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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
5 **Authors:**

6 Clara Marino^{1*} (claramarino665@gmail.com)

7 Lysandre Journiac^{1*} (lysandre.journiac@edu.mnhn.fr)

8 Chunlong Liu² (liuchunlong@ouc.edu.cn)

9 Jonathan M. Jeschke^{3,4,5} (jonathan.jeschke@gmx.net)

10 Céline Bellard¹ (celine.bellard@universite-paris-saclay.fr)

11 **Affiliations:**

12 ¹ Université Paris-Saclay, CNRS, AgroParisTech, Ecologie Systématique Evolution, Gif-sur-
13 Yvette, France

14 ² The Key Laboratory of Mariculture, Ministry of Education, College of Fisheries, Ocean
15 University of China, Qingdao 266003, China

16 ³ Leibniz Institute of Freshwater Ecology and Inland Fisheries (IGB), Berlin, Germany

17 ⁴ Institute of Biology, Freie Universität Berlin, Berlin, Germany

18 ⁵ Berlin-Brandenburg Institute of Advanced Biodiversity Research (BBIB), Berlin, Germany

19 *Authors contributed equally

20 **Corresponding author:** Clara Marino (claramarino665@gmail.com)

21

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

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

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

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52 **The Anthropocene biogeography of alien birds: drivers of their functional**
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54

55 Clara Marino*, Lysandre Journiac*, Chunlong Liu, Jonathan M. Jeschke, Céline Bellard

56 *Authors contributed equally

57 Corresponding author: Clara Marino

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. Using data on alien and native birds of 407 oceanic islands worldwide, we built
63 structural equation models to evaluate the direct and indirect influence of biotic, geographic,
64 and anthropogenic contexts on the alien birds' functional (FD) and phylogenetic diversity
65 (PD). We found that alien taxonomic richness was the main predictor of both diversities.
66 Anthropogenic factors, including colonization pressure, associated with classic
67 biogeographical variables also strongly influenced alien FD and PD. Specifically, habitat
68 modification and human connectivity markedly drove alien FD, whereas human population
69 size, gross domestic product, and native PD were crucial at explaining alien PD. Our findings
70 suggest that humans not only shape taxonomic richness but also other facets of alien diversity
71 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 for both
84 natives and aliens) (Baiser *et al.* 2018; Blackburn *et al.* 2021; Matthews *et al.* 2023).
85 However, the classic species-isolation relationship (i.e., remote islands contain less species)
86 has weakened due to a positive species-economic isolation relationship for aliens (Helmus *et*
87 *al.* 2014; Moser *et al.* 2018).

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

96 Functional diversity represents the set of ecological strategies hosted by an assemblage
97 (Mouillot *et al.* 2013), reflecting the ecological assembly rules of this assemblage (Mouchet *et*
98 *al.* 2010). By studying alien FD, we can determine how alien species mediate their response
99 to disturbances and contribute to ecosystem functioning given they may replace native species
100 (Soares *et al.* 2022). Phylogenetic diversity (PD) captures the evolutionary history of species,
101 their features and future options (Faith 1992; Purvis *et al.* 2019). Because alien species are
102 introduced by humans for specific purposes (Dyer *et al.* 2017a), we can expect that alien PD
103 is not only affected by biogeographical factors but also by human ones, and mediated by
104 native biota. By identifying the factors determining alien FD and PD, we could anticipate the
105 fate of insular diversity in a disturbed environment and provide guidelines to effective
106 conservation strategies. Our aim here is to provide the first global evaluation of the drivers of
107 FD and PD patterns for alien birds, in one single analytical framework.

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

120 Here, we investigate the spatial pattern of FD and PD for alien birds and their drivers
121 on 407 oceanic islands worldwide. Notably, we aim to test how 15 island contextual variables
122 related to the geographic (e.g., area, distance to mainland, elevation), biotic (i.e., taxonomic
123 richness, FD and PD of native birds), and anthropogenic (e.g., human population size,
124 connectivity, habitat modification, colonization pressure) contexts shape alien bird FD and
125 PD. We expect that species richness of alien assemblages will partially drive alien FD and
126 PD, but we seek to determine the direct effects of insular contexts on alien FD and PD from
127 their indirect effects through species richness. We further explore how critical the
128 anthropogenic context is compared to the biogeographic context to explain alien diversities.
129 To investigate these effects, we apply structural equation models (SEMs) by defining *a priori*
130 directional links between the contextual variables and alien diversities (Table 1; Table S1
131 describes the links connecting contextual variables). Finally, we calculate the deviations of
132 FD and PD from expected values given the taxonomic richness, allowing us to detect the
133 drivers of the relative variation of FD and PD beyond taxonomic richness (i.e., standardized
134 effect size (SES) of FD and PD) (Bach *et al.* 2022).

135 **MATERIAL AND METHODS**

136 **Alien bird diversities on oceanic islands**

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

143 islands, for a total of 188 alien bird species), which was the minimum number of species to
144 calculate FD on one island.

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

162 *Deviation from taxonomic diversity.* As we expect both FD and PD depend on alien
163 taxonomic richness, we also computed standardized effect size indices (SES-FD and SES-PD)
164 following Bach *et al.* (2022) to exclude the effect of alien taxonomic richness from these
165 indices and explore the drivers of the relative variation of FD and PD. To do so, we performed
166 null models using a matrix swap randomization by recalculating FD and PD (on 100
167 phylogenetic trees) on 100 randomly generated island-species matrices, while keeping a

168 constant number of species per assemblage. These random assemblages were simulated on the
169 global pool of birds with each species having the same chance to become alien somewhere.

170 SES indices were calculated as $SES = \frac{\text{observed value} - \text{mean}(\text{simulated values})}{\text{standard deviation}(\text{simulated values})}$. Negative values of

171 SES indicate a lower value FD or PD than expected by chance for an equal taxonomic
172 richness and, representing a more clustered assemblage in terms of traits or evolutionary
173 history.

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

175 *Geographic variables.* We extracted the geographic variables for all islands from Weigelt *et*
176 *al.* (2013). We retrieved three variables related to habitat heterogeneity (i.e., *Latitude*, *Area*,
177 *Elevation*) and two variables linked to isolation (i.e., *Distance to the continent* and
178 *Surrounding land mass*). Since native and alien bird diversities vary regarding geographic
179 regions (Holt *et al.* 2013; Dyer *et al.* 2017a), we also classified each island into the
180 corresponding zoogeographic region delineated by Holt *et al.* (2013). For islands without
181 information on the zoogeographic region (n = 260), we attributed them to the closest region
182 (Fig. S1).

183 *Biotic variables.* To account for the insular biotic context, we calculated the taxonomic
184 richness of native birds for each island by computing the spatial overlap between the native
185 ranges of all birds in the world (Birdlife International 2020) and the islands. We also
186 calculated native FD and PD following the same methodology as for alien species.

187 *Anthropogenic variables.* We compiled seven variables associated with the anthropogenic
188 context of each island. *Population size* was calculated as the sum of human population counts
189 in the area of each island using the CIESIN database (2018). *Gross domestic product (GDP)*
190 was calculated as the sum of all GDP values in the cells falling into each island using the data
191 from Wang & Sun (2022). *Human connectivity* was calculated by mirroring the surrounding

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

203 ***A priori hypotheses***

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

216 **Statistical analyses**

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

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

231 For each endogenous variable (i.e., a variable supposedly explained by one or several
232 exogenous variables), we derived a linear mixed-effects model, including the zoogeographic
233 region as a random effect. The SEMs were then built upon these individual linear mixed-
234 effects models (*psem* function from *piecewiseSEM* package). We evaluated SEM fit using
235 Fisher's C statistic and considered it incomplete if the associated P-value was below 0.05. In
236 the case of an incomplete model, we recursively added potential missing paths (i.e., paths that
237 were not included in the initial model because lacking any causal relationship), based on
238 pairwise tests of directed separation on unstated relationships between variables in the *a priori*
239 model (*dSep* function from *piecewiseSEM* package). The four final models had a Fisher's C of
240 41.5 ($p = 0.24$) for FD, 43.6 ($p=0.18$) for PD, 51.5 ($p=0.11$) for SES-FD, and 41.7 ($p=0.17$)

241 for SES-PD. They contained 51 paths between explanatory and endogenous variables, and a
242 correlated error was specified between anthropogenic variables and native biotic variables.
243 We analyzed the results of the models by retrieving the R^2 associated with each endogenous
244 variable. As we used linear mixed-effects models, R^2 values were decomposed into marginal
245 (accounting for fixed effects) and conditional (accounting for both fixed and random effects)
246 R^2 . Finally, we derived the explanatory variables' direct, indirect, and total effects on the
247 response variables by using a non-parametric bootstrapping method ($n = 10,000$ samples)
248 through the *bootEff* function from the *semEff* package (Murphy 2022).

249

250 **RESULTS**

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

252 Functional and phylogenetic diversities of alien birds varied markedly across islands
253 worldwide (Fig. 1). The Novozelandic and Hawaiian regions harbored islands with the higher
254 FD and PD values, while alien birds in Saharo-Arabian, Indo-Malayan or Sino-Japanese
255 regions were less diversified (Fig. 1A). We also observed a strong spatial variation of FD and
256 PD values within regions among islands (e.g., Papua-Melanesian and Novozelandic) (Fig. 1B,
257 C). Overall, FD and PD of alien birds were highly correlated across all islands (Pearson's
258 correlation = 0.95, $p < 0.001$, Fig. S2A), but considering each region separately, we found
259 varying shapes of relationships between both metrics (Fig. S2B). Both diversity facets were
260 also highly correlated with alien taxonomic richness (Pearson's correlation = 0.94 for FD,
261 0.96 for PD). After controlling for alien taxonomic richness, we found that both SES-FD and
262 SES-PD were significantly smaller than zero (Student tests, respectively, mean = -0.70, $t = -$
263 11.9, $p < 0.001$; mean = -1.01, $t = -29.1$, $p < 0.001$). Thus, on average and especially in the
264 Novozelandic region, alien assemblages were less phylogenetically and functionally
265 diversified than expected from random assemblages of birds with the same taxonomic

266 diversity (Fig. 2; Fig. S3). By contrast, assemblages from the Oriental, Panamanian and
267 Saharo-Arabian regions had positive SES-PD values close to zero, representing a PD that was
268 nearly expected given the taxonomic richness (Fig. 2).

269 **Drivers of alien diversities**

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

276 Overall, alien taxonomic richness had the largest total effect on alien FD and PD
277 (mean total effect = 0.58 and 0.79, respectively) followed by the geographic context (mean
278 combined total effect = 0.40 and 0.57), the anthropogenic context (mean combined total effect
279 = 0.39 and 0.44) and, to a lesser extent, by the biotic context (mean combined total effect =
280 0.15 and 0.15) (Table S2). Moreover, when anthropogenic variables were included in the
281 SEM, the R^2 of alien FD and PD were identical but the R^2 of alien taxonomic richness
282 increased by 12 to 15% compared with the SEM with biogeographical variables only (Fig.
283 S4).

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

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

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

309 The final models obtained for SES strongly differed from the ones obtained for FD and
310 PD values. While alien taxonomic richness remained a major driver of SES-FD and PD (so
311 when controlled by taxonomic richness), it had a strong negative direct effect on both alien
312 SES-FD and SES-PD (Fig. 3). This means that alien bird assemblages with higher richness
313 are more likely to be phylogenetically and functionally clustered. Anthropogenic variables
314 had a more substantial influence on the SES than biogeographic variables (Fig. 3). Among

315 biogeographic variables, only island area showed moderate evidence of a total negative effect
316 on alien SES-FD (Fig. 3). Distance to continent had a negative indirect effect on both SES-PD
317 and SES-FD, but a positive direct effect counterbalanced this effect.

318

319 **DISCUSSION**

320 **Global spatial variation of alien diversities**

321 Our study provided important insights on the global spatial variation of alien diversities.
322 Relative values of alien FD and PD varied across and within regions. The Novozelandic and
323 Hawaiian regions harbored the highest levels of alien bird FD and PD, as well as some islands
324 of Papua-Melanesia. Previous studies have pointed out the specificity of the Hawaiian
325 archipelago related to its extremely high richness of alien plant species (Denslow *et al.* 2009;
326 Wohlwend *et al.* 2021), as well as the long history of New Zealand for dealing with biological
327 invasions (Simberloff 2019). Those regions are well-known hotspots of invasions regarding
328 taxonomic (Bellard *et al.* 2017; Dawson *et al.* 2017) and phylogenetic diversity (Baiser *et al.*
329 2018), but this is the first time it is also demonstrated for the different facets of diversity at the
330 global scale. Looking at SES, we found that islands from the Novozelandic region bear
331 assemblages of aliens with less phylogenetic diversity than expected from a random
332 community assembly, as highlighted by Baiser *et al.* (2018), but also a poorer functional
333 diversity. This pattern can be explained by the invasion history of those islands for which
334 most of their exotic species were imported from Britain and belong to few families
335 (Blackburn & Duncan 2001; Baiser *et al.* 2018). Moreover, some hotspots of alien bird FD
336 and PD were not previously highlighted when focusing only on taxonomic diversity,
337 including some islands of the Papua-Melanesian and Panamanian regions.

338

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

340 While alien taxonomic richness most strongly affected alien FD and PD, both anthropogenic
341 and biogeographic contexts also had remarkable and comparable total effects on these
342 diversities. Anthropogenic variables exceed by far the effects of biogeographic variables
343 when considering SES-FD and SES-PD. This revealed that besides classical biogeographic
344 variables, the anthropogenic context is highly important to understand the absolute (FD, PD)
345 and relative (SES-FD, SES-PD) richness of birds. Therefore, neglecting anthropogenic
346 variables significantly decreased our ability to explain the observed alien diversity on islands
347 (R^2 of alien taxonomic richness reduced by 12% when not including anthropogenic variables).

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 both negatively affected by static habitat modification and connectivity. This
371 suggests that apart from increasing the number of alien species, a high human presence
372 implies a clustering of alien species in terms of traits and evolutionary history. At some point,
373 with the introduction of alien birds, a plateau is reached for alien FD and PD, and the
374 supplemental addition of species does not lead to further functional or phylogenetic novelties.
375 This also suggest that human tend to bring the same type of species in terms of evolutionary
376 history and ecological characteristics. Combined with native extinctions, alien species
377 introductions favor the global homogenization of insular biota on the multiple facets of
378 diversity (Sobral *et al.* 2016; Baiser *et al.* 2018; Sayol *et al.* 2021; Soares *et al.* 2022). The
379 introduction of alien species might thus reinforce the observed FD-area non-linear
380 relationship (i.e., the increase in area and native species richness does not imply a
381 proportional increase in trait space), with even more species clustered in already well-
382 represented parts of the trait space (Karadimou *et 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 spatial scale (Redding *et al.* 2019). For instance, the SEM analysis showed
388 that native taxonomic richness had a direct positive effect on alien PD counterbalanced by an

389 indirect negative effect through native PD. We also found a negative effect of native SES-PD
390 on alien SES-PD (and a weak negative effect on alien SES-FD), suggesting that when native
391 species are evolutionarily or ecologically clustered (negative SES), alien species are more
392 widespread across the tree of life and trait space (positive SES). Despite previous works
393 showing evidence of filters exerted by native communities on alien ones (Jeschke & Heger
394 2018), our study confirms the importance of abiotic and anthropogenic factors for shaping
395 alien 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 on species richness, farer islands favor more diverse traits. This could be

414 due either to humans that select birds with different characteristics for various purposes, or to
415 a high competition with congeners on remote islands, favoring the establishment of more
416 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, By contrast 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 on predicted alien taxonomic richness (Rojas-Sandoval *et al.* 2020). This
425 can be explained by a non-saturation of the area available for alien species to invade islands,
426 as the new alien species-area relationships seem to emphasize (Guo *et al.* 2020). Another
427 explanation is that both human population size and connectivity increase with island area as
428 well as colonization pressure. Thus, the effect of island area on alien diversities is masked by
429 the effect of anthropogenic variables (Blackburn *et al.* 2008; Moser *et al.* 2018), while area
430 has a direct effect for native diversities (Fig. S7). By decoupling direct and indirect effects,
431 this study sheds light on the importance of mediators to explain the impact of biogeographic
432 variables on alien diversities. Indeed, direct effects of biogeographic drivers on birds FD, PD,
433 SES-FD, and SES-PD were often non-significant, and their total effects were related to their
434 indirect effects mediated by anthropogenic and biotic drivers.

435

436 **Limitations**

437 Although our study provided new insights on biological invasions on islands, there are
438 limitations to be acknowledged. First, while the GAVIA database is the most comprehensive

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

454

455 **Perspectives**

456 Human arrivals and settlements on islands provoked drastic changes in ecosystem
457 compositions (Nogué *et al.* 2021), which are still ongoing. FD and PD of native and alien
458 communities determine species' ecological roles and ability to adapt. Thus, identifying the
459 drivers of multiple facets of alien diversity is a first step towards anticipating the risk posed
460 by biological invasions. Examining new insular communities in the Anthropocene is of
461 primary interest for forecasting the impacts of other global threats on islands, such as climate
462 or land-use changes.

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468

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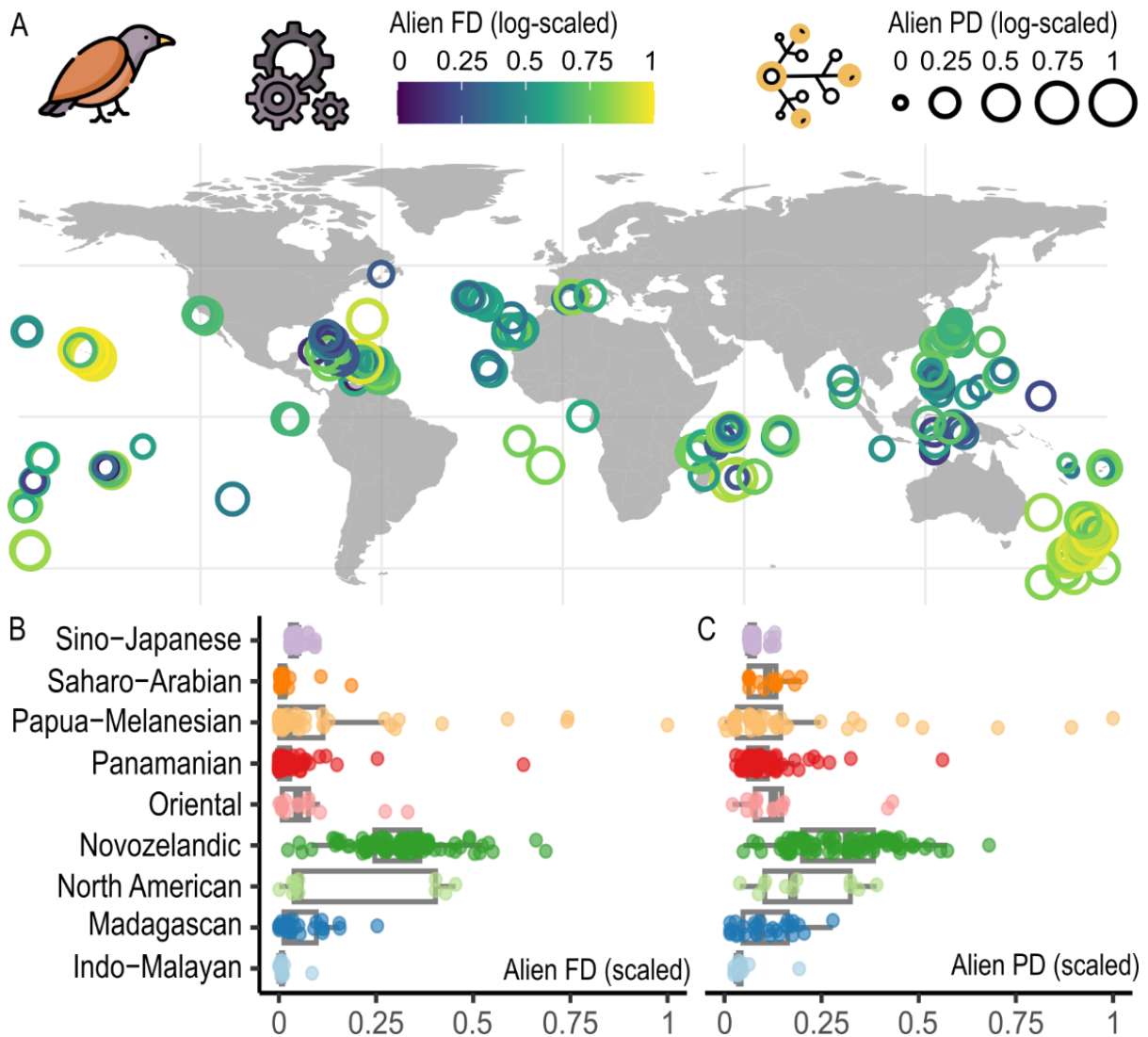
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632

633 FIGURES AND TABLES

634 **Table 1. Hypotheses on the factors driving alien bird diversities (i.e., SR: species richness; FD: functional richness; PD: phylogenetic**
635 **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)

636



637

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

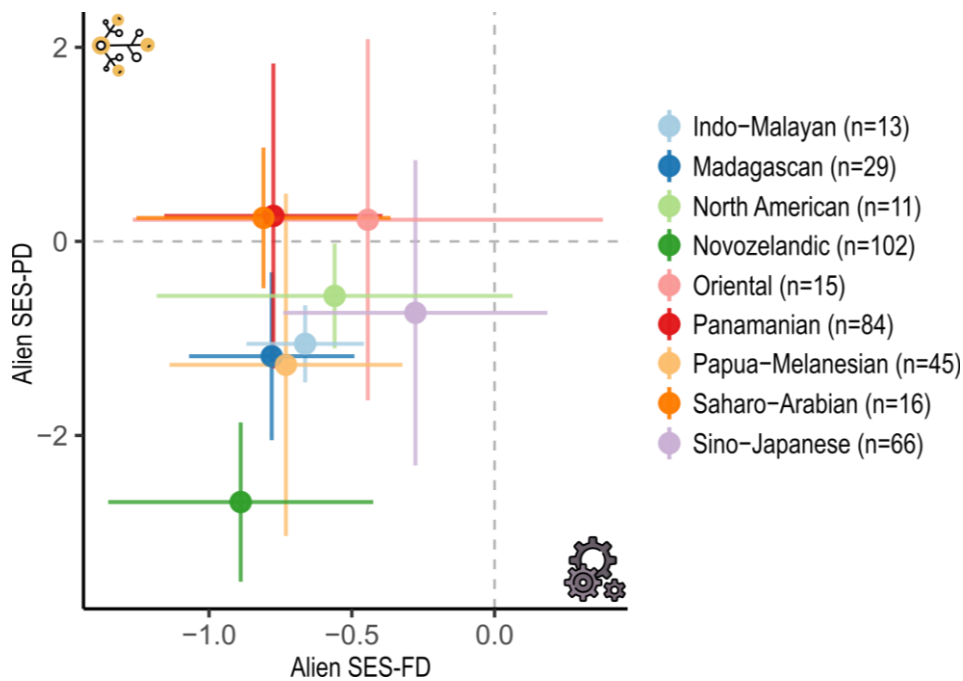
639 **oceanic islands.** (A) Spatial variation of functional diversity (Alien FD, color of the rings) and

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

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

642 shown.

643



644

645 **Figure 2. Deviations of functional and phylogenetic diversities from taxonomic diversity on**

646 **islands.** Mean standardized effect sizes (SES) of functional and phylogenetic diversities across all

647 islands separated by region. The points represent the mean SES-FD and SES-PD per region, and

648 horizontal and vertical bars represent the standard deviation of SES-FD and SES-PD within each

649 region, respectively. Only regions with more than ten islands are shown. Among the 407 islands,

650 respectively 4 and 128 islands had SES-FD and SES-PD below -1.96, which is the threshold for

651 assemblages being significantly more clustered than expected by chance. 10 islands had SES-PD

652 above 1.96, meaning their alien assemblages were significantly more dispersed than expected by

653 chance.

654



655

656 **Figure 3. Direct, indirect, and total effects of all explanatory variables on (A) functional diversity**

657 **(FD; and its associated SES) and (B) phylogenetic diversity (PD, and its associated SES) of alien**

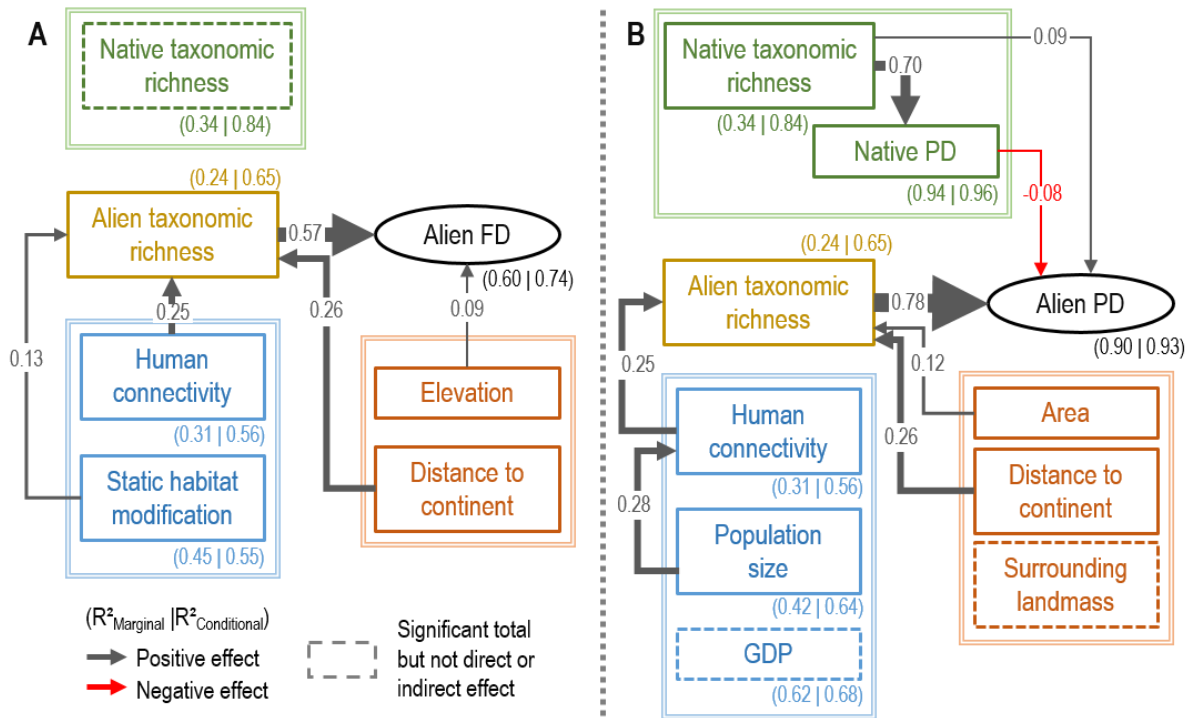
658 **birds.** The zoogeographic region for birds of each island was integrated as a random effect in all

659 relationships. Dots represent standardized mean effects, and error bars depict 95% confidence intervals

660 (shaded colors represent intervals crossing zero). Variable names are colored following their context:

661 biotic (green), human (blue), and biogeographical (orange).

662



663

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

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

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

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

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

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

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

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

672 endogenous variables are depicted in Fig. S7.