Title

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

Short title

Insular species prone to biological invasions

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Abstract

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

Keywords

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

Introduction

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

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

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

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

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

Materials and Methods

Database construction

Insular terrestrial vertebrates

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

Species information

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

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

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

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

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

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

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

Functional diversity

Rationale

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

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

Functional entities and functional space

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

Functional diversity metrics

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

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

Statistical analyses

Null models

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

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

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

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

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

Sensitivity to data imputation

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

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

Results

Functional diversity characterization of endemic insular terrestrial vertebrates associated with IAS

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

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

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

Ecological profiles of endemic insular terrestrial vertebrates exposed to IAS

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

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

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

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

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

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

Discussion

Vulnerability to IAS and ecological strategies of insular endemic species

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

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

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

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

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

Implications of data imputation for trait analyses

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

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

Functional characterization of endemic insular species vulnerable to IAS

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

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

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

Ecological and conservation implications

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

Our study is the first to evaluate, at a macroecological scale, the ecological profiles of terrestrial vertebrates at risk of extinction because of the ever-increasing IAS threat. Strategies shared by IAS-T species varied across tetrapod taxa, but we found specific profiles associated 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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Data accessibility

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

Tables

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

<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).

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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.

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Figure 2. Functional diversity metrics for endemic insular terrestrial vertebrates at a high risk of extinction due to biological invasions (IAS-T) and those that are not (IAS-NT). FRic: functional richness; FEve: functional evenness, FOR: functional over-redundancy. Bars represent observed values; points and error bars represent means and standard deviations of simulated values, respectively. Stars show significant deviations from the null hypothesis: * p-value < 0.025 or > 0.975; ** p-value < 0.010 or > 0.990; *** p-value < 0.001 or > 0.999. Values of effect sizes and associated p-values are reported in Table S2. Those results are obtained with the imputed dataset.

Figure 3. Schematic overview of the dominant characteristics shared by IAS-T species (black icons) and significantly overrepresented strategies of IAS-T species compared to the global pools (circled icons). IAS-T species are at a high risk of extinction due to biological invasions. The dominant characteristic corresponds to the prevailing trait modality shared by IAS-T species for each trait. Icons are circled when the modality is significantly overrepresented in IAS-T species compared to the global species pool. Circled gray icons show significantly overrepresented modalities compared to the global pool, but not dominant among IAS-T species. Animal icons represent the four studied taxa: amphibians, birds, mammals, and lizards. Those results are obtained with the imputed dataset.

Figure 4. Comparison between the effect sizes of ecological trait dissimilarities for IAS-T and IAS-NT species compared to the global species pool. To simplify the reading, only significantly over- and underrepresented modalities for IAS-T, IAS-NT, or both groups are represented. Points located close to the $y=x$ diagonal indicate a similar trend in trait modalities for IAS-T and IAS-NT species (gray squares). By contrast, points located in the lower right and upper left corners (in white) indicate that the directions of ES between IAS-T and IAS-NT species are opposing. For instance, IAS-NT amphibians are more habitat generalists (habitat breadth = 5+) compared to the global amphibian pool, whereas IAS-T amphibians share this characteristic less than the global pool. Ecological traits are represented by different colors. Modalities for traits overrepresented for IAS-T and/or IAS-NT groups compared to the global pools are labelled (black labels indicate relevant modalities for discussion). Those results are obtained with the imputed dataset.

Figure 5. Comparison between effect sizes of ecological trait dissimilarities for IAS-T and Other-threat-T species compared to the global species pool. To simplify the reading, only significantly over- (and under-) represented modalities for IAS-T, Other-threat-T, or both groups are represented. Gray line: $y = x$; yellow lines: $y = 3 \cdot x$ and $y = x/3$. Points located close to the $y=x$ diagonal indicate a similar trend in the trait modalities for IAS-T and Other-threat-T species (yellow zone). By contrast, points located in the lower right and upper left corners indicate that the directions of ES between IAS-T and Other-threat-T species are opposing. Ecological traits are represented by different colors. Modalities for traits overrepresented for IAS-T and/or Other-threat-T groups compared to global pools are labelled (black labels indicate relevant modalities for discussion). Those results are obtained with the imputed dataset.

Supplementary materials

879 Supplied as a separate file.