

# Global and regional nested patterns of non-native invasive floras on tropical islands

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## ABSTRACT

**Aim** Non-native species are being distributed globally as a result of human actions, but we still know little about emerging biogeographical patterns. We tested whether the distribution of plant invaders across tropical oceanic islands has a nested structure, and identified mechanisms to explain nestedness among invaders and islands.

**Location** Tropical islands world-wide.

**Methods** We analysed two datasets: a global one (350 spermatophyte species invading natural areas within 25 archipelagos) and a regional one (145 species within 12 Pacific archipelagos). We quantified island and species nestedness using the NODF metric and evaluated the contributions of each island and species to nestedness.

**Results** Globally, the distribution of invaders across islands showed a nested pattern related to island area, elevation (a proxy of habitat diversity) and invasive species richness; the pattern was weakly associated with human population density and independent of isolation from the nearest continent. Invader prevalence among islands was the best predictor of species nestedness. Nestedness was more pronounced at a regional than a global scale.

**Main conclusions** We found novel biogeographical patterns interconnecting non-native invasive floras at a global scale. Both localized and widespread species are important components of island invasive floras. Invader-rich islands host many rare invaders, and many species are invaders in only one island group, suggesting that prevention efforts should pay attention to rare invaders. We have developed a conceptual model to facilitate understanding of nestedness in island invasion. Both habitat and dispersal filtering are potential mechanisms underlying nestedness, whereas idiosyncratic factors of particular islands (e.g. habitat diversity and socio-economic history) or time-lags may explain 'invader endemicity'. Nested regional patterns may be explained by 'hub' islands that serve as early sites of introduction for many invaders, some of which subsequently spread across the region.

## Keywords

Dispersal limitation, habitat filtering, invasive flora, invasive species richness, island area, island biogeography, nestedness, tropical archipelagos.

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## INTRODUCTION

Biological invasions have been particularly detrimental on oceanic islands (Millennium Ecosystem Assessment, 2005; Reaser *et al.*, 2007), including isolated continental fragments

such as New Zealand, New Caledonia and the Seychelles; most documented extinctions promoted by non-native species (mainly vertebrates) are known from such ecosystems (e.g. Traveset & Richardson, 2006; Whittaker & Fernández-Palacios, 2007; Sax & Gaines, 2008; Caujapé-Castells *et al.*,

2010). Although there has long been an interest in biotic invasions of islands, further work is needed to describe fully and understand the biogeographical patterns of plant invasions on islands at regional to global scales (Pyšek & Richardson, 2006; Sax & Gaines, 2008; Denslow *et al.*, 2009; Kueffer *et al.*, 2010a; Richardson & Pyšek, 2012). Kueffer *et al.* (2010a) found that a combination of anthropogenic factors (e.g. the level of human settlement) and natural factors (e.g. habitat diversity) determine the species richness of invasive plants in an island group. However, we still need more integrative analyses of the community assembly of invasive floras to help us (1) predict which associations or combinations of species may be found in a given area (island or island group), and (2) determine what factors enhance or constrain the invasiveness of non-native species across islands.

One useful approach to detecting and analysing the distribution patterns of multiple species across multiple islands is nestedness analysis (e.g. Lomolino, 1996; Wright *et al.*, 1998; Greve *et al.*, 2005; Ulrich *et al.*, 2009). In particular, it is important to know whether invader-poor islands are invaded by the same species as invader-rich islands. If such a nested pattern is found, then information from highly invaded islands may be used to prevent further invasion of the less affected ones. If there is no nestedness, and invader-poor islands are invaded by a different set of species, then prevention has to be specifically tailored to those islands.

In this study, we used the data assembled by Kueffer *et al.* (2010a), with some modifications (see below), to assess whether assemblages of natural area invaders on tropical islands world-wide are hierarchically distributed, and to identify any mechanisms underlying the emerging patterns. This study is the first global-scale nestedness analysis for invasive biota, although it is restricted to tropical islands. We focused on invaders that have attained a high abundance in natural habitats and probably have an important impact. We were interested in both island and species nestedness; therefore we used a metric that quantifies the level of nestedness of a matrix separately based on columns (in our case islands) and rows (species) (Almeida-Neto *et al.*, 2008). Specifically, we tested the following hypotheses:

1. Poorly invaded islands mostly contain species that are also present on invader-rich islands. We predicted that factors such as island area, isolation, elevation (a proxy of the diversity of habitat types on an island) and human population density contribute to this nested pattern.
2. Rare invaders (defined here as those found to be invasive on only one or a few islands) are invasive on islands that contain the most widespread invaders. This nested pattern might emerge from dispersal processes (if, for instance, rare species are transported only to islands where many other species have been introduced) and also by habitat filtering (if conditions suitable for the establishment of rare invaders only occur on islands that are also suitable for more common invaders).

3. Because of similarities in the source pool of invaders across a particular region, nestedness is higher when considering a particular biogeographical region, relative to global patterns of nestedness (Greve *et al.*, 2005). To test whether this pattern holds for island invasive floras, we focused on the Pacific region, for which data from the highest number of islands exist. We also expected the geographical distance and latitudinal difference between two islands to be negatively associated with their degree of nestedness.

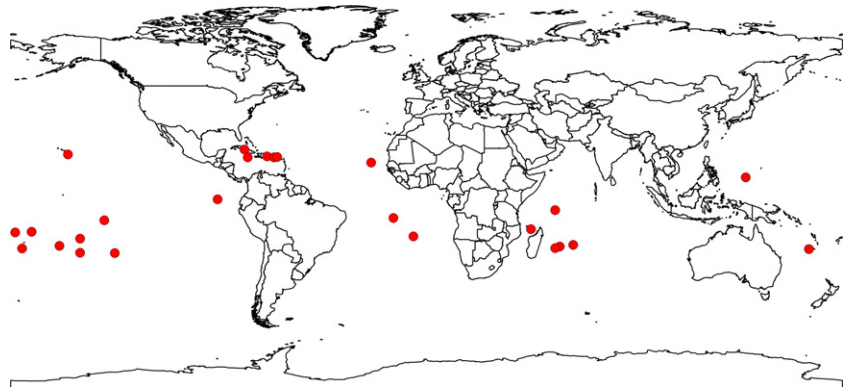
At the island and species levels, we also assessed which island and species traits affect their individual contributions to the nested pattern. For islands, we tested the effects of area, age, human population density, distance from the nearest continent, latitude and elevation, in addition to the effect of invader species richness. For species, our predictor variables were habitat affinity, life-form, growth-form and plant use, in addition to the effect of prevalence (i.e. number of islands invaded by the species).

## MATERIALS AND METHODS

### Data collection

We focused on tropical islands ( $\pm 23.4^\circ$ ; see Corlett, 2013). Ecological niche models have revealed an important influence of climate on plant distribution and potential areas of invasion (Petitpierre *et al.*, 2012, and references therein). For oceanic islands, Kueffer *et al.* (2010a) also found a strong match between the climate of the island group and the native climate range of the non-native invasive species: 82% of species on tropical or subtropical islands had a tropical or subtropical origin. Had we included islands from extreme latitudes in our analysis, we would have expected very little overlap in species composition with the tropical islands examined in our study. In fact, we found that only 11% of the plants in our dataset had a range extending considerably outside the tropics (see Appendix S1 in Supporting Information).

The original dataset used by Kueffer *et al.* (2010a) was adapted by removing six non-tropical islands. In turn, recently available data from Cuba were added (R. Oviedo, unpublished data). A total of 25 islands or archipelagos (island groups), belonging to four biogeographical regions [Atlantic Ocean (three island groups), Caribbean (five), Pacific (12) and Western Indian Ocean (five)], was included in the analyses (Fig. 1). The entire dataset included 350 spermatophyte species, belonging to 86 families, that were either moderate invaders (common invaders of natural areas, attaining a maximal relative vegetation cover of *c.* 5–25% in natural areas) or dominant invaders (reaching a maximum relative vegetation cover > 25% in natural areas). A large fraction (39%) was originally from tropical/subtropical America; 25% were from Asia and/or tropical India, 14% were from Africa, 8% were from Australia or Australasia, and only *c.* 4% were from Europe. The rest had either an obscure original range, were widespread on two or three



**Figure 1** The location of the 25 tropical ( $\pm 23.4^\circ$ ) island groups considered for the study of global and regional nested patterns of non-native invasive floras.

continents, or were small-island endemics. Further details on the dataset can be found in Kueffer *et al.* (2010a). This dataset represents the most comprehensive global list of plant invaders of natural areas on islands compiled so far, based on expert knowledge.

### Data analyses

We calculated the nestedness metric NODF (nestedness based on overlap and decreasing fill; Almeida-Neto *et al.*, 2008; Almeida-Neto & Ulrich, 2011) by using the software NODF version 2.0 (<http://www.keib.umk.pl/nodf/>). This metric was chosen to test for nestedness independently among columns (islands; i.e. community composition) and rows (species occupancy). We measured column nestedness (NODF<sub>c</sub>) to assess whether invader communities were nested among island groups, while we measured row nestedness (NODF<sub>r</sub>) to determine whether the rarest invaders were present on islands that also had the most common (widespread) invaders. NODF is dependent on the arrangement of columns and rows, which allows hypotheses about the causes of nestedness to be tested by ordering columns and rows according to criteria representing different hypotheses (Almeida-Neto *et al.*, 2008; Ulrich *et al.*, 2009; Almeida-Neto & Ulrich, 2011). To test our hypotheses, we thus arranged islands according to invasive species richness, island area, human population, isolation and elevation, but consistently kept species ordered from the most widespread to the least common. The significance of NODF values was assessed against 1000 randomizations using the fixed–fixed (FF) null model, in which entries are randomized in null matrices, but the number of invaders on each island is fixed along with the number of islands per species; this null model is appropriate for large-scale species occurrence records such as ours (Ulrich & Gotelli, 2012) and is claimed to be better than the loosely constrained models used to test nestedness in many ecological networks (see Joppa *et al.*, 2010). Additionally, we tested our matrices with another even more constrained null model, using the proportional–proportional (PP) algorithm (Ulrich & Gotelli, 2012), which has better power to detect segregated and nested matrices. The PP model creates null

matrices in which the row and column vary randomly, but the average row and column totals are unbiased and match those of the original matrix. Both these null models identify a substantially smaller number of matrices as non-random compared with the popular temperature metric (Atmar & Patterson, 1993). The temperature metric is also known to be more sensitive to the size and fill of the matrix than the NODF metric (Almeida-Neto *et al.*, 2008). In order to see how consistent and robust the results were, we examined the temperature metric and the discrepancy metric (Brualdi & Sanderson, 1999), as modified by Ulrich & Gotelli (2007). The results were obtained with the same NODF software and are given in Appendix S2.

The nestedness contribution of each island ( $\Delta_{i1}$ ) and species ( $\Delta_{sp}$ ) was obtained by subtracting the NODF value of the matrix without the island (I) or the species (Sp), respectively, from the NODF of the entire matrix (Almeida-Neto & Ulrich, 2011). We calculated these values from the matrix ordered by species richness, although they were very similar to those found when ordered by another criterion. In order to assess what island and species traits were associated with their nestedness contribution, we constructed generalized linear models (GLM) using either  $\Delta_{i1}$  or  $\Delta_{sp}$  as the dependent variable and different island and species characteristics, respectively, as predictors. In the former case, we used seven predictors: invasive species richness, island area, age, human population density, distance from nearest continent, latitude and elevation. The number of habitats in each island was highly correlated with elevation ( $r = 0.90$ ,  $P < 0.001$ ; Kueffer *et al.*, 2010a) and thus was not considered in the analysis. For species, we included five predictors in the models: number of invaded islands, habitat affinity (generalist, living in a variety of habitats; specialist, living in only one or two habitats; intermediate, between a generalist and specialist), life-form (annual, biennial or perennial), growth-form (grass, herb, vine, shrub or tree) and plant use (pasture, agriculture, ornamental or forestry). Data on the nestedness contribution were fitted to a gamma distribution in all models. The best-fitting model was determined based on the lowest Akaike information criterion (AIC) value. These analyses were performed using

the R statistical software, version 2.15.1 (R Development Core Team, 2012).

## RESULTS

### Patterns at a global level

A large fraction (*c.* 63%) of the 350 plant species in the dataset was found to invade natural areas exclusively in one island group. Large islands or archipelagos, such as Cuba and Hawai'i, contained the highest number of such 'endemic invaders', representing 56% and 39% of all invasive species, respectively. Island groups from all the biogeographical regions had endemic invaders, although the Atlantic and Caribbean regions showed higher percentages (41% and 39% of invaders, respectively) than the Pacific and Western Indian regions (22% and 27%, respectively). Despite such high levels of exclusivity of natural area invaders in particular island groups, we detected an overall nested pattern at a global scale that was significant regardless of the criterion used to order islands (Table 1). The relative contribution of island nestedness (NODF<sub>c</sub>) to the overall nestedness was consistently higher than that of species nestedness (NODF<sub>r</sub>) (Table 1).

Considering island nestedness (NODF<sub>c</sub>), different values were obtained depending upon the factor used to order the

islands. Ordering islands by species richness showed the maximum island nestedness values; ordering by island area and elevation also led to a significant nested pattern (Table 1), indicating a contribution of the last two variables to nestedness. We therefore confirmed that invader plants of small islands with a low elevation (and thus a low habitat diversity) were subsets of those found on large and high-elevation (habitat-rich) islands. Little-populated islands also tended to be nested within highly populated islands, although nestedness was only marginally significant when ordering the matrix by human population density (Table 1). In contrast, isolation did not contribute to the nested pattern, *i.e.* invaders of isolated islands were not proper subsets of those found on islands close to a mainland; this was despite the fact that less isolated islands tended to be larger ( $r_s = -0.29$ ,  $P < 0.01$ ) and showed higher human population densities ( $r_s = -0.40$ ,  $P < 0.05$ ) than more isolated islands (see Kueffer *et al.*, 2010a). Results were fairly consistent when the PP null model was used to assess the significance of the NODF<sub>c</sub> values; in this case, however, elevation contributed only marginally to island nestedness, and human population density had no significant effect (Table 1). When considering the temperature metric, determinants of the nested pattern, ordered by importance, were species richness, island area and isolation, while elevation and human

**Table 1** Nestedness parameters obtained for different matrices (islands: species), considering the complete dataset (all the islands) of invasive plants or only data from the Pacific region. In each matrix, islands (columns) were ordered with respect to different criteria: species richness, island area, isolation, human population density and elevation. Species (rows) were always ordered from the most widespread species to the rarest. NODF, total network nestedness; NODF<sub>c</sub>, column (island) nestedness; NODF<sub>r</sub>, row (species) nestedness; *P*, the probability that nestedness is different from that predicted by either the fixed-fixed (FF) or proportional-proportional (PP) null model (see Materials and Methods).

	NODF	<i>P</i>	NODF <sub>c</sub>	<i>P</i>	NODF <sub>r</sub>	<i>P</i>
Species richness						
All islands	15.06	<0.001 (FF) 0.399 (PP)	28.13	0.028 0.005	15.00	<0.001 0.391
Pacific region	25.07	<0.001 0.138	39.00	0.162 0.101	24.98	<0.001 0.135
Island area						
All islands	15.03	<0.001 0.373	20.43	0.009 0.025	15.00	<0.001 0.367
Pacific region	25.01	<0.001 0.130	30.42	0.039 0.127	24.98	<0.001 0.128
Isolation						
All islands	15.00	<0.001 0.368	15.77	0.329 0.163	15.00	<0.001 0.365
Pacific region	24.75	<0.001 0.122	13.58	0.191 0.252	24.82	<0.001 0.122
Human population density						
All islands	15.00	<0.001 0.414	15.28	0.050 0.144	15.00	<0.001 0.411
Pacific region	24.78	<0.001 0.141	18.43	0.176 0.359	24.82	<0.001 0.140
Elevation						
All islands	15.02	<0.001 0.390	20.28	0.035 0.060	15.00	<0.001 0.386
Pacific region	25.03	<0.001 0.148	32.40	0.030 0.123	24.98	<0.001 0.146



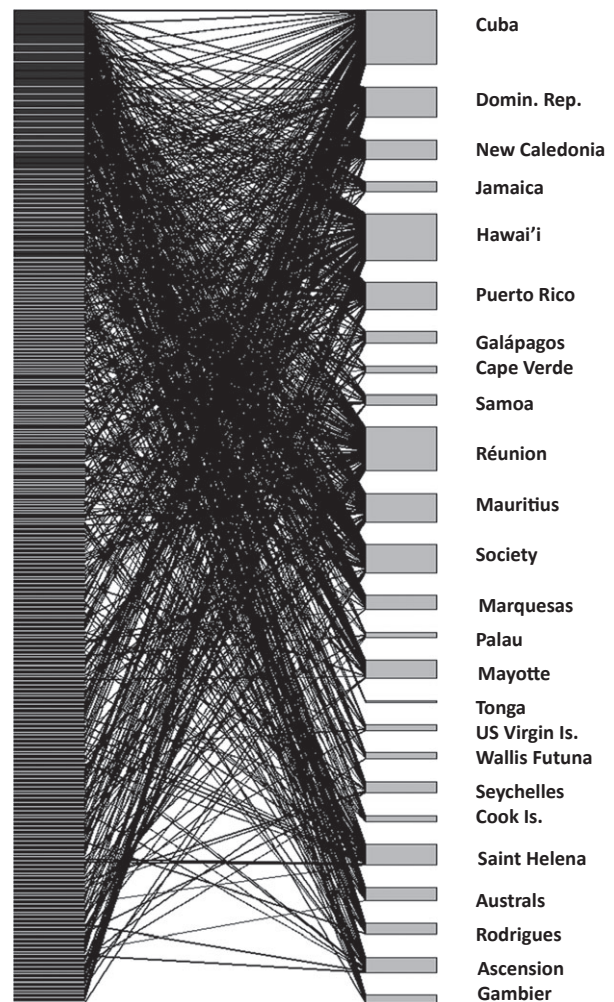
population density were not significant (see Appendix S2). Lastly, the discrepancy metric (minimum number of incidences that have to be shifted within rows or columns to achieve the maximum nestedness possible) was the same regardless of the matrix order, and was significant (see Appendix S2). Our findings thus confirmed that nestedness analyses are sensitive to the algorithm used. We believe that this should be taken into consideration in future nestedness analyses and, as suggested by Ulrich & Gotelli (2013), the most appropriate metric and null model should be employed in each study.

Although only contributing about half to overall nestedness, species nestedness ( $NODF_r$ ) was also significant, at least when using the FF null model (Table 1). Given that species were ordered from the most to the least prevalent, this implied that rare invaders tended to be found in islands that also contained common invaders. With the most restrictive PP null model, however, species nestedness was no longer significant (see Appendix S2).

The mean number of invasive species per island group ( $L_i$ ) was 25 (Table 2), although Cuba and Hawai'i, followed by Réunion, had more than twice this average (Fig. 2). There were significant differences among oceanic regions in  $L_i$ . Islands in the Caribbean and the Western Indian Ocean had higher numbers of invaders than Pacific and Atlantic islands, which did not differ (Table 2). On the other hand, the number of island groups in which a particular plant was invasive ( $L_p$ ) was on average consistently low (approximately two islands, ranging from 1 to 21; Table 2), and was higher within the Pacific and Western Indian Ocean islands than within the Caribbean and the Atlantic (Table 2). A few species were found to be invaders on a large number of islands. *Leucaena leucocephala* was by far the most widespread, invading 84% of the island groups, while other species, such as *Syzygium jambos* ( $L_p = 14$ ), *Lantana camara* ( $L_p = 13$ ), *Psidium guajava* ( $L_p = 12$ ), *Melinis minutiflora* ( $L_p = 12$ ) and *Megathyrsus maximus* ( $L_p = 12$ ), were invasive on nearly half of them. As expected, the most prevalent, widespread species were invasive in a higher number of geographical regions ( $r = 0.76$ ,  $P < 0.05$ ). However, there were also some species invasive on a low number of islands but widely distributed across four regions. For instance, *Schinus terebinthifolius* was

**Table 2** Number of plant invaders (PI) and island groups (IG) considered in each dataset analysed and for each region. The mean and standard deviation ( $x \pm SD$ ) of the prevalence of each species across islands ( $L_p$ ) as well as of the invasive species richness per island ( $L_i$ ) are given. For each of these two variables, means with the same letter are not significantly different.

	PI	IG	$L_p$ ( $x \pm SD$ )	$L_i$ ( $x \pm SD$ )
All islands	350	25	$2.09 \pm 2.35$	$29.32 \pm 22.46$
Pacific	145	12	$1.90 \pm 1.65^a$	$22.92 \pm 20.06^{ac}$
Caribbean	142	5	$1.44 \pm 0.82^b$	$41.00 \pm 31.33^b$
Atlantic	60	3	$1.17 \pm 0.38^b$	$23.33 \pm 11.59^c$
West Indian	113	5	$1.62 \pm 1.06^{ab}$	$36.60 \pm 22.01^b$



**Figure 2** The network built from the matrix data showing the 25 oceanic tropical islands (right, grey rectangles) examined in the study that were invaded by different plant species (left, black rectangles). The width of the island rectangles is proportional to the number of invaders they contained whereas the width of the species rectangles is proportional to the number of islands they invaded. Note that islands are ordered by size in this network whereas species are ordered from the most generalist (common invaders) to the most specialist (rare invaders).

an invader of natural areas on seven islands from all four regions. In contrast, other species were invaders on at least 10 islands but were restricted to only two regions (e.g. *Falcataria moluccana*).

### Regional pattern

Overall nestedness was significant for the Pacific dataset (encompassing 12 island groups and a total of 145 plants; Appendix S3); as predicted, this was even greater than when the entire dataset was considered (all  $NODF$  values were consistently higher for the Pacific dataset, except in one case; Table 1). The nested pattern emerged regardless of how the islands were ordered in the matrix (Table 1). When focusing

on island nestedness, island area and elevation were the only factors significantly influencing nestedness. Species nestedness was also significant, i.e. rare invaders in the Pacific tended to be found on the islands where the most common invaders are found. With the more restrictive PP null model, however, none of the matrices were significantly nested. The results of the widely used temperature metric were only partly consistent with the results of the FF null model: islands ordered by either area or elevation were significantly nested, as were islands ordered by isolation; the matrix ordered by species richness showed the lowest temperature, but was not significantly nested. Finally, the discrepancy index was not significant (see Appendix S2).

In the Pacific matrix (Appendix S3), a high fraction (22%) of rare invaders (found on less than four islands) occurred on the three islands with the most invaders (Hawai'i, Society and New Caledonia); 52% of the species were exclusively invasive on Hawai'i. A smaller fraction (11%) of rare invaders was exclusively from invader-poor islands (islands with less than 10 invaders).

In the Pacific region, island area was neither associated with human population density ( $r_s = -0.17$ ,  $P = 0.60$ ) nor

with isolation ( $r_s = -0.43$ ,  $P = 0.17$ ), and in turn the most isolated islands were not the least populated ones ( $r_s = 0.14$ ,  $P = 0.66$ ). Island elevation and area were positively associated ( $r_s = 0.80$ ,  $P = 0.003$ ) and were the only traits that appeared to be significantly correlated with the number of invasive plants per island in this region ( $r_s = 0.67$ ,  $P = 0.02$  and  $r_s = 0.58$ ,  $P = 0.047$ , respectively).

We further tested whether pairwise  $NODF_c$  was associated with geographical distance and latitudinal distance between island pairs in this region (Fig. 3). For both variables, a significantly negative association was found, although the pattern was stronger for geographical distance; the closer two islands were, the stronger the nestedness of plant invaders was. When both factors were included in a GLM, latitudinal distance was not significant.

### Island and species traits associated with nestedness

The model that best explained island contribution to nestedness included invasive species richness ( $t = 3.93$ ,  $P < 0.001$ ) as well as island area ( $t = 2.36$ ,  $P = 0.03$ ). In contrast, island latitude, age, elevation and human population density had non-significant effects in all models (all  $P$ -values  $> 0.05$ ).

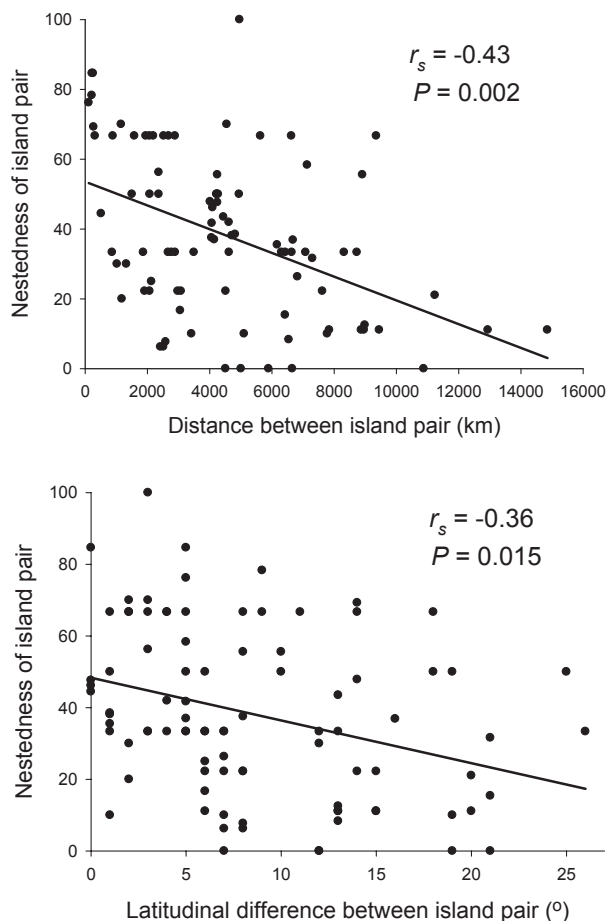
Regarding the species contribution to nestedness, prevalence of an invader across island groups was its best predictor ( $t = 30.34$ ,  $P < 0.001$ ) and the model with the lowest AIC only included this variable. The other variables, habitat affinity, life-form, growth-form and plant use, were not significant in any of the models (all  $P$ -values  $> 0.05$ ).

## DISCUSSION

### An emerging global biogeographical pattern of invasive island floras

Most plant species in the 25 tropical island groups were invasive only within one island group, although they had typically been introduced to many more island groups (Kueffer *et al.*, 2010a). Despite such a high level of invader endemicity, invasive species assemblages were significantly nested at a global scale. We have thus documented a global biogeographical pattern for invasive island floras that involves both nestedness and spatial turnover (i.e. distinct species compositions on different islands), which has been reported before for native species communities in different habitats (e.g. Baselga, 2010, 2012; Dobrovolski *et al.*, 2012; Ulrich & Gotelli, 2012, 2013).

The nested pattern is mostly the result of island nestedness rather than species nestedness, with invasive species richness, island area and elevation being the most important determinants. Therefore, the most robust pattern to emerge is that small tropical islands with a low habitat diversity and low numbers of invasive plant species tend to be invaded by species that also invade the largest, more habitat-rich and more invaded islands. Invasive species richness, known to be associated with an island's area, elevation, number of habitats



**Figure 3** The relationship between island nestedness ( $NODF_c$ ) and geographical and latitudinal distance between pairs of island groups in the Pacific region.

and human population size (Kueffer *et al.*, 2010a), was the best predictor of nestedness. Therefore, the same mechanisms might drive richness and nestedness patterns, although the effect of human population density on nestedness was only marginal: invaders of the least populated islands were not necessarily invaders of the most populated ones. It could also be that species richness contributes directly to nestedness if the presence of a large number of invasive species facilitates the invasion of additional non-native species (e.g. invasional meltdown; Simberloff, 2006). The regional analysis further substantiates the global pattern, with island area and elevation being the most important determinants of island nestedness in the Pacific region.

### Both localized and widespread species are important components of island invasive floras

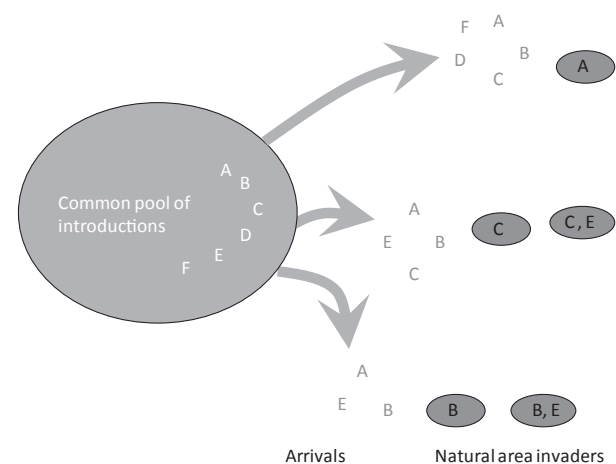
Species nestedness, although less so than island nestedness, was significant; rare invaders tended to be invasive on islands that also contained common invaders. As in the case of island nestedness, the prevalence of widespread invaders was the best predictor of species nestedness at a global scale. Thus the most widespread invaders also often invaded the least invaded islands, supporting the implicit assumption in invasive species risk assessment that the extent of an invasive species' geographical distribution is often correlated with species invasiveness.

However, many species were found only within one island group, and a small fraction (< 10%) of invaders was found exclusively on islands with low species richness (<10 invaders). Specific local colonization from the continents closest to particular islands and/or the idiosyncratic factors of particular islands might explain the invasion success of some plant species. For instance, the invasion success of cinnamon (*Cinnamomum verum*) in the Seychelles can be explained by a combination of colonial history, the introduction sequence of non-native species, disturbance and land-use history, habitat conditions (such as very nutrient-poor soils), and particular traits of cinnamon (such as strong root competition and very nutritious fruits) (Kueffer *et al.*, 2007, 2010b). Specificity in the invasive flora is also much evidenced in the Caribbean region, despite the rather short distance between Caribbean islands compared with other regions (Table 1 in Kueffer *et al.*, 2010a). For instance, 49 of the 88 (56%) invaders in Cuba are invasive only on this island, while 18 of the 49 (37%) invaders in the Dominican Republic are exclusive invaders on this island in this region. This might be explained at least partly by the relatively low prevalence of human transport between these islands as a result of contrasting socio-political histories. Further studies are needed to investigate whether the high frequency of rare invaders is more the result of a time-lag effect (i.e. recently dispersed invaders have not yet been introduced or are not yet spreading into natural areas on many islands) or the idiosyncratic history of the islands [e.g. cinnamon production in the Seychelles, the use of New Zealand flax (*Phormium tenax*) in Saint Helena]. It thus appears that both

localized and widespread species are important components of island invasive floras, and an exclusive focus in invasive species research and management on the most prevalent invasive species will neglect rare but potentially very problematic invasion threats (Kueffer *et al.*, 2013).

### A conceptual model of nestedness of island invasive floras

Both habitat and dispersal filtering may explain the distribution of invasive plants across the globe (see the conceptual model in Fig. 4). Both processes have been invoked for explaining nestedness in native plant communities, but in the case of invasive floras human action plays a major role in shaping nestedness. On the one hand, there may be *habitat filtering*: the smallest islands bear only a fraction of the habitats (often only the coastal and lowland ones) found in larger islands, and thus all invaders adapted to other types of habitats (e.g. cooler and/or humid environments found at intermediate to high elevations) are filtered out. Habitat filtering has been claimed to play a relevant role in determining nestedness in a large number of studies (e.g. Jacquemyn *et al.*, 2007; Stiles & Scheiner, 2008; Alexander *et al.*, 2011). On the other hand, an alternative explanation would be *dispersal filtering*: on the smallest, often least populated islands, humans might not have introduced 'yet' (at a magnitude or over a long enough time period to trigger an invasion) the full array of invasive plants found on more inhabited islands. Differences in natural dispersal ability among diverse taxa (seabirds, land birds, insects and plants) have been reported to determine differences in nestedness in Southern Ocean



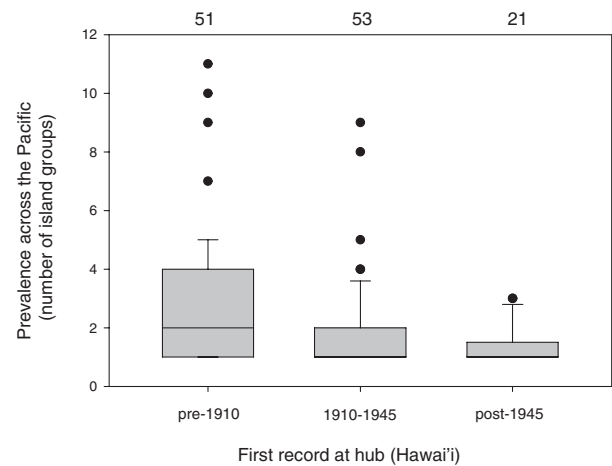
**Figure 4** A conceptual model explaining the development of nestedness patterns for invaders on islands. Introductions originate primarily from a common source pool of species (white letters) that are transported by humans. A subset of the common source pool is introduced to each island (dispersal filter; grey letters), then a subset of the introductions becomes invasive in natural areas (habitat filter; black letters). Nearer islands (horizontal pairs) are more similar than more distant islands.

islands (Greve *et al.*, 2005) and naturally dispersing plants establishing on artificial islands in an artificial reservoir lake (Kadmon, 1995). In our case, most plant invaders were deliberately dispersed by humans, so natural dispersal appears to be less important. However, we found no strong relationship between plant use (the reason for being introduced) and contribution to nestedness, suggesting that understanding any influence of human dispersal on nested patterns will require more detailed information about dispersal patterns of plants by humans.

Either dispersal or habitat filtering might also promote nestedness at the species level. In the first case, rare invaders might be transported mostly to islands where widespread invaders are present; for instance, invader-rich islands containing both rare and common invaders might be those with more diverse economic activities, including some only occurring on islands with a diverse economy. In the second case, suitable conditions for rare invaders might occur only on islands also suitable for common invaders. Indeed, some widespread species are invaders of highly disturbed low-elevation habitat (e.g. *Leucaena leucocephala*, *Lantana camara*, *Psidium guajava*, *Melinis minutiflora* and *Megathyrsus maximus*), which is present on most islands, while some rare invaders are restricted to upland habitats (e.g. *Achillea millefolium* and *Pinus radiata*) only found on larger, high-elevation islands. However, at the same time we also found widespread species that invade little-disturbed vegetation (e.g. *Hedychium gardnerianum* and *Psidium cattleianum*). It might also be that rare invaders correspond to recent introductions whereas common (more prevalent) invaders have arisen from old introductions. We tested this for the Pacific region, for which data on the first invaders of Hawai'i (a probable hub for the introduction of invaders) are available. We indeed found evidence for an increased prevalence across the Pacific island groups for species that were introduced early to Hawai'i (Fig. 5).

### The importance of regional hubs for linking regional and global species distributions

The regional study that focused on the islands of the Pacific confirmed our hypothesis that nestedness is more pronounced at a regional than a global scale, as was found in a previous study of the Southern Ocean island biotas (Greve *et al.*, 2005). Possible explanations could be that a regional area shares a homogenous species pool and all islands are linked by dispersal pathways. Indeed, at a regional scale most species were shared among several islands, and those species that occurred on only one island were almost exclusively found on the most species-rich islands (such as Hawai'i). Invaders might first invade hubs (invader-rich islands) within a region and then spread to invader-poor islands in that region. Alternatively, invaders of invader-poor islands might also soon arrive on invader-rich islands. Both scenarios highlight the importance of regional-scale dispersal networks, with species-rich islands as important nodes.



**Figure 5** A box plot showing the prevalence of plant invaders across Pacific islands in relation to the date of the first record for each species at the hub (Hawai'i). The dates of the first records were grouped into three broad periods based on introduction trends in the Pacific. Numbers at the top indicate the sample size (species) in each category. Statistical trends are as follows. Variance: pre-1910 > 1910–1945 > post-1945. Medians (Kruskal–Wallis): pre-1910 > [1910–1945 = post-1945]. Note that the variance is highest among the earliest introductions; the success of some invaders is idiosyncratic, even after being in the region for a long time.

Such dispersal and establishment between islands is unlikely to be at equilibrium (Fig. 4), which might explain the significant correlation between physical distance between islands and their pairwise nestedness found in the Pacific region. Because of the large area and wide latitudinal range covered by the Pacific region (between 22° S to 22° N; see Table 1a in Kueffer *et al.*, 2010a), many species might not yet have invaded all the islands that they potentially might invade. Castro *et al.* (2010) found lower rates of biotic homogenization in the Pacific than in other regions, which could also be explained by the greater distances among islands in the Pacific. In a separate analysis, in which we tested the association between introduced plants (not necessarily invasive) and nestedness between island pairs in this region, we found no effect of distance (results not shown). This suggests that, even though many of the invaders must reach many Pacific islands, different groups of species become established on distant island groups within this region, possibly because of time-lags between introduction and invasion. An example is *Castilla elastica*, invasive on several islands in the western and central Pacific but not invasive on others, e.g. the Galápagos and Hawai'i, where it has also been introduced. Overall, the patterns found at a regional scale highlight the importance of regional-scale invasive species prevention.

### Future research avenues and conservation implications

Human alteration of the planet is changing the biogeography of species from local to global scales. There is increasing



evidence that this is not a uniform process, i.e. it is not the case that losers of anthropogenic change disappear everywhere and winners become omnipresent. Rather, new biogeographical patterns emerge that need to be understood. While geographical barriers and plant dispersal syndromes influence nestedness in native floras, other factors such as human alteration of habitats or transportation are likely to be more important in invasive floras. As a consequence, we propose the hypothesis that native and non-native nested patterns may sometimes be decoupled, i.e. native floras of a particular habitat might be a nested subset of a broader flora, while the invasive flora in that habitat might or might not be nested, and vice versa. Whether nestedness of native and non-native floras is determined by different factors is important for understanding emerging biogeographical patterns that might be novel and complex.

Nestedness of non-native and invasive floras has important implications for conservation issues such as the homogenization of isolated and small islands: whereas their native floras are often unique, their invasive floras seem to consist mainly of widespread invaders. Our results also emphasize the importance of prevention of further invasions in currently little-invaded islands. Indeed, according to our study, information gathered from highly invaded islands can provide a robust basis for predicting invasion risks for currently poorly invaded islands. However, rare invaders on all islands require special attention: they are not widespread and thus might easily be missed by risk assessments, but they can nevertheless be problematic, bearing in mind the rule of thumb that invasive behaviour elsewhere is the best predictor of invasion in a new area (Kueffer *et al.*, 2013).

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## SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

**Appendix S1** The home ranges of the plant invaders in the dataset.

**Appendix S2** Temperature and discrepancy metrics as estimates of nestedness considering both the complete dataset (all of the islands) and just the data from the Pacific region.

**Appendix S3** The matrix for the Pacific region.

## BIOSKETCHES

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Author contributions: A.T., C.K. and C.D. conceived the idea; A.T., C.K. and C.D. compiled data; A.T. and C.D. analysed the data; and A.T. led the writing.

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