

Factors associated with alien plant richness, cover and composition differ in tropical island forests

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Abstract

Aim: To examine how native plant native communities, environment and geography are associated with alien plant species invasion in tropical island forests.

Location: Four US national parks in Hawai'i and American Samoa.

Methods: We analysed the richness, coverage and composition of alien plant species communities located across 204 plots, five islands and two archipelagos. We used generalized linear mixed-effects models and generalized dissimilarity models to determine the relative importance of native plant species communities (richness, structure and composition), environment (temperatures, precipitation, and soil age) and geography (elevation, geographical distance between plots, identity of islands and archipelagos) on alien plant species communities.

Results: Alien plant species were found in >90% of plots with on average four species covering ~15% of the understorey. Variation in alien species richness and coverage was primarily explained by archipelago and island identity and elevation. Plots located on younger islands tended to exhibit higher richness and coverage of alien plants. Native tree density and canopy height were negatively correlated with alien species coverage but not with alien species richness. Elevation was negatively correlated with both the richness and coverage of alien species. Differences in elevation, mean annual precipitation and geographical distances explained about 40% of the observed spatial turnover in alien species composition with differences in elevation being the main driver. Turnover in alien species composition was weakly correlated with turnover in native species.

Main conclusions: In the studied islands, higher elevations seem to be relatively spared from alien species invasion so far. However, our results suggest that the negative effect of elevation on alien species coverage may be larger than on alien species richness. Maintenance of tall and dense canopy may limit the coverage of alien species but not the number of alien species. Our results also support that alien species invasion may be particularly high on isolated archipelagos and younger islands.

KEYWORDS

biodiversity, climate, elevation, exotic, non-native, precipitation, resistance, richness, temperature, turnover

1 | INTRODUCTION

The invasion of native communities by alien (exotic or non-native) species is one of the main threats to biodiversity. Island biodiversity is particularly threatened and vulnerable to invasion by alien species (Caujapé-Castells et al., 2010; Denslow, 2003; Moser et al., 2018). Compared to mainland, islands have more alien species with small tropical islands exhibiting a disproportionately high number of alien species relative to their size (Dawson et al., 2017; Lonsdale, 1999; Turbelin, Malamud, & Francis, 2017; Westphal, Browne, MacKinnon, & Noble, 2008). Understanding how alien species invasions vary between and within these small tropical islands is of critical importance to managing this threat.

To establish and spread in native island communities, alien plant species have to overcome several filters. First, they must reach the island (i.e., the dispersal filter), then grow, survive and reproduce under local environmental conditions (i.e., the abiotic filter), while facing competition and other interactions with native communities (i.e., the biotic filter) (Blackburn et al., 2011; Pearson, Ortega, Eren, & Hierro, 2018; Richardson & Pyšek, 2006; Theoharides & Dukes, 2007). The dispersal filter is often overcome with the help of anthropogenic transportation supported by intentional (e.g., for horticulture, agriculture or botanical gardens) or unintentional importation to islands (Turbelin et al., 2017). The dispersal of alien species is indeed better correlated to socio-economic factors (e.g., island population, gross domestic product or degree of international trade) than geographical factors (Blackburn, Delean, Pyšek, & Cassey, 2016; Dawson et al., 2017; Kueffer et al., 2010; Moser et al., 2018; Westphal et al., 2008).

On a global scale, the abiotic filter seems to be of low importance to determining the degree of alien plant species invasion. Most studies have found no effect of climate (Kueffer et al., 2010; Moser et al., 2018) or a weak positive effect of temperature (Blackburn et al., 2016; Dawson et al., 2017) on differences in alien species richness between islands. Within islands, alien species richness tends to decrease at higher elevations (e.g., Arévalo et al., 2005; Guo et al., 2018; Jakobs, Kueffer, & Daehler, 2010; Ohlemüller, Walker, & Wilson, 2006; Tanaka & Sato, 2016). This decrease is due to the effects of several confounding factors, including decreasing temperature, human disturbance, propagule pressure and greater biotic resistance (Pauchard et al., 2009). Nutrient and water availability are additional abiotic factors likely to affect the success of alien plant species invasion within islands (Alpert, Bone, & Holzapfel, 2000). On volcanic islands, nutrient availability varies with soil age (e.g., Hughes & Denslow, 2005; Vitousek, Aplet, Turner, & Lockwood, 1992), and low nutrient availability on young soils may constitute an important filter to alien species invasion (e.g., Ostertag & Verville, 2002; Zimmerman et al., 2008). Surprisingly, the effect of water availability on alien species invasion, for example along precipitation gradients, has been hardly explored (Alpert et al., 2000; Walther et al., 2009).

The biotic filter has raised considerable interest in invasion ecology. The hypothesis that the biotic resistance of native communities to alien species invasion increases with diversity (Elton,

1958) is one of the most popular and controversial hypotheses to explain the higher degree of invasion on islands compared to mainland (Denslow, 2003; Levine & D'Antonio, 1999; Richardson & Pyšek, 2006, 2008; Simberloff, 1995; Vitousek, D'Antonio, Loope, Rejmanek, & Westbrooks, 1997). Indeed, because the factors and processes driving the invasibility of native communities vary with context (e.g., propagule pressure, environment or disturbance regime) and across spatio-temporal scales, both positive and negative relationships between native and alien species richness can be observed (Clark & Johnston, 2011; Davies, Harrison, Safford, & Viers, 2007; Fridley et al., 2007; Gurevitch, Fox, Wardle, & Taub, 2011). For instance, on a regional to global scale, more favourable or diverse environmental conditions may support higher native and alien species richness (leading to positive relationships), while on smaller scales (where biotic interactions occur and environmental conditions can be considered homogeneous), higher native species richness leaves fewer resources and niche opportunities to alien species, leading to negative relationships (Davies et al., 2007; Fridley et al., 2007; Shea & Chesson, 2002; Stohlgren et al., 1999).

Invasive alien species tend to be fast-growing and light-demanding (van Kleunen, Weber, & Fischer, 2010; Leishman, Haslehurst, Ares, & Baruch, 2007; Rejmanek & Richardson, 1996). As a result, the low level of light availability in the understorey of undisturbed forests tends to make them relatively resistant to alien species invasion (Fine, 2002). Higher light availability is also one of the factors explaining the higher degree of alien species invasion at forest edges or canopy gaps in comparison with forest interiors (e.g., Arellano-Cataldo & Smith-Ramírez, 2016; Green, Lake, & O'Dowd, 2004). However, even if the number of shade-tolerant invasive species is much lower, these species are often able to deeply invade undisturbed forests (Martin, Canham, & Marks, 2009). For instance, two of the greatest threats to the native forest of Pacific islands are the shade-tolerant tree *Miconia calvescens* (Melastomataceae) (e.g., Medieros, Loope, Conant, & McElvaney, 1997; Meyer & Florence, 1996) and shrub *Clidemia hirta* (Melastomataceae) (e.g., DeWalt, Denslow, & Ickes, 2004; Peters, 2001).

Lastly, several studies have tested whether the geophysical parameters of islands or archipelagos affect the degree of invasion on islands. The theory of island biogeography (MacArthur & Wilson, 1967) predicts that the number of species on an island results from an equilibrium between species immigration and extinction which in turn are affected by the size and isolation of islands. The general dynamic theory of oceanic island biogeography (Whittaker, Kostas, & Richard, 2008) supplemented this theory by adding the effect of island age and speciation. It predicts that the number of species on an island peaks at intermediate age, when high elevation and complex topography offer the highest diversity of environmental niches. All studies support the prediction that native and alien plant species richness increases with island size, elevation or habitat diversity (Blackburn et al., 2016; Dawson et al., 2017; Denslow, Space, & Thomas, 2009; Kueffer et al., 2010; Moser et al., 2018). However, contrary to native species, alien plant species richness tends to increase with island isolation (Denslow et al., 2009; Moser et al., 2018).

although some studies have found weak (Kueffer et al., 2010) or no effects (Traveset, Kueffer, & Daehler, 2014). Blackburn et al., (2016), suggested that isolation indirectly affects alien plant species richness through its effect on native species richness. The effect of island age on alien species richness has received less attention. Kueffer et al., (2010) found that within an archipelago, older islands tend to be less invaded and suggested that on younger islands, less diverse flora may leave more niche opportunities favouring invasions.

Here, we use plot data from forests located in Hawai'i and American Samoa, two archipelagos belonging to the Polynesia-Micronesia biodiversity hotspot (Mittermeier et al., 2005), to examine how native plant communities, environment and geography are associated with alien plant species invasion. We test the prediction that tree density, canopy height and the taxonomic richness of native plant communities play an important role in determining the resistance of native forests to invasion by alien species. We expect that (a) forests with high native tree density and high canopies prevent the establishment (i.e., lower richness) and growth (i.e., lower coverage) of alien species by decreasing light availability, and (b) the species richness and composition of native communities affect the species richness and composition of alien communities by determining available niches and levels of competition. We also expect that environment and geography should play an important role in determining the degrees of alien plant invasion. In particular, (c) the richness and coverage of alien plant species should be higher at lower elevations (higher temperature, disturbance and propagule pressure), on older soils (higher nutrient availability), in areas receiving higher precipitation (higher water availability), and on small and isolated islands (lower native plant diversity).

2 | METHODS

2.1 | Study sites

We analysed spatial variation in alien plant species richness, coverage and composition across 204 plots located in four United States National Parks. Plots were located in two archipelagos (Hawai'i and American Samoa) and five islands (Table 1). In the National Park of American Samoa, plots were located on two different islands: Tutuila and Ta'u. Each island is volcanic but differed in age, size and elevation (Figure 1). The Hawaiian and American Samoan islands are about the same distance from the nearest continent (~4,100 km west of North America and 3,900 km east of Australia, respectively); however, the Samoan archipelago (American Samoa and Samoa) is better connected to Australia and Papua New Guinea due to the presence of the Melanesian islands (e.g., Samoa is located ~850 km north-east of Fiji).

Both Hawaiian and American Samoan islands were formed by volcanic hotspots. In Hawai'i, the hotspot is currently located about 30 km south-east of the Island of Hawai'i in the vicinity of the Lō'ihi submarine volcano, and in American Samoa, the hotspot is located about 45 km east of Ta'u island in the vicinity of the Vailulu'u submarine volcano (McDougall, 2010; Neall & Trewick, 2008). Island age

increases from south-east to north-west in Hawai'i and from east to west in American Samoa.

On the Island of Hawai'i, plots were located on the active Kilauea and Mauna Loa volcanoes. This activity results in a mosaic of soils with different ages: the oldest ones originate from lava flows that occurred ~50 ka ago and the youngest ones from lava flows that occurred in 2018. No detailed map of soil ages are available for Ta'u island, but the island is ~20–70 ka (McDougall, 2010). The other islands (Maui, Molokai and Tutuila) being older (0.75–1.90 Ma), we assumed that within islands variations in soil age is of minor importance. The effect of soil age on alien species richness and coverage was therefore only explored for plots located in the Island of Hawai'i.

2.2 | Vegetation surveys

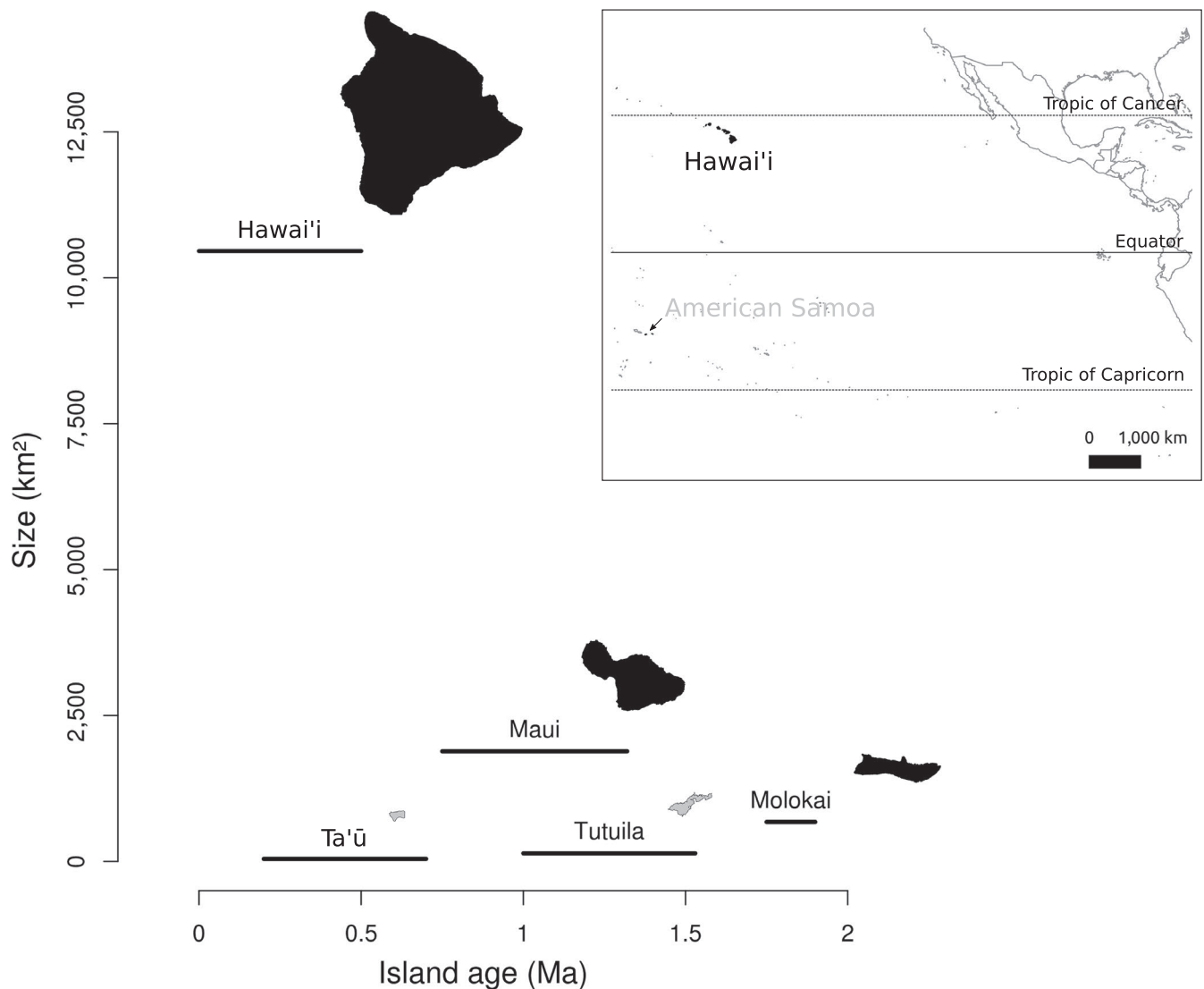
Vegetation surveys were conducted between 2010 and 2016 in relatively undisturbed wet forests (Ainsworth, Berkowitz, Jacobi, Loh, & Kozar, 2011). In each 0.1-ha plots (20 m × 50 m), all native and alien vascular plant species were inventoried. Trees and woody plants (i.e., excluding tree ferns and palms) with a stem diameter ≥10 cm at ~1.3 m above the base (DBH, diameter at breast height) were recorded. We computed native tree density as the number of native trees per plot and canopy height as the average height of three trees representative of the canopy. In most plots (>70%), the canopy was exclusively comprised of native trees. When present in the canopy, alien trees made up only 13% of trees, on average. The coverage of alien species was measured using the point-intercept method (Elzinga, Salzer, Willoughby, & Gibbs, 2001) along three 50-m transects located along the two long edges and middle of the plot. Along these transects, the presence of species was recorded every 0.5 m if one or more species intercepted a 2-m height pole. The coverage of alien species was computed as the ratio between the number of measurement points where an alien species was intercepted and the total number of measurement points (i.e., 300 points). Highly invasive alien species were identified using the "100 of the world's worst invasive alien species" species list, which encompasses 33 terrestrial plant species (Global Invasive Species Database 2018, http://www.iucngisd.org/gisd/100_worst.php).

2.3 | Environmental features

Mean annual precipitation (MAP), minimal ($T_{\min}$) and maximal temperature ($T_{\max}$) were extracted for each plot locations from the PRISM (Parameter-elevation Regressions on Independent Slopes Model) gridded climatic data (PRISM Climate Group, Oregon State University, <http://prism.oregonstate.edu>, created 4 February 2004). This data set is 15-arc-second (~450 m) spatial resolution and has been computed using 1971–2000 climatic series. Elevation was extracted from USGS 10-DEM (digital elevation model). For plots located on the Island of Hawai'i, we extracted soil age from the USGS Geologic Map of the State of Hawai'i with a spatial resolution of 1:250,000 (Sherrod, Sinton, Watkins, & Brunt, 2007; <http://pubs.usgs.gov/of/2007/1089/>).

TABLE 1 Studied national parks in Hawai'i and American Samoa

Codes	Parks	Archipelagos	Islands (age Ma)	Number of plots	Elevation (m)
HAVO	Hawai'i Volcanoes	Hawai'i	Hawai'i (0–0.50)	103	650–1,950
HALE	Haleakala	Hawai'i	Maui (0.75–1.32)	30	750–2,000
KALA	Kalaupapa	Hawai'i	Molokai (1.75–1.90)	30	900–1,250
NPSA	National Park of American Samoa	American Samoa	Ta'ū (0.02–0.07)	12	300–600
NPSA	National Park of American Samoa	American Samoa	Tutuila (1.00–1.53)	29	50–400

**FIGURE 1** Location, age and size of sampled islands in Hawai'i and American Samoa. Horizontal lines represent the minimal and maximal age of islands. Islands elevations are 4,205 m (Hawai'i), 3,055 m (Maui), 1,512 m (Molokai), 784 m (Ta'ū) and 653 m (Tutuila)

2.4 | Statistical analyses

All analyses were performed using R 3.4.4 (R Core Team, 2018). We used generalized linear mixed-effect models to examine the fixed effects of the richness and structure (tree density and canopy height) of native communities, elevation, mean annual precipitation, and the random effects of island and archipelago identity on alien species

richness and coverage (see Bunnefeld & Phillimore, 2012). Minimal and maximal temperatures were not included as explanatory variable as they strongly correlated with elevation (Figure S1).

A Poisson distribution was used for alien species richness and a Binomial distribution for alien species coverage using the *glmer* function from the *lme4* R package (Bates, Mächler, Bolker, & Walker, 2015). This analysis was also performed separately for the island of

Hawai'i to assess the effects of soil age on alien species communities. The log-transformed soil age was then added as a fixed effect and the identity of sampling frames as random effects.

We used the *MuMIn* R package (Bartoń, 2016) and the *dredge* function to generate different sets of models representing all possible combinations of subsets of fixed effects. We then selected the best models based on their corrected Akaike information criterion (AIC_c), which express the quality of a model as a function of the goodness of fit (maximum likelihood) and the number of parameters ($\Delta AIC_c < 2$ from the best models, Burnefeld & Phillimore, 2012). We used conditional R^2 (with random effects) and marginal R^2 (without random effects) to assess the relative importance of fixed and random effects in GLMMs (Nakagawa & Schielzeth, 2013).

Given that some studied plots are located close to each other (Figure 2), spatial autocorrelation in a models' residuals may violate the assumptions of the models and compromise the interpretation of the results (Dormann et al., 2007). To avoid spatial autocorrelation, we subsampled the data set before fitting the models. For each island, we built a dendrogram (*hclust* function) based on the geographical distance between plots and Ward's grouping method. We then cut the dendrogram at 1,000 m height (*cutree* function) to group plots and randomly sampled one plot per group. As a result, no plots were located closer than 300 m from another plot in the subsamples. Random subsampling was done 100 times and the parameters of the best models were averaged using the *model.avg* function. We estimated the effects of each variable as the average of averaged parameters. Averaged parameters were computed by only averaging over the models where the variables were selected within the best models. We also computed the number of times variables were selected within the best models among the 100 iterations as an indicator of the robustness of the effects of variables. Finally, we tested the spatial autocorrelation in models' residuals using the Morans' index and semivariogram computed with the *ape* (Paradis & Schiepe, 2018) and *GeoR* (Ribeiro & Diggle, 2018) R packages.

We then investigated the relative importance of environmental distances (differences in elevation and mean annual precipitation), and geographical distance between plots in driving spatial turnover in alien and native species composition (changes in species composition between plots) using generalized dissimilarity modelling (GDM, Ferrier, Manion, Elith, & Richardson, 2007) computed with the *gdm* function of the *gdm* R package (Manion et al., 2017). GDMs use monotonically increasing *l*-splines to model species turnover as a function of environmental distances and geographical distance between pairs of plots (Fitzpatrick et al., 2013; König, Weigelt, & Kreft, 2017). Species turnover was computed as the Simpson dissimilarity index (β_{sim}) using the *beta.pair* function of the *betapart* package (Baselga & Orme, 2012). We used the *gdm.varImp* function (*gdm* R package) to perform stepwise backward procedures with matrix permutation tests (50 permutations per step) and remove non-significant predictors (p -value $> .05$) from the models. To assess the effect of archipelago identity on alien species turnover, we compared the results obtained from these analyses using all pairs of plots and after removing the pairs of plots located on different archipelagos.

The proportion of variance explained by environment and geographical distance between plots was estimated by comparing the variance explained by different models computed with both environment and geographical distance as predictors (full models) and with only environment or geographical distance as predictors (Legendre, 2008). Finally, to assess whether the composition of alien communities may be affected by the composition of native communities, we tested the correlation between the residuals of the full GDMs, that is, the variance in alien and native species turnover unexplained by environment and geographical distance.

3 | RESULTS

3.1 | State of the invasion

Alien species were found in $>90\%$ of the studied plots (Figure 2). On average, four alien species covering about 15% of the understorey were found in each plot. The average alien species richness did not vary significantly between islands but their average coverage was lower on Tutuila (2.6%) and higher on the Island of Hawai'i (19.4%) (pairwise Wilcoxon rank-sum tests, p value $< .05$). A total of 107 alien species were inventoried among which six belong to the "100 of the world's worst invasive alien species": *Clidemia hirta* (Melastomataceae), *Hedygium gardnerianum* (Zingiberaceae), *Mikania micrantha* (Asteraceae), *Morella faya* (Myricaceae), *Psidium cattleianum* (Myrtaceae) and *Rubus ellipticus* (Rosaceae). At least one of these highly invasive species was present in 55% of the plots (Figure 2).

3.2 | Species richness and coverage

Elevation and native communities together with the identity of the island and archipelago explained $\sim 70\%$ and 65% of the variation in alien species richness and coverage among plots, respectively (Figure 3). About half of this variance was explained by island and archipelago identity (random effects), mostly at the archipelago scale with lower alien richness and coverage in plots located in American Samoa compared to those located on Hawaiian islands (Figure 3). At the island scale, plots located on the youngest islands, Ta'u in American Samoa and the island of Hawai'i in Hawai'i, had higher richness and coverage of alien plant species than on the other islands of their respective archipelagos.

Among the fixed effects, elevation had by far the strongest effects, with negative effects on both the richness and coverage of alien plant species (Figure 3). The effect of elevation was particularly consistent in parks located on Maui and Molokai where both the richness and coverage of alien species dramatically decrease at $\sim 1,000$ m (Figure 4). Mean annual precipitation had weak effects on both alien species coverage and richness. The richness of native species had a significant but weak positive effect on the richness of alien species, while it did not significantly affect alien species coverage. Conversely, the density of native trees and the height of the canopy both had negative effects on the coverage of alien species with weak or no effects on their richness.

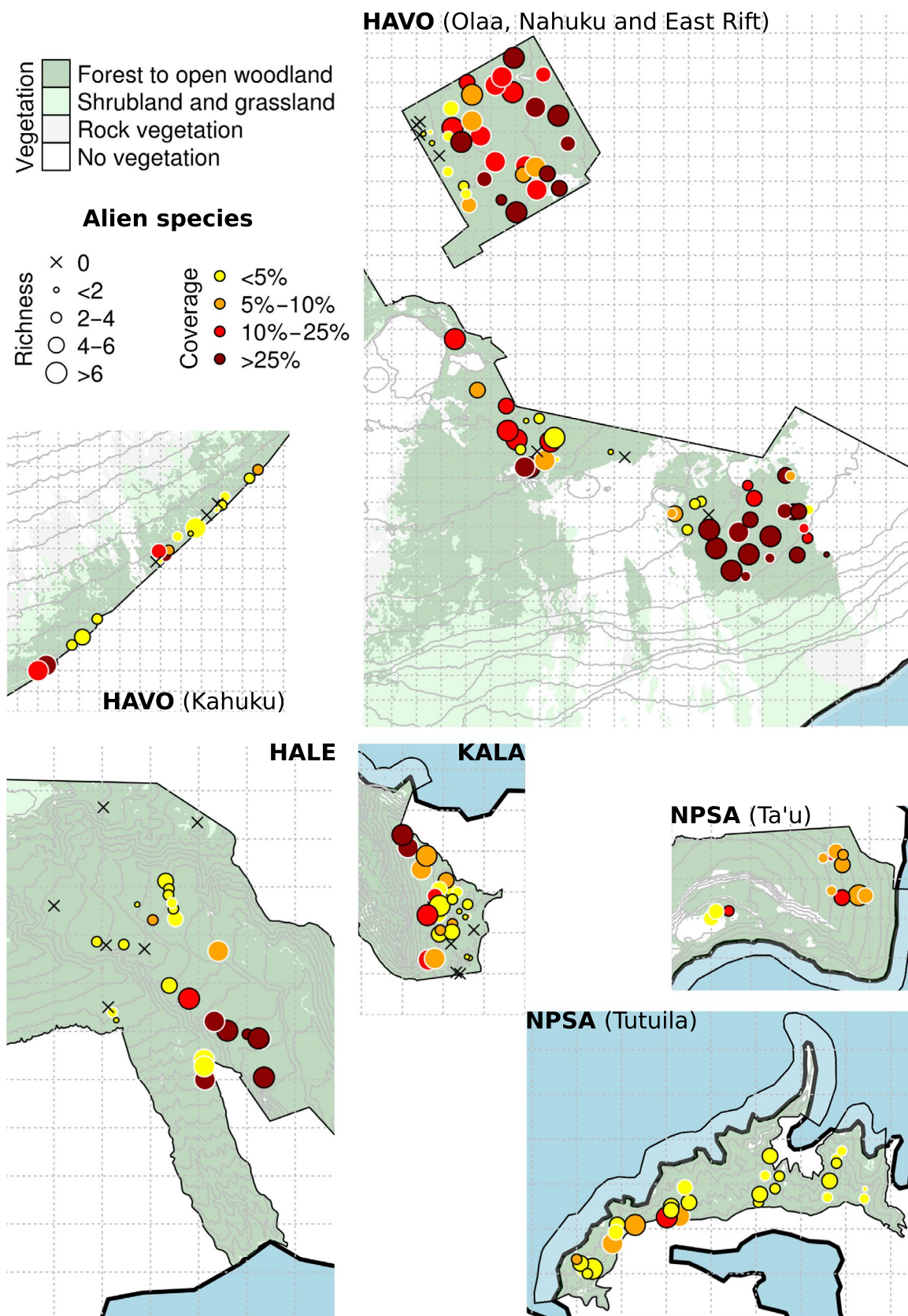
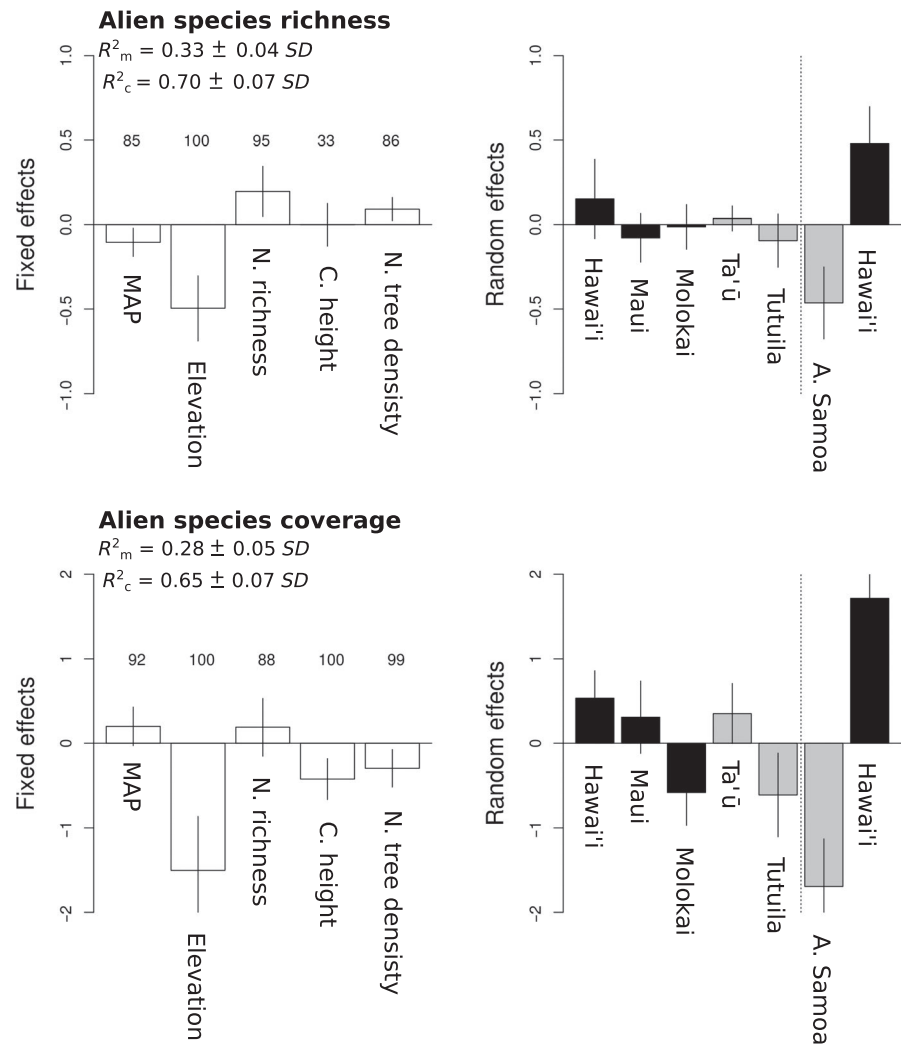


FIGURE 2 Spatial distribution of the alien plant species richness and coverage in the different parks (refer to Table 1 for the parks code). Plots where at least one alien plant species belonging to the 100 of the world's worst invasive alien species identified by the Invasive Species Specialist Group (http://www.issg.org/worst100_species.html) were inventoried are highlighted with a black point border (the other plots have a white point border). Grey lines represent 100-m elevation contours and background grids 1 km × 1 km cells

FIGURE 3 Mean fixed (mean annual precipitation, elevation, native richness, canopy height and native tree density) and random effects (island and archipelago identity) on alien species richness and coverage. Vertical segments represent 95% confidence intervals around the mean, and numbers above bars represent the percentage of iterations (among 100 iterations, $N = 78$ plots for each iteration) that retained the variable within the best model sets. R^2_m and R^2_c refer to marginal (without random effects) and conditional (with random effects) R^2 . For random effects, black and grey bars correspond to islands located in Hawaii and American Samoa, respectively. Note that within archipelagos islands are sorted in order of age (the youngest on the left hand side). Spatial autocorrelation in models' residuals was significant for only 6% and 4% of the 100 iterations (Figure S2)



On the Island of Hawai'i, 42% and 44% of the variation in alien species richness and coverage, respectively, was explained by the fixed effects (environment and native communities, Figure 5). Soil age (200–30,000 years) and elevation had negative effects on both the richness and coverage of alien species, but their effects on coverage were less consistent than on richness. Mean annual precipitation had a positive effect on alien species coverage without any effect on their richness. Native community richness and structure had a stronger effect on alien species richness than in the models with all islands together, with a negative effect of canopy height and positive effects of native species richness and tree density. Native tree density and canopy height also had negative effects on alien species coverage with notably a strong negative effect of canopy height. The random effects of sampling frame identity did not have any consistent effects on either alien species richness or coverage (Figure 5).

3.3 | Species turnover

Together, environmental and geographical distance between pairs of plots explained 87.0% of the variance in turnover of native species but only 39.5% of the variance in turnover of alien species. Moreover, contrary to turnover in alien species, turnover in native

species was primarily explained by geographical distance (Figures 6 and 7). Indeed, geographical distance only affected alien species turnover at short distances (within park) while it affected native species turnover from short (within park) to long distances (between archipelago, Figure S4). Although differences in precipitation significantly affected alien species turnover, differences in elevation were the main driver of the observed turnover (Figure 7). The unexplained variance in alien species turnover was significantly but poorly correlated with the unexplained variance in native species turnover. The strength and the significance of this correlation did not change when we considered all pairs of plots or only pairs located on the same archipelago (Pearson's $R = .11$, p value $< .001$).

4 | DISCUSSION

The high degree of invasion of Pacific islands by alien plant species (Dawson et al., 2017) was observed in relatively undisturbed tropical wet forests of Hawai'i and American Samoa. At least one alien plant species was found in the vast majority of the studied plots ($>90\%$) and at least one of the world's worst invasive alien species selected by the IUCN invasive species specialist group (Lowe, Browne,

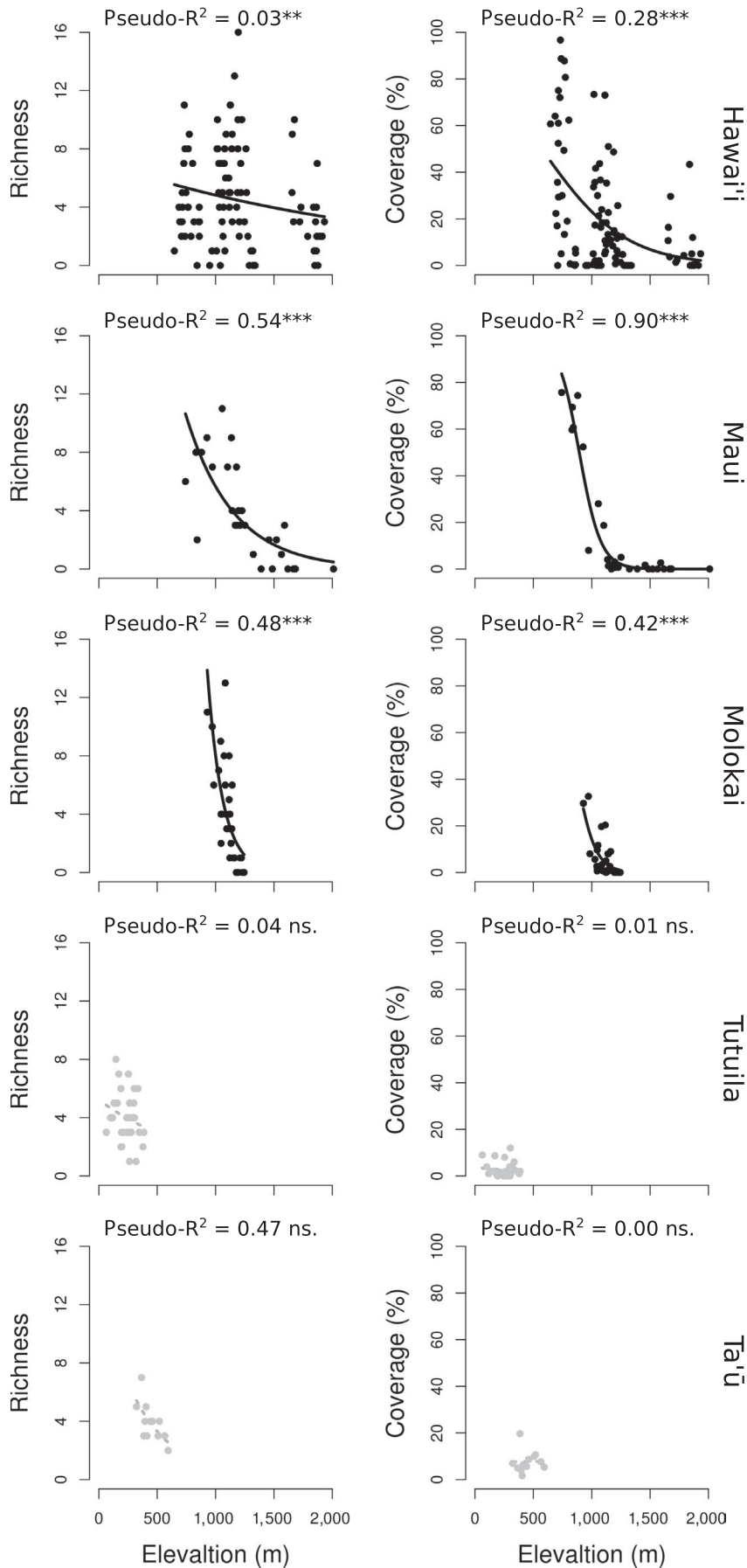
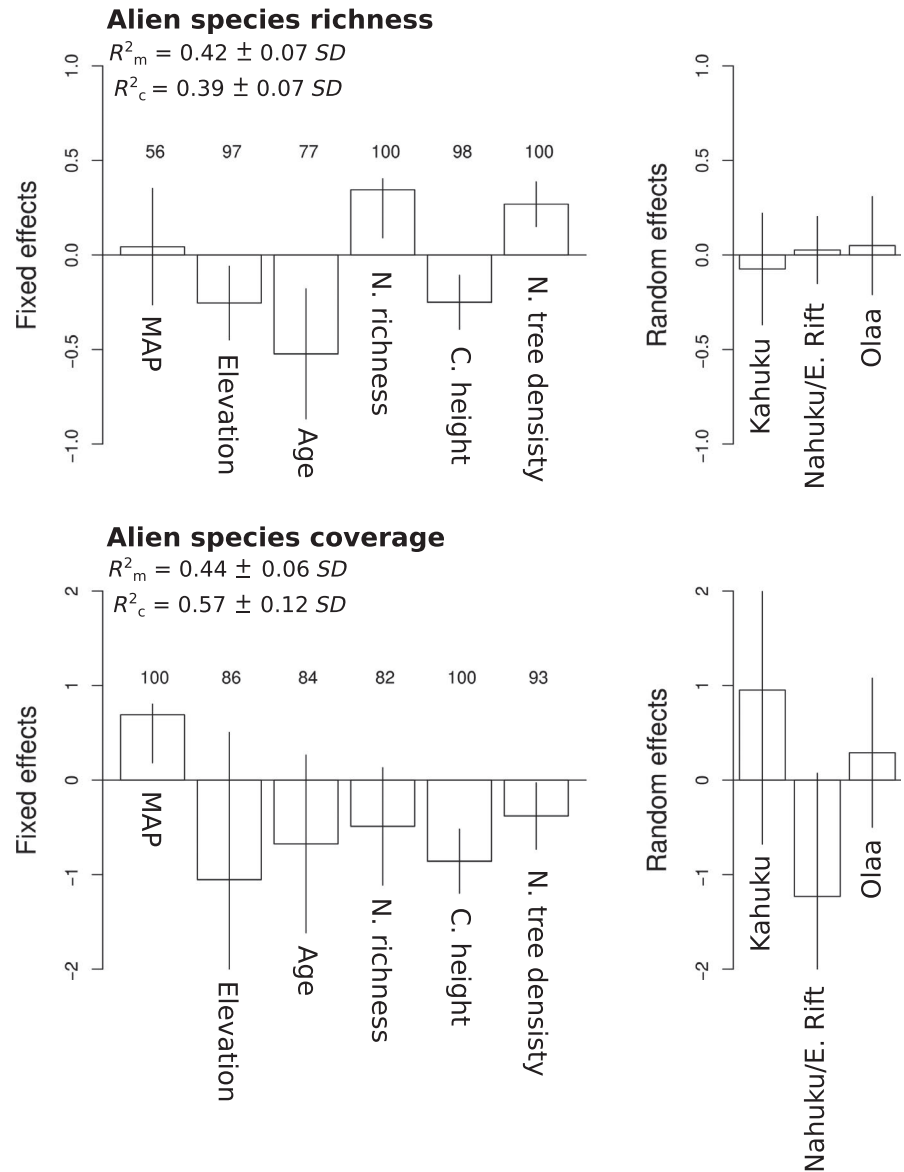


FIGURE 4 Elevational patterns of alien species richness and coverage. Lines represent fitted generalized linear models. “***” = p values <.001, “**” = p values <.01, “*” = p values <.05, ns. = p values >.05

FIGURE 5 Mean fixed (mean annual precipitation, elevation, soil age, native richness, canopy height, and native tree density) and random effects (sampling frame) on alien species richness and coverage in Hawai'i Volcanoes National Park (HAVO, Hawaii). Vertical segments represent 95% confidence intervals around the mean, and numbers above bars represent the percentage of iterations (among 100 iterations, $N = 44$ plots for each iteration) that retained the variable within the best model sets. R_m^2 and R_c^2 refer to marginal (without random effects) and conditional (with random effects) R^2 . Spatial autocorrelation in models' residuals was not significant for all of the 100 iterations (Figure S3)



Boudjelas, De, & Poorter, 2000) was observed in more than half of the plots. This high degree of invasion is particularly alarming since it is likely to be much higher outside the national park sites included in this study (see Lonsdale, 1999).

Our best models were able to explain 65%–70% of the variance in the richness and coverage of alien species across islands. In both cases, the identity of archipelagos and to a lesser extent the identity of islands explained the most variance, followed by elevation and finally native community richness or structure for alien species richness or coverage, respectively. Most of the variance in alien species composition remained unexplained, with most of the explained variance shared by environment and geographical distance.

4.1 | Archipelago and island effects

Alien species richness and coverage tended to be higher in plots located in Hawai'i compared to those located in American Samoa. This archipelago effect may have resulted from the greater isolation

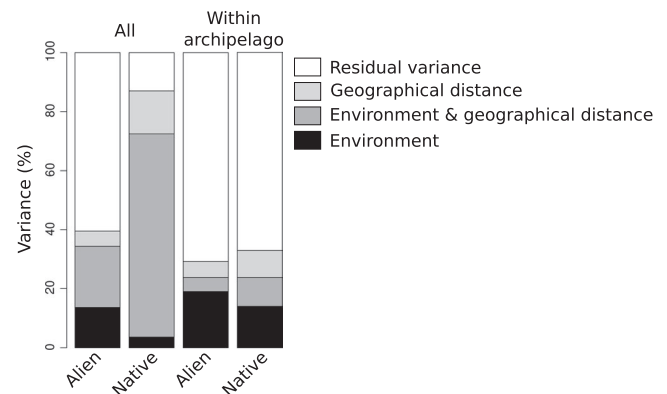


FIGURE 6 Variation partitioning (%) of alien and native species turnover. The full generalized dissimilarity models (GDM) are represented in Figure 7

of the Hawaiian archipelago, one of the most isolated land masses on earth. Indeed, as suggested by several studies (Blackburn et al., 2016; Denslow et al., 2009; Moser et al., 2018), isolation is likely to

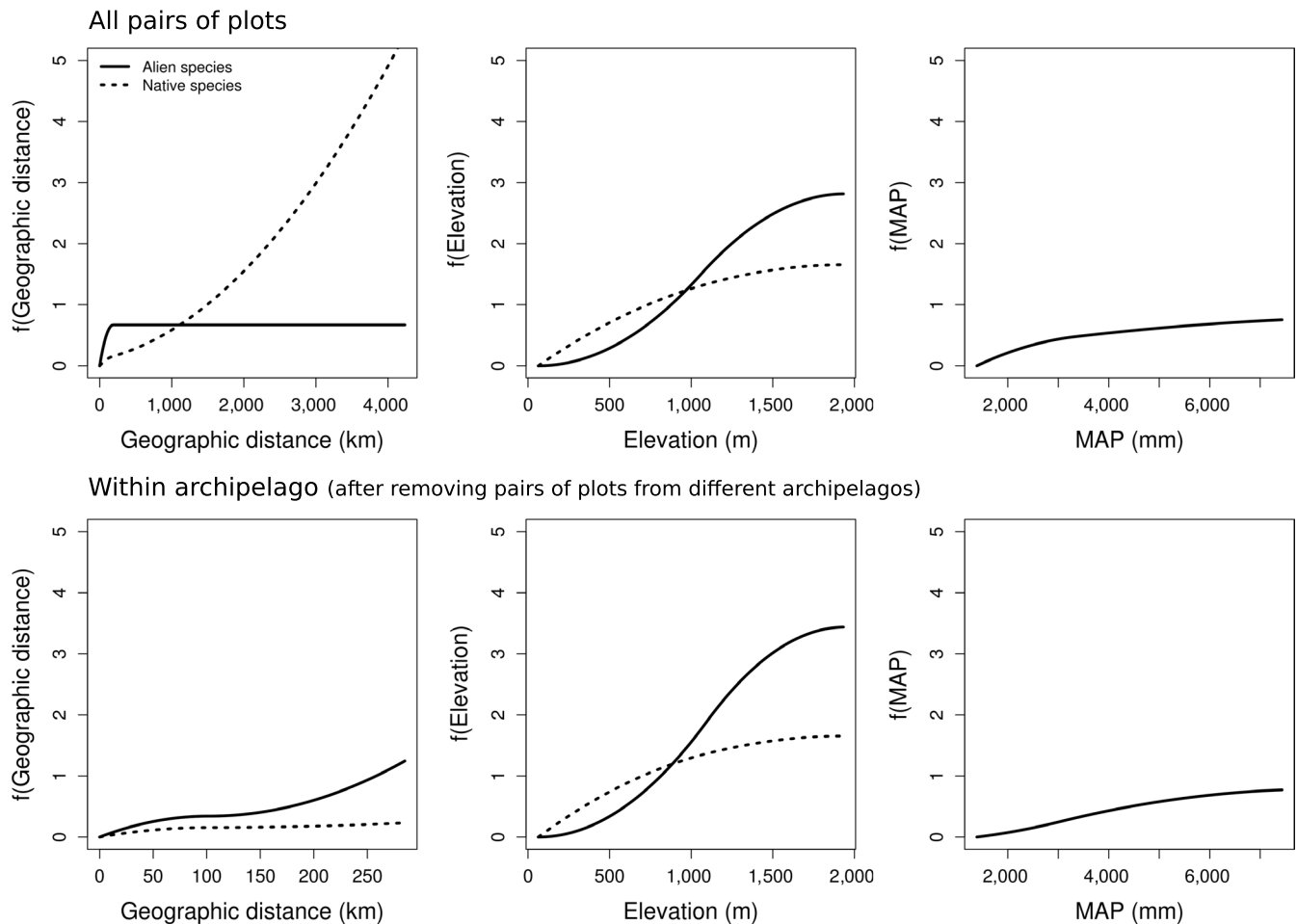


FIGURE 7 Generalized dissimilarity models (GDMs) transformation functions for alien (full lines) and native (dotted) species turnover (β_{sim}). Only significant effects are shown (p value $< .05$). MAP = mean annual precipitation

indirectly affect alien species invasion success through its effect on the diversity of native communities. Notably, due to its isolation the native Hawaiian flora originates from relatively few long-distance colonization events followed by local radiations (e.g., Gemmill, Allan, Wagner, & Zimmer, 2002). This results in a highly original flora (~90% of the flowering plants are endemic compared to ~30% in American Samoa) but with reduced genetic and functional diversity (e.g., the Hawaiian flora encompasses more species but less genera than the American Samoa), leaving more niche opportunities to invaders (see Denslow, 2003; Simberloff, 1995).

Within the archipelagos, plots located on the younger islands (the Island of Hawai'i in Hawai'i and Ta'u in American Samoa) tended to be more invaded. Kueffer et al. (2010) compared alien plant species richness between 30 island groups and also found that in younger island groups, the number of dominant invaders (i.e., those reaching maximal coverage $>25\%$ in natural areas) tended to be higher. They suggested that on younger islands, a less diverse flora may leave more niche opportunities (as supported by the general dynamic theory of oceanic island biogeography, see Whittaker et al., 2008) favouring invasion. In our case, an alternative hypothesis may be that the higher degree of invasion in Hawai'i Volcanoes National Park may result from higher accessibility and number of visitors. Lonsdale (1999) found that the

number of alien plant species in protected areas increases with the number of visitors. However, McKinney (2002) found no effect of the number of visitors on alien species richness in US parks (including National Parks). The alternative hypothesis that a higher degree of alien plant species invasion is due to higher number of visitors was not verified in this study for American Samoa. Indeed, the degree of alien species invasion was higher on the poorly accessible and less visited island of Ta'u than on the main island of Tutuila.

The effect of age also held within Hawai'i Volcanoes National Park, where plots were located on soils resulting from lava flows that occurred 200–30,000 years ago. We found that, in this range of ages, plots located on younger soils tend also to exhibit higher alien species richness and coverage. Conversely, Zimmerman et al. (2008), analysing forest growing on 50–1,500 years old lava flows, found higher degree of invasion on older soils. Low N availability on young soil may indeed limit the establishment and spread of alien species (Hughes & Denslow, 2005; Ostertag & Verville, 2002; Turner & Vitousek, 1987). Combining our results with those from Zimmerman et al., (2008), we suggest that the invasibility of these forests may rather follow a humped curve. Alien plant species may be limited by nutrient availability on young soils and competition with more diverse native communities on older soils.

4.2 | Elevation effect

Our results support the prediction that on high elevation islands, alien species invasion decreases with increasing elevation (e.g., Arévalo et al., 2005; Guo et al., 2018; Jakobs et al., 2010; Ohlemüller et al., 2006; Tanaka & Sato, 2016). Even if confounding factors may play a role (human disturbance, propagule pressure or biotic resistance, Pauchard et al., 2009), climatic constraints (e.g., lower minimal temperature or higher drought) at high elevation are likely to play a stronger role. Indeed, several studies have shown that a relaxation of climatic constraints at higher elevations due to climate change has resulted in an expansion of the range of alien species towards higher elevations on the Island of Hawai'i (Juvik, Rodomsky, Price, Hansen, & Kueffer, 2011; Koide, Yoshida, Daehler, & Mueller-Dombois, 2017). Interestingly, we found that the effect of elevation is stronger on the coverage than on the richness of alien species. Consequently, the relaxing of climatic constraints or increasing disturbance at higher elevation may then be followed by an increase in alien species competitiveness, leading to rapid spread of already established species.

4.3 | Forest structure affects alien species coverage

The vast majority of studies explore alien species invasion at large scales (e.g., between protected areas, regions or countries). Surprisingly, relatively few studies have attempted to explore how the structure of forest may affect their invasibility. Ohlemüller et al. (2006) found that forest structure had only small effects on alien species richness in forests of the South Island of New Zealand while basal area had a consistent negative effect on alien species richness. Ohlemüller et al. (2006) as well as others (e.g., Tanentzap, Bazely, & Laforzetta, 2010) found strong effects of forest fragmentation metrics on alien species richness. These effects may partly include the effect of fragmentation on forest structure as, for instance, fragmentation creates new edges that affect large trees (e.g., Laurance, Delamonica, Laurance, Vasconcelos, & Lovejoy, 2000).

Like Ohlemüller et al. (2006), we did not find a significant effect of tree density or canopy height on alien species richness. However, both these variables had a significant negative effect on alien species coverage. Thus, even if forest structure does not affect the establishment of alien species, higher tree density and canopy height likely limit their spread by limiting light availability. Ongoing change in Hawaiian forest structure due to climate change, insect outbreak or invasion (Balzotti & Asner, 2017; Barbosa & Asner, 2017) as well as dieback of ōhi'a, the Hawaiian dominant canopy tree (*Metrosideros polymorpha* Myrtaceae, which in our data set represents 75% of the inventoried trees in Hawai'i), is likely to facilitate invasions (Aplet, Hughes, & Vitousek, 1998). This threat is all the more important given that since 2010 a non-native fungus (*Ceratocystis* spp., Ceratocystaceae) has caused a rapid and widespread death of ōhi'a populations in a variety of locations on the island of Hawai'i (Asner et al., 2018).

4.4 | Turnover in alien species composition

Contrary to our expectation, native species composition did not affect alien species composition. Similar to Kueffer et al. (2010), we did not find clear patterns in alien species composition. Although environment and geographical distance had significant effects, most of the variance in alien species turnover remained unexplained. While large-scale geographical distances (between archipelagos and islands) had a strong effect on native species turnover, it did not affect alien species turnover (Leihy, Duffy, & Chown, 2018). This suggests that alien species easily reach those islands. While on a global scale climate may be a major driver of alien plant species composition, on smaller scales it may rather rely on introduction, land use history, and stochastic colonization or disturbance events (e.g., Burns, 2016; Kueffer et al., 2010; Seipel et al., 2012).

5 | CONCLUSION

Most studies on invasions by alien plant species have focused on alien species richness, while the capacity for established alien populations to expand within natural communities has retained less interest. We show that abiotic and biotic factors associated with alien species richness differed from those associated with alien species cover. Elevation was the factor that explained the most variance in the degree of invasion by alien species with higher elevations being relatively spared so far. Our results also suggest that elevation has larger effects on alien species coverage than on alien species richness. Canopy height and tree density were not associated with lower alien species richness but rather with reduced alien species coverage. Finally, our results support that this threat may be particularly high on young and isolated islands.

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DATA AVAILABILITY STATEMENT

All data are available on the Integrated Resource Management Application (IRMA) portal of the National Parks Service (<https://irma.nps.gov/Portal/>).

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BIOSKETCH

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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