

Non-native bird species will not compensate for the loss of phylogenetic and functional diversity after the extinction of threatened species

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March 14, 2023

Abstract

Human activities have altered the composition of species assemblages through the introduction of non-native species and the extinction of threatened species. However, it remains unclear whether non-native species can compensate for the loss of threatened species and thus maintain ecosystem functioning. Here we tested whether non-natives are functionally and/or phylogenetically similar (compensation hypothesis) or distinct (shift hypothesis) from native and threatened species on bird assemblages in 267 regions worldwide. We show that non-native species were more functionally distinct from threatened species than expected by chance but more phylogenetically related. Globally, this results in an increase in the functional richness of bird assemblages due to the introduction of new functional traits but a decrease in the phylogenetic richness due to the potential loss of phylogenetically unique threatened species. Furthermore, these patterns vary across continents, revealing the role of human history and footprint across the world and outlining priority areas where international bird conservation should focus. In the context of the biodiversity crisis and the increasing number of non-native species worldwide, the changes in the functional and phylogenetic structure of the bird communities might increase the vulnerability of ecosystems.

1 **Title:** Non-native bird species will not compensate for the loss of phylogenetic and functional
2 diversity after the extinction of threatened species

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13 **Short running title:** Loss of bird diversity

14 **Key Words.** Birds, introduction, extinction, functional, phylogenetic, macro-ecology

15 **Type of article:** Letter

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18

Number of words in the Abstract	145
Number of words in the main text	4997
Number of cited references	52
Number of tables	0
Number of figures	4

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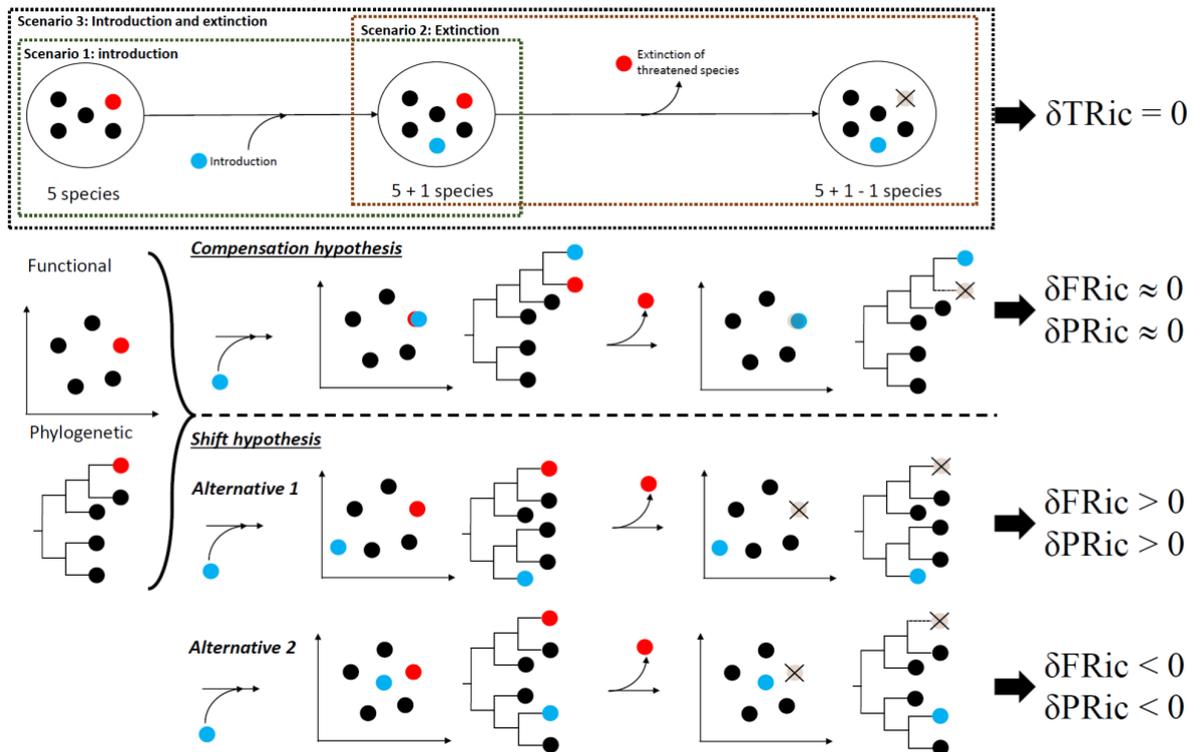
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21 **Abstract.** Human activities have altered the composition of species assemblages through the
22 introduction of non-native species and the extinction of threatened species. It remains unclear
23 whether non-native species can compensate for the loss of threatened species and thus maintain
24 ecosystem functioning. Here we tested whether non-natives are functionally and/or
25 phylogenetically similar (compensation hypothesis) or distinct (shift hypothesis) from native
26 and threatened species on bird assemblages in 267 regions. Non-native species were more
27 functionally distinct from threatened species than expected by chance but more
28 phylogenetically related. Globally, this results in an increase in functional richness but a
29 decrease in phylogenetic richness. Furthermore, these patterns vary across continents,
30 revealing the role of human footprint and outlining priority areas where conservation policies
31 should focus. In the context of the biodiversity crisis, these changes in the functional and
32 phylogenetic structure of the bird communities might increase the vulnerability of ecosystems.

33

34 **Introduction.** Through the introduction of non-native species and the extinction of threatened
35 species, human activities have contributed to a deep reorganization of species assemblages and
36 triggered the sixth biodiversity crisis (Simberloff & Vitule 2014; Capinha *et al.* 2015). While
37 many studies focused on either non-native (Gozlan *et al.* 2010; Jeschke *et al.* 2014; Martin-
38 Albarracin *et al.* 2015) or threatened species (Pimm & Raven 2000; Jenkins *et al.* 2013; Carmona
39 *et al.* 2021; Toussaint *et al.* 2021), the consequences of the coupled effects of introductions and
40 extinctions are still rarely addressed (but see Daru *et al.* (2021)). It is, however, a key aspect to
41 understanding the future composition of assemblages, its consequences for ecosystem
42 functioning, and the potential capacity of responses of organisms. Such aspects can be
43 apprehended by studying different facets of biodiversity such as the taxonomic, functional, and
44 phylogenetic diversities (Jarzyna & Jetz 2016; Pollock *et al.* 2017; Su *et al.* 2020). While
45 forecasting the future composition of assemblages under the coupled role of introductions and
46 extinctions can be mathematically calculated as a sum of introduced and extinct species (Fig
47 1), predicting the changes in functional and phylogenetic diversity depend on the
48 characteristics and the evolutionary history of the species (Sol *et al.* 2017; Su *et al.* 2019). Using
49 a recent compilation of non-native species and threatened species of birds across the world, we
50 evaluate the role of non-native species coupled with the potential extinction of threatened
51 species on the native biodiversity of birds for the taxonomic, functional, and phylogenetic
52 facets in 267 regions worldwide.

53 Recent evidence showed that compared to native species, non-native species tend to have
54 distinct functional traits (Blanchet *et al.* 2010; Van Kleunen *et al.* 2010), resulting from a human
55 selection of non-native species for specific purposes (e.g., trade, game, ornamental, pest
56 control). Conversely, large-sized, slow-paced, and slow-reproducing species of plants and
57 vertebrates tend to have higher risks to be threatened with extinction (Carmona *et al.* 2021;
58 Toussaint *et al.* 2021). While non-native species belonging to some specific clades are more
59 likely to be introduced (e.g., Anseriformes and Galliformes for bird hunting (Carpio *et al.*
60 2017), or Psittaciformes for bird trade (Cassey *et al.* 2004b; Strubbe & Matthysen 2009)), other
61 clades have higher proportions of threatened of species than expected (Bennett & Owens 1997;
62 Weeks *et al.* 2022). The future composition of species assemblages will hence result from a
63 coupled effect of both native and non-native species (Fig. 1). If non-native species have similar
64 traits and/or belong to the same clades as threatened species, the changes in species
65 composition will have little effect on functional and/or phylogenetic diversity and hardly
66 impede ecosystem functioning (hereafter called the compensation hypothesis, Fig. 1).
67 Contrastingly, if non-native and threatened species have distinct functional traits and/or belong
68 to different clades, non-native species will introduce new ecological strategies and/or
69 evolutionary histories susceptible to strongly disrupt the biodiversity and functioning of the
70 invaded assemblages (hereafter called the shift hypothesis, Fig. 1). Thus, depending on the
71 functional and phylogenetic relatedness between non-native species and threatened species, the
72 direction of the changes in functional and phylogenetic diversity can be positive or negative
73 (Fig. 1).



75

76 **Figure 1. Theoretical framework of combined effects of introductions and extinctions.**
 77 Considering an assemblage of five species (in black), we study the changes in taxonomic,
 78 functional, and phylogenetic richness following three scenarios: after the introduction of non-
 79 native species (scenario 1), after the potential extinction of threatened species (scenario 2), or
 80 after coupling the effects of introductions and extinctions (scenario 3). While there are no
 81 changes in species number in scenario 3 ($\delta TRic = 0$), changes in functional ($\delta FRic$) and
 82 phylogenetic ($\delta PRic$) can be manifold as illustrated through three theoretical situations. For
 83 the compensation hypothesis: introduced and extinct species are functionally and
 84 phylogenetically closely related and hence we expect no or few changes in FRic and PRic. For
 85 the shift hypothesis: introduced and extinct species are functionally and phylogenetically
 86 distinct. In the shift hypothesis, two alternatives can be distinguished: either non-native species
 87 is functionally and phylogenetically distinct from native species (Alternative 1) or non-native
 88 species is functionally and phylogenetically distinct from threatened species but redundant
 89 with other native species of the assemblage (Alternative 2). According to those two
 90 alternatives, the direction of the changes in FRic and PRic can be either positive (Alternative
 91 1) or negative (Alternative 2).

92

93 Changes in species composition are unevenly distributed across the world (Toussaint *et al.*
 94 2014; Dyer *et al.* 2017a), with regions highly impacted by non-native species and/or threatened
 95 species (e.g., Europe, and North America) while some others are still less impacted (e.g.,
 96 Africa). Beyond the different numbers of non-native and threatened species, the identity of
 97 species also depends on the human uses of non-native species and threats to native species
 98 (Cassey *et al.* 2004a; Dyer *et al.* 2017a). Thus, the changes in species composition might have

99 different consequences in functional and phylogenetic diversity across the world.
100 Understanding the patterns of changes in species composition in terms of taxonomic,
101 functional, and phylogenetic diversity will help to better identify the vulnerable ecosystems in
102 the world and better address conservation policies.

103 Here, we investigate how the changes in species composition through the introduction of
104 non-native species and the potential extinction of threatened species support the compensation
105 or the shift hypotheses described in Fig. 1. We first test the extent to which existing non-native
106 and threatened species are functionally and phylogenetically related by measuring the
107 dissimilarity for taxonomic, functional, and phylogenetic facets between non-native and
108 threatened species. Then, we quantify the effect of established non-native species and the
109 potential extinction of threatened species on the native biodiversity of bird assemblages
110 through three scenarios, depicting unique (scenarios 1 and 2) and coupled effects (scenario 3)
111 of introduced and threatened species (Fig. 1). The scenarios 2 and 3 depict a snapshot of what
112 the future of bird biodiversity might be, considering the actual knowledge in term of extinction
113 risks and introductions of non-native species. While introductions of new non-native species
114 are predicted for the future (Seebens *et al.* 2021), we consider only established non-native
115 species since it is still difficult to identify exactly which species could invade and where they
116 will be introduced but see Paganeli et al. (2022). We simulate extinctions of all threatened
117 species currently listed by the IUCN Red List as Critically Endangered, Endangered, and
118 Vulnerable reflecting our current knowledge of biodiversity threats. For each scenario, we
119 measure the changes in taxonomic, functional, and phylogenetic richness. We compare each
120 scenario to null hypotheses where the identity of introduced and threatened species is randomly
121 sorted among the pool of species. By doing this, we test whether the changes in functional and
122 phylogenetic richness are different from expected by chance and whether the
123 introduced/threatened species are functionally/phylogenetically redundant with the other
124 species of the assemblages.

125

126 **Methods.**

127 **Spatial database.** We collected species occurrences at the country level using the IUCN
128 spatial database “Birds of the world” (downloaded December 2020). This database allowed
129 obtaining the species list of 328 countries (defined as political borders) across the world. We
130 considered the names and the number of countries (including states or provinces for the United
131 States of America, Canada, and Australia) according to the GAVIA database (see below “Non-

132 native species”). The country and regional designations were downloaded from the Global
133 Administrative Areas (GADM) database (www.gadm.org, downloaded March 2021). From
134 here on, we will use the term of “region” to refer to countries, states, and provinces. The
135 original database encompasses 10,795 species.

136 **Non-native species.** We collected the non-native species list in each region using the
137 GAVIA database, which is considered the most complete and updated database for these
138 purposes (Dyer *et al.* 2017b). GAVIA database comprises 27,723 distribution records for 971
139 bird species for which there is some evidence of translocation outside their native range. We
140 used data on the first introduction records of non-native species between 1500 and 2000 AD
141 following the recommendation of (Dyer *et al.* 2017b). We removed the records for which there
142 is evidence that there is no established population in the country informed in the GAVIA
143 database (i.e., occurrences listed as “Extirpated” and “DiedOut”, see (Dyer *et al.* 2017b) for
144 details).

145 **Threatened species.** We collected the conservation status of species from the IUCN Red
146 List (version 2020-3, (IUCN 2020)) using the R package ‘rredlist’ (Chamberlain 2018). Such
147 information was available for 251 regions and 10,379 species. We used the IUCN classes: CR:
148 critically endangered; EN: Endangered; VU: Vulnerable; NT: Near Threatened; LC: Least
149 Concern; DD: Data Deficient.

150 **Functional traits.** We collected information on traits related to ecological functions for
151 9,683 species of birds using the AMIOTE database (Myhrvold *et al.* 2015). All the traits have
152 been selected for their ecological relevance and gathered from published studies (Myhrvold *et*
153 *al.* 2015). We selected a total of eight traits: clutch size (number of eggs), number of clutches
154 per year, adult body mass (g), incubation time (days), longevity (years), fledging age (days),
155 egg mass (g) and distance from the tip of the beak to the opening of the cloaca (cm).

156 **Phylogenetic trees.** We used the phylogeny available including 9,836 species (Jetz *et al.*
157 2012). Species for which we have functional traits but were not present in the phylogeny were
158 added to the root of the genus in the phylogeny (i.e., 2,044 species), using the
159 ‘add.species.to.genus’ from the R package ‘phytools’ (Revell 2012). By doing so, we obtained
160 10,471 species phylogenetically informed. We considered the phylogenetic uncertainties by
161 calculating the dissimilarity matrix for each of the 1,000-phylogeny based on cophenetic
162 distance and averaged those matrices in a single matrix for which we calculated the
163 eigenvectors.

164 **Functional space.** The construction of the functional space of birds followed the procedure
165 described by Carmona et al. (2021). Briefly, we identified the main axes of functional trait
166 variation by performing principal component analyses (PCA) on the log-transformed and
167 scaled functional traits. The space was built using all species for which we had trait information
168 and the two first dimensions were retained based on Horn's parallel analysis from the 'paran'
169 package (Dinno 2018). The first two axes explained 66.3% and 13.8%, respectively of the total
170 variation of functional traits (Table S1).

171 Since the functional traits were not informed for all species, we imputed the missing
172 functional traits using a machine learning approach (missForest, (Stekhoven & Bühlmann
173 2012)) combining the observed functional traits and the phylogenetic information. This way,
174 we included the evolutionary relationship between species in the imputation process by
175 including the first ten phylogenetic eigenvectors, as recommended by (Penone *et al.* 2014) (see
176 details in the following section). While phylogenetic diversity is based on the phylogenetic
177 distance between pairs of species, using phylogenetic information in the imputation considers
178 the interaction between all traits and the information, so that the positions imputed in the
179 phylogenetic space are much more accurate. However, species that are evolutionarily very far
180 apart might be very close in the functional space.

181 The accuracy of the trait imputation procedure was estimated on the subset of species for
182 which we have complete information following (Carmona *et al.* 2021). We quantified the
183 normalized root mean square error (NRMSE) according to the number of missing values (from
184 1 to the number of traits). The NRMSE error increased from $0.20 \pm 0.05\%$ for PC1 and $0.15 \pm$
185 0.03% for PC2 (when the species has only one missing trait) to $5.72 \pm 0.78\%$ for PC1 and 8.71
186 $\pm 0.56\%$ for PC2 (when the species has seven missing traits out of eight, Table S2). On average,
187 the errors were $2.95 \pm 0.23\%$ for PC1 and $3.39 \pm 0.21\%$ for PC2. Imputing the position of the
188 species based only on phylogenetic information strongly increases the error (PC1 = $63.53 \pm$
189 3.45% , PC2 = $18.75 \pm 1.07\%$), justifying the exclusion of the species for which we have only
190 phylogenetic information (representing 2,068 species).

191 We estimated the probabilistic distribution of the species within the functional space using
192 all species with spatial and functional information by performing multivariate kernel density
193 estimations with the 'TPD' R package (Carmona *et al.* 2019). We divided the 2-dimensional
194 spaces into 40,000 cells. The kernel for each species was a multivariate normal distribution
195 centered in the coordinates of the species in the functional space and bandwidth chosen using
196 unconstrained bandwidth selectors from the 'Hpi' function in the 'ks' package.

197 **Matching occurrences, functional traits, non-native, and IUCN Red List databases.**

198 Taxonomies from all the used sources were standardized using the R package ‘taxize’
199 (Chamberlain & Szöcs 2013) and names resolved against the GBIF Backbone Taxonomy. We
200 had 12,507 recognized names of bird species from the four sources of data. Among those
201 species, 10,471 species were phylogenetically informed. We had functional information (at
202 least one functional trait) for 8,718 species. The functional space was built using this subset of
203 species after the imputation of missing functional traits. We checked the reliability of the
204 functional space obtained with imputed functional trait values by comparing it with the space
205 that was based only on species with complete functional information using a Procrustes test
206 following (Carmona *et al.* 2021). The Procrustes test was highly significant ($P=0.0001$, see
207 Table S1), indicating a strong correspondence between the complete and imputed functional
208 spaces; consequently, we used the PCA based on imputed trait data in the rest of the analyses.

209 Our final set of species contained 7,685 species functionally, phylogenetically, and
210 spatially informed in 267 regions after homogenization of the country and states names. Among
211 the 971 non-native species identified worldwide, phylogenetic, functional, and spatial
212 information was available for 798 species (82%). Among the 1,376 species listed as threatened
213 by IUCN, phylogenetic, functional, and spatial information was available for 897 species
214 (65%). The proportion of species functionally and phylogenetically described varied between
215 63% and 100% of the country species composition (mean = 85%, 1st quartile = 83%, 3rd quartile
216 = 88%). 267 regions (99.6%) have received at least one non-native species and 203 regions
217 (75.5%) host at least one threatened species (Fig. S1). The proportion of introduced and
218 threatened species that were both functionally and phylogenetically informed in the 267 regions
219 was on average 92%, and 79%, respectively, compared to the original databases after species
220 and region names correction (Fig. S1).

221 We evaluated the potential uncertainties of the results of the changes in taxonomic,
222 functional, and phylogenetic richness by comparing the changes in taxonomic richness using
223 the subset of species functionally, phylogenetically, and spatially informed (i.e., 7,685 species)
224 and all spatially informed species (i.e., 9,952 species). This way, we identified the regions the
225 most potentially affected by the lack of evaluated species. For those regions, the results should
226 be taken with caution.

227 **Biodiversity indices.** Taxonomic diversity was calculated as the number of species in each
228 region (i.e., taxonomic richness, TRic). Functional diversity was measured as the amount of
229 functional space occupied by the species present in each country (i.e., functional richness,

230 FRic). Phylogenetic diversity was calculated as the sum of the branch length of species
231 occurring in each country (i.e., phylogenetic richness, PRic).

232 **Comparison between non-native and threatened species.** To test the compensation/shift
233 hypothesis between non-native and threatened species in each region (see the theoretical
234 framework in Fig. 2A), we calculated the taxonomic, functional, and phylogenetic dissimilarity
235 between all non-native and all threatened species in each region for which at least one species
236 has been introduced and at least one is threatened (N=257). The dissimilarity was measured
237 using the Jaccard dissimilarity index (Jaccard 1901) for taxonomic and phylogenetic diversities
238 using ‘betapart’ package (Baselga & Orme 2012). For functional diversity, due to the trait
239 probabilistic approach, we calculated the overlap-based dissimilarity (Carmona *et al.* 2019)
240 using ‘TPD’ package (Carmona *et al.* 2019).

241 To test whether the functional and phylogenetic dissimilarity between all non-native and
242 all threatened species was different than expected by chance, we performed null models where
243 we randomized the identity of non-native and threatened species in each region within the pool
244 of non-native and threatened species of each region, respectively. We drew 99 simulated
245 assemblages and compared the functional and phylogenetic dissimilarity of those 99
246 assemblages to the observed functional and phylogenetic dissimilarity. We calculated
247 standardized effect sizes (SES) as the difference between the observed values and the mean of
248 the simulated ones standardized by the standard deviation of the simulated values and their
249 associated P-values.

250 **Scenarios.** We built three different scenarios depicting unique (scenarios 1 and 2) and
251 coupled effects (scenario 3) of introduced/threatened species (see Fig. 1). Scenario 1: we
252 considered changes between assemblages with only native species and assemblages after
253 introduction events (i.e., native + non-native species). Scenario 2: we considered changes
254 between assemblages after introduction events (i.e., native + non-native species) and
255 assemblages after the introduction and extinctions events (i.e., native + non-native – threatened
256 species). Scenario 3: we considered changes between assemblages with only native species and
257 assemblages after the introduction and extinction events (i.e., native + non-native – threatened
258 species). For each scenario, we measured the changes in biodiversity indices (i.e., TRic, FRic,
259 PRic) and changes in dissimilarity between all pairs of assemblages (i.e., regions) as the
260 differences between two situations and expressed changes as a percentage of the initial
261 situation.

262 For each region, we compared the changes in the three biodiversity indices for the three
263 scenarios with a null model where the same number of species were randomly introduced from
264 the world's pool of species (scenario 1). This null model allows us to test whether the changes
265 in FRic and PRic observed after introductions are higher (i.e., non-native species have unique
266 functional traits and/or evolutionary history compared to the regional pool of species) or lower
267 (i.e., non-native species have redundant functional traits) than expected. For scenario 2, we test
268 whether the changes in FRic and PRic observed after the extinction of threatened species are
269 higher (i.e., threatened species have unique functional traits and/or evolutionary history
270 compared to the regional pool of species) or lower (i.e., threatened species have redundant
271 functional traits) than expected. For scenario 3, the null model allows us to test whether the
272 combined effect of non-native and threatened species contributes to higher or lower changes
273 in FRic and PRic than expected if non-native and threatened species have random functional
274 traits and evolutionary history.

275 For each country, we drew 999 simulated assemblages and compared the functional and
276 phylogenetic richness of those 999 assemblages to the observed FRic and PRic. We calculated
277 standardized effect sizes (SES) and their associated P-values.

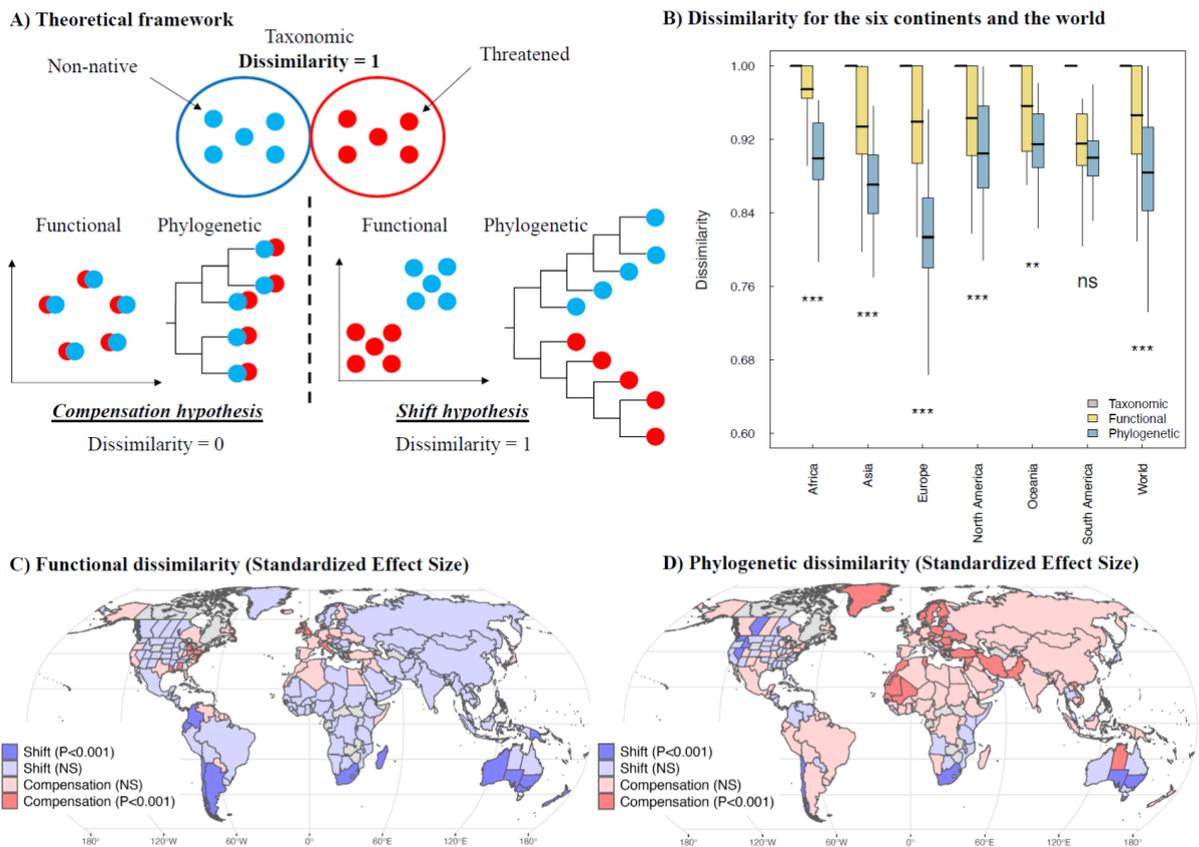
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279 **Results.**

280 To test whether non-native and threatened species are more functionally and/or
281 phylogenetically similar than expected, we investigated the taxonomic, functional, and
282 phylogenetic dissimilarity between threatened and non-native species for the regions that
283 experienced both introduction and extinction events (N=257). Taxonomic dissimilarity can be
284 only maximal since threatened and non-native species are completely distinct sets of species
285 in each region (Fig. 2A). Functional, and phylogenetic dissimilarity can vary between 0 if non-
286 native and threatened species are functionally and/or phylogenetically identical (i.e.,
287 compensation hypothesis, Fig. 2A) and 1 if non-native and threatened species are functionally
288 and/or phylogenetically completely distinct (i.e., shift hypothesis, Fig. 2A). We found that
289 functional dissimilarity varied between 0.73 and 1 and phylogenetic dissimilarity between 0.57
290 and 0.99. Functional dissimilarity was significantly higher than phylogenetic dissimilarity in
291 all continents except South America (Student tests, $P < 0.001$, Fig. 2B).

292 Comparing observed dissimilarity to null models, where the identity of non-native and
293 threatened species was randomized (see Methods), non-native and threatened species were
294 more functionally distinct than expected for 183 regions (71%, Fig. 2C), supporting the shift
295 hypothesis. For phylogenetic dissimilarity, non-native and threatened species were more

296 similar in 157 regions (61%, Fig. 2D), supporting the compensation hypothesis. Such pattern
 297 is globally congruent, except in some areas such as Western Europe, where non-native and
 298 threatened species are functionally more similar than expected, supporting the compensation
 299 hypothesis; or in Australia, South Africa, and some States in the USA, where non-native and
 300 threatened species are phylogenetically more distinct than expected, supporting the shift
 301 hypothesis.
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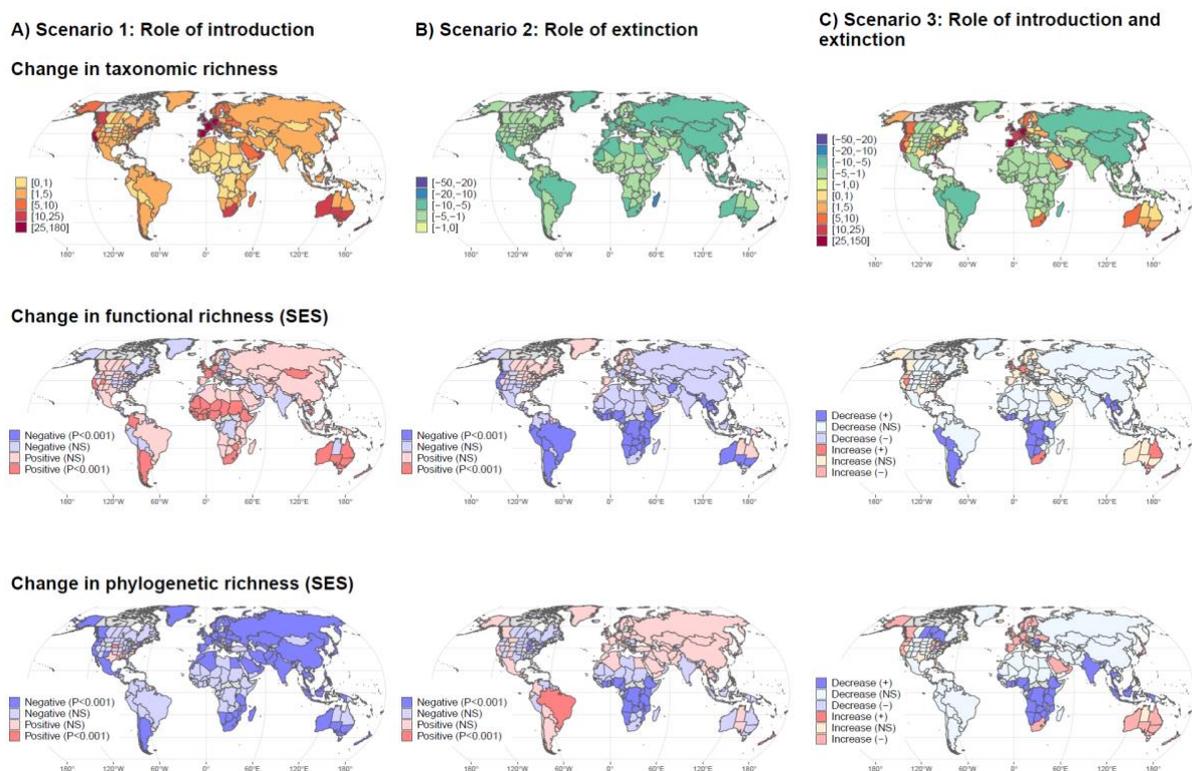
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 304 **Figure 2. Taxonomic, functional, and phylogenetic dissimilarity between non-native and**
 305 **threatened species for each region in the six continents.** A) Theoretical framework illustrating
 306 the compensation and shift hypotheses between the non-native and threatened species. The two
 307 examples are extreme cases. B) For each region experiencing at least one introduction and
 308 hosting at least one threatened species (N=257), we calculated the taxonomic, functional, and
 309 phylogenetic dissimilarity between non-native and threatened species. Box represents the 1st
 310 and 3rd quantiles; lines the 95% confidence interval; the horizontal lines the median. We
 311 compared the two distributions (functional dissimilarity, in yellow and phylogenetic
 312 dissimilarity, in blue) using Student tests (P<0.001: ***, P<0.01: **, P>0.05: ns). C and D
 313 represent the functional and phylogenetic dissimilarity, respectively, between non-native and
 314 threatened species for each region. Results are expressed in terms of Standardized effect size,
 315 where the dissimilarity was compared to a random pool of non-native and threatened species
 316 (see Methods). Blue tones mean that dissimilarity between non-native and threatened species
 317 was higher-than-expected supporting the shift hypothesis. Red tones mean that dissimilarity

318 *between non-native and threatened species was lower-than-expected supporting the*
 319 *compensation hypothesis.*

320

321 To quantify the consequences of non-native introductions and threatened species potential
 322 losses on the functional and phylogenetic richness in the 267 regions, we designed three
 323 scenarios, depicting unique (scenarios 1 and 2) and coupled effects (scenario 3) of
 324 introduced/threatened species (Fig. 1). We interpreted the Standardized Effect Sizes of null
 325 models to quantify the changes in functional and phylogenetic richness independently of the
 326 number of species introduced and/or threatened in each assemblage (see Methods).

327



328

329 **Figure 3. Changes in taxonomic, functional, and phylogenetic richness in 267 regions**
 330 **across the world following the three scenarios.** For each region, the changes were measured
 331 as the difference between the two periods according to the scenario (see details in Fig. 1 and
 332 Method). The changes are expressed as a percentage of taxonomic richness. For functional
 333 and phylogenetic richness, changes are shown in terms of Standardized Effect Size (SES),
 334 meaning that observed changes were compared to expected changes where the introduced
 335 species were randomized among a world pool of species. Negative values (blue tones) mean
 336 that the observed changes are lower-than-expected by chance whereas positive values (red
 337 tones) are higher-than-expected by chance. The results of the indices are available in
 338 Supplementary Fig. S2.

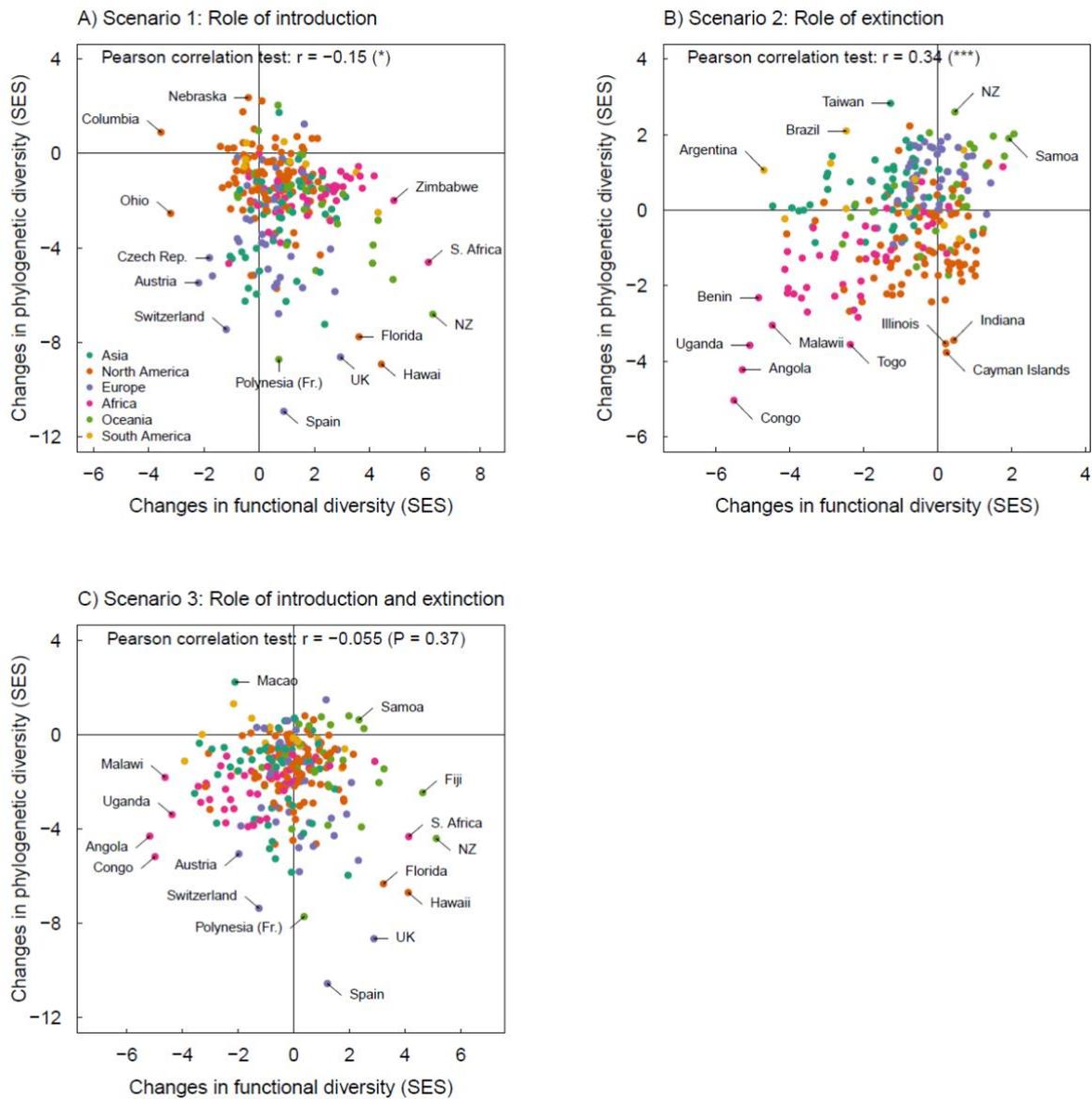
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340 The introduction of non-native species caused a significantly higher-than-expected increase
 341 in functional richness in 20% of the regions (51 regions) and a lower-than-expected increase
 342 in phylogenetic richness in 39% of the regions (106 regions, Fig. 3A, Table S3A, Table S4A).

343 This result demonstrates that non-native species are more functionally distant from native
344 species than expected (i.e., FRic SES > 0) but more phylogenetically related than expected
345 (i.e., PRic SES < 0), as supported by a negative correlation between FRic SES and PRic SES
346 (Pearson correlation test, $r = -0.15$, $P = 0.01$, Fig 4A). Moreover, the 106 regions experiencing
347 a lower-than-expected increase in phylogenetic richness were not randomly distributed
348 between continents ($\chi^2 = 20.5$, d.f. = 5, $P < 0.001$) but mainly distributed in Europe (30
349 regions), and Asia (27 regions). Similarly, the 51 regions experiencing a higher-than-expected
350 increase in functional richness were also not randomly distributed ($\chi^2 = 32.5$, d.f. = 5, $P <$
351 0.001), but they were mainly in Africa (21 regions) and Oceania (10 regions).

352 The potential loss of all threatened species revealed that extinction effects were not
353 significantly different from expected in 78% of the regions (209 regions) for functional
354 richness (Fig. 3b, Table S3B, Table S4B) and in 86% of the regions (230 regions) for
355 phylogenetic richness. The loss of functional richness was higher-than-expected mostly in
356 Africa (26 regions), Asia (13 regions), and South America (6 regions, $\chi^2 = 54.1$, d.f. = 5, $P <$
357 0.001 , Table S4B). For phylogenetic richness, the loss in phylogenetic richness was higher-
358 than-expected in Africa (N=17) and North America (N=13). Thus, the loss of threatened
359 species has a low but similar impact on both functional and phylogenetic richness ($r = 0.34$, P
360 < 0.001 , Fig. 4B).

361 Combining the effect of both introduction of non-native and extinction of threatened
362 species (scenario 3) showed that, since the number of introductions exceeds the number of
363 extinctions, dominant trends of diversity indices generally increase (Fig. 3C, Table S3C, Table
364 S4C). At the global scale, we reported an average increase of 3.15% in taxonomic richness,
365 and 3.63% and 2.89% in functional and phylogenetic richness, respectively. However, among
366 the regions experiencing a net loss of species richness, functional and phylogenetic richness
367 are decreasing more-than-expected in 18% of the regions, mainly in Africa and Asia (Fig. 3C),
368 while decreasing less-than-expected in only 3 and 1 regions, respectively. In contrast, among
369 the regions experiencing a net gain in species richness, functional richness is increasing more-
370 than-expected in 14% of the regions, while none of the regions experienced a higher-increase-
371 than expected in phylogenetic richness. Thus, combining the effect of both introduction of non-
372 native and extinction of threatened species discards the correlation between SES FRic and SES
373 PRic ($r = -0.06$, $P = 0.48$, Fig. 4C). For example, regions such as Florida, England, Germany,
374 New Zealand, or South Africa could experience higher-than-expected increases in functional
375 richness but lower than expected in phylogenetic richness (Fig. 3C).



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Figure 4. Changes in functional and phylogenetic richness in 267 regions across the world following the three scenarios. For each scenario (see details in Fig. 1 and Method), the changes in functional and phylogenetic richness are expressed in terms of Standardized Effect Size (SES), meaning that observed changes were compared to expected changes where the introduced species were randomized among a world pool of species. Colors represent the regions grouped by continents. We calculated the correlation between the SES of changes in functional and phylogenetic richness using Pearson's correlation tests ($P < 0.001$: ***, $P < 0.01$: **, $P < 0.05$: *). Some regions with the highest changes are identified. Czech Rep.: Czech Republic; NZ: New Zealand; Polynesia (Fr.): French Polynesia; UK: United Kingdom; S. Africa: South Africa.

388 **Discussion.** In this study, we seek to understand whether the replacement of non-native species
389 can offset the potential loss of threatened species in terms of functional and phylogenetic
390 diversity for bird assemblages across the world. We demonstrated that globally bird non-native
391 species are more functionally distinct from threatened species than expected (supporting the
392 shift hypothesis) but more phylogenetically clustered than expected (supporting the
393 compensation hypothesis). These changes in species composition increase the functional
394 richness of the bird assemblages due to the introduction of non-native species with distinct
395 functional traits. They might also trigger a global loss in phylogenetic richness due to the
396 potential extinction of phylogenetically unique species coupled with the introduction of species
397 closely related to native fauna. Our results highlight the need to control the introduction and
398 spread of non-native species and to protect phylogenetically unique species, which are the
399 primary drivers of changes in the functional and phylogenetic structure of bird communities.

400 Ecological consequences of the replacement of threatened species by non-native species
401 are still controversial (Wardle *et al.* 2011). Previous studies that investigated this question
402 showed that introduced species do not compensate for the loss of extinct species but instead
403 increase the functional and phylogenetic diversity of island bird assemblages (Sobral *et al.*
404 2016). Yet, other studies showed that non-native species are functionally redundant while
405 losing functionally unique species contributing to a global loss of functional diversity (Sobral
406 *et al.* 2016; Sayol *et al.* 2021). In fact, both studies support evidence for the shift hypothesis
407 following the two alternatives depicted in Fig. 1. At the global scale, we also find evidence for
408 the shift hypothesis. For functional diversity, our result supports alternative 1, indicating that
409 non-native species have unique trait syndromes. The introduction of such species can alter
410 ecosystem functioning since they can support unique ecological functions (Mouillot *et al.* 2013;
411 Violle *et al.* 2017). For phylogenetic diversity, our result supports alternative 2, indicating that
412 threatened species support unique parts of the phylogenetic diversity but are replaced by
413 species more closely related to native fauna. The loss of unique clades can weaken the capacity
414 for evolution and adaptation of an assemblage, in response to different kinds of environmental
415 disturbances. This demonstrated that functional richness does not always reflect phylogenetic
416 richness and that it is important to assess both facets of biodiversity when evaluating the
417 ecological roles and evolutionary histories of species (Losos 2008; Gerhold *et al.* 2015).

418 We find disparities between continents. In Europe and North America, introductions have
419 led to a gain of functionally distinct species that are nevertheless phylogenetically related to
420 native fauna, while Africa and South America may experience a large loss of functional

421 richness due to the loss of threatened species, supporting both variants of the shift hypothesis
422 (Fig. 1). However, increases in phylogenetic richness were mostly lower-than-expected while
423 decreases were higher-than-expected. For example, in regions that have suffered from high
424 introduction pressure (e.g., Spain), the decrease in phylogenetic richness results from an effect
425 of the loss of phylogenetically unique species (e.g., great bustard, *Otis tarda*) coupled with the
426 introduction of non-native species closely related to the native species of the recipient
427 communities (e.g., pied crow, *Corvus albus* or house sparrow, *Passer domesticus*). The
428 increases in functional richness should not be misinterpreted as introductions compensated for
429 extinctions but introduced new trait syndromes reflecting the shift hypothesis (Fig. 1). Our
430 results are in agreement with other studies on the consequences of non-native species on
431 functional diversity (e.g., Toussaint et al. 2018, Su et al. 2019), highlighting that introductions
432 of species with distinct functional traits might disrupt the trophic network and ecosystem
433 functioning.

434 With a high number of non-native and threatened species, Oceania appears to be the most
435 affected biogeographic zone and strongly supports the shift hypothesis, due to long-term
436 isolation and the presence of endemic species with unique functional traits (Toussaint *et al.*
437 2021). For instance, New Zealand, which suffers from a high level of non-native (N=119, 43%)
438 and threatened species (N=57, 21%), would experience strong shifts in functional space by
439 losing large-bodies and slow-living species such as the Hutton's shearwater (*Puffinus huttoni*)
440 or the yellow-eyed penguin (*Megadyptes antipodes*). Meanwhile, receiving small-bodied,
441 high-reproductive species such as the common quail (*Coturnix coturnix*), or the grey
442 partridge (*Perdix perdix*) helping to fill empty areas in the functional space (Fig. S3).

443 The large increases in functional richness reported in Europe and North America
444 underscore the diversity of non-native species originating worldwide and characterized by a
445 wide range of traits. This results in an expansion in all directions of functional space
446 contributing to the introduction of new trait syndromes but also an increase in functional
447 redundancy within the most densely occupied areas of functional space (>20 species, Fig. S3).
448 The potential loss of threatened species would contribute to functional space erosion by
449 increasing the proportion of functional space occupied by few species (e.g., < 5 species, Fig.
450 S3). These results show that, although the effects of extinction on functional richness are still
451 mitigated by functional redundancy of native and non-threatened species, the current
452 biodiversity crisis and future species extinctions could trigger deeper and irreversible erosion
453 of functional space, including the loss of specific ecological functions.

454 In contrast, regions less affected by non-native species (e.g., Africa, Asia, and South
455 America) are expected to lose more functional and phylogenetic richness than expected due to
456 species extinctions. This result implies that threatened species in these regions contribute
457 disproportionately to functional richness by having relatively unique traits. This situation is
458 illustrated by the introduction of non-natives that tend to be functionally redundant with native
459 species, supporting the findings on bird island assemblages (Sayol *et al.* 2021). From a
460 phylogenetic point of view, here we generalized a pattern observed for island bird assemblages
461 (Sobral *et al.* 2016), where most non-native species belonged to few clades, while threatened
462 species belonged to a diverse set of clades so that the loss of few species often leads to a loss
463 of unique parts of the phylogenetic tree.

464 The coupled effect of the extinction of threatened species and the introduction of non-native
465 species could lead to a general trend toward homogenization of the bird assemblages. We found
466 that functional homogenization exceeds the taxonomic and phylogenetic homogenization,
467 which is congruent with freshwater fishes in Europe (Villéger *et al.* 2014) or ants (Martello *et*
468 *al.* 2018). The process of biotic homogenization is amplified by the combined effect of the loss
469 of species with unique and distinct functional traits and phylogenetic clades between
470 assemblages and the introduction of similar species. These results indicate that bird
471 communities are amidst a global process of homogenization of their functional structure, which
472 is likely to be accelerated if the introduction and extinction processes are not controlled
473 (Devictor *et al.* 2007; Clavel *et al.* 2011; Toussaint *et al.* 2014).

474 Improvements in data availability will be needed to fully integrate functional and
475 phylogenetic assessments into conservation policies. Based on an estimate of changes in
476 taxonomic richness if all spatially described species were considered (Fig. S4), our results may
477 underestimate the intensity of taxonomic changes, particularly in South America and Southeast
478 Asia. In these regions, the overall decline in taxonomic richness after introduction and
479 extinction may be higher than reported primarily due to the lack of species assessed by the
480 IUCN Red List (Fig. S4c). These rare species are likely to have unique functional traits and
481 belong to unique clades and highlighting the need for additional functional and phylogenetic
482 information.

483 By altering species composition, the human footprint has become a major process
484 structuring the pattern of bird biodiversity worldwide (Ellis 2015). The increasing global trade
485 could promote an increase of non-native species across the world and mainly in countries still
486 sparsely affected such as Africa, South America, and Asia (Dawson *et al.* 2017; Seebens *et al.*

487 2018). The shifts in functional and phylogenetic structure of the bird communities reported
488 here might increase the vulnerability of ecosystems face to future changes, demonstrating the
489 urgent need for comprehensive and ambitious policies to regulate the introduction and the
490 conservation of threatened species across the world.

491

492 **Data availability Statement:** All data sets, as well as R codes involved in data processing,
493 statistical analysis, and plotting of the results (including a source data file), are available in
494 Figshare (<https://figshare.com/s/5bfe5a710cd3ea60ef2b>)

495 **Acknowledgments.** The study was financed by the Estonian Ministry of Education and
496 Research (PSG505, PSG293, MOBERC40, and PRG609) and the European Regional
497 Development Fund (Centre of Excellence EcolChange).

498 **Author Contribution:** AT and CPC conceived the study; AT and CPC collected and processed
499 the trait data and analyses. AT wrote the first draft of the manuscript and all authors contributed
500 to the interpretation of results and article writing.

501 **Conflict of interest statement.** The authors declare no competing interests.

502 **Supplementary Information** is available for this paper.

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504 **References**

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