

Anthropogenic and environmental drivers shape diversity of naturalized plants across the Pacific

Michael R. Wohlwend^{1,2}  | Dylan Craven³  | Patrick Weigelt⁴ | Hanno Seebens⁵  |
Marten Winter²  | Holger Kreft⁴  | Damaris Zurell⁶ | Juliano Sarmiento Cabral⁷ |
Franz Essl⁸  | Mark van Kleunen^{9,10}  | Jan Pergl¹¹ | Petr Pyšek^{11,12}  |
Tiffany M. Knight^{1,13,2} 

¹Institute of Biology, Martin Luther University Halle-Wittenberg, Halle (Saale), Germany

²German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Leipzig, Germany

³Centro de Modelación y Monitoreo de Ecosistemas, Universidad Mayor, Santiago, Chile

⁴Centre of Biodiversity and Sustainable Land Use (CBL), University of Goettingen, Göttingen, Germany

⁵Senckenberg Biodiversity and Climate Research Centre (SBiK-F), Frankfurt am Main, Germany

⁶Institute for Biochemistry & Biology, University Potsdam, Potsdam, Germany

⁷Center of Computational and Theoretical Biology (CCTB), University of Würzburg, Würzburg, Germany

⁸Department for Botany und Biodiversity Research, University of Vienna, Vienna, Austria

⁹Department of Biology, University of Konstanz, Konstanz, Germany

¹⁰Zhejiang Provincial Key Laboratory of Plant Evolutionary Ecology and Conservation, Taizhou University, Taizhou, China

¹¹Department of Invasion Ecology, Institute of Botany, Czech Academy of Sciences, Průhonice, Czech Republic

¹²Department of Ecology, Faculty of Science, Charles University, Prague 2, Czech Republic

¹³Department of Community Ecology, Helmholtz Centre for Environmental Research-UFZ, Halle (Saale), Germany

Correspondence

Michael R. Wohlwend, Institute of Biology,
Martin Luther University Halle-Wittenberg,
Am Kirchtor 1, Halle (Saale) 06108,
Germany.
Email: m.wohlwend@gmx.de

Funding information

Alexander von Humboldt Foundation
in the framework of the Alexander von
Humboldt Professorship; Helmholtz
Recruitment Initiative of the Helmholtz
Association; German Centre for Integrative
Biodiversity Research; German Research
Foundation, Grant/Award Number: FZT 118
– 202548816; BiodivERsA-Belmont Forum
Project “Alien Scenarios”, Grant/Award
Number: 01LC1807A; EXPRO, Grant/Award
Number: 19-28807X; Long-term Research
Development Project, Grant/Award
Number: RVO 67985939; Austrian Science
Foundation, Grant/Award Number: I 2086-
B16; DFZ, Grant/Award Number: ZU 361/1-1

Editor: Eva Knop

Abstract

Aim: The Pacific exhibits an exceptional number of naturalized plant species, but the drivers of this high diversity and the associated compositional patterns remain largely unknown. Here, we aim to (a) improve our understanding of introduction and establishment processes and (b) evaluate whether this information is sufficient to create scientific conservation tools, such as watchlists.

Location: Islands in the Pacific Ocean, excluding larger islands such as New Zealand, Japan, the Philippines and Indonesia.

Methods: We combined information from the most up-to-date data sources to quantify naturalized plant species richness and turnover across island groups and investigate the effects of anthropogenic, biogeographic and climate drivers on these patterns. In total, we found 2,672 naturalized plant species across 481 islands and 50 island groups, with a total of 11,074 records.

Results: Most naturalized species were restricted to few island groups, and most island groups have a low number of naturalized species. Island groups with few naturalized species were characterized by a set of widespread naturalized species. Several

This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

© 2021 The Authors. *Diversity and Distributions* published by John Wiley & Sons Ltd.

plant families that contributed many naturalized species globally also did so in the Pacific, particularly *Fabaceae* and *Poaceae*. However, many families were significantly over- or under-represented in the Pacific naturalized flora compared to other regions of the world. Naturalized species richness increased primarily with increased human activity and island altitude/area, whereas similarity between island groups in temperature along with richness differences was most important for beta diversity.

Main conclusions: The distribution and richness of naturalized species can be explained by a small set of drivers. The Pacific region contains many naturalized plant species also naturalized in other regions in the world, but our results highlight key differences such as a stronger role of anthropogenic drivers in shaping diversity patterns. Our results establish a basis for predicting and preventing future naturalizations in a threatened biodiversity hotspot.

KEYWORDS

anthropogenic drivers, beta diversity, island biogeography, naturalized species, Pacific Ocean, plant invasion

1 | INTRODUCTION

The Pacific ocean covers almost half of the earth's surface and contains many isolated islands with a rich and highly endemic flora that has become threatened by non-native plant species introductions (Loope, 1998; SPREP, 2016). Island floras in the Pacific region show a strong turnover in naturalized species among islands leading to the steepest regional species–area relationship in the world (van Kleunen et al. 2015), meaning that the number of naturalized species sharply increases with the number of islands analysed. Unique features of the Pacific, such as its geographic isolation, biogeographic history and spatial variation in natural and anthropogenic factors, could explain the naturalized species distribution patterns for this region. Understanding patterns and drivers that shape naturalized plant richness and composition in the Pacific is necessary for a better global understanding of naturalization processes. Further, region-specific knowledge is a prerequisite for guiding conservation planning, such as compiling regional watchlists to mitigate future invasions (Sherley et al., 2000).

Previous studies have shown that most naturalized species occur in one or a few Pacific islands and that most islands have low naturalized species richness (Denslow et al., 2009; Meyer, 2004). Species-poor islands tend to have a nested subset of the species present on species-rich islands (Traveset et al., 2014). Rarity indices that quantify the range size of species were developed for conservation research to identify areas with many endemic species (Usher, 1986; Williams, 1993). This same index can be used to quantify whether the naturalized species that are present on an island group are those with small or large ranges. If species-poor island groups have rare naturalized plant species, this could indicate strong environmental filtering for unique local conditions, whereas if they are inhabited by widespread naturalized plant species, this could indicate that dispersal limitation so far limits the arrival of rarer species due to

stochastic factors. Quantifying patterns of rarity in combination with patterns of beta diversity will elucidate the drivers of naturalized species composition, with strong implications for conservation.

The success of naturalized plant species in the Pacific is often attributed to the weak competition ability of native plant species (e.g. Gillespie et al. 2008; MacDougall et al. 2009). The extreme isolation of many island groups in this region has led to phylogenetically clustered compositions of native species, whereby some native plant lineages are absent because of dispersal limitation and other lineages are over-represented due to high rates of in situ diversification and local extinctions (Cabral et al., 2019; Cavender-Bares et al., 2009; Crisp et al., 2009; König et al., 2020; Weigelt et al., 2015). As a result, the Pacific region might have under-exploited resources (i.e. absence of species-trait combinations Denslow, 2003; Elton, 1958; Gillespie et al., 2008) that could favour the naturalization of plant species from lineages that are under-represented in the native flora of the Pacific, resulting in a disproportionate representation of certain plant families compared to global patterns. For example, the treeline in Hawai'i was low, because the typical cold-adapted functional groups (e.g. *Pinaceae*) did not arrive to these islands through natural dispersal. Analyses of the over- or under-representation of plant families in the Pacific compared to the global naturalized flora can provide a first look at these patterns and serve as an indirect indicator of the representation of certain trait combinations in the naturalized flora of the Pacific.

For native plants, climate is known to strongly influence species richness (Kreft & Jetz, 2007; Wright, 1983), and both geographic distance and climate dissimilarity strongly influence dissimilarity in species composition (often measured as beta diversity) (Keil et al., 2012; König et al., 2017; Soinenen et al., 2007). Naturalized plant diversity patterns are shaped disproportionately by other drivers (Denslow et al., 2009; Moser et al., 2018; Qian et al., 2008; Winter et al., 2010), and globally, naturalized plant

richness is strongly linked to human activity (e.g. represented by human population density and economic activity, Essl et al., 2019; Pyšek et al., 2017). Humans import and export species, purposefully and accidentally, through trade activities (Hui et al., 2017; Hulme, 2009; van Kleunen et al., 2018, 2020) and directly or indirectly create disturbances that favour their establishment (Frenot et al., 2001; Hulme, 2009; Marvier et al., 2004; Merlin & Juvik, 1992). The broad range of biogeographic (area and isolation) and anthropogenic (e.g. human density and GDP) factors present in the Pacific is uniquely suited for studying naturalized species distributions, as it includes both highly invaded (Kueffer et al., 2010) and almost untouched islands.

To understand the climatic, biogeographic and anthropogenic factors underlying diversity patterns of naturalized plant species across the Pacific, we quantify (a) naturalized species richness per island group, average distribution ranges of naturalized species per island group and naturalized species sharing between island groups in the Pacific, (b) the rarity of naturalized species present on each island group, (c) the species richness of naturalized plant families in the Pacific in relation to worldwide total and naturalized species richness, and (d) the anthropogenic, environmental and biogeographic drivers of naturalized species richness and beta diversity across Pacific island groups. Combined, these analyses provide a description of current naturalized species richness and composition in the Pacific and give insights into the forces that shape these patterns, serving as guidelines for applied conservation.

2 | METHODS

2.1 | Compilation of naturalized plant species occurrence data

In our study, the Pacific is defined as all islands between 40°N and 40°S, excluding large landmasses such as Japan, New Zealand, Indonesia, the Philippines and Papua New-Guinea as well as small islands on the Pacific-American or Australian coast. Japanese and South East Asian Islands west of Bonin/ Palau are also excluded (Table S1). We used species record data from two databases with comprehensive information on the presence of naturalized plant species, PIER and GloNAF. PIER (Pacific Island Ecosystems at Risk) contains reports of non-native species in the Pacific region at the island level (<http://www.hear.org/pier/>). GloNAF (Global Naturalized Alien Flora; van Kleunen et al., 2019) contains reports of naturalized non-native plant species across 861 geographic regions worldwide (Dawson et al. 2017; Moser et al. 2018; van Kleunen et al. 2015). The GloNAF database contains information using an island grouping based on political borders rather than the groupings we develop here (see below). We therefore used raw data at the (mostly) island level from GloNAF version 1.1 (van Kleunen et al., 2015) and aggregated them at the level of the island groups defined in this study. Table S1 gives a list of all 481 islands with species records.

Our data mostly contained information at island level, but we aggregated occurrences to island group level to ensure high completeness of the species lists analysed. We acknowledge that this reduces but does not eliminate the issue of data deficiency. To create island groups, we started with (a) political borders, including municipals or states. If political borders poorly reflected geographic borders (e.g. Samoa and American Samoa), we used (b) distance between islands and (c) ocean trenches to assign each island to one of 50 island groups. We excluded species x island records that could not be assigned to any island group with absolute certainty (e.g. when location information was imprecise). Our island groups reflect both geographic and political borders, because both are known to be important for non-native species movement. A list of all islands included in each island group is provided in Table S1.

Naturalized species were assigned accepted binomial species names using the Leipzig Catalogue of Vascular Plants (Freiberg et al., 2020) and the associated R package *lcvplants* (<https://github.com/ivid-biodiversity/lcvplants>). Different subspecies and varieties of the same species were merged to the species level. Hybrids were treated as separate species, except if no valid entry could be identified in which case they were treated as the first parent species. Species records were removed when they could not be assigned to an accepted plant species (e.g. information only at plant family level). In the rare case of more than one corresponding accepted species for a synonym, we selected the first output of the *lcvplant* function to ensure reproducibility.

Some species x island records in the databases were listed as cultivated (incl. for ornamental purposes) or native. For some species, naturalization status varies among species x island combinations (i.e. a species can be naturalized in one island group and cultivated or native in another), which we attribute to the large area of the Pacific, and the temporal nature of naturalization (i.e. a species may have escaped cultivation only in some island groups). When aggregating to island group level, we considered a species as naturalized for the island group if it has naturalized on any island within the group. When classifying the native status of species records, we averaged the expert evaluation in the sources for each island. We considered a species to be native if it is listed as native on any island within the group. Species that are not explicitly listed as naturalized in any record on the Pacific but listed as cultivated/ native at least once were excluded from our study. With these criteria, 2,672 naturalized species were included in our analyses which can be found in Table S2.

For most analyses, we evaluated our questions excluding records of species on island groups classified as native and cultivated. We show the results of the full data set (i.e. including those records) in the Figures S1–S3. Results of both approaches were comparable, indicating the robustness of our results. For beta diversity and shared species analyses, excluding records of island groups with species classified as native and cultivated would create false absences (i.e. type I errors) and may generate false negatives (i.e. type II errors). Thus, we present analyses using all data for these analyses. We did not categorize species as “invasive” or

similar (sensu Blackburn et al. 2011; Richardson et al., 2000), because this classification is not available for all species in the study region.

2.2 | Patterns of naturalized species richness, range size, rarity and composition

We first quantify basic patterns of naturalized plant species distributions in the Pacific. Compositional species sharing between each pair of the 50 island groups was quantified in two ways: (a) the total number of shared species, “(b) beta Simpson pairwise dissimilarity calculated as $\frac{\min(b,c)}{a + \min(b,c)}$, with a being the species two island groups have in common and b and c being the richness of the individual island groups; this metric considers species turnover without the influence of species richness differences (monotonic transformation as in Baselga (2010), using the betapart package in R (Baselga et al., 2020).

We used our naturalized species by island group matrix to calculate species richness per island group (n_g), species occupancy (c_i , range size of species i) and compositional species sharing. Average

(geographic) rarity per island group is defined as $\frac{\sum(\frac{1}{c_i})}{n_g}$, that is the

average over all species present in an island group of the inverse of their occupancy (Usher, 1986; Williams, 1993). We assessed whether there is a relationship between the average rarity of the naturalized species and the naturalized species richness of an island group using Pearson's product-moment correlation to assess whether species-poor island groups tend to have more common or more rare species, indicating a strong role of dispersal or environmental filtering.

2.3 | Naturalized plant family representation in the Pacific

We investigated whether the Pacific has a different naturalized plant family composition compared to other regions of the world. We assessed whether certain plant families have more or fewer naturalized species in the Pacific than expected based on (a) their global species richness and (b) their naturalized species richness in other regions of the world. Data for the number of plant species per family came from the Leipzig Catalogue of Vascular Plants (Freiberg et al., 2020). Data for naturalized plant species per family in other regions of the world came from GloNAF (van Kleunen et al., 2019). We tested whether each plant family was over- or under-represented relative to expectations from a null model using a hypergeometric distribution test. For this, we used the phyper function in R, giving the distribution of binomial probabilities comparable to a one-tailed Fisher's exact test (Johnson et al., 1992).

2.4 | Naturalized species occurrences outside the Pacific

Using GloNAF, we quantified the number of alien species in the Pacific that are also naturalized in other continents or countries. For each continent or country, we then computed the proportion of the total number of naturalized species that are shared with the Pacific. As spatial units, we used (biogeographical) continents as defined by the World Geographical Scheme for Recording Plant Distributions developed by the Biodiversity Information Standards (TDWG). We also used countries, as information exchange concerning potential non-native species exchange occurs primarily at the country level (e.g. Global Invasive Species Database; <http://issg.org/database/reference/index.asp>). Additionally, we quantified the proportion of naturalized plant species in the Pacific that are unique naturalizations to this region and compared this to other continents, to test whether there are proportionately more naturalized species exclusive the Pacific. To complete this picture, we used Pearson's correlation coefficient to test whether species that are widespread in the Pacific (occupy many island groups) are also widespread globally (occupy many countries).

2.5 | Drivers of naturalized species richness and beta diversity

We assessed the relative importance of anthropogenic, biogeographic and climatic drivers in explaining patterns of naturalized species richness and beta diversity across island groups in the Pacific. One of our main goals was to investigate which factors promote naturalized richness and compositional similarity between island groups. We used GIFT (Global Inventory of Floras and Traits, Weigelt et al., 2020), a global archive of regional plant checklists and floras including physical, geographic, bioclimatic and anthropogenic characteristics, which are computed based on the spatial polygons and summary statistics for each island group (islands with naturalized species records not yet included were added to GIFT for this purpose): land area (combined area of all islands belonging to the same island group), distance to mainland (closest distance from coast to coast) and land area in proximity (SLMP: standardized land mass in proximity, averaged among islands, that is partly reflecting the spatial arrangement of a group (Weigelt & Kreft, 2013)). Further, we extracted other variables from additional resources and assigned them to the island groups. These included the following: airport capacity (number of airports x airlines visiting them as a proxy for their size; <https://openflights.org/>), harbour capacity (number of harbours x their size in three classes (World Port Index, <https://msi.nga.mil/Publications/WPI/>)), mean annual temperature and precipitation (Chelsea (Karger et al., 2017), elevation (maximum) (WorldClim 1.4 digital elevation data (United States Geological Survey, 2011)), human population number and density (Doxsey-Whitfield et al. 2015)

and Human Footprint and Human Influence Index (WCS, 2005). Finally, we extracted a GDP Index which estimates GDP based on night light emission (NOAA et al., 2010). A low proportion of values were missing in our data set (18% for GDP Index and Human Population, 4% for precipitation and temperature), and for these, we imputed missing values using a random forest algorithm that is trained on observed values to predict missing values, using the R package “missForest” (Stekhoven & Buehlmann, 2012). We imputed missing values with 100 trees in each forest and five variables randomly sampled at each split; the estimated out-of-bag error imputation error rate across all variables was low (Out-of-bag (OOB) error = 0.144).

We assessed which variables promote naturalized species richness on Pacific island groups. Because variable importance may be biased towards correlated variables (Strobl et al., 2007), we used a two-step variable selection procedure when fitting random forest models using the R package “VSURF” (Genuer et al., 2015). The first step of this procedure ranks variables by importance and eliminates the redundant ones, where the threshold value is an estimate of the standard deviations of redundant variables. The second step selects variables that are important for interpretation, which retains variables that are strongly associated with the response variable but allows for some degree of redundancy. We used 100 trees in each forest, 10,000 forests in each interpretation step. This selection process is visualized in Figure S6.

To assess which drivers promote beta diversity of Pacific island groups, we calculated the absolute difference of each environmental and anthropogenic variable between each pair of island groups, and the geographic distance of the island groups to each other (instead of distance to continent). We included richness difference between island groups as a predictor in the random forest model to test whether pairwise beta Simpson depends on how similar or different the pairwise island groups are in their species richness. This factor must be interpreted carefully as it does not represent a biogeographical, anthropogenic or strictly environmental driver. Rather, richness difference provides meaningful information on the possible pathways in which species disperse in the Pacific. As beta Simpson examines species turnover without the influence of species richness differences, it is meaningful to examine how species richness differences influence beta Simpson. If species with similar richness have similar beta Simpson values, this could indicate that species-poor island groups all have the same composition of widespread naturalized species. Alternatively, if species with different richness values have high beta Simpson values, this could indicate that species-poor island groups contain a nested subset of the naturalized species found on species-rich island groups. When running the random forest model without the factor richness difference included, results changed only to a minor degree (Figure S7), showing the robustness of our results. To support the interpretation of our results, we included partial dependence plots of a standard random forest model in the Appendix S1, as there is no indicator of direction or shape of the drivers influence in VSURF. This function draws the

regression, which represents the effect of our drivers on naturalized species richness (Figure S8-a) or beta Simpson diversity (Figure S8-b, randomForest package in R, Liaw & Wiener, 2002). This allows us to consider trends in these regressions for a better interpretation of our results.

For all analyses and data visualization, we used R (R Core Team, 2020, version 4.0.3) and the packages ggplot2 (Wickham, 2016), raster (Hijmans, 2020), rnatualearth (South, 2017) and rgeos (Bivand & Rundel, 2020).

3 | RESULTS

3.1 | Patterns of naturalized species richness, range size and composition

On average, there were 258 species per island group (median of 182, Figure 1a). The lowest number of naturalized species was recorded for Howland and Baker (6) and the highest number for the Hawaiian Islands (1,544; Table S3). Most naturalized species were present on one or a few island groups (Figure 1b). Of the 2,672 naturalized species found in the Pacific region, only 1,377 (52%) occurred on more than one island group and only 367 (14%) occurred on more than 10.

Island groups with many naturalized species also tended to share many naturalized species with other species-rich island groups in absolute terms (Figure 2a), but this relationship was not observed for beta Simpson diversity (Figure 2b) likely because naturalized species-rich island groups had proportionally more rare species (Figure 3). Indeed, we found a positive association between the average rarity and the species richness of island groups in the Pacific ($p < .001$; Pearson's correlation estimate = 0.78; Figure 3).

3.2 | Naturalized plant family representation in the Pacific

In total, naturalized species from 228 plant families were recorded in the Pacific. Many plant families ($N = 91$) had more naturalized species in the Pacific than expected based on the global number of species in the family, such as *Poaceae*, *Arecaceae* and *Fabaceae*, whereas others ($N = 30$) had fewer naturalized species than expected, such as *Orchidaceae* and *Rubiaceae* (Figure 4a). When we considered the representation of plant families in the Pacific compared to the global number of naturalized species for the 227 families found both in the Pacific and in other regions (only *Marcgraviaceae* are exclusively naturalized in the Pacific), 94 families were over- and 31 were under-represented in the Pacific compared to other regions. For example, *Brassicaceae* and *Apiaceae* are under-represented in the Pacific, whereas *Poaceae*, *Arecaceae* and *Fabaceae* are still over-represented (Figure 4b). Five families were under-represented when the Pacific naturalized flora was compared to total global family richness, but were over-represented

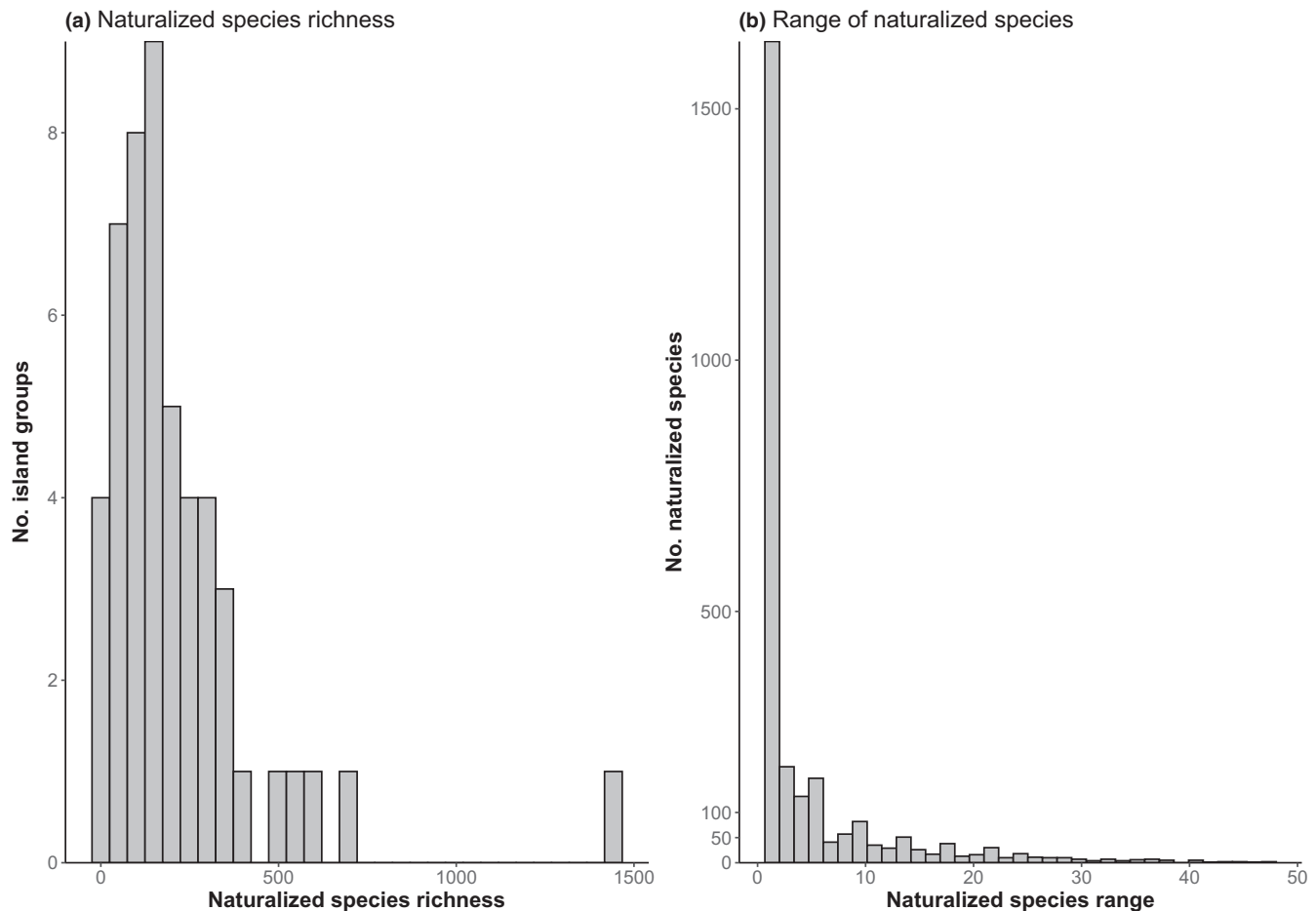


FIGURE 1 Histograms of the frequency of (a) naturalized species richness for all island groups and (b) naturalized species range (number of island groups each naturalized species is present on) for all naturalized species

when the Pacific naturalized flora was compared to the global naturalized family richness. Eight families were over-represented when the Pacific naturalized flora was compared to total global family richness, but were under-represented when the Pacific naturalized flora was compared to the global naturalized family richness. Thus, 13 families were evaluated opposingly depending on the context (Table S4), showing that naturalized families can perform very differently in the Pacific.

3.3 | Naturalized species occurrence outside of the Pacific

Twenty-one per cent of naturalized species found in the Pacific were not recorded as naturalized elsewhere in the world (Figure S4), but this is neither exceptionally high nor low (within the standard deviation). Many naturalized species in the Pacific were also found as naturalized species in South America and Africa, and in the large countries bordering the Pacific including the United States, Australia and Mexico (Table 1). The top eight countries which shared the most naturalized species with the Pacific are shown in Table 1, and these countries serve as indicators for their

larger regions (i.e. Portugal for the Mediterranean, Puerto Rico for the Caribbean). Naturalized species that were present as naturalized species in many countries outside the Pacific were also widespread within the Pacific (Figure S5).

3.4 | Drivers of naturalized species richness and beta diversity

Human footprint and airport capacity were the most important variables explaining naturalized species richness of island groups, closely followed by other drivers that also reflect human influence and economic activity (Figure 5a; $R^2 = .88$). The difference between island groups in naturalized species richness and temperature were the most important variables explaining beta Simpson across island groups (Figure 5b, $R^2 = .95$). The partial dependence plots we included to foster interpretation (Figure S8) do not provide a slope, but we observe clear trends. We can observe a generally positive trend for all drivers influencing richness (e.g. the higher the human footprint index and the land area of an island group, the higher the naturalized species richness). We observe a generally positive trend for differences in temperature and in geographic distance influencing

FIGURE 2 Pairwise patterns of shared species between island groups (more yellow colours indicate more shared species). Top (a): Total richness and total species shared between island groups. Bottom (b): Beta Simpson dissimilarity between island groups and average rarity of species on each island group

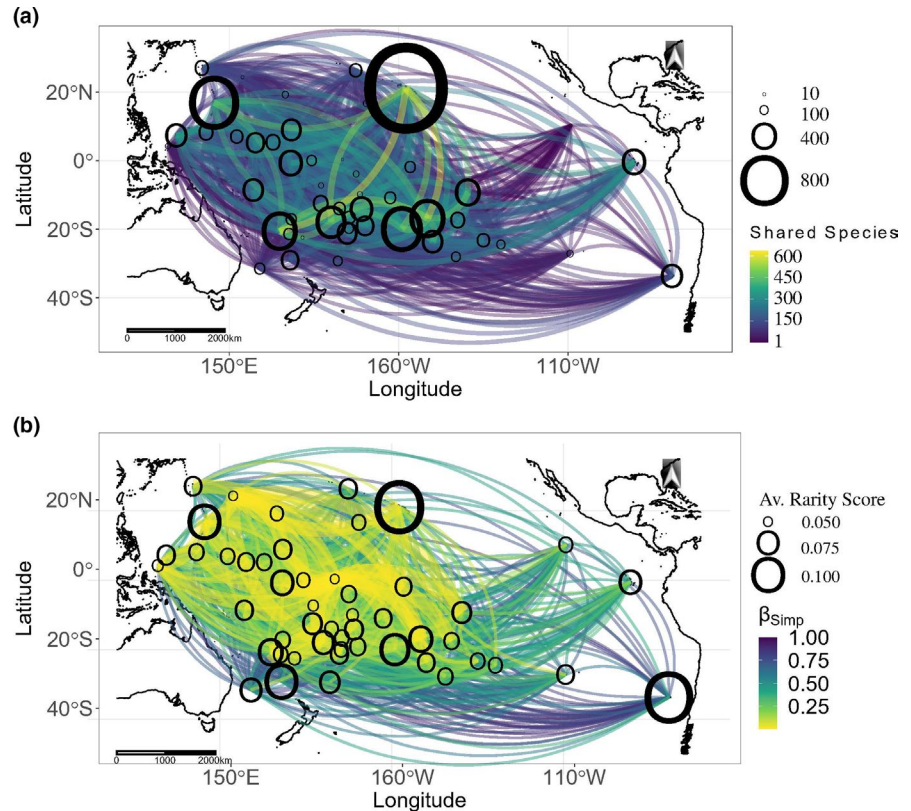
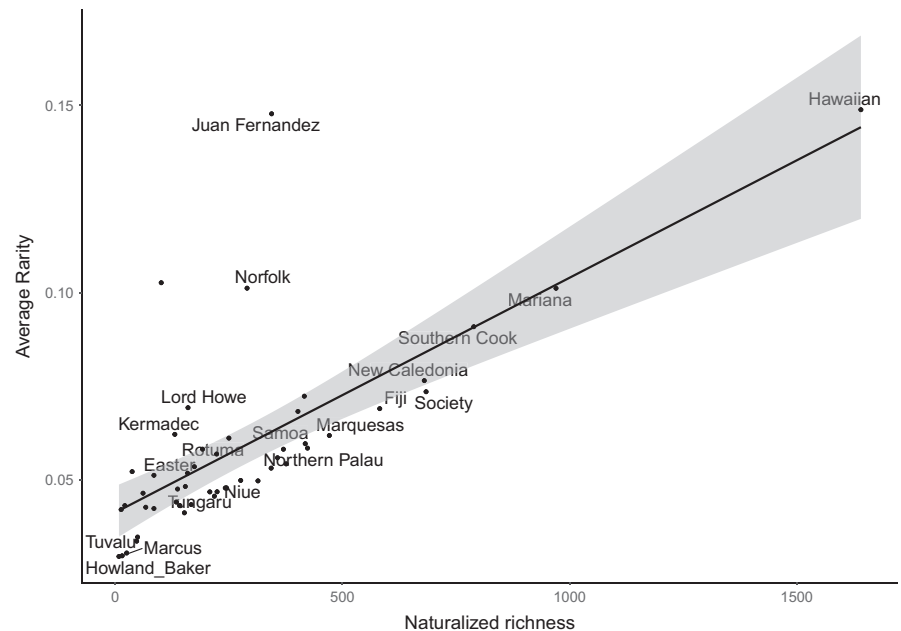


FIGURE 3 Average rarity of naturalized species on each island group in relation to naturalized species richness for each island group in the Pacific. High average rarity indicates the presence of many naturalized species that are located on few other island groups. A linear model (black line) and its 95% confidence interval are displayed. Names of many island groups with low naturalized richness are not displayed for visibility reasons



beta diversity, while we observe a generally negative trend for differences in naturalized species richness, in GDP, in airport capacity, and in population count, and for differences in the human influence index, we observe a hump-shaped pattern. Our results therefore show that the more different islands are in their naturalized species richness and GDP, the more similar they are in their naturalized species composition.

4 | DISCUSSION

In our comprehensive analysis of the naturalized flora of the Pacific region, we find 2,672 naturalized plant species from 228 different plant families. We show that the richness of naturalized plant species on island groups in the Pacific is strongly linked to anthropogenic factors, reflected in several drivers, while compositional similarity

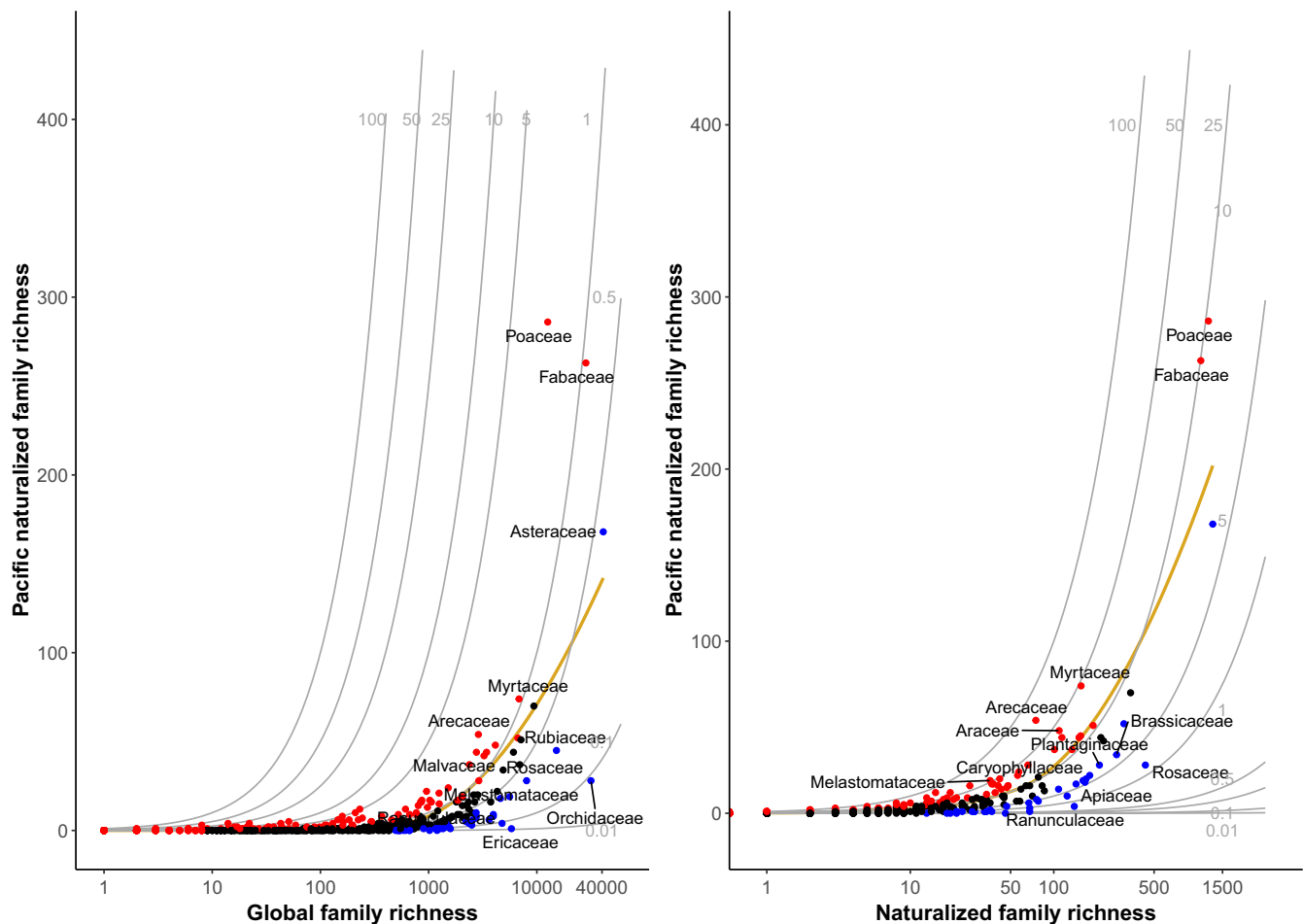


FIGURE 4 Total global species richness (a) and total naturalized global species richness excluding the Pacific (b) per plant family compared to naturalized richness per plant family in the Pacific. Coloured points indicate significantly over-represented (red) or under-represented (blue) plant families in the Pacific ($p < .05$). The names of the six most over- and under-represented families are displayed. Grey lines are for the relative per cent of species per family. Golden line shows a loess type linear model

TABLE 1 Total numbers of naturalized species recorded in the Pacific that are also naturalized elsewhere (per continent and country)

Continent	Africa	South America	North America	Australasia	Trop. Asia	Temp. Asia	Europe	Antarctic
Shared Naturalized	1,558	1,546	1,470	1,310	1,103	1,055	691	90
Total Naturalized	3,490	3,158	5,803	3,415	1,878	2,880	3,997	153
%	44.6	49	25.3	38.4	58.7	36.6	17.3	58.8
Country	USA	Australia	Mexico	Japan	New Zealand	Portugal	Puerto Rico	South Africa
Shared Naturalized	1,338	1,205	703	690	652	631	629	599
Total Naturalized	5,303	2,805	1,115	1,669	1,710	1,344	806	1,080
%	25.2	43	63	41.3	38.1	46.9	78	55.5

Note: Sorted in descending order, total naturalized richness per continent and country is given. Data for these countries do not include their Pacific territories. This table is based on GloNAF (van Kleunen et al., 2019).

between island groups is linked to richness differences and temperature similarities. The high isolation of many island groups seems to provide no barrier for naturalizations, indicating that dispersal of naturalized plant species is largely human mediated. Our findings have great potential to inform the development of applied conservation tools, such as watchlists.

Our results extend those of previous studies, in which the Pacific region showed the steepest slope for naturalized species accumulating per unit area (van Kleunen et al., 2015). This pattern emerges due to the strongly skewed distributions of richness and range size patterns. For example, 59% of all naturalized plant species found in the Pacific are present on the Hawaiian Islands

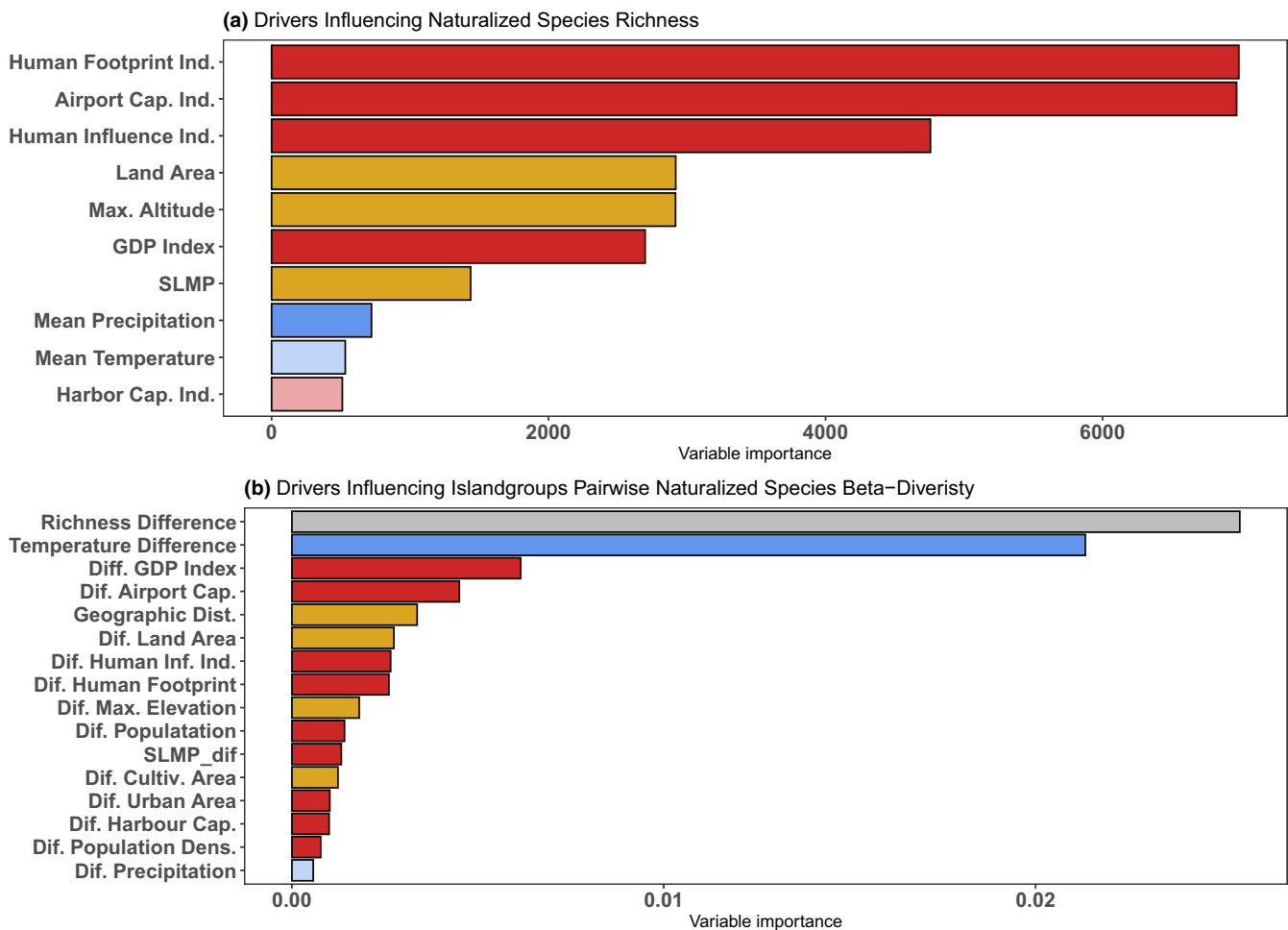


FIGURE 5 Variable importance from VSURF random forest models explaining species richness (a) and beta Simpson (b) of naturalized plant species in the Pacific. Explanatory variables are ranked by relative variable importance. Anthropogenic, biogeographic and climatic drivers are shown in red, gold and blue, respectively. Richness differences are shown in grey. Only variables retained by the variable selection process are included. Light colours (least important) indicate that these drivers were not selected as suitable, that is not included in the calculation of the R^2 , but is included in this figure to put them in a broader context

alone. We found an even more skewed distribution of naturalized plant richness across island groups than reported by Denslow et al. (2009) on 1,332 naturalized plant species. This is likely due to our larger data set that includes more rare naturalized species. The four most widespread species in our data set are all associated with anthropogenic factors and disturbed habitats, including the following: *Eleusine indica* (45/50 island groups), an agricultural weed that is resistant to glyphosate (Lee & Ngim, 2000), *Cynodon dactylon* (44/50), a graminoid which is resilient to drought, salt and trampling (Fischer et al., 2008; Kaffka, 2009), *Portulaca oleracea* (44/50), a common agricultural weed, and *Euphorbia hirta* (42/50), a weed with a wide native and naturalized ranges. Other generalist species known to thrive in disturbed ecosystems, such as species of the genus *Chenopodium*, are currently rare in the Pacific, but could spread further in the future.

Pacific island groups with few naturalized plant species are populated by "common" naturalized species (i.e. these island groups have a low average rarity score), indicating a set of notorious

species that are able to establish readily and are frequently transported, even to the most poorly connected places. This pattern has been observed for invasive naturalized species on islands globally (Traveset et al., 2014), and for native species (native species-rich islands have more endemic species) on tropical archipelagos (König et al., 2017) and in the Aegean archipelago (Kallimanis et al., 2010). As the processes that result in native species patterns are likely to be very different than those of naturalized species, a direct comparison of patterns of rarity for native and naturalized species in the Pacific and in other regions could provide insights into the underlying processes. Further, our result indicates that it is important and feasible to prioritize the prevention of the (further) spreading of common naturalized species on islands with currently low naturalized species richness and that anthropogenic introduction barriers such as trade by ship and plane, but also the availability of human-altered ecosystems, are very important.

We expected the Pacific region to contain more unique naturalized species compared to other regions due to its unique native floras

and potentially lower resistance to biological invasions (Atkinson & Cameron, 1993; L. Loope & Mueller-Dombois, 1989). In contrast, we found that a high proportion of naturalized plants in the Pacific are also naturalized in other regions. Neighbouring countries and some distant coastal countries (e.g. Portugal) and islands (e.g. Puerto Rico) share a large percentage of their naturalized species pool with the Pacific. Several smaller island regions also share a large percentage of their naturalized species with the Pacific (e.g. the Christmas Islands, which share 97% of their 176 naturalized species with the Pacific). This provides evidence that human activity overcomes geographic barriers (di Castri, 1989, 1990) and that more species in these regions could be exchanged with the Pacific, as saturation in the accumulation of naturalized species has not yet been reached (Seebens et al., 2017).

Global patterns of naturalized family richness are mirrored in the Pacific, with deviations likely resulting from the (sub-)tropical conditions and highly human-altered ecosystems. *Ranunculaceae* and *Rosaceae* are particularly under-represented in the Pacific, potentially because these families are most common in temperate latitudes (Watson & Dallwitz, 1992). *Convolvulaceae*, *Malvaceae* and *Meliaceae* are over-represented both in the Pacific naturalized flora and in the global naturalized flora. *Poaceae*, *Fabaceae* and *Arecaceae* are particularly over-represented in the Pacific, which may indicate either unique niche space or an overabundance of ubiquitous niche space available to those families in the Pacific (see e.g. Vitousek et al. 1987). Many naturalized species may have traits that favour their accidental and purposeful introductions by humans or their abilities to thrive in degraded or anthropogenic ecosystems (Doyle, 2001). There are many ecosystems or whole islands in the Pacific that have been degraded, altered or transformed entirely by human colonialization (Braje et al., 2017), and this may explain the over-representation of these families and highlights the association of naturalized species with human activity.

Variation in naturalized species richness among island groups in the Pacific was explained largely by human activity and to a lesser degree by island group size. Island size was linked to naturalized richness in the Pacific in a previous study (Denslow et al., 2009), but the other variables we consider here were heretofore largely unexplored in the Pacific. In a global analysis of islands, elevation and distance to the mainland were also linked to naturalized plant species richness (Moser et al., 2018). Our results highlight human activity (e.g. human footprint and airport capacity) as the main driver of non-native species richness, while biogeographic variables (e.g. land area and SLMP) play a secondary role. We could not show any influence of distance to mainland on naturalized species richness. This finding suggests that either naturalized species follow the similar pathways and thrive under similar conditions as humans (e.g. island groups with more area are more attractive for human activities and harbour more habitats that may host non-native species), and/or the presence of humans increases the availability and strength of introduction pathways (i.e. harbours, airports and trade volume) and suitable habitats (i.e. urban/agricultural/disturbed areas).

We find that island groups are compositionally similar to other island groups that are different in their species richness, GDP and area, but are similar in their mean annual temperature. Species-poor island groups are inhabited by widespread naturalized species. However, there is high variation in the beta diversity of species-poor islands groups, with some pairs having the exact same widespread species and others having completely different compositions. Species-poor island groups tend to have a nested subset of the species that are present on species-rich island groups (see also Traveset et al. 2014), and thus, pairings of species-poor with species-rich island groups have consistently high values of Simpson pairwise beta diversity. These results suggest that species dispersal likely follows a pathway by which species-poor and monetarily poor islands receive their naturalized species not directly from outside of the Pacific, but rather from dispersal from species- and monetarily rich island groups, which are in turn the initial introduction points of non-native species to the Pacific ("hubs" for invasion, as in Traveset et al., 2014). Naturalized species that arrive will be more likely to establish if they come from an island group of similar temperature, due to the high importance of niche constraints for establishment. In this context, it is interesting that mean annual precipitation was not considered relevant in our model. Temperature and other niche constraints such as maximum elevation are important factors shaping compositional similarity, while factors related to anthropogenic dispersal define richness.

Our analysis identified three island groups that were notable outliers in terms of richness and composition: Juan Fernandez, the Hawaiian Islands and the Solomon and Bismarck islands. Juan Fernandez has many naturalized species that are not found anywhere else in the Pacific. This could be due to the combined effects of its (a) unique colonization history, first being discovered by Spanish seafarers rather than Polynesians and later strengthening ties to Chile (Cuevas & van Leersum, 2001), (b) high isolation from other island groups and therefore poor connection to major trade routes, (c) unique biogeographic factors that shaped its highly endemic flora (Cuevas & van Leersum, 2001) and (d) lower temperatures (lowest in our data set). The Hawaiian Islands are the most invaded island group in the Pacific and contain many species that are not found anywhere else in the Pacific. The Hawaiian Islands are the third-largest island group, are heterogeneous in climate and altitude, are remote and have a unique colonization history shaped by Polynesians, British, Americans and Japanese. In contrast, the Solomon and Bismarck islands have large land area (largest in our data set) but are overall sparsely populated with a relatively low GDP Index. This island group might be understudied (e.g. no records in GloNAF) and/or might truly contain few naturalized species. These outliers help to provide a refined understanding of the patterns and the likely processes that generate them. The list of naturalized species on the Hawaiian naturalized plant species can serve as a preliminary watchlist for other island groups in the Pacific. Species-rich island groups such as Hawai'i might provide sources of naturalized species for other island groups in the Pacific and, together with the

consideration of environmental drivers, can serve as early warning sites. Future research could apply our results to (a) draw conclusions on how many species could naturalize in other island groups and (b) create more specific naturalization–risk assessments for problematic species.

The large number of naturalized plants in the Pacific gives reason to be worried, as some of them are, or will likely become invasive (Jeschke & Pyšek, 2018; Traveset et al., 2014, *sensu* Blackburn et al., 2011; Richardson et al., 2000). Even if they do not become invasive, the presence of naturalized species reduces regional floristic distinctiveness through biotic homogenization (Vitousek et al., 1997). Our results highlight the human-mediated connectivity between the Pacific and other parts of the world (see also Capinha et al., 2015) and highlights potential entry points for non-native species. There are groups of naturalized species that may be particularly suited to establish in the Pacific (e.g. because they are pre-adapted to climatic conditions or have traits associated with human use or disturbed ecosystems) and identifying additional common traits of these species holds much promise for predicting future establishment. Naturalized species patterns in the Pacific are intrinsically bound to human activities, but economic growth and naturalized species richness increase do not have to be coupled in the future, as this is a human-made connection that can be mediated using human-made measures. Management strategies to prevent undesired introduction and establishment of non-native must be put in place or strengthened and the same increased global connectivity that leads to the introduction of naturalized species can also limit it (Essl et al., 2019; Pyšek et al., 2010; Seebens et al., 2015). Cooperative initiatives to prevent and manage non-native species (e.g. “The Cooperative Islands Initiative”; <http://www.issg.org/cii/>) could be used to create specific watchlists for the Pacific, especially for invasive species, to make screening in trade easier (SPREP, 2016; Sherley et al., 2000). In this study, we provide a comprehensive overview of patterns and drivers of naturalized species establishment in the Pacific, as a foundation for future work on the processes of naturalized species spread and on applied management of naturalized species.

ACKNOWLEDGEMENTS

We appreciate the helpful comments of two anonymous reviewers to a previous version of the manuscript. This article is the result of a workshop on Pacific Naturalized plants led by TMK. The authors are grateful for members of the spatial interaction working group for valuable discussion. The authors are grateful for the support of the PIER Team. Funding was provided by the Alexander von Humboldt Foundation in the framework of the Alexander von Humboldt Professorship, by the Helmholtz Recruitment Initiative of the Helmholtz Association (both to TMK) and by the German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig funded by the German Research Foundation (DFG)—FZT 118 – 202548816. HS received funding by the BiodivERsA-Belmont Forum Project “Alien Scenarios” (BMBF grant 01LC1807A). PP and

JP were supported by EXPRO grant no. 19-28807X (Czech Science Foundation) and Long-term Research Development Project RVO 67985939 (Czech Academy of Sciences). FE appreciates funding by the Austrian Science Foundation (FWF project no I 2086-B16). DZ appreciates funding by (DFZ ZU 361/1-1).

Peer Review

The peer review history for this article is available at <https://publons.com/publon/10.1111/ddi.13260>.

DATA AVAILABILITY STATEMENT

Our data are compiled from GloNAF and PIER which are both open source. Species names and island/island group names can be found in the Table S1 and S2. We plan to publish our aggregated data set in an upcoming data publication.

ORCID

Michael R. Wohlwend  <https://orcid.org/0000-0001-7230-6058>

Dylan Craven  <https://orcid.org/0000-0003-3940-833X>

Hanno Seebens  <https://orcid.org/0000-0001-8993-6419>

Marten Winter  <https://orcid.org/0000-0002-9593-7300>

Holger Kreft  <https://orcid.org/0000-0003-4471-8236>

Franz Essl  <https://orcid.org/0000-0001-8253-2112>

Mark van Kleunen  <https://orcid.org/0000-0002-2861-3701>

Petr Pyšek  <https://orcid.org/0000-0001-8500-442X>

Tiffany M. Knight  <https://orcid.org/0000-0003-0318-1567>

REFERENCES

- Atkinson, I. A. E., & Cameron, E. K. (1993). Human influence on the terrestrial biota and biotic communities of New Zealand. *Trends in Ecology and Evolution*, 8(12), 447–451. [https://doi.org/10.1016/0169-5347\(93\)90008-D](https://doi.org/10.1016/0169-5347(93)90008-D)
- Baselga, A. (2010). Partitioning the turnover and nestedness components of beta diversity. *Global Ecology and Biogeography*, 19(1), 134–143. <https://doi.org/10.1111/j.1466-8238.2009.00490.x>
- Baselga, A., Orme, D., Villeger, S., De Bortoli, J., Leprieux, F. & Logez, M. (2020). betapart: Partitioning Beta Diversity into Turnover and Nestedness Components. R package version 1.5.2. <https://CRAN.R-project.org/package=betapart>
- Bivand, R., & Rundel, C. (2020). *rgeos: Interface to geometry engine - open source ('GEOS')* (R package version 0.5-3). Retrieved from <https://cran.r-project.org/package=rgeos>
- 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 and Evolution*, 26(7), 333–339. <https://doi.org/10.1016/j.tree.2011.03.023>
- Braje, T. J., Leppard, T. P., Fitzpatrick, S. M., & Erlandson, J. M. (2017). Archaeology, historical ecology and anthropogenic island ecosystems. *Environmental Conservation*, 44(3), 286–297. <https://doi.org/10.1017/S0376892917000261>
- Cabral, J. S., Whittaker, R. J., Wiegand, K., & Kreft, H. (2019). Assessing predicted isolation effects from the general dynamic model of island biogeography with an eco-evolutionary model for plants. *Journal of Biogeography*, 46(7), 1569–1581. <https://doi.org/10.1111/jbi.13603>
- Capinha, C., Essl, F., Seebens, H., Moser, D., & Pereira, H. M. (2015). The dispersal of alien species redefines biogeography in the Anthropocene. *Science*, 348(6240), 1248–1251. <https://doi.org/10.1126/science.aaa8913>

- Cavender-Bares, J., Kozak, K. H., Fine, P. V. A., & Kembel, S. W. (2009). The merging of community ecology and phylogenetic biology. *Ecology Letters*, 12(7), 693–715. <https://doi.org/10.1111/j.1461-0248.2009.01314.x>
- Crisp, M. D., Arroyo, M. T. K., Cook, L. G., Gandolfo, M. A., Jordan, G. J., McGlone, M. S., Weston, P. H., Westoby, M., Wilf, P., & Linder, H. P. (2009). Phylogenetic biome conservatism on a global scale. *Nature*, 458(7239), 754–756. <https://doi.org/10.1038/nature07764>
- Cuevas, J. G., & van Leersum, G. (2001). Project "Conservation, Restoration, and Development of the Juan Fernández islands, Chile". *Revista Chilena De Historia Natural*, 74(4), 899–910. <https://doi.org/10.4067/S0716-078X2001000400016>
- 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., ... Essl, F. (2017). Global hotspots and correlates of alien species richness across taxonomic groups. *Nature Ecology and Evolution*, 1(June), 1–7. <https://doi.org/10.1038/s41559-017-0186>
- Denslow, J. S. (2003). Weeds in paradise: Thoughts on the invasibility of tropical islands. *Annals of the Missouri Botanical Garden*, 90(1), 119. <https://doi.org/10.2307/3298531>
- Denslow, J. S., Space, J. C., & Thomas, P. A. (2009). Invasive exotic plants in the tropical pacific islands: Patterns of diversity. *Biotropica*, 41(2), 162–170. <https://doi.org/10.1111/j.1744-7429.2008.00469.x>
- di Castri, F. (1989). History of biological invasions with special emphasis on the Old World. In J. A. Drake, H. A. Mooney, F. di Castri, R. H. Groves, F. J. Kruger, M. Rejmánek, & M. Williamson (Eds.), *Biological invasions: A global perspective* (pp. 1–30). John Wiley and Sons.
- di Castri, F. (1990). On invading species and invaded ecosystems: The interplay of historical chance and biological necessity. In F. di Castri, A. J. Hansen, & M. Debussche (Eds.), *Biological invasions in Europe and the Mediterranean basin* (pp. 3–16). Kluwer Academic Publishers.
- Doxsey-Whitfield, E., MacManus, K., Adamo, S. B., Pistolesi, L., Squires, J., Borkovska, O., & Baptista, S. R. (2015). Taking advantage of the improved availability of census data: A first look at the gridded population of the world, version 4. *Papers in Applied Geography*, 1(3), 226–234. <https://doi.org/10.1080/23754931.2015.1014272>
- Doyle, J. J. (2001). Leguminosae. In S. Brenner & J. H. Miller (Eds.), *Encyclopedia of genetics* (pp. 1081–1085). Elsevier. <https://doi.org/10.1006/rwgn.2001.1642>
- Elton, C. S. (1958). *The ecology of invasions by animals and plants*. Methuen.
- Essl, F., Dawson, W., Kreft, H., Pergl, J., Pyšek, P., Van Kleunen, M., Weigelt, P., Mang, T., Dullinger, S., Lenzner, B., Moser, D., Maurel, N., Seebens, H., Stein, A., Weber, E., Chatelain, C., Inderjit, Genovesi, P., Kartesz, J., ... Winter, M. (2019). Drivers of the relative richness of naturalized and invasive plant species on Earth. *AoB PLANTS*, 11(5), 1–13. <https://doi.org/10.1093/aobpla/plz051>
- Fischer, M. A., Oswald, K., & Adler, W. (2008). *Exkursionsflora für Österreich, Liechtenstein und Südtirol* (3rd ed.). Land Oberösterreich, Biologiezentrum der Oberösterreichischen Landesmuseen.
- Freiberg, M., Winter, M., Gentile, A., Zizka, A., Muellner-Riehl, A. N., Weigelt, A., & Wirth, C. (2020). The Leipzig Catalogue of Vascular Plants (LCVP) – An improved taxonomic reference list for all known vascular plants. *BioRxiv*, 2020.05.08.077149. <https://doi.org/10.1101/2020.05.08.077149>
- Frenot, Y., Gloaguen, J. C., Massé, L., & Lebouvier, M. (2001). Human activities, ecosystem disturbance and plant invasions in subantarctic Crozet. *Kerguelen and Amsterdam Islands. Biological Conservation*, 101(1), 33–50. [https://doi.org/10.1016/S0006-3207\(01\)00052-0](https://doi.org/10.1016/S0006-3207(01)00052-0)
- Genuer, R., Poggi, J. M., & Tuleau-Malot, C. (2015). VSURF: An R package for variable selection using random forests. *The R Journal*, 7(2), 19–33. <https://doi.org/10.32614/RJ-2015-018>
- Gillespie, R. G., Claridge, E. M., & Roderick, G. K. (2008). Biodiversity dynamics in isolated island communities: Interaction between natural and human-mediated processes. *Molecular Ecology*, 17(1), 45–57. <https://doi.org/10.1111/j.1365-294X.2007.03466.x>
- Hijmans, R. J. (2020). *raster: Geographic data analysis and modeling (R package version 3.1-5)*. Retrieved from <https://cran.r-project.org/package=raster>
- Hui, C., Richardson, D. M., & Visser, V. (2017). Ranking of invasive spread through urban green areas in the world's 100 most populous cities. *Biological Invasions*, 19(12), 3527–3539. <https://doi.org/10.1007/s10530-017-1584-0>
- Hulme, P. E. (2009). Trade, transport and trouble: Managing invasive species pathways in an era of globalization. *Journal of Applied Ecology*, 46(1), 10–18. <https://doi.org/10.1111/j.1365-2664.2008.01600.x>
- Jeschke, J. M., & Pyšek, P. (2018). Tens rule. In J. M. Jeschke, & T. Heger (Eds.), *Invasion biology: Hypotheses and evidence* (1st ed., pp. 124–132). CABI. <https://doi.org/10.1079/9781780647647.0124>
- Johnson, N. L., Kotz, S., & Kemp, A. W. (1992). *Univariate discrete distributions* (2nd ed.). Wiley.
- Kaffka, S. R. (2009). Can feedstock production for biofuels be sustainable in California? *California Agriculture*, 63(4), 202–207. <https://doi.org/10.3733/ca.v063n04p202>
- Kallimanis, A. S., Bergmeier, E., Panitsa, M., Georgiou, K., Delipetrou, P., & Dimopoulos, P. (2010). Biogeographical determinants for total and endemic species richness in a continental archipelago. *Biodiversity and Conservation*, 19(5), 1225–1235.
- Karger, D. N., Conrad, O., Böhner, J., Kawohl, T., Kreft, H., Soria-Auza, R. W., Zimmermann, N. E., Linder, H. P., & Kessler, M. (2017). Climatologies at high resolution for the earth's land surface areas. *Scientific Data*, 4, 1–20. <https://doi.org/10.1038/sdata.2017.122>
- Keil, P., Schweiger, O., Kühn, I., Kunin, W. E., Kuussaari, M., Settele, J., Henle, K., Brotons, L., Pe'er, G., Lengyel, S., Moustakas, A., Steinicke, H., & Storch, D. (2012). Patterns of beta diversity in Europe: The role of climate, land cover and distance across scales. *Journal of Biogeography*, 39(8), 1473–1486. <https://doi.org/10.1111/j.1365-2699.2012.02701.x>
- König, C., Weigelt, P., & Kreft, H. (2017). Dissecting global turnover in vascular plants. *Global Ecology and Biogeography*, 26(2), 228–242. <https://doi.org/10.1111/geb.12536>
- 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. (2020). Source pools and disharmony of the world's island floras. *Ecography*, 44(1), 44–55. <https://doi.org/10.1111/ecog.05174>
- Kreft, H., & Jetz, W. (2007). Global patterns and determinants of vascular plant diversity. *Proceedings of the National Academy of Sciences of the United States of America*, 104(14), 5925–5930. <https://doi.org/10.1073/pnas.0608361104>
- Kueffer, C., Daehler, C. C., Torres-Santana, C. W., Laverne, 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(2), 145–161. <https://doi.org/10.1016/j.ppees.2009.06.002>
- Lee, L. J., & Ngim, J. (2000). A first report of glyphosate-resistant goosegrass (*Eleusine indica* (L) Gaertn) in Malaysia. *Pest Management Science*, 56(4), 336–339. [https://doi.org/10.1002/\(SICI\)1526-4998\(200004\)56:4<336::AID-PS123>3.0.CO;2-8](https://doi.org/10.1002/(SICI)1526-4998(200004)56:4<336::AID-PS123>3.0.CO;2-8)
- Liaw, A., & Wiener, M. (2002). Classification and Regression by random Forest. *R News*, 2(3), 18–22.
- Loope, L. L. (1998). Hawaii and Pacific islands. In M. J. Mac, P. A. Opler, C. E. Puckett Haecker, & P. D. Doran (Eds.), *Status and trends of the nation's biological resources* (Vol. 2, 2nd ed., pp. 747–774). US Geological Survey.
- Loope, L., & Mueller-Dombois, D. (1989). Characteristics of invaded islands, with special reference to Hawaii. In J. A. Drake (Ed.),

- Biological invasions: A global perspective*, (pp. 257–280). John Wiley & Sons Ltd.
- MacDougall, A. S., Gilbert, B., & Levine, J. M. (2009). Plant invasions and the niche. *Journal of Ecology*, 97(4), 609–615. <https://doi.org/10.1111/j.1365-2745.2009.01514.x>
- Marvier, M., Kareiva, P., & Neubert, M. G. (2004). Habitat destruction, fragmentation, and disturbance promote invasion by habitat generalists in a multispecies metapopulation. *Risk Analysis*, 24(4), 869–878. <https://doi.org/10.1111/j.0272-4332.2004.00485.x>
- Merlin, M. D., & Juvik, J. O. (1992). Relationships among native and alien plants on Pacific islands with and without significant human disturbance and feral ungulates. In C. P. Stone, C. W. Smith & J. T. Tunison (Eds.), *Alien plant invasions in native ecosystems of Hawaii: Management and research* (pp. 597–624). Honolulu, Hawaii, USA: The Pacific Cooperative Study Unit, University of Hawaii at Manoa.
- Meyer, J.-Y. (2004). Threat of invasive alien plants to native flora and forest vegetation of eastern Polynesia. *Pacific Science*, 58(3), 357–375. <https://doi.org/10.1353/psc.2004.0032>
- Moser, D., Lenzner, B., Weigelt, P., Dawson, W., Kreft, H., Pergl, J., Pyšek, P., van Kleunen, M., 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 of the United States of America*, 115(37), 9270–9275. <https://doi.org/10.1073/pnas.1804179115>
- NOAA, Ghosh, T., Powell, R., Elvidge, C. D., Baugh, K. E., Sutton, P. C., & Anderson, S. (2010). *Gross domestic product (GDP) from night lights*. Retrieved from <https://datacatalog.worldbank.org/dataset/gross-domestic-product-gdp-night-lights-2010>
- Patokallio, J. (2020). Retrieved from <https://openflights.org/>
- 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., & Winter, M. (2010). Disentangling the role of environmental and human pressures on biological invasions across Europe. *Proceedings of the National Academy of Sciences of the United States of America*, 107(27), 12157–12162. <https://doi.org/10.1073/pnas.1002314107>
- Pyšek, P., Pergl, J., Essl, F., Lenzner, B., Dawson, W., Kreft, H., Weigelt, P., Winter, M., Kartesz, J., Nishino, M., Antonova, L. A., Barcelona, J. F., Cablesaz, F. J., Cárdenas, D., Cárdenas-Toro, J., Castaño, N., Chacón, E., Chatelain, C., Dullinger, S., ... Kleunen, M. V. (2017). Naturalized alien flora of the world: Species diversity, taxonomic and phylogenetic patterns, geographic distribution and global hotspots of plant invasion. *Preslia*, 89(3), 203–274. <https://doi.org/10.23855/preslia.2017.203>
- Qian, H., McKinney, M. L., & Kühn, I. (2008). Effects of introduced species on floristic similarity: Comparing two US states. *Basic and Applied Ecology*, 9(6), 617–625. <https://doi.org/10.1016/j.baec.2007.11.004>
- R Core Team (2020). *R: A language and environment for statistical computing (R version 4.0.0 (2020-04-24)—“Arbor Day”)*. R Foundation for Statistical Computing. Retrieved from <https://www.r-project.org/>
- Richardson, D. M., Ek, P. P. Y. S., Rejmánek, M., Barbour, M. G., Panetta, F. D., & West, C. J. (2000). Naturalization and invasion of alien plants: Concepts and definitions. *Diversity Distributions*, 6(2), 93–107. <https://doi.org/10.1046/j.1472-4642.2000.00083.x>
- Secretariat of the Pacific Regional Environment Programme (SPREP) (2016). *Battling Invasive Species in the Pacific: Outcomes of the Regional GEF-PAS IAS Project Prevention, control and management of invasive species in the Pacific islands*. Apia, Samoa: Secretariat of the Pacific Regional Environment Programme (SPREP).
- 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-Grampow, L., Dawson, W., Dullinger, S., Fuentes, N., Jäger, H., ... Essl, F. (2017). No saturation in the accumulation of alien species worldwide. *Nature Communications*, 8, 1–9. <https://doi.org/10.1038/ncomms14435>
- Seebens, H., Essl, F., Dawson, W., Fuentes, N., Moser, D., Pergl, J., Pyšek, P., van Kleunen, M., Weber, E., Winter, M., & Blasius, B. (2015). Global trade will accelerate plant invasions in emerging economies under climate change. *Global Change Biology*, 21(11), 4128–4140. <https://doi.org/10.1111/gcb.13021>
- Sherley, G., Timmins, S., Lowe, S., Atkinson, A. E., Atkinson, T. J., Meyer, J. Y., Nishida, G. M., Evenhuis, N. L., Cowie, R. H., & Eldrege, L. G. (2000). In G. Sherley (Ed.), *Invasive species in the Pacific: A technical review and draft regional strategy* (Vol. 1, pp. 1–193). Apia, Samoa: South Pacific Regional Environment Programme. [https://doi.org/10.1016/S0378-777X\(82\)80016-4](https://doi.org/10.1016/S0378-777X(82)80016-4)
- Soininen, J., McDonald, R., & Hillebrand, H. (2007). The distance decay of similarity in ecological communities. *Ecography*, 30(1), 3–12. <https://doi.org/10.1111/j.2006.0906-7590.04817.x>
- South, A. (2017). *rnaturalearth: World map data from natural earth (R package version 0.1.0)*. Retrieved from <https://cran.r-project.org/package=rnaturalearth>
- Stekhoven, D. J., & Buehlmann, P. (2012). MissForest – Nonparametric missing value imputation for mixed-type data. *Bioinformatics*, 28, 112–118. <https://doi.org/10.1093/bioinformatics/btr597>
- Strobl, C., Boulesteix, A. L., Zeileis, A., & Hothorn, T. (2007). Bias in random forest variable importance measures: Illustrations, sources and a solution. *BMC Bioinformatics*, 8, 1–21. <https://doi.org/10.1186/1471-2105-8-25>
- Traveset, A., Kueffer, C., & Daehler, C. C. (2014). Global and regional nested patterns of non-native invasive floras on tropical islands. *Journal of Biogeography*, 41(4), 823–832. <https://doi.org/10.1111/jbi.12243>
- United States Geological Survey (2011). *Global Multi-resolution Terrain Elevation Data 2010 (GMTED2010)*. United States Geological Survey. Retrieved from <https://lta.cr.usgs.gov/GMTED2010>
- Usher, M. B. (1986). Invasibility and wildlife conservation: Invasive species on nature reserves. *Philosophical Transactions of the Royal Society of London Series B-Biological Sciences*, 314, 695–710. <https://doi.org/10.1098/rstb.1986.0081>
- van Kleunen, M., Dawson, W., Essl, F., Pergl, J., Winter, M., Weber, E., Kreft, H., Weigelt, P., Kartesz, J., Nishino, M., Antonova, L. A., Barcelona, J. F., Cabezas, F. J., Cárdenas, D., Cárdenas-Toro, J., Castaño, N., Chacón, E., Chatelain, C., Ebel, A. L., ... Pyšek, P. (2015). Global exchange and accumulation of non-native plants. *Nature*, 525(7567), 100–103. <https://doi.org/10.1038/nature14910>
- van Kleunen, M., Essl, F., Pergl, J., Brundu, G., Carboni, M., Dullinger, S., Early, R., González-Moreno, P., Groom, Q. J., Hulme, P. E., Kueffer, C., Kühn, I., Máguas, C., Maurel, N., Novoa, A., Parepa, M., Pyšek, P., Seebens, H., Tanner, R., ... Dehnen-Schmutz, K. (2018). The changing role of ornamental horticulture in alien plant invasions. *Biological Reviews*, 93(3), 1421–1437. <https://doi.org/10.1111/brv.12402>
- van Kleunen, M., Pyšek, P., Dawson, W., Essl, F., Kreft, H., Pergl, J., Weigelt, P., Stein, A., Dullinger, S., König, C., Lenzner, B., Maurel, N., Moser, D., Seebens, H., Kartesz, J., Nishino, M., Aleksanyan, A., Ansong, M., Antonova, L. A., ... Winter, M. (2019). The Global Naturalized Alien Flora (GloNAF) database. *Ecology*, 100(1), 1–2. <https://doi.org/10.1002/ecy.2542>
- van Kleunen, M., Xu, X., Yang, Q., Maurel, N., Zhang, Z., Dawson, W., Essl, F., Kreft, H., Pergl, J., Pyšek, P., Weigelt, P., Moser, D., Lenzner, B., & Frisoe, T. S. (2020). Economic use of plants is key to their naturalization success. *Nature Communications*, 11(1), 1–12. <https://doi.org/10.1038/s41467-020-16982-3>
- Vitousek, P. M., D'Antonio, C. M., Loope, L. L., Rejmánek, M., & Westbrooks, R. (1997). Introduced species: A significant component of human-caused global change. *New Zealand Journal of Ecology*, 21(1), 1–16.

- 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(4828), 802–804. <https://doi.org/10.1126/science.238.4828.802>
- Watson, L., & Dallwitz, M. J. (1992). *The families of flowering plants: Descriptions, illustrations, identification, and information retrieval*. Retrieved from <http://Biodiversity.Uno.Edu/Delta/>
- Weigelt, P., Daniel Kissling, W., Kisel, Y., Fritz, S. A., Karger, D. N., Kessler, M., Lehtonen, S., Svenning, J. C., & Kreft, H. (2015). Global patterns and drivers of phylogenetic structure in island floras. *Scientific Reports*, 5, 1–13. <https://doi.org/10.1038/srep12213>
- Weigelt, P., König, C., & Kreft, H. (2020). GIFT – A Global Inventory of Floras and Traits for macroecology and biogeography. *Journal of Biogeography*, 47(1), 16–43. <https://doi.org/10.1111/jbi.13623>
- Weigelt, P., & Kreft, H. (2013). Quantifying island isolation – Insights from global patterns of insular plant species richness. *Ecography*, 36(4), 417–429. <https://doi.org/10.1111/j.1600-0587.2012.07669.x>
- Wickham, H. (2016). *ggplot2: Elegant graphics for data analysis*. Springer-Verlag. Retrieved from <https://ggplot2.tidyverse.org>
- Wildlife Conservation Society (WCS) and the Center for International Earth Science Information Network (CIESIN) (2005). *Last of the wild project, version 2, 2005. (LWP-2): Global human footprint dataset (geographic)*. Wildlife Conservation Society (WCS) and the Center for International Earth Science Information Network (CIESIN).
- Williams, P. H. (1993). Measuring more of biodiversity for choosing conservation areas, using taxonomic relatedness. In T.-Y. Moon (Ed.), *International Symposium on Biodiversity and Conservation* (pp. 194–227). Korean Entomological Institute.
- Winter, M., Kühn, I., La Sorte, F. A., Schweiger, O., Nentwig, W., & Klotz, S. (2010). The role of non-native plants and vertebrates in defining patterns of compositional dissimilarity within and across continents. *Global Ecology and Biogeography*, 19(3), 332–342. <https://doi.org/10.1111/j.1466-8238.2010.00520.x>
- Wright, D. H. (1983). Species-energy theory: An extension of species-area theory. *Oikos*, 41, 496–506. <https://doi.org/10.2307/3544109>

BIOSKETCH

Michael R. Wohlwend is interested in the field of plant ecology and biogeography. Changing patterns and dynamics fascinated him the most. He was specialized in non-native species and their dispersal as well as experimental restoration projects, which are often sabotaged by non-native and invasive plant species. It has always been important for him to work on an applied issue on multiple scales. This project is the result of a workshop at iDiv, and his co-authors have many different backgrounds such as demography, macroecology and community ecology, sharing an interest in invasion biology.

Author contributions: T.M.K. organized the initial workshop on this topic with M.R.W., D.C., P.W., M.W., H.S., J.S.C., D.Z. and H.K. as participants. M.R.W. and D.C. compiled the data set. M.R.W., D.C. and P.W. conducted the initial analyses. M.R.W. finalized the analysis. M.R.W. and T.M.K. wrote the manuscript. All authors contributed to the final version of the manuscript.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

How to cite this article: Wohlwend MR, Craven D, Weigelt P, et al. Anthropogenic and environmental drivers shape diversity of naturalized plants across the Pacific. *Divers Distrib*. 2021;00:1–14. <https://doi.org/10.1111/ddi.13260>