Title: Interacting abiotic and biotic drivers shape woody invasions across Hawaiian forests

Running head: Alien woody invasions across Hawaii

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Abstract

The same features that generate biodiversity patterns across and within oceanic islands over evolutionary time – interactions between isolation, area, and heterogeneity – also influence their vulnerability to biological invasions. Here, we identify the factors that shape the richness and abundance of woody aliens in forest communities across the Hawaiian archipelago, and assess the relative importance of abiotic, biotic, and anthropogenic factors and their interactions on the establishment and dominance of woody alien species. Using a database of 460 forest plots distributed across the six major Hawaiian islands, we examine variation in *i*) relative alien species richness and abundance as a function of multiple factors (e.g., temperature, aridity, soil age, and the human influence index) and *ii*) establishment and dominance of alien species as a function of abiotic and anthropogenic factors, as well as phylogenetic and trait distinctiveness. We found that relative alien species richness and abundance were higher in areas where temperature was high and aridity low. Gradients in temperature, aridity, soil age, and human influence also modulated the importance of biotic factors in determining establishment of alien species. In contrast, whether these alien species could become locally dominant was not strongly influenced by abiotic or biotic factors, or their interactions. Our results suggest that environmental filtering mediates the strength of biotic filtering in determining where woody aliens are able to colonize and establish on these oceanic islands, but not whether they become dominant. The strong context dependence of multi-species invasions highlights the complexity of developing management strategies to mitigate the biodiversity and ecosystem impacts of biological invasions.

Keywords: biological invasions, context dependency, oceanic islands, Darwin's Naturalisation Hypothesis, functional traits

Introduction

On just 3 to 5% of the world's area, islands harbor a disproportionate amount (15% to 20%) of its known plant diversity (Tershy *et al.*, 2015; Whittaker *et al.*, 2017). Especially on oceanic islands, this biodiversity has emerged as a result of isolation and dynamic geophysical processes that influence island area and environmental heterogeneity (Gillespie, 2016; Schluter & Pennell, 2017; Whittaker *et al.*, 2017). However, these isolated islands are also highly susceptible to invasions by alien species (Moser *et al.*, 2018), which can alter community structure, displace endemic species, and threaten the provisioning of vital ecosystem services (Vitousek *et al.*, 1987; Sax & Gaines, 2008; Vilà *et al.*, 2011; Simberloff *et al.*, 2013; Castro-Díez *et al.*, 2019). There is no sign that the number of alien species that are successfully establishing is reaching equilibrium (Seebens *et al.*, 2017), suggesting that without prevention and management, new alien species will continue to arrive and disrupt island ecosystems. It is therefore critical to deepen current understanding of the factors that allow alien species to successfully establish and come to dominate in island ecosystems (Mack *et al.*, 2000; Pyšek *et al.*, 2010; Blackburn *et al.*, 2011; Dawson *et al.*, 2017).

Across and within oceanic islands, abiotic, biogeographical, and anthropogenic factors jointly determine where biological invasions occur. Hot spots of alien plant species are typically found on islands that are isolated, large, and topographically complex, as well as on islands with high human impacts (Sax & Gaines, 2008; Denslow *et al.*, 2009; Dawson *et al.*, 2017; Moser *et al.*, 2018; Wohlwend *et al.*, 2021). Within islands, richness and abundance of alien plants are greater at lower elevations in locations with high precipitation (Ibanez *et al.*, 2019) and where human population density is higher and land use is more intense (Denslow, 2003). However, community-level patterns of biological invasions often fail to provide mechanistic insights, in part because they overlook functional and phylogenetic differences between native and alien species (biotic filtering). A growing body of literature has emerged to fill this gap, which also highlights that biological invasions are multi-faceted processes most appropriately addressed by jointly considering multiple potential mechanisms, including environmental and biotic

filtering, propagule pressure, and human impacts (Catford *et al.*, 2009; Gallien & Carboni, 2017; Pearson *et al.*, 2018; Bennett, 2019).

Environmental filtering structures communities by influencing the establishment of species in a given place (Kraft *et al.*, 2015), via their traits that determine tolerance of abiotic factors (e.g. water availability, soil pH). This environmental filtering can result in the co-occurrence of species with similar traits. In the context of biological invasions, environmental filtering is frequently framed in terms of the pre-adaptation hypothesis (Cadotte *et al.*, 2018; Bennett, 2019), which posits that alien species should be sufficiently similar to native species in their traits or evolutionary history to allow them to establish viable populations. Support for this hypothesis is particularly expected in environments with high abiotic stress such as those with high aridity, cold temperatures, or young soils (Cornwell & Ackerly, 2009). Yet empty niche space on islands, created by the rarity and non-randomness of colonizations (Losos & Ricklefs, 2009; Carvajal-Endara *et al.*, 2017; Taylor *et al.*, 2019), may occur even in environments with high abiotic stress. For example, alien plant species were more different from native plant species in warm, arid environments on the lower slopes of Mauna Loa, Hawai'i than in cooler, wet environments, suggesting that more unfilled niche space was available in environments with greater abiotic stress (Henn *et al.*, 2019). Empirical evidence in support of the pre-adaptation hypothesis on island ecosystems (and in general) is therefore quite mixed (Schaefer *et al.*, 2011; Ma *et al.*, 2016; Marx *et al.*, 2016; Cadotte *et al.*, 2018).

On the other hand, biotic filtering can promote the co-occurrence of ecologically dissimilar species by minimizing competition (Kraft *et al.*, 2008; Kraft & Ackerly, 2010). However, these species may still not completely fill available niche space (Ashby *et al.*, 2017). For example, dispersal limitation might result in the absence of particular trait syndromes on oceanic islands (Taylor *et al.*, 2019; König *et al.*, 2021). This leaves niche space available for colonization by radiating lineages, such as the Hawaiian silversword alliance (Givnish *et al.*, 2009) and the *Periploca laevigata* complex in the Canary Islands (García-Verdugo *et al.*, 2020), or by alien species. Assuming that alien species can persist in the new

environment, Darwin's naturalisation conundrum (Darwin, 1859) predicts that alien species are more likely to establish in native communities in which they are sufficiently distinct from native species, either phylogenetically or functionally, to avoid competition by exploiting unused niche space (Cadotte *et al.*, 2018; Bennett, 2019). A meta-analysis using phylogenetic relatedness as a surrogate for niche differences found that biotic filtering influences the establishment of alien species at local spatial scales in a manner consistent with Darwin's naturalisation hypothesis (Ma et al., 2016). While phylogenetic dissimilarity is a reliable proxy for detecting differences in how species occupy multidimensional niche space (Tucker *et al.*, 2018), differences in traits associated with competition and resource use (Kunstler *et al.*, 2012; Díaz *et al.*, 2016) provide a more direct means for understanding the relationship between ecological similarity and invasion (Marx *et al.*, 2016; Carboni *et al.*, 2018; Levin *et al.*, 2020; van der Sande *et al.*, 2020).

There is a growing appreciation that biological invasions are context dependent, as they are frequently the result of interactions among abiotic, biotic, and anthropogenic factors (Ricciardi *et al.*, 2013; Pearson *et al.*, 2018; Sapsford *et al.*, 2020; Catford *et al.*, 2022). Along abiotic gradients, native communities are expected to be less invaded and alien plant species more similar to native communities where abiotic stress is high, while native communities are expected to be more invaded and alien species less similar to native communities where abiotic stress is low (Perelman *et al.*, 2007; Tecco *et al.*, 2010; Gross *et al.*, 2013; González-Moreno *et al.*, 2014; Sapsford *et al.*, 2020). Anthropogenic disturbances (or habitats) may also generate context dependent invasion outcomes (González-Moreno *et al.*, 2014; Jauni *et al.*, 2015) by favoring non-native species with disturbance-tolerant trait values (Richardson & Rejmánek, 2011; Ni *et al.*, 2021; Sperry *et al.*, 2021). Particularly on oceanic islands, island age (or soil age) - which typically has been used to address the macroevolutionary processes underlying native biodiversity patterns (Emerson, 2002; Gillespie, 2016; Whittaker *et al.*, 2017) - may further strengthen the context dependency of biological invasions by differentially shaping the biodiversity patterns for native (Whittaker *et al.*, 2008; Craven *et al.*, 2019) and alien species (Leihy *et al.*, 2018). Older islands with high native biodiversity may be more resistant to invasion ("Eltonian biotic resistance"; Fridley *et al.*, 2007),

yet there is growing evidence that more diverse native plant communities can also be more vulnerable to invasion (Stohlgren *et al.*, 2003; Qian & Sandel, 2022), possibly due to empty niche space, high habitat heterogeneity or greater resource availability. Absent disturbances, alien species are more apt to establish on older soils that usually have greater resource availability than on younger soils, which tend to be more nutrient poor (Aplet *et al.*, 1998; Hughes & Denslow, 2005; Zimmerman *et al.*, 2008). This suggests that older soils may favor stronger biotic filtering, while younger soils may act as an environmental filter of biological invasions. However, the extent to which soil age and anthropogenic and abiotic drivers underpin context-dependent biological invasions across oceanic islands remains uncertain.

Oceanic archipelagos, such as the Hawaiian islands, are frequently used as natural laboratories to disentangle ecological and evolutionary drivers of native biodiversity patterns (Emerson, 2002; Gillespie, 2016; Craven *et al.*, 2019), yet also provide a compelling template for understanding biological invasions because of their recency and severity (Barton *et al.*, 2021; Wohlwend *et al.*, 2021). Here, we examine patterns of invasions of alien woody species, which represent approximately 60% of alien species on oceanic islands (Kueffer *et al.*, 2010), and the relative importance of abiotic, biotic and anthropogenic drivers and their interactions. We first identify the abiotic and anthropogenic drivers of biological invasions (e.g., temperature, aridity, soil age, and the human influence index) in terms of alien species richness and abundance relative to native communities. We then evaluate the relative importance of phylogenetic distinctiveness and differences in traits of alien woody species to the native community along environmental and anthropogenic gradients for the establishment and dominance of alien woody species. Lastly, we test the sensitivity of the interactive effects of abiotic, biotic, and anthropogenic factors to the presence of the widespread and abundant native woody species, *Metrosideros polymorpha* (local name, Ohi'a). *Metrosideros polymorpha* is closely related to several alien and native woody species (Fig. S1; Craven *et al.*, 2018) yet is functionally unique, exhibiting greater adult plant size, heavier wood density, and lighter seeds than most native and alien woody species in Hawaiian forests. Determining if our results depend on the presence of this one native species is particularly urgent because an emerging

soil fungal pathogen (*Ceratocystis fimbriata*), also known as rapid Ohi'a death (ROD; Keith *et al.*, 2015; Fortini *et al.*, 2019), kills large numbers of *M. polymorpha* (Mortenson *et al.*, 2016), and may impact future biological invasions of native forests across Hawai'i.

Methods

Plot data selection and preparation

To examine patterns of woody plant invasion of Hawaiian forests, we used a forest plot database that compiled data from multiple sources (Zimmerman *et al.*, 2007; Ainsworth *et al.*, 2011; Gillespie Thomas W. *et al.*, 2013; Ostertag *et al.*, 2014; US Forest Service, 2016) to include species identity and size from across the Hawaiian archipelago (Craven et al. 2018). For our analyses, we used a total of 460 plots that range in area from 100 to 1,018 m^2 (median plot area = 1,000 m^2) with a minimum tree size threshold of 5 cm diameter at 1.3 m height. These plots are distributed across the six major islands in the archipelago: Hawai'i, Maui, Lana'i, Moloka'i, O'ahu, and Kaua'i (Fig. 1).

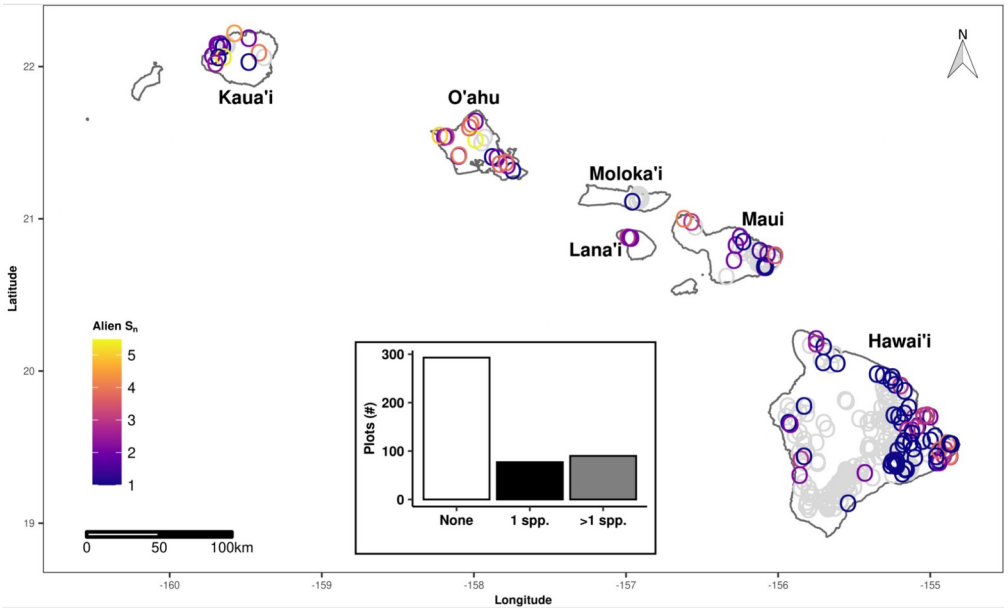

Fig. 1. Map of alien species richness in forests across the Hawaiian archipelago n= 460 plots). Color corresponds to species richness of alien woody species rarefied to 100 stems; grey circles indicate plots that have not been invaded. Inset shows the number of plots invaded by zero, one, and more than one alien woody species.

Species selection

Species names were standardized using The Plant List v 1.1 (www.theplantlist.org) with 'Taxonstand' (Cayuela *et al.*, 2017) and alien status was obtained from the flora of the Hawaiian Islands (Wagner *et al.*, 2005). While there are few non-angiosperm alien woody species in Hawai'i that have naturalized (*Pinus caribea* and *Cryptomeria japonica* (Wagner *et al.*, 2005)), their branches in a phylogeny may be longer than those of angiosperms and may result in unusual phylogenetic measures (Qian *et al.*, 2017). Similarly, monocot species likely have different ecological strategies than woody angiosperms (Spicer & Groover, 2010; Pierce *et al.*, 2013). We therefore excluded 14 non-angiosperm and monocot species from our dataset. We further excluded alien woody species that have not been reported as naturalised or whose populations are planted and have not spread widely, such as *Eucalyptus robusta* and *E. grandis* (Wagner *et al.*, 2005; Imada, 2012). In total, we included data for 129 woody species, of which 41 are alien and 88 are native (Table S1).

Levels of biological invasion

We calculated commonly used metrics that are proxies for the establishment and dominance of alien species (Catford *et al.*, 2012; Leung *et al.*, 2012). At the community level, we calculated relative alien species richness as the proportion of alien woody species to all woody species, and relative alien species abundance as the proportion of alien woody stems to all woody stems and thus indicate the extent of invasion. At the species level, we calculated presence/absence and relative abundances of each alien woody species. We classified absences as true absences if a species was reported as naturalized on an island by Wagner et al. (2005) but was not present in a plot. From here on, we refer to presence/absence as establishment and relative abundance (at the species level) as dominance.

Phylogenetic distinctiveness of alien woody species

We used an updated version of the molecular phylogeny from Zanne et al. (Jiang & Jiang 2016; Zanne et al. 2013) to build phylogenies of all species (native and alien) and only alien species. We conservatively

bound species to the backbone using dating information from congeners with the 'congeneric.merge' function in the 'pez' package (Pearse *et al.*, 2015). In total, we placed all 129 woody species in the plot database on the phylogeny (Fig. S1).

Following Thuiller et al. (2010), we calculated phylogenetic distinctiveness of alien woody species to the community of woody native species using two metrics: (i) phylogenetic distance to the nearest native species (DNNS) and (ii) mean weighted distance to native community (MWDNC). Both metrics were calculated for each alien woody species in all communities, including those in which they were not present. Because phylogenetic distinctiveness may be confounded with species richness (Kembel, 2009), both DNNS and MWDNC are likely to be smaller in more diverse communities. To correct for this, we calculated a standardized effect size (SES) by shuffling the tips of the phylogeny 1,000 times:

$$SES = (observed - mean_{null}) / standard\ deviation_{null}.$$

As DNNS is more sensitive to topological uncertainty in the phylogeny than MWDNC (Park Daniel S. *et al.*, 2020), we use MWDNC in our analyses. Lower (more negative) SES values indicate that alien woody species are more closely related to the native plant community, while higher SES values indicate that alien woody species are less closely related to the native plant community.

Functional traits

We selected three functional traits related to competitive ability to explore variation in establishment and dominance of alien woody species and that are associated with key axes of ecological variation (Díaz *et al.*, 2016): wood density, adult plant size, and seed mass. Wood density is related to interspecific variation in shade tolerance (Muller-Landau, 2004; Chave *et al.*, 2009) and growth and mortality rates (Chave *et al.*, 2009), adult plant size is associated with competition for light (King *et al.*, 2006) and seed dispersal distance (Thomson *et al.*, 2011) variation in seed mass drives the tolerance-fecundity trade-off (Muller-Landau Helene C., 2010). Data for wood density were obtained from Chave *et al.* (2009) and from the

BAAD, BIEN, and TRY databases (Falster *et al.*, 2015; Burrill *et al.*, 2018; Kattge *et al.*, 2020; Maitner, 2020). For seed mass, we obtained data from Shiels (2011) and the BIEN and TRY databases (Kattge *et al.*, 2020; Maitner, 2020). Because wood density and seed mass are strongly conserved phylogenetically (Chave *et al.*, 2009; Igea *et al.*, 2017), we calculated genus-level means when species-level data were not available. We estimated adult plant size from the plot data as the 95th percentile of diameter of all diameters ≥0.1 x maximum observed diameter ($D95_{0.1}$) for species with 20 or more stems or as the 95th percentile of diameter of all diameters for species with fewer than 20 stems (D95) following King et al. (2006). Both measures are independent of abundance, strongly correlated with maximum height, and are robust to outliers (King *et al.*, 2006).

Trait imputation

Because data were not available at the species level for all species in our data set (wood density: 5.4% unavailable; seed mass: <1% unavailable; adult plant size: 13.2% unavailable) and these gaps did not exceed 30% of our dataset (Penone *et al.*, 2014), we used phylogenetic trait imputation to fill gaps in our data set. Including imputed trait data also has been shown to reduce bias, as compared to removing species with missing trait data (Penone *et al.*, 2014). We used a random forest imputation algorithm in combination with phylogenetic information, which we optimized for each trait to minimize imputation error. For each trait, we assessed the imputation error for a range of phylogenetic eigenvectors (1 - 30) and used the imputed trait values for the number of phylogenetic eigenvectors that minimized imputation error. Prior to imputation, we log-transformed seed mass and adult plant size and back-transformed imputed values and imputation errors. We calculated imputation errors as the percent normalized root mean squared error, which were 1.95% for wood density, 13.6% for adult plant size, and 23.8% for seed mass. Our gap-filled trait data had similar distributions and mean values as the observed trait data (Fig. S2).

Trait differences

To measure trait differences among native and alien species, we calculated differences between trait values of alien species and the abundance-weighted trait values of native species for each trait (Fig. S3; van der Sande *et al.*, 2020). We standardized trait differences by calculating the log-response ratio of trait values of alien species to native species. Positive trait differences indicate that alien species had higher trait values than the native plant community and negative trait differences indicate the opposite.

Abiotic conditions and anthropogenic impacts

To understand the role of abiotic conditions in shaping woody invasions, we extracted mean annual temperature (MAT), precipitation (MAP) and potential evapotranspiration (PET; calculated using the Penman-Monteith equation) for each plot from locally interpolated climate data (Giambelluca *et al.*, 2013, 2014). We then calculated aridity, a widely used measure to assess the impacts of water availability on plant communities (e.g., Berdugo *et al.*, 2020), as the ratio of MAP to PET (Zomer *et al.*, 2008). We multiplied aridity by -1, such that low values of this index correspond to low aridity and high values to high aridity. We also extracted elevation (Jarvis *et al.*, 2008) and soil substrate age for each plot (hereon referred to as soil age; Sherrod *et al.*, 2007). On the Hawaiian archipelago, soil age is strongly related to the timing of volcanic activity over a volcanic hotspot, such that the western-most large islands (Kauai and O'ahu) are several millions of years older than the younger islands of Maui and Hawaii (Clague & Sherrod, 2014).

Because the establishment of alien woody species is facilitated by roads, and large populations of alien species can be maintained in areas where anthropogenic disturbance is high, we also included an index of human impacts in our analyses. Specifically, we extracted the human influence index (HII), a composite of human population density, land use, and infrastructure (HII ; Wildlife Conservation Society - WCS & Center for International Earth Science Information Network - CIESIN - Columbia University, 2005). .

Data analysis

Prior to model fitting, we tested for collinearity among explanatory variables using pairwise Pearson correlations. We selected variables that had a pairwise correlation below 0.7 (Dormann *et al.*, 2013). Based on this criteria, we retained mean annual temperature (MAT), aridity, soil age, and human influence index (HII) in our models examining relative alien species richness and abundance and MAT, aridity, soil age, HII, phylogenetic distinctiveness (in terms of mean weighted distance to native community (MWDNC)) and trait differences for wood density, adult plant size, and seed mass in our models examining variation in establishment and dominance.

We examined the relative importance of aridity, MAT, HII, and soil age, in determining variation in relative alien species richness and abundance using hierarchical Bayesian models with Beta and log-normal distributions, respectively. Relative alien species richness and abundance were modeled as the proportion of alien woody species or individuals in a plot. In both models we used random intercept terms for island and plot size.

Because phylogenetically closely related species are likely to share similar trait values (e.g., Felsenstein, 1985), not accounting for phylogenetic relationships may reduce estimation accuracy and increase type I error rates (Li & Ives, 2017). We therefore fit phylogenetic hierarchical Bayesian models to examine variation in establishment and dominance of alien woody species as a function of abiotic, biogeographical, and anthropogenic factors (aridity, MAT, HII, soil age), phylogenetic distinctiveness, competitive trait differences, and two-way interactions of phylogenetic distinctiveness or trait differences with abiotic conditions. We fit the model for probability of occurrence (i.e. establishment) using a Bernoulli distribution and the model for the relative abundance of alien woody species using a lognormal distribution, which fit the data better than a Beta distribution. For both models, we used a crossed random effects structure with random intercept terms for island, species and plot, as not all alien species occurred in each plot or island. In the random intercept term for plot, we nested plot identity within a group factor of plot area to account for the increased probability of occurrence in larger plots. To account for

phylogenetic correlations among species, we included two random intercept terms for species; one term models phylogenetic covariance and another term accounts for repeated measurements and other effects that may be independent of phylogenetic relationships among species. We first fit a full model with all two-way interactions and then simplified it by removing two-way interactions whose 95% credible intervals overlapped with zero.

We fit all models using weakly informative priors, four chains, and 2,500 burn-in samples per chain, after which 2,000 samples per chain were used to calculate posterior distributions of model parameters (total post-warmup samples= 8,000). Priors were flat for population-level effects. We increased the '*adapt_delta*' parameter in the 'brm' function until there were no divergent transitions. Model convergence was evaluated visually with trace plots and by estimating '*Rhat*' using the 'rhat' function, where values greater than 1.01 indicate that models have failed to converge (Tables S1 and S2). Model fit was assessed visually by comparing observed data to simulated data from the posterior predictive distribution (Fig. S4 and S5). Additionally, we estimated a Bayesian r^2 for each model to represent an estimate of the proportion of variation explained for new data (Tables S1 and S2). Model fit for establishment was also assessed by calculating ROC and AUC (Fig. S6). We evaluated spatial autocorrelation of model residuals using Moran's I. All models showed minimal evidence of spatial autocorrelation (Figs. S7 and S8). We also tested all models for scale dependence by evaluating the precision and accuracy of model estimates per plot size (Spake *et al.*, 2021); random effect estimates and their accuracy and precision did not vary systematically with plot size (Fig. S9 and S10). We also tested the sensitivity of our results to the presence of the widespread and abundant native woody species, *M. polymorpha*, by fitting the same set of models described above, but after removing *M. polymorpha* from our data set and phylogeny. All models were fitted using 'brms' (Bürkner, 2017).

For all analyses, environmental and functional trait data were visually inspected for normality; soil age was natural-log transformed. All variables were standardized using a *z*-transformation to enable comparisons across models. Analyses were performed using R v. 3.6.1 (R Core Team, 2020).

Results

Woody invasions were widespread across Hawaiian forests on all six islands (Fig. 1). Approximately 36% of forest plots were invaded, 19.6% being invaded by multiple alien woody species and 16.7% being invaded by one alien woody species. Across all plots, the most frequent woody invaders were *Psidium cattleianum, Cecropia obtusifolia, Psidium guajava*, and *Melastoma malabathricum* (Fig. S1).

Abiotic and anthropogenic drivers of woody invasions

Relative alien species richness and abundance were moderately positively correlated ($r = 0.39$, $P < 0.001$). At the community level, invasion of forests by alien woody species varied with abiotic conditions (Fig. 2). Relative species richness and abundance of alien woody species increased with MAT, and relative abundance of alien woody species decreased with increasing aridity. Relative species richness and abundance of alien woody species also showed a tendency to increase with HII, as 80% credible intervals did not overlap with zero. We found no evidence for an effect of soil age on the richness or abundance of alien woody species.

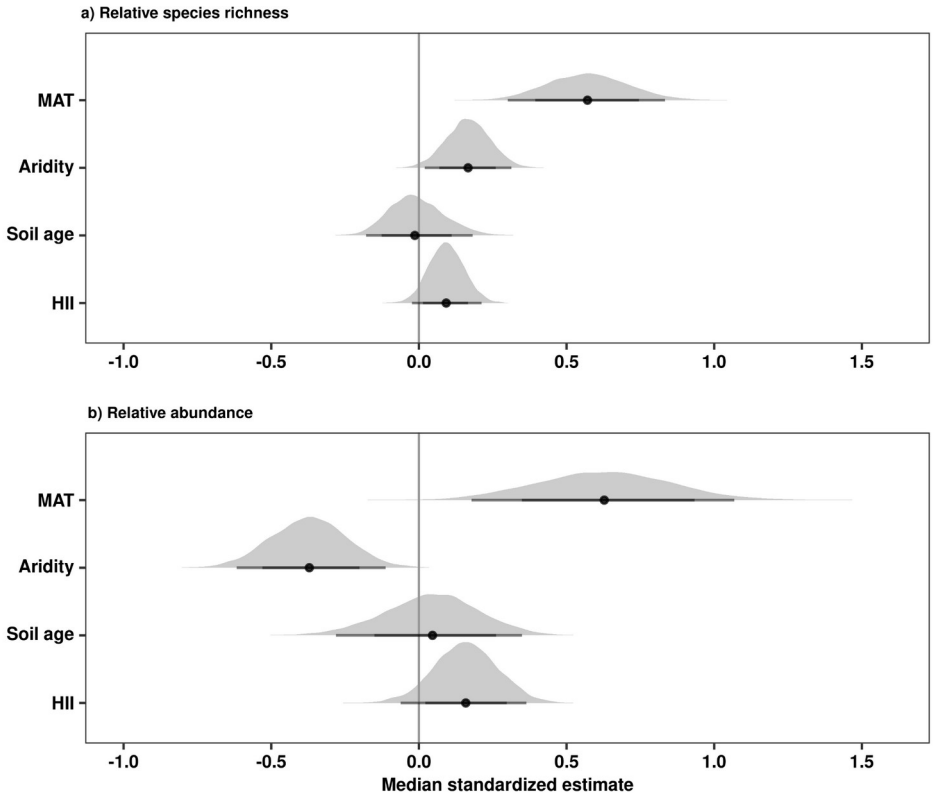

Fig. 2. Coefficient estimates of main effects used to examine **a)** relative alien woody species richness and **b)** relative alien woody species abundance across the Hawaiian archipelago. MAT is mean annual temperature, aridity is the ratio of mean annual potential evapotranspiration (PET) to mean annual precipitation, soil age is the estimated soil age, and HII is the human influence index. Medians, 80%, and 95% credible intervals of model coefficients were estimated using a phylogenetic hierarchical Bayesian with a beta distribution.

Establishment of alien woody species

Our analysis showed strong interactive effects among biotic and abiotic factors on the establishment of alien woody species across Hawaiian forests. Establishment of alien woody species increased with increasing temperature, soil age, and Δ adult plant size (Fig. 4). Yet, all biotic factors exhibited differential responses along abiotic and anthropogenic gradients (Fig. 5). At higher temperatures, alien woody species more closely related to the native plant community were more likely to occur than those distantly related to the native plant community (Fig. 5a). Likewise, alien woody species with lighter seeds and smaller adult plant size than the native plant community were more likely to establish at higher temperatures (Fig. 5b and c). In areas with high aridity, alien woody species distantly related to the native plant community were more likely to occur than less distantly related ones, whose probability of

establishment increased as aridity decreased (Fig. 5d). Alien woody species with heavier seeds and that are taller than the native plant community were more likely to occur where aridity was high, a pattern that switched sharply where aridity was low (Fig. 5e and f). Alien woody species with larger seeds and denser wood than the native plant community were more likely to occur on older soils than on younger soils (Fig. 5h and i). In areas with low human impacts, alien woody species with denser wood than the native plant community were more likely to establish than those with lighter wood than the native plant community (Fig. 5g). In contrast, alien woody species with lighter wood than the native plant community were more likely to establish in areas with higher human impacts (Fig. 5g).

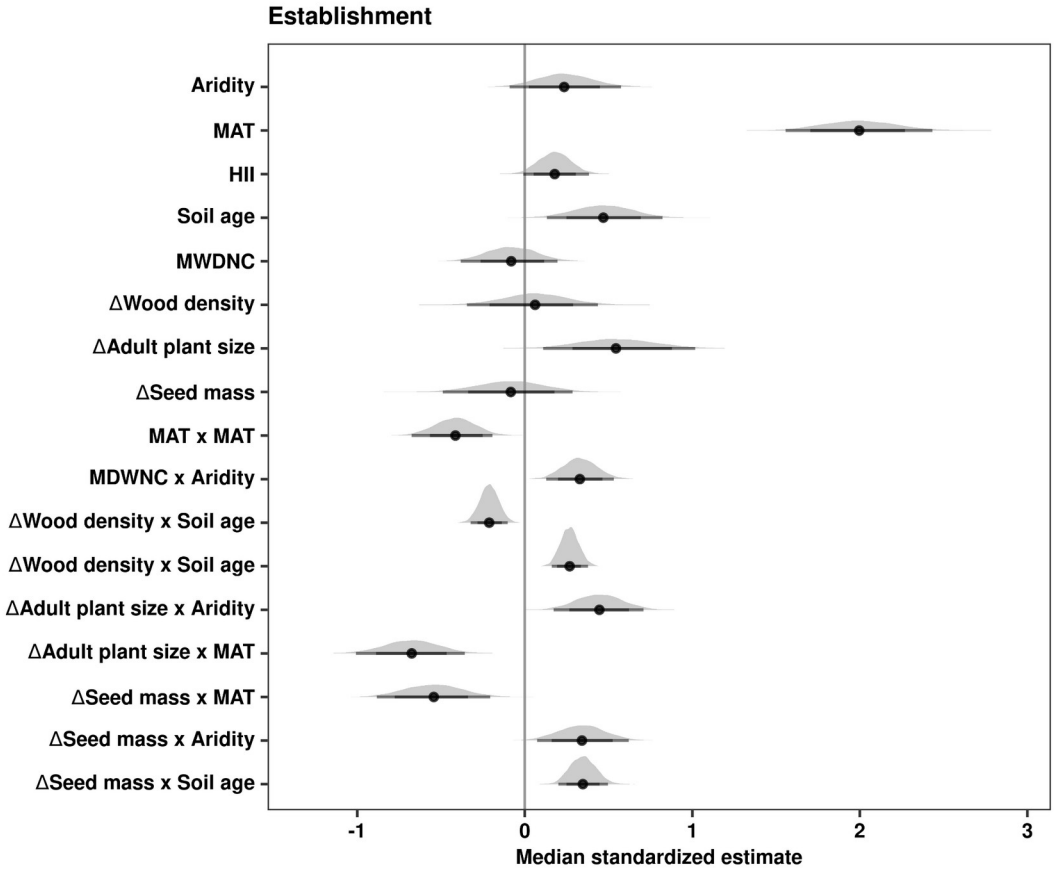

Fig. 3. Coefficient estimates of main effects used to evaluate the establishment of alien woody species across the Hawaiian archipelago. Aridity is the ratio of mean annual potential evapotranspiration (PET) to mean annual precipitation, MAT is mean annual temperature, soil age is the estimated soil age, HII is the human influence index, MWDNC is mean weighted phylogenetic distance to the native tree community, and ΔWD, Δ seed mass, and Δ adult plant size are the standardised differences in wood density, seed mass, and adult plant size, respectively, between alien woody species and the native tree community species. Medians, 80%, and 95% credible intervals of model coefficients were estimated using a phylogenetic hierarchical Bayesian model with a Bernoulli distribution.

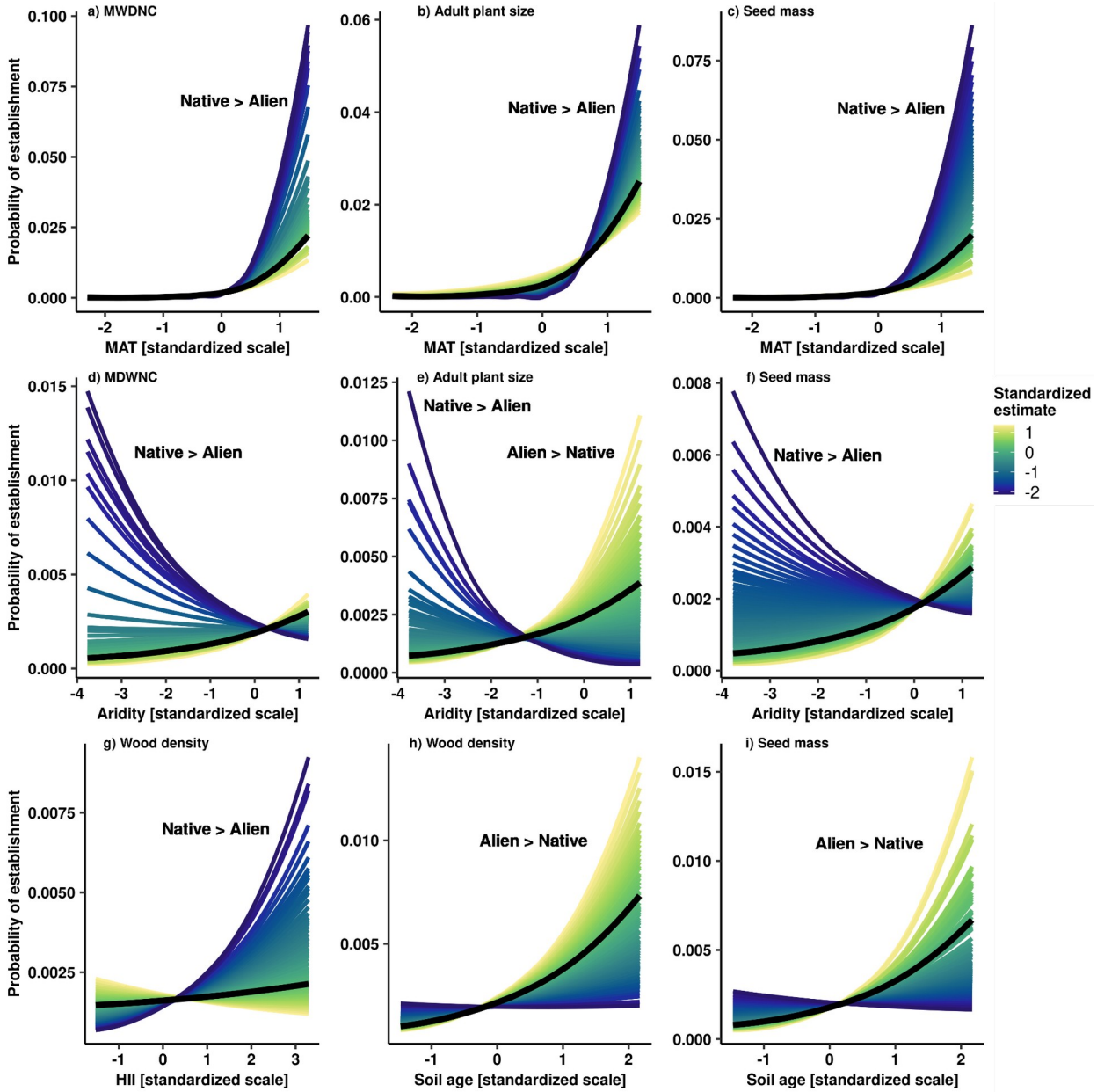

Fig. 4. The estimated effects of phylogenetic distinctiveness (MDWNC) and trait differences among alien and native species in terms of seed mass, adult plant size, and wood density along gradients of (**a,b,c**) mean annual temperature (MAT), (**d, e, f**), aridity, (**g**) human influence index (HII), and (**h & i**) soil age on the probability of establishment of alien woody species across Hawaiian forests. MDWNC is the standardized mean weighted phylogenetic distance between each alien species and the native community; positive values indicate that alien species are phylogenetically distinct from the native plant community and negative values indicate that alien species are phylogenetically similar to the native plant community. Seed mass, adult plant size, and wood density are standardized trait differences between alien woody species and the native community; positive values indicate that trait values of alien species are larger than those of the native community and negative values indicate that trait values of the alien woody species are smaller than those of the native community. Black and colored lines are marginal predictions evaluated at the 50th and 5th to the 95th quantiles of the moderator, respectively, and estimated with a phylogenetic hierarchical Bayesian model with a Bernoulli distribution. All x axes are scaled to unit variance.

Dominance of alien woody species

Abiotic and biotic factors and their interactions did not have marked impacts on dominance patterns of alien woody species (Fig. 6). Only phylogenetic distinctiveness had a moderate, negative effect on the relative abundance of alien woody species (80% credible intervals did not overlap zero), and no interactions between abiotic and biotic factors were included in the final model as the 95% credible intervals of all two-way interactions overlapped with zero.

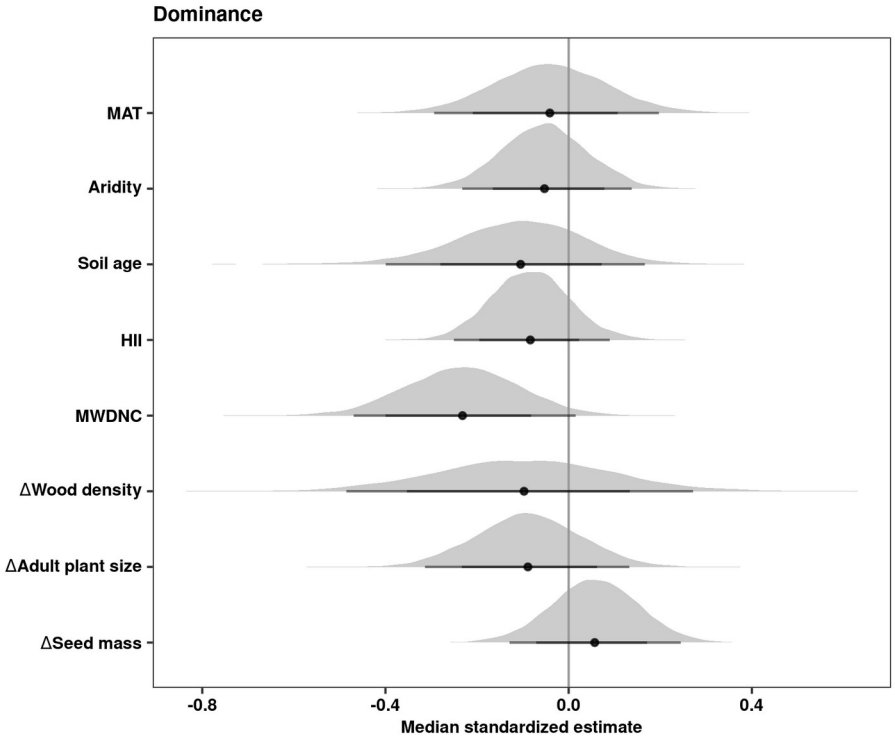

Fig. 5. Coefficient estimates of main effects used to examine dominance of alien woody species across Hawaiian forests. Aridity is the ratio of mean annual potential evapotranspiration (PET) to mean annual precipitation, MAT is mean annual temperature, soil age is the estimated soil age, HII is the human influence index, c is mean weighted phylogenetic distance to the native tree community, and ΔWD, Δ seed mass, and Δ adult plant size are the standardised differences in wood density, seed mass, and adult plant size, respectively, between alien woody species and the native tree community species. Medians and 80% and 95% credible intervals of model coefficients were estimated using a phylogenetic hierarchical Bayesian model with a log-normal distribution.

Sensitivity of context-dependent drivers of establishment and dominance

Further analyses provided added insight to the role played by *M. polymorpha* in mediating the context dependency of drivers affecting the establishment and dominance of alien woody species. When we removed *M. polymorpha* from the dataset, the influence of many interactive effects identified in the main analysis on the establishment of alien woody species was reduced considerably (Fig. S9). Indeed, only the interactions between soil age and Δ seed mass, MAT and Δ seed mass, and HII and Δ wood density retained their influence on the probability of establishment of alien woody species. Independent of the presence of *M. polymorpha*, temperature, soil age, and Δ adult plant size exhibited strong, positive effects on the probability of establishment of alien woody species, while Δ seed mass had strong, negative effects on the probability of establishment of alien woody species.

In contrast, the removal of *M. polymorpha* from the data set resulted in minimal changes to the impacts of abiotic and biotic drivers on the dominance of alien woody species (Fig. S10). The exception to this was Δ seed mass, which had a strong, positive effect on dominance. As found for the analysis of the full data set, no interactive effects were detected and phylogenetic distinctiveness had a marginally negative effect on the dominance of alien woody species.

Discussion

Our results highlight the context dependence of biological invasions (e.g., Catford et al. 2021) in forests across the Hawaiian archipelago. Abiotic factors determine the richness and abundance of alien species in communities in the expected direction, with more woody aliens in hotter and wetter locations. Interactions among biotic, abiotic, and anthropogenic factors jointly determine where alien woody species establish, but not where they become dominant. We found that alien woody species establish more readily in areas with high aridity and in older soils, which they most likely colonize successfully by exploiting niche space not occupied by native woody species. In areas with harsh abiotic conditions, such as those with younger soils, environmental filtering was usually - but not always - the likely dominant ecological mechanism operating on the establishment of alien woody species. Our results further reveal how the

impacts of soil age, a biogeographical factor often used to examine macroevolutionary processes that generate native biodiversity across and within oceanic islands (Emerson, 2002; Whittaker *et al.*, 2008; Gillespie, 2016), extend to shaping local coexistence of alien species. Together, our results suggest that the ecological mechanisms underlying both the pre-adaptation hypothesis (environmental filtering) and Darwin's naturalisation conundrum (biotic filtering) are likely to interactively shape the assembly of alien woody communities across the Hawaiian archipelago.

Abiotic drivers of multi-species woody invasions

We found that local communities are generally more invaded in forests with higher temperatures and low aridity. These findings indicate that biological invasions are more severe in lowland, moist tropical forests across the Hawaiian archipelago (Ibanez *et al.*, 2019), which have been heavily impacted by agriculture and land-use change (Jacobi *et al.*, 2017), as temperature is strongly negatively correlated with elevation (r = - 0.99). While our results show certain similarities with macroecological patterns of alien species richness and composition on oceanic islands in terms of abiotic factors, we detected weaker human impacts on the severity of biological invasions at local scales than have been reported at larger spatial scales (Moser *et al.*, 2018; Wohlwend *et al.*, 2021). Yet, the low explanatory power of our models for relative alien species richness (R^2 = 0.25, 95% credible interval: 0.15-0.33) and abundance (R^2 = 0.12, 95% credible interval: 0.06-0.20) highlights the need to include additional drivers, such as biotic interactions, historical legacies, and propagule pressure, to enhance the robustness of predictions of the severity of biological invasions at local spatial scales.

The weak, positive correlation between the two metrics of invasion impacts suggests that while in general there are more alien species when there are more alien stems, there is also a range of invaded forests across Hawai'i, including those that are heavily invaded by a small number of dominant alien woody species such as *P. cattleianum* and those dominated by native woody species, but contain several alien woody species. This finding also suggests that invasion by one species may not facilitate invasion by other alien species within the same trophic group (e.g., Zarnetske *et al.*, 2013), possibly due to niche

preemption or niche modification (Fukami, 2015). As such priority effects are often contingent upon abiotic factors (Grainger *et al.*, 2019), it is possible that high temperatures facilitate coexistence among alien woody species, while low aridity may strengthen priority effects (Fig. 2). Further studies would be needed to determine whether and how priority effects of dominant alien species such as *P. cattleianum* are influenced by their demographic traits (Fukami *et al.*, 2016) to better understand the mechanisms that underpin multi-species biological invasions.

Context dependency of alien species establishment and dominance

Our analysis suggests that the establishment of alien woody species was strongly context dependent (sensu Catford *et al.*, 2022), meaning that the impacts of phylogenetic and trait differences between alien and native species on establishment were not consistent across Hawaiian forests (Tecco *et al.*, 2010; Gross *et al.*, 2013; González-Moreno *et al.*, 2014; Sapsford *et al.*, 2020). The strength of biotic filtering is expected to shift along environmental gradients (e.g., Cornwell & Ackerly, 2009; Kraft & Ackerly, 2010), with the expectation that biotic filtering should be stronger in more favorable environments compared to harsher environments (Bertness & Callaway, 1994). In contrast, we found that environmental filtering strengthened with increasing temperature (for MWDNC, Δ seed mass, and Δ adult plant size), meaning that alien woody species that are more similar to native woody species are more likely to establish where environmental filters are weaker. In line with expectations, we found that environmental filtering strengthened with increasing human impacts (for Δ wood density) and decreasing soil age (for Δ seed mass and Δ wood density); alien woody species that are more similar to native woody species were more likely to establish in areas with stronger human impacts or with younger soils. Yet, we also found evidence that biotic filtering could be stronger in harsh environments, particularly where aridity was high (for MWDNC, Δ adult plant size, and Δ seed mass), which is consistent with results reported by Henn et al. (2019). This finding suggests that native woody communities do not fully occupy niche space in harsh environments, thereby facilitating the establishment of phylogenetically and functionally distinct alien woody species. It could also suggest that alien woody species may exhibit greater tolerance to water- or

nutrient-limited conditions than phylogenetically similar native woody species, which could be facilitated by greater intraspecific trait variation (Westerband *et al.*, 2021). Together, our results reveal that alien woody species are likely to be able to colonize native forests by competing less strongly with native woody species (Levin *et al.*, 2020), either because conditions are too harsh (i.e. where environmental filtering is strong) or empty niche space is available in places where biotic filtering is strong.

Our analysis revealed that soil age is an important underlying factor driving context dependent biological invasions across Hawaiian forests. Despite its importance for native biodiversity patterns, empirical evidence showing that soil age shapes the spatial distribution of alien species within and across islands has been limited (Aplet *et al.*, 1998; Hughes & Denslow, 2005), particularly at macroecological scales where greater emphasis is usually given to anthropogenic drivers (e.g., Dawson *et al.*, 2017; Moser *et al.*, 2018; Wohlwend *et al.*, 2021). One explanation for the positive effects of soil age on the probability of establishment of alien woody species observed in this study is that woody communities with high native plant diversity on older soils are less resistant to invasion ("the rich get richer"; Stohlgren *et al.*, 2003; Fridley *et al.*, 2007). However, once accounting for soil age, native and alien species richness exhibited a significantly negative correlation (Pearson's partial correlation = -0.11, P =0.01), indicating that more diverse woody communities are moderately more resistant to invasion than less diverse plant communities. This suggests that it not soil age per se, but rather the macroevolutionary processes associated with it, such as niche partitioning, that have generated local scale patterns of native biodiversity over millions of years (Craven *et al.*, 2019), and that this may confer resistance to biological invasions (Fridley *et al.*, 2007). Our results are also consistent with the idea that soil age directly affects biological invasions by filtering alien woody species on younger soils that have low soil nutrient content (Aplet *et al.*, 1998). Moreover, our results suggest that alien woody species successfully establish in areas with older soils by occupying different regeneration niches or acquiring soil nutrients differently than native woody species (Fig. 5h and i), strategies that may covary with either wood density or seed mass (but see Carmona *et al.*, 2021). More broadly, the importance of gradients in soil age mediating biological

invasions reveals that biogeographical factors may play an underappreciated role in shaping seemingly idiosyncratic patterns of biological invasions within and across oceanic islands.

We found little evidence that abiotic or biotic filtering consistently influenced the dominance of alien woody species across Hawaiian forests. Our results indicate that competitive outcomes between alien and native woody species are largely independent of environmental conditions or functional or phylogenetic differences. Thus, spatial variation in dominance of the alien woody community could be driven principally by dispersal, particularly if propagule pressure is high (Lockwood *et al.*, 2005; Richardson & Pyšek, 2012; Cassey *et al.*, 2018). We detected a moderate negative effect of phylogenetic distinctiveness on dominance (80% confidence intervals do not overlap with zero), which is consistent with the idea that environmental filtering is the dominant process structuring invaded forest ecosystems (Lemoine *et al.*, 2015). Nevertheless, our ability to detect the influence of abiotic and biotic filtering on dominance may have been limited by the spatial grain of our analysis (median plot area = 1,000 m^2; range of plot area: 100 to 1,018 m^2), which may be too large to capture the effects of neighborhood competition or crowding (e.g., Uriarte *et al.*, 2010). Further, we used phylogenetic distinctiveness and trait differences as proxies for competitive ability, which is rarely quantified directly (but see Levin *et al.*, 2020), and may explain further variation in dominance among alien woody species.

Presence of M. polymorpha

We found that the patterns of alien establishment critically depend on the presence of *M. polymorpha.* When we excluded *M. polymorpha* from the analysis, the factors that shape the establishment of alien woody species were markedly less context dependent; only three interactions (soil age and Δ seed mass, MAT and Δ adult plant size, and HII and Δ wood density) were retained. This result suggests that where temperature and human impacts are high, alien woody species that are phylogenetically and functionally similar to native species are more likely to establish; this is likely driven by the pervasiveness of *P. cattleianum* across Hawaiian forests and its functional similarity to *M. polymorpha* (Fig. S11, Table S6). Also, it suggests that independent of the presence of *M. polymorpha*, soil age mediates the strength of

biotic filtering. Thus, the apparent context dependency of biological invasions appears to have been driven at least in part by the broad environmental gradients across which *M. polymorpha* occurs, whose light seeds allow it to disperse widely and high wood density confers greater drought tolerance (Cordell *et al.*, 1998), and functional similarities between alien woody species and *M. polymorpha.*

Our sensitivity analysis indicates that unoccupied niche space persists even in the absence of *M. polymorpha*, as evidenced by retained interactions (soil age *x* Δ seed mass, MAT *x* and Δ adult plant size, and HII *x* Δ wood density). These results suggest that being taller, having lighter seeds or denser wood than the native community in areas with older soils or lower human impacts may confer a competitive advantage to alien woody species invading forests, regardless of whether they are dominated by *M. polymorpha.* Consequently, the growing impacts of the fungal pathogen that causes Rapid O'hia Death on *M. polymorpha* could shift alien woody invasions in Hawaiian forests (Gómez-Aparicio *et al.*, 2012; Anderegg *et al.*, 2015), potentially favoring alien woody species with lighter seeds and taller stature than the native woody community, such as *Aleurites moluccanus*, *Melia azedarach,* and *Syzygium cumini.*

Conclusions

Our results highlight that alien woody species likely establish in island ecosystems by occupying empty niche space and/or habitats that are too harsh to compete directly with native woody species. While these alien species are clearly changing the composition and dynamics of Hawaiian forests (Craven *et al.*, 2019; Barton *et al.*, 2021), our results show that biological invasions are shaped in part by the same environmental and biogeographical factors, such as climate and soil age, that generate and maintain patterns of native biodiversity. Our sensitivity analysis provides evidence that the context dependency of alien woody invasions across Hawai'i arises due to ecological interactions between abiotic, anthropogenic, and biotic factors (Catford *et al.*, 2022), particularly along gradients in soil age, human impacts, and temperature. While this context dependency makes our results difficult to generalize to other archipelagos, our results emphasize that future efforts should account for how soil age mediates biotic filtering. This strong context dependence of multi-species invasions also highlights the complexity of

developing management strategies to mitigate the biodiversity and ecosystem impacts of biological invasions.

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Data availability statement

The code and data that support the findings of this study are available in Github: https://github.com/dylancraven/Hawaii_BiologicalInvasions. These data were derived from the following resources available in Dryad: https://doi.org/10.5061/dryad.1kk02qr.

References

Ainsworth, A., Berkowitz, P, Jacobi, J.D., Loh, R.K. & Kozar, K. (2011) Focal Terrestrial Plant Communities Monitoring Protocol. *Focal Terrestrial Plant Communities Monitoring Pacific Island Network NPS/PACN/NRR–2011/410 National Park Service, Fort Collins, Colorado*.

Anderegg, W.R.L., Hicke, J.A., Fisher, R.A., Allen, C.D., Aukema, J., Bentz, B., Hood, S., Lichstein, J.W., Macalady, A.K., McDowell, N., Pan, Y., Raffa, K., Sala, A., Shaw, J.D., Stephenson, N.L., Tague, C. & Zeppel, M. (2015) Tree mortality from drought, insects, and their interactions in a changing climate. *New Phytologist*, **208**, 674–683.

Aplet, G.H., Hughes, R.F. & Vitousek, P.M. (1998) Ecosystem development on Hawaiian lava flows: biomass and species composition. *Journal of Vegetation Science*, **9**, 17–26.

Ashby, B., Watkins, E., Lourenço, J., Gupta, S. & Foster, K.R. (2017) Competing species leave many potential niches unfilled. *Nature Ecology & Evolution*, **1**, 1495–1501.

Barton, K.E., Westerband, A., Ostertag, R., Stacy, E., Winter, K., Drake, D.R., Fortini, L.B., Litton, C.M., Cordell, S., Krushelnycky, P., Kawelo, K., Feliciano, K., Bennett, G. & Knight, T. (2021) Hawai‘i Forest Review: Synthesizing the Ecology, Evolution, and Conservation of a Model

System. *Perspectives in Plant Ecology, Evolution and Systematics*, 125631.
Bennett, J.A. (2019) Similarities between invaders and native species: Moving past Darwin's naturalization conundrum. *Journal of Vegetation Science*, **30**, 1027–1034.
Berdugo, M., Delgado-Baquerizo, M., Soliveres, S., Hernández-Clemente, R., Zhao, Y., Gaitán, J.J., Gross, N., Saiz, H., Maire, V., Lehman, A., Rillig, M.C., Solé, R.V. & Maestre, F.T. (2020) Global ecosystem thresholds driven by aridity. *Science*, **367**, 787–790.
Bertness, M.D. & Callaway, R. (1994) Positive interactions in communities. *Trends in Ecology & Evolution*, **9**, 191–193.
Blackburn, T.M., Pyšek, P., Bacher, S., Carlton, J.T., Duncan, R.P., Jarošík, V., Wilson, J.R.U. & Richardson, D.M. (2011) A proposed unified framework for biological invasions. *Trends in Ecology & Evolution*, **26**, 333–339.
Bürkner, P.-C. (2017) brms: An R package for Bayesian multilevel models Using Stan. *Journal of Statistical Software*, **80**, 1–28.
Burrill, E.A., Wilson, A.M., Turner, J.A., Pugh, S.A., Menlove, J., Christiansen, G., Conkling, B.L. & David, W. (2018) *The Forest Inventory and Analysis Database: database description and user guide version 8.0 for Phase 2*, U.S. Department of Agriculture, Forest Service.
Cadotte, M.W., Campbell, S.E., Li, S., Sodhi, D.S. & Mandrak, N.E. (2018) Preadaptation and Naturalization of Nonnative Species: Darwin's Two Fundamental Insights into Species Invasion. *Annual Review of Plant Biology*, **69**, 661–684.
Carboni, M., Calderon-Sanou, I., Pollock, L., Violle, C. & Thuiller, W. (2018) Functional traits modulate the response of alien plants along abiotic and biotic gradients. *Global Ecology and Biogeography*, **27**, 1173–1185.
Carmona, C.P., Bueno, C.G., Toussaint, A., Träger, S., Díaz, S., Moora, M., Munson, A.D., Pärtel, M., Zobel, M. & Tamme, R. (2021) Fine-root traits in the global spectrum of plant form and function. *Nature*, **597**, 683–687.
Carvajal-Endara, S., Hendry, A.P., Emery, N.C. & Davies, T.J. (2017) Habitat filtering not dispersal limitation shapes oceanic island floras: species assembly of the Galápagos archipelago. *Ecology Letters*, **20**, 495–504.
Cassey, P., Delean, S., Lockwood, J.L., Sadowski, J. & Blackburn, T.M. (2018) Dissecting the null model for biological invasions: A meta-analysis of the propagule pressure effect. *PLOS Biology*, **16**, 1–16.
Castro-Díez, P., Vaz, A.S., Silva, J.S., Loo, M. van, Alonso, Á., Aponte, C., Bayón, Á., Bellingham, P.J., Chiuffo, M.C., DiManno, N., Julian, K., Kandert, S., Porta, N.L., Marchante, H., Maule, H.G., Mayfield, M.M., Metcalfe, D., Monteverdi, M.C., Núñez, M.A., Ostertag, R., Parker, I.M., Peltzer, D.A., Potgieter, L.J., Raymundo, M., Rayome, D., Reisman-Berman, O., Richardson, D.M., Roos, R.E., Saldaña, A., Shackleton, R.T., Torres, A., Trudgen, M., Urban, J., Vicente, J.R., Vilà, M., Ylioja, T., Zenni, R.D. & Godoy, O. (2019) Global effects of non-native tree species on multiple ecosystem services. *Biological Reviews*, **94**, 1477–1501.
Catford, J.A., Jansson, R. & Nilsson, C. (2009) Reducing redundancy in invasion ecology by integrating hypotheses into a single theoretical framework. *Diversity and Distributions*, **15**, 22–40.
Catford, J.A., Vesk, P.A., Richardson, D.M. & Pyšek, P. (2012) Quantifying levels of biological invasion: towards the objective classification of invaded and invasible ecosystems. *Global Change Biology*, **18**, 44–62.
Catford, J.A., Wilson, J.R.U., Pyšek, P., Hulme, P.E. & Duncan, R.P. (2022) Addressing context dependence in ecology. *Trends in Ecology & Evolution*, **37**, 158–170.
Cayuela, L., Stein, A. & Oksanen, J. (2017) Taxonstand: taxonomic standardization of plant species names. *R package version 2*.
Chave, J., Coomes, D., Jansen, S., Lewis, S.L., Swenson, N.G. & Zanne, A.E. (2009) Towards a worldwide wood economics spectrum. *Ecol Lett*, **12**, 351–66.
Clague, D.A. & Sherrod, D.R. (2014) *Growth and degradation of Hawaiian volcanoes*. *Characteristics of Hawaiian Volcanoes*, pp. 97–146. US Geological Survey Reston, VA.

Cordell, S., Goldstein, G., Mueller-Dombois, D., Webb, D. & Vitousek, P.M. (1998) Physiological and morphological variation in Metrosideros polymorpha, a dominant Hawaiian tree species, along an altitudinal gradient: the role of phenotypic plasticity. *Oecologia*, **113**, 188–196.

Cornwell, W.K. & Ackerly, D.D. (2009) Community assembly and shifts in plant trait distributions across an environmental gradient in coastal California. *Ecological Monographs*, **79**, 109–126.

Craven, D., Knight, T.M., Barton, K.E., Bialic-Murphy, L. & Chase, J.M. (2019) Dissecting macroecological and macroevolutionary patterns of forest biodiversity across the Hawaiian archipelago. *Proceedings of the National Academy of Sciences*, **116**, 16436–16441.

Craven, D., Knight, T.M., Barton, K.E., Bialic-Murphy, L., Cordell, S., Giardina, C.P., Gillespie, T.W., Ostertag, R., Sack, L. & Chase, J.M. (2018) OpenNahele: the open Hawaiian forest plot database. *Biodiversity Data Journal*, **6**, e28406.

Darwin, C. (1859) *On the origins of species by means of natural selection*, John Murray, United Kingdom.

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. *Nature Ecology & Evolution*, **1**, 0186.

Denslow, J.S. (2003) Weeds in Paradise: Thoughts on the Invasibility of Tropical Islands. *Annals of the Missouri Botanical Garden*, **90**, 119–127.

Denslow, J.S., Space, J.C. & Thomas, P.A. (2009) Invasive Exotic Plants in the Tropical Pacific Islands: Patterns of Diversity. *Biotropica*, **41**, 162–170.

Díaz, S., Kattge, J., Cornelissen, J.H.C., Wright, I.J., Lavorel, S., Dray, S., Reu, B., Kleyer, M., Wirth, C., Colin Prentice, I., Garnier, E., Bönisch, G., Westoby, M., Poorter, H., Reich, P.B., Moles, A.T., Dickie, J., Gillison, A.N., Zanne, A.E., Chave, J., Joseph Wright, S., Sheremet'ev, S.N., Jactel, H., Baraloto, C., Cerabolini, B., Pierce, S., Shipley, B., Kirkup, D., Casanoves, F., Joswig, J.S., Günther, A., Falczuk, V., Rüger, N., Mahecha, M.D. & Gorné, L.D. (2016) The global spectrum of plant form and function. *Nature*, **529**, 167–171.

Dormann, C.F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carré, G., Marquéz, J.R.G., Gruber, B., Lafourcade, B., Leitão, P.J., Münkemüller, T., McClean, C., Osborne, P.E., Reineking, B., Schröder, B., Skidmore, A.K., Zurell, D. & Lautenbach, S. (2013) Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. *Ecography*, **36**, 27–46.

Emerson, B. (2002) Evolution on oceanic islands: molecular phylogenetic approaches to understanding pattern and process. *Molecular ecology*, **11**, 951–966.

Falster, D.S., Duursma, R.A., Ishihara, M.I., Barneche, D.R., FitzJohn, R.G., Vårhammar, A., Aiba, M., Ando, M., Anten, N., Aspinwall, M.J., Baltzer, J.L., Baraloto, C., Battaglia, M., Battles, J.J., Bond-Lamberty, B., Breugel, M. van, Camac, J., Claveau, Y., Coll, L., Dannoura, M., Delagrange, S., Domec, J.-C., Fatemi, F., Feng, W., Gargaglione, V., Goto, Y., Hagihara, A., Hall, J.S., Hamilton, S., Harja, D., Hiura, T., Holdaway, R., Hutley, L.S., Ichie, T., Jokela, E.J., Kantola, A., Kelly, J.W.G., Kenzo, T., King, D., Kloeppel, B.D., Kohyama, T., Komiyama, A., Laclau, J.-P., Lusk, C.H., Maguire, D.A., Maire, G. le, Mäkelä, A., Markesteijn, L., Marshall, J., McCulloh, K., Miyata, I., Mokany, K., Mori, S., Myster, R.W., Nagano, M., Naidu, S.L., Nouvellon, Y., O'Grady, A.P., O'Hara, K.L., Ohtsuka, T., Osada, N., Osunkoya, O.O., Peri, P.L., Petritan, A.M., Poorter, L., Portsmuth, A., Potvin, C., Ransijn, J., Reid, D., Ribeiro, S.C., Roberts, S.D., Rodríguez, R., Saldaña-Acosta, A., Santa-Regina, I., Sasa, K., Selaya, N.G., Sillett, S.C., Sterck, F., Takagi, K., Tange, T., Tanouchi, H., Tissue, D., Umehara, T., Utsugi, H., Vadeboncoeur, M.A., Valladares, F., Vanninen, P., Wang, J.R., Wenk, E., Williams, R., Ximenes, F. de A., Yamaba, A., Yamada, T., Yamakura, T., Yanai, R.D. & York, R.A. (2015) BAAD: a Biomass And Allometry Database for woody plants. *Ecology*, **96**, 1445–1445.

Felsenstein, J. (1985) Phylogenies and the Comparative Method. *The American Naturalist*, **125**, 1–15.

Fortini, L.B., Kaiser, L.R., Keith, L.M., Price, J., Hughes, R.F., Jacobi, J.D. & Friday, J.B. (2019) The evolving threat of Rapid ‘Ōhi‘a Death (ROD) to Hawai‘i’s native ecosystems and rare plant species. *Forest Ecology and Management*, **448**, 376–385.

Fridley, J.D., Stachowicz, J.J., Naeem, S., Sax, D.F., Seabloom, E.W., Smith, M.D., Stohlgren, T.J., Tilman, D. & Holle, B.V. (2007) The invasion paradox: reconciling pattern and process in species invasions. *Ecology*, **88**, 3–17.

Fukami, T. (2015) Historical Contingency in Community Assembly: Integrating Niches, Species Pools, and Priority Effects. *Annual Review of Ecology, Evolution, and Systematics*, **46**, 1–23.

Fukami, T., Mordecai, E.A. & Ostling, A. (2016) A framework for priority effects. *Journal of Vegetation Science*, **27**, 655–657.

Gallien, L. & Carboni, M. (2017) The community ecology of invasive species: where are we and what’s next? *Ecography*, **40**.

García-Verdugo, C., Monroy, P., Pugnaire, F.I., Jura-Morawiec, J., Moreira, X. & Flexas, J. (2020) Leaf functional traits and insular colonization: Subtropical islands as a melting pot of trait diversity in a widespread plant lineage. *Journal of Biogeography*, **47**, 2362– 2376.

Giambelluca, T., Shuai, X., Barnes, M., Alliss, R., Longman, R., Miura, T., Chen, Q., Frazier, A., Mudd, R., Cuo, L. & others (2014) Evapotranspiration of Hawai ‘i. *Final report submitted to the US Army Corps of Engineers—Honolulu District, and the Commission on Water Resource Management, State of Hawai ‘i*.

Giambelluca, T.W., Chen, Q., Frazier, A.G., Price, J.P., Chen, Y.-L., Chu, P.-S., Eischeid, J.K. & Delparte, D.M. (2013) Online rainfall atlas of Hawai ‘i. *Bulletin of the American Meteorological Society*, **94**, 313–316.

Gillespie, R.G. (2016) Island time and the interplay between ecology and evolution in species diversification. *Evolutionary Applications*, **9**, 53–73.

Gillespie Thomas W., Keppel Gunnar, Pau Stephanie, Price Jonathan P., Jaffré Tanguy & O’Neill Kristin (2013) Scaling species richness and endemism of tropical dry forests on oceanic islands. *Diversity and Distributions*, **19**, 896–906.

Givnish, T.J., Millam, K.C., Mast, A.R., Paterson, T.B., Theim, T.J., Hipp, A.L., Henss, J.M., Smith, J.F., Wood, K.R. & Sytsma, K.J. (2009) Origin, adaptive radiation and diversification of the Hawaiian lobeliads (Asterales: Campanulaceae). *Proceedings of the Royal Society of London B: Biological Sciences*, **276**, 407–416.

Gómez-Aparicio, L., Ibáñez, B., Serrano, M.S., Vita, P.D., Ávila, J.M., Pérez-Ramos, I.M., García, L.V., Sánchez, M.E. & Marañón, T. (2012) Spatial patterns of soil pathogens in declining Mediterranean forests: implications for tree species regeneration. *New Phytologist*, **194**, 1014–1024.

González-Moreno, P., Diez, J.M., Ibáñez, I., Font, X. & Vilà, M. (2014) Plant invasions are context-dependent: multiscale effects of climate, human activity and habitat. *Diversity and Distributions*, **20**, 720–731.

Grainger, T.N., Letten, A.D., Gilbert, B. & Fukami, T. (2019) Applying modern coexistence theory to priority effects. *Proceedings of the National Academy of Sciences*, **116**, 6205–6210.

Gross, N., Börger, L., Duncan, R.P. & Hulme, P.E. (2013) Functional differences between alien and native species: do biotic interactions determine the functional structure of highly invaded grasslands? *Functional Ecology*, **27**, 1262–1272.

Henn, J.J., Yelenik, S. & Damschen, E.I. (2019) Environmental gradients influence differences in leaf functional traits between native and non-native plants. *Oecologia*, **191**, 397–409.

Hughes, R.F. & Denslow, J.S. (2005) Invasion by a N2-Fixing Tree Alters Function and Structure in Wet Lowland Forests of Hawaii. *Ecological Applications*, **15**, 1615–1628.

Ibanez, T., Hart, P., Ainsworth, A., Gross, J. & Monello, R. (2019) Factors associated with alien plant richness, cover and composition differ in tropical island forests. *Diversity and Distributions*, **25**, 1910–1923.

Igea, J., Miller, E.F., Papadopulos, A.S.T. & Tanentzap, A.J. (2017) Seed size and its rate of evolution

correlate with species diversification across angiosperms. *PLOS Biology*, **15**, 1–16.
Imada, C.T. (2012) Hawaiian native and naturalized vascular plants checklist. *Honolulu: Hawaii Biological Survey, Bishop Museum*.
Jacobi, J.D., Price, J.P., Fortini, L.B., Gon, S.M. & Berkowitz, P. (2017) Baseline land cover. *Baseline and projected future carbon storage and carbon fluxes in ecosystems of Hawai'i. US Geological Survey Professional Paper 1834. Reston, VA: US Department of the Interior, US Geological Survey*, 9–20.
Jarvis, A., Reuter, H., Nelson, A. & Guevara, E. (2008) *SRTM 90m Digital Elevation Database v4. 1*, CGIAR-CSI.
Jauni, M., Gripenberg, S. & Ramula, S. (2015) Non-native plant species benefit from disturbance: a meta-analysis. *Oikos*, **124**, 122–129.
Kattge, J., Bönisch, G., Díaz, S., Lavorel, S., Prentice, I.C., Leadley, P., Tautenhahn, S., Werner, G.D.A., Aakala, T., Abedi, M., Acosta, A.T.R., Adamidis, G.C., Adamson, K., Aiba, M., Albert, C.H., Alcántara, J.M., C, C.A., Aleixo, I., Ali, H., Amiaud, B., Ammer, C., Amoroso, M.M., Anand, M., Anderson, C., Anten, N., Antos, J., Apgaua, D.M.G., Ashman, T.-L., Asmara, D.H., Asner, G.P., Aspinwall, M., Atkin, O., Aubin, I., Baastrup-Spohr, L., Bahalkeh, K., Bahn, M., Baker, T., Baker, W.J., Bakker, J.P., Baldocchi, D., Baltzer, J., Banerjee, A., Baranger, A., Barlow, J., Barneche, D.R., Baruch, Z., Bastianelli, D., Battles, J., Bauerle, W., Bauters, M., Bazzato, E., Beckmann, M., Beeckman, H., Beierkuhnlein, C., Bekker, R., Belfry, G., Belluau, M., Beloiu, M., Benavides, R., Benomar, L., Berdugo-Lattke, M.L., Berenguer, E., Bergamin, R., Bergmann, J., Carlucci, M.B., Berner, L., Bernhardt-Römermann, M., Bigler, C., Bjorkman, A.D., Blackman, C., Blanco, C., Blonder, B., Blumenthal, D., Bocanegra-González, K.T., Boeckx, P., Bohlman, S., Böhning-Gaese, K., Boisvert-Marsh, L., Bond, W., Bond-Lamberty, B., Boom, A., Boonman, C.C.F., Bordin, K., Boughton, E.H., Boukili, V., Bowman, D.M.J.S., Bravo, S., Brendel, M.R., Broadley, M.R., Brown, K.A., Bruelheide, H., Brumnich, F., Bruun, H.H., Bruy, D., Buchanan, S.W., Bucher, S.F., Buchmann, N., Buitenwerf, R., Bunker, D.E., Bürger, J., Burrascano, S., Burslem, D.F.R.P., Butterfield, B.J., Byun, C., Marques, M., Scalon, M.C., Caccianiga, M., Cadotte, M., Cailleret, M., Camac, J., Camarero, J.J., Campany, C., Campetella, G., Campos, J.A., Cano-Arboleda, L., Canullo, R., Carbognani, M., Carvalho, F., Casanoves, F., Castagneyrol, B., Catford, J.A., Cavender-Bares, J., Cerabolini, B.E.L., Cervellini, M., Chacón-Madrigal, E., Chapin, K., Chapin, F.S., Chelli, S., Chen, S.-C., Chen, A., Cherubini, P., Chianucci, F., Choat, B., Chung, K.-S., Chytrý, M., Ciccarelli, D., Coll, L., Collins, C.G., Conti, L., Coomes, D., Cornelissen, J.H.C., Cornwell, W.K., Corona, P., Coyea, M., Craine, J., Craven, D., Cromsigt, J.P.G.M., Csecserits, A., Cufar, K., Cuntz, M., Silva, A.C. da, Dahlin, K.M., Dainese, M., Dalke, I., Fratte, M.D., Dang-Le, A.T., Danihelka, J., Dannoura, M., Dawson, S., Beer, A.J. de, Frutos, A.D., Long, J.R.D., Dechant, B., Delagrange, S., Delpierre, N., Derroire, G., Dias, A.S., Diaz-Toribio, M.H., Dimitrakopoulos, P.G., Dobrowolski, M., Doktor, D., Dřevojan, P., Dong, N., Dransfield, J., Dressler, S., Duarte, L., Ducouret, E., Dullinger, S., Durka, W., Duursma, R., Dymova, O., E-Vojtkó, A., Eckstein, R.L., Ejtehadi, H., Elser, J., Emilio, T., Engemann, K., Erfanian, M.B., Erfmeier, A., Esquivel-Muelbert, A., Esser, G., Estiarte, M., Domingues, T.F., Fagan, W.F., Fagúndez, J., Falster, D.S., Fan, Y., Fang, J., Farris, E., Fazlioglu, F., Feng, Y., Fernandez-Mendez, F., Ferrara, C., Ferreira, J., Fidelis, A., Finegan, B., Firn, J., Flowers, T.J., Flynn, D.F.B., Fontana, V., Forey, E., Forgiarini, C., François, L., Frangipani, M., Frank, D., Frenette-Dussault, C., Freschet, G.T., Fry, E.L., Fyllas, N.M., Mazzochini, G.G., Gachet, S., Gallagher, R., Ganade, G., Ganga, F., García-Palacios, P., Gargaglione, V., Garnier, E., Garrido, J.L., Gasper, A.L. de, Gea-Izquierdo, G., Gibson, D., Gillison, A.N., Giroldo, A., Glasenhardt, M.-C., Gleason, S., Gliesch, M., Goldberg, E., Göldel, B., Gonzalez-Akre, E., Gonzalez-Andujar, J.L., González-Melo, A., González-Robles, A., Graae, B.J., Granda, E., Graves, S., Green, W.A., Gregor, T., Gross, N., Guerin, G.R., Günther, A., Gutiérrez, A.G., Haddock, L., Haines, A., Hall, J., Hambuckers, A., Han, W., Harrison, S.P., Hattingh, W., Hawes, J.E., He, T., He, P., Heberling, J.M., Helm, A., Hempel, S., Hentschel, J., Hérault, B., Hereş, A.-M., Herz, K.,

Heuertz, M., Hickler, T., Hietz, P., Higuchi, P., Hipp, A.L., Hirons, A., Hock, M., Hogan, J.A., Holl, K., Honnay, O., Hornstein, D., Hou, E., Hough-Snee, N., Hovstad, K.A., Ichie, T., Igić, B., Illa, E., Isaac, M., Ishihara, M., Ivanov, L., Ivanova, L., Iversen, C.M., Izquierdo, J., Jackson, R.B., Jackson, B., Jactel, H., Jagodzinski, A.M., Jandt, U., Jansen, S., Jenkins, T., Jentsch, A., Jespersen, J.R.P., Jiang, G.-F., Johansen, J.L., Johnson, D., Jokela, E.J., Joly, C.A., Jordan, G.J., Joseph, G.S., Junaedi, D., Junker, R.R., Justes, E., Kabzems, R., Kane, J., Kaplan, Z., Kattenborn, T., Kavelenova, L., Kearsley, E., Kempel, A., Kenzo, T., Kerkhoff, A., Khalil, M.I., Kinlock, N.L., Kissling, W.D., Kitajima, K., Kitzberger, T., Kjøller, R., Klein, T., Kleyer, M., Klimešová, J., Klipel, J., Kloeppel, B., Klotz, S., Knops, J.M.H., Kohyama, T., Koike, F., Kollmann, J., Komac, B., Komatsu, K., König, C., Kraft, N.J.B., Kramer, K., Kreft, H., Kühn, I., Kumarathunge, D., Kuppler, J., Kurokawa, H., Kurosawa, Y., Kuyah, S., Laclau, J.-P., Lafleur, B., Lallai, E., Lamb, E., Lamprecht, A., Larkin, D.J., Laughlin, D., Bagousse-Pinguet, Y.L., Maire, G. le, Roux, P.C. le, Roux, E. le, Lee, T., Lens, F., Lewis, S.L., Lhotsky, B., Li, Y., Li, X., Lichstein, J.W., Liebergesell, M., Lim, J.Y., Lin, Y.-S., Linares, J.C., Liu, C., Liu, D., Liu, U., Livingstone, S., Llusià, J., Lohbeck, M., López-García, Á., Lopez-Gonzalez, G., Lososová, Z., Louault, F., Lukács, B.A., Lukeš, P., Luo, Y., Lussu, M., Ma, S., Pereira, C.M.R., Mack, M., Maire, V., Mäkelä, A., Mäkinen, H., Malhado, A.C.M., Mallik, A., Manning, P., Manzoni, S., Marchetti, Z., Marchino, L., Marcilio-Silva, V., Marcon, E., Marignani, M., Markesteijn, L., Martin, A., Martínez-Garza, C., Martínez-Vilalta, J., Mašková, T., Mason, K., Mason, N., Massad, T.J., Masse, J., Mayrose, I., McCarthy, J., McCormack, M.L., McCulloh, K., McFadden, I.R., McGill, B.J., McPartland, M.Y., Medeiros, J.S., Medlyn, B., Meerts, P., Mehrabi, Z., Meir, P., Melo, F.P.L., Mencuccini, M., Meredieu, C., Messier, J., Mészáros, I., Metsaranta, J., Michaletz, S.T., Michelaki, C., Migalina, S., Milla, R., Miller, J.E.D., Minden, V., Ming, R., Mokany, K., Moles, A.T., Molnár, A., Molofsky, J., Molz, M., Montgomery, R.A., Monty, A., Moravcová, L., Moreno-Martínez, A., Moretti, M., Mori, A.S., Mori, S., Morris, D., Morrison, J., Mucina, L., Mueller, S., Muir, C.D., Müller, S.C., Munoz, F., Myers-Smith, I.H., Myster, R.W., Nagano, M., Naidu, S., Narayanan, A., Natesan, B., Negoita, L., Nelson, A.S., Neuschulz, E.L., Ni, J., Niedrist, G., Nieto, J., Niinemets, Ü., Nolan, R., Nottebrock, H., Nouvellon, Y., Novakovskiy, A., Nystuen, K.O., O'Grady, A., O'Hara, K., O'Reilly-Nugent, A., Oakley, S., Oberhuber, W., Ohtsuka, T., Oliveira, R., Öllerer, K., Olson, M.E., Onipchenko, V., Onoda, Y., Onstein, R.E., Ordonez, J.C., Osada, N., Ostonen, I., Ottaviani, G., Otto, S., Overbeck, G.E., Ozinga, W.A., Pahl, A.T., Paine, C.E.T., Pakeman, R.J., Papageorgiou, A.C., Parfionova, E., Pärtel, M., Patacca, M., Paula, S., Paule, J., Pauli, H., Pausas, J.G., Peco, B., Penuelas, J., Perea, A., Peri, P.L., Petisco-Souza, A.C., Petraglia, A., Petritan, A.M., Phillips, O.L., Pierce, S., Pillar, V.D., Pisek, J., Pomogaybin, A., Poorter, H., Portsmuth, A., Poschlod, P., Potvin, C., Pounds, D., Powell, A.S., Power, S.A., Prinzing, A., Puglielli, G., Pyšek, P., Raevel, V., Rammig, A., Ransijn, J., Ray, C.A., Reich, P.B., Reichstein, M., Reid, D.E.B., Réjou-Méchain, M., Dios, V.R. de, Ribeiro, S., Richardson, S., Riibak, K., Rillig, M.C., Riviera, F., Robert, E.M.R., Roberts, S., Robroek, B., Roddy, A., Rodrigues, A.V., Rogers, A., Rollinson, E., Rolo, V., Römermann, C., Ronzhina, D., Roscher, C., Rosell, J.A., Rosenfield, M.F., Rossi, C., Roy, D.B., Royer-Tardif, S., Rüger, N., Ruiz-Peinado, R., Rumpf, S.B., Rusch, G.M., Ryo, M., Sack, L., Saldaña, A., Salgado-Negret, B., Salguero-Gomez, R., Santa-Regina, I., Santacruz-García, A.C., Santos, J., Sardans, J., Schamp, B., Scherer-Lorenzen, M., Schleuning, M., Schmid, B., Schmidt, M., Schmitt, S., Schneider, J.V., Schowanek, S.D., Schrader, J., Schrodt, F., Schuldt, B., Schurr, F., Garvizu, G.S., Semchenko, M., Seymour, C., Sfair, J.C., Sharpe, J.M., Sheppard, C.S., Sheremetiev, S., Shiodera, S., Shipley, B., Shovon, T.A., Siebenkäs, A., Sierra, C., Silva, V., Silva, M., Sitzia, T., Sjöman, H., Slot, M., Smith, N.G., Sodhi, D., Soltis, P., Soltis, D., Somers, B., Sonnier, G., Sørensen, M.V., Sosinski, E.E., Soudzilovskaia, N.A., Souza, A.F., Spasojevic, M., Sperandii, M.G., Stan, A.B., Stegen, J., Steinbauer, K., Stephan, J.G., Sterck, F., Stojanovic, D.B., Strydom, T., Suarez, M.L., Svenning, J.-C., Svitková, I., Svitok, M., Svoboda, M., Swaine, E., Swenson, N., Tabarelli, M., Takagi, K., Tappeiner, U., Tarifa, R., Tauugourdeau, S., Tavsanoglu, C., Beest,

M. te, Tedersoo, L., Thiffault, N., Thom, D., Thomas, E., Thompson, K., Thornton, P.E., Thuiller, W., Tichý, L., Tissue, D., Tjoelker, M.G., Tng, D.Y.P., Tobias, J., Török, P., Tarin, T., Torres-Ruiz, J.M., Tóthmérész, B., Treurnicht, M., Trivellone, V., Trolliet, F., Trotsiuk, V., Tsakalos, J.L., Tsiripidis, I., Tysklind, N., Umehara, T., Usoltsev, V., Vadeboncoeur, M., Vaezi, J., Valladares, F., Vamosi, J., Bodegom, P.M. van, Breugel, M. van, Cleemput, E.V., Weg, M. van de, Merwe, S. van der, Plas, F. van der, Sande, M.T. van der, Kleunen, M. van, Meerbeek, K.V., Vanderwel, M., Vanselow, K.A., Vårhammar, A., Varone, L., Valderrama, M.Y.V., Vassilev, K., Vellend, M., Veneklaas, E.J., Verbeeck, H., Verheyen, K., Vibrans, A., Vieira, I., Villacís, J., Violle, C., Vivek, P., Wagner, K., Waldram, M., Waldron, A., Walker, A.P., Waller, M., Walther, G., Wang, H., Wang, F., Wang, W., Watkins, H., Watkins, J., Weber, U., Weedon, J.T., Wei, L., Weigelt, P., Weiher, E., Wells, A.W., Wellstein, C., Wenk, E., Westoby, M., Westwood, A., White, P.J., Whitten, M., Williams, M., Winkler, D.E., Winter, K., Womack, C., Wright, I.J., Wright, S.J., Wright, J., Pinho, B.X., Ximenes, F., Yamada, T., Yamaji, K., Yanai, R., Yankov, N., Yguel, B., Zanini, K.J., Zanne, A.E., Zelený, D., Zhao, Y.-P., Zheng, J., Zheng, J., Ziemińska, K., Zirbel, C.R., Zizka, G., Zo-Bi, I.C., Zotz, G. & Wirth, C. (2020) TRY plant trait database – enhanced coverage and open access. *Global Change Biology*, **26**, 119–188.

Keith, L.M., Hughes, R.F., Sugiyama, L.S., Heller, W.P., Bushe, B.C. & Friday, J.B. (2015) First Report of Ceratocystis Wilt on `Ōhi`a (Metrosideros polymorpha). *Plant Disease*, **99**, 1276.

Kembel, S.W. (2009) Disentangling niche and neutral influences on community assembly: assessing the performance of community phylogenetic structure tests. *Ecology Letters*, **12**, 949–960.

King, D.A., Davies, S.J. & Noor, N.S.M. (2006) Growth and mortality are related to adult tree size in a Malaysian mixed dipterocarp forest. *Forest Ecology and Management*, **223**, 152–158.

König, C., Weigelt, P., Taylor, A., Stein, A., Dawson, W., Essl, F., Pergl, J., Pyšek, P., van Kleunen, M., Winter, M., Chatelain, C., Wieringa, J.J., Krestov, P. & Kreft, H. (2021) Source pools and disharmony of the world's island floras. *Ecography*, **44**, 44–55.

Kraft, N.J.B. & Ackerly, D.D. (2010) Functional trait and phylogenetic tests of community assembly across spatial scales in an Amazonian forest. *Ecological Monographs*, **80**, 401–422.

Kraft, N.J.B., Adler, P.B., Godoy, O., James, E.C., Fuller, S. & Levine, J.M. (2015) Community assembly, coexistence and the environmental filtering metaphor. *Functional Ecology*, **29**, 592–599.

Kraft, N.J.B., Valencia, R. & Ackerly, D.D. (2008) Functional Traits and Niche-Based Tree Community Assembly in an Amazonian Forest. *Science*, **322**, 580–582.

Kueffer, C., Daehler, C.C., Torres-Santana, C.W., Lavergne, C., Meyer, J.-Y., Otto, R. & Silva, L. (2010) A global comparison of plant invasions on oceanic islands. *Perspectives in Plant Ecology, Evolution and Systematics*, **12**, 145–161.

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. *Ecology Letters*, **15**, 831–840.

Leihy, R.I., Duffy, G.A. & Chown, S.L. (2018) Species richness and turnover among indigenous and introduced plants and insects of the Southern Ocean Islands. *Ecosphere*, **9**, e02358.

Lemoine, N.P., Shue, J., Verrico, B., Erickson, D., Kress, W.J. & Parker, J.D. (2015) Phylogenetic relatedness and leaf functional traits, not introduced status, influence community assembly. *Ecology*, **96**, 2605–2612.

Leung, B., Roura-Pascual, N., Bacher, S., Heikkilä, J., Brotons, L., Burgman, M.A., Dehnen-Schmutz, K., Essl, F., Hulme, P.E., Richardson, D.M., Sol, D. & Vilà, M. (2012) TEASIng apart alien species risk assessments: a framework for best practices. *Ecology Letters*, **15**, 1475–1493.

Levin, S.C., Crandall, R.M., Pokoski, T., Stein, C. & Knight, T.M. (2020) Phylogenetic and functional distinctiveness explain alien plant population responses to competition. *Proceedings of the Royal Society B: Biological Sciences*, **287**, 20201070.

Li, D. & Ives, A.R. (2017) The statistical need to include phylogeny in trait-based analyses of community

composition. *Methods in Ecology and Evolution*, **8**, 1192–1199.
Lockwood, J.L., Cassey, P. & Blackburn, T. (2005) The role of propagule pressure in explaining species invasions. *Trends in Ecology & Evolution*, **20**, 223–228.
Losos, J.B. & Ricklefs, R.E. (2009) Adaptation and diversification on islands. *Nature*, **457**, 830.
Ma, C., Li, S., Pu, Z., Tan, J., Liu, M., Zhou, J., Li, H. & Jiang, L. (2016) Different effects of invader–native phylogenetic relatedness on invasion success and impact: a meta-analysis of Darwin's naturalization hypothesis. *Proceedings of the Royal Society B: Biological Sciences*, **283**, 20160663.
Mack, R.N., Simberloff, D., Lonsdale, W.M., Evans, H., Clout, M. & Bazzaz, F.A. (2000) Biotic Invasions: Causes, Epidemiology, Global Consequences, and Control. *Ecological Applications*, **10**, 689–710.
Maitner, B. (2020) BIEN: tools for accessing the botanical information and ecology network database. *R package version 1.2.5*.
Marx, H.E., Giblin, D.E., Dunwiddie, P.W. & Tank, D.C. (2016) Deconstructing darwin's naturalization conundrum in the san juan islands using community phylogenetics and functional traits. *Diversity and Distributions*, **22**, 318–331.
Mortenson, L.A., Flint Hughes, R., Friday, J.B., Keith, L.M., Barbosa, J.M., Friday, N.J., Liu, Z. & Sowards, T.G. (2016) Assessing spatial distribution, stand impacts and rate of Ceratocystis fimbriata induced ʻōhiʻa (Metrosideros polymorpha) mortality in a tropical wet forest, Hawaiʻi Island, USA. *Forest Ecology and Management*, **377**, 83–92.
Moser, D., Lenzner, B., Weigelt, P., Dawson, W., Kreft, H., Pergl, J., Pyšek, P., Kleunen, M. van, Winter, M., Capinha, C., Cassey, P., Dullinger, S., Economo, E.P., García-Díaz, P., Guénard, B., Hofhansl, F., Mang, T., Seebens, H. & Essl, F. (2018) Remoteness promotes biological invasions on islands worldwide. *Proceedings of the National Academy of Sciences*, **115**, 9270–9275.
Muller-Landau, H.C. (2004) Interspecific and Inter-site Variation in Wood Specific Gravity of Tropical Trees. *Biotropica*, **36**, 20–32.
Muller-Landau Helene C. (2010) The tolerance–fecundity trade-off and the maintenance of diversity in seed size. *Proceedings of the National Academy of Sciences*, **107**, 4242–4247.
Ni, M., Deane, D.C., Li, S., Wu, Y., Sui, X., Xu, H., Chu, C., He, F. & Fang, S. (2021) Invasion success and impacts depend on different characteristics in non-native plants. *Diversity and Distributions*, **27**, 1194–1207.
Ostertag, R., Inman-Narahari, F., Cordell, S., Giardina, C.P. & Sack, L. (2014) Forest structure in low-diversity tropical forests: a study of Hawaiian wet and dry forests. *PLOS ONE*, **9**, 1–18.
Park Daniel S., Feng Xiao, Maitner Brian S., Ernst Kacey C. & Enquist Brian J. (2020) Darwin's naturalization conundrum can be explained by spatial scale. *Proceedings of the National Academy of Sciences*, **117**, 10904–10910.
Pearse, W.D., Cadotte, M.W., Cavender-Bares, J., Ives, A.R., Tucker, C.M., Walker, S.C. & Helmus, M.R. (2015) pez: phylogenetics for the environmental sciences. *Bioinformatics*, **31**, 2888–2890.
Pearson, D.E., Ortega, Y.K., Eren, Ö. & Hierro, J.L. (2018) Community Assembly Theory as a Framework for Biological Invasions. *Trends in Ecology & Evolution*, **33**, 313–325.
Penone, C., Davidson, A.D., Shoemaker, K.T., Marco, M.D., Rondinini, C., Brooks, T.M., Young, B.E., Graham, C.H. & Costa, G.C. (2014) Imputation of missing data in life-history trait datasets: which approach performs the best? *Methods in Ecology and Evolution*, **5**, 961–970.
Perelman, S.B., Chaneton, E.J., Batista, W.B., Burkart, S.E. & León, R.J.C. (2007) Habitat stress, species pool size and biotic resistance influence exotic plant richness in the Flooding Pampa grasslands. *Journal of Ecology*, **95**, 662–673.
Pierce, S., Brusa, G., Vagge, I. & Cerabolini, B.E.L. (2013) Allocating CSR plant functional types: the use of leaf economics and size traits to classify woody and herbaceous vascular plants. *Functional Ecology*, **27**, 1002–1010.
Pyšek, P., Jarošík, V., Hulme, P.E., Kühn, I., Wild, J., Arianoutsou, M., Bacher, S., Chiron, F., Didžiulis, V., Essl, F., Genovesi, P., Gherardi, F., Hejda, M., Kark, S., Lambdon, P.W., Desprez-Loustau,

M.-L., Nentwig, W., Pergl, J., Poboljšaj, K., Rabitsch, W., Roques, A., Roy, D.B., Shirley, S., Solarz, W., Vilà, M. & Winter, M. (2010) Disentangling the role of environmental and human pressures on biological invasions across Europe. *Proceedings of the National Academy of Sciences*, **107**, 12157–12162.

Qian, H., Jin, Y. & Ricklefs, R.E. (2017) Patterns of phylogenetic relatedness of angiosperm woody plants across biomes and life-history stages. *Journal of Biogeography*, **44**, 1383–1392.

Qian, H. & Sandel, B. (2022) Darwin's preadaptation hypothesis and the phylogenetic structure of native and alien regional plant assemblages across North America. *Global Ecology and Biogeography*, **31**, 531–545.

R Core Team (2020) *R: A Language and Environment for Statistical Computing*, R Foundation for Statistical Computing, Vienna, Austria.

Ricciardi, A., Hoopes, M.F., Marchetti, M.P. & Lockwood, J.L. (2013) Progress toward understanding the ecological impacts of nonnative species. *Ecological Monographs*, **83**, 263–282.

Richardson, D.M. & Pyšek, P. (2012) Naturalization of introduced plants: ecological drivers of biogeographical patterns. *New Phytologist*, **196**, 383–396.

Richardson, D.M. & Rejmánek, M. (2011) Trees and shrubs as invasive alien species – a global review. *Diversity and Distributions*, **17**, 788–809.

van der Sande, M.T., Bruelheide, H., Dawson, W., Dengler, J., Essl, F., Field, R., Haider, S., van Kleunen, M., Kreft, H., Pagel, J., Pergl, J., Purschke, O., Pyšek, P., Weigelt, P., Winter, M., Attorre, F., Aubin, I., Bergmeier, E., Chytrý, M., Dainese, M., De Sanctis, M., Fagundez, J., Golub, V., Guerin, G.R., Gutiérrez, A.G., Jandt, U., Jansen, F., Jiménez-Alfaro, B., Kattge, J., Kearsley, E., Klotz, S., Kramer, K., Moretti, M., Niinemets, Ü., Peet, R.K., Penuelas, J., Petřík, P., Reich, P.B., Sandel, B., Schmidt, M., Sibikova, M., Violle, C., Whitfeld, T.J.S., Wohlgemuth, T. & Knight, T.M. (2020) Similar factors underlie tree abundance in forests in native and alien ranges. *Global Ecology and Biogeography*, **29**, 281–294.

Sapsford, S.J., Brandt, A.J., Davis, K.T., Peralta, G., Dickie, I.A., Gibson, R.D., Green, J.L., Hulme, P.E., Nuñez, M.A., Orwin, K.H., Pauchard, A., Wardle, D.A. & Peltzer, D.A. (2020) Towards a framework for understanding the context dependence of impacts of non-native tree species. *Functional Ecology*, **34**, 944–955.

Sax, D.F. & Gaines, S.D. (2008) Species invasions and extinction: the future of native biodiversity on islands. *Proceedings of the National Academy of Sciences*, **105**, 11490–11497.

Schaefer, H., Hardy, O.J., Silva, L., Barraclough, T.G. & Savolainen, V. (2011) Testing Darwin's naturalization hypothesis in the Azores. *Ecology letters*, **14**, 389–396.

Schluter, D. & Pennell, M.W. (2017) Speciation gradients and the distribution of biodiversity. *Nature*, **546**, 48–55.

Seebens, H., Blackburn, T.M., Dyer, E.E., Genovesi, P., Hulme, P.E., Jeschke, J.M., Pagad, S., Pyšek, P., Winter, M., Arianoutsou, M., Bacher, S., Blasius, B., Brundu, G., Capinha, C., Celesti-Grapow, L., Dawson, W., Dullinger, S., Fuentes, N., Jäger, H., Kartesz, J., Kenis, M., Kreft, H., Kühn, I., Lenzner, B., Liebhold, A., Mosena, A., Moser, D., Nishino, M., Pearman, D., Pergl, J., Rabitsch, W., Rojas-Sandoval, J., Roques, A., Rorke, S., Rossinelli, S., Roy, H.E., Scalera, R., Schindler, S., Štajerová, K., Tokarska-Guzik, B., van Kleunen, M., Walker, K., Weigelt, P., Yamanaka, T. & Essl, F. (2017) No saturation in the accumulation of alien species worldwide. *Nature Communications*, **8**, 14435.

Sherrod, D.R., Sinton, J.M., Watkins, S.E. & Brunt, K.M. (2007) *Geologic map of the State of Hawaii*, Geological Survey (US).

Shiels, A.B. (2011) Frugivory by introduced black rats (Rattus rattus) promotes dispersal of invasive plant seeds. *Biological Invasions*, **13**, 781–792.

Simberloff, D., Martin, J.-L., Genovesi, P., Maris, V., Wardle, D.A., Aronson, J., Courchamp, F., Galil, B., García-Berthou, E., Pascal, M., Pyšek, P., Sousa, R., Tabacchi, E. & Vilà, M. (2013) Impacts of biological invasions: what's what and the way forward. *Trends in Ecology & Evolution*, **28**, 58–66.

Spake, R., Mori, A.S., Beckmann, M., Martin, P.A., Christie, A.P., Duguid, M.C. & Doncaster, C.P. (2021) Implications of scale dependence for cross-study syntheses of biodiversity differences. *Ecology Letters*, **24**, 374–390.

Sperry, J.H., O'Hearn, D., Drake, D.R., Hruska, A.M., Case, S.B., Vizentin-Bugoni, J., Arnett, C., Chambers, T. & Tarwater, C.E. (2021) Fruit and seed traits of native and invasive plant species in Hawai'i: implications for seed dispersal by non-native birds. *Biological Invasions*, **23**, 1819–1835.

Spicer, R. & Groover, A. (2010) Evolution of development of vascular cambia and secondary growth. *New Phytologist*, **186**, 577–592.

Stohlgren, T.J., Barnett, D.T. & Kartesz, J.T. (2003) The rich get richer: patterns of plant invasions in the United States. *Frontiers in Ecology and the Environment*, **1**, 11–14.

Taylor, A., Weigelt, P., König, C., Zotz, G. & Kreft, H. (2019) Island disharmony revisited using orchids as a model group. *New Phytologist*, **223**, 597–606.

Tecco, P.A., Díaz, S., Cabido, M. & Urcelay, C. (2010) Functional traits of alien plants across contrasting climatic and land-use regimes: do aliens join the locals or try harder than them? *Journal of Ecology*, **98**, 17–27.

Tershy, B.R., Shen, K.-W., Newton, K.M., Holmes, N.D. & Croll, D.A. (2015) The importance of islands for the protection of biological and linguistic diversity. *BioScience*, **65**, 592–597.

Thomson, F.J., Moles, A.T., Auld, T.D. & Kingsford, R.T. (2011) Seed dispersal distance is more strongly correlated with plant height than with seed mass. *Journal of Ecology*, **99**, 1299–1307.

Thuiller, W., Gallien, L., Boulangeat, I., Bello, F.D., Münkemüller, T., Roquet, C. & Lavergne, S. (2010) Resolving Darwin's naturalization conundrum: a quest for evidence. *Diversity and Distributions*, **16**, 461–475.

Tucker, C.M., Davies, T.J., Cadotte, M.W. & Pearse, W.D. (2018) On the relationship between phylogenetic diversity and trait diversity. *Ecology*, **99**, 1473–1479.

Uriarte, M., Swenson, N.G., Chazdon, R.L., Comita, L.S., Kress, W.J., Erickson, D., Forero-Montaña, J., Zimmerman, J.K. & Thompson, J. (2010) Trait similarity, shared ancestry and the structure of neighbourhood interactions in a subtropical wet forest: implications for community assembly. *Ecology Letters*, **13**, 1503–1514.

US Forest Service (2016) Forest inventory and analysis national core field guide, Volume 1: Field data collection procedures for Phase 2 Plots, version 7.1.

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. *Ecology Letters*, **14**, 702–708.

Vitousek, P.M., Walker, L.R., Whiteaker, L.D., Mueller-Dombois, D. & Matson, P.A. (1987) Biological invasion by Myrica faya alters ecosystem development in Hawaii. *Science*, **238**, 802–804.

Wagner, W., Herbst, D. & Lorence, D. (2005) Flora of the Hawaiian Islands website. *(https://naturalhistory2.si.edu/botany/hawaiianflora/)*.

Westerband, A.C., Knight, T.M. & Barton, K.E. (2021) Intraspecific trait variation and reversals of trait strategies across key climate gradients in native Hawaiian plants and non-native invaders. *Annals of Botany*, **127**, 553–564.

Whittaker, R.J., Fernández-Palacios, J.M., Matthews, T.J., Borregaard, M.K. & Triantis, K.A. (2017) Island biogeography: Taking the long view of nature's laboratories. *Science*, **357**.

Whittaker, R.J., Triantis, K.A. & Ladle, R.J. (2008) A general dynamic theory of oceanic island biogeography. *Journal of Biogeography*, **35**, 977–994.

Wildlife Conservation Society - WCS & Center for International Earth Science Information Network - CIESIN - Columbia University (2005) Last of the Wild Project, Version 2, 2005 (LWP-2): Global Human Influence Index (HII) Dataset (Geographic).

Wohlwend, M.R., Craven, D., Weigelt, P., Seebens, H., Winter, M., Kreft, H., Zurell, D., Cabral, J.S., Essl, F., Kleunen, M. van, Pergl, J., Pyšek, P. & Knight, T.M. (2021) Anthropogenic and environmental drivers shape diversity of naturalized plants across the Pacific. *Diversity and*

Distributions, **27**, 1120– 1133.
Zarnetske, P.L., Gouhier, T.C., Hacker, S.D., Seabloom, E.W. & Bokil, V.A. (2013) Indirect effects and facilitation among native and non-native species promote invasion success along an environmental stress gradient. *Journal of Ecology*, **101**, 905–915.
Zimmerman, N., Flint Hughes, R., Cordell, S., Hart, P., Chang, H.K., Perez, D., Like, R.K. & Ostertag, R. (2008) Patterns of primary succession of native and introduced plants in lowland wet forests in eastern Hawai ‘i. *Biotropica*, **40**, 277–284.
Zimmerman, N., Hughes, R., Cordell, S., Hart, P., Chang, H., Perez, D., Like, R. & Ostertag, R. (2007) *Data from: Patterns of primary succession of native and introduced plants in lowland wet forests in eastern Hawai‘i*, Dryad Digital Repository.
Zomer, R.J., Trabucco, A., Bossio, D.A. & Verchot, L.V. (2008) Climate change mitigation: A spatial analysis of global land suitability for clean development mechanism afforestation and reforestation. *Agriculture, Ecosystems & Environment*, **126**, 67–80.