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1 **Conservation priorities for functionally unique and specialized terrestrial vertebrates**  
2 **threatened by biological invasions**

3

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13 **Keywords** conservation, functional traits, invasive non-native species, irreplaceability,  
14 prioritization, tetrapods

15

16 **Article Impact Statement** Including species traits in conservation metrics helps prioritize  
17 species and sites endangeredby biological invasions.

18

19 **Abstract**

20 Invasive non-native species (INS) continue to pose a significant threat to biodiversity,  
21 including native population declines, which can ultimately disrupt ecosystem processes.  
22 Although there is growing evidence of the impacts of INS on functional diversity, most of the  
23 existing approaches to prioritization of species for conservation still focus on taxonomic  
24 diversity, neglecting the ecological role of species. We developed the functionally unique,  
25 specialized, and endangered by invasive non-native species (FUSE INS) score to fill this gap  
26 by combining functional irreplaceability (i.e., uniqueness and specialization) of species with  
27 their extinction risk due to INS. We calculated this score for 3,642 terrestrial vertebrates  
28 exposed to INS by assessing how INS affect them based on the IUCN Red List and  
29 evaluating their specialization and uniqueness in a multidimensional functional space. Thirty-  
30 eight percent of native species were both at high extinction risk because of INS and  
31 functionally unique and specialized, making them priority species for INS impacts mitigation.  
32 Priority species of amphibians concentrated in Central America and Madagascar and of  
33 lizards in the Caribbean islands, northern Australia, New Zealand, and New Caledonia.  
34 Priority bird and mammal species were more widespread (birds, mostly in coastal areas, on  
35 Pacific islands, and in northern India and New Zealand; mammals, in southwestern Europe,  
36 Central, East, and southern Africa, Southeast Asia, and eastern Australia). Seventy-eight  
37 species were also highly irreplaceable but not yet threatened by INS, suggesting that  
38 preventive conservation measures may help protect these species. For the 50 birds of the  
39 highest priority, 64% required conservation actions to mitigate the INS threat. The FUSE INS  
40 score can be used to help prioritize indigenous species representing large amounts of  
41 functional diversity. Incorporating functional diversity into the conservation prioritization of  
42 species and associated areas is key to accurately reducing and mitigating the impacts of INS  
43 on native biodiversity.

## 44 **Introduction**

45 According to the International Union for Conservation of Nature (IUCN) Red List, 333  
46 contemporary extinctions have occurred worldwide due to biological invasions and nearly  
47 7,000 species are currently at risk of extinction or extirpation due to the effects of invasive  
48 non-native species (INS) (defined by Pyšek et al. [2020]). It is expected that 2,301 species  
49 will go extinct within the next 50 years (IUCN, 2022). The consequences of biological  
50 invasions go far beyond a simple number of declining species; they represent profound  
51 changes in the functional diversity of vertebrate communities (Bellard et al., 2021). For  
52 instance, Sayol et al. (2021) found that non-native bird species lead to the functional  
53 homogenization of insular avian communities. The number of introduced bird species is often  
54 equal to or higher than the number of extinct birds on islands; however, they do not seem to  
55 compensate for the functional loss due to the extinction of functionally distinct birds (such as  
56 large-bodied birds with low flight ability and animal- or nectar-based diets [Sayol et al.,  
57 2020; Soares et al., 2022]). Invasive non-native species threaten 10% of the taxonomic and  
58 50% of the functional diversity of insular amphibians (Marino et al., 2022). Thus, focusing on  
59 taxonomic diversity greatly underestimates the impacts of INS, especially regarding the  
60 maintenance of ecosystem functions and services (Egerer et al., 2018). Therefore, other  
61 dimensions of diversity need to be accounted for in the establishment of conservation  
62 priorities to ensure they cover the complete picture of INS impacts on native biota.

63 Taxonomic diversity has been for decades the main indicator of the state of biodiversity  
64 (Purvis et al., 2019); thus, most conservation initiatives have relied on this dimension (e.g.,  
65 global biodiversity hotspots [Myers et al., 2000]). This practice disregards species' functional  
66 role and evolutionary history (Bonn et al., 2002; Rodrigues & Gaston, 2002). Moreover,  
67 taxonomic diversity is an unreliable indicator of other diversity dimensions, such as  
68 phylogenetic and functional diversity (Brum et al., 2017); therefore, it is even more important

69 to integrate them into conservation prioritizations (Diamond & Roy, 2023; Gaüzère et al.,  
70 2022).

71 New metrics have been developed to better integrate the multidimensionality of diversity,  
72 accounting for species' evolutionary history or functional diversity, in conservation measures  
73 (Cui et al., 2023; Gumbs et al., 2023; Hidasi-Neto et al., 2015; Isaac et al., 2007; Pimiento et  
74 al., 2020). For example, the evolutionarily distinct and globally endangered (EDGE) metric,  
75 which accounts for species' evolutionary distinctiveness and extinction risk, has been applied  
76 to many taxa and integrated into conservation schemes (Gumbs et al., 2018). In parallel,  
77 Pimiento et al. (2020) developed the “functionally unique, specialized and endangered”  
78 (FUSE) metric and applied it to marine megafauna to identify species of critical importance  
79 for functional diversity and at high extinction risk. Nevertheless, the integration of functional  
80 features into conservation policies remains anecdotal, especially the FUSE metric that has, to  
81 our knowledge, never been applied to any other taxon besides marine megafauna and  
82 elasmobranchs (i.e., sharks, rays, and skates) (Pimiento et al., 2023). Although conservation  
83 measures require identification of the threats species face, most prioritization measures do  
84 not account for the specificity of threats. For instance, INS have caused the extinction of  
85 native species with unique functional traits, some of which no longer exist in the current  
86 fauna (e.g., birds: Matthews et al., 2022). Once identified, INS need to be controlled or  
87 eradicated to save native species' from extinction. It is thus crucial to define a species  
88 conservation prioritisation strategy that takes into account the traits of species and their  
89 uniqueness and specialization among their taxonomic group from a threat perspective.

90 We developed the FUSE INS score to identify species endangered by INS and functionally  
91 unique and specialized, meaning they are irreplaceable in terms of functional strategies in the  
92 global functional space. Taking advantage of recent improvements in the FUSE and EDGE  
93 frameworks (Gouhier & Pillai, 2020; Griffin et al., 2020 [preprint]; Gumbs et al., 2023), we

94 implemented a new method to calculate the FUSE INS score of species and applied it to  
95 almost all (not crocodiles, turtles, or snakes) extant terrestrial vertebrates ( $n = 27,841$   
96 species). We relied on two major improvements that consider the uncertainty associated with  
97 the extinction probability of assessed species, recently developed by Gumbs et al. (2023)  
98 (EDGE2) and the severity of the impact of INS on native species, based on the IUCN Red  
99 List.

100 To date, all the major international institutions agree that biological invasion represents one  
101 of the main direct drivers of biodiversity loss (Bellard et al., 2022). In December 2022,  
102 COP15 of the Convention on Biological Diversity adopted a specific target for reducing and  
103 mitigating the impacts of INS on native biodiversity (Secretariat of the United Nations  
104 Convention on Biological Diversity, 2021). To achieve this goal, it is essential to identify the  
105 species and areas most vulnerable to INS impacts (Essl et al., 2020), not only by considering  
106 the imperiled taxonomic diversity but also by accounting for the functional value of species  
107 and ecosystems. In this context, this index dedicated to species affected by INS will help  
108 identify and prioritize functionally irreplaceable vertebrates at high risk of extinction due to  
109 INS and identify and monitor species (and associated sites) that are not yet threatened by INS  
110 but have a high functional irreplaceability, representing an opportunity for the future of  
111 biodiversity. Preserving species that present exceptional traits will directly contribute to the  
112 conservation of global functional diversity. Because INS involve specific measures of  
113 prevention, control, and eradication relative to habitat loss or overexploitation, which require  
114 other types of conservation measures, we focused only on INS threat.

115

## 116 **Methods**

### 117 *Rationale*

118 Inspired by the FUSE approach, we built the FUSE INS score to focus on species that have a  
119 high extinction risk due to INS and are of particular importance for functional diversity  
120 (Pimiento et al., 2020). We took advantage of the recent development of the EDGE2 metric  
121 to quantify the uncertainty associated with the species' probability of extinction. The FUSE  
122 INS score of a given species is the product of its extinction risk due to INS ( $P_{INS}$ ) and its  
123 functional irreplaceability accounting for all species in the taxonomic group. Species that are  
124 strongly threatened by INS and functionally irreplaceable will have a high FUSE INS score,  
125 whereas species that are less affected by INS or less exceptional in terms of ecological  
126 characteristics will have a lower score. Specifically, we defined the FUSE INS score of a  
127 given species as the log-transformed combination of its extinction probability due to INS  
128 threat ( $P_{INS}$ ) and functional irreplaceability, captured by functional specialization (FSp) and  
129 functional uniqueness (FUn), as follows:

$$130 \text{ FUSE INS} = \ln(1 + P_{INS} \times \text{FSp} + P_{INS} \times \text{FUn}) \quad (1)$$

131 (Fig. 1)

### 132 *Species threats and conservation status*

133 We characterized species threats, conservation status, and conservation actions with the  
134 advanced research tool from the IUCN Red List of Threatened Species (IUCN, 2022). First,  
135 we identified the terrestrial vertebrates exposed to INS as all species associated with the  
136 threats "Invasive non-native/alien species/diseases" or "Problematic species/diseases of  
137 unknown origin" (the latter, only when we could determine the non-native origin of the  
138 named problematic species). This process identified 1,895 amphibians, 816 birds, 508 lizards,  
139 and 423 mammals affected by INS (3,642 total species). Vertebrates not exposed to INS  
140 ( $n=24,199$ ) received a  $P_{INS}$  of 0 and thus a FUSE INS of 0. We also collected information  
141 regarding the other threats these species face. We then extracted information about the scope

142 and severity of the INS threat specifically to quantify the INS impact magnitude. Species  
143 with >50% of their total population experiencing a significant decline (i.e., slow, rapid, or  
144 very rapid) due to INS were classified as sustaining a high impact from INS, whereas species  
145 with <50% of their population experiencing fluctuations or no declines were classified as  
146 experiencing a low impact. Species that had no information for the INS impact magnitude  
147 were classified as NA.

148 Second, we collected the IUCN Red List category (i.e., global conservation status) of species  
149 affected by INS: least concern (LC), near threatened (NT), vulnerable (VU), endangered  
150 (EN), critically endangered (CR), or data deficient (DD). Finally, we extracted the  
151 conservation actions needed (which indicate the conservation actions or measures needed for  
152 the concerned animal), based on category “invasive/problematic species control” from the  
153 Conservation Actions Classification Scheme (version 2.0), as conservation actions for INS  
154 management.

### 155 *Extinction probability of species associated with INS threat*

156 Following the EDGE2 protocol, we incorporated uncertainty in extinction probability  
157 (Gumbs et al., 2023). Specifically, we computed a smoothed distribution of extinction  
158 probabilities as in Gumbs et al. (2023). The median probability of extinction was 0.06 for LC,  
159 0.12 for NT, 0.24 for VU, 0.49 for EN, and 0.97 for CR species (Mooers et al., 2008;  
160 Appendices S1, S2). Thus, each IUCN Red List category had an associated range of  
161 extinction probabilities (e.g., 0.0001 to 0.09 for LC species and 0.7 to 0.9999 for CR species)  
162 (ranges of all categories in Appendix S1). The size of probability ranges differed among the  
163 categories, introducing a higher variance in extinction probability for intermediate categories.  
164 A species at very high (or low) extinction risk is more likely to become extinct (or not), with  
165 very low uncertainty, as illustrated by a low variance in  $P_{INS}$ . In contrast, a species at



166 moderate extinction risk could become extinct but could also thrive longer than within 50  
167 years. In such cases, the associated uncertainty is higher at those intermediate risk of  
168 extinctions, illustrated by a larger range of  $P_{INS}$ . This method for deriving  $P_{INS}$  presents  
169 several advantages: extinction probabilities are continuous, avoiding a strong bias in the final  
170 score due to a coarse categorization of species extinction risk and allowing a smooth  
171 changing of categories; some uncertainty is attributed to each probability; and the amount of  
172 uncertainty depends on the IUCN Red List category (Gumbs et al., 2023).

173 We further divided each IUCN Red List category into two subcategories based on the INS  
174 impact magnitude. We then drew 1,000 values of  $P_{INS}$  for each species by randomly selecting  
175 1,000  $P_{INS}$  in the range corresponding to the species' subcategory, considering both  
176 conservation status and INS impact magnitude (Figure 1a, Appendix S2). For instance, if a  
177 species is CR with a high INS impact magnitude,  $P_{INS}$  would be randomly picked from 0.874  
178 to 0.9999, whereas for a CR species with a low impact magnitude it would be picked from  
179 0.7 to 0.874. For NA species regarding the INS impact magnitude,  $P_{INS}$  values were selected  
180 in the whole range of extinction probabilities of the species' conservation status. For DD  
181 species,  $P_{INS}$  was selected in the whole range of the 10 categories (0.0001-0.9999), regardless  
182 of conservation status and INS impact magnitude.

### 183 *Functional irreplaceability definition*

184 The functional value of species was measured in a functional space, which was defined as a  
185 multidimensional space containing all species from a taxonomic group, where axes are a  
186 combination of species traits. The functional irreplaceability represents the degree of  
187 specialization and uniqueness of species in the functional space (Pimiento et al., 2020).

188 Functional specialization (FSp) accounts for species' distance from the average strategies of

189 the taxonomic group, and functional uniqueness (FUn) measures the level of isolation of each  
190 species in the functional space of its respective taxon (Mouillot et al., 2013).

191 *Trait data and functional spaces*

192 We combined a global list of 27,841 terrestrial vertebrates (6,492 amphibians, 10,943 birds,  
193 5,505 mammals, and 4,901 lizards) for which we had trait information from Marino et al.  
194 (2022) for amphibians, lizards, and mammals and from Marino and Bellard (2023) for birds.  
195 Because reptile traits were poorly reported for major groups, such as snakes, turtles, and  
196 crocodiles, we focused on lizard species for this taxon. Traits were related to species  
197 morphology, life history, and ecology, which together reflect species functional strategies  
198 (Marino et al., 2022; Marino & Bellard, 2023). We ended up with a total of four traits for  
199 amphibians, 10 traits for birds, and five traits for both lizards and mammals (details on trait  
200 definition and sources are in Appendix S3). These traits are commonly used in studies  
201 evaluating functional diversity and summarizing the effects of species on ecological  
202 processes and their responses to environmental change (Bellard et al., 2021; Cooke et al.,  
203 2019; Marino et al., 2022).

204 We built a multidimensional functional space for each taxonomic group separately with a  
205 two-step approach that allowed us to consider various types of variables (e.g., continuous,  
206 ordinal, factorial). First, we computed pairwise trait-based distances between species with the  
207 Gower (1971) dissimilarity index. Second, we calculated species coordinates in the functional  
208 space by applying a principal coordinate analysis (PCoA) on the distance matrix to reduce the  
209 number of dimensions. The trait-based distance matrix was obtained with the `funct.dist()`  
210 function from the `mFD` package, and the PCoA was computed with the `pcoa()` function from  
211 the `ape` package (Magneville et al., 2021; Paradis & Schliep, 2019). Then, we evaluated the  
212 quality of spaces with an increasing number of principal components to build them. Quality

213 was assessed by the root mean square deviation (rmsd) between trait-based distances and  
214 distances in the PCoA-based space, and the best functional space was obtained for the lowest  
215 rmsd score (Maire et al., 2015). The best functional spaces contained three dimensions for  
216 amphibians (rmsd = 0.070), seven dimensions for birds (rmsd = 0.032), and five dimensions  
217 for lizards (rmsd = 0.071) and mammals (rmsd = 0.069) (Appendix S4). The cumulated  
218 variance explained by the final functional spaces ranged between 69% to 74% (Appendix  
219 S4).

### 220 *Functional specialization and uniqueness*

221 Finally, for a given species  $i$ , we calculated FSp as the Euclidean distance between  $i$  and the  
222  $n$ -dimensional functional space centroid and FUn as the sum of the Euclidean distances  
223 between  $i$  and its five nearest neighbors (Figure 1b). When combined, FSp and FUn represent  
224 the functional irreplaceability of a given species within its own taxonomic group (Pimienta et  
225 al., 2020). Both metrics were normalized from 0 to 1. For FSp, 0 represented the most central  
226 species in the functional space, whereas 1 was the most distant species from the centroid  
227 (Appendix S5). For FUn, 0 represented the least isolated species (given the distance from its  
228 five nearest neighbors), and 1 was the most isolated species (Appendix S6). The two metrics  
229 were not correlated because they were complementary for all taxonomic groups (Appendix  
230 S7).

### 231 *Final metric and priority lists*

232 We calculated the FUSE INS score for each species with equation (1) and used the values of  
233  $P_{INS}$ , FSp, and FUn calculated previously. Because all three metrics ranged from 0 to 1, the  
234 FUSE INS score ranged from 0 to  $\ln(3) \approx 1.1$ . We also calculated FUSE INS scores with two  
235 alternative formulas to quantify the sensitivity of this index to different formulations  
236 (Appendix S8). Each species received 1,000 FUSE INS scores, one for each of the 1,000

237 generated  $P_{\text{INS}}$ , from which we calculated the median score per species and its standard  
238 deviation. Furthermore, for each taxonomic group, we calculated the median score based on  
239 all species of the taxonomic group to classify species in priority lists based on different  
240 conservation objectives (Gumbs et al. 2023) (Figure 1c): core, research, watch, and  
241 borderline lists. The core list contained threatened species with a CR, EN, or VU  
242 conservation status that had more than 95% of their scores above the median score of all  
243 species of their respective group. Species in this list were of high functional value and would  
244 require an urgent and adapted conservation response to prevent their extinction. The research  
245 list contained data deficient (DD) species with more than 95% of their scores above the  
246 median score of their respective group. This list would help target species that are of high  
247 functional value but have not yet received enough research to have a proper conservation  
248 evaluation. The watch list contained nonthreatened species with an NT or LC conservation  
249 status that had more than 95% of their scores above the median score of their respective  
250 group. Species in this list were of high functional value but not immediately prone to  
251 extinction; however, they would benefit from proactive conservation strategies. Finally, the  
252 borderline list contained threatened species with a CR, EN, or VU conservation status that  
253 had 80-95% of their scores above the median score of their respective group. Species in this  
254 list had a high extinction risk but were not as functionally exceptional as the species from the  
255 core list. However, if species in the core list became extinct, they would be the next species  
256 on the verge of extinction harboring the most functionally distinct features.

257 We derived the four lists for each taxon (i.e., amphibians, birds, lizards, and mammals). We  
258 also analyzed the lists' sensitivity to the 80% and 95% thresholds by building the lists based  
259 on thresholds of 75% (or 85%) and 90% (or 97.5%) (results in Appendix S9).

260 *Species distribution ranges and richness maps*

261 We collected the distribution range of amphibians and mammals from the IUCN Red List, of  
262 birds from Birdlife, and of lizards from the GARD database (BirdLife International &  
263 Handbook of the Birds of the World, 2020; IUCN, 2022; Roll et al., 2017). We considered  
264 only range polygons where the species were considered extant, native, or reintroduced and  
265 resident or breeding. We then extracted the species' potential presence in hexagonal cells of  
266 110 km long (dimension of 1° cells at the equator) to derive maps of species richness. At the  
267 cell level, we evaluated the correlation between the species richness of FUSE INS species  
268 and the sum of FUSE INS scores of all present species. Because the two metrics were highly  
269 correlated (Pearson's correlation coefficient > 0.80 for all groups) (Appendix S10), we  
270 displayed only the maps based on the species richness of FUSE INS species.

271 All analyses were conducted with R 4.2.2 (R Core Team, 2022). Data and codes supporting  
272 the results in the paper are archived in Zenodo and linked to a Github public repository:  
273 <https://zenodo.org/doi/10.5281/zenodo.10716188>.

274

## 275 **Results**

276 We calculated the FUSE INS score of 3,642 terrestrial vertebrates listed as associated with  
277 the INS threat on the IUCN Red List (the scores for all 3,642 species are available from  
278 Zenodo [<https://zenodo.org/doi/10.5281/zenodo.10716188>]). The scores ranged from 0 to  
279 0.992, thus never reaching the maximum possible value. The highest score was for kakapo  
280 (*Strigops habroptila*), a large, flightless, endemic, ground-nesting, nocturnal parrot from New  
281 Zealand. Median scores for each group were low overall: 0.05 (SD 0.13) for amphibians, 0.06  
282 (SD 0.11 and 0.13) for birds and lizards, and 0.04 (SD 0.09) for mammals. The FUSE INS  
283 scores calculated with alternative formulas were highly correlated with the main formula

284 (Pearson's correlation coefficient > 0.99 for all taxonomic groups and formulas) (Appendix  
285 S8) and resulted in the same ranking of species.

286 We identified 1,378 species in the FUSE INS core list: 684 amphibians, 343 birds, 199  
287 lizards, and 152 mammals (Figure 2). These represented 38% of all species exposed to INS  
288 (complete lists with species scores are in Appendix S15). We did not identify any species  
289 belonging to the FUSE INS research list (i.e. species with high FUSE INS score but of DD  
290 status; 211 out of 3,642 species were DD). However, 78 species were listed on the FUSE INS  
291 watch list (non-threatened species with high FUSE INS scores), and the large majority was  
292 classified as NT. Forty-three species were assigned to the borderline list, including five  
293 critically endangered species. The thresholds used for defining the four lists had a negligible  
294 effect on the species included on the lists, except for the FUSE INS research list for  
295 amphibians, which contained 39 species with lower thresholds (i.e., 70% and 90% [Appendix  
296 S9]). In all taxonomic groups, most species across the three lists were associated with only  
297 one INS. Except for amphibians, which were mostly associated with two fungi  
298 (*Batrachochytrium dendrobatidis* and *Batrachochytrium salamandrivorans*), invasive  
299 mammals stood out as the most commonly identified INS group across all lists and taxa.  
300 However, for 29% of species, INS were referenced as "unspecified species."

301 Throughout all taxonomic groups and lists, most species tended to be associated with other  
302 threats besides INS (details in Appendix S11). Seventy-eight species were threatened by INS  
303 alone (i.e., not threatened by any other pressure): 11 amphibians, 19 birds, 26 lizards, and  
304 eight mammals on the core list; one amphibian, three birds, four lizards, and one mammal on  
305 the watch list; and three birds and two lizards on the borderline list (Appendix S12). On  
306 average, species on the core list were associated with more than four threats, including the  
307 INS threat (mean [SD]=4.1 [1.8]), except lizards that were on average associated with three  
308 threats. Biological resource use and agriculture and aquaculture were among the most

309 common other threats associated with amphibians, birds, and mammals. Lizards were  
310 threatened mostly by agriculture and aquaculture, followed by natural system modifications.  
311 Birds and mammals were the only groups associated with climate change and severe weather.  
312 Overall, information on INS impact magnitude was lacking. Information was missing for  
313 88% of amphibians, 67% of mammals, 53% of lizards, and 21% of birds on the core list.  
314 Because birds had more information than other taxa, we focused on the 50 birds on the core  
315 list of the highest conservation priority to illustrate associated threats and conservation  
316 actions needed based on the IUCN Red List classification (Figure 3). More than half of them  
317 were threatened only by one INS. Invasive mammals affected 56% of the species, followed  
318 by invasive birds (22%), plants (12%), and other taxa to a lesser extent. Almost all of these  
319 species were threatened by other threats besides INS (92%). The most commonly identified  
320 threats were biological resource use (70%) and climate change and severe weather (56%),  
321 followed by agriculture and aquaculture (48%), natural system modifications (38%), and  
322 pollution (34%). All 50 species were cited as in need of conservation action (i.e., land and  
323 water protection or management) by the IUCN. Specifically, 64% of the 50 birds of the  
324 highest conservation priority were associated with unimplemented INS control.

325 Birds and mammals on the core list were widespread, whereas amphibians and lizards were  
326 regionally clustered (Figure 4). We detected hotspots of core list species in Central America  
327 (especially Guatemala, Costa Rica, northern Ecuador, and northern Colombia) and eastern  
328 Madagascar for amphibians and in the Caribbean islands, northern Australia, New Zealand,  
329 and New Caledonia for lizards. For birds areas with the highest density of core list species  
330 were the coasts of the Southern Hemisphere, Pacific islands; including Hawaii and  
331 Galapagos; northern India, and New Zealand. For mammals, species on the core list occurred  
332 mostly in the East African Rift, Zambia, Botswana, the Pyrenees, Madagascar, Himalayas,  
333 Southeast Asia, and eastern Australia. Species on the watch list occurred all over the world

334 for birds and mammals, but amphibians and lizards were restricted to a few areas (e.g.,  
335 northern Andes, Madagascar, New Zealand) (Appendix S13). In contrast, all species on the  
336 borderline list, regardless of taxa, were restricted to areas, such as Madagascar or western  
337 Pacific islands, with species with small range sizes (Appendix S14).

338

## 339 **Discussion**

340 Across terrestrial vertebrates, we identified more than 1,300 species with high functional  
341 irreplaceability at high risk of extinction, partly because of INS (including 78 with INS as the  
342 only threat). On the core lists, amphibians represented most of the species with high FUSE  
343 INS scores, followed by birds, lizards, and mammals. In general, amphibians have the highest  
344 amount of taxonomic and functional diversity threatened by biological invasions (Bellard,  
345 Genovesi, et al., 2016; Marino et al., 2022), which our FUSE INS scores confirmed. Overall,  
346 the high number of species on these priority lists reinforces the vulnerability of these  
347 taxonomic groups to biological invasions (Bellard et al., 2016). Moreover, it highlights the  
348 importance of considering species traits when evaluating the INS threat because many of  
349 their impacts jeopardize more than taxonomic richness alone. The FUSE -INS scores can be  
350 used to identify species and areas of high conservation priority relative to the threat of INS.  
351 This approach also has the potential to be used for the other conservation goals listed, along  
352 with warnings and recommendations, in Table 1.

353

354 Identification of priority species and areas with the FUSE INS score

355 Assessing the spatial distribution of species from the FUSE INS core lists allowed us to  
356 identify areas that concentrated functionally irreplaceable vertebrates at high risk of  
357 extinction due to INS. Core list birds occurred mostly along coastlines of the Southern



358 Hemisphere but were also present on many Pacific islands and New Zealand. Pacific islands  
359 are the object of several conservation initiatives, including marine protected areas, to protect  
360 bird reproduction and ensure population persistence for key species. For instance, important  
361 bird and biodiversity areas (IBA) are defined based on their contribution to global avifauna  
362 preservation (Donald et al., 2019) and highlight zones of high irreplaceability in terms of  
363 taxonomic richness (Di Marco et al., 2016). These areas could gain importance and receive  
364 even more attention if other facets of diversity were added as a criterion, for example with the  
365 FUSE INS score, which considers species functional irreplaceability.

366 We identified some hotspots of core list species that, despite the exceptional species they  
367 host, are not represented in any IBAs, such as New Zealand or coastlines. An extreme  
368 example is the kakapo, the species with the highest FUSE INS score. This species has  
369 particular ecological characteristics that are generally associated with a high vulnerability to  
370 INS, such as ground-dwelling foraging, habitat specialism, large size, and plant-based diet  
371 (Marino et al., 2022). As the largest parrot in the world and the only one that does not fly, this  
372 species is certainly exceptional in terms of functional strategies at the global scale. Coastal  
373 birds are also distinct regarding functional traits. For instance, the New Zealand storm-petrel  
374 (*Fregetta maoriana*), Guadalupe storm-petrel (*Hydrobates macrodactylus*), and  
375 MacGillivray's prion (*Pachyptila macgillivrayi*) are seabirds that nest on islands and, together  
376 with the kakapo, are among the 50 birds of the highest conservation priority on the core list  
377 that are threatened only by INS (i.e., not by other threats according to the IUCN Red List).

378 Apart from birds, most species on core lists had no information regarding their INS impact  
379 magnitude; up to 88% of amphibian species lacked information. This large deficiency is  
380 likely to reduce the importance of the INS impact compared with the conservation status  
381 itself in the final calculations of the FUSE INS score. Despite the limited information, we still  
382 found that amphibians represented half of the species on the core lists. Amphibians affected

383 by INS are mostly threatened by the two chytrid fungi responsible for the chytridiomycosis  
384 disease, which has caused declines in more than 500 amphibian species worldwide (Scheele  
385 et al., 2019). The chytrid is widespread throughout the world but has the greatest effect on  
386 large-size and range-restricted amphibians from the tropical climates in the Americas.  
387 Therefore, it was not surprising to find that amphibians on the core list were restricted to  
388 zones in Central America and the northern Andes.

389 Lizards on the core list were almost all from northern Australia or native to islands (oceanic  
390 islands in the Caribbean and Pacific, New Zealand, New Caledonia), of which 81% were  
391 insular endemics. These findings are consistent with the facts that insular endemic species are  
392 more prone to extinction than continental species and threatened predominantly by INS  
393 (Leclerc et al., 2018). Moreover, endemic species also tend to have unique characteristics due  
394 to their isolated evolutionary histories, such as gigantism or dwarfism, inability or poor  
395 ability to fly, and reduced clutch size (Fernández-Palacios et al., 2021; Whittaker et al.,  
396 2017).

397 Finally, we found that the hotspots of core-list mammals were localized in different areas  
398 compared with the global hotspots of mammals sensitive to INS obtained with taxonomic  
399 diversity alone (Bellard, Genovesi, et al., 2016). In line with previous findings, eastern  
400 Australian mammals contributed significantly to the core list. However, new areas, such as  
401 the Pyrenees, eastern and southern Africa, and the Himalayas, were revealed to be important  
402 based on the FUSE INS score. Moreover, our score corroborates some priority areas  
403 identified to preserve the global phylogenetic diversity of mammals in Amazonia, central,  
404 eastern, and southern Africa; Madagascar, and Southeast Asia (Robuchon et al., 2021). Yet,  
405 the importance of areas such as southwestern Europe or eastern Australia was specific to the  
406 INS threat and the functional dimension of diversity; thus, they were excluded in previous

407 conservation prioritization strategies that are highly biased toward taxonomic diversity  
408 (Llorente-Culebras et al., 2023).

409

410 Using the FUSE INS score for conservation guidance

411 Once identified based on an FUSE INS score, priority species and areas can be the object of  
412 conservation measures dedicated to mitigating INS threat. Identifying which INS are  
413 threatening each species would allow direct targeting of INS for management actions.

414 Information about associated INS was unavailable or incomplete for most native species on  
415 the IUCN Red List, even for birds, which have the most comprehensive data. In those cases,  
416 we suggest complementing the IUCN Red List with other sources, such as the Global  
417 Invasive Species Database (<https://www.iucngisd.org/gisd/>), to identify the associated INS  
418 and then implementing an appropriated conservation action targeting the given INS.

419 For specific predators (e.g., introduced rodents and cats) or habitat disruptors (e.g.,  
420 introduced herbivores or plants), eradication campaigns can benefit core-list species,  
421 especially if they are endemic species. Although costly to implement, eradications can yield  
422 real benefits for native diversity when the context of INS presence and its integration into  
423 native ecosystems is properly identified (Philippe-Lesaffre et al., 2023). However, this  
424 control measure is mainly effective in isolated systems, such as islands, where INS are the  
425 main threat to the species and their numbers are low (maximum 2 to 3 species), making them  
426 easier to eradicate (Glen et al., 2013). Our results showed that almost half of the birds and the  
427 majority of reptiles from the core lists were insular endemics, offering high hopes for the  
428 potential use of this strategy (Barbraud et al., 2021; Medina et al., 2011). For instance, the  
429 Tristan albatross (*Diomedea dabbenena*), ranking third in the bird core list, would highly  
430 benefit from a mice eradication program on Gough Island, an important reproductive area

431 where mice threaten their eggs (Wanless et al., 2009). An eradication would also benefit  
432 MacGillivray's prion, which also inhabits this island (Dilley et al., 2015).

433 Eradication is only possible when the INS is a visible organism, therefore it can not be  
434 applied to introduced diseases. Moreover, pathogens, such as chytrids, pose a major  
435 management challenge because traditional area-based conservation methods, such as habitat  
436 protection, are ineffective. Consequently, new strategies must be designed, such as the  
437 translocation of populations, which requires sufficient knowledge to ensure its efficacy in the  
438 long term, especially in the context of chytrid disease (Scheele et al., 2021).

439 Species with high FUSE INS scores were also threatened by other pressures, predominantly  
440 biological resource use and agriculture or aquaculture. There was, on average, a higher  
441 number of threats associated with the core-list species than with endangered species in  
442 general (Berglund et al., 2013; Capdevila et al., 2022; Leclerc et al., 2018). The recognition  
443 of threat co- occurrences and interactions through networks could greatly facilitate the  
444 decision- making processes of practitioners by prioritizing conservation actions linked to one  
445 or more threats (Geary et al., 2019). Besides, removing INS pressure for core-list species  
446 could increase the ability of these species to recover from other global threats (Capdevila et  
447 al., 2021).

448

449 Making the most of FUSE INS watch and borderline lists

450 The FUSE INS watch list contained species of high functional value (i.e., functionally unique  
451 or specialized) that are affected by INS but have a low global extinction risk. This list  
452 therefore included species with strategies not frequently associated with other species that  
453 seem to resist (or to be less exposed to) INS or other threats. In contrast, species on the  
454 borderline list are threatened and have a high extinction risk but are less functionally

455 exceptional relative to core-list species. However, if the species on the core list become  
456 extinct, these are the next species on the verge of extinction that harbor functionally distinct  
457 features and thus represent great amounts of functional diversity.

458 Species on both the watch and borderline lists may therefore need proactive conservation  
459 strategies to prevent them from being more exposed to INS threats and consequently facing  
460 an increased extinction risk. In contrast, core list species require reactive conservation  
461 measures following an INS threat already in place. In fact, protecting the watch-list species  
462 can be a less expensive option to guaranteeing the preservation of functional diversity.

463 Applying less costly conservation actions, such as habitat protection or monitoring, to protect  
464 functionally distinct species that still maintain viable populations and large distribution areas  
465 can provide high benefits at low cost. By simply overlapping the zones where these species  
466 occur (Appendices S13, S14) with the current protected area (PA) coverage, one can identify  
467 the extent to which a PA could contribute to the protection of these species (Daru et al.,  
468 2019). Moreover, one could determine zones where a small increase in PA size would have  
469 large benefits by encompassing significant regions of these species distribution ranges.

470 Although current protected areas do not fully address species conservation needs, at least for  
471 mammals (Williams et al., 2022), these are still an efficient way to protect native species  
472 from INS and ensure a high level of resilience (Liu et al., 2020). We emphasize the urgent  
473 need to improve the network of PAs by making them adaptable to the different threats and  
474 conservation priorities identified.

475 Applications of the FUSE INS scoreThe FUSE INS score represents a promising approach to  
476 inform conservation priorities regarding the threat of INS on a macroecological scale because  
477 it allows the identification of functionally irreplaceable species at high risk of extinction due  
478 to INS. The list of warnings and recommendations in Table 1 can help one make the most of  
479 the FUSE INS score in conservation planning (Table 1). By definition, the FUSE INS score

480 depends on the probability of extinction due to INS and on the traits used to calculate the  
481 functional spaces and indices. Therefore, those two components need to be carefully defined  
482 and might be adjusted based on the final conservation objective. For instance, if the study is  
483 global, one might use a small amount of broad traits that have large taxonomic coverage.  
484 However, if the study is conducted at a smaller taxonomic or spatial extent, the traits can be  
485 selected to better represent the ecological or functional role of species within a particular  
486 ecosystem.

487 Although defined within a global perspective, the FUSE INS score and lists can be useful to  
488 prioritize functionally irreplaceable species and associated areas at a national or state-island  
489 scale. Moreover, they can be complemented with other prioritization tools, such as the EDGE  
490 score, for comparing or reaching a consensus list across the several facets of diversity (i.e.,  
491 taxonomic, phylogenetic, and functional). Finally, this index can be constructed to prioritize  
492 species at local scales simply by creating a functional space that reflects the local species  
493 community. The FUSE INS score is an adaptable index that can be applied to all taxonomic  
494 groups with sufficient trait data and downscaled to focus on smaller spatial scales to meet the  
495 project's conservation objectives.

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503

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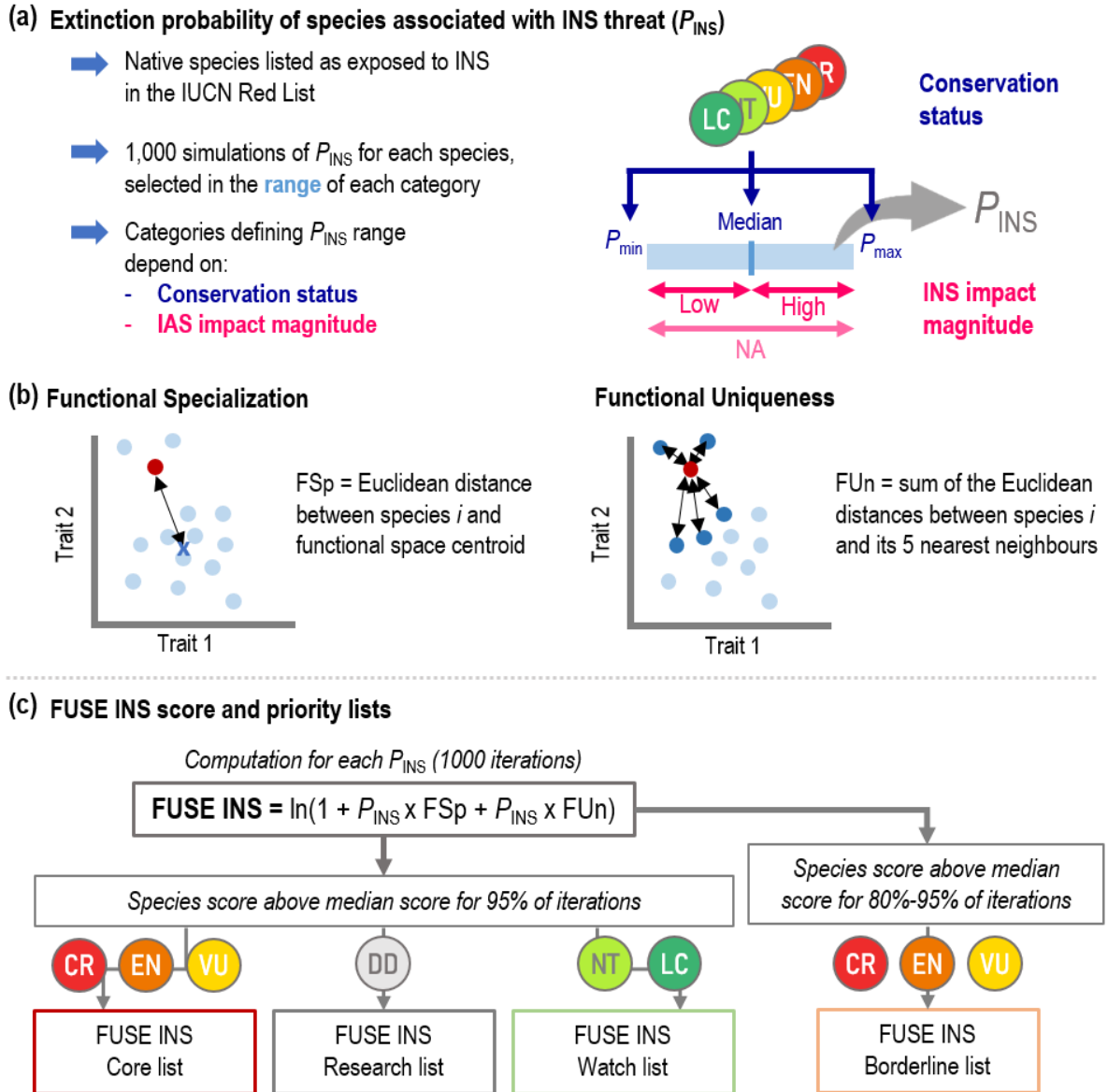
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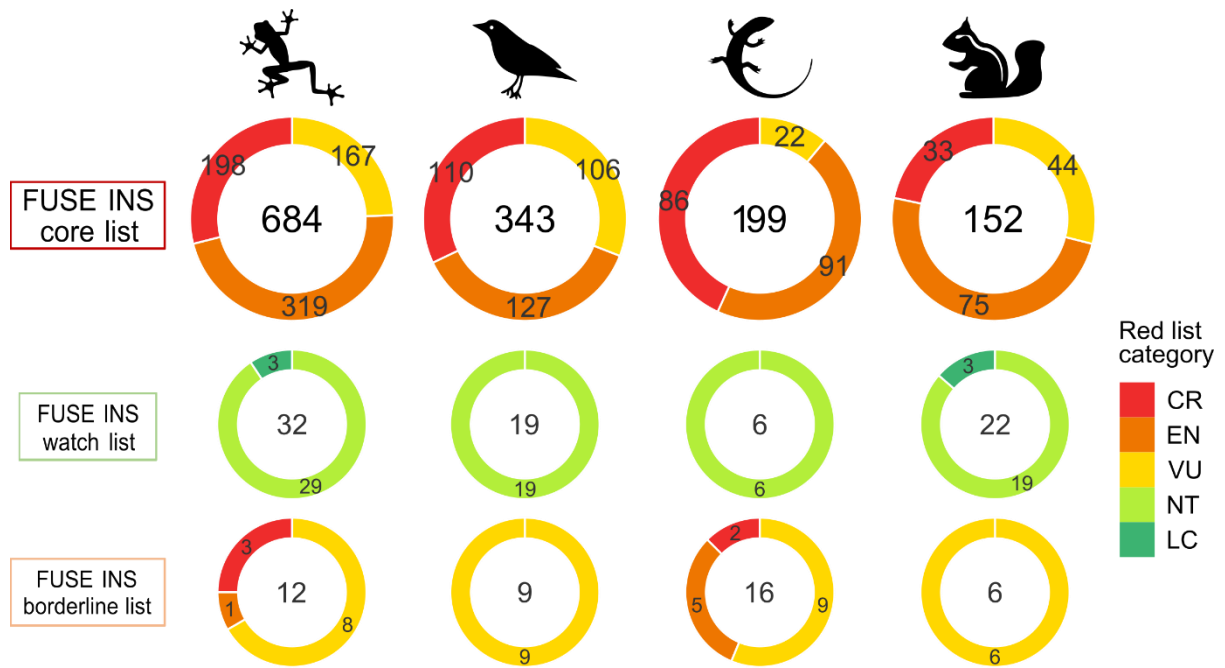
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**Figure 1.** Schematic workflow of the FUSE INS (functionally unique, specialized, and endangered by invasive non-native species) score calculation: (a) estimated extinction probabilities ( $P_{INS}$ ) randomly selected within the range of probability values of an International Union for Conservation of Nature (IUCN) Red list category and the INS impact magnitude (details on ranges of probability values in Appendix S2), (b) functional specialization (FSp) and functional uniqueness (FUn) measured in a functional space of  $n$  dimensions, adapted to each taxonomic group, and normalized (range 0 to 1), and (c) 1,000 FUSE INS scores computed as the combination of  $P_{INS}$ , FSp, and FUn for each species and

720 species lists built based on the median FUSE INS score of each taxonomic group and the  
721 conservation status of species (types of lists described in *Final metric and priority lists*).

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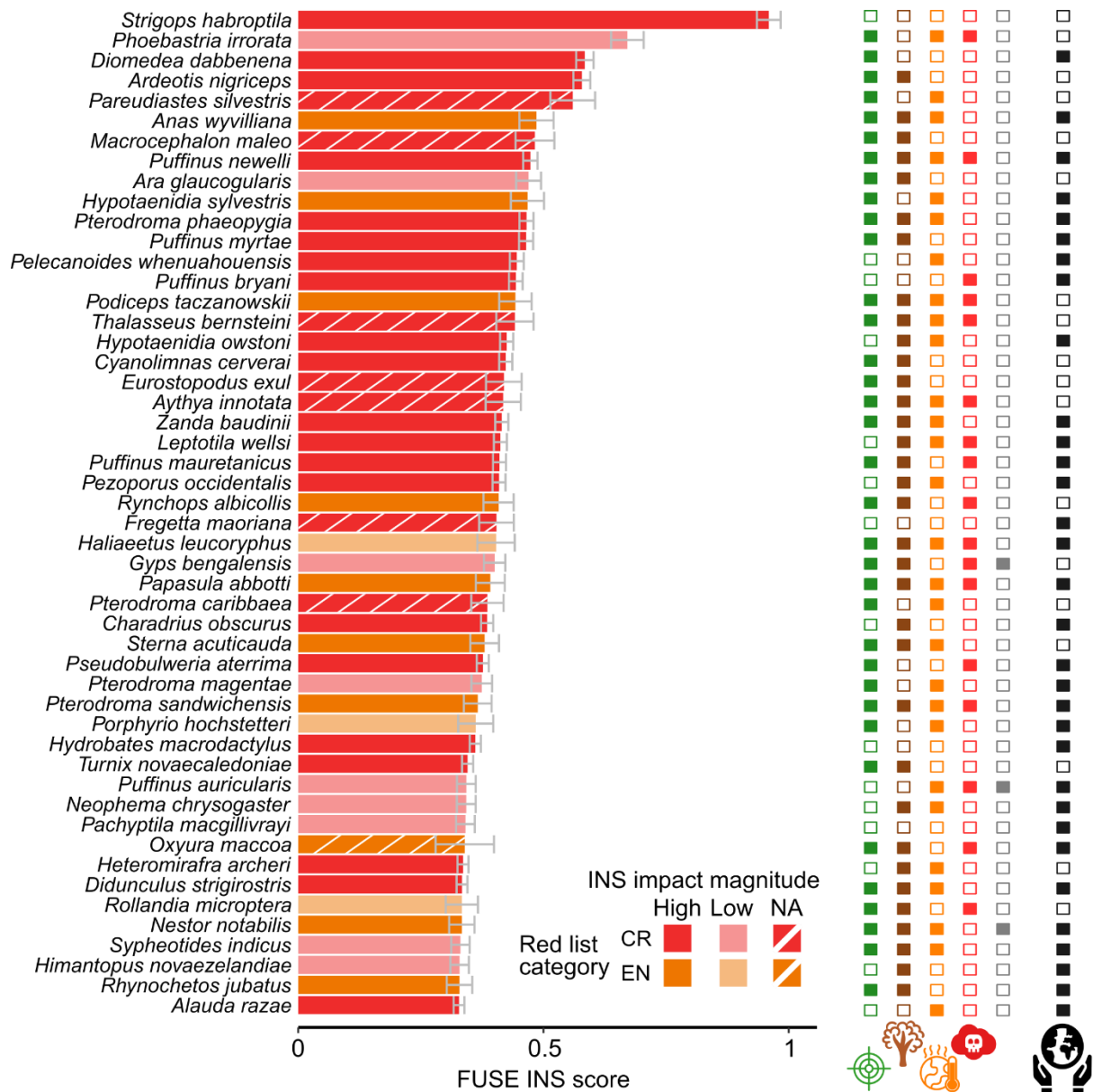
724 **Figure 2.** Number of species in the core, watch and borderline lists (lists described in *Final*

725 *metric and priority lists*) (circles, all species in the lists for each taxon; numbers inside

726 circles, number of species; CR, critically endangered; EN, endangered; VU, vulnerable; NT,

727 near threatened; LC, least concern).

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**Figure 3.** Functionally unique, specialized, and endangered by invasive non-native species

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(FUSE INS) scores for the 50 birds of the highest conservation priority on the core list (i.e.,

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species of high functional value and at high extinction risk due to INS) (bars, median score;

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error bars, standard deviation of the 1,000 scores computed for each species; CR, critically

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endangered ; EN, endangered; NA, missing impact information) (left), other threats besides

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INS to species, and conservation actions needed for INS management (green, biological

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resource use; brown, habitat loss and degradation [combined residential and commercial

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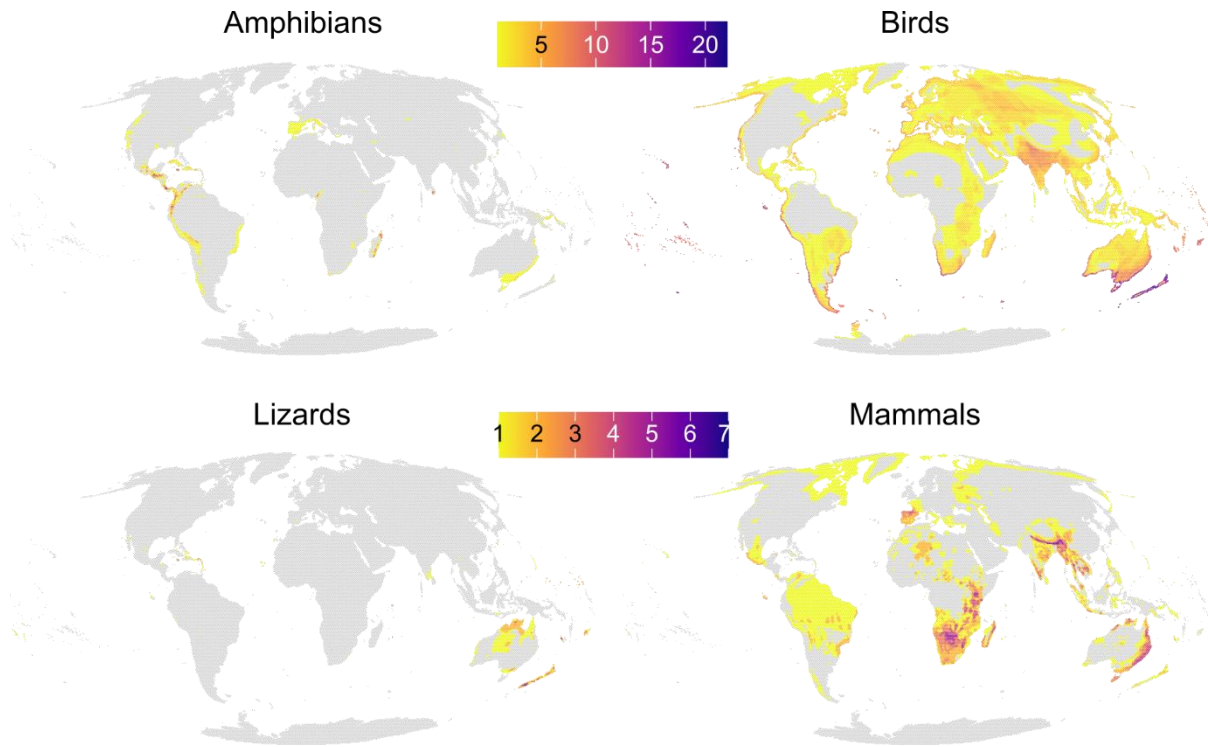
development, agriculture and aquaculture, energy production and mining, transportation and

738 service corridors, human intrusion and disturbance, and natural system modification]; orange,  
739 climate change and extreme weather; red, pollution; gray, other threat types; black:  
740 conservation actions needed; filled square, existence of a threat or conservation action need  
741 related to that species) (right).

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745 **Figure 4.** Global maps of species in the core list (i.e., species of high functional value and at  
 746 high extinction risk due to INS) for each taxon (values, taxonomic richness of species ranging  
 747 from 1 to 22 for amphibians and birds and from 1 to 7 for lizards and mammals; gray, no  
 748 species on the core list).

749

750 **Table 1.** Warnings, recommendations, and ways to adapt the functionally unique, specialized,  
 751 and endangered by invasive non-native species (FUSE INS) score to set conservation goals.

<b>Score construction</b>	
Warning	Traits used for functional space construction must encompass species' ecological niches to better represent their role in the ecosystem. Thus, in general, the number of traits to consider must be >3.
Warning	Use at least one continuous trait to avoid a patchy distribution of species in the functional space.
Recommendation	Data on species extinction risks, threats, or traits are regularly updated. The score can be recalculated to match the most updated information.
Possible adaptation	For taxa with fewer available traits at a global scale, such as plants or arthropods, the score can be calculated on a taxonomic or geographic subset. In that case, regional International Union for Conservation of Nature (IUCN) assessments be used instead of the global IUCN Red List.
Possible adaptation	Criteria for establishing priority lists are fully adaptable: the threshold of 95% of score values above the median can be adjusted to fit the project's specific objectives.
<b>Score interpretation and priority lists</b>	
Warning	Absolute value of the index is not informative per se. Use the ranking of species to obtain priorities based on the conservation objectives.
Recommendation	Report other threats associated with species on the lists to manage the INS threat.
Recommendation	Consider providing proactive conservation guidance for species in the watch list* and not restraining conservation efforts to core list* species.
Recommendation	Score ranks species based on their functional irreplaceability, but one could incorporate species' evolutionary history. The score can thus be combined and compared with other metrics, such as the EDGE score adapted to INS threat.

752 \*Watch list, species of high functional value but not immediately prone to extinction (LC and  
 753 NT); core list, species of high functional value and at high extinction risk due to INS (CR,  
 754 EN, or VU).