1 **Title: Contrasting impacts of non-native and threatened species on morphological, life-**

2 **history, and phylogenetic diversity in birds' assemblages.**

3

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18

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20

21 **Abstract**. Human activities have altered the species composition of assemblages through
22 introductions and extinctions, but it remains unclear how those changes can affect the different
23 facets of biodiversity. Here we assessed the impact of changes in species composition on
24 taxonomic, functional, and phylogenetic diversity across 281 bird assemblages worldwide. To
25 provide a more nuanced understanding of functional diversity, we distinguished morphological
26 from life-history traits. We showed that shifts in species composition could trigger a global
27 decline in avian biodiversity due to the high number of potential extinctions. Moreover, these
28 extinctions were not random but unique in terms of function and phylogeny at the regional
29 level. Our findings demonstrated that non-native species cannot compensate for these losses,
30 as they are both morphologically and phylogenetically close to the native fauna. In the context
31 of the ongoing biodiversity crisis, such alterations in the functional and phylogenetic structure
32 of bird assemblages could heighten ecosystem vulnerability.

33

34 **Introduction**. Through the introduction of non-native species and the extinction of threatened
35 species, human activities contribute to a deep reorganization of species assemblages and
36 triggered the sixth biodiversity crisis (Capinha *et al.* 2015; Simberloff & Vitule 2014). 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 (Carmona *et al.* 2021; Jenkins *et al.* 2013; Pimm
39 & Raven 2000; Toussaint *et al.* 2021), few studies have explored their combined effects (but
40 see Daru et al. (2021). These combined effects are key to understanding the future composition
41 of assemblages, its consequences for ecosystem functioning, and the potential capacity of
42 responses of organisms. Such aspects can be apprehended by studying different facets of
43 biodiversity such as the taxonomic, functional, and phylogenetic diversities (Jarzyna & Jetz
44 2016; Pollock *et al.* 2017; Su *et al.* 2020). While forecasting the future composition of
45 assemblages under the coupled role of introductions and extinctions can be mathematically
46 calculated as a sum of introduced and extinct species, predicting the changes in functional and
47 phylogenetic diversity depends on the functional traits and the evolutionary history of the
48 species (Sol *et al.* 2017; Su *et al.* 2019). Using a recent compilation of non-native species and
49 threatened species of birds across the world, we evaluated the role of non-native species
50 coupled with the potential extinction of threatened species on the native biodiversity of birds
51 for the taxonomic, functional, and phylogenetic facets in 281 regions worldwide.
52   Previous evidence showed that non-native species often support unique traits due to human
53 selection for specific uses like trade or pest control (Sobral et al. 2016; Sayol et al. 2021). In
54 contrast, species with traits like large size and slow reproduction are more likely to be

55 threatened (Carmona *et al.* 2021; Toussaint *et al.* 2021). For birds, some clades are more prone

56 to introduction (e.g., Anseriformes for hunting; Carpio et al. 2017) while others (e.g., Rallidae)

57 have higher proportions of threatened species (Weeks *et al.* 2022). Thus, the future composition

58 of species assemblages will result from the coupled effect of both native and non-native

59 species. The net effect on biodiversity and ecosystem function depends on the functional and

60 phylogenetic similarities between non-native and threatened species.

61   The ecological consequences of the replacement of threatened species by non-native

62 species are controversial (Wardle *et al.* 2011). Some studies on island bird assemblages occupy

63 different positions than native species in the functional space and in the phylogeny (Sobral *et*

64 *al.* 2016). By contrast, other studies have shown that non-native species are functionally

65 redundant so biotic invasions have not offset the extinction of functionally unique species on

66 oceanic archipelagos (Sayol et al. 2021). However, those studies mainly investigated the effects

67 of species that have already been extinct and considered only island assemblages. While island

68 ecosystems have already experienced a significant loss of endemic species (approximately

69 8%), the extinction rate for non-island species remains relatively low (estimated at 0.002%,

70 Matthews et al. 2022), indicating that substantial changes are likely to occur in the future. Thus,

71 understanding how global species losses will impact ecological function remains a major

72 challenge (Ali *et al.* 2023).

73   Here, we investigated how changes in species composition through the introduction of non-

74 native species and the potential extinction of threatened species impact the functional and

75 phylogenetic structure of bird assemblages across the world. To comprehensively assess

76 functional diversity, we used two distinct sets of traits: morphological diversity from the

77 AVONET database (Tobias *et al.* 2022), and life-history diversity from the AMNIOTE

78 database (Myhrvold *et al.* 2015). By dissecting functional diversity in this manner, our study

79 aimed to provide a more nuanced understanding of how different facets of biodiversity are

80 affected by the introduction of non-native species and the loss of threatened species. This

81 approach allowed us to identify specific ecological functions that may be disproportionately

82 impacted, thereby offering more targeted recommendations for conservation strategies.

83

84   **Methods**.

85   **Spatial Resolution.** Spatial entities were identified at the Biodiversity Information

86 Standards (TDWG) level 3 according to the Global Administrative Areas (GADM) database

87 (www.gadm.org, downloaded March 2021), resulting in 369 spatial entities worldwide. For

88 each spatial entity, we retrieved the continental divisions also provided within the GADM

89   database to assign the appropriate continent to each spatial entity. To mitigate the potential
90   effects of small islands, those with an area below 70 square kilometers, as well as islands in
91   the "seven seas" and Antarctica, were excluded. This refinement yielded a subset of 281 entities
92   for subsequent analyses, hereafter named as regions.

93   **Functional Traits.** Functional diversity is a multi-faceted concept that encompasses a
94   range of traits affecting species' roles in ecosystems. Traditionally, studies have aggregated
95   traits into a single measure of functional diversity. We adopted a different approach by
96   dissecting functional diversity into two morphological diversity and life-history diversity.

97   We collected morphological traits from the AVONET database for 9,981 species (Tobias
98   *et al.* 2022). The selected traits included 11 morphological traits relative to beak length
99   (Culmen and Nares), width, and depth, tarsus length, wing length, kipps distance, hand-wing
100 index, tail length, secondary, and body mass (Table S1). These traits influence various
101 ecological functions like seed dispersal, predation, and resource utilization (McGill et al.,
102 2006).

103 Life-history traits were retrieved from the AMNIOTE database for 8,940 species
104 (Myhrvold *et al.* 2015). We selected a total of eight traits (Table S1): clutch size (number of
105 eggs), number of clutches per year, incubation time (days), longevity (years), fledging age
106 (days), egg mass (g) and distance from the tip of the beak to the opening of the cloaca (cm) and
107 body mass (g).

108 Since life-history traits were not informed for all species, we imputed the missing life-
109 history trait values using a machine learning approach ("*missForest*", Stekhoven & Bühlmann
110 2012) combining the observed life-history traits and the phylogenetic information as explained
111 in Carmona *et al.* (2021). This way, we included the evolutionary relationship between species
112 in the imputation process by including the first ten phylogenetic eigenvectors, as recommended
113 by Penone et al. (2014). While phylogenetic diversity is based on the phylogenetic distance
114 between pairs of species, using phylogenetic information in the imputation considers the
115 interaction between all traits and the information, so that the positions imputed in the
116 phylogenetic space are much more accurate (Stewart *et al.* 2023). We used the imputed traits
117 to project species onto the life-history space, utilizing the complete dataset.

118 We assessed the accuracy of our imputation method using the Normalized Root Mean
119 Square Error (NRMSE), which quantifies the average deviation between the "real" and
120 imputed trait values as a fraction of the trait value range. To conduct this assessment, we
121 intentionally removed 10% of trait values from a subset of species with complete data. We then
122 randomly selected a species with incomplete data and applied the same pattern of missing

4

123 values to it, thereby maintaining the original dataset's missing value pattern. We ran the
124 imputation process using the full dataset, which included both species with incomplete trait
125 data and those with complete data (i.e., 90% of species with complete data and an additional
126 10% with artificially induced missing values). This approach resulted in a higher ratio of
127 missing to complete data in the simulations compared to the original dataset, providing a
128 conservative evaluation of our imputation quality. We repeated this procedure 100 times and
129 found that the standard error of the NRMSE was consistently below 1%, indicating the
130 robustness of our method (see Table S2).

131 After standardization of the species taxonomy and nomenclature according to BirdTree
132 (Jetz *et al.* 2012) for AMNIOTE species, 8,502 species were common between AVONET and
133 AMNIOTE. To assess the impact of utilizing a subset of species (i.e., 8,502 species), we
134 performed supplementary analyses revealing strong correlations with the two sets of data
135 (Spearman's rank correlation tests: $r > 0.94$, $P < 0.001$, Fig. S1).

136 **Phylogenetic Information.** We used a comprehensive phylogeny including 9,993 bird
137 species (Jetz *et al.* 2012). We extracted data from 100 individual phylogenetic trees available
138 in the R package "*rtree*" (Li 2023) and integrated it into a single consensus tree using the
139 consensus function from the R package "*ape*" (Paradis *et al.* 2004). This approach allowed us
140 to account for phylogenetic uncertainty by summarizing the topological and branch-length
141 variations across the multiple trees. All species for which we have trait information (i.e., 9,981
142 species) were included in the phylogeny.

143 **Species Occurrences.** Species occurrences of the 9,981 species were retrieved for each
144 region from the comprehensive "Birds of The World" spatial database (Billerman *et al.* 2022).
145 We considered only the species with presence categories 1 (i.e., resident), 2 (i.e., seasonal),
146 and 3 (i.e., vagrant, or occasional) and origin of 1 (i.e., native from the region).

147 **Conservation Status.** The conservation status was obtained from the IUCN Red List
148 (version 2020-3, (IUCN 2020)) using the R package "*rredlist*" (Chamberlain 2018). We
149 retrieved information for 9,432 species with IUCN status: CR: critically endangered; EN:
150 Endangered; VU: Vulnerable; NT: Near Threatened; LC: Least Concern; DD: Data Deficient.
151 Since we considered current and future changes in species composition, we do not consider
152 extinct species.

153 We used the regional IUCN Red List when available (i.e., for 167 regions, 60%), otherwise,
154 we used the global status. Regional assessments provide a finer resolution, accounting for
155 localized threats, population dynamics, and ecological conditions that may vary across
156 different regions. This approach allows for a more precise evaluation of the conservation status

157 of species, considering region-specific factors that might not be adequately reflected in the
158 global assessment.

159 **Non-Native Species.** The GAVIA database considered the most comprehensive and
160 updated source for non-native species of birds, was utilized to compile a list of non-native bird
161 species for each region. This database included 27,723 distribution records for 970 bird species
162 with evidence of translocation outside their native range. Only records of the first introductions
163 between 1500 and 2000 AD were considered, in line with the recommendations of Dyer et al.
164 (2017). Records indicating no established population in the region (e.g., listed as "Extirpated"
165 and "DiedOut") were excluded (see Dyer et al. (2017) for details). While introductions of new
166 non-native species are predicted for the future (Seebens *et al.* 2021), we considered only
167 established non-native species since it is still difficult to identify exactly which species could
168 invade and where they will be introduced see Paganeli et al. (2022).

169 The GAVIA database, originally compiled at the country level 1, posed a spatial challenge
170 as our analysis required data at a finer resolution. To bridge this gap, we implemented a
171 structured framework. For the 255 regions where the spatial resolution remained consistent
172 between country level 1 and country level 3, we used the species list of the GAVIA database.
173 United States of America, Canada, and Australia were available at the states or provinces'
174 spatial resolution in the GAVIA database in agreement with the spatial resolution of country
175 level 3. For 18 regions, where country level 3 encompassed multiple regions at level 1, we
176 combined the species list of these individual regions at level 1 to create a comprehensive list
177 at level 3. For the nine regions where the borders are smaller in level 3 than level1 (e.g.,
178 Argentina, Brazil, Chile, China, France, Russia, Mexico, Italy, and South Africa), we first used
179 the species list of GAVIA at the level 1, then used the species' ranged maps also provide by
180 GAVIA. Since this information was available only for 362 species (Dyer *et al.* 2017), we
181 completed the database by using GBIF to retrieve the occurrences of the other non-native
182 species listed in GAVIA at a smaller spatial scale. Given the potential for misidentifications in
183 GBIF records, we adopted a conservative approach, restricting our selection to records labeled
184 as 'HUMAN OBSERVATION' with accurate geographic coordinates to mitigate potential
185 errors. At the global scale, 802 species were identified as non-native in at least one of the 281
186 regions. Among them, 789 (98%) were morphologically and phylogenetically informed.

187 **Functional space.** The construction of the morphological and life-history spaces of birds
188 followed the procedure described by Carmona et al. (2021). Briefly, we identified the main
189 axes of functional trait variation by performing principal component analyses (PCA) on the
190 log-transformed and scaled traits. The spaces were built using all species for which we had trait

191 information and the two first dimensions were retained based on Horn's parallel analysis from

192 the "*paran*" package (Dinno 2018). For the life-history space, the first two axes explained

193 66.3% and 13.8%, respectively of the total variation of the life-history traits (Table S1). For

194 the morphological space, the first two axes explained 68.4% and 14.7%, respectively of the

195 total variation of the morphological traits (Table S1).

196 We estimated the probabilistic distribution of the species within the spaces by performing

197 multivariate kernel density estimations with the "*TPD*" R package (Carmona *et al.* 2019). We

198 divided the 2-dimensional spaces into 40,000 cells. The kernel for each species was a

199 multivariate normal distribution centered in the coordinates of the species in the functional

200 space and bandwidth chosen using unconstrained bandwidth selectors from the *Hpi* function in

201 the "*ks*" package.

202 Additional analyses indicate a positive correlation between the functional spaces

203 constructed from both databases (PERMANOVA: r = 0.78, P < 0.001), suggesting that the

204 relative position of species within each functional space is consistent. However, when we

205 delved deeper into the correlation of each Principal Component (PC) axis, we observed

206 divergent patterns. For PC1, which is influenced by body size in both functional spaces, we

207 found a high correlation (Spearman rank correlation test: r > 0.9, P < 0.001). In contrast, the

208 correlation for Principal Component axis 2 was not significant (r = -0.01, P = 0.47). This was

209 explained by the fact that in the life-history space, PC2 is related to reproductive strategies,

210 while in the morphological space, PC2 is related to the shape of the bird (Table S1). This lack

211 of correlation underscores the importance of treating the trait separately to capture the full

212 spectrum of functional diversity impacts.

213 **Data Standardization.** Taxonomies from all sources were standardized according to

214 BirdTree, the most recent global bird phylogeny (Jetz *et al.* 2012). The final dataset

215 encompassed 8,143 species (82%). The proportion of species described in the subset of species

216 (including non-native species) in each region varied between 81% and 100% of the number of

217 species in the complete set of data (mean = 93.5%, 1st quartile = 92.1%, 3rd quartile = 95.5%,

218 Fig. S2). The proportion of non-native species varied from 67% and 100% (mean = 96.3%, 1st

219 quartile = 94.4%, 3rd quartile = 100%) and the proportion of threatened species varied from

220 67% and 100% (mean = 94.2%, 1st quartile = 90.9%, 3rd quartile = 100%).

221 We evaluated the potential uncertainties of the results by comparing the changes in

222 taxonomic richness using the subset of species (i.e., 8,143 species) and all species (i.e., 9,881

223 species). This way, we identified the regions the most potentially affected by the lack of

224 evaluated species. For those regions, the results should be taken with caution (Fig. S3).

225   **Scenario of species composition changes:** We considered changes between assemblages
226   with only native species and assemblages after the introduction and extinction events (i.e.,
227   native + non-native – threatened species). To reflect the varying degrees of extinction risk, we
228   removed species classified as critically endangered (CR), representing the highest risk
229   category, and progressively proceeded to eliminate species with lower threat statuses (i.e.,
230   endangered (EN), vulnerable (VU), and near threatened (NT)). Each step in the simulation
231   sequentially removed species, creating a gradient of extinction risk scenarios (see Toussaint et
232   al. 2021). For simplicity, scenarios were denoted by the least threatened category considered.

233   In addition, we quantified the impact of introduced non-native species and the extinction
234   of threatened species independently considering 1) changes between assemblages with only
235   native species and assemblages after introduction events (i.e., native + non-native species); and
236   2) changes between assemblages after introduction events (i.e., native + non-native species)
237   and assemblages after the introduction and extinctions events (i.e., native + non-native –
238   threatened species).

239   **Biodiversity indices.** Taxonomic diversity was calculated as the number of species in each
240   region (i.e., taxonomic richness). Morphological and life-history diversity was measured as the
241   amount of morphological and life-history space, respectively, occupied by the species present
242   in each region (i.e., functional richness). Phylogenetic diversity was calculated as the sum of
243   the branch length of species occurring in each region (i.e., phylogenetic richness). We
244   measured the changes in biodiversity indices as the differences between the two situations and
245   expressed changes as a percentage of the initial situation.

246   Taxonomic, morphological, life-history, and phylogenetic dissimilarities were assessed for
247   each region between assemblages with only native species and assemblages after the
248   introduction and extinction events (i.e., native + non-native – threatened species). The
249   dissimilarity was measured using the Jaccard dissimilarity index (Jaccard 1901) for taxonomic
250   and phylogenetic diversities using the "*betapart*" package (Baselga & Orme 2012). For
251   morphological and life-history diversity, due to the trait probabilistic approach, we calculated
252   the overlap-based dissimilarity using the "*TPD*" package (Carmona *et al.* 2019).

253   Morphological and life-history uniqueness of non-native and threatened species were
254   calculated in the functional spaces and for each PC axis. Uniqueness was calculated for each
255   region and standardized to the center of the native species of each country using the R package
256   "*funrar*" (Grenié *et al.* 2017). By doing this, we were able to compare the morphological and
257   life-history uniqueness of the two functional spaces as well as for each PC axis.

258   **Null models.** For each region, we compared the changes in morphology, life-history, and
259   phylogenetic richness and dissimilarity with null models. Null models were built to assess
260   whether the combined influence of non-native species introductions and threatened species
261   extinctions resulted in higher or lower changes in morphology, life-history, and phylogenetic
262   richness and dissimilarity than would be expected by chance. In the null models, we maintained
263   the number of native species as in the community and we introduced the same number of
264   species as observed but randomly sorted from the global pool of species. Additionally, we
265   randomized the IUCN status among the native species pool (see Carmona et al. 2021; Toussaint
266   et al. 2021 for similar approaches). We generated 999 simulated assemblages for each region.
267   We then compared the changes in morphology, life-history richness, and dissimilarity values
268   of these 999 simulated assemblages with the observed changes in morphology, life-history and
269   phylogenetic richness, and dissimilarity. To quantify the degree of deviation from random
270   expectations, we calculated standardized effect sizes (SES), providing a measure of how
271   observed changes compared to the null model. Additionally, we determined associated P-
272   values to assess the statistical significance of these deviations.

273

274   **Results.**
275   The cumulative impact of non-native species introduction and potential extinctions of
276   threatened species led to a net decrease in global biodiversity of 5.26% in taxonomic, 2.04%
277   in morphological, 1.02% in life-history, and 3.39% in phylogenetic richness (Fig. 1, Fig. S4,
278   Table S3). However, this trend was not uniform across regions since Europe and Oceania
279   experienced milder declines in biodiversity, with occasional gains in life-history and
280   morphological richness. In contrast, Africa, Asia, and South America exhibited more
281   substantial decreases in all aspects of biodiversity. These regional disparities can be explained
282   by a lower introduction pressure (0.9±1.4, 3.6±6.8, and 2.0±2.0 species per region on average)
283   in Africa, Asia, and South America, respectively. This stands in contrast to Europe, North
284   America, and Oceania, where introduction pressures were higher (9.37±14.9, 4.05±8.8, and
285   15.25±15.9 species per region on average, respectively). Even when considering other
286   categories of threatened species, the patterns remained consistent, suggesting that the trends
287   identified in the most severe scenario aligned across different threat levels (Fig. S5).
288   As those changes were affected by the number of non-native species and/or threatened in
289   each assemblage, Standardized Effect Sizes (SES) from null models were used (Fig. 1). While
290   the SES in morphological and phylogenetic richness were correlated (r = 0.65, P < 0.001, Fig.
291   S6), life-history traits showed a lower proportion of regions with significantly higher-than-

292   expected losses (i.e., $SES_{LH} < 0$, $P < 0.001$). Such a pattern was consistent across threat levels
293   (Fig. S5) despite differences between facets of biodiversity were even more pronounced at
294   lower threat levels (e.g., Critically Endangered [CR] and Endangered [EN]). This indicated that
295   the most endangered species were often more unique in morphology and phylogeny than in
296   life-history traits.

297   Our analysis revealed that the higher-than-expected decrease in all facets of biodiversity
298   was more marked in Asia, Africa, and South America (Fig. 1, Fig. S6) than in Europe and
299   Oceania and, to a lesser extent, in North America. In those regions, changes in species
300   composition resulted in higher-than-expected losses in morphological (i.e., $SES_{Morpho} < 0$, $P <$
301   0.05) and phylogenetic richness (i.e., $SES_{Phylo} < 0$, $P < 0.05$) but non-significant or even a
302   lower-than-expected changes in life-history richness in 6 regions (i.e., $SES_{LHT} > 0$, $P < 0.05$,
303   Fig. 1, Table S4).

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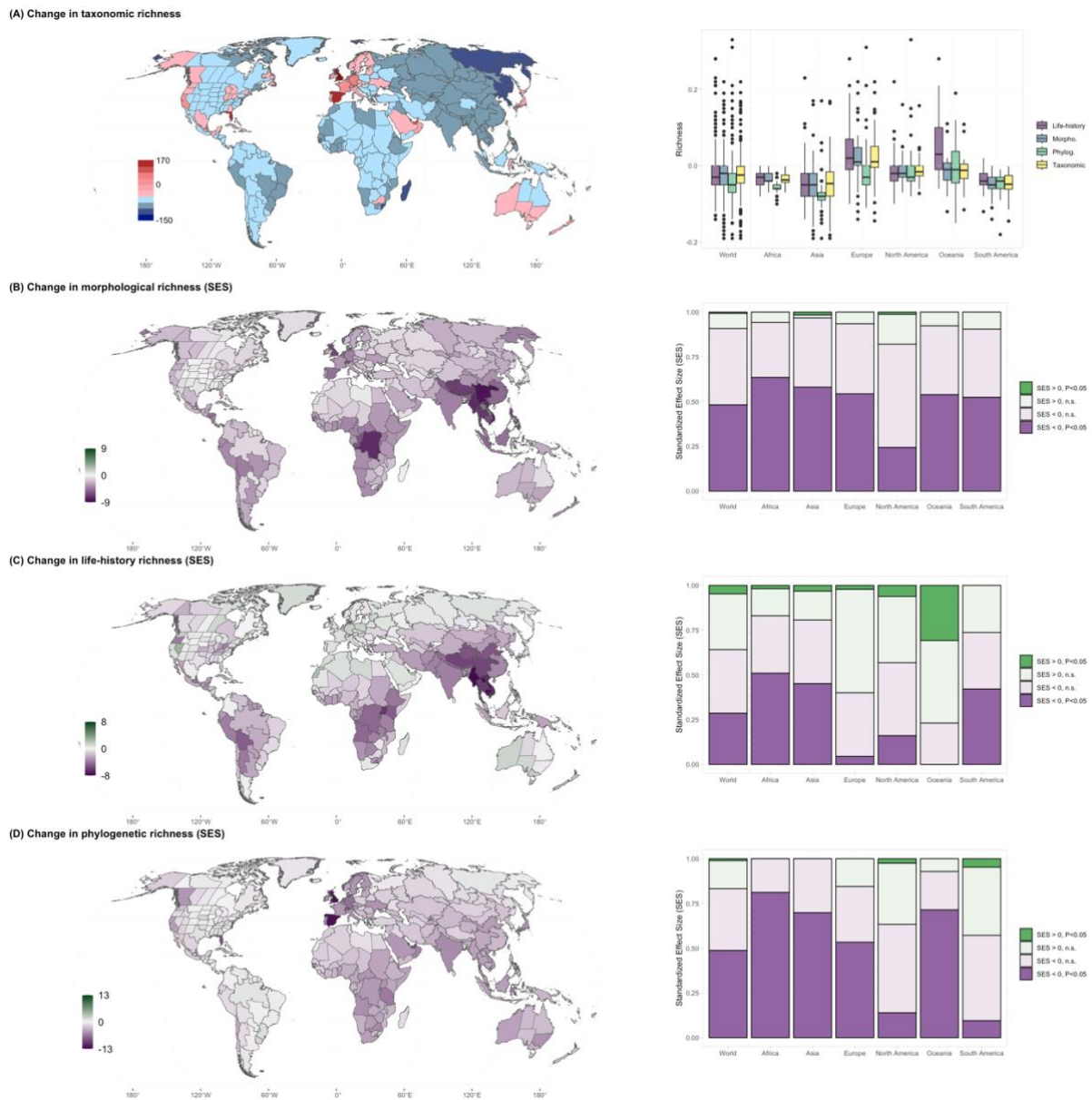
Figure 1. Changes in taxonomic, morphological, life-history, and phylogenetic richness in 281
regions across the world. *For each region, the changes were measured as the difference between the*
two periods (i.e., native species vs. natives + non-natives – threatened). Changes in richness are shown
for taxonomic in map (A) and for all facets in the boxplot. Changes for morphological (B), life-history
(C), and phylogenetic (C) are also expressed in terms of Standardized Effect Size (SES), meaning that
observed changes were compared to 999 expected changes where the introduced species were
randomized among a world pool of species. Purple tones mean that changes in morphological, life-
history, and phylogenetic richness were lower-than-expected. Green tones mean changes in
morphological, life-history, and phylogenetic richness were higher-than-expected. Threatened species
are species classified as CR, EN, VU, and NT by IUCN. Maps of changes in biodiversity facets are
provided in Fig. S4. Scenarios with different classes of IUCN are provided in Fig. S5.

317

318   This pattern can be explained by a contrasting impact of non-native and threatened species

319   (Fig. 2). Indeed, non-native species exhibited life-history traits that diverged significantly from

320   native fauna in 56 regions (i.e., $SES_{LH} > 0$, P < 0.05, Fig. 2B) while non-native species were

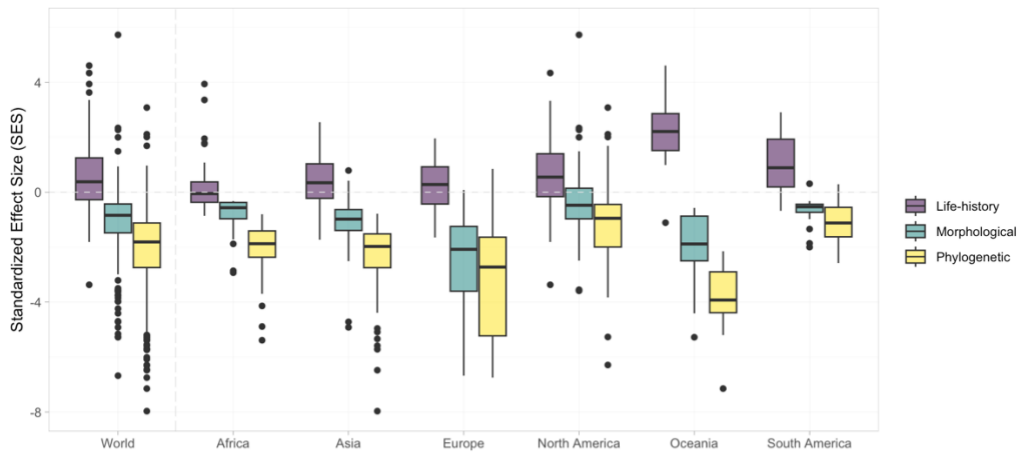321   more morphologically or phylogenetically closer to the native species than expected in 70 and

322 136 regions, respectively (i.e., SES_{Morpho} and $SES_{Phylo} < 0$, $P < 0.05$). Such a nuanced interplay

323 between biodiversity facets was particularly pronounced in Oceania (78% of the regions

324 depicted opposite patterns between SES_{Morpho} and $SES_{LH,}$ Fig. 2B), underscoring the region-

325 specific complexities in the impact of species composition changes on various facets of

326 biodiversity.

327 In contrast, threatened species exhibited more consistent relationships across biodiversity

328 facets, particularly between life-history and morphological traits (Spearman rank correlation

329 test: $r = 0.64$, $P < 0.001$, Fig. 2C). We found a dominant trend of negative Standardized Effect

330 Sizes (SES), with 90% of regions showing negative SES in at least one biodiversity facet. In

331 41% of regions, the loss of threatened species correlated with a higher-than-expected decline

332 in at least one facet, while only two regions showed the opposite trend. This accelerated loss

333 of biodiversity was most pronounced in Africa, Asia, and South America, underscoring the

334 geographic variability in the impact of threatened species on biodiversity. This pattern was also

335 evident across levels of threat (Fig. S5B), especially in Africa, Asia, and South America, where

336 even the loss of the most critically endangered species impacted significantly avian
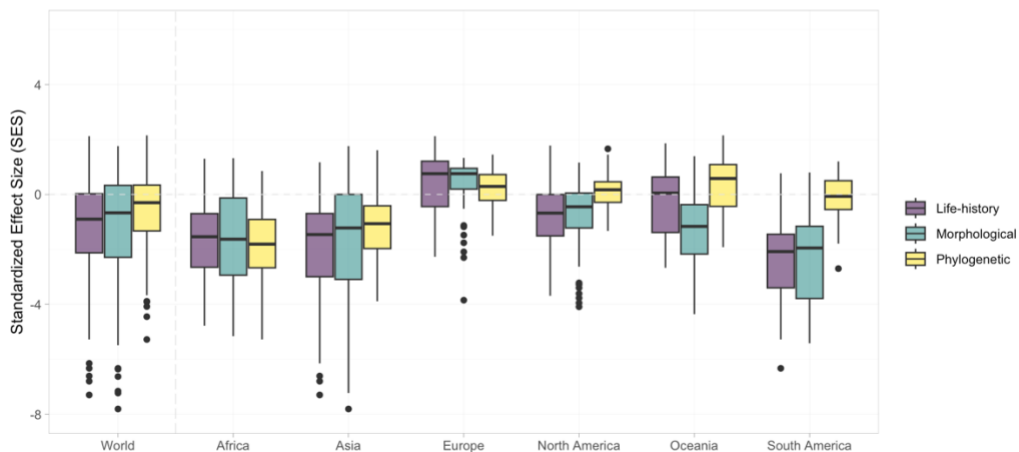
337 biodiversity.

(A) Combined introduction and extirpation
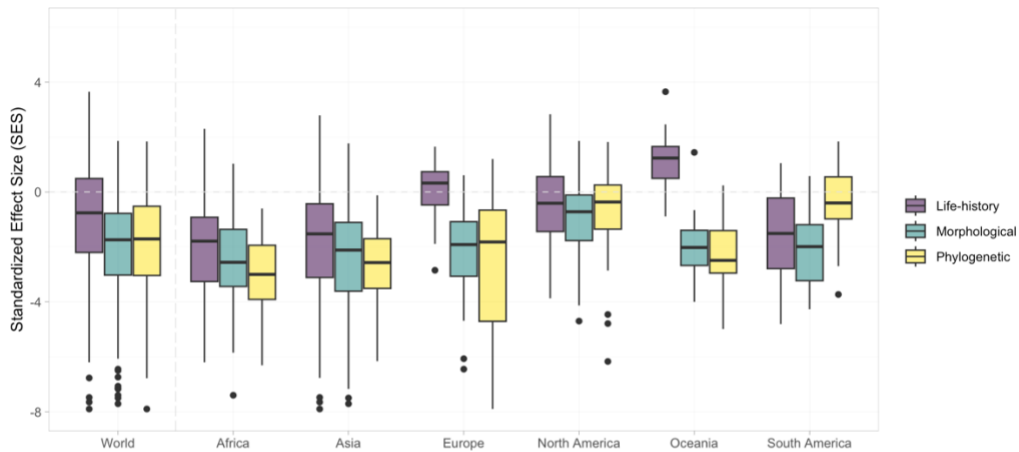

(B) After introduction of non-native species

(C) After extinction of threatened species

Figure 2 Changes in morphological, life-history, and phylogenetic richness in 281 regions across the world and for the six continents. For each scenario (see Method), the changes in morphological, life-history, and phylogenetic richness are expressed in terms of Standardized Effect Size (SES), meaning that observed changes were compared to 999 expected changes where the introduced species were randomized among a world pool of species. Threatened species are species classified as CR, EN, VU, and NT by IUCN. Scenarios with different classes of IUCN are provided in Supplementary.

13

Beyond the net loss in biodiversity, changes in species composition contributed to the reorganization of biodiversity at the community level, measured as the dissimilarity between native assemblages and assemblages after potential species composition changes (i.e., introduction and threatened species). Globally, the dissimilarity values were low as demonstrated by taxonomic dissimilarity (mean ± SD: 13.6% ± 8.4). The other facets of biodiversity were highly correlated (Spearman rank correlation tests: $r > 0.7$, $P < 0.001$).
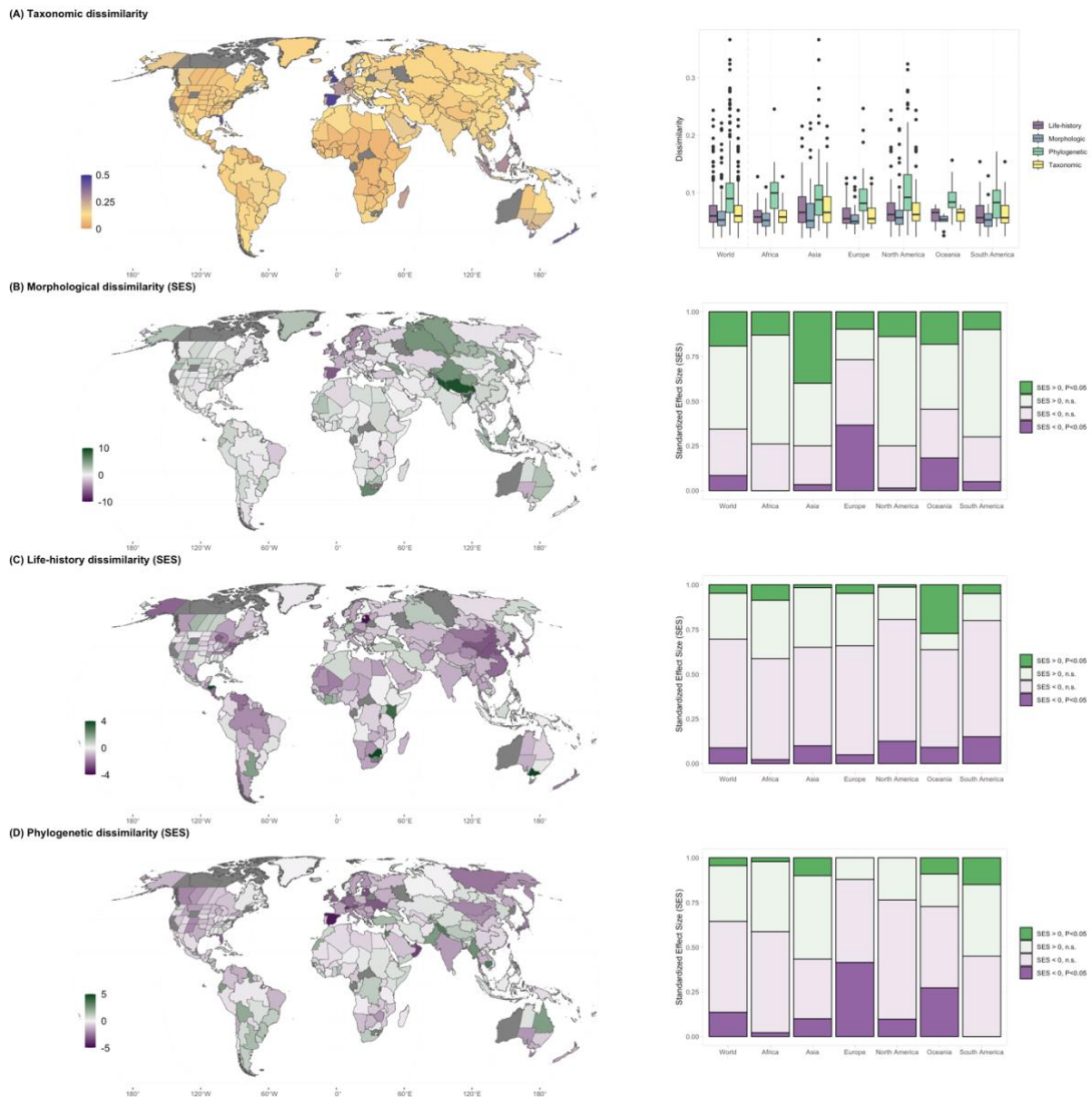
Figure 3. Changes in taxonomic, morphological, life-history, and phylogenetic dissimilarity in 281 regions across the world. For each region, the changes were measured as the difference between the two periods (i.e., native species vs. natives + non-natives – threatened). Changes in dissimilarity are shown for taxonomic in map (A) and for all facets in the boxplot. Changes for morphological (B), life-history (C), and phylogenetic (C) are also expressed in terms of Standardized Effect Size (SES), meaning that observed changes were compared to 999 expected changes where the introduced species were randomized among a world pool of species. Purple tones mean that changes in morphological, life-history, and phylogenetic dissimilarity were lower-than-expected. Green tones mean changes in

morphological, life-history, and phylogenetic dissimilarity were higher-than-expected. Threatened species are species classified as CR, EN, VU, and NT by IUCN.

The changes in species composition led to deeper variations in morphological dissimilarity and phylogenetic dissimilarity (r = 0.45, P < 0.001, Fig. 4A) than in life-history dissimilarity, which showed only a weak correlation with other diversity facets (r < 0.20, P < 0.01, Fig. 4B, C). For instance, in Asia, the decrease in morphological dissimilarity was lower-than-expected in 37% of regions while the life-history dissimilarity was not significant. In contrast, in Western Europe, 36% of the regions experienced a decrease lower-than-expected in morphological dissimilarity but not in life-history dissimilarity.
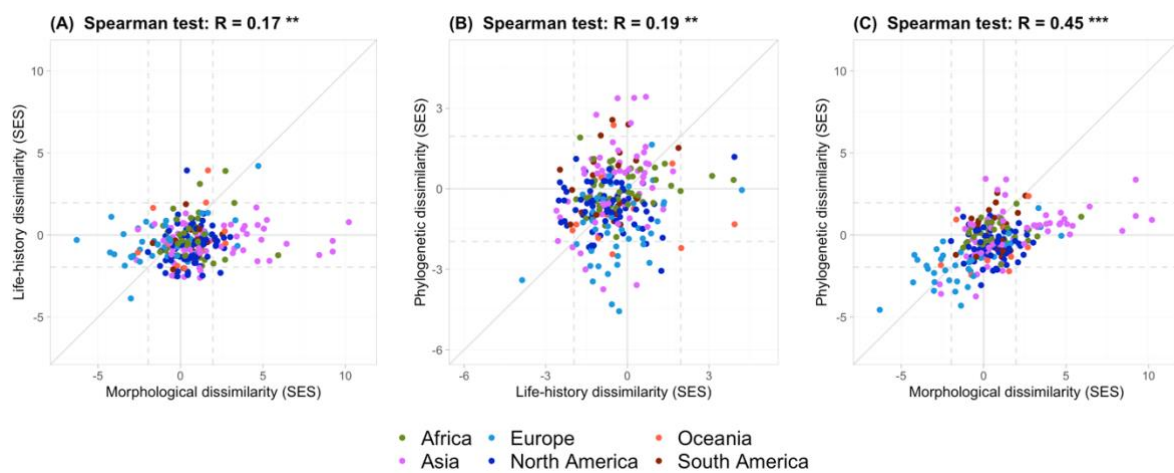

Figure 4. Correlation between standardized effect sizes between morphological, LH, and phylogenetic dissimilarity. Each dissimilarity metric was computed between native and native + non-native – threatened species in each country, independently. The standardized effect sizes (SES) were calculated between the observed dissimilarity and 999 expected changes if the non-native and threatened species were randomly selected (see Methods for details). Colors correspond to the continent each country belongs and are indicated in the legend. Spearman rank correlation tests were used between each standardized effect size of dissimilarity indices and indicated in the title of each panel. Threatened species are species classified as CR, EN, VU, and NT by IUCN.

The observed discrepancies between morphological and life-history traits can be attributed to the distribution of species within the morphological and life-history spaces (Fig. 5). Indeed, non-native species were more distant from native fauna in terms of life-history traits than morphological traits, with these differences being especially pronounced along the PC2 axis. This accounted for the higher-than-expected losses observed in life-history richness but also for the higher-than-expected decrease in dissimilarity for morphological traits. Conversely, for threatened species, we did not observe significant differences between the two sets of traits in the functional spaces and PC2 and even slightly higher for PC1 in morphological traits, explaining higher congruence in patterns for threatened species (Fig. 2B).

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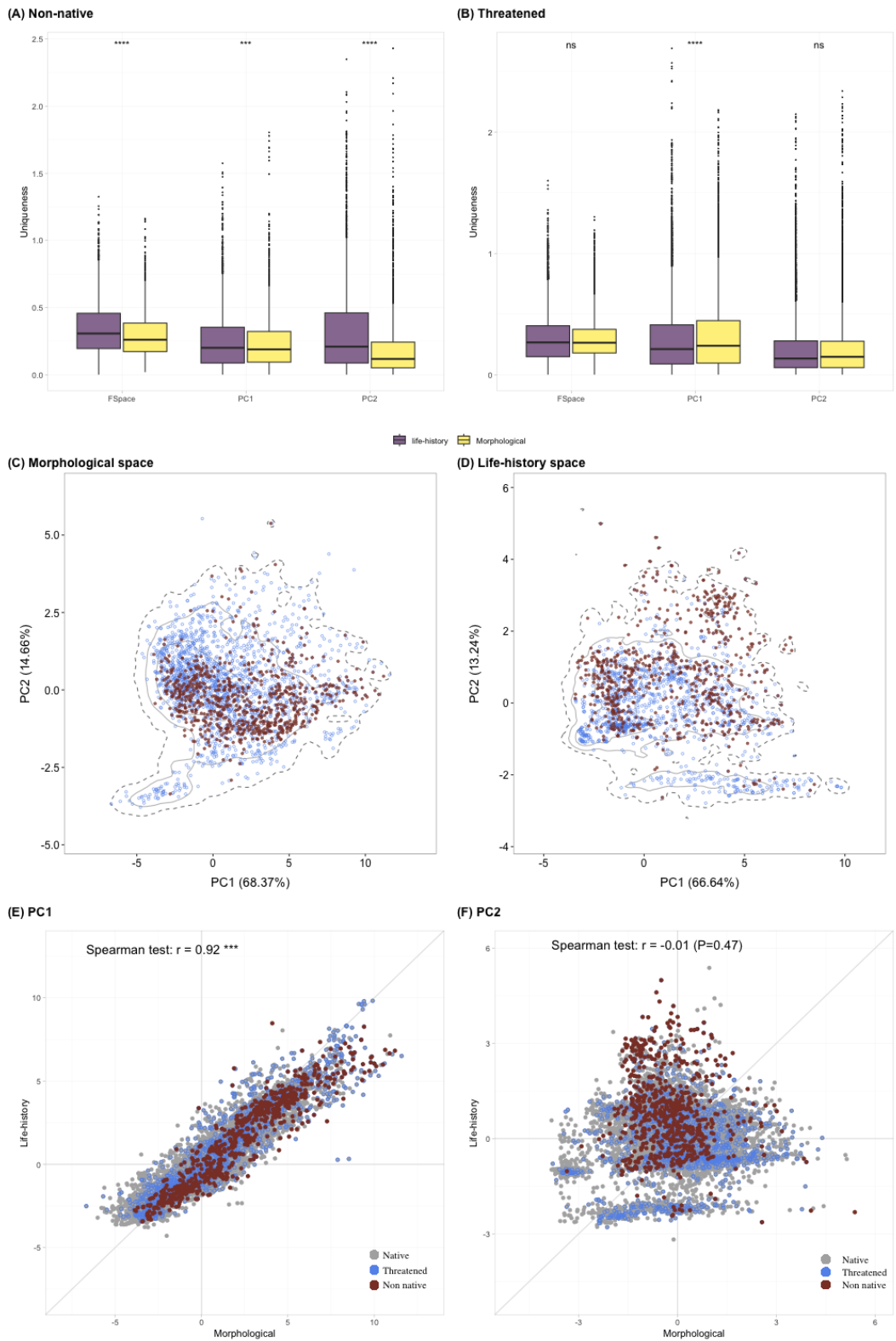
Figure 5. Functional uniqueness of non-native and threatened species between morphological and life-history traits. *Functional uniqueness was calculated for non-native (A) and threatened species (B) in the morphological (purple) and life-history (yellow) space as well as for each PC axis. The functional uniqueness of non-native and threatened species was calculated for each region and standardized to the center of the native species of each region. Threatened (blue) and non-native species (red) are positioned in the morphological (B) and life-history space (C). Relationships between morphological*

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and life-history are presented for each PC axis (E: PC1 and F: PC2) and tested using Spearman rank
correlation tests. Threatened species are species classified as CR, EN, VU, and NT by IUCN.

Discussion. Amid growing concerns about global biodiversity loss, the impacts of non-native species and the extinction of native species on ecosystems have garnered attention (Sobral *et al.* 2016; Su *et al.* 2021). We focus on bird assemblages worldwide to evaluate whether the introduction of non-native species could potentially offset losses in morphological, life-history, and phylogenetic diversity stemming from the extinction of threatened species. Our findings indicate that shifts in species composition could trigger a global decline in avian biodiversity due to the high number of threatened species. Furthermore, these losses are not random; they disproportionally involve species that are functionally and phylogenetically unique at the regional scale. Our results show that non-native species are not able to offset these changes because they are morphologically and phylogenetically close to native fauna. Consequently, our results emphasize the need for both controlling non-native species and preserving phylogenetically unique native species, which are the primary drivers of changes in the functional and phylogenetic structure of bird communities. These findings contribute to our understanding of the complex dynamics shaping global biodiversity and inform conservation strategies.

Our study reveals distinctive roles of non-native and threatened species in shaping the morphological, life-history, and phylogenetic facets of avian biodiversity. Extending a pattern observed in island bird assemblages (Sobral *et al.* 2016), we found that non-native species often clustered within a limited number of phylogenetic clades, whereas threatened species were scattered across a diverse array of clades. Because of this, even the extinction of a few threatened species often leads to the loss of unique parts of the phylogenetic tree. Importantly, our findings highlight that functional traits and phylogenetic richness are not always congruent. Therefore, a comprehensive understanding of species' ecological roles and evolutionary histories requires evaluating both dimensions of biodiversity (Gerhold *et al.* 2015; Losos 2008).

The choice of functional traits is critical, as it shapes our results and their ecological implications. Our data reveals a weak correlation between morphological and life-history traits. For instance, while non-native birds displayed distinct life-history traits compared to natives, they did not necessarily introduce new morphological traits into the existing assemblages. In both functional spaces, the dominant axis was related to body size, but the secondary axes diverged significantly, each capturing different aspects of bird ecological strategies. Notably, the non-native species showed greater uniqueness in the secondary axis of the life-history space. Such distinct reproductive strategies among non-natives could have far-reaching

435   implications, potentially affecting ecosystem functioning (Leitão *et al.* 2016; Loiseau *et al.*
436   2020; Mouillot *et al.* 2013).

437   Furthermore, compared to changes in life-history traits, changes in morphological diversity
438   correlated more strongly with changes in phylogenetic richness. This implies that variation in
439   life-history traits among closely related species is larger than morphological variation which
440   can be attributed to higher phylogenetic conservatism in morphological traits than for life-
441   history traits. This finding deepens our understanding of the multifaceted impacts of species
442   composition changes on biodiversity and underscores the need for nuanced conservation
443   strategies that consider these complex relationships. This also calls for considering a large
444   range of traits. Indeed, even if the chosen traits are known to be strongly related to the
445   ecological strategies of species (Pigot *et al.* 2019), there are some ecological functions that are
446   not included such as the diet traits which might be also relevant to assess the ecological role of
447   bird species (Wilman *et al.* 2014).

448   The importance of threatened species in this complex puzzle cannot be overstated. The
449   potential loss of threatened species has a more uniform impact on all facets of biodiversity
450   compared to the effect of non-native species. The congruence between levels of threats
451   demonstrates that threatened species contribute significantly to both functional and
452   evolutionary diversity, irrespective of their threat levels. The loss of endangered species not
453   only leads to a reduction in the diversity of ecological functions but also weakens the potential
454   for evolution and adaptation in response to different kinds of environmental disturbances. This
455   has implications for ecosystem stability and resilience, as phylogenetic diversity often plays a
456   crucial role in enhancing the adaptability of ecosystems to environmental changes (Cadotte &
457   Tucker 2018; Losos 1996; Sobral *et al.* 2014; Winter *et al.* 2013).

458   Beyond the net biodiversity loss, the generally low dissimilarity values suggest that
459   introductions or extinctions do not drastically shift the occupation of the functional spaces or
460   the evolutionary relationships among remaining bird species. This general pattern, however,
461   varied across the biodiversity indices. For example, Western Europe is poised for significant
462   shifts in morphological and phylogenetic structure but not in life-history. This result can be
463   attributed to the introduction of non-natives that tend to be morphologically redundant
464   compared to native species, a pattern also seen in island assemblages (Sayol *et al.* 2021).
465   Opposite patterns were found for several regions in central Asia depicting a turnover in the
466   morphological and phylogenetic structure of those assemblages.

467   However, the full scope of this biotic reorganization may still be underestimated due to
468   gaps in current data. Improvements in data availability are crucial for accurate functional and

phylogenetic assessments in conservation policies. Particularly in regions like South America and Southeast Asia (Fig. S4), our results may underestimate the intensity of taxonomic changes due to gaps in coverage of the IUCN Red List (Fig. S4c). The development of a complete database such as AVONET marks a significant step forward. However, our findings indicate that certain facets of ecological functions, such as reproduction may exhibit different patterns. Therefore, it's crucial to also consider these unaddressed aspects and make further progress in characterizing species traits.

In conclusion, the human impact on the global landscape of avian biodiversity is clear and presents a pressing need for action (Ellis 2015). The surge in global trade has the potential to significantly boost the spread of non-native species across the world, particularly in countries still sparsely affected such as Africa, South America, and Asia (Dawson *et al.* 2017; Seebens *et al.* 2018). The shifts in functional and phylogenetic structure of bird assemblages reported here might increase the vulnerability of ecosystems to future changes, demanding immediate, region-specific conservation policies. This study underscores the critical need for ambitious, comprehensive strategies to regulate both species introduction and the conservation of threatened species across the world.

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