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# Conservation priorities for functionally unique and specialized terrestrial vertebrates threatened by biological invasions

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1 **Title**

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

4

5 **Article Impact Statement**

6 Including species traits in conservation metrics help to prioritize in a context of biological  
7 invasions.

8

9 **Keywords**

10 Conservation, functional traits, invasive alien species, irreplaceability, prioritization, tetrapods

11

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22

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31

32 **Abstract**

33 Invasive alien species (IAS) continue to pose a significant threat to biodiversity, leading to  
34 native population declines, which can ultimately disrupt ecosystem processes. Even though  
35 there is growing evidence of the impacts of IAS on functional diversity, most of the existing  
36 conservation prioritization approaches still focus on taxonomic diversity, neglecting the  
37 ecological role of species. We have refined the FUSE-IAS score to fill this gap by combining  
38 functional irreplaceability (measured by uniqueness and specialization) of species with their  
39 extinction risk due to IAS. Applying this score to 3,642 terrestrial vertebrates exposed to IAS,  
40 we found that 38% of those species showed high functional irreplaceability, making them  
41 priority species for conservation actions targeting IAS. These priority species were concentrated  
42 in specific areas in the case of amphibians (Central America and Madagascar) and lizards  
43 (Caribbean islands, North Australia, New Zealand, and New Caledonia), whereas birds (mostly  
44 coastal and on Pacific islands, North India, and New Zealand) and mammals (Southwest  
45 Europe, Central, East and South Africa, Southeast Asia, and East Australia) were more  
46 widespread. We further identified 79 species that were also highly irreplaceable but not yet  
47 threatened by IAS, suggesting that preventive conservation measures can ensure the protection  
48 of these species and their future biodiversity value. Finally, focusing on the Top 50 priority  
49 birds, we found that 64% of species still require the implementation of conservation actions to  
50 mitigate the IAS threat. This score helps prioritize species that represent large amounts of  
51 functional diversity and thus contribute to the conservation of global functional diversity.  
52 Incorporating functional diversity into the conservation prioritization of species and associated  
53 areas is key to accurately reducing and mitigating the impacts of IAS on native biodiversity, a  
54 target defined in the Kunming-Montreal Global Biodiversity Framework.

## 56 **Introduction**

57 According to the IUCN Red List, 333 contemporary extinctions have already occurred  
58 worldwide due to biological invasions and nearly 7,000 species are currently at risk of  
59 extinction partly due to the actions of invasive alien species (IAS, defined following Pyšek et  
60 al. (2020)), with 2,301 species expected to go extinct within 50 years (IUCN, 2022). Recent  
61 studies have shown that the consequences of biological invasions go far beyond a simple  
62 number of declining species, describing profound changes in the functional diversity of  
63 vertebrate communities (Bellard et al., 2021). Sayol and colleagues found that alien bird species  
64 led to the functional homogenization of insular avian communities (Sayol et al., 2021).  
65 Introduced birds are often equal or higher than the number of extinct birds on islands, however  
66 they do not seem to compensate for the functional loss due to the extinction of functionally  
67 distinct birds (such as, large bodied birds with low flight ability and animal- or nectar-based  
68 diets; Sayol et al., 2020; Soares et al., 2022). Recent evidence suggests that IAS threaten 10%  
69 of the taxonomic but 50% of the functional diversity of insular amphibians (Marino et al., 2022).  
70 Thus, focusing on taxonomic diversity greatly underestimates the impacts caused by IAS,  
71 especially regarding the maintenance of ecosystem functions and services (Egerer et al., 2018).  
72 Therefore, other dimensions of diversity need to be accounted for in the establishment of  
73 conservation priorities to ensure they cover the complete picture of IAS impacts on native biota.

74 Taxonomic diversity has been for decades the main indicator of the state of biodiversity (Purvis  
75 et al., 2019), causing most conservation initiatives to rely on this dimension (e.g., the global  
76 biodiversity hotspots; Myers et al., 2000), and thus disregarding species' functional role and  
77 evolutionary history (Bonn et al., 2002; Rodrigues & Gaston, 2002). Moreover, taxonomic  
78 diversity has been shown to be an unreliable indicator of other diversity dimensions, such as  
79 phylogenetic and functional diversity (Brum et al., 2017), therefore it is even more urgent to  
80 integrate them into conservation priorities (Diamond & Roy, 2023; Gaüzère et al., 2022).

81 Recently, new metrics have been developed to better integrate the multidimensionality of  
82 diversity, accounting for species' evolutionary history or functional diversity into conservation  
83 measures (Cui et al., 2024; Gumbs et al., 2023; Hidasi-Neto et al., 2015; Isaac et al., 2007;  
84 Pimienta et al., 2020). For example, the 'Evolutionarily Distinct and Globally Endangered'  
85 (EDGE) metric, which accounts for species' evolutionary distinctiveness and extinction risk,  
86 has been applied to many taxa and integrated into conservation schemes (Gumbs et al., 2018).  
87 In parallel, Pimienta et al. (2020) developed the 'Functionally Unique, Specialized and  
88 Endangered' (FUSE) metric, applying it to marine megafauna to identify species of critical  
89 importance for functional diversity and at high extinction risk. Nevertheless, the integration of  
90 functional features into conservation policies remains anecdotal, especially the FUSE metric  
91 that has, to our knowledge, never been applied to any other taxon besides marine megafauna  
92 and elasmobranchs (i.e., sharks, rays, and skates) (Pimienta et al., 2023). Although conservation  
93 measures are local and require to identify the threats that species face, most of prioritization  
94 measures do not account for the specificity of threats. For instance, IAS are known to have  
95 caused the extinction of distinct native species with unique functional traits, some of which no  
96 longer exist in the current fauna (e.g., birds: Matthews et al., 2022). It is thus crucial to define  
97 a species conservation prioritisation strategy that takes into account the traits of species, as well  
98 as their uniqueness and specialization among their taxonomic group in a threat perspective.

99 Here, we develop the FUSE-IAS score to identify species that are endangered by IAS and  
100 functionally unique and specialized, being therefore irreplaceable in terms of functional  
101 strategies and roles in the ecosystem. Taking advantage of recent improvements in the FUSE  
102 and EDGE frameworks (Gouhier & Pillai, 2020; Griffin et al., 2020 [preprint]; Gumbs et al.,  
103 2023), we developed a new method to calculate the FUSE-IAS score of species and applied it  
104 to almost all extant terrestrial vertebrates ( $n = 27,841$  species). Specifically, our index relies on  
105 two major improvements that consider: (i) the uncertainty associated with the extinction

106 probability of assessed species, recently developed by EDGE2 (Gumbs et al., 2023); and (ii)  
107 the severity of the impact of IAS on threatened species, using the IUCN Red List scheme. To  
108 date, all the major international institutions agree that biological invasions represent one of the  
109 main direct drivers of biodiversity loss (Bellard et al., 2022). In December 2022, COP15 of the  
110 Convention on Biological Diversity adopted a specific target for reducing and mitigating the  
111 impacts of IAS on native biodiversity (Secretariat of the United Nations Convention on  
112 Biological Diversity, 2021). To achieve this goal, it is essential to identify the species and areas  
113 most vulnerable to IAS impacts (Essl et al., 2020), not only by considering the imperilled  
114 taxonomic diversity but also by accounting for the functional value of species and ecosystems.  
115 In this context, this improved index will help to (1) identify and prioritize functionally  
116 irreplaceable vertebrates at high risk of extinction due to IAS, and (2) identify and monitor  
117 species (and associated sites) that are not yet threatened by IAS but have a high functional  
118 irreplaceability, representing an opportunity for the future of biodiversity. Preserving species  
119 that present exceptional traits will directly contribute to the conservation of global functional  
120 diversity.

121

## 122 **Material and Methods**

123 *Rationale.* Inspired by the FUSE approach, we built the FUSE-IAS score to focus on species  
124 that have a high extinction risk due to IAS, and are of particular importance for functional  
125 diversity (Griffin et al., 2020). We took advantage of the recent development of the EDGE2  
126 metric to quantify the uncertainty associated with the species' probability of extinction. The  
127 FUSE-IAS score of a given species is the product of its extinction risk due to IAS ( $P_{IAS}$ ) and its  
128 functional irreplaceability accounting for all species in the taxonomic group. Species that are  
129 strongly threatened by IAS and functionally irreplaceable will have a high FUSE-IAS score,  
130 while species that are less impacted by IAS or less exceptional in terms of ecological

131 characteristics will have a lower score. Specifically, we defined the FUSE-IAS score of a given  
132 species as the log-transformed combination of its extinction probability due to IAS threat ( $P_{IAS}$ )  
133 and functional irreplaceability, captured by functional specialization (FSp) and functional  
134 uniqueness (FUn), as follows:

$$135 \quad \text{FUSE-IAS} = \ln(1 + P_{IAS} \times \text{FSp} + P_{IAS} \times \text{FUn}) \quad (1)$$

136 The main steps of the FUSE-IAS score calculation are detailed in the next paragraphs and  
137 illustrated in Figure 1.

138 *Species threats and conservation status.* We used the IUCN Red List categories to identify all  
139 the terrestrial vertebrates exposed to IAS as all species associated with the threats *8.1 Invasive*  
140 *non-native/alien species/diseases* or *8.4 Problematic species/diseases of unknown origin* (the  
141 latter, only when we could determine the exotic origin of the named problematic species)  
142 (IUCN, 2022). We identified 1,895 amphibians, 816 birds, 508 lizards, and 423 mammals  
143 affected by IAS using the IUCN Threats Classification Scheme (version 3.3). We collected their  
144 global conservation status based on the IUCN Red List: Least Concern (LC), Near Threatened  
145 (NT), Vulnerable (VU), Endangered (EN), Critically Endangered (CR), or Data Deficient (DD).  
146 We extracted information about the scope and the severity of the IAS threat to quantify the  
147 impact native species sustain from IAS: species with more than 50% of their total population  
148 experiencing a significant decline (i.e., slow, rapid, or very rapid) due to IAS were classified as  
149 sustaining a high impact from IAS; whereas species with less than 50% of their population  
150 experiencing fluctuations or no declines were classified as supporting a low impact. Finally, we  
151 collected information regarding the other threats species are facing and the conservation actions  
152 needed. Threats were taken from the IUCN Red List summary (IUCN, 2022), following the  
153 Threats Classification Scheme (version 3.3). Conservation actions needed (which indicate the  
154 conservation actions or measures that are needed for the animal concerned) were also extracted  
155 from the IUCN Red List and we considered the category *2.2. Invasive/problematic species*



156 *control* from the Conservation Actions Classification Scheme (version 2.0) as conservation  
157 actions for IAS management.

158 *Extinction probability of species associated with IAS threat.* Following the EDGE2 protocol,  
159 we incorporated uncertainty in extinction probability to avoid a strong bias in the final score  
160 due to a coarse categorization of species extinction risk (Gumbs et al., 2023). Specifically, we  
161 fitted a quartic distribution on 20,000 ranked values for the five IUCN categories, with a  
162 probability of extinction of 0.06 for LC, 0.12 for NT, 0.24 for VU, 0.49 for EN and 0.97 for CR  
163 species (Mooers et al., 2008; Appendix S1). We removed the two extrema of the fitted values to  
164 avoid picking a probability of 0 or 1. We further divided each IUCN category into two blocks  
165 of fitted values based on their ranks to represent the IAS impact magnitude (low and high,  
166 Appendix S2). Extinction probabilities for species with low IAS impact are picked in the block  
167 of inferior values, while those for species with high IAS impact are picked in the block of  
168 superior values. We ended up with 10 categories defined both by the conservation status and  
169 the impact magnitude (Figure 1a, Appendix S2). We then drew 1,000 values of  $P_{IAS}$  for each  
170 species, by randomly selecting  $P_{IAS}$  in the block corresponding to the species' category,  
171 considering both conservation status and IAS impact. For species without information about  
172 the impact magnitude,  $P_{IAS}$  was selected within the two blocks corresponding to the two  
173 categories of the same conservation status. For DD species,  $P_{IAS}$  was selected in the whole range  
174 of the 10 categories (0.0001-0.9999), regardless of conservation status and IAS impact.

175 *Functional irreplaceability definition.* The functional value of species was measured in a  
176 functional space, which was defined as a multidimensional space containing all species from a  
177 taxonomic group, where axes are a combination of species traits. The functional irreplaceability  
178 represents the degree of specialization and uniqueness of species within the functional space  
179 (Pimiento et al., 2020). Functional specialization (FSp) accounts for species' distance from  
180 average strategies of the taxonomic group, while functional uniqueness (FUn) measures the

181 level of isolation of each species in the functional space of its respective taxon (Mouillot et al.,  
182 2013). The definition and calculation protocol of both metrics are detailed below.

183 *Trait data and functional spaces.* We combined a global list of 27,841 terrestrial vertebrates  
184 (6,492 amphibians, 10,943 birds, 5,505 mammals, and 4,901 lizards) for which we had  
185 complete trait information from Marino et al. (2022). Because reptile traits were poorly reported  
186 for major groups such as snakes, turtles, and crocodiles, we focused on lizard species for this  
187 taxon. Traits were related to species morphology, life history and ecology, which together  
188 reflect species functional strategies (Marino et al., 2022; Marino & Bellard, 2023). We ended  
189 up with a total of four traits for amphibians, 10 traits for birds, and five traits for both lizards  
190 and mammals (all details on trait sources are provided in Appendix S3). These traits are  
191 commonly used in studies evaluating functional diversity and summarizing the effects of  
192 species on ecological processes and their responses to environmental change (Marino et al.,  
193 2022; Sayol et al., 2021; Soares et al., 2022).

194 We built a multidimensional functional space for each taxonomic group separately, with a two-  
195 step approach that enables us to consider various types of variables (e.g., continuous, ordinal,  
196 factorial). First, we computed pairwise trait-based distances between species using the Gower  
197 dissimilarity index (Gower, 1971). Second, we calculated species coordinates in the functional  
198 space by applying a principal coordinate analysis (PCoA) on the distance matrix to reduce the  
199 number of dimensions. The trait-based distance matrix was obtained with the *daisy()* function  
200 from the *cluster* package, and the PCoA was computed with the *pcoa()* function from the *ape*  
201 package (Maechler et al., 2018; Paradis & Schliep, 2019). The final functional spaces explained  
202 more than 50% of the variance with three dimensions for amphibians (54.1% of cumulated  
203 explained variance), seven dimensions for birds (50.2%), and five dimensions for mammals  
204 and lizards (53.7% and 54.0%, respectively).

205 *Functional specialization and uniqueness.* Finally, for a given species  $i$ , we calculated FSp as  
206 the Euclidean distance between  $i$  and the  $n$ -dimensional functional space centroid, and FUn as  
207 the sum of the Euclidean distances between  $i$  and its five nearest neighbors. When combined,  
208 FSp and FUn represent the functional irreplaceability of a given species within its own  
209 taxonomic group (Pimienta et al., 2020). Both metrics were normalized between 0 and 1: for  
210 FSp, 0 represents the most central species in the functional space, whereas 1 is the most distant  
211 species from the centroid (Appendix S4); for FUn, 0 represents the least isolated species (given  
212 the distance from its five nearest neighbors), and 1 is the most isolated species (Appendix S5).  
213 The two metrics were not correlated, being complementary for all taxonomic groups considered  
214 (Appendix S6).

215 *Final metric and priority lists.* We calculated the FUSE-IAS score for each species using  
216 equation (1) with the values of  $P_{IAS}$ , FSp, and FUn previously calculated. As all three metrics  
217 ranged between 0 and 1, the FUSE-IAS score ranged between 0 and  $\ln(3) \approx 1.1$ . Each species  
218 obtained 1,000 FUSE-IAS scores, one for each of the 1,000 generated  $P_{IAS}$ , from which we  
219 calculated the median score per species with its associated standard deviation. Furthermore, for  
220 each taxonomic group, we obtained the median score using all species of the taxonomic group  
221 to classify species in priority lists based on different conservation objectives (Figure 1c; Gumbs  
222 et al. 2023):

- 223 - FUSE-IAS Core list: threatened species with a CR, EN, or VU conservation status that  
224 have more than 95% of their score values above the median score of all species of their  
225 respective group. Species in this list are of high functional value and would require an  
226 urgent and adapted conservation response to prevent their extinction;
- 227 - FUSE-IAS Research list: data deficient species regarding conservation status that have  
228 more than 95% of their score values above the median score of their respective group.

229 This list would help target species that are of high functional value but have not yet  
230 received enough research effort for having a proper conservation evaluation;

- 231 - FUSE-IAS Watch list: non-threatened species with a NT or LC conservation status that  
232 have more than 95% of their score values above the median score of their respective  
233 group. Species in this list are of high functional value but not immediately prone to  
234 extinction, however, they would benefit from proactive conservation strategies;
- 235 - FUSE-IAS Borderline list: threatened species with a CR, EN, or VU conservation status  
236 that have between 80% and 95% of their score values above the median score of their  
237 respective group. Species in this list have a high extinction risk but are not as  
238 functionally exceptional as the species from the Core list. However, if Core list species  
239 become extinct, they are the next species on the verge of extinction that harbor the most  
240 functionally distinct features.

241 We derived the four lists for each taxon (i.e., amphibians, birds, lizards, and mammals).

242 *Species distribution ranges and richness maps.* We collected the native distribution range of  
243 amphibians and mammals from the IUCN, birds from Birdlife, and lizards from the GARD  
244 database (BirdLife International & Handbook of the Birds of the World, 2020; IUCN, 2022;  
245 Roll et al., 2017). We then extracted the species' potential presence in cells of 110 km resolution  
246 to derive maps of species richness. At the cell level, we evaluated the correlation between the  
247 species richness of FUSE-IAS species and the sum of FUSE-IAS scores of all present species.  
248 As the two metrics were highly correlated (Appendix S7, Pearson's correlation coefficient >  
249 0.80 for all groups), we only displayed the maps based on the species richness of FUSE-IAS  
250 species.

251 All analyses were conducted using R software version 4.2.2 (R Core Team, 2022).

252

## 253 **Results**

254 We calculated the FUSE-IAS score of 3,642 terrestrial vertebrates listed as associated with IAS  
255 threat in the IUCN Red List (complete lists with species scores are provided in Supplementary  
256 Information for the four taxa). The scores ranged from 0 to 0.992, thus never reaching the  
257 maximum possible value, with the highest score obtained for the Kākāpō (*Strigops habroptila*),  
258 a large, flightless, ground-nesting nocturnal parrot from New Zealand. Median scores for each  
259 group were overall low: 0.05 (SD 0.13) for amphibians, 0.06 (SD 0.11 and 0.13) for birds and  
260 lizards, and 0.04 (SD 0.09) for mammals.

261 We identified 1,378 species in the FUSE-IAS Core list, namely 684 amphibians, 343 birds, 199  
262 lizards, and 152 mammals (Figure 2), representing 38% of all species exposed to IAS. We did  
263 not identify any species belonging to the FUSE-IAS Research list, i.e. species with high FUSE-  
264 IAS score but DD for conservation status (although 211 out of 3,642 species were DD).  
265 However, 79 species were listed in the FUSE-IAS Watch list (non-threatened species with high  
266 FUSE-IAS scores) and the large majority was classified as Near Threatened. Finally, we found  
267 43 species belonging to the FUSE-IAS Borderline list, including five that were critically  
268 endangered. In all taxonomic groups, most species across the three lists were associated with  
269 only one IAS. Except for amphibians, which were mostly associated with two fungi  
270 (*Batrachochytrium dendrobatidis* and *Batrachochytrium salamandrivorans*), invasive  
271 mammals stood out as the most commonly identified IAS group across all lists and taxa.  
272 However, for 29% of species, IAS were referenced as “unspecified species”, meaning that they  
273 were not reported in the IUCN classification.

274 Throughout all taxonomic groups and lists, most species tended to be associated with other  
275 threats besides IAS (Appendix S8 for details). A total of 78 species were threatened by IAS  
276 alone (i.e., not threatened by any other pressure): representing 11 amphibians, 19 birds, 26

277 lizards and eight mammals in the Core list; one amphibian, three birds, four lizards and one  
278 mammal in the Watch list; and three birds and two lizards in the Borderline list (Appendix S9).  
279 On average, species from the Core list were associated with more than four threats, including  
280 the IAS threat (mean (SD)=4.1 (1.8)), except lizards that were on average associated with three  
281 threats. *Biological resource use* and *Agriculture and aquaculture* were among the most  
282 common other threats associated with amphibians, birds, and mammals. Lizards were  
283 threatened mostly by *Agriculture and aquaculture*, followed by *Natural system modifications*.  
284 Birds and mammals were the only groups associated with *Climate change and severe weather*.

285 Overall, we found that IAS impact magnitude was poorly informed with missing information  
286 for 88% of amphibians in the Core list, 67% of mammals, 53% of lizards, and 21% of birds.  
287 Because birds were more informed than other taxa, we focused on the Top 50 birds in the Core  
288 list to illustrate associated threats and conservation actions needed based on the IUCN Red List  
289 classification (Figure 3). More than half of them were threatened only by one IAS, with invasive  
290 mammals affecting 56% of the species, followed by invasive birds (22%), plants (12%), and  
291 other taxa to a lesser extent. Almost all of these species were threatened by other threats besides  
292 IAS (92%). The most commonly identified threats were *Biological resource use* (70%) and  
293 *Climate change and severe weather* (56%), followed by *Agriculture & aquaculture* (48%),  
294 *Natural system modifications* (38%) and *Pollution* (34%). All 50 species had conservation  
295 actions needed in the IUCN Red List regarding land/water protection or management.  
296 Specifically, 64% of the Top 50 birds have conservation actions regarding IAS control that still  
297 need to be implemented.

298 By investigating the spatial distribution of the Core list species, we found that birds and  
299 mammals were widespread, while amphibians and lizards were regionally clustered (Figure 4).  
300 We detected hotspots of Core list species within Central America (especially Guatemala, Costa  
301 Rica, and the north of Equator and Columbia) and the east part of Madagascar for amphibians,

302 and in the Caribbean islands, North Australia, New Zealand, and New Caledonia for lizards.  
303 For birds, the areas with the highest density of Core list species were the coasts of the southern  
304 hemisphere, Pacific islands including Hawaii and Galapagos, north India, and New Zealand.  
305 For mammals, species from the Core list occurred mostly in the East African Rift, Zambia,  
306 Botswana, and also the Pyrenees, Madagascar, Himalayas, South East Asia, and East Australia.  
307 Species from the Watch list occurred all over the world for birds and mammals, but amphibians  
308 and lizards were restricted to a few specific areas (e.g., north Andes, Madagascar, New Zealand;  
309 Appendix S10). In contrast, all species from the Borderline list, regardless of taxa, were  
310 restricted to specific areas like Madagascar or West Pacific islands with low-range size species  
311 (Appendix S11).

312

### 313 **Discussion**

314 Across tetrapods, we identified more than 1,300 species that showed high functional  
315 irreplaceability but were at high risk of extinction, partly because of IAS (including 64 with  
316 IAS as the only threat). We found that among the Core lists, amphibians represented most of  
317 the species with high FUSE-IAS scores, followed by birds, lizards and mammals. Another study  
318 following a similar approach on phylogenetic diversity to assess evolutionary distinct and  
319 globally endangered (EDGE) mammals identified 645 species in the EDGE Core list (Gumbs  
320 et al., 2023). We found 152 mammals in the FUSE-IAS Core list just by focusing on species  
321 that are exposed to IAS. This suggests that IAS are threatening many species considered  
322 endangered and that are functionally exceptional, not only for mammals but for all tetrapods  
323 given the results on the other taxonomic groups. Overall, the high proportion of species in these  
324 priority lists reinforces the vulnerability of these taxonomic groups to biological invasions  
325 (Bellard, Cassey, et al., 2016). Moreover, it highlights the importance of considering the  
326 ecological characteristics of species when evaluating the IAS threat since many of their impacts

327 jeopardize more than taxonomic richness alone. Here we discuss the relevance of FUSE-IAS  
328 score to identify priority species and areas regarding the IAS threat, but this approach has the  
329 potential to be used for other conservation goals, which we highlighted in Table 1, additionally  
330 with warnings and recommendations.

331

### 332 **Identification of priority species and areas thanks to the FUSE-IAS score**

333 Assessing the spatial distribution of species from the FUSE-IAS Core lists allows us to identify  
334 areas that concentrate functionally irreplaceable vertebrates at high risk of extinction due to  
335 IAS. Core list birds were mostly in the coastlines of the Southern Hemisphere but also present  
336 on many Pacific islands and New Zealand. Pacific islands are the object of several conservation  
337 initiatives, that include marine areas, for ensuring bird reproduction and population persistence  
338 for key species. For instance, the Important Bird and Biodiversity Areas (IBA) are defined  
339 regarding their contribution to global avifauna preservation (Donald et al., 2019), and permit to  
340 secure zones of high irreplaceability in terms of taxonomic richness (Di Marco et al., 2016).  
341 Those areas could greatly be improved if other facets of diversity were added as a criterion, for  
342 example by using the FUSE-IAS score that considers species functional irreplaceability.  
343 However, we identified some hotspots of the Core list species that, despite the exceptional  
344 species they host, are not at all represented by IBAs, such as New Zealand or coastlines. An  
345 extreme example is the Kākāpō, the species with the highest FUSE-IAS score and endemic to  
346 New Zealand. This species has particular ecological characteristics that are generally associated  
347 with a high vulnerability to IAS, such as ground-dwelling foraging, habitat specialism, large  
348 size and plant-based diet (Marino et al., 2022). As the largest parrot in the world and the only  
349 one that does not fly, this species is certainly exceptional in terms of functional strategies at the  
350 global scale. Coastal birds are also distinct regarding functional traits, for instance, the New  
351 Zealand Storm-petrel (*Fregatta maoriana*), the Guadalupe Storm-petrel (*Hydrobates*



352 *macrodactylus*), and the MacGillivray's Prion (*Pachyptila macgillivrayi*) are seabirds nesting  
353 on islands and, together with the Kakapo, correspond to four species in the Top 50 birds of the  
354 Core list threatened only by IAS (i.e., not by other threats according to the IUCN Red List).

355 Apart from birds, species in the Core list were mostly data deficient regarding the IAS threat  
356 impact magnitude, reaching up to 88% of uninformed species for amphibians. This high rate of  
357 deficiency is likely to reduce the importance of the IAS impact compared to the conservation  
358 status itself in the final calculations for the FUSE-IAS score. Despite the limited information,  
359 we still found that amphibians represented half of the species present in the Core lists.  
360 Amphibians impacted by IAS are mostly threatened by two chytrid fungi that are responsible  
361 for the chytridiomycosis disease, which has caused declines in more than 500 amphibian species  
362 worldwide (Scheele et al., 2019). The chytrid is widespread throughout the world but has the  
363 greatest effect on large-size and range-restricted amphibians from the tropical climates in the  
364 Americas. Therefore, it was not surprising to find that the Core list amphibians are restricted to  
365 zones of central America and northern Andes.

366 Lizards from the Core list were almost all from North Australia or native to islands (oceanic  
367 islands from the Caribbean and Pacific, New Zealand, New Caledonia), of which 81% are  
368 insular endemics. These findings are consistent with the fact that insular endemic species are  
369 known to be more prone to extinction than continental ones, with IAS being a predominant  
370 threat (Leclerc et al., 2018). Moreover, endemic species also tend to have specific  
371 characteristics due to their isolated evolutionary histories, like gigantism or dwarfism, naivety  
372 to predators, inability or poor ability to fly, and reduced clutch size, all of which rend them  
373 unique (Fernández-Palacios et al., 2021; Whittaker et al., 2017).

374 Finally, we found that the hotspots of Core list mammals were very different from the global  
375 hotspots of mammals sensitive to IAS obtained using taxonomic diversity alone (Bellard,  
376 Genovesi, et al., 2016). In line with previous findings, we found a significant contribution of

377 East-Australian mammals to the Core list. However, new areas like the Pyrenees, East and  
378 South Africa, and the Himalayas were revealed to be important thanks to the FUSE-IAS score.  
379 Thus, contrarily to birds, mammals sensitive to IAS are not necessarily the mammals with the  
380 highest functional values. Moreover, our score corroborates some priority areas that were  
381 identified to preserve the global phylogenetic diversity of mammals, like Amazonia, Central,  
382 East and South Africa, Madagascar and Southeast Asia (Robuchon et al., 2021). Yet, the  
383 importance of areas like Southwest Europe or East Australia were specific to the IAS threat and  
384 the functional dimension of diversity, thus they remained excluded in previous conservation  
385 prioritization strategies.

386

### 387 **Using the FUSE-IAS score for conservation guidance**

388 Once identified thanks to the FUSE-IAS score, priority species and areas can be the object of  
389 conservation measures dedicated to mitigating IAS threat. Identifying which IAS are  
390 threatening each species would allow direct targeting of IAS for management actions. Note that  
391 information about associated IAS was unavailable or incomplete for most native species in the  
392 IUCN Red List, even for birds that are the most comprehensive group in terms of data. In those  
393 cases, we suggest complementing the Red List with other sources such as the Global Invasive  
394 Species Database (<https://www.iucngisd.org/gisd/>) to identify the associated IAS and then,  
395 implement an adapted response.

396 For specific predators (e.g., introduced rodents and cats) or habitat disruptors (e.g., introduced  
397 herbivores or plants), eradication campaigns can benefit Core list species, especially if they are  
398 endemics. Although costly to implement, eradications can yield real benefits for native diversity  
399 when the context of IAS presence and its integration into native ecosystems is properly  
400 identified (Philippe-Lesaffre et al., 2023). However, this control measure is mainly effective in

401 isolated systems, such as islands, when IAS are the main threat to the species and their numbers  
402 are low (maximum 2 to 3 species), making them easier to eradicate (Glen et al., 2013). Our  
403 results showed that almost half of the birds and the majority of reptiles from the Core lists were  
404 insular endemics, offering high hopes for the potential use of this strategy (Barbraud et al.,  
405 2021; Medina et al., 2011). For instance, the Tristan albatross (*Diomedea dabbenena*), ranking  
406 third in the bird Core list, would highly benefit from a mice eradication program on Gough  
407 Island, an important reproductive area where mice threaten their eggs (Wanless et al., 2009).  
408 An eradication that would also benefit the MacGillivray's Prion, which also inhabits this island  
409 (Dilley et al., 2015).

410 Eradication is only possible when the IAS is a visible organism, therefore it can not be applied  
411 to introduced diseases. Moreover, pathogens like chytrids pose a major management challenge  
412 because traditional area-based conservation methods, such as habitat protection, are poorly  
413 effective. Consequently, new strategies must be designed, like the translocation of populations,  
414 which requires an appropriate amount of knowledge to ensure its efficacy in the long term,  
415 especially in the context of chytrid disease (Scheele et al., 2021).

416 Finally, we found that species with high FUSE-IAS scores were also threatened by other  
417 pressures, namely biological resource use and agriculture/aquaculture. We found that there is,  
418 on average, a higher number of threats associated with the Core list species than with  
419 endangered species in general (Berglund et al., 2013; Capdevila et al., 2022; Leclerc et al.,  
420 2018). The recognition of threat co-occurrences and interactions through networks could largely  
421 facilitate the decision-making processes of practitioners by prioritizing conservation actions  
422 linked to one or more threats (Geary et al., 2019). Besides, removing the pressure sustained by  
423 IAS on the Core list species can alleviate these species, allowing them to increase their  
424 resistance and resilience to the other global threats they face.

425

426 **Make the most of FUSE-IAS Watch and Borderline lists**

427 The FUSE-IAS Watch list contains species of high functional value that are not yet threatened  
428 by IAS. This list therefore includes species that ensure strategies that are not frequently  
429 performed by other species but they seem to have currently some resistance (or are not highly  
430 exposed) to IAS or other threats. In contrast, species in the Borderline list are threatened and  
431 have a high extinction risk, but are less functionally exceptional compared to the Core list  
432 species. However, if the species in the Core list become extinct, these are the next species on  
433 the verge of extinction that harbor functionally distinct features and thus represent great  
434 amounts of functional diversity.

435 Species from both the Watch and Borderline lists may therefore need proactive conservation  
436 strategies, that would prevent species from being more exposed and consequently threatened  
437 by IAS threat, in contrast with Core list species that require reactive conservation measures  
438 following a threat already in place. In fact, protecting the Watch list species can be a less  
439 expensive option to guarantee the preservation of functional diversity. Applying less costly  
440 conservation actions, such as habitat protection or monitoring, to protect functionally distinct  
441 species that still maintain viable populations and large distribution areas, can provide high  
442 benefits at low cost. By simply overlapping the zones where these species occur (Figures S6,  
443 S7) with the current protected area (PA) coverage, we can identify to which extent PA could  
444 contribute to the protection of these species (Daru et al., 2019). Moreover, we can also  
445 determine the zones where a small increase in PA size would have large benefits by  
446 encompassing significant regions of these species distribution ranges. Although current  
447 protected areas do not fully address species conservation needs, at least for mammals (Williams  
448 et al., 2022), these are still an efficient way to protect native species from IAS and ensure a high  
449 level of resilience (Liu et al., 2020). We emphasize the urgent need to improve the network of  
450 PAs, making them adaptable to the different threats following conservation priorities.

## 451 **Conclusion**

452 The FUSE-IAS score represents a promising approach to inform conservation priorities  
453 regarding the threat of IAS on a macro-ecological scale. By allowing the identification of  
454 functionally irreplaceable species at high risk of extinction due to IAS, this index can contribute  
455 to address the objective of reducing by 50% the number of species threatened by IAS on the  
456 IUCN Red List, included in the European Union's Biodiversity Strategy for 2030. We provide  
457 a list of warnings and recommendations to make the most of the FUSE-IAS score in  
458 conservation guidance (Table 1). Although defined within a global perspective, the FUSE-IAS  
459 score and lists can be useful to prioritize functionally irreplaceable species and associated areas  
460 at a national or state-island scale. Moreover, they can be complemented with other prioritization  
461 tools like the EDGE score for comparing or reaching a consensual list across the several facets  
462 of diversity (i.e., taxonomic, phylogenetic and functional). Lastly, this index can be constructed  
463 to prioritize species at local scales simply by creating a functional space that reflects the local  
464 species community. The FUSE-IAS score is an adaptive index that can be applied to all  
465 taxonomic groups with sufficient trait data and downscaled to focus on smaller spatial scales in  
466 order to meet the project's conservation objectives.

467

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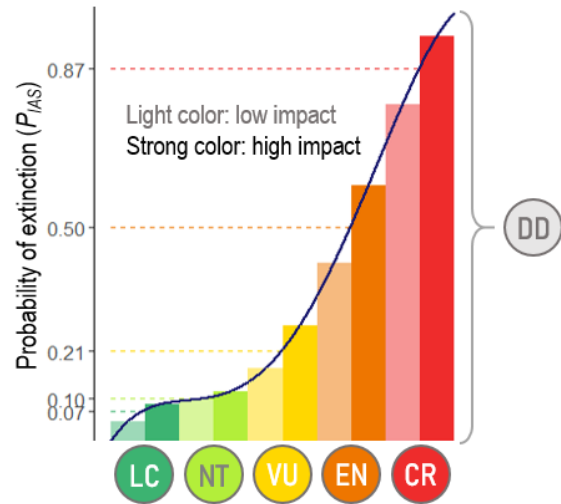
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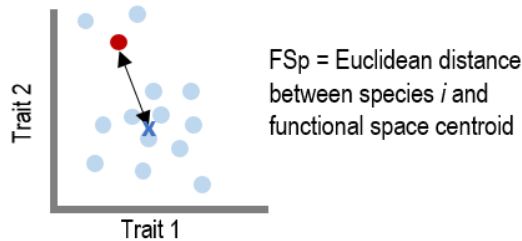
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**(a) Extinction probability of species associated with IAS threat**

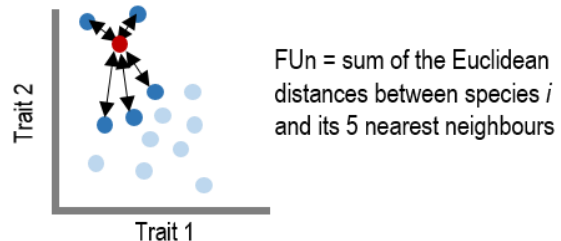
- ➔ Native species listed as exposed to IAS in the IUCN RedList
- ➔  $P_{IAS}$  is dependent on:
  - Conservation status
  - IAS-impact magnitude
- ➔  $P_{IAS}$  is randomly selected in the value range of each category
- ➔ 1000 simulations of  $P_{IAS}$  for each species



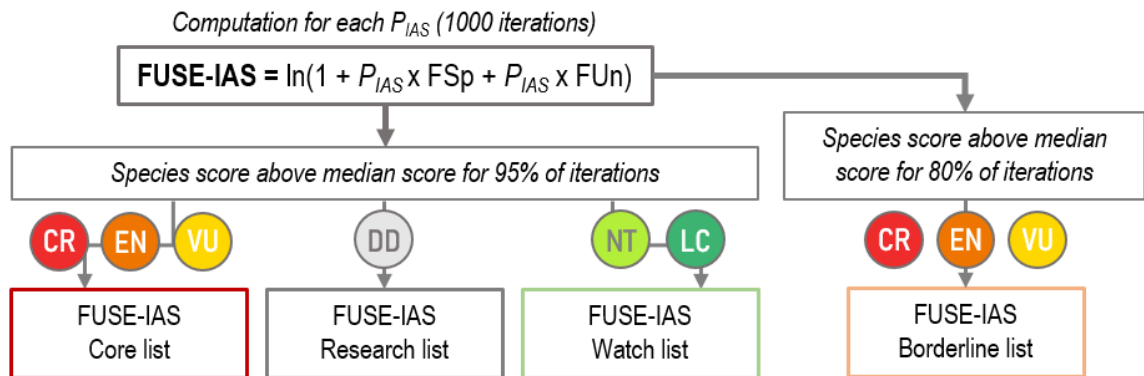
**(b) Functional Specialization**



**Functional Uniqueness**



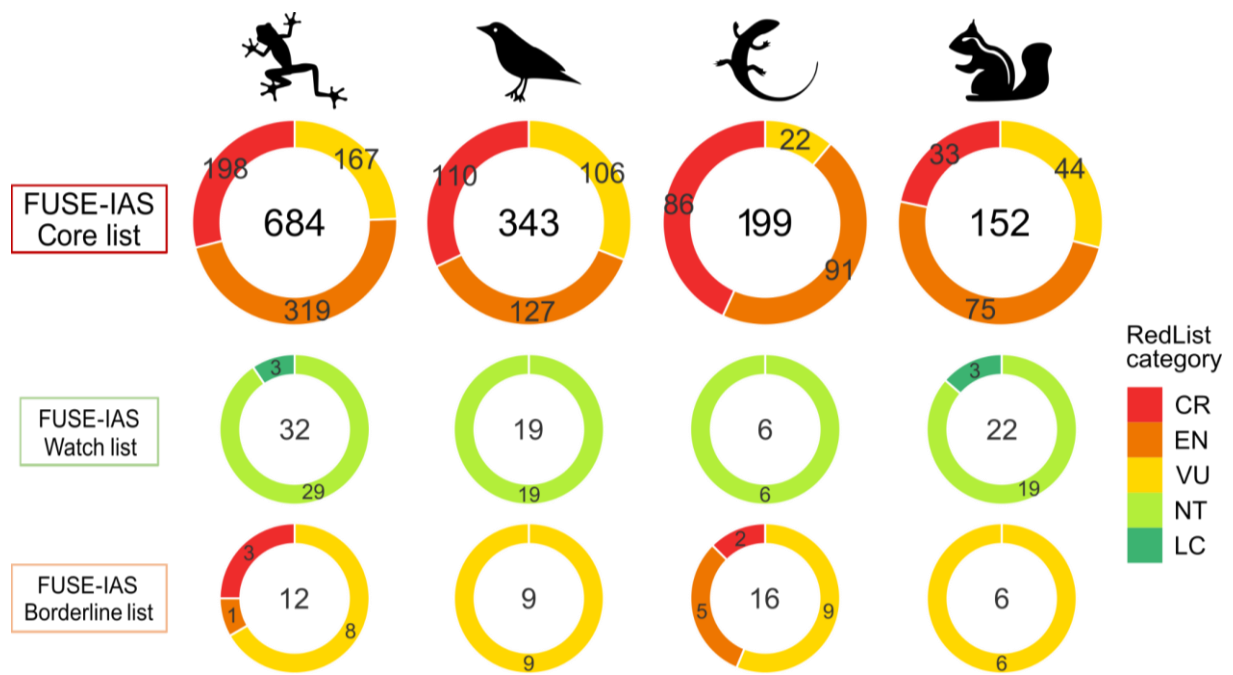
**(c) FUSE-IAS score and priority lists**



680

681 **Figure 1. Schematic workflow of the FUSE-IAS score calculation.** For each species, we calculated  
 682 functional specialization (FSp) and functional uniqueness (FUn), and estimated 1000 extinction  
 683 probabilities ( $P_{IAS}$ ). (a)  $P_{IAS}$  was drawn from a quartic distribution adjusted to the extinction probabilities  
 684 of the five IUCN conservation statuses (adapted from Gumbs et al. 2023). In detail,  $P_{IAS}$  was randomly  
 685 selected within the range of values of a category, defined by the conservation status and the IAS impact  
 686 magnitude. For DD species,  $P_{IAS}$  was selected within the whole range (0.0001-0.9999). (b) FSp and FUn  
 687 were measured in a functional space of n-dimensions, adapted to each taxonomic group, and normalized  
 688 between 0 and 1. Then, 1,000 FUSE-IAS scores were computed as the combination of  $P_{IAS}$ , FSp and  
 689 FUn. (c) Species lists were built based on the median FUSE-IAS score of each taxonomic group and the  
 690 conservation status of species.

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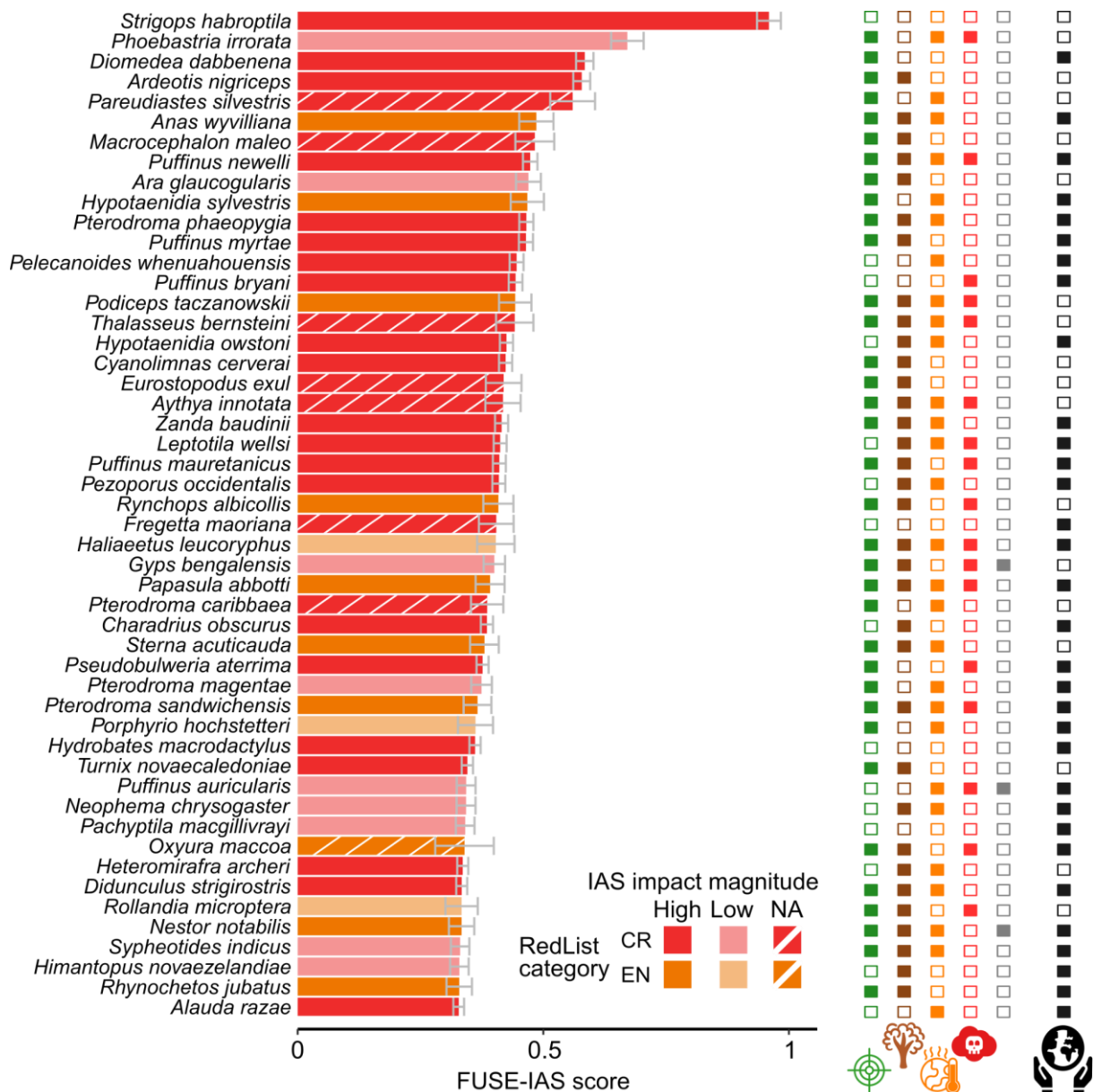


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694 **Figure 2. Number of species in the Core, Watch and Borderline lists.** Circles represent all of the  
 695 species in the lists for each taxon (species numbers are shown inside each circle). Colors represent the  
 696 associated conservation status obtained from the Red List categories (CR: Critically Endangered; EN:  
 697 Endangered; VU: Vulnerable; NT: Near Threatened; LC: Least Concerned).

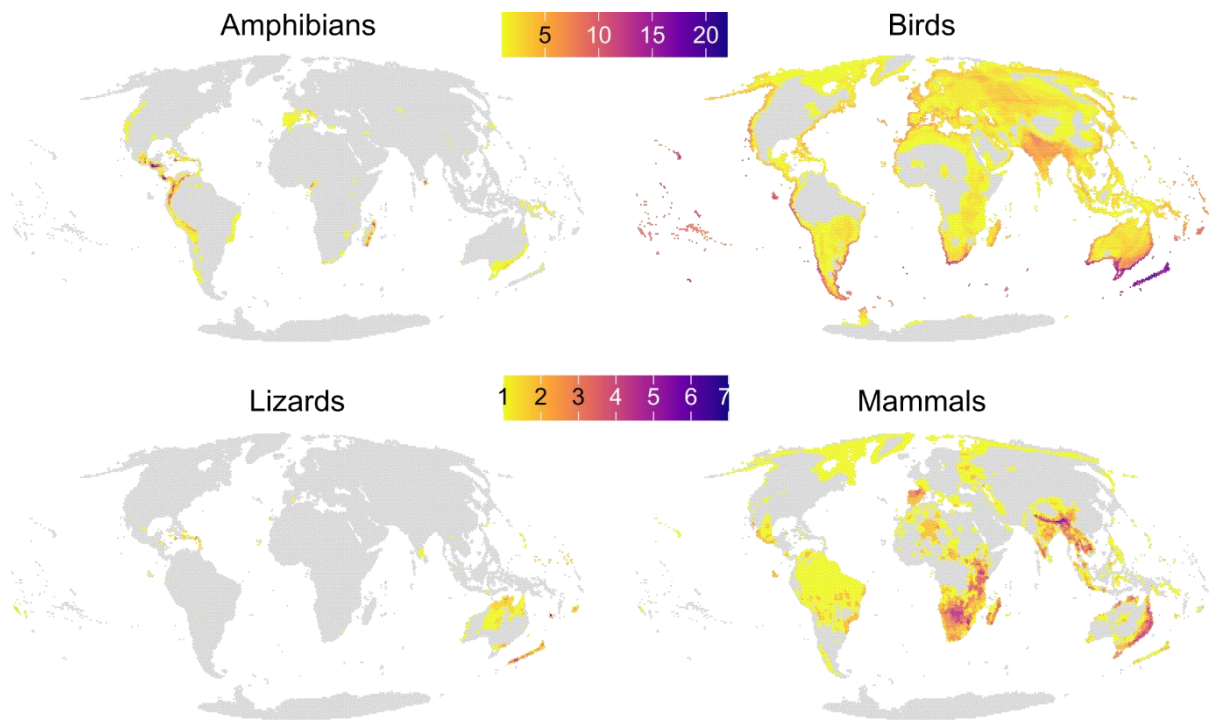
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700 **Figure 3. FUSE-IAS scores, threats and conservation actions of Top 50 birds in the Core list.** Left  
 701 part: Species were ordered by decreasing FUSE-IAS score. Bars and error bars represent, respectively,  
 702 the median FUSE-IAS score and the standard deviation of the 1,000 scores computed for each species.  
 703 Colors represent the Red List category and the impact magnitude of the IAS threat: Critically endangered  
 704 (CR) with high impact magnitude (strong red), low impact magnitude (light red), and missing impact  
 705 information (stripped red); Endangered (EN) with high impact magnitude (strong orange), low impact  
 706 magnitude (light orange), and missing impact information (stripped orange). Right part: Other threats  
 707 besides IAS are represented by the first five columns: biological resource use (green), habitat loss and  
 708 degradation (brown); climate change and extreme weather (orange); pollution (red); other threat types  
 709 (grey). Conservation actions needed for IAS management are represented by the black column. In all  
 710 columns, a filled box indicates the existence of a threat or conservation action need related to that  
 711 species. Threats were aggregated in broad categories: habitat loss and degradation is a combination of  
 712 residential and commercial development, agriculture and aquaculture, energy production and mining,  
 713 transportation and service corridors, human intrusion and disturbance, and natural system modification.

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717 **Figure 4. Global maps of the FUSE-IAS Core list species for each taxon.** The color pattern represents  
 718 the taxonomic richness of species from the FUSE-IAS Core list. Note the differences in values between  
 719 groups, which range from one to 22 species for amphibians and birds, and one to seven species for  
 720 lizards and mammals. Grey areas represent zones without any species from the FUSE-IAS Core list.

721

722 **Table 1. Conservation guide: Warnings, recommendations, and possible ways to adapt**  
 723 **the FUSE-IAS score to conservation goals.**

<b>FUSE-IAS score construction</b>	
Warning	Traits used for the 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 higher than three.
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, like plants or arthropods, the score can be calculated on a taxonomic or geographic subset. In that case, regional assessments of IUCN can be used instead of the global Red List of threatened species.
Possible adaptation	The 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>FUSE-IAS score interpretation and priority lists</b>	
Warning	The 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 the other threats associated with species on the lists to manage the IAS threat.
Recommendation	Consider providing proactive conservation guidance for species in the Watch list and not restraining conservation efforts to Core list species.
Recommendation	The FUSE-IAS 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, like the EDGE score, adapted to IAS threat.

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