adriaens et al. 2015; Reaney et al. 2019; Schade et al. 2019; Wallace et al. 2016.
^{ID} Photo Upload (P)	App has access to the onboard camera, and the user can take the picture and upload an image of the encountered IAS with timestamp and GPS data.	0 = not present; 3 = present.	Adriaens et al. 2015; Andrachuk et al. 2019; Schade et al. 2019; Schneider 2014; Wallace et al. 2016.
^{1D} Report Verification (Q)	Reports submitted via app are verified by trained authority before being added to the database or posted on the user interface.	0 = none or relies on user selection of species from list; 1 = expert only or AI only verification; 2 = multiple levels of verification; 3 = multiple levels of verification that are indicated on observation/record within app.	Adriaens et al. 2015; Schade et al. 2019; Wallace et al. 2016.
^{ID} Search/List Filter (R)	User interface allows searching for specific IAS taxa, IAS type or by geographic region.	0 = not present; 3 = present.	Zamberg et al. 2020.
^{ID} Unknown Reporting (S)	Previously undocumented or unidentified IAS can be reported. Allows reports of unknown species that are not listed in the app.	0 = not present; 3 = present.	Rowley et al. 2019.
RepAutomated Outlier Rejection (T)	App uses algorithms combined with internal or external sensors to exclude non-targeted data/ reports (i.e., uses GPS to exclude reports of desert species in tidal marsh).	0 = not present; 3 = present.	Kvapilova et al. 2019; Pastick et al. 2020; Wu et al. 2019.
RepIntegrates Previous Reports (U)	Data from established IAS reports/sightings and historical presence/absence data, which can be visualized by users	0 = not present; 1 = data available as a static distribution map; 2 = data integrate user observations that were previously submitted; 3 = data integrate user observations that were previously submitted plus data from other sources (e.g., government surveys)	Wallace et al. 2016.
^{Rep} Offline Reporting (V)	App stores data from reports when offline to be uploaded when the user returns to service.	0 = not present; 3 = present.	Adriaens et al. 2015; Wallace et al. 2016; Schade et al. 2019.
RepReporting Form (W)	App has a formatted reporting structure that includes all data required for EDRR/ report has required fields to standardize the data reported.	0 = not present; 3 = present.	Wallace et al. 2016.
RepReports to Central Database (X)	Reports are submitted to a national IAS database for verification and use by appropriate IAS decision- making entities.	0 = no database; 1 = Stores data that could be accessed and filtered for IAS data; 2 = App/project has dedicated IAS database; 3 = App sends data directly to central/ national or management/ agency IAS-centric database.	Adriaens et al. 2015; Schade et al. 2019; Wallace et al. 2016; Wallace et al. 2020; Zamberg et al. 2020.
^{Rep} Website/ Dashboard (Y)	Website reporting component and online frontend user dashboard to access IAS information and support the IAS app.	0 = not present; 1 = link to parent site with program or developer info only; 2 = link to parent program site w/ reporting ability; 3 = link to program site with reporting and user interface	Adriaens et al. 2015; Rowley et al. 2019; Schneider 2014; Wallace et al.,2016.
^{Eng} Device Compatibility (Z)	Available on both IOS platforms (Android/ iPhone). Users are not limited by the type of smartphone owned.	0 = not available; 1 = One IOS platform only; 3 = both major platforms	Adriaens et al. 2015; Wallace et al. 2016; Zamberg et al. 2020.
^{Eng} Feedback Feature (AA)	Users can contact admin or developer with comments or suggestions and this feature is readily accessible within the user interface.	0 = not present; 2 = buried in secondary screens; 3 = accessible from main menu	
EngGamification (AB)	App includes features to promote user engagement through competition (i.e., Leader Boards, Rankings, Quizzes, or Contests to promote use. Badges, Trophies, Unlockable Content, Tracking Progress).	0 = not present; 3 = present.	Aebli 2019; Adriaens et al. 2015; Andrachuk et al. 2019; Bayuk and Altobello 2019; Cellina et al. 2019; Szinay et al. 2020; Wallace et al. 2016.

Dimension	Definition	Rubric Scoring Scale	Relevant Literature
EngHelp Content (AC)	App includes guidance materials on how to use the app or link to Frequently Asked Questions / troubleshooting solutions for common questions and user-related concerns.	0 = not present; 2 = a help link is available to separate support page; 3 = in-app help functionalities and information are available	Adriaens et al. 2015.
^{Eng} IAS Related Title (AD)	App title implies purpose is IAS reporting.	0 = title has no mention or indication of relation to IAS; 1 = mentions an invasive species or taxon; 2 = uses the acronym IAS in the title; 3 = includes the term "invasive" or "invasion"	Wallace et al. 2016.
^{Eng} News Feed/ Notifications (AE)	In-app feature to build a sense of community. Interface where recent sightings are highlighted, and app or IAS related news can be viewed by the end user/ In app notifications from admin to user or via social media notifications.	0 = not present; 3 = present.	Joseph et al. 2020; Szinay et al. 2020.
EngSocial Media Outlet (AF)	Users can upload/post verified reports to social media platforms directly from the IAS app. Allows users to share status, trophies, number of verified reports. App allows login using social media platform login info to connect directly to users' social media outlet of choice.	0 = none; 1 = Function to share observations or keep private within the app; 2 = has a share icon that allows user to send messages or share via individual's personal social media accounts; 3 = App has dedicated social media platform accounts for posting shared observations	Adriaens et al. 2015; Andrachuk et al. 2019; Cellina et al. 2019; Joeckel and Dogruel 2020; Martinez et al. 2020; Szinay et al. 2020.
^{Eng} Updated Regularly (AG)	Developers and Admin regularly update the app to fix bugs and add new dimensions as they become available and relevant.	0 = Last updated four or more years ago; 1 = Last updated three years ago, 2 = Last updated two years ago; 3 = Updated in the last year	Castaneda et al. 2019.
^{Eng} User Account/ Login (AH)	Users can create a private unique user ID and password to protect information stored on the app. Can be set to stay logged in or prefill login info to increase ease of reporting via preferences.	0 = no user account system; 1 = users log in for every use; 2 = user ID's saved for automatic login; 3 = User ID's saved and linked to e-mail address or other contact information	Andrachuk et al., 2019; Joeckel and Dogruel, 2020; Schade et al. 2019; Wallace et al. 2016.
^{Eng} User-Centered Design (AI)	User-friendly interface. Easily navigable design. Users can easily send reports without going through a bunch of screens or submitting unnecessary information.	0 = text only; 1 = simple user interface with report form; 2 = basic and intuitive user interface; 3 = multiple-page user interface with buttons, images, visual guides, and dropdowns	Adriaens et al. 2015; Bergquist et al. 2020; Birnie et al. 2019; Scott et al. 2020; Wallace et al. 2016.

Next, we compiled a list of all free, English-language IAS reporting apps on the Google Play and Apple iTunes online app stores using a methodised search (Fig. 1). We defined IAS reporting apps as those which were specifically focused on detecting and monitoring IAS and offered user functionality to report an IAS occurrence. The final eligibility of each app was determined by the ability to report observations directly from the app, to eliminate apps that were not used for IAS reporting (e.g. apps only for identification and outreach and no reporting functionality were excluded). We also specifically included iNaturalist, Flora Incognita and Plantnet, which are recommended and commonly used for reporting invasives by some agencies, though they were not specifically designated for IAS reporting. This yielded a final sample of 41 IAS apps (Fig. 1).

We then collected additional information from online store descriptions and metadata for all apps to gain insight into regional trends, the types of agencies using app data, app publishers, download trends and temporal trends in app release and availability. Download statistics were based on Google downloads and were not available for four apps. Download statistics are reported by Google in numerical bins (i.e. ≥ 5 , \geq 100, \geq 1,000), so we calculated summary statistics as approximations. Apps were then downloaded and three reviewers independently applied our rubric to each app. Scores for each rubric dimension were determined, based upon the presence and functionality of each feature within the app and feature descriptions from mobile app stores. Each reviewer received training in how to interpret dimension scores and categories to increase consistency. Reviewers then completed the rubric for all apps independently. We assessed the concordance amongst reviewer scores to check for any major inconsistencies using Spearman's non-parametric correlation with the package Hmisc (Harrell Jr 2021) implemented in R (version 4.0.3; R Core Team 2021). We assessed reviewer concordance for all total, subtotal and dimension-specific scores and used these as the primary method of comparison and ranking among apps.

We then examined the distribution of rubric scores for individual apps, as well as within domains and individual dimensions. For domain- and dimension-specific scores, we report scores for the top apps after reporting scores for the entire sample. This allows for comparison of overall app corpus performance and top apps with respect to the idealised suite of mobile app functionalities specified in our rubric and with respect to the top-performing apps being used. Here, we present total rubric scores and domain subtotal scores as percentages and provide raw scores in parentheses.

Results

We found strong concordance between app total scores amongst all three reviewers, with pairwise Spearman's correlation values ranging from 0.72 to 0.82 (p values, all < 0.0001; Suppl. material 2: Table S2). This concordance held for individual dimension scores, with rank correlations ranging from 0.78 to 0.93 (p values, all < 0.0001; Suppl. material 2: Table S2). Total rubric scores for the 41 IAS reporting apps in our sample ranged from 27.93% to 66.35% of the maximum score (29.33 – 69.67 points; Fig. 2), with a mean of 46.64% \pm 10.88% (48.98 \pm 11.42 points; Fig. 2). Total rubric scores amongst all apps followed a near-normal distribution (Fig. 2). The top five apps were: GLEDN, ED-DMapS, IveGot1, MAEDN, Outsmart Invasive and Species. Total scores for these top-performing apps ranged from 61.90% to 66.35% of maximum (65.00 – 69.67 points) with a mean of 63.56% \pm 1.83% (66.73 \pm 1.92; Fig. 2). Raw data for all reviewed apps are available in supplemental materials (Suppl. material 3, 4: Table S3, S4).

The Data Collection Domain had 36 available points from 12 dimensions (Table 1). Scores in this domain across all apps ranged from 18.53% to 68.61% of maximum (6.67 – 24.70 points) with a mean of $39.97\% \pm 13.22\%$ (14.39 \pm 4.76; Fig. 3a), while scores for the top-performing apps ranged from 50.00% to 68.53% (18.00 – 24.67 points) with a mean of 57.78% \pm 9.04% (20.80 \pm 3.25; Fig. 3a). No apps were readily compatible with external sensors and only seven apps included documentation of the sampling method by which species were detected. Other app dimensions with relatively low implementation (< 40% of sampled apps) included documentation of Catch per Unit Effort (13 apps) and Climate and Habitat data and Absence reporting (implemented by 15 and 14 apps respectively; Fig. 3a; see Table 1 for definitions).

Apps could score a maximum of 30 points from 10 dimensions in the User Engagement domain. Observed scores ranged from 16.67% to 65.57% of available points (5.00 – 19.67 points) with a mean of 44.20% \pm 12.67% (13.26 \pm 3.80; Fig. 3d) and top scores from 47.77% to 65.57% (14.33 – 19.67) with a mean of 57.33% \pm 6.74% (17.20 \pm 2.02; Fig. 3b). Only two apps (iNaturalist and Squishr; 5% of sampled apps) included gamification functionalities and only eight (< 20%; Invasive Plants of Arizona, ERWP Invasives Reporter, PlantNet, iNaturalist, Squishr, CSMON-LIFE Observation, FeralScan Pest Mapping and NJ Invasives) included compatibility with social media (Fig. 3d).

Eighteen possible points from six dimensions were available within the Reporting domain. Observed scores ranged from 22.22% to 77.78% (4.00 - 14.00 points) with a mean of 54.65% \pm 16.13% (9.84 ± 2.90 ; Fig. 3c) and top-performing apps ranging from 70.39% to 77.78% (12.67 - 14.00) with a mean of 74.44% \pm 3.31% (13.40 ± 0.60 ; Fig. 3c). The lowest scoring dimension within this domain (with mean ~ 1 or below) across all apps was Automated outlier rejection (only iNaturalist and Report Invasives BC or ~ 5% of our sample included this feature; Fig. 3c).

The Identification domain had a maximum of 21 points from seven dimensions and observed scores ranged from 9.52% to 88.90% of maximum (2.00 – 18.67 points) with a mean of 54.70% \pm 18.23% (11.49 \pm 3.83 points; Fig. 3b) of available domain points, while top-performing apps ranged from 68.24% to 77.76% (14.33 – 16.33 points) with a mean of 73.02% \pm 4.05% (15.33 \pm 0.85; Fig. 3d). Only seven apps (Aqua Invaders; AquaHunter; Asian Hornet Watch; EDDMapS; Flora Incognita; iNaturalist; PlantNet or ~ 17% of sampled apps) implemented an artificial intelligence or machine learning approach to photo identification, which was the lowest scoring dimension in this domain of functionality.



Figure 2. Distribution of total rubric scores across all apps. Rubric scores were near-normally distributed around the mean (dashed vertical line).

We found that 28 of 41 (68.29%) sampled apps were from North America, followed by five apps from the European Union, two apps from the United Kingdom, three from Australia and one app focused on Eastern and Southern Africa (Suppl. material 3: Table S3). Data collected via 21 of 41 (51.22%) apps are sent to govern-



Figure 3. Distributions for domain subtotal scores across all reviewed apps w/ distribution of scores for each dimension within the domain **a** Data collection **b** User engagement **c** Reporting **d** Identification. Mean is indicated by the dashed vertical line for domain subtotals and by the points for dimensions.

ment agencies while nine apps were associated with NGOs, four with university programmes, two with the European Union International Invasives Programme and three apps with private entities. All five of the top-performing (i.e. highest scoring) apps were released by Bugwood LLC (University of Georgia Center for Invasive Species and Ecosystem Health, Tifton, Georgia, USA). We found that 28 apps (68.39%) allowed reporting of any taxon and did not specify a habitat type (i.e. focused on all taxa and biomes); three apps (7.32%) focused on all taxon types, but within the aquatic biome only; five apps (12.20%) focused only on plants; three apps (7.32%) focused on invertebrates only; one app focused on a single animal species (Suppl. material 3: Table S3).

The number of downloads for each app was highly right-skewed and ranged from 5 to 1,000,000 (mean = $27,600 \pm 162,000$). Only two apps (iNaturalist and Asian Hornet Watch) exceeded 100,000 downloads and two other apps had more than 10,000 downloads. Twenty-seven of the reviewed apps had 1,000 or fewer downloads (Suppl. material 3: Table S3). Four apps did not have download information available. The earliest two released apps in our review were released in 2010 and 2011, respectively, both released by Bugwood LLC and most apps released before 2015 were published by this developer.

Discussion

We synthesised existing literature in invasion biology, citizen science and mobile app development to generate a rubric describing the functionality of an idealised IAS reporting app and applied this rubric to the available, free, English language IAS reporting apps on two major app-indexing software platforms (Google Play and Apple App Store). We measured the breadth of implementation of various technologies and functionalities amongst the current corpus of IAS reporting apps to identify opportunities for improvement and innovation in mobile apps for IAS detection and monitoring.

Our review highlights the major implementation gaps and provides a formalised rubric for holistically and quantitatively assessing app design, relative to best practices and recommendations from literature and the scientific community. The repeatability and transparency of this rubric for future assessments is especially helpful given the proliferation of IAS reporting apps and their variable use lifetimes. Five of the 24 European IAS apps, reviewed by Adriaens et al. (2015), no longer existed a year later (Schade and Tsinaraki 2016). Furthermore, a careful assessment of existing app functions and re-use of knowledge is important to prevent "re-inventing the wheel" as app development continues in a piecemeal and fragmented fashion (Johnson et al. 2020). Our review also further indicates that even top IAS reporting mobile apps make use of only about 70% of the useful features and functionalities mentioned and recommended in the literature, suggesting that there is substantial room to improve the performance of IAS mobile apps, even with existing technology and knowledge.

A worthwhile caveat is that, although our rubric summarises current suggested features and best practices for IAS mobile reporting apps, an app need not receive a perfect score to be functional and effective. A hypothetical app achieving a perfect score in our rubric would be easy to use, include value-added and gaming functionalities to encourage user uptake and sustained participation, enlist multiple onboard smartphone sensors to collect ancillary information, use machine-learning functionalities for automated taxonomic identification, provide visualisations of past reports and sightings for target taxa, facilitate researcher-user interaction to reduce data collection bias and would collect data in standard formats that enabled data sharing and interoperability with other monitoring systems. This is no doubt much to ask of any developer or project, but patterns and trends in our study nonetheless point in the direction of helpful innovations for invasive species apps going forward.

Many important functionalities found in only a few sampled apps, reinforcing the notion that better use of available technology could make major contributions to IAS research and management, particularly the implementation of EDRR approaches (Lahoz-Monfort et al. 2019; Martinez et al. 2020). Notably, artificial intelligence or machine learning for photo identification was a poorly implemented functionality present in a small proportion of surveyed apps, despite its great success in driving user uptake and participation in apps like iNaturalist. This represents a major implementation gap for invasive species apps, both in that it would greatly enhance species identification and, thus, the reliability of species reports and that it might provide a functionality that increases public participation and utility to users.

The substantial variation observed amongst rubric scores for sampled apps further suggests that there is little consistency in app functionality and design between developers, a finding that echoes the observations of other researchers that IAS mobile app development is not well coordinated amongst projects (Adriaens et al. 2015; Johnson et al. 2020). Better coordination and consistency amongst IAS reporting app developers would prevent duplication of effort and accelerate innovation and implementation of useful functionalities. The availability of open-source code or templates for local agencies to develop apps, based on frameworks developed by larger and better-funded organisations, might address this need while also reducing implementation gaps.

The five top-scoring apps were set apart by including functionality for reporting absences or non-detections, unknown or unidentified taxa and detection metadata (i.e. survey method, time and effort). Rubric dimensions and corresponding mobile app functionalities that were absent from this higher-scoring subgroup are indicative of major gaps in IAS reporting app implementation and development. These also included automated quality control features like outlier flagging (to highlight potential first detections of an unreported species in an area for expert review) or rejection (for species that cannot occur in the indicated area; for example, a marine species on top of a mountain), the use of integrated mobile device sensors (e.g. thermometer, altimeter and barometer) and user-focused elements, such as social media compatibility and game features.

We observed the lowest proportional rubric performance in the Data Collection domain, which includes app features pertaining to how and what data are included in a user report. These low scores were driven by only a small number of apps allowing absence (non-detection) or abundance reporting or collecting ancillary information on habitat variables and little use of onboard sensor technology (even amongst top apps, as noted above). Absence (or non-detection) data are important in their own right for biosurveillance (i.e. confirming that a species has not reached or established in an area); such periodic verification of IAS absence or non-detection constitutes the biosurveillance needed for EDRR implementation.

Beyond monitoring (biosurveillance), absence data are also valuable as a complement to presence data, enabling much more robust statistical modelling of species distributions (Elith et al. 2017). Such models lie at the core of a proactive approach to IAS research and management because they enable spatially-explicit risk assessment and forecasting (Latombe et al. 2017; Battini et al. 2019; van Rees et al., in press). Many existing databases and reporting apps collect and accommodate presence-only data (Adriaens et al. 2015; Wallace et al. 2016). Although distribution models are constructed using presence-only data from community science data and mobile reporting apps (Kress et al. 2018; Malek et al. 2018), limitations exist compared to presence-absence distribution models. Presence-only modelling involves more statistical assumptions, with a higher likelihood of inaccurate model outputs and over-inflated model evaluation statistics due to the necessity of defining background or pseudo-absence points (Elith et al. 2017). Finally, a more systematic sampling and reporting of non-detections could greatly improve the modelling potential of IAS mobile app-generated data (Wallace et al. 2016).

Abundance and other quantitative data can, in turn, enable more explicit modelling of population behaviour, facilitating a mechanistic understanding of invasion dynamics (Latombe et al. 2017; McGeoch and Jetz 2019). Ancillary information on weather or other physical habitat characteristics can provide in-situ environmental covariates to enhance these types of modelling or even downscale spatial covariates derived from remote-sensing data (Atkinson 2013).

The onboard sensors and instrumentation available in contemporary mobile devices are increasing in diversity and quality and now include a barometer, gyroscope, accelerometer, microphone and ambient light sensor, along with gigabytes of data storage capacity (Lane et al. 2010). Bioacoustic analysis can detect and identify species in targeted and passive recordings (e.g. Platenberg et al. 2020), a process that can be increasingly automated using machine-learning approaches (Martinez et al. 2020). Camera traps, infrared cameras and other external sensors can now readily be linked to smartphones and could enhance IAS detection by allowing for the capture of images remotely and allow for the detection of cryptic species, based on thermal signatures, respectively (Martinez et al. 2020).

Reviewed apps also had generally low scores in the User Engagement domain, indicating that there is substantial room for innovation and growth in the degree and manner in which the volunteer community is engaged in IAS data collection. At the time of review, Invasive Plants of Arizona, ERWP Invasives Reporter, PlantNet, iNaturalist, Squishr, CSMON-LIFE Observation, FeralScan Pest Mapping and NJ Invasives allowed users to share observations via social media feeds. Other apps have begun to include this feature in more recent updates (e.g. Flora Incognita). Only iNaturalist and Squishr integrate leaderboards which introduce a competitive element to promote user engagement and retention. iNaturalist allows users to access and comment on reports/ confirm or dispute taxonomic identification (Pimm et al. 2015).

The success and efficacy of highly popular reporting apps like eBird (Sullivan et al. 2014) and iNaturalist show the volumes of data that can be generated where user

participation is high (e.g. > 1 million records on iNaturalist within ~ 7 years; Pimm et al. 2015); although these apps record more than just invasive species, their success is testament to what can be done with biodiversity apps when useful functionalities are provided to users. Limited implementation of such user engagement and user experience features is no doubt a major obstacle to similarly mainstreaming IAS monitoring amongst the nature-interested public. User motivation is a primary factor influencing the uptake and sustained use of mobile apps (Luna et al. 2018) and gamification (adding competitive or progress-orientated elements to the user experience) and social media connections (allowing socialisation and sharing of the activity) are effective motivators (Adriaens et al. 2015). The Budburst app (Han et al. 2011) offers badges and ranks to app users, based on their level of activity and performance in locating plant species and allows users to share their findings on the social media site Flickr. The social and aspirational motivations provided by game elements and sharing were the highestranked sources of motivations amongst surveyed contributors (Han et al. 2011); the potential for competitive 'listing', which has long been popular amongst birdwatchers, was captured in the eBird app, which is no doubt part of its enthusiastic and sustained uptake amongst users (Sullivan et al. 2014).

In addition to increasing user engagement and increasing data submissions, gamification elements could also allow better coordination between researchers and community scientists, increasing the value of individual reports for management and policy objectives (Groom et al. 2019). For example, gamification features could increase rewards for community science surveys and reporting in areas where data are more helpful for modelling or biosurveillance. These could include places with scarce data, lower visitation rates or for which repeated visits are needed for time-series analysis (Callaghan et al. 2019). Such mechanisms could be integrated with value-of-information analyses to provide spatiotemporal prioritisations and corresponding rewards to data collection that maximises value to decision-making or related statistical modelling (Dietze et al. 2018). Game elements and rewards could also encourage absence reporting to combat biases against reporting negative results or promote the validation and verification of flagged reports through follow-up visits. The latter feature was poorly represented amongst our surveyed mobile apps. Rewards, such as badges, contest rankings, personal lists or social media recognition, align well with researcher needs to increase sustained use and activity within apps, while increasing the benefit to volunteer participants. It is also worth acknowledging that there is a potential trade-off between user motivation, app usability and data quality, wherein highly effective gamification methods may provide perverse incentives to generate data that maximise rewards, even if the data themselves are not authentic (Adriaens et al. 2015).

Certain key functionalities for reporting data and automating quality control were also largely absent from our sampled apps: few apps allowed users to submit reports offline or save them for later submission and only two included automated quality control mechanisms, such as outlier rejection or flagging. Inclusion of these features could increase the quantity and quality of data from IAS reporting apps. For example, the use of machine learning to flag or eliminate false reports, could reduce the time spent on verification of submitted reports, especially where data volume exceeds the capabilities of experts or trained volunteers who are typically responsible for verification (e.g. Kress et al. 2018; Malek et al. 2018). Offline reporting capabilities are necessary to avoid spatial biases in reporting, wherein remote areas outside of typical mobile phone service are under-reported (Graham et al. 2011). Detecting novel invaders is an additional priority for EDRR risk analysis and horizon scanning (Roy et al. 2020). The ability to report an unknown species using an app provides real-time accurate data to support these processes. For example, the non-native Central American milk snake, recently discovered by community scientists in the Everglades (Brasilero 2021) would not have been reportable via many current IAS apps because it was not on their list of potential invasive taxa.

Taxonomic identification is a priority for EDRR risk assessment and eliciting the proper level of response to a detection. Photo ID and machine-learning algorithms could streamline the reporting process by cutting out the need for users to identify an IAS prior to being able to submit a report and improving report accuracy (Terry et al. 2020). For example, iNaturalist users can take a picture with their phone and are then offered possible taxa that match the uploaded image (Pimm et al. 2015). This type of functionality can increase reporting rates by reducing the burden of effort on users and provides an incentive for app use by providing reference photos and information on encountered organisms. Choe et al. (2020) developed a mobile app for identifying endangered parrots at customs checkpoints using a cognitive neural network algorithm and similar image recognition technology could help users learn to identify and report species of concern as they are encountered.

Additional data collected from app descriptions indicated that non-standardised data from many mobile apps are being sent to a plethora of non-interconnected regional or local databases (Luna et al. 2018; Johnson et al. 2020). This corroborates findings from other reviews of community-sourced IAS data (Adriaens et al. 2015; Luna et al. 2018; Johnson et al. 2020) that, although large volumes of data are being collected, their storage and management is highly fragmented and inconsistent. With few exceptions, we also found little information on the metadata and data management practices used by each app developer, echoing findings by Schade et al. (2017) in Europe that most apps are opaque with respect to data use and not amenable to data reuse. IAS occurrence databases amongst different apps and organisations are designed to meet different goals, objectives and standards (Ricciardi et al. 2000; Latombe et al. 2017), but data must ultimately be standardised and centralised to make them useful for EDRR applications at larger scales (Fuller and Nielson 2015; Reaser 2020; Wallace et al. 2020). The interoperability of community science IAS data from mobile apps and transparency by app developers as to how and where data are stored are high priorities for the field (Groom et al. 2017; Johnson et al. 2020). Apps built on the EDDMapS platform (Laforest et al. 2011), which send data to a national database, are a notable exception and a positive example for future reporting apps.

This review was limited to English language IAS reporting apps available in North America through the Apple App Store and Google Play, introducing a geographical and linguistic bias to our study sample. Further work should expand this review to apps in other languages and available in other parts of the world, although the number of existing IAS mobile apps and their users are also strongly biased towards Western Europe and North America (Johnson et al. 2020). Our data were also somewhat biased by the uneven distribution of apps amongst developers, including one developer (Bugwood LLC, n = 15 apps) which accounted for the majority of top-scoring apps.

Another caveat is the need for more publicly available information (e.g. use metrics), which could greatly facilitate further analysis of app performance and sustained use. In the absence of such data on actual use for each sampled app, this analysis was limited to their range of functionalities and basic information on number of downloads. Download statistics are, however, a flawed metric of the success or performance of an app, as effective data collection could take place on a small-scale, regional basis with relatively few downloads with an enthusiastic user base. Our inability to access user statistics or submitted data for the surveyed apps made such metrics unfeasible, but finding ways to share such information in ways that protect the privacy of users would help scientists investigate correlates of success across biodiversity apps. Despite these limitations, our results provide a useful framework for investigating the functionality of existing IAS apps and the degree to which they manifest best practices from EDRR and app development literature.

Future efforts in IAS reporting app development should emphasise better use of existing technologies, data sharing and management and interoperability and game features that can both increase user participation and coordination between researchers and app users. The development and implementation of gamification functionalities could greatly increase app uptake and sustained use and is compatible with potential mechanisms to improve the quality of data recorded by non-professionals through spatial prioritisation and reward systems. Further research on the prevalence of different motivating factors in IAS reporting app participation would support efforts to increase uptake and provide valuable guidance for marketing and gamification. Given the bellicose terminology and adversarial popular thinking around invasive species (Janovsky and Larson 2019), the optimal strategies for effective and ethical management and community science research of IAS could differ substantially from work in other systems of ecological community science for ethical reasons (e.g. Han et al. 2011). In other words, very different lessons might be learned about user motivations and how they can best be managed for citizen science applications, given that efforts are focused on detection and hopeful eradication, rather than preservation. Increasing the implementation of machine learning for image and sound recognition and, thus, the automation of detection from community science observations is also a major priority (Schade et al. 2019).

The cost of designing apps, especially ones providing the multitude of functionalities described above, is a potential obstacle to further innovation. App design and creation often cost in the order of tens to hundreds of thousands of US dollars (Odenwald 2019). The development of a generalised, customisable app template with multiple options for functionalities (including gamification and user rewards), but with consistent metadata, back-end data management and storage infrastructure could simultaneously reduce the data fragmentation amongst IAS mobile apps (Johnson et al. 2020), while also encouraging their use and uptake by regional organisations and the larger citizen science community. Such a centralised app template could be financially
supported by governments, philanthropists and a group or consortium of organisations, thus reducing the financial burden on any one group and allowing a pooling of institutional and monetary resources. Importantly, the broader economic benefits of any successful IAS reporting app with large and consistent community participation would far outweigh initial investment costs, when considering avoided ecological, agricultural and other costs.

Although our framework gave greater credit to apps with larger taxonomic ranges, regionally-focused apps may have an advantage in connecting and identifying with the interests and attitudes of local users, increasing the volume and quality of participation. For example, Aquahunter, an app produced by a county-level invasive species department in Minnesota (USA), integrates features of larger focal scale apps, such as a photo recognition tool, the ability to share an observation on Twitter/Facebook and an interactive map with observations. Such implementations of social media may be more effective at smaller scales, where users are more likely to be socially connected prior to using the app. A template model allowing customisation for regional applications would maintain these advantages, while overcoming ongoing problems of data fragmentation and lack of interoperability amongst existing apps.

Conclusions

Smartphone apps, if widely used, are amongst the most promising approaches to monitor, predict and reduce the spread of invasive alien species. Wide-spread use of mobile apps could massively increase the spatiotemporal coverage of IAS data collection, yielding new modelling insights into invasion dynamics. Future apps would attract a greater and more consistent user base with the addition of gaming functions (e.g. leaderboards, reward systems), social media connections (e.g. sharing functionalities), the ability to report absences and valuable ancillary data on surrounding habitats, survey methods and survey effort. With broader participation, more informative reporting forms and more consistent and structured data management, IAS reporting apps could make much larger contributions to Early Detection and Rapid Response efforts worldwide. This, in turn, could save local, regional and national economies millions to billions of dollars annually, while protecting valuable ecological and agricultural systems for future generations.

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Supplementary material I

Table S1. Search parameters

Authors: Leif Howard, Charles van Rees

Data type: metadata

Explanation note: Literature review search terms and filtering.

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Link: https://doi.org/10.3897/neobiota.71.79597.suppl1

Supplementary material 2

Table S2. Reviewer correlation

Authors: Leif Howard, Charles van Rees

Data type: statistics

Explanation note: Reviewer correlation results.

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Link: https://doi.org/10.3897/neobiota.71.79597.suppl2

Supplementary material 3

Table S3. App Metadata

Authors: Leif Howard, Charles van Rees

Data type: metadata

Explanation note: Metadata, total rubric scores and scores by domain for each reviewed app.

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Link: https://doi.org/10.3897/neobiota.71.79597.suppl3

Supplementary material 4

Table S4. Mean dimension scores by app

Authors: Leif Howard, Charles van Rees

Data type: metadata

Explanation note: Mean dimension scores by app.

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