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1 **Title page for:**

2 **The Anthropocene biogeography of alien birds on islands: drivers of their**
3 **functional and phylogenetic diversities**

4

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47 (https://github.com/claramarino/biogeo_alien_FD_PD). Data include all variables used in the

48 SEM, such as alien diversity values on each island for the three facets (i.e., taxonomic,

49 phylogenetic and functional) as well as insular anthropogenic, biotic and geographic contexts.

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51

52 **The Anthropocene biogeography of alien birds: drivers of their functional**
53 **and phylogenetic diversities on islands**

54

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58

59 **Abstract**

60 A branch of island biogeography has emerged to explain alien species diversity in the light of
61 the biogeographic and anthropogenic context, yet overlooking the functional and phylogenetic
62 facets. Evaluating alien and native birds of 407 oceanic islands worldwide, we built structural
63 equation models to assess the direct and indirect influence of biotic, geographic, and
64 anthropogenic contexts on alien functional (FD) and phylogenetic diversity (PD). We found
65 that alien taxonomic richness was the main predictor of both diversities. Anthropogenic
66 factors, including colonization pressure, associated with classic biogeographical variables also
67 strongly influenced alien FD and PD. Specifically, habitat modification and human
68 connectivity markedly drove alien FD, especially when controlled by taxonomic richness,
69 whereas human population size, gross domestic product, and native PD were crucial at
70 explaining alien PD. Our findings suggest that humans not only shape taxonomic richness but
71 also other facets of alien diversity in a complex way.

72

73 INTRODUCTION

74 Natural eco-evolutionary processes have shaped insular ecosystems and biota for millions of
75 years. Since MacArthur and Wilson's book *The Theory of Island Biogeography* (MacArthur
76 & Wilson 1967), there has been a growing interest in estimating and predicting species
77 taxonomic richness on islands using geophysical factors (Whittaker *et al.* 2017). However,
78 human arrivals on islands disturbed the natural processes by accelerating the introduction of
79 alien species (Fernández-Palacios *et al.* 2021). A new branch of insular biogeography in the
80 Anthropocene has thus emerged to study the diversity of alien species, such as birds,
81 mammals, and plants (van Kleunen *et al.* 2015; Capinha *et al.* 2017; Dawson *et al.* 2017;
82 Dyer *et al.* 2017a; Seebens & Kaplan 2022). This branch has shown several consistent
83 patterns with the theory of island biogeography (e.g., species-area relationship) (Baiser *et al.*
84 2018; Blackburn *et al.* 2021; Matthews *et al.* 2023). However, the classic species-isolation
85 relationship (i.e., remote islands contain less species) has weakened due to more alien species
86 established in remote islands (Helmus *et al.* 2014; Moser *et al.* 2018).

87 Previous studies of alien diversity on islands have focused on only one facet of diversity
88 (i.e., taxonomic diversity). There are only few studies assessing functional and phylogenetic
89 diversities of native and alien biota with a special focus on diversity-area relationships
90 (Matthews *et al.* 2023; Sayol *et al.* 2021; Soares *et al.* 2022), and to our knowledge, there is
91 no study to date that investigated how the multiple facets of alien diversity on islands,
92 including functional (FD) and phylogenetic (PD) diversity, are affected by biogeographic and
93 anthropogenic drivers. This knowledge gap is surprising, as both FD and PD are crucial to
94 understand invasion dynamics and properly explore island biogeography in the Anthropocene.

95 Functional diversity represents the set of ecological strategies hosted by an assemblage
96 (Mouillot *et al.* 2013), reflecting the ecological assembly rules of this assemblage (Mouchet *et*

97 *al.* 2010). By studying alien FD, we can determine how alien species mediate their response
98 to disturbances and contribute to ecosystem functioning given they may replace native species
99 (Soares *et al.* 2022). Phylogenetic diversity (PD) captures the evolutionary history of species,
100 their features and future options (Faith 1992; Purvis *et al.* 2019). Because alien species are
101 introduced by humans for specific purposes (Dyer *et al.* 2017a), we can expect that alien PD
102 is not only affected by biogeographical factors but also by human ones, and mediated by
103 native biota. By identifying the factors determining alien FD and PD, we could anticipate the
104 fate of insular diversity in a disturbed environment and provide guidelines to effective
105 conservation strategies. Our aim here is to provide the first global evaluation of the drivers of
106 FD and PD patterns for island alien birds, in one single analytical framework.

107 Birds are taxonomically well described and are the object of the most comprehensive
108 resource on the global distribution of alien species (Jetz *et al.* 2012; Dyer *et al.* 2017b; Tobias
109 *et al.* 2021). During European colonization, many birds were intentionally introduced,
110 particularly specific families (e.g., Galliniformes) originating from Western Europe (Cassey *et*
111 *al.* 2015), and species with peculiar traits (e.g., diurnal and granivorous birds foraging on the
112 ground and in artificial terrestrial habitats (Soares *et al.* 2021). This period resulted in
113 numerous introductions on remote islands marked by a taxonomic selection for probability of
114 alien establishment (Lockwood 1999), representing a biased sample of global avian
115 evolutionary history and ecology. Moreover, Dyer *et al.* (2017a) showed that the identity of
116 introduced birds and the relative importance of colonization pressure, i.e., the number of
117 species introduced to an area (Blackburn *et al.* 2020), varied through time. Birds are thus an
118 excellent model for exploring global distribution of FD and PD of alien species.

119 Here, we investigate the spatial pattern of FD and PD for alien birds and their drivers
120 on 407 oceanic islands worldwide. Notably, we aim to test how 15 island contextual variables

121 related to the geographic (e.g., area, distance to mainland, elevation), biotic (i.e., taxonomic
122 richness, FD and PD of native birds), and anthropogenic (e.g., human population size,
123 connectivity, habitat modification, colonization pressure) contexts shape alien bird FD and
124 PD. We expect that species richness of alien assemblages will partially drive alien FD and
125 PD. Moreover, we seek to determine the effects of insular contexts on alien FD and PD which
126 may be mediated by species richness. We further explore how critical the anthropogenic
127 context is compared to the biogeographic context to explain alien diversities. To investigate
128 these effects, we apply structural equation models (SEMs) by defining *a priori* directional
129 links between the contextual variables and alien diversities (Table 1; Table S1 describes the
130 links connecting contextual variables). Finally, we calculate the deviations of FD and PD
131 from expected values given the taxonomic richness, allowing us to detect the drivers of the
132 relative variation of FD and PD beyond taxonomic richness (i.e., standardized effect size
133 (SES) of FD and PD) (Bach *et al.* 2022).

134 **MATERIAL AND METHODS**

135 **Alien bird diversities on oceanic islands**

136 *Study islands and species.* Our dataset is based on the oceanic islands from Weigelt *et al.*
137 (2013), defined as land masses larger than one km² not connected to the mainland during the
138 last glacial maximum. Alien assemblages were obtained by overlapping the distribution of
139 current established alien bird populations from the global avian invasion atlas (GAVIA) (Dyer
140 *et al.* 2017b) and the oceanic island contours from GADM (<http://www.gadm.org/version1>).
141 We restricted our dataset to oceanic islands that harbored at least four alien birds (n = 407
142 islands, for a total of 188 alien bird species), which was the minimum number of species to
143 calculate FD on one island.

144 *Functional and phylogenetic diversities.* We defined an alien assemblage as the pool of all
145 alien birds with an established population on an island. Alien bird FD of an island was the
146 ratio between the convex hull encompassing species from the alien assemblage and the
147 convex hull encompassing the global bird pool in a three-dimensional trait space (Mouillot *et*
148 *al.* 2013). To calculate alien FD, we collected seven species-level traits related to morphology
149 (i.e., beak length, beak depth, hand-wing index, body mass) and ecological preferences (i.e.,
150 trophic level, foraging niche and habitat breadth) for 10,862 bird species from AVONET
151 (Tobias *et al.* 2021) and IUCN (2022). Then, we reduced the dimensionality of the species-
152 trait matrix by computing a Principal Coordinate Analysis (PCoA) on the Gower's distance
153 between species. We finally obtained a synthesized 3D-trait space representing 54.1% of the
154 total variation among bird species (see Supporting text, Tables S2, S3 in SI for more details
155 on functional space computation). Alien FD was computed for each island using the
156 *alpha.fd.multidim* function from the *mFD* package (Magneville *et al.* 2021). We calculated
157 alien PD as the minimum total length of all phylogenetic branches required to span all alien
158 birds in the assemblage on a phylogenetic tree. Phylogenetic trees were extracted from
159 VertLife database (<https://vertlife.org>), and PD was calculated on 1,000 trees using the *pd*
160 function from the *picante* package (Kembel *et al.* 2010).

161 *Deviation from taxonomic diversity.* As we expect both FD and PD depend on alien
162 taxonomic richness, we also computed standardized effect size indices (SES-FD and SES-PD)
163 following Bach *et al.* (2022) to exclude the effect of alien taxonomic richness from these
164 indices and explore the drivers of the relative variation of FD and PD. To do so, we performed
165 null models using a matrix swap randomization by recalculating FD and PD (on 100
166 phylogenetic trees) on 100 randomly generated island-species matrices, while keeping a
167 constant number of species per assemblage. These random assemblages were simulated on the
168 global pool of alien birds documented in GAVIA ($n = 952$) with each species having the same

169 chance to become alien in each of the islands. SES indices were calculated as

170 $SES = \frac{\text{observed value} - \text{mean}(\text{simulated values})}{\text{standard deviation}(\text{simulated values})}$. Negative values of SES indicate a lower value FD

171 or PD than expected by chance for an equal taxonomic richness, representing a more clustered

172 assemblage in terms of traits or evolutionary history.

173 **Potential drivers of functional and phylogenetic diversities of alien birds on islands**

174 *Geographic variables.* We extracted the geographic variables for all islands from Weigelt *et*

175 *al.* (2013). We retrieved three variables related to habitat heterogeneity (i.e., *Latitude*, *Area*,

176 *Elevation*) and two variables linked to isolation (i.e., *Distance to the continent* and

177 *Surrounding land mass*). Since native and alien bird diversities vary regarding geographic

178 regions (Holt *et al.* 2013; Dyer *et al.* 2017a), we also classified each island into the

179 corresponding zoogeographic region delineated by Holt *et al.* (2013). For islands without

180 information on the zoogeographic region (n = 260), we attributed them to the closest region

181 (Fig. S1).

182 *Biotic variables.* To account for the insular biotic context, we calculated the taxonomic

183 richness of native birds for each island by computing the spatial overlap between the native

184 ranges of all birds in the world (Birdlife International 2020) and the islands. We also

185 calculated native FD and PD following the same methodology as for alien species.

186 *Anthropogenic variables.* We compiled seven variables associated with the anthropogenic

187 context of each island. *Population size* was calculated as the sum of human population counts

188 in the area of each island using the CIESIN database (2018). *Gross domestic product (GDP)*

189 was calculated as the sum of all GDP values in the cells falling into each island using the data

190 from Wang & Sun (2022). *Human connectivity* was calculated by mirroring the surrounding

191 landmass as a metric of human isolation of each island. We summed each island's number of

192 ports (<https://data.humdata.org/dataset/world-port-index>) and airports

193 (<http://www.partow.net/miscellaneous/airportdatabase/>) within the island and in a buffer of
194 100 km around the perimeter of the island. Finally, we retrieved two metrics related to habitat
195 modification by human activities (Theobald *et al.* 2020). *Static habitat modification* refers to
196 the median value of the current state of habitat modified by humans in 2017, while *Change*
197 *habitat modification* depicts the dynamics of habitat modifications between 1990 and 2015.
198 Both variables were aggregated at the island scale as the median of the values of habitat
199 modification. Using the GAVIA dataset, we also retrieved information of *Colonization*
200 *pressure* (i.e., the total number of alien species introduced to each island) for 96 islands, and
201 of *Time since first introduction* for 83 islands (see Supporting text for details on the method).

202 ***A priori* hypotheses**

203 We set 17 hypotheses to assess the links among the different variables (Table S1), including
204 10 hypotheses of direct links between absolute and relative values of alien diversities and the
205 insular contexts (Table 1). For instance, larger and more remote islands are known to host a
206 higher number of alien species, following known species-area and reverse species-isolation
207 relationships (Blackburn *et al.* 2016; Moser *et al.* 2018). Besides the absolute values of
208 FD/PD, we also seek to understand the variation and the drivers of FD/PD that are not
209 explained by species richness (i.e., SES-FD/PD). For instance, islands containing
210 heterogeneous habitats are the place for hosting species with more diversified ecological
211 strategies (Kadmon & Allouche 2007) and hypothetically more FD than expected given their
212 taxonomic richness (positive SES-FD). Moreover, native communities are likely to exert a
213 biotic filter on alien species and we can hypothesize lower SES-FD/PD than expected, if
214 competition or human selection exert a filter on alien species.

215 **Statistical analyses**

216 All statistical analyses were conducted in R (version 4.2.1) (R Core Team 2022).

217 To assess the direct, indirect, and total effects of biogeographic, anthropogenic, and
218 biotic factors on alien bird diversities, we performed SEMs using the *piecewiseSEM* package
219 (Lefcheck 2016). We built four SEMs on the 407 islands to explain each of the endogenous
220 variables related to alien diversity, i.e., alien FD, PD, SES-FD, and SES-PD, using our set of
221 *a priori* hypotheses (Tables 1, S1), excluding *Colonization pressure* and *Time since first*
222 *introduction* due to the existence of missing data in the two variables. We conducted models
223 with and without those two variables on sub-samples of islands (n=96 and n=83, respectively,
224 when data were available) to compare the effects of those variables on the outputs
225 (Supplementary text). All variables with a right-skewed distribution were log-transformed
226 (*Area*, *Distance to the continent*, *Surrounding landmass*, *Elevation*, *Native richness*, *Native*
227 *PD*, *Native FD*, *Alien richness*, *Alien PD*, and *Alien FD*), and *Latitude* was converted as an
228 absolute value. Finally, we scaled all the variables ($\mu = 0$, $\sigma = 1$) to get comparable
229 effects.

230 For each endogenous variable (i.e., a variable supposedly explained by one or several
231 exogenous variables), we derived a linear mixed-effects model, including the zoogeographic
232 region as a random effect. The SEMs were then built upon these individual linear mixed-
233 effects models (*psem* function from *piecewiseSEM* package). We evaluated SEM fit using
234 Fisher's C statistic and considered it incomplete if the associated P-value was below 0.05. In
235 the case of an incomplete model, we recursively added potential missing paths (i.e., paths that
236 were not included in the initial model because lacking any causal relationship), based on
237 pairwise tests of directed separation on unstated relationships between variables in the *a priori*
238 model (*dSep* function from *piecewiseSEM* package). The four final models had a Fisher's C of
239 41.5 ($p = 0.24$) for FD, 43.6 ($p=0.18$) for PD, 50.8 ($p=0.12$) for SES-FD, and 40.9 ($p=0.19$)
240 for SES-PD. They contained 51 paths between explanatory and endogenous variables, and a
241 correlated error was specified between anthropogenic variables and native biotic variables.

242 We analyzed the results of the models by retrieving the R^2 associated with each
243 endogenous variable. As we used linear mixed-effects models, R^2 values were decomposed
244 into marginal (accounting for fixed effects) and conditional (accounting for both fixed and
245 random effects) R^2 . Finally, we derived the explanatory variables' direct, indirect, and total
246 effects on the response variables by using a non-parametric bootstrapping method ($n = 10,000$
247 samples) through the *bootEff* function from the *semEff* package (Murphy 2022).

248

249 **RESULTS**

250 **Functional and phylogenetic diversities of alien birds**

251 Functional and phylogenetic diversities of alien birds varied markedly across islands
252 worldwide (Fig. 1). The Novozelandic and Hawaiian regions harbored islands with the higher
253 FD and PD values, while alien birds in Saharo-Arabian, Indo-Malayan or Sino-Japanese
254 regions had a lower diversity (Fig. 1A). We also observed a strong spatial variation of FD and
255 PD values within regions among islands (e.g., Papua-Melanesian and Novozelandic) (Fig. 1B,
256 C). Overall, FD and PD of alien birds were highly correlated across all islands (Pearson's
257 correlation = 0.95, $p < 0.001$, Fig. S2A), but considering each region separately, we found
258 varying shapes of relationships between both metrics (Fig. S2B). Both diversity facets were
259 also highly correlated with alien taxonomic richness (Pearson's correlation = 0.94 for FD,
260 0.96 for PD). After controlling for alien taxonomic richness, we found that both SES-FD and
261 SES-PD were significantly smaller than zero (Student tests, respectively, mean = -0.92, $t = -$
262 33.6, $p < 0.001$; mean = -0.89, $t = -13.6$, $p < 0.001$). Thus, on average and especially in the
263 Novozelandic region, alien assemblages were less phylogenetically and functionally
264 diversified than expected from random assemblages of birds with the same taxonomic
265 diversity (Fig. 2; Fig. S3). By contrast, assemblages from the Oriental, Panamanian and

266 Saharo-Arabian regions had positive SES-PD values close to zero, representing a PD that was
267 nearly expected given the taxonomic richness (Fig. 2).

268 **Drivers of alien diversities**

269 Six variables had a significant total effect on alien FD (R^2 marginal = 0.60), namely alien
270 taxonomic richness, native taxonomic richness, static habitat modification, human
271 connectivity, elevation, and distance to continent (confidence intervals (CI) at 95% not
272 crossing zero, Fig. 3A, 4A). Eight variables had a significant total effect on alien PD (R^2
273 marginal = 0.90), namely alien taxonomic richness, native PD, human connectivity,
274 population size, GDP, surrounding landmass, distance to continent, and area (Fig. 3B, 4B).

275 Overall, alien taxonomic richness had the largest total effect on alien FD and PD
276 (mean total effect = 0.58 and 0.79, respectively) followed by the geographic context (mean
277 combined total effect = 0.40 and 0.57), the anthropogenic context (mean combined total effect
278 = 0.39 and 0.44) and, to a lesser extent, by the biotic context (mean combined total effect =
279 0.15 and 0.15) (Table S4). Moreover, when anthropogenic variables were included in the
280 SEM, the R^2 of alien FD and PD were identical but the R^2 of alien taxonomic richness
281 increased by 12 to 15% compared with the SEM with biogeographical variables only (Fig.
282 S4).

283 Alien taxonomic richness had a substantial direct effect on both alien FD (95% CI:
284 [0.46; 0.72]; Fig. 3A, 4A) and PD (95% CI: [0.76; 0.90]; Fig. 3B, 4B). By contrast, native
285 taxonomic richness had a total negative effect on alien FD (95% CI: [-0.22; -0.04]; Fig. 3A)
286 and a weak negative effect on alien PD (95% CI: [-0.22; 0.04]; Fig. 3B). Moreover, native PD
287 had a moderate direct negative effect on alien PD (95% CI: [-0.20; -0.03]; Fig. 3B), whereas
288 native FD had no significant effect on alien FD (Fig. 3A).

289 Regarding anthropogenic drivers, connectivity, population size, and GDP had a total
290 positive effect on alien PD mediated by positive effects on alien taxonomic richness. By
291 contrast, connectivity and static habitat modification positively affected alien FD (Figs. 3, 4).
292 Human connectivity was the anthropogenic driver with the most considerable total effect on
293 both alien FD and PD (95% CI: [0.04; 0.23] and [0.04; 0.23], respectively; Figs. 3, 4). When
294 considering colonization pressure (and time since first introduction) on the subset of 96 (83)
295 informed islands for this variable, colonization pressure had the strongest total effect on alien
296 FD and PD among anthropogenic drivers (Fig. S5), while time since first introduction had no
297 effect (Fig. S6). The presence of colonization pressure in the predictors led to a decrease in
298 the importance of the other anthropogenic effects compared to models without it, for both
299 alien FD and PD. However, confidence intervals largely overlapped in the two types of
300 models for all predictors.

301 Biogeographic variables posed different effects on alien FD and PD. Distance to
302 continent had a positive direct effect on alien taxonomic richness and a positive indirect effect
303 on both alien FD and PD (95% CI: [0.11; 0.30] and [0.10; 0.28], respectively; Figs. 3, 4).
304 Island area had a total positive effect on alien PD (95% CI: [0.06; 0.17]), but not on alien FD,
305 while island elevation had a positive direct effect on alien FD (95% CI: [0.08; 0.22]), but not
306 on alien PD (Fig. 3). The total effect of biogeographic variables was similar in models
307 accounting for colonization pressure. Moreover, the zoogeographic regions included as a
308 random effect increased the explanatory power of the SEMs (conditional R^2 : 0.74 for FD;
309 0.93 for PD).

310 The final models obtained for SES strongly differed from the ones obtained for FD and
311 PD values. While alien taxonomic richness remained a major driver of SES-FD and SES-PD
312 (so when controlled by taxonomic richness), it had a strong negative direct effect on both
313 SES-FD and SES-PD (Fig. 3). This means that alien bird assemblages with higher richness

314 are more likely to be phylogenetically and functionally clustered. Anthropogenic variables
315 had a more substantial influence on the SES than biogeographic variables (Fig. 3), with
316 evidence of a total negative effect of human connectivity on SES-FD and SES-PD and of
317 static modification on SES-FD. Among biogeographic variables, only island area showed
318 moderate evidence of a total negative effect on SES-FD (Fig. 3).

319

320 **DISCUSSION**

321 **Global spatial variation of alien diversities**

322 Our study provided important insights on the global spatial variation of alien diversities.
323 Relative values of alien FD and PD varied across and within regions. The Novozelandic and
324 Hawaiian regions harbored the highest levels of alien bird FD and PD, as well as some islands
325 of Papua-Melanesia. Previous studies have pointed out the specificity of the Hawaiian
326 archipelago related to its extremely high richness of alien plant species (Denslow *et al.* 2009;
327 Wohlwend *et al.* 2021), as well as the long history of New Zealand for dealing with biological
328 invasions (Simberloff 2019). Those regions are well-known hotspots of invasions regarding
329 taxonomic (Bellard *et al.* 2017; Dawson *et al.* 2017) and phylogenetic diversity (Baiser *et al.*
330 2018), but this is the first time it is also demonstrated for the different facets of diversity at the
331 global scale. Looking at SES, we found that islands from the Novozelandic region bear
332 assemblages of aliens with less phylogenetic diversity than expected from a random
333 community assembly, as highlighted by Baiser *et al.* (2018), but also a poorer functional
334 diversity. This pattern can be explained by the invasion history of those islands for which
335 most of their exotic species were imported from Britain and belong to few families
336 (Blackburn & Duncan 2001; Baiser *et al.* 2018). Moreover, some hotspots of alien bird FD

337 and PD were not previously highlighted when focusing only on taxonomic diversity,
338 including some islands of the Papua-Melanesian and Panamanian regions.

339

340 **The relative contribution of biogeographic, anthropogenic and biotic factors**

341 While alien taxonomic richness most strongly affected alien FD and PD, both anthropogenic
342 and biogeographic contexts also had remarkable and comparable total effects on these
343 diversities. Anthropogenic variables exceed by far the effects of biogeographic variables
344 when considering SES-FD and SES-PD. This revealed that besides classical biogeographic
345 variables, the anthropogenic context is highly important to understand the absolute (FD, PD)
346 and relative (SES-FD, SES-PD) richness of birds. Therefore, neglecting anthropogenic
347 variables significantly decreased our ability to explain the observed alien diversity on islands.

348

349 **Including anthropogenic factors to fully address the diversity patterns of alien species**

350 Our results suggest a substantial effect of anthropogenic factors on alien FD and PD, which
351 have also been documented for alien species from several taxa on continents (Pyšek *et al.*
352 2010). First, we found a strong positive effect of human connectivity on absolute and relative
353 alien bird richness, indirectly affecting alien FD, PD, SES-FD and SES-PD. Human
354 connectivity reshapes environmental barriers between isolated places, the distance to a human
355 facility that introduces species on islands being a primary determinant of alien distribution
356 (Gleditsch *et al.* 2023). Human connectivity is also a proxy of colonization pressure, a critical
357 factor in alien taxonomic richness (Blackburn *et al.* 2020). Indeed, when included, we found
358 that colonization pressure was the most important anthropogenic factor in the SEMs
359 contributing to alien FD and PD, and it reduced the direct effect of connectivity on alien
360 species richness and thus the indirect effect on alien PD (Figure S5).

361 Second, habitat modification positively influenced alien taxonomic richness and
362 indirectly alien FD. Habitats with stronger human activities are considered more favorable for
363 alien species establishment, partly because alien species do not have to compete with native
364 species that are excluded from those disturbed habitats (Sol *et al.* 2022). Moreover, aliens
365 adapt more to human-associated habitats due to their proximity and evolution with societies.
366 The effect of habitat modification on FD rather than PD supports the idea that alien species
367 exploit environmental niches in disturbed environments that differ from native ones (Soares *et*
368 *al.* 2021).

369 We also observed contrasting effects of specific factors on SES-PD and SES-FD,
370 which were negatively affected by static habitat modification and connectivity. This suggests
371 that apart from increasing the number of alien species, a high human presence implies a
372 clustering of alien species in terms of traits and evolutionary history. At some point, with the
373 introduction of alien birds, a plateau is reached for alien FD and PD, and the supplemental
374 addition of species does not lead to further functional or phylogenetic novelties. This also
375 suggests that humans tend to bring the same type of species in terms of evolutionary history
376 and ecological characteristics. Combined with native extinctions, alien species introductions
377 favor the global homogenization of insular biota on the multiple facets of diversity (Sobral *et*
378 *al.* 2016; Baiser *et al.* 2018; Sayol *et al.* 2021; Soares *et al.* 2022). The introduction of alien
379 species might thus reinforce the observed FD-area non-linear relationship (i.e., the increase in
380 area and native species richness does not imply a proportional increase in trait space), with
381 even more species clustered in already well-represented parts of the trait space (Karadimou *et*
382 *al.* 2016; Matthews *et al.* 2023).

383

384 **Native communities as a weak biotic filter to alien diversities**

385 Our study confirms that the biotic context (native taxonomic richness or their associated FD
386 and PD) has a weaker influence on invasion success than anthropogenic or biogeographic
387 contexts at this scale (Redding *et al.* 2019). For instance, the SEM analysis showed that native
388 taxonomic richness had a direct positive effect on alien PD counterbalanced by an indirect
389 negative effect through native PD. We also found a negative effect of native SES-PD on alien
390 SES-PD (and a weak negative effect on alien SES-FD), suggesting that when native species
391 are evolutionarily or ecologically clustered (negative SES), alien species are more widespread
392 across the tree of life and trait space (positive SES). Despite previous works showing
393 evidence of filters exerted by native communities on alien ones (Jeschke & Heger 2018), our
394 study confirms the importance of abiotic and anthropogenic factors for shaping alien
395 diversities.

396

397 **Biogeographic factors continue to drive alien diversities**

398 Distance to the closest continent was the strongest biogeographic driver explaining alien FD
399 and PD, and also negatively affected alien SES-FD and SES-PD. Remote islands tend to
400 contain more alien species than closer islands following a reverse species-isolation
401 relationship (SIR), and thus a more diverse alien assemblage regarding traits or evolutionary
402 history. Our results are consistent with previous findings for other groups like plants or
403 reptiles (Blackburn *et al.* 2016; Moser *et al.* 2018; Gleditsch *et al.* 2023). Interestingly, this
404 pattern has never been confirmed for alien birds, with contrasting effects of remoteness on
405 alien bird richness, either a negative indirect effect through native taxonomic richness
406 (Blackburn *et al.* 2016), no effect (Moser *et al.* 2018), or a positive effect (Blackburn *et al.*
407 2008). We can confirm that reverse SIR is also validated for alien birds globally, thanks to the
408 SEM analysis. For native birds, the original SIR was verified: taxonomic richness on islands
409 declined with distance to continent (Fig. S7). The negative indirect effect of distance to

410 continent on alien SES-FD and SES-PD suggests that remote islands with higher alien species
411 richness also tend to contain more redundant species in terms of traits or evolutionary history.
412 Yet we also found a positive direct effect of distance to continent on alien SES-FD, meaning
413 that, independently of species richness, islands farther from continents favor more diverse
414 traits. This could be due either to humans that select birds with different characteristics for
415 various purposes, or to a high competition with congeners on remote islands, favoring the
416 establishment of more diverse traits.

417 We additionally found that both surrounding land mass and area positively affected
418 alien PD indirectly through alien taxonomic richness but had no total effect on alien FD. The
419 overall effect of island area was weak, suggesting that this is not a primary determinant in
420 alien bird diversities, contrasting with previous studies (Blackburn *et al.* 2008, 2016). The
421 log-log species-area relationship stands for alien species in many taxa, such as plants (Rojas-
422 Sandoval *et al.* 2020) and insects (Mally *et al.* 2022). Still, the slope of the relationship is
423 steeper than for native species with anthropogenic variables complementing the effect of
424 biogeographic ones (Rojas-Sandoval *et al.* 2020), the available area for alien species to invade
425 islands being non-saturated (Guo *et al.* 2020). Another explanation is that both human
426 population size and connectivity increase with island area as well as colonization pressure.
427 Thus, the effect of island area on alien diversities is masked by the effect of anthropogenic
428 variables (Blackburn *et al.* 2008; Moser *et al.* 2018), while area has a direct effect for native
429 diversities (Fig. S7). Our study sheds light on the importance of mediators to explain the
430 impact of biogeographic variables on alien diversities. Indeed, direct effects of biogeographic
431 drivers on birds FD, PD, SES-FD, and SES-PD were often non-significant, and their total
432 effects were related to indirect effects mediated by anthropogenic and biotic drivers.

433

434 **Limitations**

435 Although our study provided new insights on biological invasions on islands, there are
436 limitations to be acknowledged. First, while the GAVIA database is the most comprehensive
437 source for alien bird distributions worldwide, it is not regularly being updated, and for ten
438 species known to have an established population on an oceanic island, the alien range map
439 was not available. We were able to retrieve the colonization pressure only for 96 out of 407
440 islands, partly limiting our analyses using this variable. Yet, we could prove it was a critical
441 factor for explaining alien taxonomic richness, but which did not have any direct effect on
442 alien FD or PD (Supplementary text, Fig. S5). Second, SEM is usually designed for causal
443 relationships. However, it is unlikely to precisely get the direct links between predictors at
444 such a spatial scale, forcing us to deal with many latent variables. As such, model
445 construction led to the inclusion of a correlated error between the human-related variables and
446 the native biotic context, based on two a priori hypotheses: (i) expert-derived maps for
447 calculating native richness tend to overestimate species presence on islands, scaling with
448 human presence (Nori *et al.* 2022); (ii) islands with more resources and thus with a higher
449 native richness are more attractive to humans, resulting in an increased human presence (Luck
450 2007).

451

452 **Conclusion**

453 We found that humans provoked drastic changes in ecosystem compositions across all facets
454 of diversity. Our study allowed us to identify the drivers of multiple facets of alien diversity
455 as a first step towards anticipating the risk posed by biological invasions. We believe that
456 examining new insular communities, thus rethinking the island biogeography in the
457 Anthropocene, is of primary interest for forecasting the impacts of other global threats on
458 islands, such as climate or land-use changes.

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465

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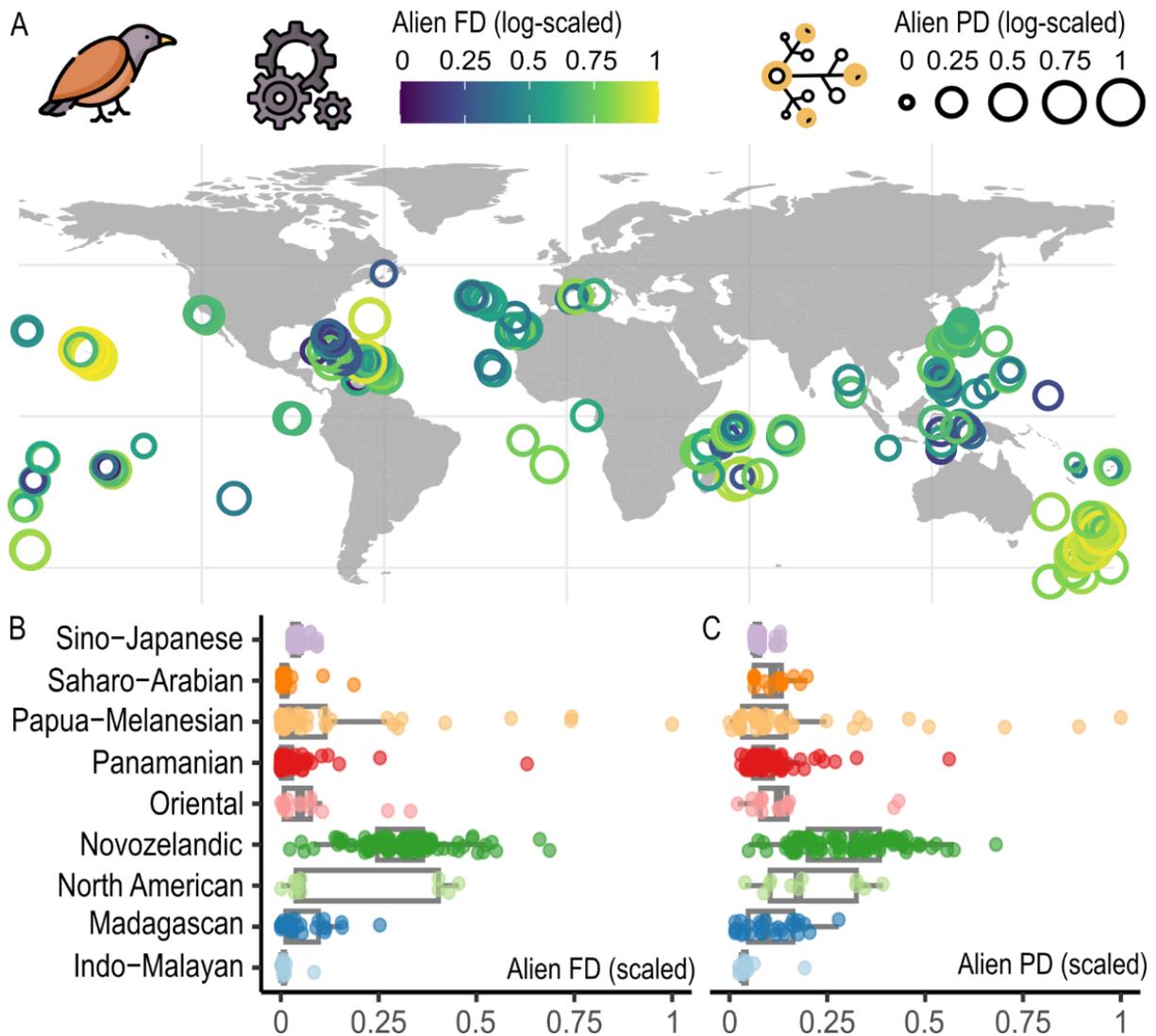
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628

629 FIGURES AND TABLES

630 **Table 1. Hypotheses on the factors driving alien bird diversities (i.e., SR: species richness; FD: functional richness; PD: phylogenetic**
631 **richness)**

Response	Driver	Variable	Hypothesized relationship	Source
Alien FD, PD	Alien taxonomic richness	Alien SR	(+) Alien FD and PD are partially dependent on alien SR	(Faith 1992; Mouchet <i>et al.</i> 2010)
Alien SES-FD, SES-PD	Alien taxonomic richness	Alien SR	(+/-) Depending on the assembly rules, species close to each other can be favored by habitat filtering or disfavored to limit competition	(Tilman 2004; Mouchet <i>et al.</i> 2010)
Alien SR, FD	Area	Area	(+) Species-area relationship applied to aliens (alien SR) (+) FD-area relationship posits that FD will increase with area but will reach a plateau because of functional redundancy between species (alien FD)	(MacArthur & Wilson 1967; Case 1996; Blackburn <i>et al.</i> 2008, 2016)
Alien FD, PD	Elevation	Elevation	(+) Habitat heterogeneity promotes the establishment of species with distinct traits	(Case 1996; Walsh <i>et al.</i> 2012)
Alien SR	Latitude	Latitude	(+) Alien taxonomic richness higher toward temperate zones	(Dyer <i>et al.</i> 2020)
Alien SR	Isolation	Distance to continent; Surrounding landmass	(+) Isolated islands more prone to alien species introduction and establishment	(Moser <i>et al.</i> 2018)
Alien SR, FD, PD	Native biota	Native taxonomic richness; Native FD; Native PD	(-) <i>Biotic resistance</i> hypothesis (+) <i>Rich-get-richer</i> hypothesis	(Levine & D'Antonio 1999; Stohlgren <i>et al.</i> 2006; Dyer <i>et al.</i> 2017)
Alien SR	Colonization pressure	Alien CP	(+) A high number of introduced species promotes a high number of established species	(Dyer <i>et al.</i> 2017a; Blackburn <i>et al.</i> 2020)
Alien SR, FD, PD	Human exchanges and intensity of presence	GDP; Population size; Human connectivity	(+) Colonization pressure increases with human exchanges which are driven by population density, tourism, island accessibility and wealth	(Dawson <i>et al.</i> 2017; Dyer <i>et al.</i> 2017a)
Alien SR, FD	Habitat modification	Static habitat modification; Change habitat modification	(+) Alien species thrive in disturbed habitats (alien SR) (+) Disturbed habitats offer new niches and favor new species traits (alien FD)	(Sánchez-Ortiz <i>et al.</i> 2020)

632



633

634 **Figure 1. Global association between functional and phylogenetic diversities of alien birds on**

635 **oceanic islands.** (A) Spatial variation of functional diversity (Alien FD, color of the rings) and

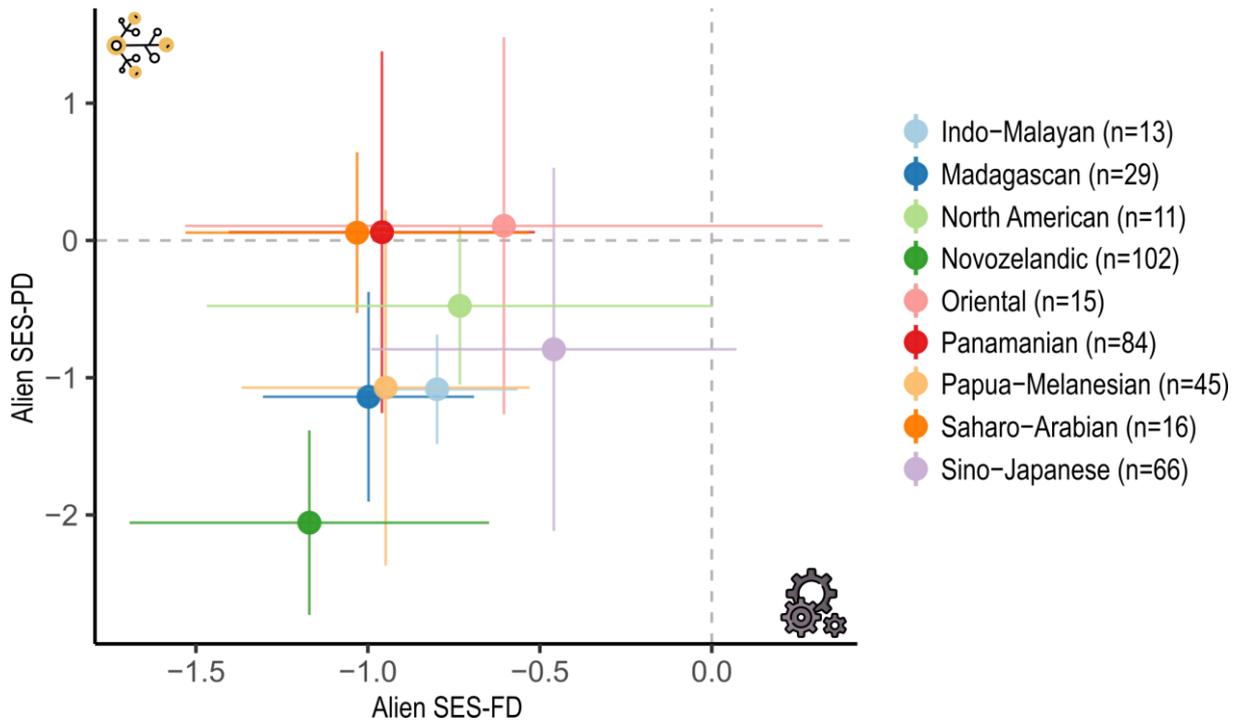
636 phylogenetic diversity (Alien PD, size of the rings) of alien birds on the 407 islands. Values of alien

637 FD (B) and alien PD (C) for islands within each region. Only regions with more than ten islands are

638 shown.

639

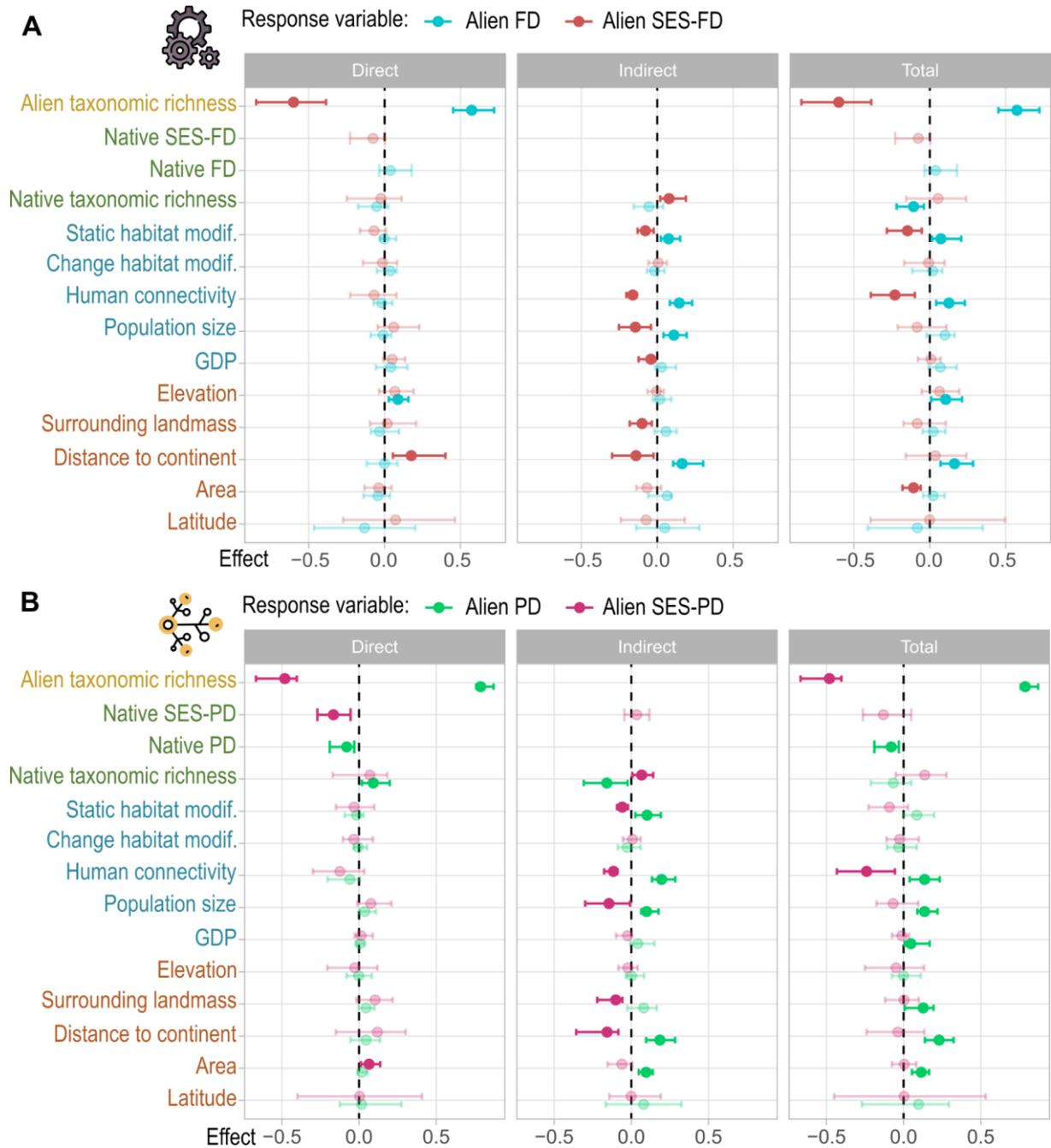
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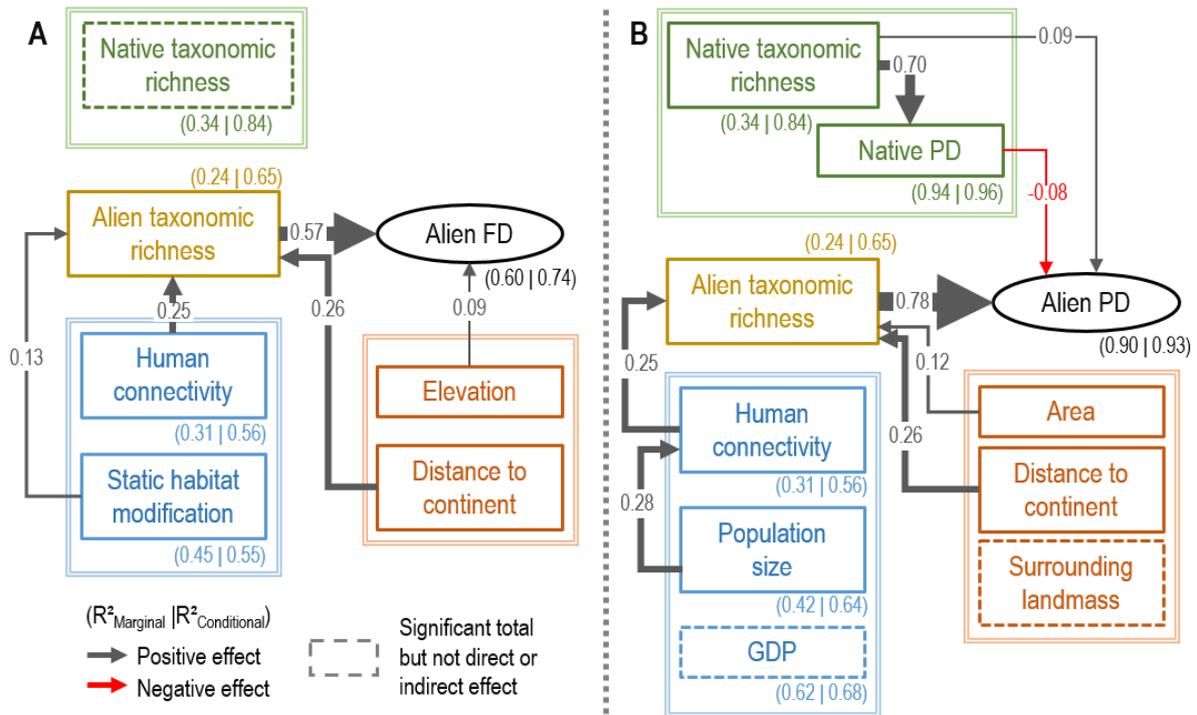
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642 **Figure 2. Deviations of functional and phylogenetic diversities from taxonomic diversity on**
643 **islands.** Mean standardized effect sizes (SES) of functional and phylogenetic diversities across all
644 islands separated by region. The points represent the mean SES-FD and SES-PD per region, and
645 horizontal and vertical bars represent the standard deviation of SES-FD and SES-PD within each
646 region, respectively. Only regions with more than ten islands are shown. Among the 407 islands,
647 respectively 15 and 100 islands had SES-FD and SES-PD below -1.96, which is the threshold for
648 assemblages being significantly more clustered than expected by chance. 3 islands had SES-PD above
649 1.96, meaning their alien assemblages were significantly more dispersed than expected by chance.

650



651
 652 **Figure 3. Direct, indirect, and total effects of all explanatory variables on (A) functional diversity**
 653 **(FD; and its associated SES) and (B) phylogenetic diversity (PD, and its associated SES) of alien**
 654 **birds.** The zoogeographic region for birds of each island was integrated as a random effect in all
 655 relationships. Dots represent standardized mean effects, and error bars depict 95% confidence intervals
 656 (shaded colors represent intervals crossing zero). Variable names are colored following their context:
 657 biotic (green), human (blue), and biogeographical (orange).
 658



659

660 **Figure 4. Schematic path diagram representing causal relationships between the geological,**

661 **human, and biotic insular context and the alien functional diversity (FD, panel A) and**

662 **phylogenetic diversity (PD; panel B). Line width is scaled to the absolute value of effects.**

663 Standardized R^2 coefficients are specified in brackets for each endogenous variable. Variable names

664 are colored following their context: biotic (green), human (blue), and biogeographical (orange). We

665 only represented the effects for variables with a significant total effect on FD or PD. Dashed lines

666 represent variables with a significant total effect (resulting from adding direct and multiple indirect

667 effects through other variables), but no direct or indirect significant effect. All links between

668 endogenous variables are depicted in Fig. S7.