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1 **Title**

2 Profiling insular vertebrates prone to biological invasions: what makes them vulnerable?

3 **Short title**

4 Insular species prone to biological invasions

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19

20 **Abstract**

21 Invasive alien species (IAS) are a major threat to insular vertebrates, although the ecological
22 characteristics that make insular communities vulnerable to IAS are poorly understood. After
23 describing the ecological strategies of 6,015 insular amphibians, birds, lizards and mammals,
24 we assessed the functional and ecological features of vertebrates exposed to IAS. We found
25 that at least 50% of insular amphibian functional richness was hosted by IAS-threatened
26 amphibians and up to 29% for birds. Moreover, all IAS-threatened groups except birds
27 harbored a higher functional richness than species groups threatened by other threats.
28 Disentangling the ecological strategies threatened by IAS, compared to those associated with
29 other threats, we showed that birds, lizards, and mammals were more likely to be terrestrial
30 foragers and amphibians to have larval development. By contrast, large-bodied species and
31 habitat specialists were universally threatened. By considering the functional aspect of
32 threatened insular diversity, our work improves our understanding of global IAS impacts.
33 This new dimension proves essential for undertaking relevant and effective conservation
34 actions.

35

36 **Keywords**

37 Biological invasions; Ecological traits; Functional diversity; Islands; Vertebrates;
38 Vulnerability.

39

40 **Introduction**

41 Human activities continue to impact biodiversity worldwide at an accelerating rate (Ceballos
42 et al., 2015). Among various drivers that negatively affect global biodiversity, invasive alien
43 species (IAS) are considered to be the primary cause of extinctions (Blackburn et al., 2019).
44 Because almost nine out of ten extinctions associated with IAS involve insular endemic
45 species (Bellard, Cassey, et al., 2016), insular systems are particularly impacted by this threat.
46 Moreover, intrinsic island features such as simplified ecosystems and high endemism due to a
47 specific eco-evolutionary history promote the high extinction proneness of insular species
48 (Tershy et al., 2015). Combined with the ongoing IAS threat, this puts strong pressure on
49 contemporary insular biodiversity. For example, IAS are currently associated with more than
50 a quarter of critically endangered insular terrestrial vertebrates (Dueñas et al., 2021). Since the
51 rate of introduction of alien species into new ecosystems is currently increasing and does not
52 appear to be slowing down (Seebens et al., 2017), it is of primary importance to understand
53 the vulnerability of insular ecosystems to biological invasions.

54 Species vulnerability to threats depends on extrinsic factors such as stress intensity as well as
55 intrinsic factors such as ecological traits (e.g., body size, type of habitat, diet), which affect
56 the capacity of species to adapt and thrive under changing environments (Clavel et al., 2011).
57 The link between species traits and vulnerability to major threats has been widely
58 documented. For instance, universal characteristics associated with a “slow-living” pace
59 (correlated to large body size) or a small geographical range have been shown to be
60 particularly important to explain the species extinction risk (Chichorro et al., 2019). However,
61 the interaction between species traits and their vulnerability depends on the threat involved
62 (Chichorro et al., 2020). The ability of species to survive habitat loss is affected by their
63 habitat breadth and geographic range, whereas wildlife exploitation and hunting preferentially
64 threaten very large species (Gonzalez-Suarez et al., 2013; Ruland & Jeschke, 2017; Tingley et

65 al., 2013). To our knowledge, the link between species traits and vulnerability to IAS has been
66 poorly assessed at a global scale for terrestrial vertebrates (but see Evans et al. (2021) for
67 birds and Liu et al. (2017) for fishes). To date, the vast majority of the literature focuses on
68 plants and is based on experimental works (Fried et al., 2019; Hejda, 2013). Analyzing which
69 ecological strategies of species are particularly threatened by IAS in insular ecosystems is
70 crucial in order to anticipate a potential functional shift due to extinctions (Carmona et al.,
71 2021; Cooke et al., 2019; Oliveira et al., 2020). Although the functional vulnerability of
72 insular birds and mammals to major biodiversity threats has been assessed (Leclerc et al.,
73 2020), special attention should be paid to IAS in particular. IAS impact systems in various
74 ways, depending – among other parameters – on the
75 features of the recipient community (Ricciardi et al., 2013). Evaluating species vulnerability
76 to invasions across the whole group of tetrapods would complete the existing knowledge on
77 the impacts of invasions. This could prove valuable in order to implement more effective
78 conservation measures for worldwide insular biodiversity vulnerable to IAS threat.

79 Here, we focus on the ecological attributes of endemic insular terrestrial vertebrates that make
80 them vulnerable to IAS threats. We collected information on six ecological traits for 6,015
81 endemic insular terrestrial vertebrates (1,423 amphibians, 2,020 birds, 1,151 mammals, and
82 1,421 lizards). First, we assessed the functional diversity of insular vertebrates associated with
83 IAS compared to the global pool of endemic insular species. We considered a group of
84 species declining due to biological invasions (IAS-T) and a group of species that is not
85 significantly declining despite the presence of this threat (IAS-NT). Our assumption is that
86 IAS-T and IAS-NT are both characterized by a functional richness that is lower than expected
87 by chance (i.e. than assemblages composed of random sets of species), indicating that both
88 assemblages contain species with relatively similar functional traits. Indeed, species sharing
89 certain properties (i.e., vulnerability to a threat) tend to aggregate into a few functional groups

90 (Mouillot et al., 2014), because the threat often filters particular traits. We then investigated
91 the prevailing and specific ecological profiles of endemic species threatened by IAS
92 compared to the global pool of endemic insular vertebrates. We disentangled the effects of
93 other major threats on biodiversity by comparing the attributes of species threatened by IAS
94 and species threatened by other threats. As IAS impact native fauna through various
95 mechanisms (e.g., predation, competition, habitat alteration), we expect endemic species to
96 present general features of vulnerability to this threat. For instance, we assume that species
97 with a restricted habitat breadth will be vulnerable to IAS, similarly to other threats like
98 habitat loss. Finally, we expect that endemic species with fragile stages of their life cycle
99 (e.g., egg, larvae) will be more prone to experience pressure from invasive predators, thus
100 making these traits sensitive to IAS (Allen et al., 2004).

101

102 **Materials and Methods**

103 **Database construction**

104 *Insular terrestrial vertebrates*

105 We extracted the occurrences of species from the spatial data of the IUCN Red List (IUCN,
106 2020) for amphibians and mammals, BirdLife International (BirdLife International &
107 Handbook of the Birds of the World, 2020) for birds, and GARD (Roll et al., 2017) for
108 lizards. We then determined the insularity status of each species, because we limited our study
109 to endemic insular tetrapods, i.e., terrestrial vertebrates occurring only on islands and not on
110 continents. Islands were defined as land masses surrounded by water, larger than 1 km² and
111 smaller than Greenland (Weigelt et al., 2013). This resulted in 1,423 amphibians, 2,020 birds,
112 1,151 mammals, and 1,421 lizards that were extant, native, or reintroduced, and resident on
113 islands.

114 *Species information*

115 *Extinction risk & biological invasion threat.* The IUCN Red List provides the category of
116 extinction risk for each species: least concerned (LC), near threatened (NT), vulnerable (VU),
117 endangered (EN), critically endangered (CR), extinct (EX), extinct in the wild (EW), and data
118 deficient (DD). As we considered only extant species, we removed species from EX and EW
119 categories. CR, EN, and VU categories were grouped into a single “threatened species”
120 category. LC and NT categories were grouped together in a “non-threatened species”
121 category. In addition, for a wide range of species, the IUCN Red List offers a description of
122 all threats to which species are currently exposed based on the IUCN Threats Classification
123 Scheme that proposes a unified categorization of threats to biodiversity (Salafsky et al., 2008).
124 We identified species exposed to invasive alien species (IAS) as those associated with threat 8
125 *Invasive & other problematic species, genes & diseases* from the IUCN Threats Classification
126 Scheme (version 3.2). However, this category also includes threats due to problematic native
127 species or diseases, which do not correspond to the established definition of invasive alien
128 (i.e., non-native) species (Blackburn et al., 2011). We therefore considered only the
129 subcategories *8.1 Invasive non-native/alien species/diseases* and *8.4 Problematic*
130 *species/diseases of unknown origin* (when we were able to determine the exotic origin of the
131 named problematic species).

132 Thus, we defined the three following categories: IAS-threatened (IAS-T), IAS-non-threatened
133 (IAS-NT), and Other-threat-T species. IAS-T species suffer from a decline in population size
134 or range due to a biological invasion threat. IAS-NT species are not considered at risk of
135 extinction despite being exposed to a biological invasion threat according to the IUCN Red
136 List criteria. The Other-threat-T set constitutes a control category composed of species
137 exposed to one or several other threats (except biological invasions) and at high risk of
138 extinction. Data deficient species were excluded from these three pools but not from the
139 global species pool.

140 *Ecological traits.* We described four to five species-level traits for amphibians, birds,
141 mammals, and lizards that are detailed below (see Table S1 for more details on the trait
142 categories). These were chosen according to their ecological importance regarding the
143 biological invasion threat and the percentage of missing values. Traits were related to life
144 history (i.e., body mass, reproductive mode) or resource use and habitat occupation (i.e., diet,
145 foraging niche, period of activity, habitat breadth). They also affect various ecosystem
146 processes (food web functioning, nutrient cycles, seed dispersal, etc.) that build ecological
147 communities and drive their responses to biotic and abiotic factors (Harrison et al., 2014).
148 Habitat breadth was represented by the number of habitat types used by each species. Habitat
149 types were based on the IUCN Habitats Classification Scheme (version 3.1). Habitat breadth
150 was coded using five ordered categories, ranging from one to five or more habitats. Body size
151 was defined for each taxon by five ordered categories (very small, small, medium, large, very
152 large), which were determined so as to each contain 20% of the overall distribution of body
153 mass or body length (depending on the group). The foraging niche was coded by five to seven
154 categories depending on the taxon (Table S1 for category details). This trait represented the
155 preferred stratum of each species, coded as “Multiple” if none was dominant. The period of
156 activity was coded by six factors for mammals: crepuscular, diurnal, nocturnal, crepuscular-
157 diurnal, crepuscular-nocturnal, and crepuscular-diurnal-nocturnal. Lizards were coded as
158 diurnal, nocturnal, or cathemeral, and birds as diurnal or nocturnal. As this trait lacked
159 information for amphibians, we did not consider it in our analyses. The main diet was
160 described for birds and mammals only, and it was characterized as the dominant type of food
161 (>50%) consumed by the species. This trait involved five categories: herbivore, invertebrates,
162 vertebrates and carrions, mixed carnivore, and omnivore. Finally, reproductive mode was
163 compiled for lizards and amphibians, indicated the way in which species reproduce and

164 develop. It was coded by three factors: viviparous, oviparous, and mixed for lizards;
165 viviparous, larval, and direct for amphibians.

166 Except for the habitat breadth extracted from the IUCN database (IUCN, 2020) for all
167 tetrapod species, ecological trait values were compiled from multiple sources: amphibian
168 traits from the AmphiBIO database (Oliveira et al., 2017); bird traits from the Elton trait
169 database (Wilman et al., 2014); mammal traits from both the PHYLACINE database (Faurby
170 et al., 2020) (diet and body size) and the Elton trait database (period of activity and foraging
171 niche); and lizard traits from published datasets (Slavenko et al. (2016) for body size and
172 Meiri (2018) for reproductive mode, activity period, and foraging niche). Because reptile
173 traits were poorly reported for major groups such as snakes, turtles, and crocodiles (only body
174 size was described), we focused on lizard species for this taxon. Other global databases
175 contained information on reptile life-history (e.g. Amniote database (Myhrvold et al., 2015)),
176 but at this time there is no existing database on reptile ecological traits except Meiri (2018)
177 for lizards only. Considering the whole class of reptiles in our study would have introduced a
178 too severe phylogenetic bias in trait completion, and thus decreased the quality of data
179 imputation and analyses. For trait data compilation and the merging of databases from
180 different sources, we verified species synonyms using both the *rl_synonyms* function from the
181 *rredlist* package (Chamberlain, 2020) for searches in the IUCN database and the *synonyms*
182 function from *taxise* package (Chamberlain & Szocs, 2013) for searches in the Integrated
183 Taxonomic Information System.

184 *Data imputation for missing trait values.* Functional diversity analyses require an exhaustive
185 dataset with no missing values. However, only birds had complete trait data, while mammals
186 contained 7% of missing values, amphibians 13%, and lizards 15% (percentages varying from
187 0% to 34% depending on the traits; Table S1). To avoid bias due to the data depletion of
188 species with missing values (Taugourdeau et al., 2014), we decided to impute missing data

189 using phylogeny, as closely related species tend to be more similar to each other. We thus
190 computed for each trait its associated phylogenetic signal (Pagel's lambda calculated with the
191 *Phylosig* function from the *phytools* package (Revell, 2012)). All imputed traits had a Pagel's
192 lambda higher than 0.70 (Table S1). Phylogenetic information was therefore summarized by
193 the first 10 phylogenetic eigenvectors computed from 1,000 trees for each taxon obtained
194 from Vertlife.org (amphibians (Jetz & Pyron, 2018); mammals (Upham et al., 2019);
195 squamates, including lizards (Tonini et al., 2016)). Eigenvectors extracted from principal
196 component analysis (using *PVR* (Santos, 2018) and *RSpectra* (Qiu & Mei, 2019) packages)
197 represent the variation in the phylogenetic distances between species. Here, the first 10
198 selected eigenvectors explained more than 50% of the phylogenetic variance between species
199 for each taxon. We generated imputed values with the *mice* function from the *mice* package
200 (van Buuren & Groothuis-Oudshoorn, 2011) using the predictive mean matching method
201 based on the ecological (traits and insular character) and phylogenetic (first 10 phylogenetic
202 eigenvectors) relationships between species (Cooke et al., 2019; Penone et al., 2014). We
203 evaluated the performance of the imputation method for each trait of each taxon (see
204 Appendix S1 for more details). Data imputation was computed for worldwide species pools
205 (not only species from islands). Considering only insular endemic species, the final complete
206 trait datasets contained 1,423 amphibians, 2,020 birds, 1,151 mammals, and 1,421 lizards
207 (total of 6,015 terrestrial vertebrates) and are available online (Marino et al., 2021). An
208 outline of the different stages of data compilation is provided in Figure 1.

209 **Functional diversity**

210 *Rationale*

211 Ecological traits determine most of the functions and processes that species can accomplish in
212 an ecosystem (Harrison et al., 2014). Their responses to disturbances (and thus to biological
213 invasions) depend directly or indirectly on functional trait diversity and variety (Hevia et al.,

214 2017). Hence, an adequate characterization of functional diversity is necessary to encapsulate
215 trait variation between IAS-T and IAS-NT groups. In this study, we considered functional
216 diversity as the distribution of species and their relative representation in a functional space
217 (Mason et al., 2005). A functional space is a multidimensional space where the axes are
218 ecological traits along which species are distributed according to their trait values (Mouillot et
219 al., 2013).

220 *Functional entities and functional space*

221 To represent the distances between combinations of trait values, we classified the 6,015
222 insular endemic amphibians, birds, mammals, and lizards into functional entities (FEs) for
223 each taxon. FEs are groups with a unique combination of functional trait values for the
224 considered traits. Then, we arranged these FEs into multidimensional functional spaces based
225 on the value of their ecological traits. To do so, the pairwise functional distances between FEs
226 were computed using the Gower dissimilarity index (Gower, 1971), which allowed us to
227 calculate the distances between categorical traits while giving the same weight to all traits.
228 Then, we calculated all multidimensional functional spaces from 2 to 10 dimensions using
229 Principal Coordinates Analysis. Finally, we selected the best functional space for each taxon,
230 i.e. the space giving the most accurate representation of trait values. A functional space is of
231 high quality when the distance between each pair of species in the space (Euclidean distance
232 for multidimensional functional space) is close to the initial functional distance (Gower's
233 distance). For each taxon, we kept the functional space having the smaller mean square
234 deviation (mSD), the quality criteria of Maire et al. (2015), which reflects the minimum
235 deviation between the Euclidean distances and the Gower's distances.

236 *Functional diversity metrics*

237 Because of its complexity, functional diversity cannot be reported by a single metric (Villéger
238 et al., 2008). We used several indices to describe how the functional space is filled and how

239 the relative representation of a species set is allocated within the functional space. We adopted
240 three metrics to characterize functional diversity: functional richness (FRic), functional
241 evenness (FEve), and functional over-redundancy (FOR). All these metrics take a value
242 between 0 and 1, and their theoretical and ecological interpretations are detailed in Table 1.
243 We used scripts from Villéger (2017) to compute the functional spaces and functional
244 diversity metrics. FRic and FEve were computed as in Villéger et al. (2008) whereas FOR
245 followed Mouillot et al. (2014) formula.

246 **Statistical analyses**

247 *Null models*

248 To test whether the observed values of the functional diversity indices were significantly
249 different from the hypothesis that all species were randomly distributed, we ran null models.
250 This test allowed us to quantitatively assess the characterization of functional diversity of
251 IAS-T and IAS-NT sets specifically compared to the global pool, i.e. all the endemic insular
252 species. From the global pool, we randomly assigned FEs and species into IAS-T and IAS-NT
253 sets 999 times, while keeping constant the number of FEs and species in each set. As an
254 example, if the IAS-T set contained 100 species distributed in 60 FEs while the global pool
255 contained 1,000 species distributed in 300 FEs, simulating an assemblage consists in
256 randomly selecting 60 FEs among the 300 and fill them with 100 species picked randomly
257 among the 1,000. The process is then repeated 999 times to get rid of the effect of
258 randomization. Functional diversity metrics were computed for each random set. Null models
259 were run independently on amphibian, bird, mammal, and lizard functional spaces.

260 The observed values of functional diversity indices were compared to the simulated values
261 using a two-sided test ($\alpha = 5\%$) to measure deviations from the null hypothesis. We calculated
262 p-values directly from the null distribution of simulated metrics as $p = (b+1)/(n+1)$, with b the
263 number of random values equal or above the observed value and n the number of simulations

264 (Veech, 2012). We then calculated effect-size (ES) values as probit transformed p-values to
265 indicate departure from the random expectation following Botta-Dukát (2018). For extreme
266 observed values ($b < 6$ or $b > n-6$), we applied p-calculation by fitting generalized Pareto-
267 distribution of the most extreme simulated values and estimating p from this new distribution
268 (Knijnenburg et al., 2009) (Appendix S2 for a detailed method of p and ES calculation).

269 An observed value of FRic, FEve or FOR emerges as significantly different from the
270 simulated values if the observed value is in one of the 2.5% tails of the simulated value
271 distribution. For instance, an observed value of FRic $< 2.5\%$ of the simulated values (i.e.,
272 expected values under a null hypothesis) means that FEs (and thus species) from this set are
273 more functionally clustered than expected by chance (negative ES and p-value > 0.975). On
274 the contrary, an observed value $> 97.5\%$ of simulated values indicates that FEs from this set
275 are less clustered (and thus more widespread) than expected under a null hypothesis (positive
276 ES and p-value < 0.025).

277 To determine whether the traits of species exposed to biological invasions were significantly
278 different from the global pool of insular endemic species, we also performed null models on
279 the trait distribution among species, independently for each taxon. From the global pool, we
280 randomly assigned FEs of IAS-T and IAS-NT species and broke down these entities to count
281 the number of species per trait modality for each set. Simulations were run 9,999 times while
282 keeping a constant number of species and FEs for each set. The observed values of the
283 number of species per trait modality for IAS-T and IAS-NT sets were compared to simulated
284 values using p-values and ES as described above. To assess the effect of biological invasion
285 versus other threats that could affect biodiversity, we computed an identical null model for
286 Other-threat-T sets.

287 *Sensitivity to data imputation*

288 To ensure the obtained results were not biased by data imputation, we rerun all our analyses
289 without imputed data. Thus, we considered 879 amphibians, 2,020 birds, 923 mammals, and
290 711 lizards for which we had complete informed traits before imputation.

291 All analyses were performed with R software (version 4.0.3) (R Core Team, 2020).

292

293 **Results**

294 **Functional diversity characterization of endemic insular terrestrial vertebrates** 295 **associated with IAS**

296 We found that IAS-threatened (IAS-T) amphibians represented 50% of worldwide insular
297 endemic functional richness followed by birds (29%), lizards (26%), and mammals (16%)
298 (Figure 2, Table S2). Our results showed that functional richness hosted by insular species
299 vulnerable to IAS (IAS-T) was always higher compared to that hosted by species not at risk of
300 extinction (IAS-non-threatened – IAS-NT). In all cases, statistical analyses revealed that
301 functional richness hosted by insular endemic species associated with IAS threat (either
302 threatened or not) occupied smaller functional spaces than expected given their respective
303 taxonomic richness (except for IAS-NT mammals) (Figure 2, Table S2). Species in IAS-T and
304 IAS-NT sets were therefore more clustered than anticipated under the null hypothesis. When
305 controlling the FRic by the taxonomic richness (i.e. number of species), the IAS-T groups
306 hold more functional diversity than the IAS-NT ones, except for amphibians for which the
307 ratio is equivalent. Moreover, all IAS-T groups except birds harbored a higher FRic than
308 groups of species exposed to one or several other threats (except biological invasions) and at
309 high risk of extinction (Other-threat-T), with IAS-T lizards representing a functional diversity
310 six times greater than Other-threat-T lizards.

311 Concerning the other metrics of functional diversity, we expected a functional space filled
312 with more regularity for IAS-NT sets than for IAS-T. This would result in lower functional

313 evenness (FEve) and higher functional over-redundancy (FOR) for IAS-T species compared
314 to IAS-NT. However, we did not detect such differences (Figure 2, Table S2). Only birds and
315 mammals showed differences in regularity between IAS-T and IAS-NT groups: in both taxa,
316 FOR was twice as high for IAS-T than for IAS-NT (ca. 26% vs ca. 13% for both taxa,
317 respectively). Functional diversity metrics were almost identical with and without imputed
318 data for all groups (Figure 2, Figure S1). The relationships between IAS-T, IAS-NT and
319 Other-threat-T metrics were preserved despite the imputation process.

320 **Ecological profiles of endemic insular terrestrial vertebrates exposed to IAS**

321 The performance of the data imputation for global species characteristics varied depending on
322 the trait modalities and the taxon. Body size was correctly imputed with a very low RMSE for
323 all taxa (Table S3). Reproductive mode for amphibians had a great prediction rate for both
324 direct and larval strategies, as well as foraging niche and main diet for mammals (Figure S3).
325 However, nocturnal activity period for mammals and terrestrial foraging strategy for lizards
326 tended to be over-predicted by the data imputation (Figure S3). With that in mind, we
327 analyzed the ecological strategies shared by IAS-T endemic insular tetrapods at a global scale
328 for the six studied traits using the imputed dataset (Figure 3). Overall, IAS-T species of the
329 four taxa were mainly habitat specialists (habitat breadth [HB] of one or two) and had a large
330 or very large body size. These strategies were overrepresented among IAS-T species
331 compared to the global pool for certain taxa (positive effect size [ES], p -value < 0.025). All
332 IAS-T groups except amphibians were characterized by a dominant and overrepresented
333 terrestrial foraging niche (birds: $p = 0.010$, $ES = 2.32$; lizards: $p = 0.001$, $ES = 3.01$;
334 mammals: ns). IAS-T amphibians were more likely to occur in multiple foraging niches,
335 including aquatic habitats, compared to the global pool ($p = 0.003$, $ES = 2.71$). Concerning
336 the period of activity, IAS-T mammals were more nocturnal ($p = 0.001$, $ES = 2.99$), whereas
337 lizards were more diurnal ($p = 0.001$, $ES = 2.98$) than the global pool. IAS-T birds consumed

338 more invertebrates, while IAS-T mammals consumed more plant materials than their
339 respective global pools (birds: $p = 0.022$, $ES = 2.01$; mammals: $p = 0.006$, $ES = 2.51$). Finally,
340 IAS-T amphibians had a dominant and overrepresented larval reproductive mode ($p = 0.004$,
341 $ES = 2.64$).

342 All the cited results about IAS-T species strategies generally stand out when compared to the
343 analysis without data imputation (Figure S2). We noticed few exceptions when considering
344 only complete data (i.e. without imputation). For instance, larval reproductive mode was no
345 longer overrepresented among IAS-T amphibians and IAS-T lizards were no longer more
346 terrestrial than global lizard pool.

347 All the strategies shared by IAS-T species were broadly shared by IAS-NT species (see the
348 dots in gray squares in Figure 4, meaning that ES values had the same sign in both IAS-T and
349 IAS-NT sets). However, we found a few exceptions to this pattern. For instance, IAS-NT sets
350 showed an overrepresentation of habitat generalists, while this modality was underrepresented
351 in IAS-T amphibians, birds, and lizards. Several strategies were characterized by a difference
352 in ES magnitude between IAS-T and IAS-NT sets, being more associated with IAS-T species.
353 This was the case for very large body size in birds. Moreover, terrestrial and water foraging
354 niches were more than twice as overrepresented in IAS-T birds than in IAS-NT birds;
355 nocturnal activity was more than three times as overrepresented in IAS-T mammals than in
356 IAS-NT mammals compared to the global pool.

357 Finally, to disentangle the traits that may play a role in insular vertebrate vulnerability to
358 biological invasions in particular, we compared the traits shared by IAS-T species and species
359 at high risk of extinction exposed to one or several other threats, except biological invasions
360 (Other-threat-T, Figure 5). Habitat specialization was associated with a high extinction risk
361 for all threatened species (high ES for both Other-threat-T and IAS-T sets for $HB = 1$ for
362 birds, mammals and lizards). Very large lizards were overrepresented in IAS-T but

363 underrepresented in Other-threat-T. Terrestrial foraging niche (as well as water foraging niche
364 for birds) was specific to IAS threat for birds, mammals, and lizards. Diet of IAS-T birds was
365 overrepresented by invertebrates compared to Other-threat-T birds. Lastly, regarding
366 reproductive mode, IAS-T lizards did not share any specific profile, while Other-threat-T
367 lizards were significantly more oviparous than the global pool. Nevertheless, IAS-T
368 amphibians showed a significant overrepresentation of larval reproductive mode, whereas
369 Other-threat-T amphibians had more a direct development than the global pool.

370

371 **Discussion**

372 **Vulnerability to IAS and ecological strategies of insular endemic species**

373 Ecological traits related to habitat, life history, or foraging behavior are keys to triggering the
374 adequate response and adaptation of species to IAS pressures (Berthon, 2015). IAS-T species
375 from the four studied taxa presented common characteristics such as the predominance of a
376 specialized habitat and a large body mass. These features are consistent with the profiles of
377 globally endangered terrestrial vertebrates (Cooke et al., 2019; Slavenko et al., 2016), as large
378 species are particularly vulnerable to hunting, habitat destruction, or human pressure in
379 general (Rapacciuolo et al., 2017). This can be correlated with a slow-living pace that makes
380 species unable to recover from fast and impacting disturbances like IAS (Slavenko et al.,
381 2016). Since IAS-NT species do not share such traits, it would appear that these are more
382 specific to a high extinction risk than to IAS threat in particular.

383 More importantly, we found that foraging niche was a crucial trait of species vulnerability to
384 IAS compared to other global threats. First, terrestrial niche was a dominant and
385 overrepresented feature among all IAS-T birds, lizards, and mammals. Various IAS have
386 major impacts at the ground level. For instance, IAS plants can change ground cover very
387 rapidly, which disrupts the habitat of native species, thus making ground-level species more

388 vulnerable (Ceradini & Chalfoun, 2017). Moreover, IAS that impact mammals are mainly
389 predators or competitors on the ground (feral cats, rats, feral dogs, etc.) (Doherty et al., 2016).
390 Predation pressure by an IAS was also shown to reduce ground-level foraging for insular
391 lizards (Delaugerre et al., 2019). However, for this group the data imputation we performed
392 tended to over predict the terrestrial strategy, thus it can explain why this strategy is
393 prevailing. The negative impacts of IAS on terrestrial birds are numerous; for example, they
394 can affect nesting or foraging strategies as in the case of invasive ants disturbing complete
395 insular ecosystems (Davis et al., 2008). Second, water foraging birds were also
396 overrepresented among IAS-T species. This is consistent with field observations that
397 acknowledge the severe IAS impacts on seabirds such as rat predation (Jones et al., 2008).
398 Studies at a larger scale confirm that specialist pelagic birds with a slow reproductive mode
399 (e.g., large water foraging species) are sensitive to stresses like IAS that impact survival and
400 reproductive success (Richards et al., 2021). Third, IAS-T amphibians were more likely to
401 live in multiple niches, including an aquatic habitat. This ecological strategy is concomitant
402 with an aquatic life stage during which amphibians are highly vulnerable to introduced fishes
403 (Bucciarelli et al., 2014).

404 Studies on the involvement of the oviparous reproductive mode of reptiles and amphibians in
405 response to invasions are lacking (Martin & Murray, 2011). Here, we showed that at the
406 global scale, the larval reproductive mode is a trait shared by IAS-T amphibians. Although the
407 over-representation of larval stage among IAS-T amphibians was not significant when
408 considering data without imputation, the good quality of prediction for this modality invites
409 us to consider this result as very likely. Larval strategy involves the tadpole stage, which is
410 highly vulnerable. First, it is sensitive to water pollutants and composition that can be
411 influenced by invasive plant species (Maerz et al., 2005). Second, tadpoles are exposed to fish
412 predation, which is considerable in the case of alien fish introductions into freshwater systems

413 (Falaschi et al., 2020). Finally, amphibians are generally threatened by *Batrachochytrium*
414 *dendrobatidis* (*Bd*), a worldwide spread disease classified as IAS (Scheele et al., 2019). Since
415 *Bd* is present in aquatic habitats, amphibians with a larval (i.e., aquatic) stage are also more
416 exposed to this disease (Scheele et al., 2019). Globally, aquatic amphibians are more impacted
417 by population decline than terrestrial ones (Lips et al., 2003). However, the multiple processes
418 involved in the vulnerability of larval and aquatic strategy to IAS (predation, disease
419 transmission, habitat alteration) require very different conservation actions (Falaschi et al.,
420 2020). Conversely, we did not find any strong correlation between IAS vulnerability and
421 reproductive mode within lizards. In fact, oviparity in endangered lizards was strongly
422 associated with other threats. This result is concomitant with previous studies on reptiles,
423 showing that IAS threat had no effect on traits, probably because at a global scale, habitat loss
424 is the most severe threat for this taxon (Böhm et al., 2016). Furthermore, it is probable that
425 disparities in ecological strategies among IAS-T species are present within taxa due to the
426 different mechanisms by which IAS impact native species (e.g. predation, competition). Thus,
427 not detecting any effect on the whole group of lizards regarding the reproductive mode might
428 also be a reflection of opposite effects in vulnerability to different IAS mechanisms.

429 **Implications of data imputation for trait analyses**

430 Gaps in trait data remain an ongoing issue for macroecological studies, especially for
431 amphibians and reptiles (Etard et al., 2020). Thus, data imputation was a good way to include
432 more species and decrease bias in the represented strategies (Taugourdeau et al., 2014). Plus,
433 data imputation enables better calculations of functional diversity metrics than data with
434 depleted species with missing values (Kim et al., 2018). However, we need to carefully
435 interpret our findings on traits in light of the performance of data imputation. For instance, we
436 observed that the imputation of lizard foraging niche tends to over-predict terrestrial strategy.
437 As a consequence, the observed effect of IAS-T lizards being more terrestrial than the global

438 pool might be due to artificial over-prediction through data imputation. Second, a sample size
439 effect due to the addition of species into the IAS-T and global pools thanks to data imputation
440 can emphasize differences between imputed and non-imputed datasets. For instance, in the
441 lizard dataset, habitat breadth and body size were barely imputed. However, we found several
442 differences with these traits being overrepresented in the IAS-T pool compared to the global
443 pool with and without imputation. In short, data imputation allowed us to include more
444 species in our dataset and improve the conclusions, although we call for a preliminary
445 verification of well and poorly predicted traits before applying data imputation in order to be
446 able to disentangle the imputation effect from the size effect. Some traits were rather poorly
447 imputed with our method (e.g. foraging strategy of amphibians and lizards). Yet, the potential
448 deleterious consequences of this low performance were limited by the fact that we imputed
449 data only for relatively low percentages of species, with weak phylogenetic bias. Following
450 Johnson et al. (2021) we excluded clades that had no information at all (i.e. focusing on
451 lizards instead of the whole Reptilia class) not to impute totally random trait values. We had
452 to restrain the studied traits to well informed traits, but we hope that further data collection on
453 poorly informed taxa will improve the quality of available global trait data. A higher data
454 completeness combined with an appropriate development of open science principles regarding
455 trait data should greatly enhance future studies on functional diversity (Gallagher et al., 2020).

456 **Functional characterization of endemic insular species vulnerable to IAS**

457 Our results emphasize that IAS-threatened amphibians represented a disproportionate amount
458 of the total functional richness (FRic) of this taxon (50%), while the other taxa showed a
459 lower ratio (e.g., 16% for mammals). The FRic rate for IAS-T amphibians largely
460 encompasses the proportion of taxonomic diversity associated with IAS threats within this
461 taxon (Bellard, Genovesi, et al., 2016). The prevalence of predation as an impact mechanism
462 may lead to the increased susceptibility of amphibians to IAS (Nunes et al., 2019), not to

463 mention exposure to *Bd* (Falaschi et al., 2020), which is the IAS impacting the largest number
464 of vertebrates worldwide (Bellard, Genovesi, et al., 2016). Conversely, FRic associated with
465 IAS-T mammals is lower compared to other taxa. However, many insular mammals have
466 already become extinct because of IAS (Bellard, Cassey, et al., 2016). This can give the false
467 impression that mammals are less vulnerable, but many already disappeared, thus shrinking
468 the functional space associated with IAS-T species. All IAS-T groups except birds harbored a
469 higher FRic than Other-threat-T ones when controlling by the taxonomic richness. Therefore,
470 FRic levels for all taxa point toward a worrying amount of ecological strategies threatened by
471 IAS specifically, possibly impacting ecosystem processes carried out using these strategies
472 (Cadotte et al., 2011). This functional vulnerability might even be underestimated, because we
473 only considered species with a Red List category and removed data deficient species from
474 pools associated with IAS. However, in reality, a large number of data deficient species have
475 a high extinction risk, reaching 50% of species for amphibians (González-del-Pliego et al.,
476 2019; Gumbs et al., 2020). We also explored functional evenness (FEve) and over-
477 redundancy (FOR), which provide information on species distribution among functional
478 strategies. These metrics are likely to change following a disturbance in the ecosystem: for
479 instance, FEve is expected to decrease when the disturbance increases (Mouillot et al., 2013).
480 Here, we found no great difference between IAS-T and IAS-NT species regarding FEve in all
481 the studied taxa. Vulnerability of IAS-T insular vertebrates to invasion threat was thus not
482 linked to an uneven global assemblage, as previously found for freshwater fish along an
483 invasion gradient (Shuai et al., 2018). However, our study considered species from all islands
484 (oceanic and continental) pooled together. We may expect that the functional diversity indices
485 differ between the different types of islands, with oceanic islands showing lower functional
486 redundancy than continental ones. In addition, we may expect an important role of island area
487 and distance to mainland to explain the functional diversity observed in this study (Jacquet et

488 al., 2017). Therefore, such a pooling is likely to hide the differences between the IAS-T and
489 IAS-NT groups at a finer scale, notably because of the scaling of functional diversity with
490 island area or isolation.

491 **Ecological and conservation implications**

492 Terrestrial vertebrates are involved in various ecosystem processes such as seed dispersal,
493 nutrient cycling, and pest control, which are directly linked to their traits (Harrison et al.,
494 2014). As IAS threaten a specific part of these traits, we may ask whether ecosystem
495 processes will remain unchanged or whether some are particularly at risk if IAS-T species
496 disappear. For instance, in addition to maintaining physical and chemical conditions around
497 them as larvae, amphibians play a critical role in nutrient flow when moving from water to
498 land during metamorphosis (Ford et al., 2020). However, we showed that amphibians with
499 aquatic larval stages were likely to be associated with IAS threat specifically, thus rendering
500 these functions uncertain if IAS-T species go extinct. Finally, IAS mechanisms (e.g.
501 predation, competition, etc.) are likely to select specific profiles and filter species according to
502 their traits: the traits needed to escape predation are not the same as those used to be more
503 competitive (Evans et al., 2021). The future identification of the association between
504 mechanism type and ecological trait might be of substantial interest to our understanding of
505 IAS functional consequences. From the perspective of developing effective conservation
506 strategies for insular biodiversity, considering native species traits in light of island properties
507 or human pressure would greatly improve the risk assessment of IAS threats (Spatz et al.,
508 2017).

509 Our study is the first to evaluate, at a macroecological scale, the ecological profiles of
510 terrestrial vertebrates at risk of extinction because of the ever-increasing IAS threat. Strategies
511 shared by IAS-T species varied across tetrapod taxa, but we found specific profiles associated
512 with a high vulnerability to IAS in all four taxa. Consequently, the responses of insular

513 systems to future IAS are likely to be affected by the number of vulnerable traits harbored by
514 their species. In addition, if such species vulnerable to IAS were to disappear, ecosystem
515 integrity may not be preserved. We thus recommend integrating native species characteristics
516 into impact assessments of future biological invasions.

517

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804 **Data accessibility**

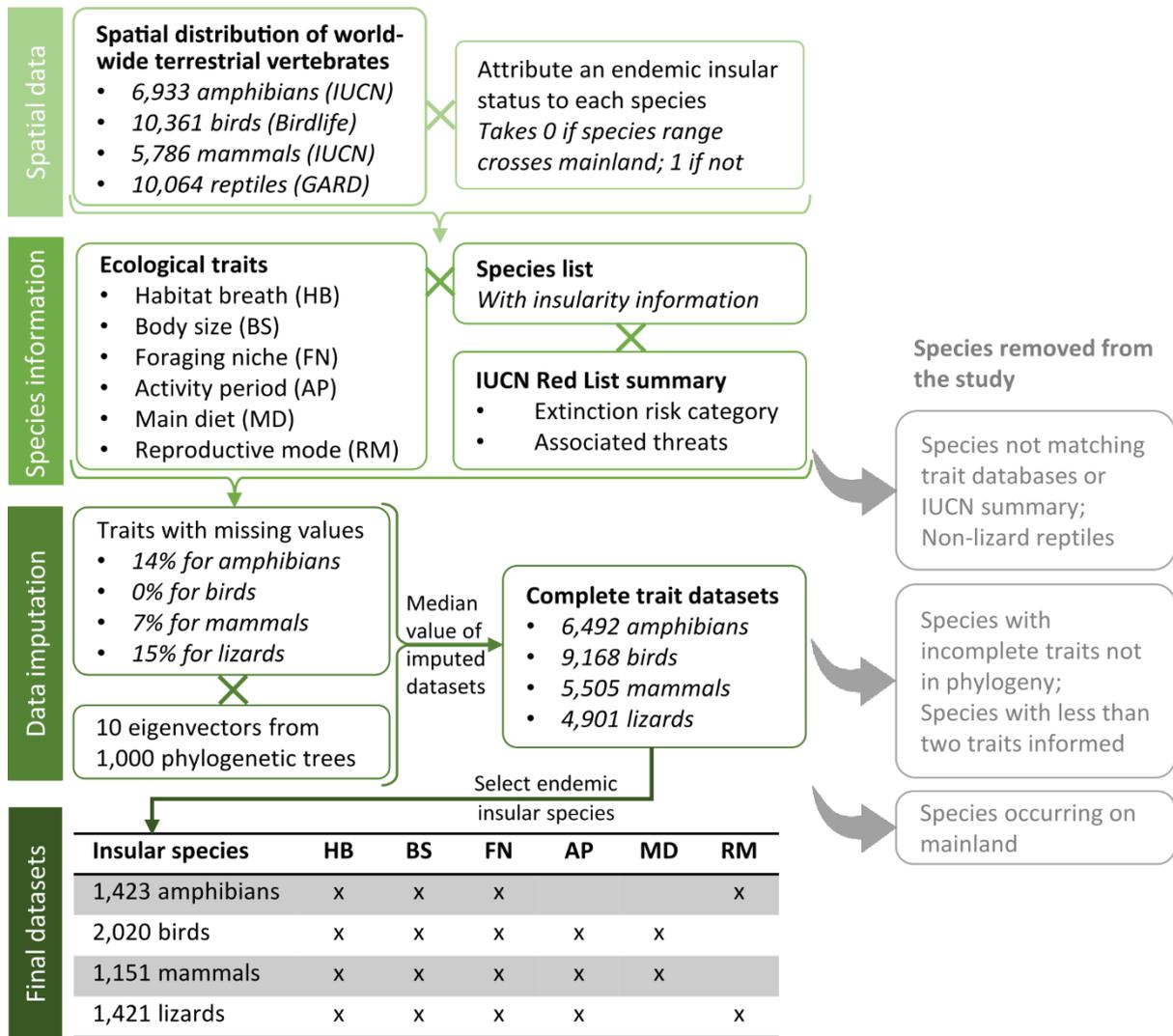
805 The IUCN Red List data are available from the IUCN website
806 (<https://www.iucnredlist.org/search>), which includes information about IUCN Red List status,
807 identity of the threat, list of occupied habitats, and species range maps for amphibians and
808 mammals. Range maps for birds were obtained upon request from BirdLife
809 (<http://datazone.birdlife.org/species/requestdis>); lizard ranges were obtained from GARD
810 (<http://www.gardinitiative.org/data.html>). All traits used in this study are freely available from
811 AmphiBIO (Oliveira et al., 2017), Elton traits (Wilman et al., 2014), PHYLACINE (Faurby et
812 al., 2020), and published databases (Meiri, 2018; Slavenko et al., 2016). We also used
813 phylogenies for amphibians, mammals, and lizards, available from the open access source
814 www.Vertlife.org (Jetz & Pyron, 2018; Tonini et al., 2016; Upham et al., 2019). The data and
815 the code that support the findings of this study are openly available in Zenodo at
816 <https://doi.org/10.5281/zenodo.5571529>, reference number 5571529.

817 **Tables**

818 **Table 1. Description of the three metrics used to characterize functional diversity of**
 819 **endemic insular terrestrial vertebrates at a high risk of extinction due to biological**
 820 **invasions (IAS-T) and those that are not (IAS-NT).**

821

<i>Metric</i>	<i>Theoretical definition</i>	<i>Theoretical interpretation of a high value (close to 1)</i>	<i>Ecological interpretation of a high value</i>	<i>Hypothesis regarding IAS-T and IAS-NT sets</i>
<i>Functional richness (FRic)</i>	Volume occupied by functional entities (FEs) of a set of species in the functional space, expressed as a proportion of the total functional space.	FEs from the set cover a large part of the total functional space	Species from the set share a large part of the total ecological strategies.	FRic is low for IAS-T and IAS-NT sets, but lower for IAS-T (Mouillot et al., 2014).
<i>Functional evenness (FEve)</i>	Regularity with which the functional space is filled in by FEs. This integrates the distance between FEs and the distribution of abundances among FEs in the minimum spanning tree from the functional space.	Species are evenly distributed among FEs, and distances between FEs are entirely regular.	Species from the set evenly share all ecological strategies, and their ecological strategies regularly cover the potential strategies from the global pool.	FEve is low for the IAS-T set but high for IAS-NT (Mouillot et al., 2013).
<i>Functional over-redundancy (FOR)</i>	Percentage of species contained in FEs above the average level of functional redundancy (FR, which is the mean number of species per FE). Its calculation does not depend on the functional space.	Species are densely packed into a few FEs, while many FEs contain a limited number of species.	A large number of species share a limited range of ecological strategies (overrepresentation of strategies in terms of species richness), while many species have unique ecological strategies.	FOR is low for both groups, but lower for the IAS-NT set (Mouillot et al., 2014).

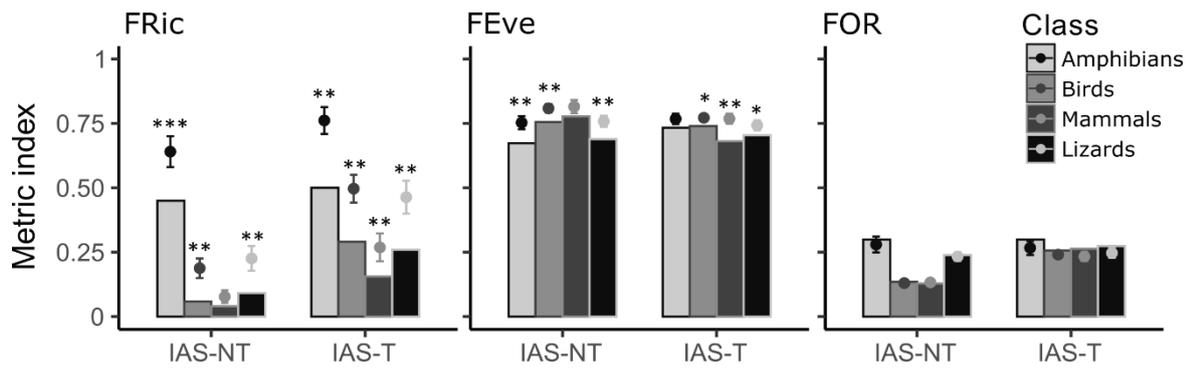


823
824

825 **Figure 1. Different steps of database compilation.** During all the data cleaning process, we
826 excluded some species from the study to ensure the best possible quality for the considered
827 data in our analyses.

828

829



830

831 **Figure 2. Functional diversity metrics for endemic insular terrestrial vertebrates at a**

832 **high risk of extinction due to biological invasions (IAS-T) and those that are not (IAS-**

833 **NT). FRic: functional richness; FEve: functional evenness, FOR: functional over-redundancy.**

834 Bars represent observed values; points and error bars represent means and standard deviations

835 of simulated values, respectively. Stars show significant deviations from the null hypothesis:

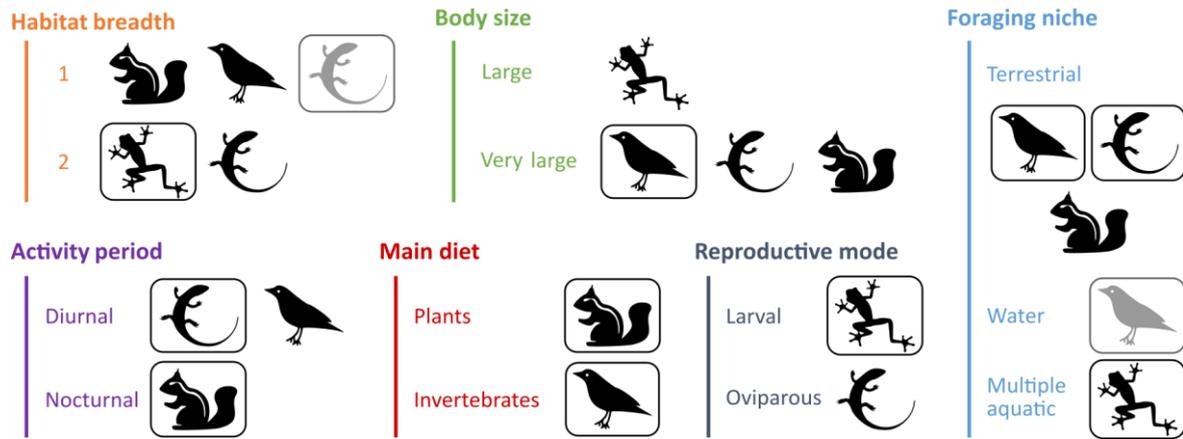
836 * p-value < 0.025 or > 0.975; ** p-value < 0.010 or > 0.990; *** p-value < 0.001 or > 0.999.

837 Values of effect sizes and associated p-values are reported in Table S2. Those results are

838 obtained with the imputed dataset.

839

840



841

842 **Figure 3. Schematic overview of the dominant characteristics shared by IAS-T species**

843 **(black icons) and significantly overrepresented strategies of IAS-T species compared to**

844 **the global pools (circled icons). IAS-T species are at a high risk of extinction due to**

845 biological invasions. The dominant characteristic corresponds to the prevailing trait modality

846 shared by IAS-T species for each trait. Icons are circled when the modality is significantly

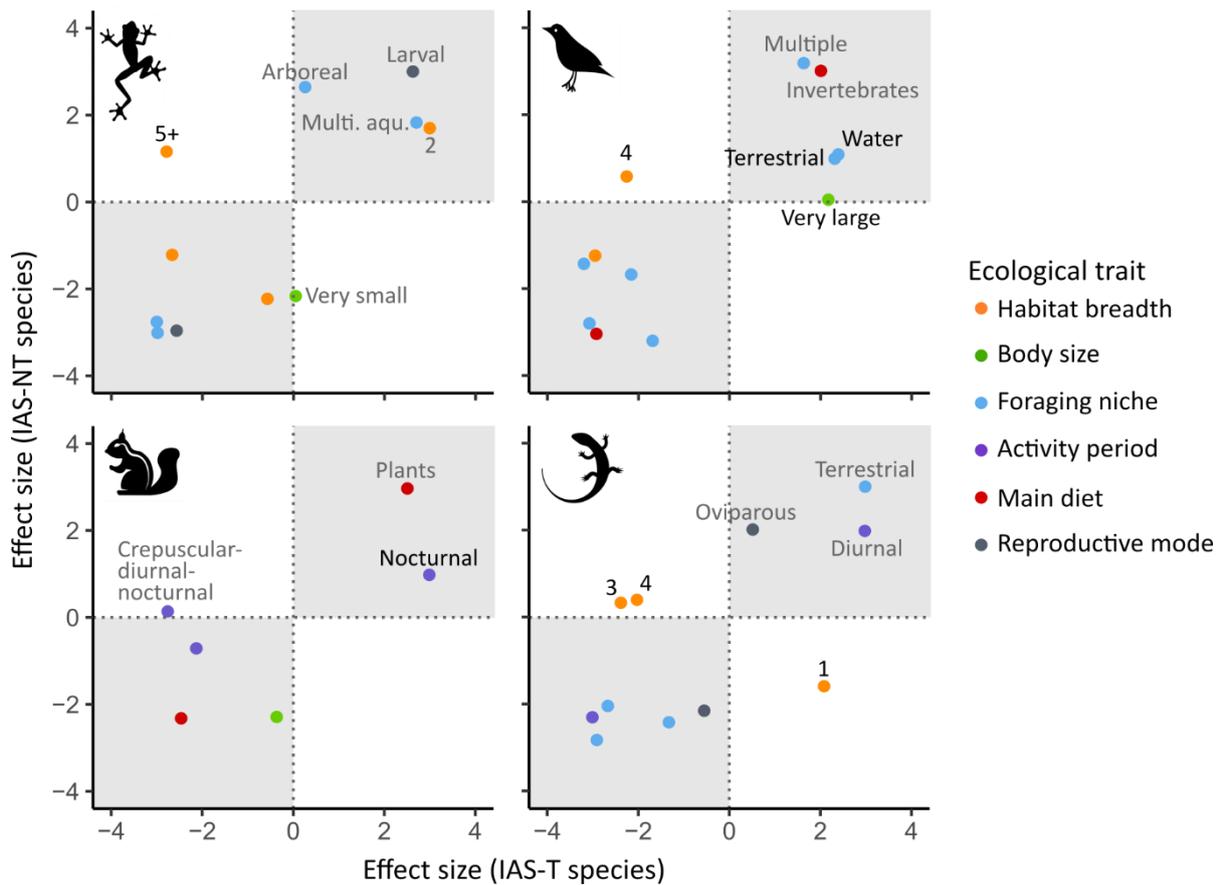
847 overrepresented in IAS-T species compared to the global species pool. Circled gray icons

848 show significantly overrepresented modalities compared to the global pool, but not dominant

849 among IAS-T species. Animal icons represent the four studied taxa: amphibians, birds,

850 mammals, and lizards. Those results are obtained with the imputed dataset.

851



852

853 **Figure 4. Comparison between the effect sizes of ecological trait dissimilarities for IAS-T**

854 **and IAS-NT species compared to the global species pool.** To simplify the reading, only

855 significantly over- and underrepresented modalities for IAS-T, IAS-NT, or both groups are

856 represented. Points located close to the $y=x$ diagonal indicate a similar trend in trait

857 modalities for IAS-T and IAS-NT species (gray squares). By contrast, points located in the

858 lower right and upper left corners (in white) indicate that the directions of ES between IAS-T

859 and IAS-NT species are opposing. For instance, IAS-NT amphibians are more habitat

860 generalists (habitat breadth = 5+) compared to the global amphibian pool, whereas IAS-T

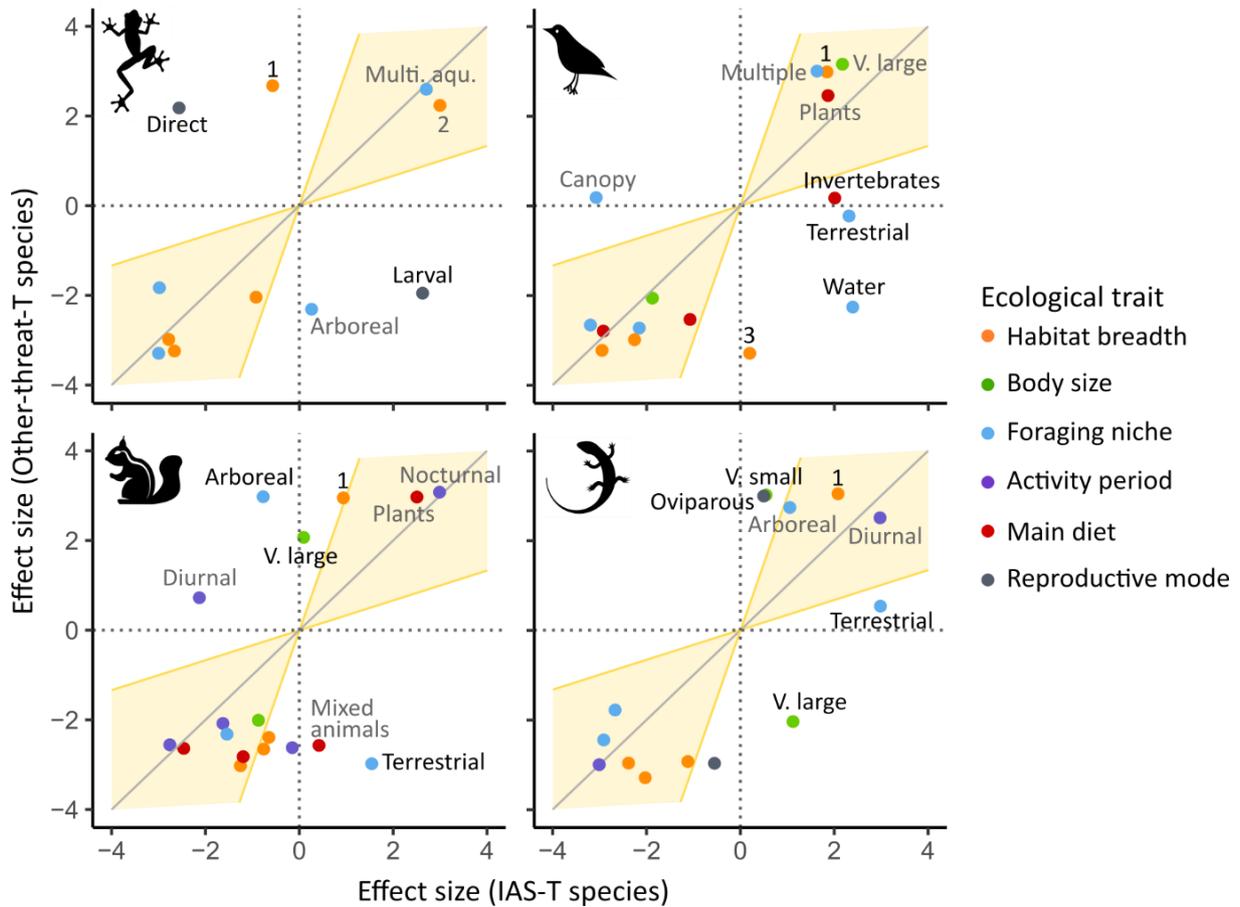
861 amphibians share this characteristic less than the global pool. Ecological traits are represented

862 by different colors. Modalities for traits overrepresented for IAS-T and/or IAS-NT groups

863 compared to the global pools are labelled (black labels indicate relevant modalities for

864 discussion). Those results are obtained with the imputed dataset.

865



866

867 **Figure 5. Comparison between effect sizes of ecological trait dissimilarities for IAS-T**

868 **and Other-threat-T species compared to the global species pool.** To simplify the reading,

869 only significantly over- (and under-) represented modalities for IAS-T, Other-threat-T, or both

870 groups are represented. Gray line: $y = x$; yellow lines: $y = 3*x$ and $y = x/3$. Points located

871 close to the $y=x$ diagonal indicate a similar trend in the trait modalities for IAS-T and Other-

872 threat-T species (yellow zone). By contrast, points located in the lower right and upper left

873 corners indicate that the directions of ES between IAS-T and Other-threat-T species are

874 opposing. Ecological traits are represented by different colors. Modalities for traits

875 overrepresented for IAS-T and/or Other-threat-T groups compared to global pools are labelled

876 (black labels indicate relevant modalities for discussion). Those results are obtained with the

877 imputed dataset.

878 **Supplementary materials**

879 Supplied as a separate file.