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1 **Looming extinctions due to invasive species: Irreversible loss of ecological strategy and**
2 **evolutionary history**

3 **Running title:** Functional and phylogenetic extinctions due to biological invasions

4

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23 **Abstract**

24 Biological invasions are one of the main drivers of biodiversity decline worldwide.
25 However, many associated extinctions are yet to occur, meaning that the ecological debt
26 caused by invasive species could be considerable for biodiversity. We explore extinction
27 scenarios due to invasive species and investigate whether paying off the current extinction
28 debt will shift the global composition of mammals and birds in terms of ecological strategy
29 and evolutionary history. Current studies mostly focus on the number of species potentially at
30 risk due to invasions without taking into account species characteristics in terms of ecological
31 or phylogenetic properties. We found that 11% of phylogenetic diversity worldwide is
32 represented by invasive-threatened species. Further, 14% of worldwide trait diversity is
33 hosted by invasive-threatened mammals and 40% by invasive-threatened birds, with
34 Neotropical and Oceanian realms being primary risk hotspots. Projected extinctions of
35 invasive-threatened species result in a smaller reduction in ecological strategy space and
36 evolutionary history than expected under randomized extinction scenarios. This can be
37 explained by the strong pattern in the clustering of ecological profiles and families impacted
38 by invasive alien species (IAS). However, our results confirm that IAS are likely to cause the
39 selective loss of species with unique evolutionary and ecological profiles. Our results also
40 suggest a global shift in species composition away from those with large body mass, which
41 mostly feed in the lower foraging strata and have a herbivorous diet (mammals). Our findings
42 demonstrate the potential impact of biological invasions on phylogenetic and trait dimensions
43 of diversity, especially in the Oceanian realm. We therefore call for a more systematic
44 integration of all facets of diversity when investigating the consequences of biological
45 invasions in future studies. This would help to establish spatial prioritizations regarding IAS
46 threats worldwide and anticipate the consequences of losing specific ecological profiles in the
47 invaded community.

49 **Introduction**

50 Invasive alien species (IAS) are considered to be the second most important cause of
51 worldwide extinctions (C. Bellard, Genovesi, & Jeschke, 2016; Gurevitch & Padilla, 2004;
52 Maxwell, Fuller, Brooks, & Watson, 2016). Invasive predators alone have contributed to 58%
53 of modern extinctions (Doherty, Glen, Nimmo, Ritchie, & Dickman, 2016). Most of these
54 extinctions occurred on islands, but mainland areas also suffer from the presence of IAS
55 (Céline Bellard, Cassey, & Blackburn, 2016; Clavero, Brotons, Pons, & Sol, 2009). The
56 global threat of species invasions continues to increase with the spread of new emerging
57 invaders (Seebens et al., 2017, 2018).

58 Over the past decades, several review articles and global analyses have investigated the
59 ecological impact of IAS, ranging from local population declines to global extinctions
60 (Lapiedra, Sol, Traveset, & Vilà, 2015; McCreless et al., 2016). However, most studies focus
61 on the number of species prone to extinctions without taking into account species
62 characteristics in terms of ecological or phylogenetic properties, even though all three facets
63 (taxonomic, phylogenetic, trait) are advocated as essential for conservation (Mazel et al.,
64 2014). Indeed, phylogenetic and trait diversity provide a more direct link to ecosystem
65 properties compared to species diversity (e.g., Sekercioglu, 2006; Cadotte, Cardinale &
66 Oakley, 2008). Extinctions and population declines are not random, and as a result, they are
67 more likely to be associated with specific lineages or ecological profiles (i.e., combinations of
68 morphological, phenological, or behavioral features) (Cooke, Eigenbrod, & Bates, 2019;
69 Davis, Faurby, & Svenning, 2018; Pavoine, Bonsall, Davies, & Masi, 2019).

70 Previous assessments showed that climate change may lead to uncompensated phylogenetic or
71 functional losses, causing further biotic homogenization (Buisson, Grenouillet, Villéger,

72 Canal, & Laffaille, 2013; Thuiller et al., 2011), although this has not yet been explored in the
73 context of biological invasions. In other words, the manner in which species extinctions due
74 to IAS affect the ecological and evolutionary dimensions of biodiversity mostly remains an
75 open question (but see Lapiedra *et al.*, 2015; Sunday *et al.*, 2015; Longman, Rosenblad &
76 Sax, 2018). This issue is particularly important, as shown by the recent surge in interest
77 among international experts of the Intergovernmental Science-Policy Platform on Biodiversity
78 and Ecosystem Services (IPBES), who advocated that including ecological and phylogenetic
79 components of biodiversity is essential in biodiversity assessments (IPBES, 2019).

80 Moreover, taxonomic diversity often fails to capture phylogenetic and ecological diversity
81 (Devictor et al., 2010; Leclerc, Villéger, Marino, & Bellard, 2020; Mazel et al., 2014); it is
82 thus highly important to consider multiple dimensions of diversity when providing
83 recommendations on spatial conservation priorities (Brum et al., 2017; Pollock, Thuiller, &
84 Jetz, 2017). Indeed, biodiversity is a multifaceted concept, and the emerging consensus is that
85 a macro-ecological approach is needed to understand the impact of IAS worldwide. With
86 increasing information about the phylogenetic and life history traits of species, it is now
87 possible to conduct such an assessment and provide a clear picture of the consequences of
88 IAS on multiple dimensions of diversity.

89 A critical aspect of biodiversity assessments is thus to identify and characterize the diversity
90 elements most likely to go extinct, thus inferring the future state of biodiversity. Here, we aim
91 to provide such an assessment of at-risk biodiversity related to biological invasions with a
92 focus on the trait and phylogenetic diversity of birds ($n = 8,113$) and mammals ($n = 4,804$).
93 Trait diversity (TrD) represents how species are distributed in a multidimensional niche space
94 and provides a way to assess the ecological strategy adopted by species. We measured the
95 amount of trait space occupied by invasive-threatened species compared to the global pool
96 worldwide following the methodology of Villéger, Mason, and Mouillot (2008) based on five

97 ecological traits (Table 1). In other words, for TrD, we calculate how much of the total trait
98 space is occupied by invasive-threatened mammals and birds. Phylogenetic diversity (PD)
99 captures the evolutionary history of species (Pavoine et al., 2011) and potentially the species
100 contribution to feature diversity (Faith, 1992). We measured the amount of evolutionary
101 history represented by invasive-threatened species at a global scale for both birds and
102 mammals. We expect that species losses due to IAS may result in the loss of ecosystem
103 functions and/or adaptive features, which are indispensable in a changing environment. We
104 also investigate the contribution of invasive-threatened birds and mammals to the total PD and
105 TrD in different realms. Because all invasive-threatened species are unlikely to go extinct in
106 the near future, we further investigate extinction scenarios related to IAS worldwide. We
107 specifically explore the potential level of phylogenetic and ecological erosion in IAS
108 extinction scenarios over the next 50 and 100 years as well as under randomized extinction
109 scenarios. Finally, we determine the ecological profiles and species families most likely to be
110 lost because of IAS.

111

112 **Methods**

113 **Species studied**

114 We used the IUCN Red List of Species to identify the species considered to be the most
115 threatened by IAS (Version 3, accessed in August 2019). We considered species classified as
116 critically endangered (CR), endangered (EN), vulnerable (VU), near-threatened (NT), or least
117 concern (LC) by the IUCN Red List. We focused on the threatened species defined by the
118 IUCN (CR, EN, VU) for which IAS are listed as a threat (hereafter, invasive-threatened) and
119 excluded NT and LC species, which only represent “potentially threatened” species for two
120 reasons. Therefore, we filtered out species for which IAS is listed as a future threat or when

121 the threat is due to a problematic species/disease (including viral or prion) of unknown origin
122 or native. First, we want to focus our analyses on the threatened species (CR, EN, VU) facing
123 imminent extinctions so as to be conservative in our study following the methodology of
124 Toussaint *et al.* (2016). Second, IUCN only assigns a specific extinction probability to VU,
125 EN, and CR. No quantitative analyses of the probability of extinction are required for NT or
126 LC, while the latter category does not specify the major threat faced, which will add
127 uncertainty to our analyses of the IAS threat (IUCN, 2012). Moreover, we focused our
128 analysis on the most comprehensively assessed vertebrate groups by the IUCN: birds and
129 mammals (Meiri & Chapple, 2016). This resulted in a total of 207 invasive-threatened
130 mammals out of 5,708 mammals assessed by the IUCN Red List and 499 invasive-threatened
131 birds out of 10,965 birds (IUCN, 2017). Note that it is impossible to disentangle the effects of
132 IAS from other threats. IAS threat is mostly associated with biological resource use and
133 agriculture. In fact, the vast majority of species threatened by IAS are also likely to be
134 threatened by other threats with an average of 3.9 threats co-occurring for IAS-threatened
135 birds and mammals; thus, IAS-threatened species are species for which IAS is listed as a
136 threat, although other threats might also occur. In fact, 837 mammals and 736 birds are
137 threatened by other threats. We also used the mechanisms documented for each invasive-
138 threatened species based on the IUCN information (e.g., competition, hybridization, reduced
139 reproductive success, species mortality, ecosystem degradation) to assess the contribution of
140 each mechanism to the potential loss of PD and TrD. We considered the top three
141 mechanisms for both birds and mammals, which represent more than 80% of all mechanisms
142 documented for each taxon. We considered species mortality, competition, and ecosystem
143 degradation for mammals and ecosystem degradation, species mortality, and reduction in
144 reproductive success for birds. We considered each mechanism when cited alone or in
145 association with another mechanism. Therefore, our indicator of mechanisms represents the

146 documented occurrences of a given mechanism for each species. We also used the realm
147 associated with each species extracted from the IUCN database to conduct analyses at the
148 realm scale (i.e., Afrotropical, Australasian, Indomalayan, Nearctic, Neotropical, Oceanian,
149 and Palearctic).

150

151 **Trait diversity analysis**

152 To quantify TrD associated with invasive-threatened species, we used the five following
153 traits: body size, habitat breadth, foraging strata, main diet, and period of activity (Table 1 for
154 modalities), which are associated with the key ecological strategies of species (e.g., carcass
155 removal, seed dispersal, soil fertility, pollination; Sekercioglu, 2010; Hevia et al., 2017; see
156 also Appendix S3). All traits were extracted from the Elton trait database (Wilman et al.,
157 2014) except for habitat types, which were taken from the IUCN habitat classification scheme
158 (version 3.1). Main diet category for mammals is based on the majority of diet consumed by
159 each species, with a 50% threshold (following Wilman et al. (2014)). For instance, the mixed
160 herbivore category represents all species whose diet consists of more than 50% of plant
161 material, seeds, fleshy fruits, and nectar. The omnivore (mixed) category includes all species
162 that are 50% mixed herbivore and 50% mixed animal. Foraging strata category for birds is
163 based on the location of the different items consumed by each species with a 50% threshold
164 (following Wilman et al. (2014)). If the foraging strata include several categories, we kept the
165 foraging strata represented by more than 50% of the whole foraging strata; and if there is no
166 main foraging stratum represented by more 50%, it is designated as “multiple”. Body mass
167 category for birds and mammals is based on their respective quantiles with the very large
168 category representing the largest 20% of species. Overall, we extracted trait data for 4,804
169 mammals, including 186 invasive-threatened mammals, and 8,113 birds, including 360

170 invasive-threatened birds (Fig. S2). The two continuous variables (i.e., main diet and body
171 size) were categorized as discrete variables following the method of Leclerc *et al.* (2020) (see
172 also Table 1 for details).

173

174 To compute and investigate TrD for each invasive-threatened species assemblage, we
175 followed different steps:

176 (i) First, we grouped species as ecological entities, which represent groups of species
177 sharing the same trait values (Table 1), methodology that has been successfully
178 applied in functional analyses (Keyel & Wiegand, 2016; David Mouillot *et al.*,
179 2014). This step allowed us to calculate trait vulnerability, which is related to the
180 number of species included in each ecological entity. Trait vulnerability is high
181 when ecological entities have a small number of species and low when ecological
182 entities host a high number of species, which indicates high redundancy.

183 (ii) To build the trait space, we also calculated pairwise trait distances using the
184 Gower metric, which allowed us to deal with data of mixed types (Pavoine, Vallet,
185 Dufour, Gachet, & Daniel, 2009). We then used principal coordinate analysis
186 (PCoA) on the trait distance matrix to build a multidimensional trait space, where
187 the position of ecological entities corresponds to their differences. We selected the
188 best functional space by choosing the number of PCoA axes that provided the most
189 faithful representation of the initial functional trait values. In other terms, we
190 selected the number of axes that minimized the mean squared-deviation metric
191 (i.e., average deviation between Euclidean distance and Gower distance; Maire *et*
192 *al.*, 2015), which allowed us to compute the indices in a reasonable timeframe. In
193 this study, we selected five axes for mammals, which represent an average error of
194 3.6% (average deviation between original and transformation data) and three axes

195 for birds, which had an average error of 5.6%, indicating functional spaces of high
196 qualities.

197 (iii) Based on these trait spaces for birds and mammals, we calculated TrD (more
198 commonly known as functional richness following the definition of Villéger *et al.*
199 (2008)), which represents the volume of trait space occupied by invasive-
200 threatened species within the PCoA compared to the total pool of species. This
201 metric is widely applied in functional studies (Leclerc *et al.*, 2020; David Mouillot
202 *et al.*, 2014; Toussaint *et al.*, 2016). It has been demonstrated as the best
203 performing index and is highly correlated to other functional diversity measures
204 (Mouchet, Villéger, Mason, & Mouillot, 2010). This step was also conducted at
205 the realm scale.

206 (iv) We also performed statistical analyses to compare the trait modalities associated
207 with invasive-threatened species and those associated with either non-invasive-
208 threatened species worldwide and species threatened by threats other than IAS
209 (i.e., other-threatened species). Specifically, we compared the trait distributions of
210 invasive-threatened species with a random sample (with replacement) of an equal
211 number of species that are not invasive-threatened within the global pool (999
212 repetitions). We also compared the trait distributions of invasive-threatened
213 species with a random sample of an equal number of other-threatened species
214 within the global pool. These two comparisons allowed us to disentangle whether
215 the trait modalities were specific to the invasive threat or whether there were
216 related to threatened species (Table S1).

217 To test the significance of the results, we applied Chi-squared tests when the number of
218 species in each modality was ≥ 5 for all the samples. Otherwise, a Fisher's exact test was

219 used. If at least 95% of tests had a p-value <0.05 , the two distributions were considered to
220 significantly differ. We repeated the same analyses for both mammals and birds.

221

222 **Phylogenetic diversity analyses**

223 To compute PD hosted by invasive-threatened species, we used the PHYLACINE 1.2
224 complete phylogeny by Faurby *et al.* (2018) for mammals. This built phylogeny relies on the
225 morphological and genetic data of 5,831 known mammal species that have lived since the last
226 interglacial period. It also contains 1,000 trees that represent the uncertainties in topology and
227 branch lengths. We also verified species synonyms using the `rl_synonyms()` functions in the
228 `rredList` package (Chamberlain, 2019), and we pruned the original phylogenetic tree
229 ($n = 5,831$) to the species of the IUCN Red List included in the tree for mammals. In total,
230 5,529 species, including 205 invasive-threatened species, were included in the phylogenetic
231 trees (Fig. S1 for the sample size of each analysis). For birds, we used the tree version (V2.iii,
232 Ericson backbone) with the complete phylogeny of Jetz *et al.* (2014) and extracted 1,000
233 trees. The built phylogeny combines the relaxed clock molecular trees of well-supported avian
234 clades with a fossil-calibrated backbone with representatives from each clade. Similar to
235 mammals, we also searched for synonyms and pruned the original phylogenetic tree to 8,113
236 birds, including 360 invasive-threatened species (Fig. S1). Then, to measure PD associated
237 with invasive-threatened species for both mammals and birds, we used the Faith Index (using
238 the `pd()` function of the `picante` package; Kembel *et al.*, 2010) and calculated the average PD
239 across the 1,000 trees. Ultimately, we calculated the percentage for the invasive-threatened
240 species PD value compared to the total PD value of the sample in order to compare between
241 taxa. We also conducted PD analysis for each realm.

242

243 **Null model analyses for both phylogenetic and trait diversity measures**

244 For both mammals and birds, we tested whether the observed values of TrD were significantly
245 different from the null hypothesis that species are randomly distributed into ecological
246 entities. We used null models here to examine if TrD values are related to the number of
247 species or to the ecological profile of species. In each invasive-threatened sample, we
248 simulated a random assignment of species to ecological entities, while ensuring that each
249 ecological entity has at least one species. We simulated 999 random assemblages, while
250 keeping the number of species and ecological entities constant.

251 We also randomized the phylogenetic information between the invasive-threatened species for
252 both mammals and birds. For this purpose, we considered a constrained null model that
253 randomizes the names of taxa to the phylogeny. Thus, it randomizes which species are most
254 closely related to each other, although it does not alter the actual branch lengths or their
255 distributions. The rationale for this null model is to investigate if the species at risk of
256 extinction due to IAS are more closely related than expected randomly given their number.
257 The randomization was repeated 999 times over 1,000 trees each time.

258 More specifically, we calculated the deviation from the null expectation by computing the
259 standardized effect size (SES) and associated p-value. SES represents the difference between
260 the observed values of TrD or PD and the mean of predicted values by the null model divided
261 by the standard deviation of predicted values. The significance of the difference between
262 observed values and null expectations was tested using a bilateral test at a level of 5%. In
263 short, an observed value is considered significantly different from null expectations if the
264 observed value is in the top or bottom 2.5% of the null expectation distribution.

265

266 **Projected extinction scenarios**

267 We considered two extinction scenarios based on the IUCN Red List categories over the next
268 50 and 100 years. The IUCN Red List designed probabilities of extinctions for the three
269 threatened categories that are evaluated under criterion E: Prob(ext)CR = 0.5 in 10 years,
270 Prob(ext)EN = 0.2 in 20 years, and Prob(ext)VU = 0.1 in 100 years (Mooers, Faith, &
271 Maddison, 2008). Based on these probabilities of extinction, in the first scenario (50 years),
272 we assigned a probability of extinction for all species (even if there are not evaluated under
273 criterion E) of 97% for CR invasive-threatened species, 42% for EN, and 5% for VU
274 following Mooers *et al.* (2008) and Cooke *et al.* (2019). Similarly, the probability of
275 extinction under the second scenario (100 years) was 99% for CR invasive-threatened species,
276 66.7% for EN, and 10% for VU following Mooers *et al.* (2008). The randomized extinction
277 scenario assigned an equivalent number of species that were predicted to go extinct (from the
278 global pool) over the next 50 and 100 years but randomly with respect to species identity and
279 traits (Cooke *et al.*, 2019). All three extinction scenarios (100 years, 50 years, and random)
280 were each repeated 999 times. Finally, we compared the potential level of phylogenetic and
281 ecological erosion obtained under both scenarios with that obtained from a randomized
282 extinction scenario.

283 We used R version 3.6.1 to conduct the analyses and the ggplot2 package to plot the figures
284 (Wickham, 2016).

285

286 **Results**

287 *Trait and phylogenetic diversity hosted by invasive-threatened species worldwide and within*
288 *realms.* Our results showed that invasive-threatened birds occupy 40% of the total trait space
289 (TrD) for birds worldwide. By contrast, invasive-threatened mammals represented only 14%
290 of the total trait space for mammals (Table 2). The contribution of invasive-threatened species

291 to the total PD worldwide was 10.2% for mammals and 11.4% for birds. In all cases, the PD
292 values for invasive-threatened mammals and birds were significantly lower than expected
293 given the number of species (standardized effect size (SES = -7.294 and $P > 0.99$ for
294 mammals, and SES = -4.542 and $P > 0.99$ for birds)). Similarly, TrD values were significantly
295 lower than expected given the number of species (SES = -4.177 and $P > 0.99$ for mammals
296 and SES = -3.672 and $P > 0.99$ for birds). Both diversity metrics were thus more clustered
297 than expected under the null scenario.

298 We also calculated diversity measures for the top three mechanisms associated with invasive-
299 threatened species (Fig. 1). We found that the contribution of invasive-threatened birds
300 worldwide to TrD and PD was largely driven by ecosystem degradation (36.8% for TrD and
301 11.1% for PD) and mortality induced by IAS. The reduction in reproduction success was also
302 an important mechanism associated with the potential loss of TrD and PD in birds worldwide.
303 Conversely, the contribution of invasive-threatened mammals to TrD and PD worldwide was
304 mostly driven by mortality (12.05% for TrD and 8.8% for PD) induced by IAS, while
305 competition and ecosystem degradation were less likely to lead to mammal TrD losses.

306
307 By analyzing the diversity represented by invasive-threatened birds and mammals for each
308 realm, we found clear spatial differences (Fig. 2). The contribution of invasive-threatened
309 birds located in the Oceanian realm to the total bird TrD worldwide is nearly 30%. The
310 contributions of invasive-threatened birds in the Afrotropical and Neotropical realms to total
311 bird TrD was also high with 20% and 17%, respectively, whereas the contribution of
312 invasive-threatened mammals in the Neotropical realm to total mammal TrD was only 4%.
313 We found that all the realms showed low PD values for invasive-threatened mammals (0.7%-
314 4.2%) and birds (0.93%-5.4%). In addition, we found an average of 1.4 invasive-threatened
315 species for each ecological entity (groups of species sharing the same combinations of traits)

316 for mammals and 1.2 for birds within realms, while we estimated 6.8 species per ecological
317 entity in the rest of the species sample for mammals and 13.7 for birds.

318

319

320 ***Extinction scenarios of invasive-threatened species compared to random scenarios.*** Because
321 all the invasive-threatened species are unlikely to go extinct in the near future, we considered
322 extinction scenarios following the methodology of Cooke *et al.* (2019). On average, 6.5% to
323 7.7% of worldwide PD associated with invasive-threatened mammals is expected to be lost
324 over the next 50-100 years, while the percentage is slightly higher under the randomized
325 extinction scenarios for mammals (7.7% to 9.3%). Loss of PD worldwide for birds is
326 projected to be of a similar order of magnitude with 6.1% to 7.2%, which is also slightly
327 lower compared to randomized extinction scenarios (6.5% to 7.8%). The potential loss is
328 more pronounced for TrD, which may reach 5.8% to 7.8% for mammals (11.3% to 15.0%
329 under the randomized extinction scenarios) and 27.4% to 30.6% for birds worldwide (32.5%
330 to 36.3% under the randomized extinction scenarios) over the next 50-100 years due to IAS.
331 In all cases, the potential loss of both facets of diversity (PD and TrD) induced by IAS is
332 lower than expected given the species richness under the random extinction scenarios (Fig. 3).

333

334 ***Profile of species at risk of extinctions.*** We further analyzed the phylogenetic and ecological
335 properties of invasive-threatened species for both mammals and birds and compared them to
336 the characteristics of the pool of non-invasive-threatened species (hereafter, global pool) and
337 species threatened by threats other than IAS. We found that the 186 invasive-threatened
338 mammals represent 109 ecological entities (groups of species sharing the same combinations
339 of traits, with 14 ecological entities exclusively represented by invasive-threatened mammals

340 and not found in the global pool) (Table S1). Four families were comprised exclusively of
341 species threatened by IAS, although other threats may also be involved: Solenodontidae,
342 Myrmecobiidae, Phascolarctidae, and Thylacomyidae. Muridae and Cricetidae were the most
343 represented families among invasive-threatened mammals as well as among the global pool of
344 mammals. Similarly, the 360 invasive-threatened birds represented 149 ecological entities
345 (including 10 ecological entities exclusively hosted by invasive-threatened birds), which
346 belong to 92 families, including 5 families (i.e., Balaenicipitidae, Strigopidae, Rhynochetidae,
347 Notiomystidae, and Pedionomidae) that were exclusively found in the invasive-threatened
348 pool. The two most represented families within invasive-threatened birds were Procellariidae
349 and Psittacidae, although they were respectively ranked 59th and 4th when considering the
350 global pool of birds.

351 A closer investigation of the ecological profile of invasive-threatened species revealed that
352 mammals were represented by mostly large to very large species (68%), specialists with only
353 one or two habitats (65%), only nocturnal species (61%), those feeding on the ground (76%),
354 and those with a primarily or exclusively herbivorous diet (62%) (Fig. 4; see also Table S2).
355 We observed some significant differences with the global pool of mammals regarding
356 foraging strata (i.e., species were mostly aerial in the global pool), diet regime (species mostly
357 feed on invertebrates) and body size (species have a very small body size) (Fig. 4; see also
358 Table S4), while significant differences were also detected for the period of activity and
359 habitat breadth when compared to other-threatened species (See Fig. 4 and Table S4). We
360 found a significantly higher percentage of ground-foraging species within invasive-threatened
361 mammals compared to both the global pool and the other-threatened species pool (Fig. 4). By
362 contrast, invasive-threatened mammals were significantly less represented in the arboreal
363 foraging strata compared to the global pool and the other-threatened pool of mammals. Our
364 results also revealed that invasive-threatened species were less likely to be diurnal and less

365 likely to be specialized to one habitat compared to other-threatened species. In addition, it
366 appears that invasive-threatened mammals were significantly more represented among very
367 large species and significantly less among very small species in comparison with the global
368 pool, although these characteristics were not specific to invasive-threatened species, as other-
369 threatened species were also very large species. Finally, our results also revealed that
370 invertebrate diets were less represented among invasive-threatened mammals compared to the
371 global pool (Fig. 4). This was also the case with other-threatened species, although the
372 difference was not statistically significant.

373 Invasive-threatened birds were mostly large to very large species (63%) and habitat specialists
374 with three or less habitats (81%); the majority foraged in multiple strata (57%), were active
375 during the day (97%), and mostly fed on animals (41%) (Fig. 5; see also Table S3). Again,
376 invasive-threatened species had similar ecological characteristics compared to the rest of the
377 species pool but with a few notable exceptions (Fig. 5; see also Tables S6-7). For instance, a
378 significantly higher percentage of invasive-threatened birds forages below the water surface
379 compared to both the global pool and the other-threatened species pool, while a significantly
380 lower percentage forages in multiple strata compared to the other samples (Fig. 5). Invasive-
381 threatened species were also significantly less represented among very small species
382 compared to both the global pool and the other-threatened species pool (Fig 4). Moreover, we
383 also observed that invasive-threatened species mostly feed on animals. We also found that
384 invasive-threatened birds were less likely to be habitat specialists compared to other-
385 threatened species and more likely to live in three or four habitats, although we did not detect
386 such differences when comparing these results to the global pool (Table S6-7).

387

388

389 **Discussion**

390 Our results highlight the global contribution of invasive-threatened species to
391 biodiversity worldwide and illustrate the magnitude of the extinction debt related to biological
392 invasions. As such, our results reveal that biological invasion is potentially a major threat to
393 both the phylogenetic and trait diversity of birds and mammals worldwide. The contribution
394 of invasive-threatened birds and mammals to the total PD reaches 11%. Moreover, invasive-
395 threatened birds represent 40% of the total trait space for birds, which is considerable given
396 the number of invasive-threatened birds worldwide (~4.5% of all known birds). Our results
397 confirm that birds are more vulnerable to biological invasions compared to mammals (C.
398 Bellard et al., 2016; Céline Bellard et al., 2016), not only in terms of the number of species at
399 risk of extinction but also in terms of ecological and evolutionary diversity. Given the role of
400 birds for ecosystem services like pollination, seed dispersal, predation, and/or food-web
401 structure (C.H. Sekercioglu, 2010; Cagan H Sekercioglu, Schneider, Fay, & Loarie, 2008), we
402 expect that these losses will have important implications in the near future. Our results
403 contrast with the recent assessment of the IPBES, which ranks IAS as one of the last drivers
404 of change among global change components in the global state of nature (IPBES, 2019). We
405 demonstrate that it is crucial not to overlook biological invasions as a top driver of
406 biodiversity loss given the potential extinction debt. Note that on average, 3.9 threats were
407 associated with invasive-threatened species (Appendix S1). We observed that biological
408 resource use or agriculture and aquaculture are often associated with IAS threats for both
409 birds and mammals (see also Leclerc, Courchamp & Bellard, 2018; Leclerc *et al.*, 2020 for
410 insular ecosystems). In this context, our results suggest that IAS associated with these two
411 threats may lead to an important ecological and evolutionary debt worldwide.

412 Because all the species threatened by IAS are unlikely to disappear, we also conducted
413 50- and 100-year extinction scenarios to provide an initial approximation of the potential cost
414 of the current extinction debt due to biological invasions while considering only the imminent

415 extinctions. The potential losses might be tremendous with around 7% of PD worldwide for
416 both mammals and birds as well as 6% (mammals) and up to 27% (birds) of TrD worldwide.
417 It is worth noting that we only considered species that are facing imminent extinction
418 according to the IUCN Red List criteria, thus ignoring near-threatened, least concern, or data-
419 deficient species that might be at risk of extinctions in the near future due to IAS such as the
420 Reunion Bulbul (International., 2017). For instance, data-deficient species represent 15% of
421 the entire mammal dataset. Consequently, we potentially underestimated the extinction debt
422 due to IAS in this regard. On the contrary, the potential percentage of diversity predicted to
423 become extinct due to IAS is significantly lower than expected under the projected
424 randomized scenario given the species richness. The main explanation is that invasive-
425 threatened species are clustered in both the phylogenetic and trait space and that the projected
426 diversity losses associated with mammals and birds will not be random. In fact, a selective
427 process will occur across the phylogenetic tree and the ecological strategy space (Thuiller et
428 al., 2011; Yessoufou & Davies, 2016).

429 We found that both invasive-threatened mammals and birds have a significantly larger
430 body size than the rest of the pool but not when compared to other-threatened mammals.
431 Large body mass has already been highlighted as a life history trait that is strongly associated
432 with increasing extinction risks due to the slow reproductive rate associated with large body
433 mass (Hanna & Cardillo, 2013; Leclerc et al., 2020; Ripple et al., 2017). But note that body
434 mass may hide the effects of other variables linked to reproduction, locomotion or survival.
435 Therefore, the effects of body size could not be direct but reflect the impact of other variables
436 on species extinction risk. We also found that invasive-threatened species were more likely to
437 feed in the lower strata (i.e., ground level or below the water surface) and less likely to feed in
438 the higher strata (i.e., aerial or arboreal) compared to the other-threatened species, and more
439 generally, the global pool. This pattern has recently been highlighted for insular species

440 (Leclerc et al., 2020). Because most invasive-threatened species are found on islands, one
441 possible explanation could be related to the naïveté syndrome. Indeed, ground species are
442 more exposed to the introduction of nocturnal predators and are less capable of changing their
443 behavior to develop new defenses (Doherty et al., 2016), while higher-strata species may
444 develop avoidance strategies with the invasive mammals. We also found that invasive-
445 threatened species live in a limited number of habitats and are more likely to be specialist
446 species than generalist ones (Foden et al., 2018; Gonzalez-Suarez, Gomez, & Revilla, 2013;
447 Pacifici et al., 2017), but this tendency was not significantly different compared to the rest of
448 the species. In fact, we found that other-threatened mammals are more likely to be specialized
449 to a single habitat than invasive-threatened mammals, which are more likely to live in four
450 different habitats. We also found that most invasive-threatened mammals are primarily
451 herbivorous, which confirms the results of a recent study showing that large-bodied
452 herbivorous mammals are more at risk of extinctions due to global threats, including
453 biological invasions (Atwood et al., 2020). However, it would appear that the vast majority of
454 mammals are herbivorous, meaning that this characteristic is not particularly associated with
455 threatened species. By contrast, we did not observe that invasive-threatened bird species are
456 more likely to be herbivorous, whereas Atwood *et al.* (2020) detected that large-bodied
457 herbivorous birds are more at risk of extinctions with biological invasions. In fact, we found a
458 disproportionately higher number of invasive-threatened birds that feed on animals compared
459 to the rest of the species. More specifically, our findings suggest that habitat specialists and
460 species with lower-strata feeding strategies are more likely to be filtered out of the global pool
461 of mammals and birds. This is confirmed by the higher frequency of birds that feed on
462 multiple strata in the global pool compared to those that are threatened by IAS. Because these
463 traits have also been identified as highly vulnerable to other components of global changes,
464 we can expect that IAS will further affect the global composition of bird and mammal species.

465 In the near future, we may observe a shift in the global composition of birds and mammals
466 toward species that have a lower body mass. Indeed, the average size of invasive-threatened
467 species is four and eight times larger than the rest of the pool of birds and mammals,
468 respectively. Recently, Cooke *et al.* (2019) predicted a potential ecological downsizing within
469 mammals and birds due to global changes (Ripple *et al.*, 2017). Forecast shifts in ecological
470 traits could help us to identify the potential ecological consequences of extinctions for
471 community and ecosystem services (D. Mouillot, Graham, Villéger, Mason, & Bellwood,
472 2013). Moreover, the predicted loss of habitat specialists and species with restricted foraging
473 strata may lead to a shift toward generalist species, which may result in a global process of
474 homogenizing ecological strategies (Clavel, Julliard, & Devictor, 2011; Qian & Ricklefs,
475 2006; Sébastien Villéger, Blanchet, Beauchard, Oberdorff, & Brosse, 2011). In other words,
476 biological invasions have the potential to disrupt the ecosystem structure and function.

477 One of the most prominent findings of this study is that the evolutionary and
478 ecological implications of the extinction debt go far beyond a simple number of lost species.
479 Indeed, species at risk of extinctions due to IAS will impact the ecological and evolutionary
480 composition of future communities. We observed a clear ecological and evolutionary profile
481 of species vulnerable to invasions. While we know that IAS is one of the most important
482 drivers of species extinctions on islands (Bellard *et al.*, 2016a), this is the first time that we
483 documented the need to further investigate the ecological and adaptive consequences of the
484 biological invasion threat worldwide. For this reason, we investigated whether these losses
485 might result in the disappearance of particular profiles and/or lead to a shift in the
486 composition of mammals and birds worldwide. Our results point to the potential
487 disappearance of specific lineages of mammals (e.g., Myrmecobiidae, Thylacomyidae) and
488 birds (e.g., Notiomystidae, Rhynochetidae), because all species in these families are
489 threatened by IAS. This also includes families that are currently represented by a single

490 species. For instance, the sole member of the Myrmecobiidae family is *Myrmecobius*
491 *fasciatus*, which now has fewer than 800 individuals in Australia and continues to be
492 threatened by several IAS (Woinarski & Burbidge, 2016). Even if IAS appear to be the
493 primary threat to these species, other threats such as habitat degradation or natural system
494 modifications like fire regime changes are also involved in population decline; indeed, IAS is
495 rarely the sole threat responsible for the increasing risk of extinctions (Leclerc *et al.*, 2018 see
496 also Appendix S1). In fact, IAS is the only threat in less than 8% of cases in our dataset.

497 The potential implications of our results are multiple. For instance, we expect that the
498 extinction debt due to IAS in terms of PD will reduce future options to adapt in a changing
499 environment. Indeed, PD links evolutionary history to the conservation of feature diversity
500 and potential future options (IPBES, 2019). TrD represents the ecological properties
501 embodied by different species, which are of high concern to comprehend how ecosystems
502 may persist in a changing world. The potential loss of TrD associated with invasive-
503 threatened birds is very high concern for this group and may result in a reduced ability to
504 adapt in the future. Specifically, large bird species that mostly feed in the lower foraging
505 strata should be monitored and benefit from conservation measures. To better understand the
506 threat posed by biological invasions, we also conducted a spatial analysis of TrD and PD
507 threatened by biological invasions, which is a first step when establishing spatial prioritization
508 for research and conservation actions. We found that invasive-threatened bird species located
509 in the Oceanian realm, which is mostly comprised of islands, contribute to about half of the
510 total invasive-threatened bird space for both PD and TrD. Moreover, the Neotropical and
511 Australasian realms also represent hotspots of invasive-threatened mammals regarding TrD
512 and PD. This pattern is very similar to what was observed in previous studies focusing on
513 conservation priorities for birds and mammals (Jetz *et al.*, 2014; Pollock *et al.*, 2017),
514 although it has never been revealed specifically for biological invasions. Therefore, our

515 results imply that TrD and PD show clear differences across taxonomic groups and realms
516 regarding the biological invasion threat, which should be considered when establishing spatial
517 prioritizations.

518 Although our study brings potentially important insights into the role played by
519 biological invasions in biodiversity losses, it is important to extend this study to other
520 taxonomic groups before making decisions about conservation planning. The choice of life
521 history traits or the number of modalities and how they are categorized may also affect the
522 results, although our sensitivity analyses of body mass modalities showed that our results are
523 robust (Appendix S2). In addition, TrD or PD could be divided into multiple indicators
524 (richness, divergence, originality, specialization, rarity), all of which give complementary
525 information that is necessary to establish a clear spatial prioritization. Because conservation is
526 mostly undertaken at a local level, this study should be complemented with local assessments
527 of community vulnerability to biological invasions. Moreover, IAS rarely acted alone and
528 were often accompanied by other threats such as overexploitation and agriculture (Appendix
529 S1). To date, it is impossible to disentangle the specific contribution of IAS compared to other
530 threats, because the large majority of threatened species are at risk of extinction due to the
531 actions of simultaneous threats. However, our results suggest that at a minimum, IAS
532 associated with other threats could be an important driver of TrD and PD losses in the near
533 future. We were also able to compare ecological traits that are specifically associated with
534 IAS compared to other threats.

535 Our study is a first attempt at a global scale to study the potential consequences of IAS on
536 phylogenetic and functional diversity for birds and mammals. This study represents a first
537 step toward integrating the multidimensional nature of diversity. We thus appeal to ecologists
538 to investigate the consequences of biological invasions on multiple indicators of diversity and
539 then transform this knowledge into local conservation initiatives.

540 **Data availability:** All traits used in this study are included in the github repository and can be
541 extracted from the Elton trait database (Wilman et al., 2014). We also used phylogeny for
542 both birds and mammals; the data are freely available (Faurby et al., 2018; Jetz et al., 2014).

543

544 **Code availability:** Original codes for conducting the functional analyses are available at
545 (<http://villeger.sebastien.free.fr/Rscripts.html>). The R codes used to calculate TrD and PD are
546 available on github (https://github.com/cbellard/FDPD_IAST).

547

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553

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750 *Table 1: Description of the traits used to measure the trait diversity of birds and mammals as*
 751 *well as their modalities.*

753

Trait	Modality (Abbr.)	Taxa concerned	
Main diet	Plant material and seeds (Plant-seeds)	B, M	
	Fleshy fruits and nectar (Fruits-nect)	B, M	
	Invertebrates (Invert)	B, M	
	Vertebrate prey and carrion (Vert)	B, M	
	Omnivore (Mixed)	B, M	
	Mixed herbivore (Main veg)	B, M	
	Mixed animal (Main ani)	B, M	
Foraging strata	Water (W)	B	
	Ground-level (G)	B	
	Understory (U)	B	
	Mid-high (Mi)	B	
	Canopy (Ca)	B	
	Aerial (A)	B	
	Multiple strata (Mult)	B	
		Scansorial (S)	M
		Ground-level (G)	M
		Marine (M)	M
		Arboreal (Ar)	M
		Aerial (A)	M
	Period of activity	Crepuscular (C)	M
		Diurnal (D)	B, M
Nocturnal (N)		B, M	
Crepuscular / Diurnal (CD)		M	
Crepuscular / Nocturnal (CN)		M	
Crepuscular / Diurnal / Nocturnal (CDN)		M	
Habitat breadth	Number of habitats used	B, M	
Body mass	Very small (Vsmall)	B, M	
	Small	B, M	
	Medium	B, M	
	Large	B, M	
	Very large (Vlarge)	B, M	

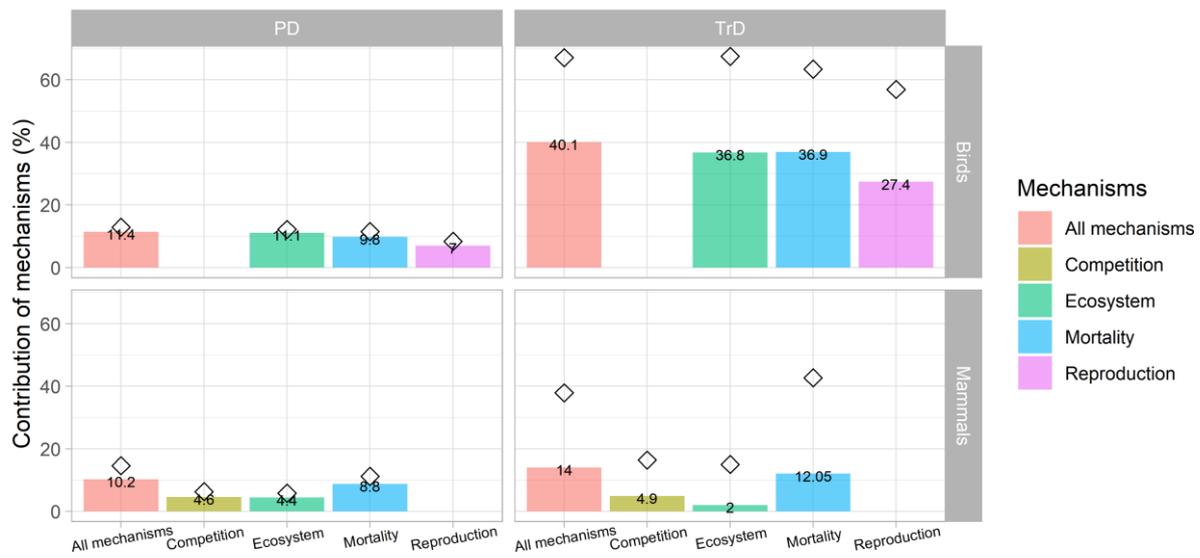
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756 *Table 2: Trait and phylogenetic diversity observed in worldwide invasive-threatened*
 757 *mammals and birds with their standardized effect size (SES) and p-value.*

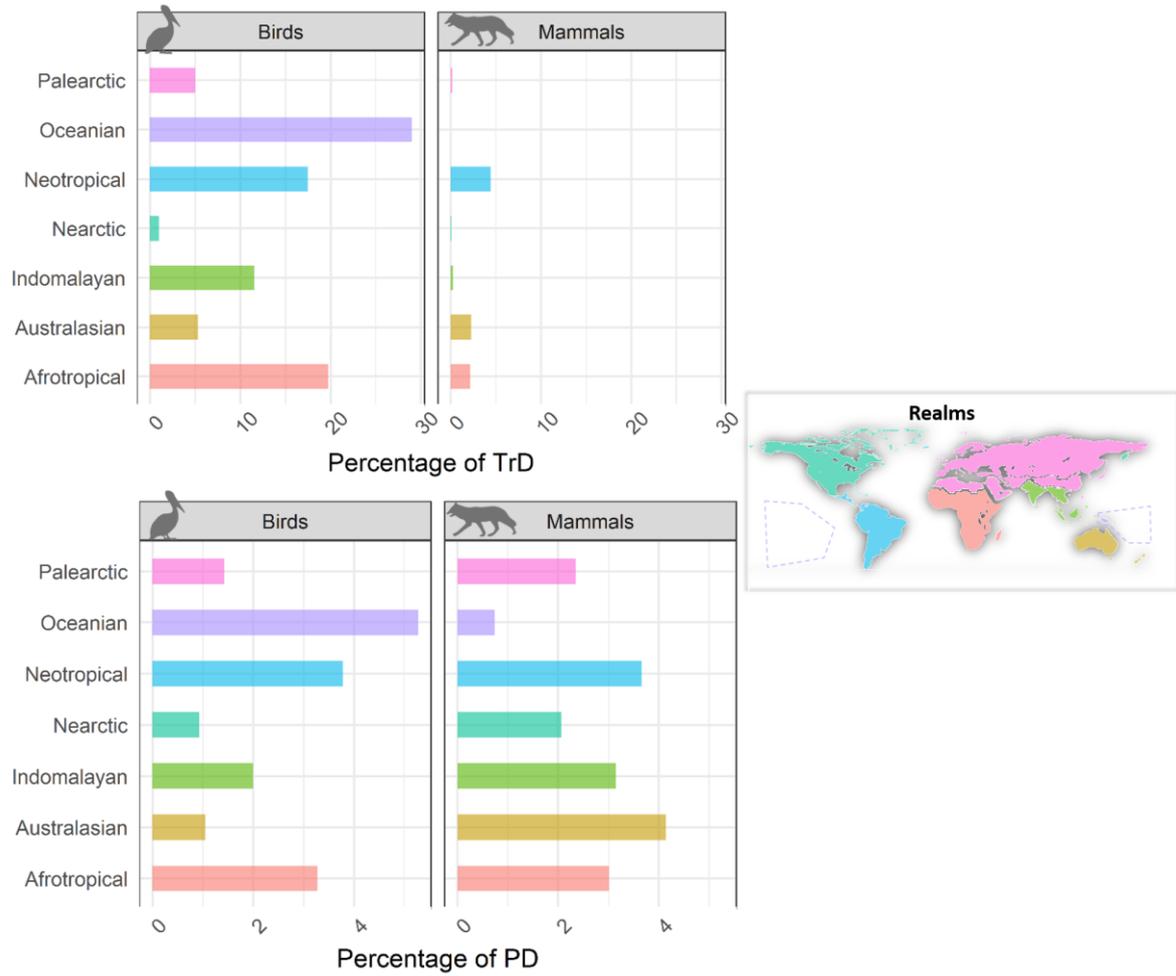
Taxa	Type of diversity	Observed (%)	Expected under null scenario (%)	SES	p-value	
Mammals	Trait	14.0	37.9	-4.177	> 0.999	***
	Phylogenetic	10.2	14.6	-7.294	> 0.999	***
Birds	Trait	40.1	67.1	-3.672	> 0.999	***
	Phylogenetic	11.4	12.9	-4.057	> 0.990	***

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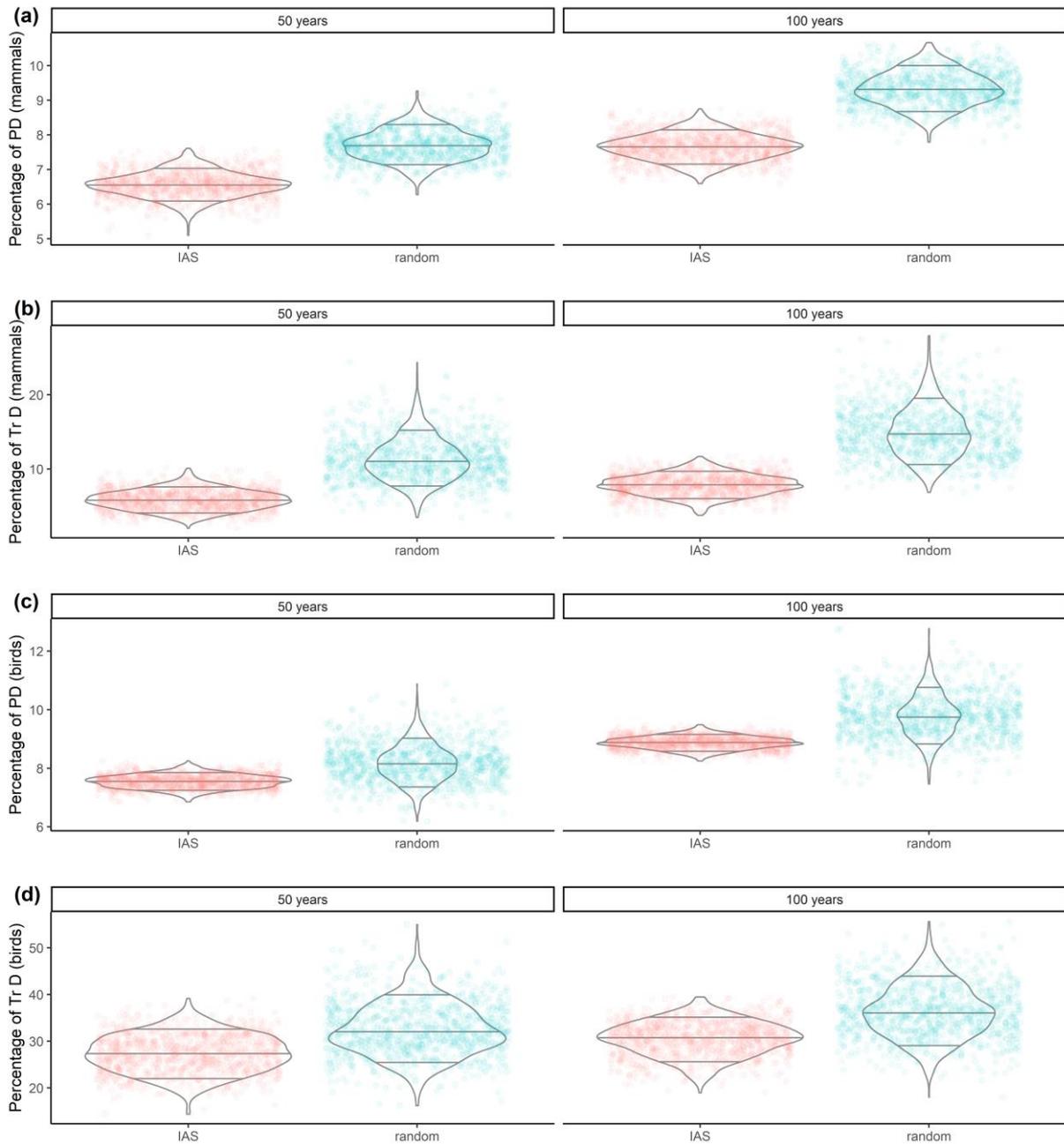
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760 *Figure 1: Contribution of the mechanisms (i.e., all mechanisms, competition, ecosystem*
 761 *degradation, mortality, and/or reduction in reproduction success) impacting invasive-*
 762 *threatened species to the total bird (or mammal) trait (TrD) and phylogenetic diversity (PD)*
 763 *in percentage. We only considered the top three mechanisms for each taxon. Bar plots*
 764 *represent the observed values of diversity, while the diamonds represent the null models*
 765 *(expected values when species identity is randomized).*



766

767 *Figure 2: Contribution of invasive-threatened species located in each realm to the total bird*
 768 *(or mammal) diversity for both trait (TrD) and phylogenetic diversity (PD).*



769

770 *Figure 3: Contribution of mammals and birds to the total phylogenetic (PD) and trait*
 771 *diversity (TrD) expressed in percentages under 50- and 100-year extinction scenarios. These*
 772 *values represent potential losses of PD and TrD under different extinctions scenarios. We*
 773 *considered two samples of species: invasive-threatened species and random species (species*
 774 *taken from the total pool of mammal and bird species worldwide that are not invasive-*
 775 *threatened species). We included jittered points for each of the 999 repetitions; the median*
 776 *and quantiles (0.10 and 0.90) are also shown.*

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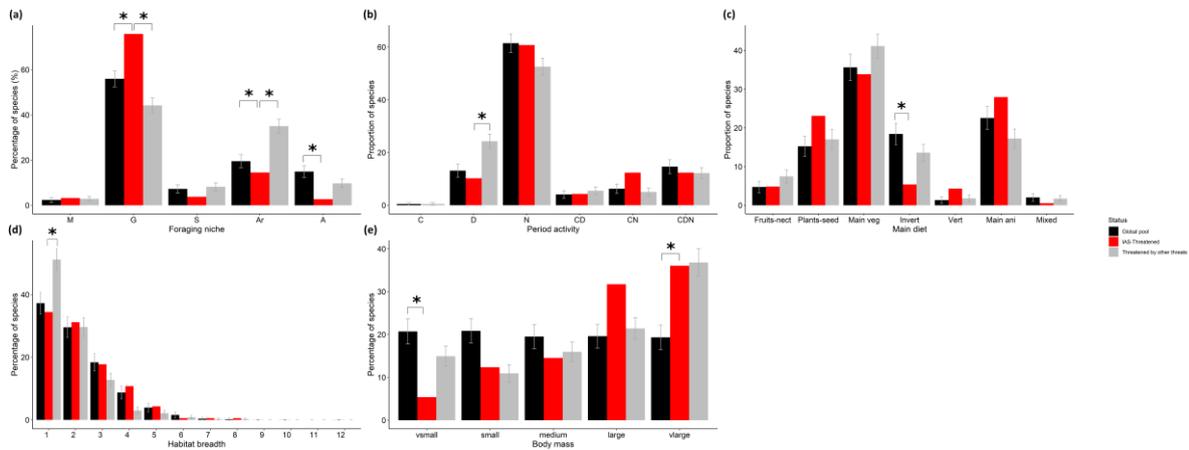
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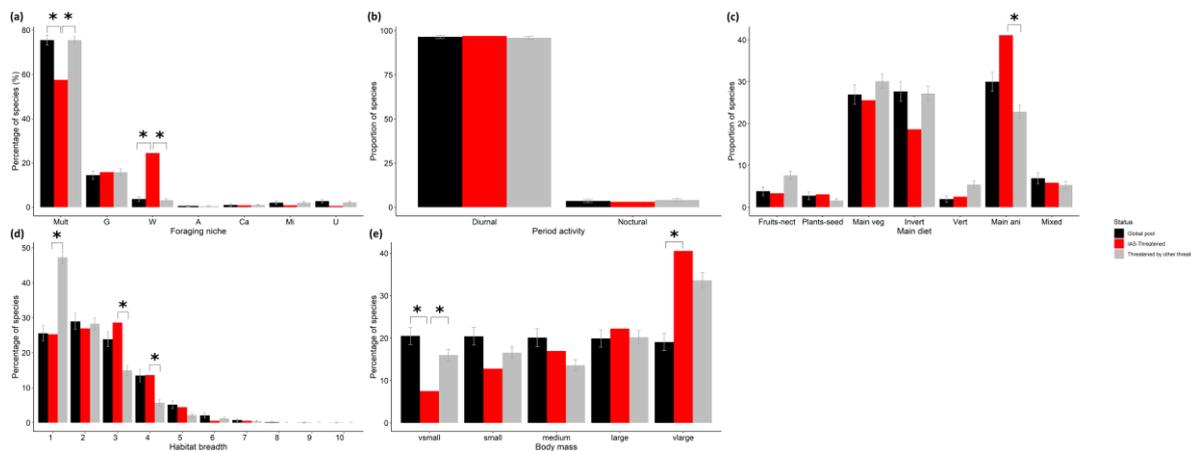
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784 *Figure 4: Percentage of invasive-threatened mammals (in red) for the five traits considered:*
 785 *A. Foraging strata (with M: marine, G: ground-level, S: scansorial, Ar: arboreal, A: aerial);*
 786 *B. Period of activity (with C: crepuscular, D: diurnal, N: nocturnal, CD: crepuscular-*
 787 *diurnal, CN: crepuscular-nocturnal, CDN: crepuscular-diurnal-nocturnal); C. Main diet; D.*
 788 *Habitat breadth; E. Body size. Their associated modalities are compared to the global pool*
 789 *(black bars with standard deviation errors bars) and other-threatened species (gray bars).*
 790 *See Table 1 for the modality descriptions and abbreviations. * indicates the percentage of*
 791 *trait modalities that are significantly different between invasive-threatened and other*
 792 *mammal species. A difference is significant when 95% of tests have a p-value < 0.05 (see*
 793 *Tables S4-5 for value details).*



794

795 *Figure 5: Percentage of invasive-threatened birds (in red) for the five traits considered: A.*
 796 *Foraging strata (with M: multiple strata, G: ground-level, W: water, A: aerial, Ca: canopy,*
 797 *Mi: mid-high, U: understory); B. Period of activity; C. Main diet; D. Habitat breadth; E.*
 798 *Body size. Their associated modalities are compared to the global pool (black bars with*
 799 *standard deviation errors bars) and the other-threatened species group (in gray). See Table 1*
 800 *for the modality descriptions and abbreviations. * indicates the percentage of trait*
 801 *modalities that are significantly different between invasive-threatened and other mammal species. A*
 802 *difference is significant when 95% of tests have a p-value < 0.05 (see Tables S6-7 for value*
 803 *details).*

804