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Closely related aliens lead to greater extinction risk

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ABSTRACT

Alien species are considered a major driver of extinction risk. Preventing high-impact aliens from being introduced is more necessary than ever to mitigate the current biodiversity crisis. Invasive species risk assessments look at the characteristics of potential invaders but rarely consider how different they are from the native residents that they might threaten. Therefore, we tested whether the impacts of an alien species on a native species can be predicted using the pairwise phylogenetic distance (PPD) between them. Specifically, we analysed whether the PPD of 1407 pairs of native–invasive alien plants is related to the extinction risk of the native plants. We showed that natives threatened by close alien relatives have a significantly higher extinction risk, especially on oceanic islands. This finding argues for consideration of PPD, or at least the presence of congeneric or confamilial native species, in risk assessment of potential impacts of newly introduced alien species and priorization of management of already naturalized alien species.

1. Introduction

As a consequence of globalisation and the associated cross-border exchange of goods and people, biological invasions are now one of the characterising features of the Anthropocene (Dawson et al., 2017). In addition to causing severe economic and health damages, alien species pose a significant threat to native biodiversity and are considered a common cause of recent extinctions, especially in the last century (Bellard et al., 2016). No less than ~4 % of all extant vascular plant species (van Kleunen et al., 2015) and ~ 2 % of birds are now considered to be naturalized (Blackburn et al., 2015), i.e. have established wild populations outside of their native distributions. Moreover, the number of naturalized species that are considered invasive (i.e. that spread rapidly over long distances from introduction sites and negatively impact native biodiversity) is also substantial and increasing dramatically (McGeoch et al., 2010).

Preventing high-impact alien species from being introduced is the most cost-effective way to avoid their deleterious impacts (e.g. reduced fitness, growth, abundance and diversity of native species, altered primary production) (Reaser et al., 2020). Risk assessments of alien species are essential for informing prevention and control (McGeoch et al., 2016), but we often lack complete knowledge on species' ecology and impacts. Moreover, context-dependency relating to recipient native communities and ecosystems have generated invasion impacts that vary from region to region. Therefore, the search for new readily available predictors of high-impact alien species must consider the match between characteristics of the invader and those of members of the native community to inform more effective conservation strategies.

Invasive species risk assessments are particularly important for islands. Because the endemic species richness among native plants and vertebrates on islands is ~ 9 times higher than on continents (Kier et al., 2009), the conservation value and the possible consequences of invasions on islands are comparatively large. Moreover, as islands have remained isolated for millions of years, island biota are particularly vulnerable to alien species. Indeed, biological invasions are implicated in 86 % of all recorded extinctions on islands (Bellard et al., 2016), and 100 % of recorded cases of recent plant extinctions facilitated by alien species occurred on islands (Sax and Gaines, 2008). Despite these challenges, there are also opportunities for the prevention of biological invasions because islands typically have only few entry points (e.g. air and sea ports) through which all traffic must pass. Therefore, islands are theoretically more amenable to monitoring introductions than continents (Russell et al., 2017).

Charles Darwin observed that introduced species are more likely to

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become naturalized in native communities where phylogenetically close relatives, which would provide competitive resistance, are absent (Darwin, 1859). This prediction is now referred to as 'Darwin's naturalization hypothesis' (Daehler, 2001). On the other hand, Darwin also discussed the importance of the abiotic environment and hypothesized that traits that pre-adapt alien species to their new environment are more likely to be shared with phylogenetically close native relatives (Darwin, 1859). These apparently opposing predictions have been termed 'Darwin's naturalization conundrum'. A number of studies have since searched for empirical evidence that phylogenetic relatedness between native and alien species can predict naturalization (e.g. Duncan and Williams, 2002; Malecore et al., 2019) and invasion success (e.g. Schaefer et al., 2011; Park et al., 2020), but without reaching a consensus. Recently, Omer et al. (2022) showed that the direction of the effect of phylogenetic relatedness can depend on the invasion stage, at least in Southern Africa. There, humans have, for cultivation purposes, predominantly introduced aliens that are phylogenetically distant to the native flora (and thus are likely to harbour novel traits), but the introduced ones that have close native relatives were more likely to naturalize, whereas subsequent spread was negatively associated with phylogenetic relatedness (Omer et al., 2022). So, each specific stage of invasion success must be considered individually.

Although predicting impacts of alien species is critical for invasion risk assessment, very few studies have investigated whether phylogenetic relatedness is associated with the impact of invasion on native communities. A notable exception is a study conducted by Li et al. (2015) who examined the long-term invasion dynamics of 480 vegetation plots in New Jersey, USA. The authors showed that native residents phylogenetically close to invasive alien species were more likely to be extirpated from the plots after 40 years. This finding suggests that phylogenetic relatedness can serve as a predictor positively related to local extinction risk due to invasion. However, phylogenetic patterns of community assembly, such as predicted by the hypotheses that constitute Darwin's naturalization conundrum, are often scale dependent (Procheş et al., 2008; Thuiller et al., 2010). Results obtained at fine spatial scales (e.g. local extirpation) are therefore not necessarily applicable to large-scale patterns (e.g. global extinction). Furthermore, several thresholds have to be crossed before a species that has lost one or more populations in the wild will have a complete loss of all individuals and propagules (Downey and Richardson, 2016). The extinction thresholds may be crossed more easily on islands, where the limited distributions and small populations of island endemics make them more prone to global extinction. Comparisons between the impacts of invasive species on islands and continental regions could test the context dependence of an association between phylogenetic relatedness and global extinction risk.

In this study, we evaluated whether phylogenetic relatedness can help predict impacts of alien species on native species, distinguishing species occurring on islands from those occurring on continents. We used the global extinction risk as provided in the IUCN Red List of Threatened Species as a measure of invasion impact. We calculated the pairwise phylogenetic distance (PPD) of coexisting native and alien seed plants, i.e. the total branch length of the shortest path between the two species in the phylogeny, as well as a normalized and standardised version of PPD ($\mathrm{PPD_S}$). Then we asked whether $\mathrm{PPD_S}$ is related to the extinction risk of native plants threatened by alien plants and if so, in which direction (positively or negatively). Given that competition and reproduction interference are expected to be strongest among phylogenetically similar species with shared functional traits and overlapping niches, we predict a negative relationship between $\mathrm{PPD_S}$ and extinction risk. Moreover, regarding the fundamental biotic differences between islands and continents, we predict a significantly stronger relationship between $\mathrm{PPD_S}$ and extinction risk on islands, particularly on the most isolated ones, than on continents.

2. Materials and methods

2.1. Associations between threatened native and invasive alien plants

Invasive alien species has been shown to significantly impact biodiversity. However, the direction and magnitude of change has been found to be inconsistent across alien species and invaded ecosystems (Vilà et al., 2011). These inconsistencies make it difficult to develop a unified method to quantify the impact of alien species on native species (Davis and Chew, 2017; Russell and Blackburn, 2017; Tassin et al., 2017). Many studies have quantified the impact by documenting how the spread of alien species affects native plant community diversity, e.g., species richness, phylogenetic diversity, functional diversity (Hejda et al., 2009; Cadotte et al., 2010; Hejda and de Bello, 2013; Powell et al., 2013). Unfortunately, to date, none of these impact indicators is available at a global scale (McGeoch et al., 2010). However, a database on the extinction risk of native species and the threats they face at a global scale is provided by the IUCN Red List of Threatened Species.

One of the threat categories in the IUCN Red List is invasive alien species. Due to the limited amount of specific research on threats, the nature of the threat reported in the IUCN Red List is mainly based on expert knowledge. Consequently, studies that analyse the information on threats provided by the IUCN Red List can only test correlationals. However, as we expect that the uncertainties due to the lack of dedicated research should mainly add random noise to the relationship between alien-native phylogenetic distance and alien impact, a significant correlation will most likely be an underestimate of the strength of the true relationship. So, in spite of the limitations of the threat-category assignment in the IUCN Red List, it represents a unique and underutilised resource to assess the presence of a pattern in the phylogenetic relationship linking alien species with the native ones that they impact.

Using the R package 'rredlist' (Chamberlain, 2020), we identified all terrestrial seed-plant species in the categories near threatened (NT), vulnerable (VU), endangered (EN), critically endangered (CR), extinct in the wild (EW) and extinct (EX) for which invasive alien species are cited as a threat (24 September 2021), i.e. in category number 8.1.2 'Named invasive non-native/alien species/diseases' of the IUCN Threats Classification Scheme (Salafsky et al., 2008). Plant species threatened by organisms other than seed-plants (e.g. animals, viruses) were not considered. Alien seed plants identified at the genus level (e.g. 'unspecified *Lantana*') were assigned to the most commonly reported alien species in the genus (e.g. *Lantana camara*). The same approach was applied at the family level (e.g. 'unspecified Pinaceae' was assigned to *Pinus patula*). This approach should not affect the PPD values, because the PPD of the native species is the same to all species in the invader's family, and no native species was threatened by an unspecified confamilial alien. However, alien species identified at a higher taxonomic level (e.g. 'unspecified Pinales' or 'undefined Plantae') were not considered.

Six native–alien species pairs were congeneric. According to their assessment reports, those in the genera *Centaurea*, *Centranthus*, *Hyophorbe* and *Juniperus* (two pairs) were associated with a risk of hybridization. As hybridization falls outside the scope of Darwin's naturalization conundrum, these congeneric pairs were excluded from analysis. However, as the threat of *Cirsium vulgare* to *C. vinaceum* was explicitly associated with interspecific competition and not hybridization, we kept this congeneric pair. Our final dataset had 1407 unique native–alien species pairs involving 558 native species of which 289 species are threatened by more than one alien species (51.8 %; Table S1). The dataset includes 285 alien species of which 142 species threaten more than one native species (49.8 %; Table S1).

Although islands cover only ~5 % of the world's land surface area, 70.9 % of the native plants threatened by alien plants were native to islands, and particulary to islands of the Hawaiian archipelago (50.2 %; Fig. 1). So, island floras were over-represented in the dataset. However,

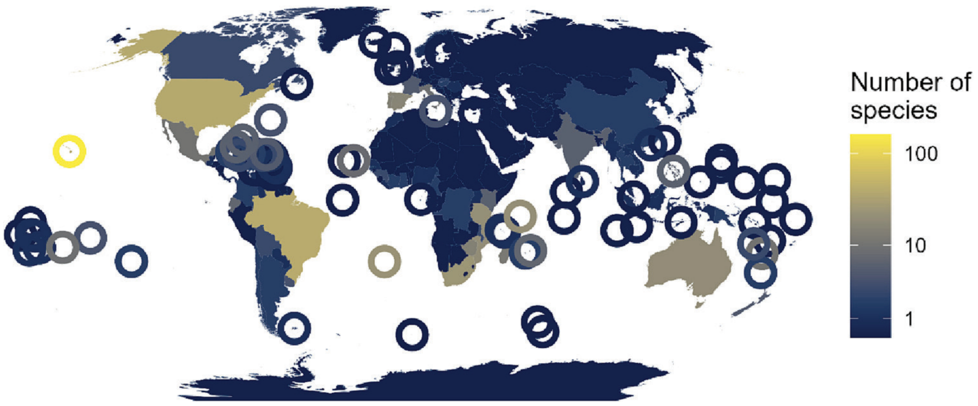

Fig. 1. Global map of the number of native seed-plant species reported as threatened by a named alien seed-plant species in the global IUCN Red List database. To facilitate readability, small island regions are represented by a circle. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

the assessment effort (i.e. the proportion of known species in a region that have currently been assessed with regard to their global threat status) was similar on islands and continents ($P = 0.746$; Wilcoxon signed rank test; Fig. S1). Therefore, the over-representation of islands appears not to be a simple reflection of island floras being more comprehensively assessed. To test whether island native floras are more susceptible to close alien relatives or to phylogenetically distant alien species than species in continental floras, we split the dataset into two: native–alien pairs occurring on islands (70.9 %) versus those occurring on continents or on both continents and islands (29.1 %). Moreover, to determine whether island isolation influences the relationship between phylogenetic distance and extinction risk, we further divided the set of native–alien pairs occurring on islands into two subsets: those occurring on oceanic islands (i.e. islands that formed over oceanic plates and were never connected to continental landmasses) and those occurring on continental islands (i.e. islands formed from ancient continental fragments or on continental shelves; Kreft et al., 2008). Furthermore, to ensure that our results were not solely driven by Hawaii, which included half of the threatened native species in our dataset, we further distinguished Hawaiian and non-Hawaiian islands.

Among the 558 native species threatened by alien species, a large majority (90 %) were also affected by other threats (e.g. overexploitation, agricultural activity, urban development, pollution). Extinction risk was found to be uncorrelated to the number of threats that affect the species ($P = 0.136$; one-way ANOVA). However, native species occurring only on islands were affected by a significantly smaller number of threats (mean = 2.1) than those occurring on continents (3.5; $P < 0.001$; Wilcoxon signed rank test) and by a different set of threats (Fig. S2). Compared to continental native species, island native species were less likely to be affected by seven of the 11 threat categories, but they were more likely to be affected by 'geological events', 'climate change and severe wheather', and by the category 'other options' (Table S2).

Because the IUCN classifies certain species as threatened based exclusively on their small geographic range, we tested whether this could affect our results by first performing the analyses on all species and then on the subset of native species for which IUCN criterion B 'geographic range size' had not been used. This subset included 42.5 % of the native species, involved in 50.0 % of the native–alien pairs. We also considered the currently observed population trend as given by the IUCN as a complementary measure of impact imposed by alien species to native ones. To do so, native species with decreasing populations (60.4 % of the native species, 71.6 % of the native-alien pairs) were compared to those whose populations are stable or increase (8.1 % of the species, 4.8 % of the pairs). The species with unknown population trends (31.5 % of the native species, 23.6 % of the native-alien pairs) were then not considered.

2.2. Phylogenetic analyses

We used a recently generated time-calibrated megatree including all families of seed plants (spermatophytes) as a backbone to generate a phylogeny for the native and alien species in our dataset (Smith and Brown, 2018). Almost half (46 %) of the species and all genera in our dataset were present in the megatree. We added the species in our dataset that were absent from the megatree to their respective genera using the scenario 3 option implemented in the R package 'V.PhyloMaker' (Jin and Qian, 2019), which binds species at the halfway point of the genus branch. We then calculated the cophenetic matrix of the phylogenetic tree using the '*cophenetic.phylo*' function of the package 'ape' and derived PPD of each native–alien pair (Paradis et al., 2004).

2.3. Statistical analyses

PPD had a non-normal distribution. Hence, it was normalized and standardised with a mean of 0 and a standard deviation of 1 (hereafter abbreviated PPD_S) using ordered quantile normalization (Beasley et al., 2009). According to the R package 'bestNormalize' (Peterson, 2021), this transformation minimized the deviations of our data from normality. Ordered quantile normalization is a rank-based procedure in which the values of a vector are mapped to their percentile, which is then mapped to the same percentile of the normal distribution.

We tested whether PPD_S decreased or increased with increasing extinction risk of the native species (our measure of impact). To this end, we converted the risk categories to an ordinal index ranging from 1 for NT species to 5 for EW and EX species (these two categories were merged into a single 'extinct' category) (Ducatez et al., 2020). Then we built a linear mixed-effect (LME) model with PPD_S as the response variable and the ordinal index of threat as an explanatory variable. In addition, identities of the native and alien species were included as random factors since some of them were included in multiple species pairs. Linear mixed-effect analyses were performed using the R package 'lme4' (Bates et al., 2015).

3. Results

Among the 1407 native–alien species pairs compiled from the IUCN Red List of Threatened Species, 51.4 % included NT, VU and EN species, 48.1 % included CR species, and only 0.5 % (i.e. 7 pairs) included EW and EX species (Table 1). The EW and EX species were all single-island endemics (Table 2). The three native plant species threatened by the largest number of alien plants were the Hawaiian endemics *Isodendrion*

Table 1
Numbers and proportions of native–alien species pairs reported in the IUCN Red List of Threatened Species in each extinction risk category of the native species. All = all species in the IUCN categories NT, VU, EN, CR and EX, NT = near threatened, VU = vulnerable, EN = endangered, CR = critically endangered and EX = extinct in the wild or completely extinct.

IUCN Red List category	Number of native–alien species pairs	Proportion of native–alien species pairs
NT	107	7.6
VU	175	12.4
EN	442	31.4
CR	676	48.1
EX	7	0.5
All	1407	100.0

Table 2
List of plant species gone extinct in the wild (EW) or completely extinct (EX) following the introduction of alien plant species according to the IUCN Red List of Threatened Species. The pairwise phylogenetic distance (PPD) and standardised pairwise phylogenetic distance (PPD$_{\mathrm{s}}$) of each native–alien pair are indicated.

Extinct species	IUCN Red List category	Native range	Alien species	PPD (My)	PPD$_{\mathrm{s}}$
Abutilon pitcairnense	EW	Pitcairn	*Lantana camara*	124	0.02
〃	〃	〃	*Syzygium jambos*	117	−0.84
Melicope macropus	EX	Kauai (HI)	*Hedychium gardnerianum*	136	0.68
〃	〃	〃	*Kalanchoe pinnata*	123	−0.55
〃	〃	〃	*Rubus argutus*	119	−0.82
〃	〃	〃	*Rubus rosifolius*	119	−0.81
Logania depressa	EX	NZ's North Island	*Pilosella officinarum*	107	−1.15

longifolium (threatened by 32 alien species), *Astelia argyrocoma* (19) and *Polyscias waimeae* (14). The three alien species that threaten the largest numbers of native plant species were *Psidium cattleianum* (threatening 86 native species), *Lantana camara* (79) and *Clidemia hirta* (68).

Pairwise phylogenetic distance ranged from 3.5 My (PPD$_{\mathrm{s}}$ 3.39) between the native *Cirsium vinaceum* and the alien *Cirsium vulgare* to 325 My (PPD$_{\mathrm{s}} > 1.66$) for 74 pairs involving an angiosperm (native in 57 pairs and alien in 17 pairs) and a gymnosperm species (Fig. 2; Table S1). Across all native-alien species pairs, PPD$_{\mathrm{s}}$ decreased with increasing extinction risk (Fig. 3; *t* 3.169, *P* 0.002, pseudo-R^2 0.622, LME). In other words, native residents co-occurring with close alien relatives were found to be more likely to be threatened with extinction. However, for the subset of native species that occur on continents, PPD$_{\mathrm{s}}$ was not significantlly related to extinction risk (*t* 0.629, *P* 0.529, pseudo-R^2 0.575, *n* 401). For native species restricted to islands, the PPD$_{\mathrm{s}}$-extinction relationship was significant, irrespective of whether extinct species were included in the analysis (*t* 2.276, *P* 0.023, pseudo-R^2 0.655, *n* 1006, LME here and herefater) or not (*t* 2.199, *P* 0.028, pseudo-R^2 0.654, *n* 999). However, separate analyses for oceanic and continental islands showed that the negative PPD$_{\mathrm{s}}$–extinction risk relationship was significant for species pairs on oceanic islands (Fig. 3; *t* 2.042, *P* 0.041, pseudo-R^2 0.636, *n* 909) but not on continental islands (*t* 0.130, *P* 0.529, pseudo-R^2 0.972, *n* 88). Furthermore, the negative PPD$_{\mathrm{s}}$-extinction risk relationship was significant on non-Hawaiian islands (*t* 1.976, *P* 0.048, pseudo-R^2 0.676, *n* 291) but not on Hawaiian islands alone (*t* 0.130, *P* 0.636, pseudo-R^2 0.593, *n* 706).

The same patterns were found when excluding species classified as threatened based exclusively on IUCN-red-list criterion B ('geographic range size') and those with unknown criteria (Fig. 3). We found a negative relationship between PPD$_{\mathrm{s}}$ and extinction risk for the full dataset including both the native species on islands and the native species on continents (*t* 4.667, *P* < 0.001, pseudo-R^2 0.792, *n* 291), and for the subset of native species that occur on islands only (*t* 3.368, *P* < 0.001, pseudo-R^2 0.811, *n* 583). However, there was no significant relationship for native species that occur on continents only (*t* 1.529, *P* 0.126, pseudo-R^2 0.711, *n* 121).

PPD$_{\mathrm{s}}$ was also significantly lower for threatened native species with decreasing populations than for the ones with stable or increasing populations, but only when species with narrow ranges and those with unknown criteria were not considered (Fig. 3; *t* 3.387, *P* < 0.001, pseudo-R^2 0.767, *n* 589). Again, this relationship was clearly driven by island species whose PPD$_{\mathrm{s}}$ decreased with increasing extinction risk

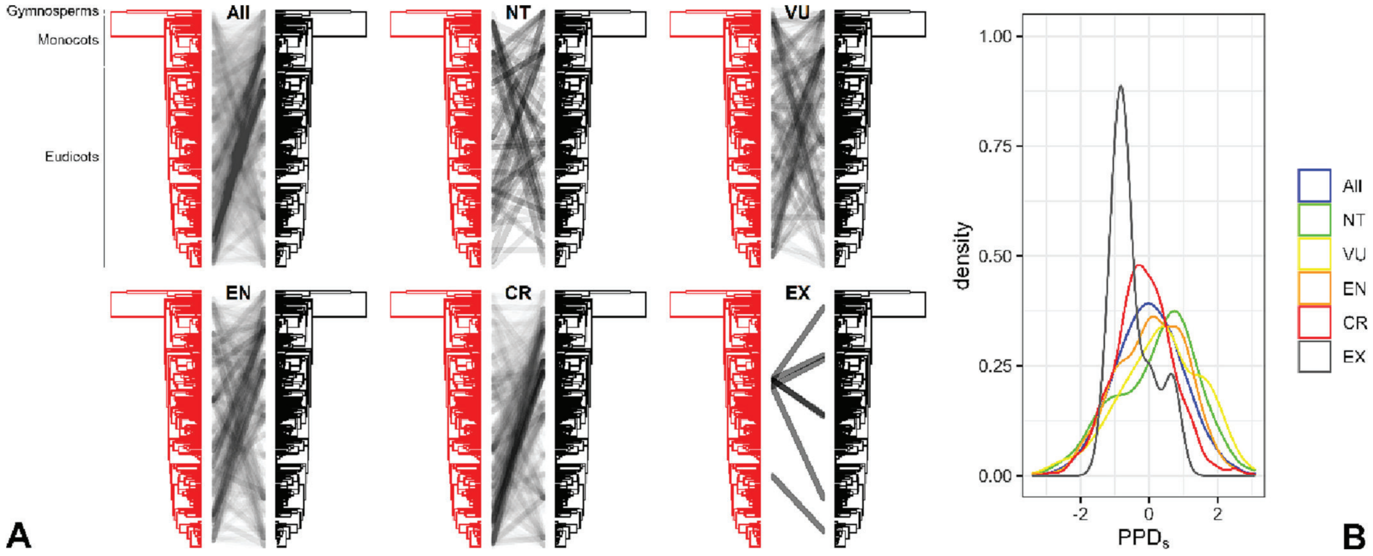

Fig. 2. Pairwise associations between threatened native (red, on the left) and invasive alien species (black, on the right) reported in the global IUCN Red List database mapped on a seed plant phylogeny (A) and density distributions of the standardised pairwise phylogenetic distances (PPD$_{\mathrm{s}}$) between native and alien species by threat status of native species (B). All = all species in the IUCN categories NT, VU, EN, CR and EX, NT = near threatened, VU = vulnerable, EN = endangered, CR = critically endangered and EX = extinct in the wild or completely extinct. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

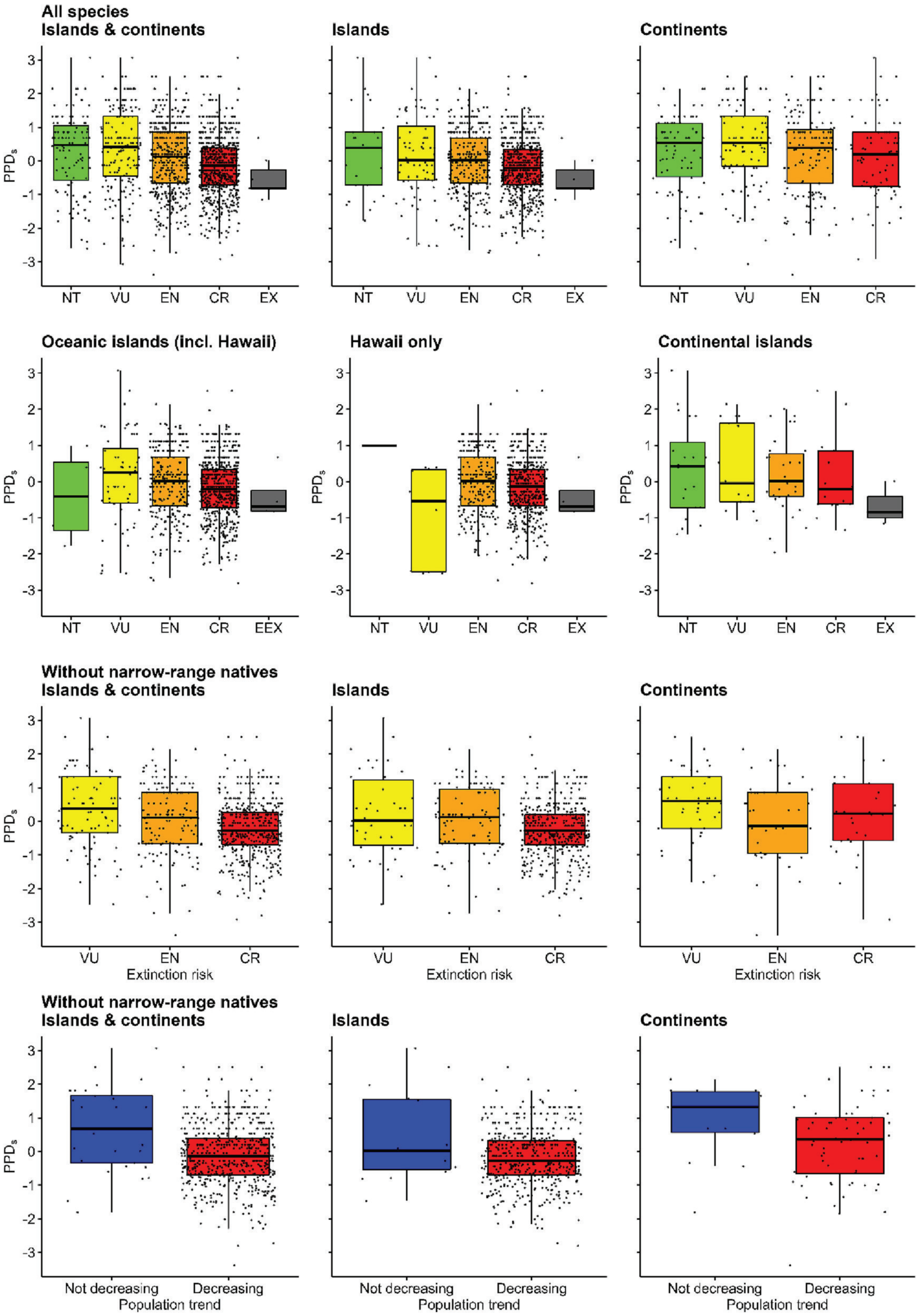

Fig. 3. Standardised phylogenetic distance (PPD$_S$), i.e. branch length between native plants reported as threatened by alien plants in the global IUCN Red List database and the associated alien plants. Native–alien pairs are sorted by threat status of native species (NT = near threatened, VU = vulnerable, EN = endangered, CR = critically endangered, EX = extinct in the wild or completely extinct) in the first three rows, and by population trend of native species ('not decreasing' includes stable and increasing populations) in the last row. All species were considered in the first two rows while only those classified as threatened based on criteria other than criterion B ('geographic range size') were considered in the third and fourth rows. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

($t = 3.844$, $P < 0.001$, pseudo-$R^2 = 0.795$, $n = 511$), while no significant relationship was found for continental species ($t = 1.076$, $P = 0.282$, pseudo-$R^2 = 0.711$, pseudo-$R^2 = 0.769$, $n = 78$).

4. Discussion

We evaluated how the impact of invasive alien seed plants on native ones is related to their phylogenetic relatedness. We showed that the extinction risk as well as the population decline of native species threatened by alien species decreased with their phylogenetic distance at the global scale. We further found that this relationship is driven by species on oceanic islands, and that the relationship was not significant for species on continents or continental islands.

Our findings thus contribute to completion of the picture of how phylogenetic distance to native residents influences the success of alien species along the different stages of the invasion process: i) the probability of introduction for cultivation is higher for distantly related species, ii) the probability of subsequent naturalization is higher for closely related introduced species, iii) the probability of spread is higher for distantly related naturalized species (Omer et al., 2022), and iv) the probability of driving native species extinct is higher for closely related invasive species (Fig. 4).

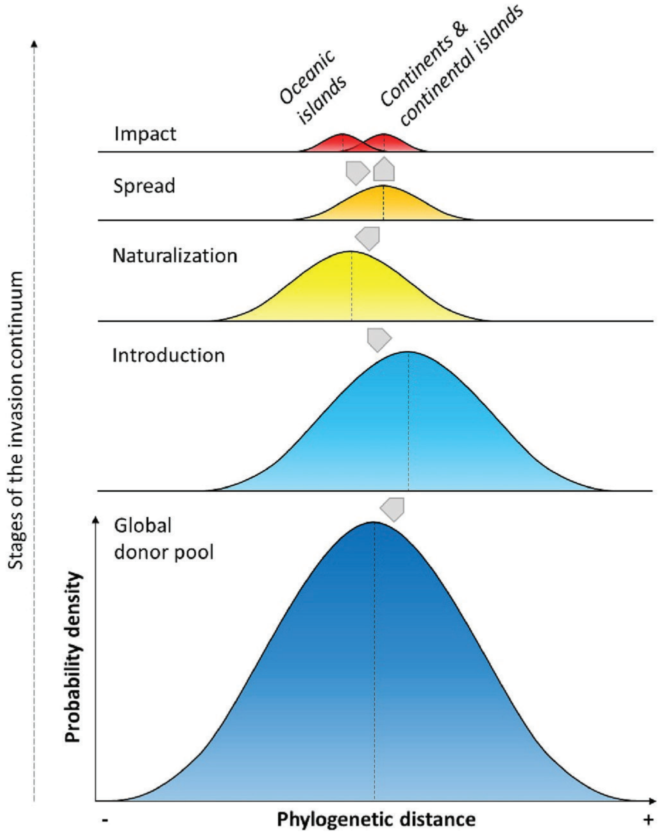

Fig. 4. Conceptual representation of how phylogenetic distance between native and alien species is expected to vary along the stages of the invasion process. Variation in the earliest stages of the invasion continuum (from blue to orange), i.e. introduction, naturalization and spread, has been the focus of several studies synthesised and developed in Omer et al. (2022). Our study of the last stage (in red), i.e. invasion impact on native species, contributes to complete the picture. We showed that the level of impact exerted by alien species on native ones increases with their phylogenetic relatedness on oceanic islands but not on continents and continental islands. The grey arrows show the direction of the change in phylogenetic distance relative to the preceding stage, the area under the curves indicates that the number of species gets smaller at each stage and warmer colour that species get more problematic. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

As species restricted to islands are likely to have small ranges, this may make them more susceptible to alien species compared to continental native species, which may benefit from greater distributions and the buffering effects of meta-population dynamics (Gillespie et al., 2008). However, the negative relationship between phylogenetic distance and the impact of aliens on natives was found both with and without species for which the threat status was based on criterion B ('geographic range size'). Our results thus indicate that narrow distributional ranges are not the sole reason for the susceptibility of island plants to alien plants.

Darwin reasoned that phylogenetically close species tend to have similar traits and therefore occupy similar ecological niches, and that niche overlap between more closely related species would hinder their coexistence (Darwin, 1859). This line of reasoning might suggest that, among other possible mechanisms, certain alien plants can outcompete phylogenetically close natives, and ultimately drive them to extinction. Interestingly, Carlquist hypothesized that selective pressure for competitive ability would be low on islands due to the low plant diversity there (Carlquist, 1974), which decreases with island isolation (MacArthur & Wilson 1967). As a consequence, competitive ability may be lower for native species restricted to islands than for continental species. For the same reason, species from oceanic islands would be more likely to be outcompeted by aliens than those from continental islands. Following the same logic, the evolutionary imbalance hypothesis predicts that successful invaders are more likely to originate from regions of high genetic potential with independent lineages of large population size, experiencing historical stability and under strong competition from other lineages (Fridley and Sax, 2014; Fristoe et al., 2023). This might also partly explain the success of alien species from continental origin on islands.

Interestingly, previous studies on native and invasive herbaceous species (Dostál, 2011), as well as on native forest trees (Kunstler et al., 2012), have shown that phylogenetic similarity does not explain competitive interactions well. This indicates that the relationship between phylogenetic distance and competition can actually be much more complex than predicted by Darwin's naturalization hypothesis. Competitive interactions are notoriously difficult to quantify, and relatedness might also influence many species interactions other than resource competition (Barton and Wong, 2019). For example, closely related alien plants could dilute pollination and dispersal services if they attract native pollinators or seed dispersers at the expense of native plants (Spotswood et al., 2012; Vanbergen et al., 2018). Moreover, it has been reported that heterospecific pollen interference (i.e. the negative effect of heterospecific pollen deposition on fruit and seed production) is larger when the alien pollen donor is closely related to the native pollen recipient (Arceo-Gómez and Ashman, 2016 but see Malecore et al., 2021). Invasive plants can also act as reservoirs of novel pathogens contributing to diseases in closely related native plants (Stewart et al., 2018). Ultimately, the impacts that species have on one another should not be driven by phylogenetic relatedness per se but by the functional traits that they share (and which are correlated with phylogeny). Future studies should aim to identify those functional traits. Furthermore, as assignment of the different threat categories in the IUCN Red List is based on expert opinions, further research is needed to assess the contributions of alien species to the threat of native species (e.g. by resource use, demographic effects in neighbourhoods; Barton and Fortunel, 2023).

The profound human alterations that most ecosystems have recently experienced may further contribute to native plant declines and alien plant performance via eutrophication, habitat alteration or loss, and climate change (Caujapé-Castells et al., 2010). Losses in pollination and seed dispersal due to the extinction of native insects and frugivorous vertebrates may also have negative effects on native plant dynamics, especially on islands (Cox and Elmqvist, 2000; Albert et al., 2022). Therefore, ecosystem modification is likely to influence interaction outcomes between native and alien species, thus challenging identification of the primary drivers of extinction risk (Barton and Shiels, 2020; Macinnis-Ng et al., 2021). Nevertheless, if alien plants reported as a threat to native plants in the IUCN Red List database were mostly passengers of anthropogenic environmental change, without directly threatening native plants, a random phylogenetic relationship between native and alien species would have been expected. Moreover, we also showed that island species were on average affected by a lower diversity of threats not related to alien species than continental species. Hence, our results suggest that alien plants are important contributors to the decline of native plants, particularly on islands, but that it is also likely that other simultaneously acting anthropogenic pressures contribute.

Showing that phylogenetic relatedness influences the ecological impacts of alien species on native ones does not reveal the underlying mechanisms. However, our findings suggest that pairwise phylogenetic distance can, to a certain extent, help predict potential impacts of alien invaders, at least on islands. Position in the phylogenetic tree is a readily available attribute and pairwise distances can be easily calculated for all members of a community, while functional traits or pairwise interactions would be extremely difficult to obtain for a large number of species within a limited period of time. Phylogenetic distance between potential alien invaders and native plants can therefore guide the identification of taxa that should be prioritized for further assessment of potential impacts. However, we found a lot of variation in phylogenetic distance within the different threat categories. This means that some distantly related species can also have strong impacts and that phylogenetic distance cannot be used as the sole basis for building lists of alien species likely to pose risks to native species.

This study is the first to document that native species co-occurring with close alien relatives are more likely to be threatened with global extinction, especially on oceanic islands. Since phylogenetic relatedness is associated with increased extinction risk in native species, this simple attribute could theoretically help predict potential impacts of alien species in conjunction with other attributes. This calls for integrating phylogenetic relatedness or at least for considering the presence of congeneric or confamilial native species in invasive species risk assessments. This could help to predict potential impacts of newly introduced alien species and to prioritize management efforts of already naturalized alien species.

CRediT authorship contribution statement

RP conceived the study, compiled and analysed the data, and wrote the manuscript with helpful input from MvK. All authors gave final approval for publication.

Declaration of competing interest

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

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References

Albert, S., Flores, O., Stahl, M., Guilhabert, F., Strasberg, D., 2022. Tree recruitment after native frugivore extinction? A field experiment to test the impact of fruit flesh persistence in a tropical oceanic island. J. Trop. Ecol. 38, 370–376.

Arceo-Gómez, G., Ashman, T.-L., 2016. Invasion status and phylogenetic relatedness predict cost of heterospecific pollen receipt: implications for native biodiversity decline. J. Ecol. 104, 1003–1008.

Barton, K.E., Fortunel, C., 2023. Island plant functional syndromes and competition with invasive species. J. Biogeogr. 50, 641–653.

Barton, K.E., Shiels, A.B., 2020. Additive and non-additive responses of seedlings to simulated herbivory and drought. Biotropica 52, 1217–1228.

Barton, K.E., Wong, A., 2019. Plant competition as a mechanism of invasion on islands: revisiting the conclusions of Kuebbing and Nunez (2016). Biotropica 51, 316–318.

Bates, D., Machler, M., Bolker, B., Walker, S., 2015. Fitting linear mixed-effects models using lme4. J. Stat. Softw. 67, 1–48.

Beasley, T.M., Erickson, S., Allison, D.B., 2009. Rank-based inverse normal transformations are increasingly used, but are they merited? Behav. Genet. 39, 580.

Bellard, C., Cassey, P., Blackburn, T.M., 2016. Alien species as a driver of recent extinctions. Biol. Lett. 12, 20150623.

Blackburn, T.M., Dyer, E., Su, S., Cassey, P., 2015. Long after the event, or four things we (should) know about bird invasions. J. Ornithol. 156, 15–25.

Cadotte, M.W., Borer, E.T., Seabloom, E.W., Cavender-Bares, J., Harpole, W.S., Cleland, E., Davies, K.F., 2010. Phylogenetic patterns differ for native and exotic plant communities across a richness gradient in Northern California. Divers. Distrib. 16, 892–901.

Carlquist, S.J., 1974. Island Biology. Columbia University Press, New York.

Caujapé-Castells, J., Tye, A., Crawford, D.J., Santos-Guerra, A., Sakai, A., Beaver, K., Lobin, W., Vincent Florens, F.B., Moura, M., Jardim, R., Gómes, I., Kueffer, C., 2010. Conservation of oceanic island floras: present and future global challenges. In: Perspectives in Plant Ecology, Evolution and Systematics, Comparative Ecological Research on Oceanic Islands, vol. 12, pp. 107–129.

Chamberlain, S., 2020. rredlist: 'IUCN' Red List Client. R package Version 0.7.0. *https://CRAN.R-project.org/package rredlist* (accessed 11 May 2022).

Cox, P.A., Elmqvist, T., 2000. Pollinator extinction in the Pacific Islands. Conserv. Biol. 14, 1237–1239.

Daehler, C.C., 2001. Darwin's naturalization hypothesis revisited. Am. Nat. 158, 324–330.

Darwin, C., 1859. On the Origin of Species by Means of Natural Selection. John Murray, London.

Davis, M.A., Chew, M.K., 2017. 'The denialists are coming!' Well, not exactly: A response to Russell and Blackburn. Trends Ecol. Evol. 32, 229–230.

Dawson, W., Moser, D., van Kleunen, M., Kreft, H., Pergl, J., Pyšek, P., Weigelt, P., Winter, M., Lenzner, B., Blackburn, T.M., Dyer, E.E., Cassey, P., Scrivens, S.L., Economo, E.P., Guénard, B., Capinha, C., Seebens, H., García-Díaz, P., Nentwig, W., García-Berthou, E., Casal, C., Mandrak, N.E., Fuller, P., Meyer, C., Essl, F., 2017. Global hotspots and correlates of alien species richness across taxonomic groups. Nat. Ecol. Evol. 1, 1–7.

Dostál, P., 2011. Plant competitive interactions and invasiveness: searching for the effects of phylogenetic relatedness and origin on competition intensity. Am. Nat. 177, 655–667.

Downey, P.O., Richardson, D.M., 2016. Alien plant invasions and native plant extinctions: a six-threshold framework. AoB PLANTS 8.

Ducatez, S., Sol, D., Sayol, F., Lefebvre, L., 2020. Behavioural plasticity is associated with reduced extinction risk in birds. Nat. Ecol. Evol. 4, 788–793.

Duncan, R.P., Williams, P.A., 2002. Darwin's naturalization hypothesis challenged. Nature 417, 608–609.

Fridley, J.D., Sax, D.F., 2014. The imbalance of nature: revisiting a Darwinian framework for invasion biology. Glob. Ecol. Biogeogr. 23, 1157–1166.

Fristoe, T.S., Bleilevens, J., Kinlock, N.L., Yang, Q., Zhang, Z., Dawson, W., Essl, F., Kreft, H., Pergl, J., Pyšek, P., Weigelt, P., Dufour-Dror, J.-M., Sennikov, A.-N., Wasowicz, P., Westergaard, K.B., van Kleunen, M., 2023. Evolutionary imbalance, human history, and the global biogeography of alien plants. Nat. Ecol. Evol. (in press).

Gillespie, R.G., Claridge, E.M., Roderick, G.K., 2008. Biodiversity dynamics in isolated island communities: interaction between natural and human-mediated processes. Mol. Ecol. 17, 45–57.

Hejda, M., de Bello, F., 2013. Impact of plant invasions on functional diversity in the vegetation of Central Europe. J. Veg. Sci. 24, 890–897.

Hejda, M., Pyšek, P., Jarošík, V., 2009. Impact of invasive plants on the species richness, diversity and composition of invaded communities. J. Ecol. 97, 393–403.

Jin, Y., Qian, H., 2019. V.PhyloMaker: an R package that can generate very large phylogenies for vascular plants. Ecography 42, 1353–1359.

Kier, G., Kreft, H., Lee, T.M., Jetz, W., Ibisch, P.L., Nowicki, C., Mutke, J., Barthlott, W., 2009. A global assessment of endemism and species richness across island and mainland regions. PNAS 106, 9322–9327.

van Kleunen, M., Dawson, W., Essl, F., Pergl, J., Winter, M., Weber, E., Kreft, H., Weigelt, P., Kartesz, J., Nishino, M., Antonova, L.A., Barcelona, J.F., Cabezas, F.J., Cárdenas, D., Cárdenas-Toro, J., Castano, N., Chacón, E., Chatelain, C., Ebel, A.L., Figueiredo, E., Fuentes, N., Groom, Q.J., Henderson, L., Inderjit, Kupriyanov, A., Masciadri, S., Meerman, J., Morozova, O., Moser, D., Nickrent, D.L., Patzelt, A., Pelser, P.B., Baptiste, M.P., Poopath, M., Schulze, M., Seebens, H., Shu, W., Thomas, J., Velayos, M., Wieringa, J.J., Pyšek, P., 2015. Global exchange and accumulation of non-native plants. Nature 525, 100–103.

Kreft, H., Jetz, W., Mutke, J., Kier, G., Barthlott, W., 2008. Global diversity of island floras from a macroecological perspective. Ecol. Lett. 11, 116–127.

Kunstler, G., Lavergne, S., Courbaud, B., Thuiller, W., Vieilledent, G., Zimmermann, N.E., Kattge, J., Coomes, D.A., 2012. Competitive interactions between forest trees are driven by species' trait hierarchy, not phylogenetic or functional similarity: implications for forest community assembly. Ecol. Lett. 15, 831–840.

Li, S., Cadotte, M.W., Meiners, S.J., Hua, Z., Shu, H., Li, J., Shu, W., 2015. The effects of phylogenetic relatedness on invasion success and impact: deconstructing Darwin's naturalisation conundrum. Ecol. Lett. 18, 1285–1292.

Macinnis-Ng, C., Mcintosh, A.R., Monks, J.M., Waipara, N., White, R.S., Boudjelas, S., Clark, C.D., Clearwater, M.J., Curran, T.J., Dickinson, K.J., Nelson, N., Perry, G.L., Richardson, S.J., Stanley, M.C., Peltzer, D.A., 2021. Climate-change impacts exacerbate conservation threats in island systems: New Zealand as a case study. Front. Ecol. Environ. 19, 216–224.

Malecore, E.M., Dawson, W., Kempel, A., Müller, G., van Kleunen, M., 2019. Nonlinear effects of phylogenetic distance on early-stage establishment of experimentally introduced plants in grassland communities. J. Ecol. 107, 781–793.

Malecore, E.M., Berthelot, S., van Kleunen, M., Razanajatovo, M., 2021. Reciprocal heterospecific pollen interference among alien and native species. In: Perspectives in Plant Ecology, Evolution and Systematics, vol. 50, p. 125610.

McGeoch, M.A., Butchart, S.H.M., Spear, D., Marais, E., Kleynhans, E.J., Symes, A., Chanson, J., Hoffmann, M., 2010. Global indicators of biological invasion: species numbers, biodiversity impact and policy responses. Divers. Distrib. 16, 95–108.

McGeoch, M.A., Genovesi, P., Bellingham, P.J., Costello, M.J., McGrannachan, C., Sheppard, A., 2016. Prioritizing species, pathways, and sites to achieve conservation targets for biological invasion. Biol. Invasions 18, 299–314.

Omer, A., Fristoe, T., Yang, Q., Razanajatovo, M., Weigelt, P., Kreft, H., Dawson, W., Dullinger, S., Essl, F., Pergl, J., Pyšek, P., van Kleunen, M., 2022. The role of phylogenetic relatedness on alien plant success depends on the stage of invasion. Nat. Plants 8, 906–914.

Paradis, E., Claude, J., Strimmer, K., 2004. APE: analyses of phylogenetics and evolution in R language. Bioinformatics 20, 289–290.

Park, D.S., Feng, X., Maitner, B.S., Ernst, K.C., Enquist, B.J., 2020. Darwin's naturalization conundrum can be explained by spatial scale. Proc. Natl. Acad. Sci. 117, 10904–10910.

Peterson, R.A., 2021. bestNormalize: Normalizing Transformation Functions Version 1.8.2. https://cran.r-project.org/web/packages/bestNormalize/index.html (accessed 11 May 2022).

Powell, K.I., Chase, J.M., Knight, T.M., 2013. Invasive plants have scale-dependent effects on diversity by altering species-area relationships. Science 339, 316–318.

Procheş, Ş., Wilson, J.R.U., Richardson, D.M., Rejmánek, M., 2008. Searching for phylogenetic pattern in biological invasions. Glob. Ecol. Biogeogr. 17, 5–10.

Reaser, J.K., Burgiel, S.W., Kirkey, J., Brantley, K.A., Veatch, S.D., Burgos-Rodríguez, J., 2020. The early detection of and rapid response (EDRR) to invasive species: a conceptual framework and federal capacities assessment. Biol. Invasions 22, 1–19.

Russell, J.C., Blackburn, T.M., 2017. The rise of invasive species denialism. Trends Ecol. Evol. 32, 3–6.

Russell, J.C., Meyer, J.-Y., Holmes, N.D., Pagad, S., 2017. Invasive alien species on islands: impacts, distribution, interactions and management. Environ. Conserv. 44, 359–370.

Salafsky, N., Salzer, D., Stattersfield, A.J., Hilton-Taylor, C., Neugarten, R., Butchart, S.H. M., Collen, B., Cox, N., Master, L.L., O'connor, S., Wilkie, D., 2008. A standard lexicon for biodiversity conservation: unified classifications of threats and actions. Conserv. Biol. 22, 897–911.

Sax, D.F., Gaines, S.D., 2008. Species invasions and extinction: the future of native biodiversity on islands. PNAS 105, 11490–11497.

Schaefer, H., Hardy, O.J., Silva, L., Barraclough, T.G., Savolainen, V., 2011. Testing Darwin's naturalization hypothesis in the Azores. Ecol. Lett. 14, 389–396.

Smith, S.A., Brown, J.W., 2018. Constructing a broadly inclusive seed plant phylogeny. Am. J. Bot. 105, 302–314.

Spotswood, E.N., Meyer, J.-Y., Bartolome, J.W., 2012. An invasive tree alters the structure of seed dispersal networks between birds and plants in French Polynesia. J. Biogeogr. 39, 2007–2020.

Stewart, J.E., Ross-Davis, A.L., Graça, R.N., Alfenas, A.C., Peever, T.L., Hanna, J.W., Uchida, J.Y., Hauff, R.D., Kadooka, C.Y., Kim, M.-S., Cannon, P.G., Namba, S., Simeto, S., Pérez, C.A., Rayamajhi, M.B., Lodge, D.J., Arguedas, M., Medel-Ortiz, R., López-Ramirez, M.A., Tennant, P., Glen, M., Machado, P.S., McTaggart, A.R., Carnegie, A.J., Klopfenstein, N.B., 2018. Genetic diversity of the myrtle rust pathogen (Austropuccinia psidii) in the Americas and Hawaii: global implications for invasive threat assessments. For. Pathol. 48, e12378.

Tassin, J., Thompson, K., Carroll, S.P., Thomas, C.D., 2017. Determining whether the impacts of introduced species are negative cannot be based solely on science: a response to Russell and Blackburn. Trends Ecol. Evol. 32, 230–231.

Thuiller, W., Gallien, L., Boulangeat, I., De Bello, F., Münkemüller, T., Roquet, C., Lavergne, S., 2010. Resolving Darwin's naturalization conundrum: a quest for evidence. Divers. Distrib. 16, 461–475.

Vanbergen, A.J., Espíndola, A., Aizen, M.A., 2018. Risks to pollinators and pollination from invasive alien species. Nat. Ecol. Evol. 2, 16–25.

Vilà, M., Espinar, J.L., Hejda, M., Hulme, P.E., Jarošík, V., Maron, J.L., Pergl, J., Schaffner, U., Sun, Y., Pyšek, P., 2011. Ecological impacts of invasive alien plants: a meta-analysis of their effects on species, communities and ecosystems. Ecol. Lett. 14, 702–708.