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5 **Global and regional nested patterns of non-native invasive floras on**
6 **tropical islands**

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23 **ABSTRACT**

24

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

29

30 **Location** Tropical islands world-wide.

31

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

36

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

41 Nestedness was more pronounced at a regional than a global scale.

42

43 **Main conclusions** We found novel biogeographical patterns interconnecting non-native
44 invasive floras at a global scale. Both localized and widespread species are important components
45 of island invasive floras. Invader-rich islands host many rare invaders, and many species are

46 invaders in only one island group, suggesting that prevention efforts should pay attention to rare
47 invaders. We have developed a conceptual model to facilitate understanding of nestedness in
48 island invasion. Both habitat and dispersal filtering are potential mechanisms underlying
49 nestedness, whereas idiosyncratic factors of particular islands (e.g. habitat diversity and socio-
50 economic history) or time-lags may explain ‘invader endemicity’. Nested regional patterns may
51 be explained by ‘hub’ islands that serve as early sites of introduction for many invaders, some of
52 which subsequently spread across the region.

53

54 **Keywords**

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

57

58 INTRODUCTION

59
60 Island ecosystems are particularly vulnerable to invasive species, which can substantially modify
61 the structure and composition of colonized ecosystems (Millennium Ecosystem Assessment,
62 2005; Reaser *et al.*, 2007). Biological invasions have been particularly detrimental on oceanic
63 islands, including isolated continental fragments such as New Zealand, New Caledonia and the
64 Seychelles; most documented extinctions promoted by non-native species (mainly vertebrates)
65 are known from such ecosystems (e.g. Traveset & Richardson, 2006; Whittaker & Fernández-
66 Palacios, 2007; Sax & Gaines, 2008; Caujapé-Castells *et al.*, 2010). Although there has long been
67 an interest in biotic invasions of islands, further work is needed to describe fully and understand
68 the biogeographical patterns of plant invasions on islands at regional to global scales (Pyšek &
69 Richardson, 2006; Sax & Gaines, 2008; Denslow *et al.*, 2009; Kueffer *et al.*, 2010a; Richardson
70 & Pyšek, 2012). Kueffer *et al.* (2010a) found that a combination of anthropogenic factors (e.g.
71 the level of human settlement) and natural factors (e.g. habitat diversity) determine the species
72 richness of invasive plants in an island group. However, we still need more integrative analyses
73 of the community assembly of invasive floras to help us (1) predict which associations or
74 combinations of species may be found in a given area (island or island group), and (2) determine
75 what factors enhance or constrain the invasiveness of non-native species across islands.

76 One useful approach to detecting and analysing the distribution patterns of multiple
77 species across multiple islands is nestedness analysis (e.g. Lomolino, 1996; Wright *et al.*, 1998;
78 Greve *et al.*, 2005; Ulrich *et al.*, 2009). In particular, it is important to know whether invader-
79 poor islands are invaded by the same species as invader-rich islands. If such a nested pattern is
80 found, then information from highly invaded islands may be used to prevent further invasion of

81 the less affected ones. If there is no nestedness, and invader-poor islands are invaded by a
82 different set of species, then prevention has to be specifically tailored to those islands.

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

92 **1.** Poorly invaded islands mostly contain species that are also present on invader-rich islands. We
93 predicted that factors such as island area, isolation, elevation (a proxy of the diversity of habitat
94 types on an island) and human population density contribute to this nested pattern.

95 **2.** Rare invaders (defined here as those found to be invasive on only one or a few islands) are
96 invasive on islands that contain the most widespread invaders. This nested pattern might emerge
97 from dispersal processes (if, for instance, rare species are transported only to islands where many
98 other species have been introduced) and also by habitat filtering (if conditions suitable for the
99 establishment of rare invaders only occur on islands that are also suitable for more common
100 invaders).

101 **3.** Because of similarities in the source pool of invaders across a particular region, nestedness is
102 higher when considering a particular biogeographical region, relative to global patterns of
103 nestedness (Greve *et al.*, 2005). To test whether this pattern holds for island invasive floras, we
104 focused on the Pacific region, for which data from the highest number of islands exist. We also

105 expected the geographical distance and latitudinal difference between two islands to be
106 negatively associated with their degree of nestedness.

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

113

114

115 **MATERIALS AND METHODS**

116

117 **Data collection**

118

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

128 The original dataset used by Kueffer *et al.* (2010a) was adapted by removing six extra-

129 tropical islands. In turn, recently available data from Cuba were added (Ramona Oviedo,
130 unpub.dat.). A total of 25 islands or archipelagos (island groups), belonging to four
131 biogeographical regions [Atlantic Ocean (three island groups), Caribbean (five), Pacific (12) and
132 Western Indian Ocean (five)], was included in the analyses (Fig. 1). The entire dataset included
133 350 spermatophyte species, belonging to 86 families, that were either moderate invaders
134 (common invaders of natural areas, attaining a maximal relative vegetation cover of *c.* 5–25% in
135 natural areas) or dominant invaders (reaching a maximum relative vegetation cover > 25% in
136 natural areas). A large fraction (39%) was originally from tropical/subtropical America; 25%
137 were from Asia and/or tropical India, 14% were from Africa, 8% were from Australia or
138 Australasia, and only *c.* 4% were from Europe. The rest had either an obscure original range,
139 were widespread on two or three continents, or were small-island endemics. Further details on the
140 dataset can be found in Kueffer *et al.* (2010a). This dataset represents the most comprehensive
141 global list of plant invaders of natural areas on islands compiled so far, based on expert
142 knowledge.

143

144 **Data analyses**

145

146 We calculated the nestedness metric NODF (nestedness based on overlap and decreasing fill;
147 Almeida-Neto *et al.*, 2008; Almeida-Neto & Ulrich, 2011) by using the software NODF version
148 2.0 (<http://www.keib.umk.pl/nodf/>). This metric was chosen to test for nestedness independently
149 among columns (islands; i.e. community composition) and rows (species occupancy). We
150 measured column nestedness (NODF_c) to assess whether invader communities were nested
151 among island groups, while we measured row nestedness (NODF_r) to determine whether the

152 rarest invaders were present on islands that also had the most common (widespread) invaders.

153 NODF is dependent on the arrangement of columns and rows, which allows hypotheses about the

154 causes of nestedness to be tested by ordering columns and rows according to criteria representing

155 different hypotheses (Almeida-Neto *et al.*, 2008; Ulrich *et al.*, 2009; Almeida-Neto & Ulrich,

156 2011). To test our hypotheses, we thus arranged islands according to invasive species richness,

157 island area, human population, isolation and elevation, but consistently kept species ordered from

158 the most widespread to the least common. The significance of NODF values was assessed against

159 1000 randomizations using the fixed–fixed (FF) null model, in which entries are randomized in

160 null matrices, but the number of invaders on each island is fixed along with the number of islands

161 per species; this null model is appropriate for large-scale species occurrence records such as ours

162 (Ulrich & Gotelli, 2012) and is claimed to be better than the loosely constrained models used to

163 test nestedness in many ecological networks (see Joppa *et al.*, 2010). Additionally, we tested our

164 matrices with another even more constrained null model, using the proportional–proportional

165 (PP) algorithm (Ulrich & Gotelli, 2012), which has better power to detect segregated and nested

166 matrices. The PP model creates null matrices in which the row and column vary randomly, but

167 the average row and column totals are unbiased and match those of the original matrix. Both

168 these null models identify a substantially smaller number of matrices as non-random compared

169 with the popular temperature metric (Atmar & Patterson, 1993). The temperature metric is also

170 known to be more sensitive to the size and fill of the matrix than the NODF metric (Almeida-

171 Neto *et al.*, 2008). In order to see how consistent and robust the results were, we examined the

172 temperature metric and the discrepancy metric (Brualdi & Sanderson, 1999), as modified by

173 Ulrich & Gotelli (2007). The results were obtained with the same NODF software and are given in

174 Appendix S2.

175 The nestedness contribution of each island (Δ_{I}) and species (Δ_{Sp}) was obtained by
176 subtracting the NODF value of the matrix without the island (I) or the species (Sp), respectively,
177 from the NODF of the entire matrix (Almeida-Neto & Ulrich, 2011). We calculated these values
178 from the matrix ordered by species richness, although they were very similar to those found when
179 ordered by another criterion. In order to assess what island and species traits were associated with
180 their nestedness contribution, we constructed generalized linear models (GLM) using either
181 Δ_{I} or Δ_{Sp} as the dependent variable and different island and species characteristics,
182 respectively, as predictors. In the former case, we used seven predictors: invasive species
183 richness, island area, age, human population density, distance from nearest continent, latitude and
184 elevation. The number of habitats in each island was highly correlated with elevation ($r = 0.90$,
185 $P < 0.001$; Kueffer *et al.*, 2010a) and thus was not considered in the analysis. For species, we
186 included five predictors in the models: number of invaded islands, habitat affinity (generalist,
187 living in a variety of habitats; specialist, living in only one or two habitats; intermediate, between
188 a generalist and specialist), life-form (annual, biennial or perennial), growth-form (grass, herb,
189 vine, shrub or tree) and plant use (pasture, agriculture, ornamental or forestry). Data on the
190 nestedness contribution were fitted to a gamma distribution in all models. The best-fitting model
191 was determined based on the lowest Akaike information criterion (AIC) value. These analyses
192 were performed using the R statistical software, version 2.15.1 (R Development Core Team,
193 2012).

194

195 **RESULTS**

196

197 **Patterns at a global level**

198

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

210 Considering island nestedness (NODF_c), different values were obtained depending upon
211 the factor used to order the islands. Ordering islands by species richness showed the maximum
212 island nestedness values; ordering by island area and elevation also led to a significant nested
213 pattern (Table 1), indicating a contribution of the last two variables to nestedness. We therefore
214 confirmed that invader plants of small islands with a low elevation (and thus a low habitat
215 diversity) were subsets of those found on large and high-elevation (habitat-rich) islands. Little-
216 populated islands also tended to be nested within highly populated islands, although nestedness
217 was only marginally significant when ordering the matrix by human population density (Table 1).
218 In contrast, isolation did not contribute to the nested pattern, i.e. invaders of isolated islands were
219 not proper subsets of those found on islands close to a mainland; this was despite the fact that less
220 isolated islands tended to be larger ($r_s = -0.29$, $P < 0.01$) and showed higher human population

221 densities ($r_s = -0.40$, $P < 0.05$) than more isolated islands (see Kueffer *et al.*, 2010a). Results
222 were fairly consistent when the PP null model was used to assess the significance of the NODF_c
223 values; in this case, however, elevation contributed only marginally to island nestedness and
224 human population density had no significant effect (Table 1). When considering the temperature
225 metric, determinants of the nested pattern, ordered by importance, were species richness, island
226 area and isolation, while elevation and human population density were not significant (see
227 Appendix S2). Lastly, the discrepancy metric (minimum number of incidences that have to be
228 shifted within rows or columns to achieve the maximum nestedness possible) was the same
229 regardless of the matrix order, and was significant (see Appendix S2). Our findings thus
230 confirmed that nestedness analyses are sensitive to the algorithm used. We believe that this
231 should be taken into consideration in future nestedness analyses and, as suggested by Ulrich &
232 Gotelli (2013), the most appropriate metric and null model should be employed in each study.

233
234 Although only contributing about half to overall nestedness, species nestedness (NODF_r)
235 was also significant, at least when using the FF null model (Table 1). Given that species were
236 ordered from the most to the least prevalent, this implied that rare invaders tended to be found in
237 islands that also contained common invaders. With the most restrictive PP null model, however,
238 species nestedness was no longer significant (see Appendix S2).

239 The mean number of invasive species per island group (L_i) was 29 (Table 2), although
240 Cuba and Hawai'i, followed by Réunion, had more than twice this average (Fig. 2). There were
241 significant differences among oceanic regions in L_i . Islands in the Caribbean and the Western
242 Indian Ocean had higher numbers of invaders than Pacific and Atlantic islands, which did not
243 differ (Table 2). On the other hand, the number of island groups in which a particular plant was
244 invasive (L_p) was on average consistently low (approximately two islands, ranging from 1 to 21;

245 Table 2), and was higher within the Pacific and Western Indian Ocean islands within the
246 Caribbean and the Atlantic (Table 2). A few species were found to be invaders on a large number
247 of islands. *Leucaena leucocephala* was by far the most widespread, invading 84% of the island
248 groups, while other species, such as *Syzygium jambos* ($L_p = 14$), *Lantana camara* ($L_p = 13$),
249 *Psidium guajava* ($L_p = 12$), *Melinis minutiflora* ($L_p = 12$) and *Megathyrsus maximus* ($L_p = 12$),
250 were invasive on nearly half of them. As expected, the most prevalent, widespread species were
251 invasive in a higher number of geographical regions ($r = 0.76$, $P < 0.05$). However, there were
252 also some species invasive on a low number of islands but widely distributed across four regions.
253 For instance, *Schinus terebinthifolius* was an invader of natural areas on seven islands from all
254 four regions. In contrast, other species were invaders on at least 10 islands but were restricted to
255 only two regions (e.g. *Falcataria moluccana*).

256

257 **Regional pattern**

258

259 Overall nestedness was significant for the Pacific dataset (encompassing 12 island groups and a
260 total of 145 plants; Appendix S3); as predicted, this was even greater than when the entire dataset
261 was considered (all NODF values were consistently higher for the Pacific dataset, except in one
262 case; Table 1). The nested pattern emerged regardless of how the islands were ordered in the
263 matrix (Table 1). When focusing on island nestedness, island area and elevation were the only
264 factors significantly influencing nestedness. Species nestedness was also significant, i.e. rare
265 invaders in the Pacific tended to be found on the islands where the most common invaders are
266 found. With the more restrictive PP null model, however, none of the matrices were significantly
267 nested. The results of the widely used temperature metric were only partly consistent with the
268 results of the FF null model: islands ordered by either area or elevation were significantly nested,

269 as were islands ordered by isolation; the matrix ordered by species richness showed the lowest
270 temperature, but was not significantly nested. Finally, the discrepancy index was not significant
271 (see Appendix S2).

272 In the Pacific matrix (Appendix S3), a high fraction (22%) of rare invaders (found on less
273 than four islands) occurred on the three islands with the most invaders (Hawai'i, Society and
274 New Caledonia); 52% of the species were exclusively invasive on Hawai'i. A smaller fraction
275 (11%) of rare invaders was exclusively from invader-poor islands (islands with less than 10
276 invaders).

277 In the Pacific region, island area was neither associated with human population density
278 ($r_s = -0.17$, $P = 0.60$) nor with isolation ($r_s = -0.43$, $P = 0.17$), and in turn the most isolated
279 islands were not the least populated ones ($r_s = 0.14$, $P = 0.66$). Island elevation and area were
280 positively associated ($r_s = 0.80$, $P = 0.003$) and were the only traits that appeared to be
281 significantly correlated with the number of invasive plants per island in this region ($r_s = 0.67$,
282 $P = 0.02$ and $r_s = 0.58$, $P = 0.047$, respectively).

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

288

289 **Island and species traits associated with nestedness**

290

291 The model that best explained island contribution to nestedness included invasive species
292 richness ($t = 3.93$, $P < 0.001$) as well as island area ($t = 2.36$, $P = 0.03$). In contrast, island

293 latitude, age, elevation and human population density had non-significant effects in all models
294 (all P -values > 0.05).

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

299

300 **DISCUSSION**

301

302 **An emerging global biogeographical pattern of invasive island floras**

303

304 Most plant species in the 25 tropical island groups were invasive only within one island group,
305 although they had typically been introduced to many more island groups (Kueffer *et al.*, 2010a).

306 Despite such a high level of invader endemicity, invasive species assemblages were significantly
307 nested at a global scale. We have thus documented a global biogeographical pattern for invasive
308 island floras that involves both nestedness and spatial turnover (i.e. distinct species compositions
309 on different islands), which has been reported before for native species communities in different
310 habitats (e.g. Baselga, 2010, 2012; Dobrovolski *et al.*, 2012; Ulrich & Gotelli, 2012, 2013).

311 The nested pattern is mostly the result of island nestedness rather than species nestedness,
312 with invasive species richness, island area and elevation being the most important determinants.

313 Therefore, the most robust pattern to emerge is that small tropical islands with a low habitat
314 diversity and low numbers of invasive plant species tend to be invaded by species that also

315 invade the largest, more habitat-rich and more invaded islands. Invasive species richness, known

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

325

326 **Both localized and widespread species are important components of island** 327 **invasive floras**

328

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

335 However, many species were found only within one island group, and a small fraction (<
336 10%) of invaders was found exclusively on islands with low species richness (< 10 invaders).

337 Specific local colonization from the continents closest to particular islands and/or the
338 idiosyncratic factors of particular islands might explain the invasion success of some plant
339 species. For instance, the invasion success of cinnamon (*Cinnamomum verum*) in the Seychelles

340 can be explained by a combination of colonial history, the introduction sequence of non-native
341 species, disturbance and land-use history, habitat conditions (such as very nutrient-poor soils),
342 and particular traits of *C. verum* (such as strong root competition and very nutritious fruits)
343 (Kueffer *et al.*, 2007, 2010b). Specificity in the invasive flora is also much evidenced in the
344 Caribbean region, despite the rather short distance between Caribbean islands compared with
345 other regions (Table 1 in Kueffer *et al.*, 2010a). For instance, 49 of the 88 (56%) invaders in
346 Cuba are invasive only on this island, while 18 of the 49 (37%) invaders in the Dominican
347 Republic are exclusive invaders on this island in this region. This might be explained at least
348 partly by the relatively low prevalence of human transport between these islands as a result of
349 contrasting socio-political histories. Further studies are needed to investigate whether the high
350 frequency of rare invaders is more the result of a time-lag effect (i.e. recently dispersed invaders
351 have not yet been introduced or are not yet spreading into natural areas on many islands) or the
352 idiosyncratic history of the islands [e.g. cinnamon production in the Seychelles, the use of New
353 Zealand flax (*Phormium tenax*) in Saint Helena]. It thus appears that both localized and
354 widespread species are important components of island invasive floras, and an exclusive focus in
355 invasive species research and management on the most prevalent invasive species will neglect
356 rare but potentially very problematic invasion threats (Kueffer *et al.*, 2013).

357

358 **A conceptual model of nestedness of island invasive floras**

359

360 Both habitat and dispersal filtering may explain the distribution of invasive plants across the
361 globe (see the conceptual model in Fig. 4). Both processes have been invoked for explaining
362 nestedness in native plant communities, but in the case of invasive floras human action plays a
363 major role in shaping nestedness. On the one hand, there may be *habitat filtering*: the smallest

364 islands bear only a fraction of the habitats (often only the coastal and lowland ones) found in
365 larger islands, and thus all invaders adapted to other types of habitats (e.g. cooler and/or humid
366 environments found at intermediate to high elevations) are filtered out. Habitat filtering has been
367 claimed to play a relevant role in determining nestedness in a large number of studies (e.g.
368 Jacquemyn *et al.*, 2007; Stiles & Scheiner, 2008; Alexander *et al.*, 2011). On the other hand, an
369 alternative explanation would be *dispersal filtering*: on the smallest, often least populated islands,
370 humans might not have introduced ‘yet’ (at a magnitude or over a long enough time period to
371 trigger an invasion) the full array of invasive plants found on more inhabited islands. Differences
372 in natural dispersal ability among diverse taxa (seabirds, land birds, insects and plants) have been
373 reported to determine differences in nestedness in Southern Ocean islands (Greve *et al.*, 2005)
374 and naturally dispersing plants establishing on artificial islands in an artificial reservoir lake
375 (Kadmon, 1995). In our case, most plant invaders were deliberately dispersed by humans, so
376 natural dispersal appears to be less important. However, we found no strong relationship between
377 plant use (the reason for being introduced) and contribution to nestedness, suggesting that
378 understanding any influence of human dispersal on nested patterns will require more detailed
379 information about dispersal patterns of plants by humans.

380 Either dispersal or habitat filtering might also promote nestedness at the species level. In
381 the first case, rare invaders might be transported mostly to islands where widespread invaders are
382 present; for instance, invader-rich islands containing both rare and common invaders might be
383 those with more diverse economic activities, including some only occurring on islands with a
384 diverse economy. In the second case, suitable conditions for rare invaders might occur only on
385 islands also suitable for common invaders. Indeed, some widespread species are invaders of
386 highly disturbed low-elevation habitat (e.g. *Leucaena leucocephala*, *Lantana camara*, *Psidium*
387 *guajava*, *Melinis minutiflora* and *Megathyrsus maximus*), which is present on most islands, while

388 some rare invaders are restricted to upland habitats (e.g. *Achillea millefolium* and *Pinus radiata*)
389 only found on larger, high-elevation islands. However, at the same time we also found
390 widespread species that invade little-disturbed vegetation (e.g. *Hedychium gardnerianum* and
391 *Psidium cattleianum*). It might also be that rare invaders correspond to recent introductions
392 whereas common (more prevalent) invaders have arisen from old introductions. We tested this
393 for the Pacific region, for which data on the first invaders of Hawai'i (a probable hub for the
394 introduction of invaders) are available. We indeed found evidence for an increased prevalence
395 across the Pacific island groups for species that were introduced early to Hawai'i (Fig. 5).

396

397 **The importance of regional hubs for linking regional and global species** 398 **distributions**

399

400 The regional study that focused on the islands of the Pacific confirmed our hypothesis that
401 nestedness is more pronounced at a regional than a global scale, as was found in a previous study
402 of the Southern Ocean island biotas (Greve *et al.*, 2005). Possible explanations could be that a
403 regional area shares a homogenous species pool and all islands are linked by dispersal pathways.
404 Indeed, at a regional scale most species were shared among several islands, and those species that
405 occurred on only one island were almost exclusively found on the most species-rich islands (such
406 as Hawai'i). Invaders might first invade hubs (invader-rich islands) within a region and then
407 spread to invader-poor islands in that region. Alternatively, invaders of invader-poor islands
408 might also soon arrive on invader-rich islands. Both scenarios highlight the importance of
409 regional-scale dispersal networks, with species-rich islands as important nodes.
410 Such dispersal and establishment between islands is unlikely to be at equilibrium (Fig. 4), which
411 might explain the significant correlation between physical distance between islands and their

412 pairwise nestedness found in the Pacific region. Because of the large area and wide latitudinal
413 range covered by the Pacific region (between 22° S to 22° N; see Table 1a in Kueffer *et al.*,
414 2010a), many species might not yet have invaded all the islands that they potentially might
415 invade. Castro *et al.* (2010) found lower rates of biotic homogenization in the Pacific than in
416 other regions, which could also be explained by the greater distances among islands in the
417 Pacific. In a separate analysis, in which we tested the association between introduced plants (not
418 necessarily invasive) and nestedness between island pairs in this region, we found no effect of
419 distance (results not shown). This suggests that, even though many of the invaders must reach
420 many Pacific islands, different groups of species become established on distant island groups
421 within this region, possibly because of time-lags between introduction and invasion. An example
422 is *Castilla elastica*, invasive on several islands in the western and central Pacific but not invasive
423 on others, e.g. the Galápagos and Hawai'i, where it has also been introduced. Overall, the
424 patterns found at a regional scale highlight the importance of regional-scale invasive species
425 prevention.

426

427 **Future research avenues and conservation implications**

428 Human alteration of the planet is changing the biogeography of species from local to global
429 scales. There is increasing evidence that this is not a uniform process, i.e. it is not the case that
430 losers of anthropogenic change disappear everywhere and winners become omnipresent. Rather,
431 new biogeographical patterns emerge that need to be understood. While geographical barriers and
432 plant dispersal syndromes influence nestedness in native floras, other factors such as human
433 alteration of habitats or transportation are likely to be more important in invasive floras. As a
434 consequence, we propose the hypothesis that native and non-native nested patterns may

435 sometimes be decoupled, i.e. native floras of a particular habitat might be a nested subset of a
436 broader flora, while the invasive flora in that habitat might or might not be nested, and vice versa.
437 Whether nestedness of native and non-native floras is determined by different factors is important
438 for understanding emerging biogeographical patterns that might be novel and complex.

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

449
450

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452
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461

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555

556 **SUPPORTING INFORMATION**

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

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

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

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

562 -----

563

564 **BIOSKETCHES**

565 **Anna Traveset** is a professor at the Spanish Research Council. Her current research centres on
566 the impact of different drivers of global change, mainly biological invasions, on the native biota
567 and interactions of island ecosystems.

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569 **Christoph Kueffer** is a senior scientist at ETH Zurich. His research interests include plant
570 invasions on islands and mountains, island ecology and transdisciplinary research on
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572

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574 population biology and plant–animal interactions.

575

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

578

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580

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

	NODF	<i>P</i>	NODF _c	<i>P</i>	NODF _r	<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

588

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

	PI	IG	$L_p (x \pm SD)$	$L_i (x \pm SD)$
All islands	350	29	2.09 ± 2.35	29.32 ± 22.46
Pacific	145	12	1.90 ± 1.65^a	22.92 ± 20.06^{ac}
Caribbean	142	5	1.44 ± 0.82^b	41.00 ± 31.33^b
Atlantic	60	3	1.17 ± 0.38^b	23.33 ± 11.59^c
West Indian	113	5	1.62 ± 1.06^{ab}	36.60 ± 22.01^b

593

594 **FIGURE LEGENDS**

595
596 **Figure 1** The location of the 25 tropical ($\pm 23.4^\circ$) island groups considered for the study of global
597 and regional nested patterns of non-native invasive floras.

598
599 **Figure 2** The network built from the matrix data showing the 25 oceanic tropical islands (right,
600 grey rectangles) examined in the study that were invaded by different plant species (left, black
601 rectangles). The width of the island rectangles is proportional to the number of invaders they
602 contained whereas the width of the species rectangles is proportional to the number of islands
603 they invaded. Note that islands are ordered by size in this network whereas species are ordered
604 from the most generalist (common invaders) to the most specialist (rare invaders).

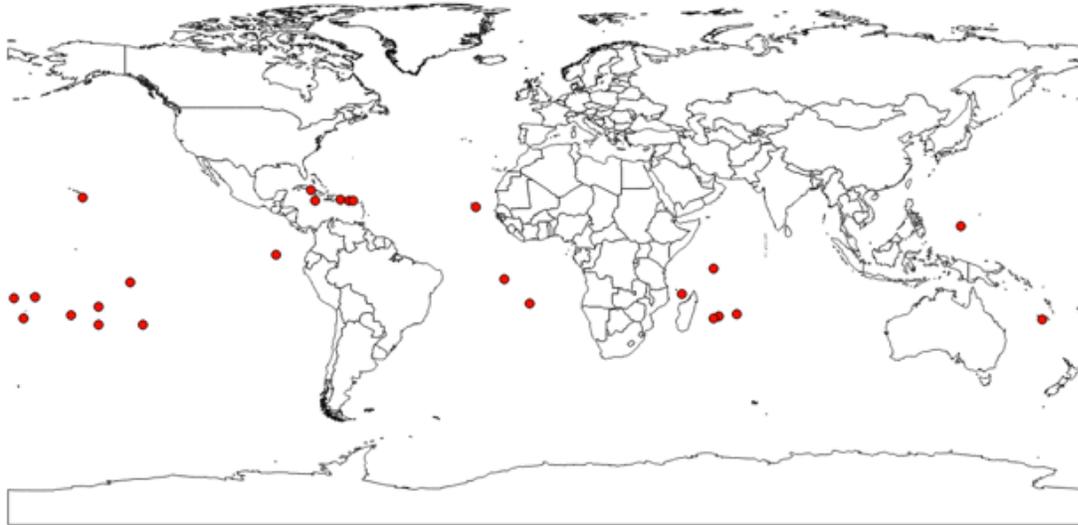
605
606 **Figure 3** The relationship between island nestedness (NODF_c) and geographical and latitudinal
607 distance between pairs of island groups in the Pacific region.

608
609 **Figure 4** A conceptual model explaining the development of nestedness patterns for invaders on
610 islands. Introductions originate primarily from a common source pool of species (white letters)
611 that are transported by humans. A subset of the common source pool is introduced to each island
612 (dispersal filter; grey letters), then a subset of the introductions becomes invasive in natural areas
613 (habitat filter; black letters). Nearer islands (horizontal pairs) are more similar than more distant
614 islands.

615

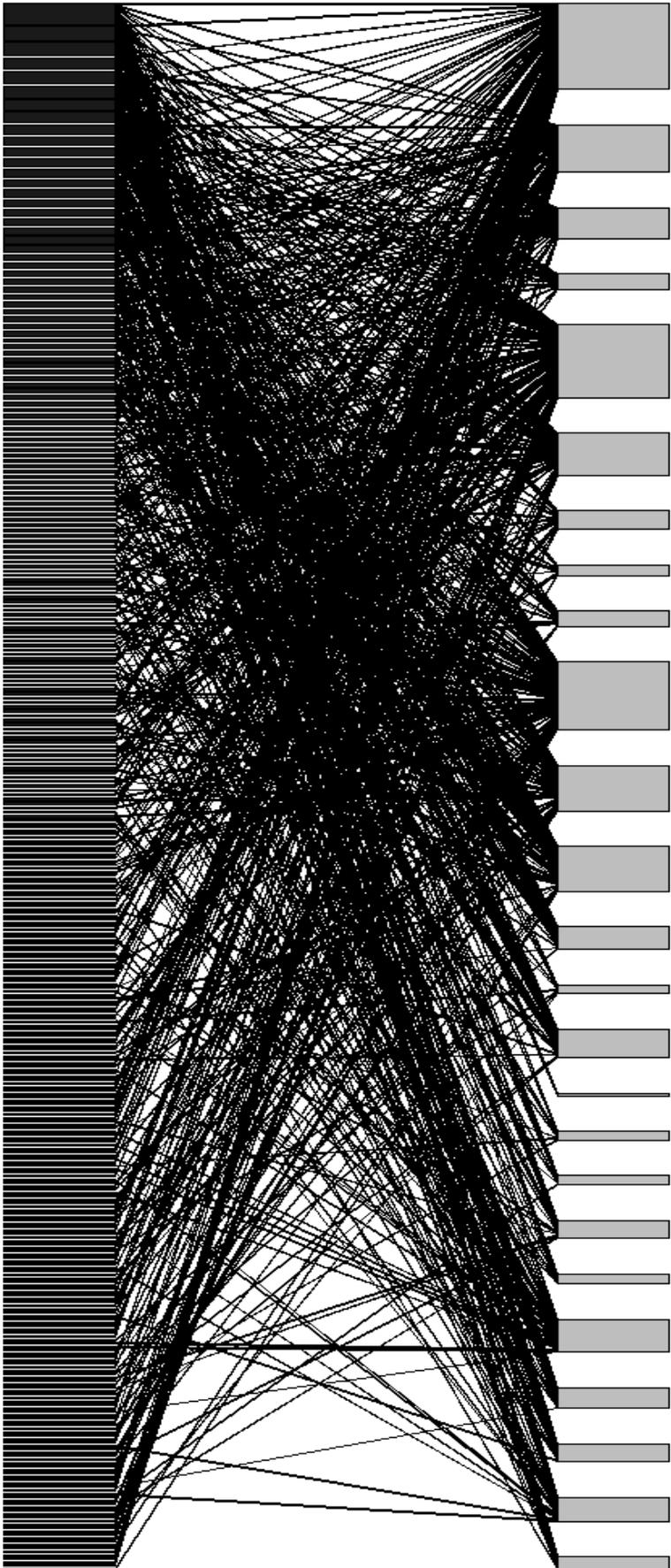
616 **Figure 5** A box plot showing the prevalence of plant invaders across Pacific islands in relation to
617 the date of the first record for each species at the hub (Hawai'i). The dates of the first records
618 were grouped into three broad periods based on introduction trends in the Pacific. Numbers at the
619 top indicate the sample size (species) in each category. Statistical trends are as follows. Variance:
620 pre-1910 > 1910-1945 > post-1945. Medians (Kruskal–Wallis): pre-1910 > [1910-1945 = post-
621 1945]. Note that the variance is highest among the earliest introductions; the success of some
622 invaders is idiosyncratic, even after being in the region for a long time.
623
624

625 **Fig.1**



626

Fig. 2



Cuba
Domin. Rep.
New Caledonia

Jamaica

Hawai'i

Puerto Rico

Galápagos
Cape Verde

Samoa
Réunion

Mauritius
Society

Marquesas

Palau

Mayotte

Tonga
US Virgin Is.
Wallis Futuna

Seychelles
Cook Is.

Saint Helena

Australs

Rodrigues

Ascension
Gambier

Fig. 3

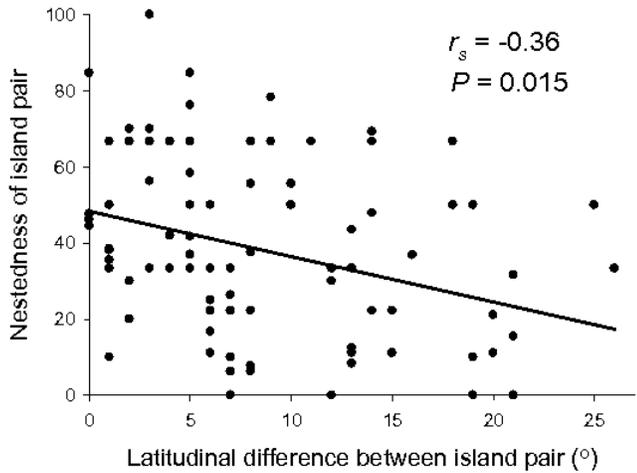
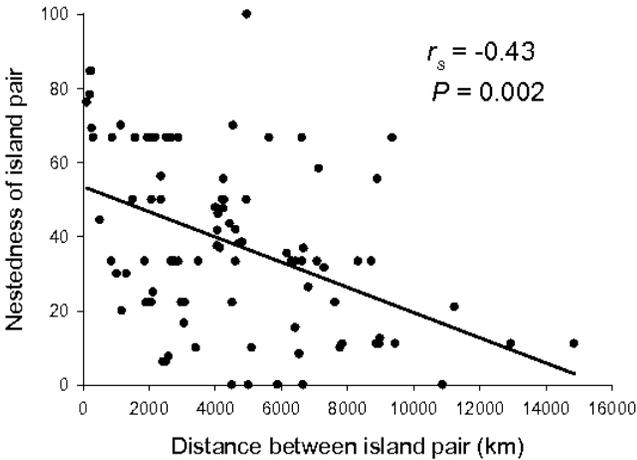


Fig. 4

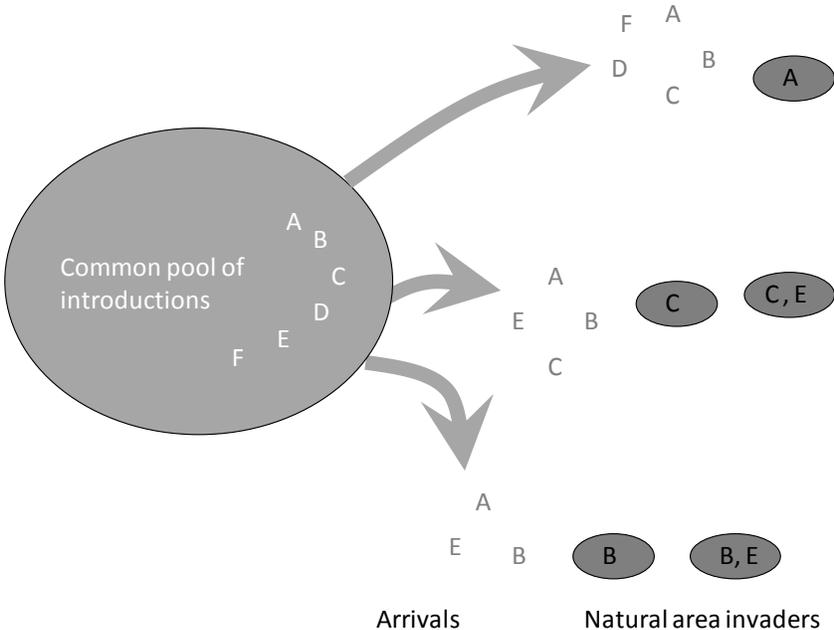


Fig. 5

