

## Research

### Phylogenetic composition of native island floras influences naturalized alien species richness

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## Ecography

2022: e06227

doi: 10.1111/ecog.06227

Subject Editor:

Catherine H Graham

Editor-in-Chief:

Jens-Christian Svenning

Accepted 4 July 2022



[www.ecography.org](http://www.ecography.org)

Islands are hotspots of plant endemism and are particularly vulnerable to the establishment (naturalization) of alien plant species. Naturalized species richness on islands depends on several biogeographical and socioeconomic factors, but especially on remoteness. One potential explanation for this is that the phylogenetically imbalanced composition of native floras on remote islands leaves unoccupied niche space for alien species to colonize. Here, we tested whether the species richness of naturalized seed plants on 249 islands worldwide is related to the phylogenetic composition of their native floras. To this end, we calculated standardized effect size (ses) accounting for species richness for three phylogenetic assemblage metrics (Faith's phylogenetic diversity (PD), PDses; mean pairwise distance (MPD), MPDses; and mean nearest taxon distance (MNTD), MNTDses) based on a phylogeny of 42 135 native island plant species and related them to naturalized species richness. As covariates in generalized linear mixed models, we included native species richness and biogeographical, climatic and socioeconomic island characteristics known to affect naturalized species richness. Our analysis showed an increase in naturalized species richness with increasing phylogenetic clustering of the native assemblages (i.e. native species more closely related

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than expected by chance), most prominently with MPDses. This effect, however, was smaller than the influence of native species richness and biogeographical factors, e.g. remoteness. Further, the effect of native phylogenetic structure (MPDses) on naturalized species richness was stronger for smaller islands, but this pattern was not consistent across all phylogenetic assemblage metrics. This finding suggests that the phylogenetic composition of native island floras may affect naturalized species richness, particularly on small islands where species are more likely to co-occur locally. Overall, we conclude that the composition of native island assemblages affects their susceptibility to plant naturalizations in addition to other socioeconomic and biogeographical factors, and should be considered when assessing invasion risks on islands.

Keywords: biological invasions, biotic resistance, Darwin's naturalization hypothesis, naturalized species, phylogenetic structure, species composition

## Introduction

In the era of globalization, biodiversity is threatened by intensifying anthropogenic environmental changes (Díaz et al. 2019). One driver of the endangerment and ultimately the extinction of species is the introduction and spread of alien species (Blackburn et al. 2019, IPBES 2019, Pyšek et al. 2020). Global increases in connectivity via human transportation and trade networks have led to the breakdown of biogeographical dispersal barriers, enabling the spread of species beyond their native ranges (Helmus et al. 2014, Seebens et al. 2017). Furthermore, horticulture, agriculture, forestry and other human activities facilitate the introduction and establishment of alien plant species (Reichard and White 2001, van Kleunen et al. 2020). At least 3.9% of all known vascular plants have already become naturalized outside their native ranges, a number that is likely to increase in the coming decades (van Kleunen et al. 2015). Islands are particularly prone to biological invasions, harbouring six times more alien plant species per native species than mainland regions (Essl et al. 2019), and alien species are one of the main drivers of species extinctions on islands (Bellard et al. 2016). To avoid extinctions and improve the effectiveness of alien plant management, it is essential to identify the ecological and biogeographical factors that can predict the numbers of naturalized species on islands, as larger numbers of alien species may lead to a higher likelihood that some of them become harmful (i.e. invasive; Blackburn et al. 2011).

The species richness of naturalized alien plants on islands is shaped by a combination of biogeographical, environmental and socioeconomic factors. For instance, larger island area, greater topographic heterogeneity and warmer and wetter climates potentially increase the environmental niche space, thereby increasing naturalized species richness (Kumar et al. 2006, Denslow et al. 2009, Blackburn et al. 2016). Additionally, the number of naturalized species is affected considerably by socioeconomic activities, which influence propagule and colonization pressure (Helmus et al. 2014, Moser et al. 2018, Essl et al. 2019). More specifically, measures describing human activity, such as human population density (Pyšek et al. 2010, Banks et al. 2015, Dawson et al. 2017), income (Hulme 2009) and the connectedness to global transport networks (Seebens et al. 2015) are positively related to naturalized species richness. However, these factors strongly influence both mainland regions and islands, and

they therefore do not explain the higher richness of naturalized species per native species on islands (Essl et al. 2019).

Naturalized species richness on islands is known to increase with island remoteness for several taxa (Moser et al. 2018), while native species richness generally decreases with remoteness (MacArthur and Wilson 1963, Kreft et al. 2008, Weigelt and Kreft 2013). A possible explanation for the positive effect of remoteness on naturalized species richness is the reduced biotic resistance of the relatively depauperate recipient native floras on remote islands (Elton 1958, Denslow et al. 2009). In particular, on oceanic islands that emerged from the seafloor due to volcanic activity or uplift, limited dispersal, environmental filtering and in situ speciation have led to the development of unique island floras (Weigelt et al. 2015). These floras are characterized by a disharmonic representation of taxa compared with source pools and are often phylogenetically clustered, with many species concentrated in a limited number of lineages (Carlquist 1974, Taylor et al. 2019, König et al. 2021). Native species on islands with phylogenetically clustered floras, i.e. with species more closely related to each other than expected by chance, may not fully occupy the available niche space, thereby offering lower resistance to introductions compared with more phylogenetically diverse island or mainland floras (Elton 1958, Weigelt et al. 2015, Moser et al. 2018). The expected relationship between phylogenetic clustering and naturalized species richness is therefore positive.

According to Darwin's naturalization hypothesis (Darwin 1859), alien species are less likely to naturalize in new regions if close relatives are present, assuming that they compete for similar resources (Diez et al. 2008, Ma et al. 2016). With increasing phylogenetic clustering of native island floras, the likelihood of interacting with a closely related species decreases for introduced species, and hence the number of successful alien species might increase. At the same time, the opposite relationship might be found because resource requirements and environmental adaptations shared between alien and related native species make it more likely for alien species to establish if a close relative has already managed to thrive (Marx et al. 2016, Cadotte et al. 2018). Particularly regionally, successful invaders might share adaptations with the native flora (Carboni et al. 2018) because environmental filters select for functionally more similar native and alien species (Levine and D'Antonio 1999, Ma et al. 2016). However, at smaller spatial scales (i.e. plot to landscape) where native

and alien species are more likely to interact, competition between these two groups is thought to play a greater role, often reducing naturalization success (Divišek et al. 2018, Park et al. 2020). The same rationale applies to island area. Since larger areas decrease the chance of alien species meeting a close relative, the proposed positive effect of phylogenetic clustering of the native island floras on the number of naturalized species should decrease with increasing island area.

Here, we used a global dataset of 249 island seed plant floras to examine the effects of native species richness and phylogenetic structure at the island level on the richness of successfully naturalized alien species, while controlling for biogeographical and socioeconomic drivers known to affect naturalized species richness. Based on Darwin's naturalization hypothesis (Darwin 1859) and Elton's concept of biotic resistance (Elton 1958), we hypothesized that 1) phylogenetically more clustered native island floras harbour more naturalized plant species; and 2) the effect of the phylogenetic assemblage structure of native plant species on naturalized species richness is greater for smaller islands, where closely related native and alien species are more likely to co-occur locally.

## Material and methods

### Species distribution data

We used the Global Inventory of Floras and Traits (GIFT; Weigelt et al. 2020) as the primary source for seed plant (Spermatophyta) species checklists per island. GIFT contains standardized information on the composition of 1852 island floras collated from published floras, checklists and online databases. The floristic status (native or naturalized alien) is indicated within GIFT, although the availability of this information varies among regions. Specifically, regions with information on naturalized species are considerably less common than regions with information on native species. We therefore also used the most comprehensive collection of naturalized plant species checklists, the Global Naturalized Alien Flora database, to fill data gaps (GloNAF; van Kleunen et al. 2019). GloNAF contains checklists of naturalized species, i.e. species that have established self-sustaining populations in new areas outside their native range (Richardson et al. 2000), for 1029 geographic regions (e.g. countries, islands, archipelagos) worldwide (Pyšek et al. 2017, van Kleunen et al. 2019).

We initially extracted seed plant checklists for 1108 oceanic, continental shelf and continental fragment islands with data on native species from GIFT (ver. 2.0; Supporting information for references to all checklists), 580 of which also had information on naturalized species. In addition, we extracted naturalized alien seed plant species for 223 islands from GloNAF (ver. 1.2), adding information for another 98 islands without naturalized species in GIFT. If naturalized species information for an island was available in both GIFT and GloNAF, and the absolute difference in  $\ln(\text{species number} + 1)$  between GIFT and GloNAF was  $< 0.5$ , we used data from GIFT because they come from the same resources as the

native species information. If the difference was  $\geq 0.5$  ( $n = 27$  islands), we compared the checklists manually and, in all cases except one, used the checklist with the higher naturalized species richness. The exception was La Réunion, where we decided to keep the lower value, 660 species (Strahm 1996), which we consider to be a realistic representation of naturalized species richness on that island (Baret et al. 2006). We excluded spatially overlapping island polygons, and preferred smaller single islands over island groups, leading to a total of 645 non-overlapping islands and a few small island groups with information on native and naturalized species composition.

### Phylogenetic assemblage structure

To calculate phylogenetic assemblage metrics for native island floras, we matched a megaphylogeny comprising 353 185 seed plant taxa from GenBank and Open Tree of Life and a backbone from Open Tree of Life ver. 9.1 (Smith and Brown 2018) to the overall native island species pool of 42 732 native species across 645 islands. We removed hybrids or taxa not identified to the species level from the island checklists. All infraspecific taxa were treated at the species level. A total of 34 542 native species from the checklists (80.8%) could be matched to the tree directly. An additional 7593 (17.5%) native species present in GIFT were missing from the tree and were conservatively added to their respective genera using the 'congeneric.merge' function in the R package *pez* (Pearse et al. 2015), allowing these genera to form polytomies. The resulting phylogenetic tree included 42 135 (98.6%) species. The remaining 597 species (1.4%) belonged to genera that were not present in the tree and were excluded (Supporting information).

To capture the phylogenetic structure and diversity of native island floras, we calculated three commonly used phylogenetic assemblage metrics per island: 1) unrooted Faith's phylogenetic diversity (PD) (Faith 1992); 2) mean pairwise distance (MPD); and 3) mean nearest taxon distance (MNTD) (Webb 2000, Tucker et al. 2017). PD is the sum of branch lengths and reflects richness in terms of the evolutionary history of an assemblage, while MPD and MNTD represent the branching structure of the phylogeny but are sensitive to changes at different depths of the phylogenetic tree (Mazel et al. 2016, Tucker et al. 2017). We calculated standardized effect size (ses) of the phylogenetic assemblage metrics to account for variation in species richness among islands using the R package *PhyloMeasures* (Tsirogiannis and Sandel 2017). Null models were based on all possible species combinations (equal probability) from the complete island species pool maintaining species richness of the target island (Tsirogiannis and Sandel 2017). All subsequent analyses were based on the ses of the phylogenetic assemblage metrics (hereafter PDses, MPDses and MNTDses). Positive values of PDses, MPDses and MNTDses indicate phylogenetic overdispersion and negative values indicate phylogenetic clustering compared with an assemblage expected at random based on the null models (Webb et al. 2002).

We chose a global island species pool for the null models to reflect that alien species can be introduced from anywhere (van Kleunen et al. 2015). It therefore matters if the recipient species assemblages are clustered compared to hypothetical assemblages, including species from all over the world.

As a sensitivity analysis, we calculated the phylogenetic assemblage metrics based on the phylogenetic tree, including only the 80.8% of the native island species that were originally included in the phylogeny (Smith and Brown 2018), i.e. retaining the original relationships in all genera and without manual addition of missing species leading to polytomies. The two versions of PDses, MPDses and MNTDses calculated from phylogenetic trees with or without missing species added were highly correlated ( $r \geq 0.967$ ; see Supporting information, indicating only marginal effects of introduced polytomies versus missing species on the phylogenetic assemblage metrics. Additionally, we calculated phylogenetic assemblage metrics based on a global island and mainland species pool (Supporting information). Analyses were repeated using the metrics based on the island and mainland species pool, but the metrics using the two different species pools were highly correlated (Pearson correlation  $> 0.9$ , Supporting information). Subsequent analyses were, therefore, based on the phylogenetic assemblage metrics calculated using the phylogenetic tree with missing species added and the global island species pool. To account for the fact that island assemblages might appear phylogenetically less clustered if they are compared with only climatically similar source pools, we included climatic covariates accounting for environmental similarity among islands in our statistical models (below).

Phylogenetic assemblage metrics may still be correlated with species richness after null-model standardization, particularly when filtering mechanisms are strong (Sandel 2018). This may bias analyses of phylogenetic assemblage structure along environmental gradients, as the same strength of filters can lead to different values of phylogenetic clustering for assemblages with different numbers of species. Therefore, we added a sensitivity analysis with rarefied phylogenetic assemblage metrics. Rarefied metrics were calculated as the mean of the phylogenetic assemblage metrics across 100 assemblages with a fixed number of 25 native species randomly drawn from a given island's set of species (Sandel 2018). We excluded islands with fewer than 25 species, reducing the number of islands to 238. Since we were not interested in how environmental filtering influences the phylogenetic composition of island floras, but rather how their phylogenetic composition affects naturalized species richness, we present results based on the unrarefied standardized metrics of phylogenetic diversity in the main text but mention differences among the results based on the different standardization methods (see Supporting information for additional results based on rarefied phylogenetic assemblage metrics).

### **Biogeographical and socioeconomic variables**

Along with species richness and phylogenetic structure of the native island floras, our models accounted for biogeographical

and socioeconomic factors known to affect naturalized alien plant species richness globally, and on islands in particular (Moser et al. 2018, Essl et al. 2019). Island area, environmental heterogeneity and macroclimate influence an island's carrying capacity and environmental niche space, and hence limit the number of species that can coexist (Kreft et al. 2008, Denslow et al. 2009). Island remoteness and geological history affect the likelihood of establishment directly via an island's accessibility for potential introduction agents and indirectly via the set of native species present (Moser et al. 2018). Oceanic islands emerged as new landmasses due to volcanic activity or uplift, and all native biota had to either colonize or evolve in situ (Weigelt et al. 2015). This distinguishes oceanic from continental islands, which are situated on continental shelves and have repeatedly been connected to the mainland during periods of low sea level, and from continental fragments, which have separated from their original landmass as a result of tectonic movements (Ali 2017). We included island area ( $\text{km}^2$ ; Weigelt et al. 2020), environmental heterogeneity (terrain ruggedness index, calculated based on a digital elevation model at a 15 arcsec resolution; Riley et al. 1999, USGS 2011), geological island type (oceanic, continental, fragment; Weigelt et al. 2020), and mean annual precipitation (mm) and temperature ( $^{\circ}\text{C}$ ) (Karger et al. 2017) as biogeographical variables in the models. Area was calculated based on polygons contained within GIFT, while temperature and precipitation were calculated based on raster data aggregated per spatial polygon from the respective sources. We also included geographical remoteness as distance to the closest mainland in km (Weigelt and Kreft 2013, Moser et al. 2018). As proxies for propagule and colonization pressure, we used a set of socioeconomic factors representing economic activity and connectedness of the islands to global trade networks (Helmus et al. 2014, Moser et al. 2018, Essl et al. 2019). We used a proxy for regional, island-specific gross domestic product, derived from night light emissions measured via satellite imaging, averaged per island, to represent the enhanced risk of species introductions in economically highly developed regions due to imported goods, tourism and horticulture (Hulme 2009, Ghosh et al. 2010). For islands, gross domestic product (GDP) estimated from night light emissions is more suitable because GDP is commonly available at the level of administrative units but not at the level of larger individual islands. To more directly capture the connectedness of islands to global transport networks and the accompanying risk of importing more individuals and species (Seebens et al. 2015), we additionally counted the number of seaports (World Port Index 2019) and the number of airports (Open Flights 2015) on each island.

### **Data analysis**

To test whether the species richness and phylogenetic structure of native island floras are related to the number of naturalized species, we fitted six separate generalized linear mixed models (GLMMs). As response variables, we used either the number of naturalized species or the proportion of naturalized species

in the total island flora in separate models. As fixed-effect predictor variables, we used one of the three phylogenetic assemblage metrics (in separate models), native species richness and the biogeographical and socioeconomic covariables. We only included islands larger than 1 km<sup>2</sup> (to match the resolution of the climate data), with at least one naturalized species and no missing values for any of the biogeographical and socioeconomic covariables. Due to the presence of many small islands in the initial dataset and missing values for some of the biogeographical and socioeconomic variables, the dataset retained for analyses included 249 islands with at least 15 native species (Fig. 1).

Before analysis, we transformed some of the predictor variables to reduce skewness of their distributions and meet the

model assumption of homoscedasticity of the residuals. Native species richness, island area, remoteness, terrain ruggedness index and night light-based GDP were log-transformed. Precipitation was square root-transformed. We then standardized all predictor variables to zero mean and unit variance (z-transformation) to make model coefficients comparable. To account for idiosyncratic differences in the biogeographical histories of the archipelagos and potential differences in sampling completeness of their floras, we included archipelago membership as a random intercept (Bunnefeld and Phillimore 2012). To test the hypothesis that the effect of the phylogenetic structure of native species on naturalized species richness decreases with increasing island area, we included an interaction term between the phylogenetic assemblage metric and island area. All six GLMMs were fitted using the ses of the phylogenetic assemblage metrics and those of the rarefied phylogenetic assemblage metrics. We used a Poisson error distribution for naturalized species richness and a binomial error distribution and total species richness (native + naturalized species richness) as weights for naturalized species proportion. GLMMs with naturalized species richness as the response variable exhibited only small amounts of overdispersion ( $0.29 < \text{dispersion} < 0.33$ , for all models  $p = 0.04$ ), and GLMMs with naturalized species proportion as the response variable exhibited no significant overdispersion ( $1 < \text{dispersion} < 1.01$ , for all models  $p > 0.8$ , Hartig 2019). In addition to assessing the effect sizes of all predictor variables in the full models, we identified optimized models by performing model selection based on the Akaike information criterion (AIC) (Akaike 1998; Supporting information).

Including native species richness as a predictor variable in the alien species proportion models might appear problematic because naturalized species proportions must logically decrease if native species richness increases when naturalized species richness is constant. However, the native species richness on the islands considered here is not modified directly but rather is the result of complex biogeographical and macroclimatic conditions and histories. An island with a richer native flora can potentially host more alien species, and it is possible that alien species richness differs even more strongly than native species richness when comparing across islands. We would, therefore, assume either a constant proportion of alien species with varying native species richness, while controlling for all other factors as a null expectation, or a negative effect of native species richness if richer native island floras show a higher biotic resistance against naturalized species. An alternative explanation for a negative effect of native species richness, which cannot be ruled out completely, is that naturalized species richness is lower than native species richness on species-rich islands because the global set of frequently introduced species is limited. The effect of native species richness in the proportion models should, therefore, be interpreted with caution. In any case, we consider native species richness to be an important biotic predictor variable that is needed to correctly model the effects of the other covariables (Morrissey and Ruxton 2018), particularly the phylogenetic assemblage metrics.

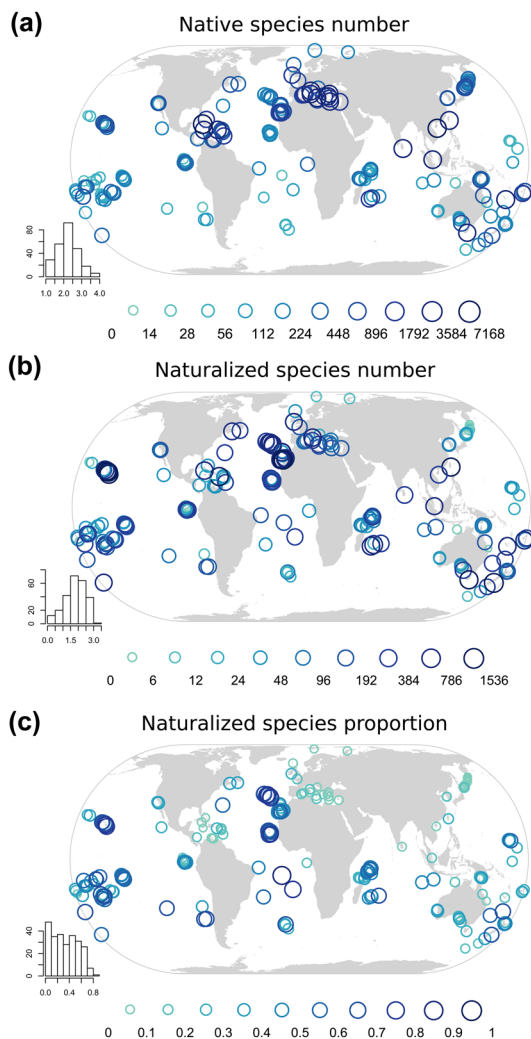


Figure 1. Numbers of native (a) and naturalized alien (b) seed plant species and the proportion of naturalized species (c) across 249 islands worldwide. Values range from low (blue) to high (red) in (a) and (b), and from 0 (light blue) to 1 (dark blue) in (c). Circle sizes are scaled according to the number of naturalized species (a) and (b) or the proportion of naturalized species out of all species (c). Numbers in the legends indicate category borders, and histograms show the frequency of values (at log-scale in (a) and (b)).

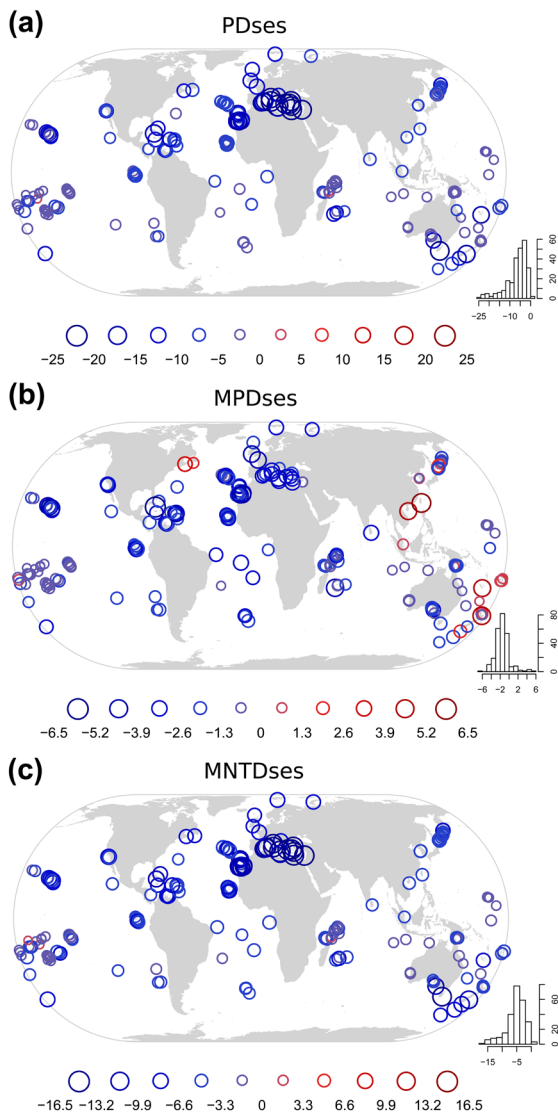


Figure 2. Standardized effect size (ses) of (a) Faith's phylogenetic diversity (PDses), (b) mean pairwise distance (MPDses) and (c) mean nearest taxon distance (MNTDses) of native plant species assemblages on 249 islands worldwide. Negative values (larger blue circles) indicate phylogenetic clustering, positive values (larger red circles) indicate overdispersion, and values close to zero (smaller circles) indicate that values match those expected based on a null model drawing from a global island species pool. Numbers in the legends indicate category borders and histograms show the frequency of values.

As the results from the GLMMs were not consistent across the different phylogenetic assemblage metrics, we fitted an additional set of statistical models. The residuals of an analogous generalized linear model (GLM), fit without archipelago affiliation as a random effect, showed significant spatial autocorrelation (global Moran's I statistic of model residuals for Faith's PD=0.22, MPD=0.23, MNTD=0.23,  $p < 0.05$ ; Dormann et al. 2013). We therefore also used GLMs with a residual autocovariate weighted by inverse geographical distance (spatial models). As we detected phylogenetic overdispersion in the Poisson GLMs with a spatial autocovariate,

we corrected the standard errors using quasi-GLM models, where the variance is given by  $\phi \times \mu$ , where  $\mu$  is the mean and  $\phi$  the dispersion parameter. Results from the spatial models were largely consistent with the GLMM results (Supporting information). We focus our results and discussion on aspects that clearly emerged across models and sensitivity analyses.

To assess multicollinearity, we calculated variance inflation factors (VIF) for all models (Fox and Monette 1992). All models showed comparatively high degrees of multicollinearity (GLMMs VIF < 10; GLMMs with rarefied phylogenetic assemblage metrics VIF < 7; spatial models VIF < 15; Supporting information). However, in multiple regression, multicollinearity does not necessarily indicate a problem or justify deletion of variables, particularly when sample sizes are large. In fact, removing collinear variables that are hypothesized to have an effect on the response variable might cause other variables to have unrealistic direct effects (Morrissey and Ruxton 2018). We therefore retained all variables with distinct hypothesized effects in our models. As the spatial models showed the highest multicollinearity, we do not present their output as the main results.

All analyses were performed using R ver. 3.6.0 (<www.r-project.org>) with the packages *lme4* (Bates et al. 2019), *MuMIn* (Barton 2019) and *spdep* (Bivand 2019). We evaluated all models using residual diagnostics implemented in the R package *DHARMA* (Hartig 2019).

## Results

Across all islands, naturalized species richness ranged from 1 (several small islands) to 1341 (South Island of New Zealand), and the proportion of naturalized species ranged from 4% (Urup Island, Kuriles) to 89% (Ascension Island in the South Atlantic) (Fig. 1; see Data availability statement for link to a table with all values). Most native island floras showed strong phylogenetic clustering (median values: Faith's PDses = -5.22; MPDses = -1.61; MNTDses = -4.84; Fig. 2). Similar patterns emerged for phylogenetic assemblage metrics calculated using the phylogenetic tree, before adding missing taxa and rarefied phylogenetic assemblage metrics, which suggest an even stronger effect of native flora clustering (Supporting information).

Overall, the results for naturalized species number and proportion across islands were similar for the different models and across phylogenetic assemblage metrics (Fig. 3; Supporting information). Naturalized species numbers and proportion increased with phylogenetic clustering of native floras across models. This effect, however, was mostly small and only statistically significant across model types for MPDses (Fig. 3 and 4; Supporting information). Phylogenetic metrics calculated with the island and mainland species pool showed the same negative effect of MPDses on naturalized species richness as the main analyses (Supporting information). Rarefied phylogenetic assemblage metrics showed slightly stronger negative effects on naturalized species richness, which were all statistically significant except

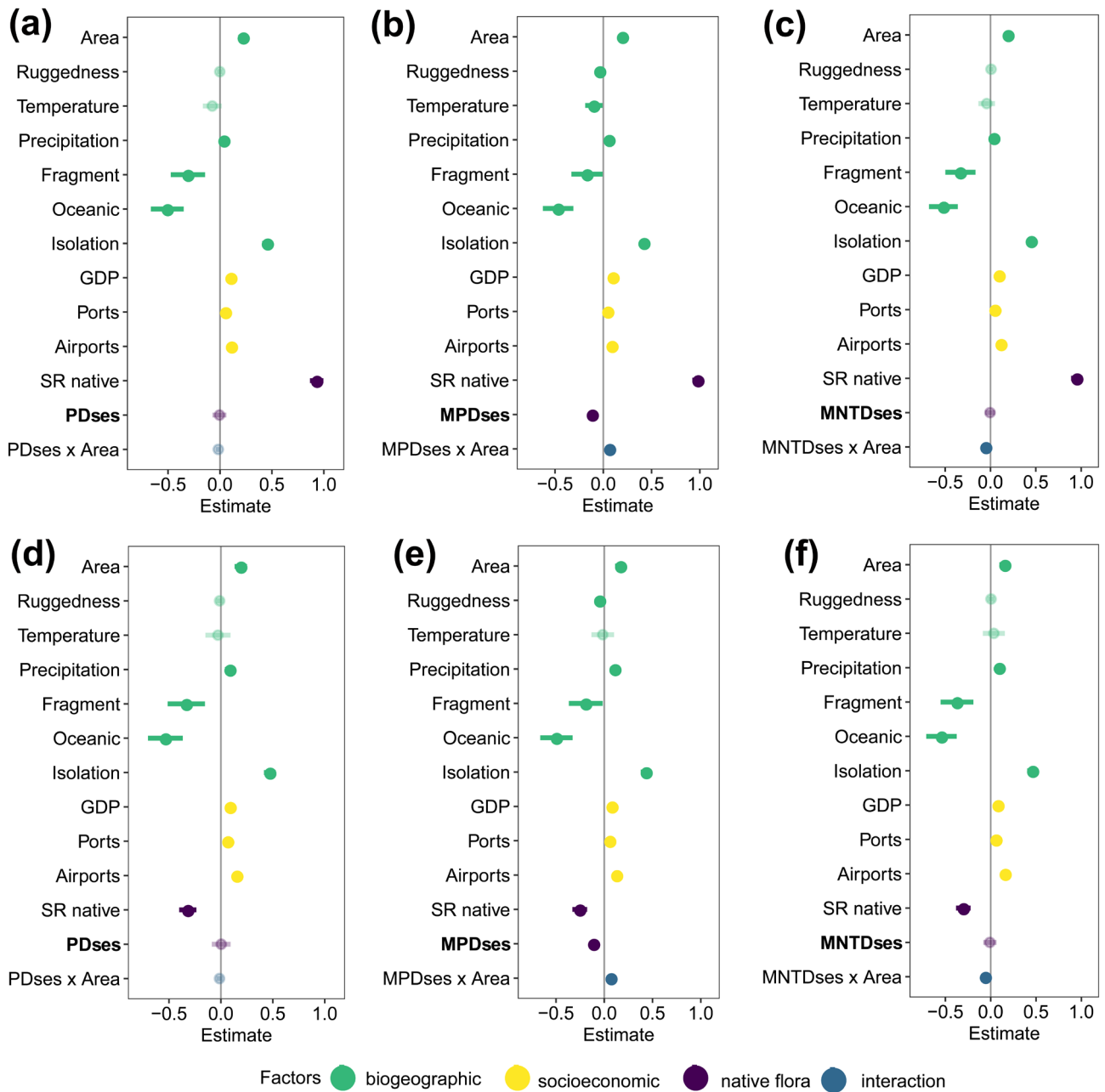


Figure 3. Effects of native species richness (SR native), phylogenetic assemblage structure (in bold), and biogeographical and socioeconomic factors on naturalized alien seed plant diversity on 249 islands worldwide. Standardized coefficient plots show the relative importance of standardized effect size of phylogenetic diversity (PDses) (a) and (d), mean pairwise distance (MPDsdes) (b) and (e) and mean nearest taxon distance (MNTDsdes) (c) and (f) in generalized linear mixed models in determining the number (a)–(c) and proportion (d)–(f) of naturalized species. Regression coefficients (points) and 95% confidence intervals (bars) have been standardized using a z-transformation. GDP refers to night light-based gross domestic product. Light colours indicate non-significant effects.

for MNTDsdes in the proportion model (Supporting information). Naturalized species number consistently increased with increasing native species richness, but the proportion of naturalized species decreased. Native species richness was included in all optimized GLMMs ( $\Delta AIC < 2$ ), and the phylogenetic assemblage metrics were included in all optimized GLMMs, apart from PDses (missing from proportion model; Supporting information).

Model results showed less consistency regarding the effect of the interaction between the phylogenetic assemblage metrics and island area. Only MPDsdes showed the expected positive interaction for both naturalized species number and proportion, indicating a stronger increase in naturalized species diversity with phylogenetic clustering on smaller islands than on larger islands (Fig. 4). This interactive effect was, however, not present in the spatial models (Supporting

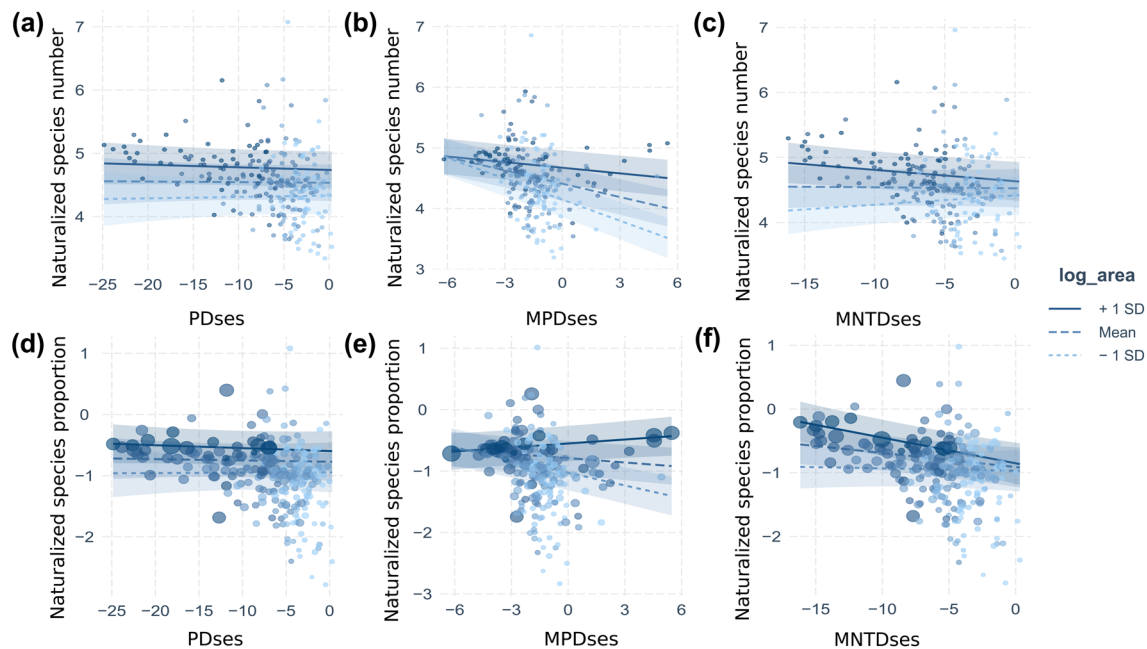


Figure 4. Interactive effects of phylogenetic assemblage structure and island area ( $\log_{10}$ ) on naturalized alien seed plant species diversity on 249 islands worldwide. Depicted are the effects of the phylogenetic assemblage metrics phylogenetic diversity standardized effect size (PDses) (a) and (d), mean pairwise distance (MPDses) (b) and (e), and mean nearest taxon distance (MNTDses) (c) and (f) on the number (a)–(c) and proportion (d)–(f) of naturalized species in a generalized linear mixed model. Points represent partial residuals and lines are predicted slopes and their respective 95% confidence intervals including native species richness and biogeographical and socioeconomic covariables. Points are also scaled according to total species richness in (d)–(f). Dashed lines represent islands with the mean area, solid lines represent +1 standard deviation (large islands), and dotted lines represent –1 standard deviation (small islands).

information) nor in models with rarefied MPDses (Supporting information).

Of the biogeographical variables considered, island remoteness and island area had the strongest positive effects on both naturalized species richness and proportion across all models. Island geology showed unexpected trends in the GLMMs, with oceanic islands and continental fragments having fewer naturalized species than continental shelf islands (Fig. 3; Supporting information). However, these results were not confirmed with the spatial models, in which geology did not have a marked effect (Supporting information). Neither topographic ruggedness nor the climatic variables had a strong effect on naturalized species numbers and proportion across models. The socioeconomic variables consistently showed positive effects on both naturalized species numbers and proportion, except for the number of ports, which had no effect in the spatial models (Supporting information). The strongest socioeconomic predictors for naturalized species numbers and proportion were the number of airports and the area-weighted night light-based GDP across all phylogenetic assemblage metrics. The fixed effects of the GLMMs, including the non-rarefied phylogenetic assemblage metrics, explained 57% of the variation in naturalized species richness (PDses, MPDses and MNTDses), but only 5% (PDses) and 4% (MPDses and MNTDses) of the variation in the proportion of naturalized species, rendering the proportion models less informative.

## Discussion

Our analysis provides empirical support for the long-standing hypothesis that the composition of native island floras affects naturalized species richness. We found an increase in naturalized alien seed plant richness with increasing clustering of the native floras on 249 islands worldwide. Even though this effect was small, and native species richness and other biogeographical factors were more important, it suggests that phylogenetically clustered island biotas are less resistant to plant naturalizations (Darwin 1859, Elton 1958).

### Native floras influence naturalized species richness

We observed phylogenetic clustering due to the presence of many closely related species, indicating compositional imbalance for the majority of native island floras (Weigelt et al. 2015). This is likely to be the result of dispersal, environmental filtering and in situ speciation, e.g. adaptive radiations. Low interspecific competition and potentially available niche space in clustered island floras may foster the establishment of alien species (Elton 1958, Cronk 1997). In fact, clustering may indicate an overlap of ecological niches between closely related species, suggesting that coexistence is driven by filtering rather than by competition (Webb 2000). Since clustered island floras are products of a limited number of colonizing lineages, entire phylogenetic groups might be missing from the native floras, decreasing the odds that close relatives of

an alien species are present (Daehler 2001). For introduced alien species, clustering of the native flora thus decreases the likelihood of facing a strong native competitor, and increases the chances of naturalization. As we accounted for climatic, socioeconomic and biogeographical covariables in our models, the observed increase in naturalized species richness with greater phylogenetic clustering (represented by MPDs) is hence in line with expectations based on both Darwin's naturalization hypothesis (Darwin 1859) and Elton's concept of biotic resistance (Elton 1958). Given that these covariables and their effect on propagule pressure are expected to have a strong influence on the introduction and establishment of alien species on islands (Moser et al. 2018, Essl et al. 2019), it is remarkable that the phylogenetic composition shows an effect on naturalized species richness, even though the observed effect is small.

MPDs was the phylogenetic assemblage metric that most consistently showed a relationship between native phylogenetic structure and naturalized species richness across the models in our study, even though this effect was secondary to native richness and biogeographical factors like isolation. MPDs is a divergence-based phylogenetic assemblage metric that reflects the distinction between all species in an assemblage at a comparatively deep branching level (Mazel et al. 2016, Tucker et al. 2017). MPDs has previously been shown to respond differently to variation in phylogenetic assemblage structure compared with PDs and MNTDs, which behave similarly to each other (Mazel et al. 2016), and our results confirm this pattern (Supporting information). MNTDs reflects divergence in relatively recent evolutionary history, while PDs reflects phylogenetic richness more than divergence patterns. Here, the generally consistent effect of MPDs might indicate that closer relatedness among all species of an assemblage, and hence the presence of larger 'phylogenetic gaps' (e.g. entire genera or even larger clades missing), is of greater importance for alien plant naturalization than the relatedness among more recently diverging lineages in native floras.

Naturalized species richness increased with native species richness more strongly than with phylogenetic assemblage metrics. This indicates that factors limiting the carrying capacity of an island constrain both native and naturalized species richness (Stohlgren et al. 2003, Kreft et al. 2008). The effect of these limiting factors on native and alien species could be either direct, e.g. by fostering competition for limited resources; or indirectly, e.g. by climatic conditions similarly influencing native and alien species. The decrease in the naturalized species proportion with increasing native species richness, however, suggests that the richness of native floras also has a direct negative effect on the establishment of new alien species. When holding macroclimate and other island biogeographical island characteristics constant, native assemblages with fewer species and hence more potentially empty niche space show a lower biotic resistance against invaders (Fig. 3; Elton 1958, Bennett 2019). Consequently, we conclude that biotic resistance and niche saturation affect the establishment of alien species in island floras at a global scale via the number of native species present and their phylogenetic relationships.

## Abiotic drivers of naturalized species richness

Our models indicate a positive effect of island remoteness on naturalized species richness, even after accounting for native species richness and phylogenetic assemblage structure. This positive effect of remoteness is in line with recent findings (Pyšek et al. 2017, Moser et al. 2018), suggesting that it may be explained by the impoverished and phylogenetically imbalanced native floras of isolated islands. When directly accounting for these factors by including native species richness and phylogenetic structure in models, the effect of remoteness as such should diminish. The fact that remoteness was still important in our models, therefore, indicates that the phylogenetic assemblage metrics used here might not fully account for all factors related to remoteness. For instance, certain herbivores may be missing or underrepresented on more remote islands, promoting alien species establishment (Funk and Throop 2010). Further, the approach of regressing phylogenetic assemblage metrics at the island level with naturalized species richness might be limited; assessing the relatedness among naturalized alien and native species at the local scale may be a way to address the effect of phylogenetic relatedness on alien species establishment more directly (Marx et al. 2016).

Regarding socioeconomic factors, night light-based GDP and the number of airports consistently increased naturalized species richness, although these effects were small compared with biogeographical factors and native species richness. A possible explanation for the only moderate effects of socioeconomic factors is that we only used indirect measures of propagule and colonization pressure (Blackburn et al. 2016). Moreover, the number of ports or airports does not capture the intensity of traffic as well as the size of the port and socioeconomic factors might have a higher impact on the richness of invasive alien species, as opposed to naturalized species (Essl et al. 2019). Aside from these considerations, the characteristics of the native floras and biogeographical factors, such as area and remoteness, may indeed be more important than previously anticipated for understanding plant naturalizations on remote oceanic islands.

## Effect of spatial scale

We found a positive effect of native phylogenetic clustering on naturalized species richness, even though we investigated entire island assemblages, in which individual species do not necessarily co-occur and compete for resources, rather than local communities where this positive effect would be expected to be strongest (Ma et al. 2016, Park et al. 2020). In fact, Darwin's naturalization conundrum predicts both phylogenetic dissimilarity among native and alien species, resulting from competition between close relatives, and phylogenetic similarity, resulting from environmental filtering. When both competition and environmental filtering act simultaneously, this may result in the absence of establishment or in non-linear patterns of establishment success with increasing relatedness between alien and native species (Malecore et al. 2019). The positive interaction between MPDs and island

area found here hence suggests that both sides of Darwin's naturalization conundrum operate simultaneously in shaping patterns of alien species naturalization on islands. On smaller islands, where close relatives are more likely to co-occur, our findings indicate that phylogenetic clustering promotes naturalized species richness, possibly due to the absence of closely related competitors (Carboni et al. 2013). On larger islands, where close relatives are less likely to co-occur locally, we found this effect to be smaller, suggesting that environmental filtering for particular trait values that facilitate the naturalization of closely related species might be more important in that setting (Thuiller et al. 2010, Marx et al. 2016).

Notably, the interaction between phylogenetic clustering and island area was not consistently supported across all model types and phylogenetic assemblage metrics. One potential explanation for this mixed signal is that the smallest islands included in the analyses ( $\sim 1 \text{ km}^2$ ) might still have been too large to capture interactions between native and naturalized species. An alternative explanation is that abiotic conditions mediate biotic interactions like competition (González-Moreno et al. 2014, Craven et al. 2019).

### A call for a functional approach

The concept of biotic resistance relies on the assumption that taxonomically or phylogenetically diverse assemblages are also functionally diverse and fill more available niche space as a result of high interspecific competition. Similarly, Darwin's naturalization hypothesis relies on the assumption that phylogenetically close species share similar functional traits and, therefore, occupy similar potential ecological niches. However, phylogenetically closely related species are not necessarily functionally similar (Marx et al. 2016), particularly on islands, where radiations frequently result in functionally different but related species. Adaptive radiations increase phylogenetic clustering but may also fill gaps in the niche space of an island (Givnish 2010), leading to higher functional diversity and possibly greater biotic resistance. On the contrary, radiations are not always adaptive, and the potential for a small number of lineages to evolve into an unoccupied niche space within a given amount of time is limited (Czekanski-Moir and Rundell 2019). In addition, evolution under relaxed competitive conditions potentially leads to island species being less competitive compared with their mainland counterparts. Using functional traits to characterize a flora's functional composition would be a promising step forward in understanding how the composition of native island floras affects their resistance against alien species and whether diversification on islands leads to higher or lower biotic resistance. Our finding that the phylogenetic structure of native species, represented by mean pairwise distance (MPDs), influences naturalized species richness suggests that the phylogenetic structure on these islands represents at least parts of the functional structure of the assemblages, particularly those conserved in more ancestral relationships of the phylogeny. As more information on the functional traits of island plants becomes available, the effects of functional

assemblage structure and functional similarity of native and alien species on alien species establishment could be investigated more explicitly to deepen our understanding of the susceptibility of island floras to naturalization.

### Conclusions

Our results indicate that the phylogenetic structure of native seed plant assemblages on islands influences their resistance to the naturalization of alien plant species, even at the island scale. This highlights the importance of information on native assemblage composition for understanding the introduction and naturalization of alien species. While the phylogenetic structure of native assemblages can explain at least part of the observed variation in naturalized species richness on islands worldwide, the processes driving its effect on the establishment success of alien species remain elusive. As a way forward to identify these processes, we suggest assessing the phylogenetic and functional similarity among alien and native species across spatial scales, from the local to the island level.

*Acknowledgement* – We thank M. Dawes for language editing.

*Funding* – PP and JP were supported by EXPRO grant no. 19-28807X (Czech Science Foundation) and long-term research development project RVO 67985939 (Czech Academy of Sciences). MvK acknowledges funding from the German Research Foundation DFG (project no. 264740629). FE and BL appreciate funding from the Austrian Science Foundation FWF (grant no. I 3757-B29). CM acknowledges funding from the Volkswagen Foundation through a Freigeist Fellowship (A118199). CM and MW acknowledge funding from iDiv through the German Research Foundation (DFG–FZT 118, grant no. 202548816). HK acknowledges funding from the Deutsche Forschungsgemeinschaft in the context of the research unit FOR 2716 DynaCom (project no. 379417748). JS acknowledges funding from the Deutsche Forschungsgemeinschaft through a Research Fellowship (grant no. SCHR 1672/1-1). HEM was supported by an NSF Graduate Research Fellowship (grant no. DGE-1144254), an NSF Graduate Research Opportunities Worldwide (GROW) Fellowship, and a Chateaubriand Fellowship. DC received funding from the Agencia Nacional de Investigación y Desarrollo (Chile; FONDECYT Regular grant no. 1201347). We acknowledge support by the Open Access Publication Funds of the Göttingen University.

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### Transparent peer review

The peer review history for this article is available at <<https://publons.com/publon/10.1111/ecog.06227>>.

### Data availability statement

Data to replicate the statistical analyses are available from the dryad digital repository (<https://datadryad.org/stash/dataset/doi:10.5061/dryad.h44j0zpp5>). Species occurrence lists for alien species can be retrieved from the GloNAF database (van Kleunen et al. 2019). Original checklists of native species are available via the GIFT database (Weigelt et al. 2020). An R package to retrieve data from GIFT is under development.

### Supporting information

The Supporting information associated with this article is available with the online version.

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