

1 **On the island biogeography of aliens: a global analysis of the richness of plant and bird**
2 **species on oceanic islands**

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24

25 **Abstract**

26 **Aim** To (1) characterize the relationship(s) between species richness and area for alien plant
27 and bird species on islands, and to identify commonalities and differences in the relationships
28 for these different taxa, and between alien and native species; (2) test whether area per se,
29 native species richness or human factors related to area is the primary determinant of alien
30 species richness; and (3) explore the effects of isolation, productivity, and the time since first
31 European landfall, on alien island biogeography.

32

33 **Location** Islands around the world.

34

35 **Methods** We used structural equation modeling (SEM; supported by generalized linear
36 models) to interrogate data on the alien and native species richness of birds and plants on
37 islands.

38

39 **Results** Alien plant and bird species richness were both strongly correlated with island area,
40 with similar slopes on logarithmic axes. SEMs for both plants and birds revealed positive direct
41 effects of native species richness and human population size, and positive indirect effects of
42 area, on alien species richness. The models also identified indirect effects of temperature
43 (positive) and isolation (negative) on alien species richness. Native plant and bird species
44 richness were both predicted by direct effects of area (positive), temperature (positive) and
45 isolation (negative). However, native plant richness was the only direct predictor of native, and
46 the strongest direct predictor of alien, bird species richness for islands with both plant and
47 bird richness data.

48

49 **Main conclusions** Our analyses recover the species-area, species-isolation and productivity
50 relationships in native richness. Alien species richness was most strongly related to native

51 species richness, with additional effects of human population size. Human population size most
52 likely determines the number of alien species that arrive on an island, while the effect of native
53 species richness may be driven by the influence of habitat heterogeneity on the likelihood that
54 those populations persist (establishment success).

55

56 **Key words:** Alien species; bird; human population size; island biogeography; native species
57 richness; plant; species-area relationship; structural equation model

58

59 **Running Head:** The island biogeography of alien species

60 **Introduction**

61 Species richness shows substantial spatial variation, but all such variation is the result of the
62 interaction of four key processes: immigration, emigration, speciation and extinction. There is
63 a large body of published research devoted to understanding exactly why these processes vary
64 over space and time, and how they interact to determine species richness (see reviews in
65 Rosenzweig 1995; Whittaker 1998; Kalmar & Currie 2006). Much of this work has focused on
66 variation in species richness across islands, especially since the publication of the seminal
67 work by MacArthur & Wilson (1967) on island biogeography. Islands constitute well defined
68 but restricted spatial units, which make ideal natural laboratories to study the processes that
69 lead to different numbers of species inhabiting different spatial locations.

70

71 Species richness on islands shows several consistent patterns of variation (Whittaker 1998;
72 Kreft *et al.* 2008; Whittaker *et al.* 2008; Triantis *et al.* 2012) and (all else being equal) is higher:
73 (i) on larger islands (the species-area relationship), (ii) on islands with higher primary
74 productivity, (iii) on islands closer to the continental mainland, (iv) on land-bridge islands than
75 on oceanic islands, and (v) on geologically older islands than on younger islands, although
76 richness can decline again with age on very old islands. The caveat of “all else being equal” here
77 includes the geological and evolutionary history of the islands, the taxon concerned, and the
78 interaction of different features (e.g. size versus isolation). Nevertheless, on average we expect
79 larger, older (but not too old), less isolated, more productive, land-bridge islands to be home to
80 more species.

81

82 These consistent patterns have in turn led to a variety of hypotheses regarding how the
83 processes of immigration, emigration, speciation and extinction may act to determine island
84 species richness. However, while islands make excellent natural laboratories, using them to
85 test different hypotheses for observed patterns in species richness is difficult: the processes

86 concerned are not readily amenable to controlled experimental manipulation, while tests of
87 different predictions using observational data on richness patterns are unlikely to be clear-cut.
88 Given these issues, one potentially valuable opportunity to study the processes underlying
89 island species richness patterns is to exploit the large-scale experiment in nature that is
90 provided by alien species. A recent upsurge of interest in the island biogeography of alien
91 species has followed from the observation that they may provide valuable information on the
92 natural processes structuring the assemblage of island biotas (Brown & Sax, 2004; Sax &
93 Gaines, 2005; Blackburn *et al.* 2008).

94

95 Alien species are species whose presence in a region is attributable to human actions, which
96 have enabled them to overcome fundamental biogeographical boundaries (Blackburn *et al.*
97 2011; Richardson *et al.* 2011). Their species richness will therefore be determined by human
98 factors, but potentially also in part by the same natural processes that determine native species
99 richness. We might expect quantitatively similar relationships in the island biogeography of
100 native and alien species if assemblages of both sets of species are responding to common
101 structuring processes, but differences where those structuring processes differ between these
102 groups (Hulme 2008). For example, Blackburn *et al.* (2008) found that alien bird species on 41
103 islands and archipelagoes worldwide had a species – area relationship (log-log axes) of similar
104 slope ($z = 0.18$ vs 0.25) but lower intercept ($c = 0.18$ vs 0.79) to that for native bird species
105 from the same locations. The relationships between species richness and isolation from the
106 nearest continental mainland were weakly (and not significantly) negative for native bird
107 species but significantly positive for aliens. Taken at face value, this might suggest that
108 common processes determine the slopes of native and alien species-area relationships (e.g.
109 common extinction processes acting on established populations), while different processes
110 determine their intercepts and the forms of species-isolation relationships (e.g. the different
111 drivers of immigration in natives versus aliens). However, at present it is difficult to draw

112 conclusions about the generality of different processes as determinants of alien species
113 richness on islands, as few studies have tested alternative hypotheses for these patterns. Those
114 that have have tended to compare measures of three potential correlates of richness: island
115 area, native species richness, and human population size.

116

117 Island area is a convenient surrogate for the same area-related natural processes that
118 determine native species richness. For example, extinction probability is thought to be higher
119 on smaller islands, as these tend to house smaller populations more likely to be affected by
120 demographic and environmental stochasticity or Allee effects; such effects will apply equally to
121 both native and alien species. Nevertheless, some natural processes are unlikely to influence
122 alien species richness, including anything linked to the rate or magnitude of speciation. The
123 influence of island area may therefore be altered depending on the extent to which these
124 processes underlie species-area relationships.

125

126 Native species richness may be positively or negatively related to alien species richness.
127 Islands rich in native species may limit the establishment of alien species through negative
128 biotic interactions such as competition or predation (termed biotic resistance; Elton 1958).
129 Conversely, areas that can support many native species may also be able to support many alien
130 species, leading to positive relationships between native and alien species richness (“the rich
131 get richer”, *sensu* Stohlgren *et al.* 2003). Such relationships might be expected if a key
132 restriction on native species richness is dispersal limitation, such that total species richness
133 can increase markedly if this limitation is overcome by the anthropogenic movement of species
134 (Hulme 2009). Native species richness may also affect human responses to alien species, for
135 example if depauperate native biotas have stimulated intentional efforts to increase local
136 biodiversity for hunting or aesthetic reasons.

137

138 Finally, given that the presence of alien species is attributable to human actions, a range of
139 factors relating to the magnitude of human impacts in an area might influence alien species
140 richness. For example, the volume of trade to an island (often analyzed in terms of Gross
141 Domestic Product) may determine the number of species deliberately or accidentally imported
142 (i.e., human-mediated immigration), whereas the extent of anthropogenic habitat modification
143 might relate to the opportunities for alien species to establish viable populations. Many of
144 these factors will correlate strongly with human population size (e.g. Kummu & Varis 2011),
145 which is therefore a convenient surrogate for human influence on alien species richness. Since
146 most movements of alien species have occurred in the period since Europeans started to
147 navigate and explore the globe (di Castri 1989; Hulme 2009), the time since the first European
148 landfall may also relate positively to the number of species that have had the opportunity to
149 colonize an island (Blackburn *et al.* 2008).

150

151 Different empirical studies of the richness of alien species on islands have found different
152 effects of human factors, area and native species richness, for both plants (e.g. Lonsdale 1999;
153 Sax *et al.* 2002; Long *et al.* 2009; Kueffer *et al.* 2010; Pretto *et al.* 2012) and animals (e.g. Case
154 1996; Chown *et al.* 1998; Sax *et al.* 2002; Blackburn *et al.* 2008; Ficetola & Padoa-Schioppa
155 2008). The increasing number of studies of alien species richness on islands, and the lack of
156 consistent comparisons or outcomes from them, suggests to us that a synthetic analysis of
157 available data would be timely. Therefore, here we compile and analyze data on the richness of
158 plant and bird species derived from previous studies from oceanic islands worldwide. We focus
159 on plants and birds because data for both native and alien species richness are available from a
160 large number of islands, relative to other taxa.

161

162 Our aims were threefold. First, we wished to characterize the relationship(s) between species
163 richness and area for alien species, to identify commonalities and differences in the

164 relationships for different taxa, and between alien and native species. Second, we wanted to
165 test for the effects of different drivers of area-related variation in alien species. Specifically, we
166 were interested in whether area per se is a primary determinant of alien species richness, or
167 whether native species richness or human factors related to area underlie variation in alien
168 species richness across islands. We also collated information on the isolation of islands from
169 mainland regions, metrics of productivity, and the time since first European landfall on an
170 island. As pointed out above, isolation and productivity have been shown to be key
171 determinants of native species richness on oceanic islands. Time since first European landfall
172 may influence alien richness independently of area-related effects. Our third aim was to
173 explore the effects of these additional factors on alien species richness. The synthetic approach
174 allows us to test these different hypotheses across broader ranges of variation than has been
175 possible before, which may allow us to extract some generalities despite the range of outcomes
176 from previous studies.

177

178 **Methods**

179 We analyzed data on the alien and native species richness of birds from 68 island locations,
180 and on plants from 62 island locations around the world. This represents a total of 90 islands,
181 of which 40 islands included data for both taxa. Some locations represent single islands, and
182 some whole archipelagoes, but each individual island is included in each taxon dataset only
183 once. Locations were distributed within the Atlantic (n = 14), Caribbean (n = 7) Indian (n = 12),
184 Pacific (n = 37) and Southern (n = 20) oceans. We included data only for islands >90 km from a
185 continental mainland, so that as much as possible we are considering oceanic islands (in effect,
186 if not necessarily in geological origin). Alien species richness refers to naturalized or
187 established species, from sources published since 1995 (to minimize variation in numbers due
188 to time available to establish). For birds, native species richness refers to terrestrial species
189 breeding on the island, including recently extinct species (since 1500 AD).

190

191 In addition to species richness, we obtained the following data for all islands in the data set:
192 area (km²), distance from the nearest continental mainland (km), distance from the nearest
193 landmass larger than the island/archipelago (km), temperature (°C), precipitation (mm),
194 latitude (degrees from the Equator), time since first European arrival (2013 minus date of first
195 European landing if possible, otherwise first sighting or first attempt to colonize), and human
196 population size. Data on temperature and precipitation were obtained from Mitchell & Jones
197 (2005). Distances were calculated using the Google Maps Distance Measurement tool. Other
198 data were sourced from internet fact pages including the CIA Factbook and Wikipedia (or
199 linked reference in a few cases). The data and sources are available as online Supplementary
200 Material (Appendix 1). We use natural logarithm transforms (hereafter, log) of alien and native
201 species richness, island area, human population size, distance from land and time since
202 colonization variables for all statistical analyses.

203

204 We used structural equation models (SEM; Grace, 2006) to investigate direct and indirect
205 effects of island area, human population size, latitude, environment (temperature and
206 precipitation), distance from land (nearest larger island and nearest continental land mass),
207 and time since European colonization on alien and native species richness on islands. In
208 addition to alien and native species richness, the hypothesized inter-relationships among the
209 variables resulted in human population size and the environment variables (temperature and
210 precipitation) also being treated as endogenous (i.e., response) variables in our model. We
211 used the SEM to partition the correlations between the exogenous explanatory variables and
212 endogenous response variables into direct and indirect effects using a recursive path analysis
213 (Grace 2006).

214

215 We developed our SEM model a priori based on hypothesized relationships from theoretical
216 and empirical evidence (Figure S1, Appendix 2; online Supplementary Material). We were
217 specifically interested in evaluating the relative importance of native species richness, island
218 area and human population size on alien species richness. However, the SEM approach allowed
219 simultaneous testing of theoretical native species-area relationships and the hypothesized
220 effects of biogeographical, environmental and historical variables on both alien and native
221 species richness. We also assessed relationships between human population size and island
222 area and biogeography within the model. We tested for differences in SEM path relationships
223 between birds and plants by contrasting a model with additive taxon effects to a model where
224 relationships differed between taxon groups, using BIC.

225

226 We assessed the fit of our theoretical SEM using a χ^2 goodness-of-fit test of the difference
227 between the observed data and hypothesized model, the root mean square error of
228 approximation (RMSEA), and the comparative fit index (CFI). A satisfactory model fit was
229 indicated by (1) a non-significant χ^2 goodness- of-fit test ($\alpha = 0.05$), (2) CFI > 0.9, and (3) lower
230 90% confidence intervals of RMSEA < 0.05 (Zhang 2013). In the case of poor model fit, we used
231 large residual covariances and high modification indices (and/or standardized expected
232 parameter change values) to identify missing paths or residual correlations and to respecify
233 the model. A parametric bootstrap approach was used to estimate 95% confidence intervals of
234 path coefficients (direct and indirect) and derived estimates of total effects (i.e. the sum of
235 direct and indirect effects). After identifying an adequate respecified SEM (based on our
236 criteria above; Table S1, Appendix 2; online Supplementary Material), we simplified the model
237 by removing terms with direct path coefficients for which their bootstrap 95% confidence
238 intervals included zero.

239

240 The SEM approach has the advantage of estimating the (total) effects of the explanatory
241 variables on the multiple response variables simultaneously (and additionally assesses the
242 relationships between response variables). However, with this approach we are forced to
243 logarithmically-transform the species richness variables (which are counts) prior to the
244 analysis (including the addition of +1 to those variables that take zero values). Therefore, we
245 also analysed the data using a set of independent hypothesis-specific generalized linear models
246 (GLM). These models are fitted using a negative binomial variance function and log link, and
247 hence properly account for the variation (including overdispersion) of the count variables. We
248 include the results of the more conservative GLM approach in the online Supplementary
249 Material (Appendix 2) to support the SEM findings.

250

251 Kissling *et al.* (2008) found, using SEM, that native plant species richness affects native bird
252 species richness in Kenya. Therefore, we further examined how relationships between native
253 and alien bird species richness were associated with native plant species richness, using the
254 subset of islands ($n = 40$) for which both bird and plant species richness data were available.
255 We used the final path model identified for bird species richness relationships from the full
256 data set as a starting model, and included the following additional sets of paths: (1) exogenous
257 paths for the effects of native plant species richness on both native and alien bird species
258 richness endogenous variables, and (2) exogenous paths for the effects of island area,
259 temperature, and distance to nearest continental mainland on native plant species richness (as
260 identified for native plant species richness relationships from models fitted to the full data set).
261 The full SEM model for this analysis is presented in Figure S2 (Appendix 2; online
262 Supplementary Material), and was simplified as described above.

263

264 All statistical analyses were conducted using R 3.1.0 (R Core Team 2014). The structural
265 equation models were calculated with the R package `lavaan` 0.5-16 (Rosseel 2012).

266

267 **Results**

268 Figure 1 shows the species-area relationships for alien and native plant and bird species on
269 oceanic islands around the world. Both alien plant and alien bird species-area relationships
270 have slopes (z) that are statistically indistinguishable, and that are also indistinguishable from
271 0.25, which is often cited as the canonical slope for native island species-area relationships
272 (plants: z [95% confidence intervals] = 0.24 [0.15, 0.33]; birds: z = 0.27 [0.17, 0.36]). Native
273 plant and bird species-area relationships also have statistically indistinguishable slopes, but
274 these are steeper than those for the alien species in the same taxon, with confidence intervals
275 that do not overlap 0.25 (plants: z = 0.39 [0.32, 0.46]; birds: z = 0.36 [0.28, 0.43]).

276

277 The comparison between full SEM path models with additive taxon effects and independent
278 models, where the relationships differed between taxa, suggested that the latter was more
279 likely given the data (Δ BIC = 133.4). Model simplification for each taxon (described in
280 Appendix 2; online Supplementary Material) resulted in the models presented in Figure 2. The
281 standardized coefficient estimates relating to each path in these figures are also given in Table
282 1.

283

284 The SEM path model for alien bird species richness identified strong positive direct effects of
285 both human population size and native bird species richness (Figure 2a, Table 1). There was
286 also a negative direct effect of precipitation. The effect of island area on alien bird species
287 richness was indirect, acting through the positive effects of area on native species richness and
288 human population size. The standardized effect sizes of human population size, native bird
289 species richness and island area were all of similar magnitude, albeit that the effect of area was
290 indirect. There was also an indirect positive effect of temperature, and an indirect negative
291 effect of distance from the nearest continent, on alien bird species richness (Figure 2a, Table 1).

292 The indirect effect of temperature acted through its positive effects on native species richness
293 and human population size, while the indirect effect of distance from the nearest continent
294 acted through its negative effect on native species richness (Table 1). Thus, bird native species
295 richness was predicted by positive direct effects of area and temperature, and a negative direct
296 effect of distance from the nearest continent. Human population size was predicted by positive
297 direct effects of area and temperature (Table 1). Each model term contributed either a direct or
298 indirect effect only as their total contribution to the simplified SEM path model.

299

300 The SEM path model for alien plants was similar to that for birds, but differed in including a
301 small direct negative effect of island area, and in lacking an effect of precipitation, on alien
302 plant species richness (Figure 2b, Table 1). Each model term contributed either a direct or
303 indirect effect only as their total contribution to the simplified SEM path model, apart from the
304 effect of island area on alien plant species richness: the total effect of area was 0.471 (95%
305 confidence intervals = 0.288, 0.629). The total standardized effect sizes of human population
306 size, native plant species richness and island area were all of similar magnitude, as for birds.
307 However, the largest direct effect on alien plant species richness in the model was that of
308 native plant species richness, versus human population size for alien bird species richness
309 (Table 1). The indirect positive effect of temperature on alien plant species richness was
310 stronger than the equivalent effect for birds, with only marginally overlapping confidence
311 intervals (Table 1). This stronger indirect effect of temperature was the result of stronger
312 direct positive effects of temperature on native species richness and human population size in
313 the plant model. The paths and their associated coefficients for native species richness and
314 human population size were otherwise very similar for the bird and plant models (Figure 2,
315 Table 1).

316

317 The results of the GLM analysis were consistent with the SEM analysis. GLMs identified strong
318 effects of native species richness, human population size and island area on alien bird and
319 plant species richness, in models that treated each of these predictor variables separately
320 (Tables S3 – S5, Figure S3, Appendix 2; online Supplementary Material). Across the three
321 model sets for alien species richness, the best supported models were those that included
322 native species richness as a predictor (Table S6, Appendix 2). Effects of taxon, precipitation and
323 temperature are also consistently included in the most likely models, along with interactions
324 between taxon and the continuous predictor variables. The most likely model in terms of
325 human population size included a negative effect of time since European colonization and its
326 interaction with taxon (more recently colonized islands have more alien bird species, but alien
327 plant species richness is independent of colonization time), but these effects were only
328 included in two of the 12 models with $\Delta AIC_c < 4$ (Table S4, Appendix 2). The most likely model
329 set for native species richness included effects of area, taxon, temperature and precipitation,
330 with the best supported model including all these variables except precipitation (Tables S7 - S8,
331 Figure S4, Appendix 2).

332

333 For the subset of 40 islands with data on both plant and bird species, the simplified SEM
334 showed that native plant species richness was strongly positively correlated with alien bird
335 species richness (Figure 3, Table 2), and indeed replaces the effects of native bird species and
336 human population size identified from the taxon-specific analysis of the full data set (Figure 2).
337 The species-area relationship for native plants was retained in this model, but a strong positive
338 effect of native plant species richness on native bird species richness negated the influence of
339 island area on the latter (Figure 3, Table 2). In addition, the direct effects of temperature and
340 distance to the nearest continental mainland on native bird species richness were replaced by
341 indirect effects through native plant richness. Indeed, aside from a negative direct effect of

342 precipitation on alien bird species richness, the only direct effects on native or alien bird
343 species richness in the simplified model are effects of native plant richness (Figure 3, Table 2).

344

345 **Discussion**

346 The positive relationship between the area of an island and the number of native species found
347 there is one of the canonical relationships in ecology (Rosenzweig 1995; Whittaker 1998). The
348 relationship is not restricted to native species. We found that alien species richness also
349 increases with island area, for both plants and birds (Figure 1a), as has been shown elsewhere
350 (e.g. Case 1996; Blackburn *et al.* 2008; Ficetola & Padoa-Schioppa 2008; Long *et al.* 2009;
351 Kueffer *et al.* 2010). The existence of an alien species-area relationship has raised the hope that
352 similarities and differences between this and native species-area relationships could provide
353 valuable insight into the causes of the latter. However, any such insight depends on us also
354 understanding what causes there to be more alien species on larger islands. Our results
355 provide some relevant information in this regard.

356

357 Previous studies of spatial variation in alien species richness have generally considered it in
358 terms of one or more of land area, native species richness, or a measure of human activity such
359 as human population size (but see e.g. McKinney 2006). These variables are inter-correlated in
360 our data, which motivated our approach of using structural equation modeling to explore their
361 effects simultaneously. The SEM models of the full data set reveal that all three of these
362 variables have positive effects on both plant and bird alien species richness, but that the effects
363 of native species richness and human population size are direct, while the effect of area is
364 largely indirect (Figure 2, Table 1). The SEM analyses identified strong effects of area, distance
365 to the nearest continental landmass, and temperature on native species richness (Figure 2,
366 Table 1), such that they recover the well-known species-area relationship, species-isolation
367 relationship and latitudinal/productivity gradient in species richness (see Introduction). These

368 outcomes give us confidence that our results for alien species are also likely to be sensible, as
369 do the relatively high goodness of fit values (r^2) for each endogenous variable in both models
370 (Figure 2). Our results imply that alien species-area relationships arise because the area of an
371 island influences the number of native species and the number of humans that inhabit it.

372

373 Alien species introductions are ultimately a consequence of human activities. Islands with
374 more people should generate more trade and more transport interchange with mainland areas,
375 all else being equal, producing more opportunities to import (and export) novel species (Pyšek
376 *et al.* 2010). The strong positive path linking human population size to alien species richness in
377 both plant and bird models (Table 1) confirms this expectation. In addition to this effect,
378 however, areas rich in native plants are also rich in alien plants, and likewise for birds (Table 1,
379 2; see also Lonsdale 1999; Sax *et al.* 2002). This suggests that at larger spatial scales, external
380 factors affect the richness of native and alien species in the same way, and provides little
381 support for the action of biotic resistance, whereby islands rich in native species resist the
382 establishment of alien species (e.g. Elton 1958). Rather, rich islands get richer (cf. Stohlgren *et*
383 *al.* 2003). Thus, it appears that the alien species richness of islands is produced by a
384 combination of anthropogenic and natural processes (but see below). We can interpret these
385 findings in terms of the influence of these different processes on different stages of the
386 pathway to invasion by alien species (Blackburn *et al.* 2011).

387

388 The number of alien species on an island is a positive function of the number of species
389 introduced ('colonization pressure') and the probability that an introduced species then
390 establishes a viable population (Lonsdale 1999; Lockwood *et al.* 2009). These processes are the
391 equivalents of immigration and (one minus) extinction rates for native species. It is not obvious
392 how native species richness would have a positive effect on colonization pressure, and so
393 native richness is therefore most likely to act through effects on the probability that introduced

394 species then successfully establish viable populations. There are at least two possible
395 mechanisms. First, native species may directly determine opportunities for alien species
396 establishment, such that islands with more native species end up also with more alien species.
397 Second, the environment may influence the likelihood that both native species and alien
398 species will persist in the same way, causing the positive relationship between the two to arise
399 indirectly.

400

401 Direct effects of native species on opportunities for alien species establishment may include
402 facilitation through shared mutualisms (Richardson *et al.* 2000). Rich plant assemblages may
403 have promoted (or been promoted by) the existence of pollinators or mycorrhizal fungi that
404 could then also be utilized by alien species (Richardson *et al.* 2000). In contrast, we can think of
405 no good ecological reason why native bird species richness should directly promote
406 establishment by alien bird species (Figure 2). Our SEM models suggest that the indirect
407 effects are unlikely to include area per se, temperature, isolation, or precipitation. If these
408 variables influenced both native and alien species richness, we would expect to observe direct
409 paths between them and both richness variables (Figure 2, Table 1). For plants, where the
410 overwhelming role of habitat on alien species richness in a region has recently been
411 emphasized (Chytrý *et al.* 2008a, 2008b), the most likely mechanism underlying the positive
412 relationship at the large spatial scale is increasing habitat heterogeneity with area, which
413 results in higher species numbers of both native and alien species. While indirect, this effect
414 could appear as a direct path between native and alien plant richness in our models: indeed, if
415 native plants do indeed respond to habitat heterogeneity as strongly as argued (Chytrý *et al.*
416 2008a, 2008b), then native plant richness would be an excellent proxy for it.

417

418 Further evidence of a role for habitat is provided by our subsequent analyses on the subset of
419 40 islands for which data on both plant and bird species richness are available. Our models of

420 the full data set showed a direct effect of native bird richness on alien bird richness (Table 1,
421 Figure 2). In the subset analysis, this is replaced by a strong direct effect of native plant
422 richness: indeed, native plant richness is the only direct positive predictor of alien bird species
423 richness, and the only direct predictor of native bird richness (Table 2, Figure 3). Links
424 between native bird and native plant richness were present indirectly in the separate analyses
425 of each taxon through the common effects of species area relationships, latitudinal
426 temperature gradients and distance from nearest mainland on native richness for each taxon
427 (Table 1, Figure 2). In the subset analyses, the direct effects of these variables on native bird
428 richness are replaced by indirect effects through native plant richness, and their indirect
429 effects on alien bird richness are retained. Previous studies have also shown positive
430 relationships between native plant and native bird species richness over large spatial scales
431 (e.g. Kissling *et al.* 2008; Jetz *et al.* 2009), which have been suggested to be a consequence of
432 greater niche opportunities for birds provided by the increased structural complexity of richer
433 plant assemblages (Kissling *et al.* 2008). Our analyses suggest that higher habitat heterogeneity,
434 as indexed by native plant richness, may be a significant part of the reason why rich islands get
435 richer in terms of both alien plant and alien bird richness, and indeed why some islands are
436 richer than others in native bird species.

437

438 The impact of human population size on alien species richness is more likely to act through its
439 effect on immigration, via colonization pressure. For most alien taxa, we do not know how
440 many species were introduced to a location but failed to establish: we lack this information for
441 plants for the great majority of our islands (and for birds for many). Nevertheless, it is likely
442 that colonization pressure is a positive function of the scale of human activities (e.g. trade
443 volume, GDP), as these will increase the opportunities for accidental and deliberate
444 introduction of species (Pyšek *et al.* 2010). Blackburn *et al.* (2008) have previously shown, for
445 a subset of the data on alien birds analyzed here, that colonization pressure was higher on

446 islands with higher human population sizes. Human population size could also directly affect
447 establishment probability, for example by increasing the niche space for human-commensal
448 alien species (Chapple et al. 2012).

449

450 Interestingly, the effect of human population size disappears from our analyses of the subset of
451 islands with both plant and bird richness data (Table 2, Figure 3), seemingly as a result of the
452 correlation with island area: area had an indirect effect on alien richness through human
453 population size, as well as through native bird richness, in the original analysis (Table 1, Figure
454 2). Immigration by alien species increased dramatically after European nations started to
455 colonize other parts of the world in the middle of the eighteenth century (di Castri 1989;
456 Hulme 2009; Blackburn *et al.* 2015). We therefore expected to see a positive effect of time since
457 European colonization on alien species richness in our data. The SEM models identify no such
458 effect, although the associated GLMs do find that islands colonized more recently have *more*
459 species of alien birds (Appendix 2) for reasons that are unclear. All of this suggests that
460 immigration may be less important as a driver of alien species richness than establishment
461 success (i.e. 1 – extinction rate), but the relative contributions will be difficult to determine
462 with certainty in the absence of data on colonization pressure.

463

464 Our analysis of the full data set found that alien species richness was better fitted by separate
465 SEMs for plants and birds, but there are nonetheless striking commonalities in the path
466 structure for the two taxa (Figure 2). The only two differences are negative direct effects of
467 precipitation on alien bird species richness, and of area on plant species richness. The latter
468 effect is weak, and is likely to be an artefact of inter-correlation between area, native species
469 richness and human population size. The former effect shows that alien bird species richness is
470 higher on drier islands. Rolett & Diamond (2004) showed that islands in the Pacific with lower
471 annual rainfall suffered higher deforestation in the period between first human and first

472 European colonization, while Duncan et al. (2013) found that drier islands had suffered higher
473 extinction rates in the native avifauna in this period. If these relationships generalize, they
474 would imply that drier islands could have more opportunities for alien bird species to colonize,
475 as a result of either habitat alteration or higher native bird species extinction.

476

477 We also found striking commonalities in the slopes of the species-area relationships for alien
478 plants and birds ($z = 0.24$ and 0.27 , respectively), and for native plants and birds ($z = 0.39$ and
479 0.36 , respectively; Figure 1). Thus, alien species richness increases with area at the same rate
480 for both plants and birds, as does native species richness, although native richness increases
481 with area more quickly. It is interesting that the processes that lead to plant and bird richness
482 produce common relative increases with area for alien species, and higher but still common
483 relative increases with area for native species. Given the timescales involved, speciation and
484 emigration can make only a trivial contribution to alien species richness in these data, and as
485 noted above, the slopes of the alien species-area relationships must be determined just by
486 immigration (colonization pressure) and extinction (via establishment success). These
487 processes will be ongoing, as more alien species will be added to islands, while inevitably some
488 will go extinct after shorter or longer residence times. The slopes of the alien species-area
489 relationships are likely to change as a result, and it will be interesting to see whether or not
490 they ultimately converge on native patterns. Our models imply that immigration and extinction
491 act differently on alien plants and birds (Table 1, 2), and that there is actually no direct positive
492 effect of area on alien species richness, but that the outcome is nevertheless common species-
493 area slopes. The precise influence of these processes would be fundamentally informed by data
494 for colonization pressure. Nevertheless, our analyses suggest that not only do different
495 processes underlie similar native and alien species-area relationships, but also that the same
496 processes act differently to produce similar species-area relationships in different alien taxa.
497 Common pattern is no guarantee of common process at any level of comparison.

498

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507

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625

626

627 **Biosketch**

628 Tim Blackburn is an ecologist with interests in human-mediated biological invasions,
629 extinction, and other topics relating to the large-scale distribution and abundance of species.

630 He mainly works on birds.

631

632 Steve Delean is an environmental biostatistician and wildlife ecologist.

633

634 Phill Cassey is an invasion ecologist with interests in the distribution, transport and trade of
635 alien species, particularly vertebrates.

636

Table 1. Structural equation model standardized path coefficient estimates for the simplified model for each taxon. Italicized numbers in parentheses are 95% parametric bootstrap confidence intervals. Indirect effects are composite effects of all indirect paths in the model for each exogenous variable. Using the simplified model, each model term contributed either a direct or indirect effect only as their total contribution. The single exception to this was that island area contributed both directly and indirectly (through its effect on native species richness) to plant alien species richness; the total effect was 0.471 (95% confidence intervals = 0.288, 0.629). ‘Not Included’ indicates that the term was not included in the simplified model for that particular taxon.

Taxon		Birds		Plants	
Endogenous	Exogenous	Direct	Indirect	Direct	Indirect
Alien Species Richness	Area		0.518 <i>(0.404, 0.617)</i>	-0.234 <i>(-0.427, -0.038)</i>	0.705 <i>(0.541, 0.886)</i>
	Human Population	0.428 <i>(0.190, 0.647)</i>		0.495 <i>(0.282, 0.697)</i>	
	Native Richness	0.411 <i>(0.169, 0.632)</i>		0.561 <i>(0.365, 0.747)</i>	
	Precipitation	-0.223 <i>(-0.381, -0.066)</i>		Not included	
	Temperature		0.359 <i>(0.258, 0.459)</i>		0.600 <i>(0.457, 0.729)</i>
	Distance Continent		-0.107 <i>(-0.197, -0.035)</i>		-0.125 <i>(-0.242, -0.037)</i>
	Area		0.577 <i>(0.450, 0.697)</i>		0.630 <i>(0.465, 0.771)</i>
Native Species Richness	Temperature	0.338 <i>(0.213, 0.470)</i>		0.496 <i>(0.341, 0.654)</i>	
	Distance Continent	-0.261 <i>(-0.393, -0.124)</i>		-0.224 <i>(-0.381, -0.072)</i>	
	Area	0.657 <i>(0.545, 0.758)</i>		0.710 <i>(0.574, 0.848)</i>	
Human Population Size	Temperature	0.514 <i>(0.408, 0.629)</i>		0.649 <i>(0.509, 0.797)</i>	

Table 2. Structural equation model standardized path coefficient estimates for the simplified model of bird-plant inter-relationships. Italicized numbers in parentheses are 95% parametric bootstrap confidence intervals. Indirect effects are composite effects of all indirect paths in the model for each exogenous variable.

Endogenous	Exogenous	Direct	Indirect	
Alien Bird Species Richness	Island Area		0.441 (0.284, 0.606)	
	Precipitation	-0.196 (-0.393, -0.015)		
		Temperature		0.350 (0.198, 0.501)
		Distance Continent		-0.179 (-0.328, -0.018)
		Native Plant Richness	0.798 (0.659, 0.897)	
	Native Bird Species Richness	Island Area		0.509 (0.339, 0.686)
Temperature			0.405 (0.236, 0.561)	
Distance Continent			-0.207 (-0.380, -0.022)	
Native Plant Richness		0.922 (0.862, 0.958)		
Native Plant Species Richness		Island Area	0.552 (0.366, 0.740)	
	Temperature	0.439 (0.259, 0.615)		
	Distance Continent	-0.224 (-0.409, -0.023)		
	Human Population Size	Island Area	0.609 (0.452, 0.759)	
	Temperature	0.656 (0.500, 0.805)		

FIGURE LEGENDS

Figure 1. Model fitted estimates of the species-area relationship for (a) alien (Plants: $\log S = 3.79 + 0.24 \cdot \log A$; Birds: $\log S = 0.16 + 0.27 \cdot \log A$) and (b) native species richness (Plants: $\log S = 3.24 + 0.39 \cdot \log A$; Birds: $\log S = 0.77 + 0.36 \cdot \log A$) for each taxon. The red line shows the relationship for plants, the blue line for birds; points show partial deviance residuals for birds (blue circles) and plants (red triangles). Grey shading shows 95% confidence intervals.

Figure 2. Simplified path analysis model for (a) bird and (b) plant species richness after excluding paths with parametric bootstrap 95% confidence intervals that include zero. Endogenous variables are shown in ellipses and exogenous variables in boxes; arrows indicate direction of effects. The model r^2 values for each endogenous variable are: (a) log alien species richness = 0.61, log native species richness = 0.77, log human population size = 0.84; (b) log alien species richness = 0.70, log native species richness = 0.65, log human population size = 0.81. Standardized path coefficient estimates from the models are shown for each path.

Figure 3. Simplified path analysis model (after excluding paths with parametric bootstrap 95% confidence intervals that include zero) for bird species richness including plant species richness as an endogenous variable, for the subset of islands for which both plant and bird richness data were available. Endogenous variables are shown in ellipses and exogenous variables in boxes; arrows indicate direction of effects. Standardized path coefficient estimates from the models are shown for each path.

Fig. 1

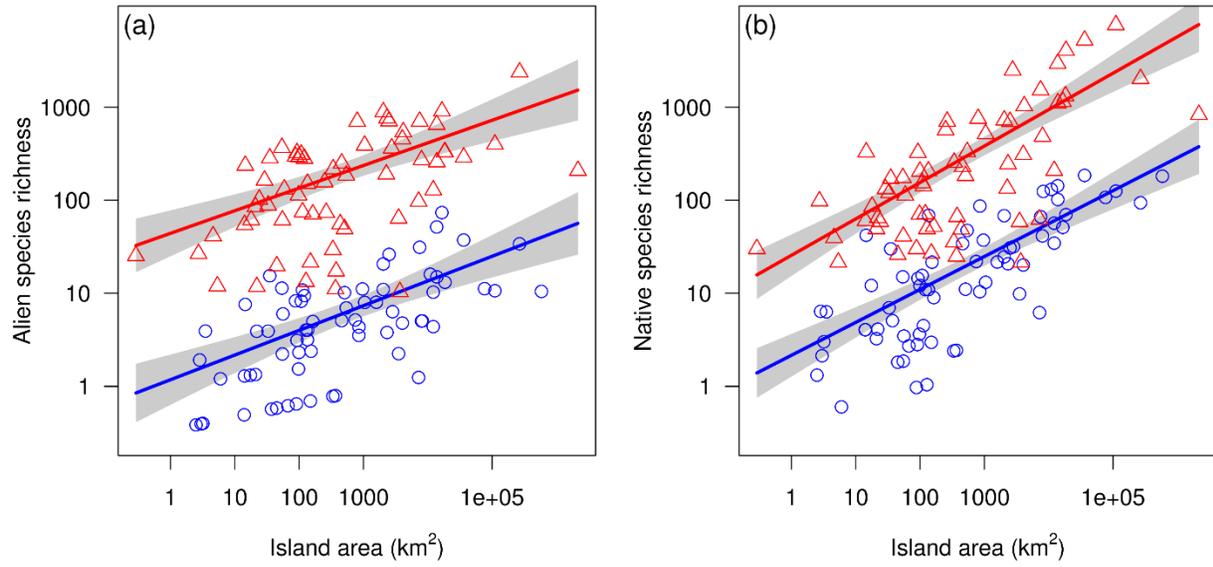


Fig. 2

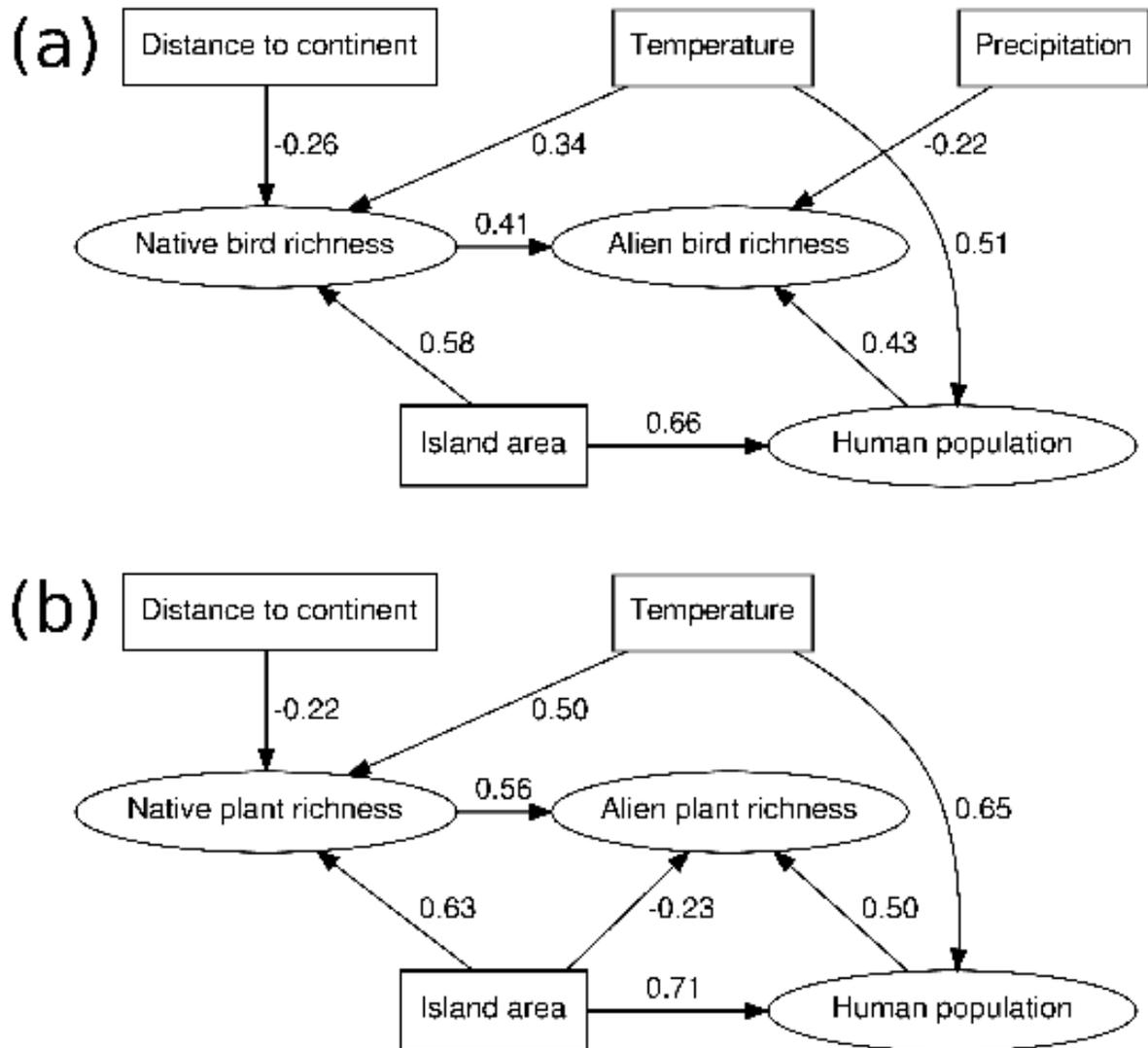


Fig. 3

