

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

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Abstract

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

KEYWORDS

extinction risk, invasive species, phylogenetic diversity, scenarios, trait diversity

1 | INTRODUCTION

Invasive alien species (IAS) are considered to be the second most important cause of worldwide extinctions (Bellard, Genovesi, et al.,

2016; Gurevitch & Padilla, 2004; Maxwell et al., 2016). Invasive predators alone have contributed to 58% of modern extinctions (Doherty et al., 2016). Most of these extinctions occurred on islands, but mainland areas also suffer from the presence of IAS (Bellard,

Cassey, et al., 2016; Clavero et al., 2009). The global threat of species invasions continues to increase with the spread of new emerging invaders (Seebens et al., 2017, 2018).

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

Previous assessments showed that climate change may lead to uncompensated phylogenetic or functional losses, causing further biotic homogenization (Buisson et al., 2013; Thuiller et al., 2011), although this has not yet been explored in the context of biological invasions. In other words, the manner in which species extinctions due to IAS affect the ecological and evolutionary dimensions of biodiversity mostly remains an open question (but see Lapiedra et al., 2015; Longman et al., 2018; Sunday et al., 2015). This issue is particularly important, as shown by the recent surge in interest among international experts of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES), who advocated that including ecological and phylogenetic components of biodiversity is essential in biodiversity assessments (IPBES, 2019).

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

A critical aspect of biodiversity assessments is thus to identify and characterize the diversity elements most likely to go extinct, thus inferring the future state of biodiversity. Here, we aim to provide such an assessment of at-risk biodiversity related to biological invasions with a focus on the trait and phylogenetic diversity (PD) of birds ($n = 8113$) and mammals ($n = 4804$). TrD represents how species are distributed in a multidimensional niche space and provides a way to assess the ecological strategy adopted by species. We measured the amount of trait space occupied by invasive-threatened species compared to the global pool worldwide following the methodology of Villéger et al. (2008) based on five ecological traits (Table 1). In other

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

2 | METHODS

2.1 | Species studied

We used the IUCN Red List of Species to identify the species considered to be the most threatened by IAS (Version 3, accessed in August 2019). We considered species classified as critically endangered (CR), endangered (EN), vulnerable (VU), near-threatened (NT), or least concern (LC) by the IUCN Red List. We focused on the threatened species defined by the IUCN (CR, EN, and VU) for which IAS are listed as a threat (hereafter, invasive-threatened) and excluded NT and LC species, which only represent “potentially threatened” species for two reasons. Therefore, we filtered out species for which IAS is listed as a future threat or when the threat is due to a problematic species/disease (including viral or prion) of unknown origin or native. First, we want to focus our analyses on the threatened species (CR, EN, and VU) facing imminent extinctions so as to be conservative in our study following the methodology of Toussaint et al. (2016). Second, IUCN only assigns a specific extinction probability to VU, EN, and CR. No quantitative analyses of the probability of extinction are required for NT or LC, while the latter category does not specify the major threat faced, which will add uncertainty to our analyses of the IAS threat (IUCN, 2012). Moreover, we focused our analysis on the most comprehensively assessed vertebrate groups by the IUCN: birds and mammals (Meiri & Chapple, 2016). This resulted in a total of 207 invasive-threatened mammals out of 5708 mammals assessed by the IUCN Red List and 499 invasive-threatened birds out of 10,965 birds (IUCN, 2017). Note that it is impossible to disentangle the effects of IAS from other threats. IAS threat is mostly associated with biological resource use and agriculture. In fact, the vast majority of species threatened by IAS are also likely to be threatened by other threats with an average of 3.9 threats co-occurring for IAS-threatened birds and mammals; thus, IAS-threatened species are species for which IAS is listed as a threat, although other threats might also occur. In fact,

TABLE 1 Description of the traits used to measure the trait diversity of birds and mammals as well as their modalities

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

837 mammals and 736 birds are threatened by other threats. We also used the mechanisms documented for each invasive-threatened species based on the IUCN information (e.g., competition, hybridization, reduced reproductive success, species mortality, and ecosystem degradation) to assess the contribution of each mechanism to the potential loss of PD and TrD. We considered the top three mechanisms for both birds and mammals, which represent more than 80% of all mechanisms documented for each taxon. We considered species mortality, competition, and ecosystem degradation for mammals and ecosystem degradation, species mortality, and reduction in reproductive success for

birds. We considered each mechanism when cited alone or in association with another mechanism. Therefore, our indicator of mechanisms represents the documented occurrences of a given mechanism for each species. We also used the realm associated with each species extracted from the IUCN database to conduct analyses at the realm scale (i.e., Afrotropical, Australasian, Indomalayan, Nearctic, Neotropical, Oceanian, and Palearctic).

2.2 | TrD analysis

To quantify TrD associated with invasive-threatened species, we used the five following traits: body size, habitat breadth, foraging strata, main diet, and period of activity (Table 1 for modalities), which are associated with the key ecological strategies of species (e.g., carcass removal, seed dispersal, soil fertility, and pollination; Sekercioglu, 2010; Hevia et al., 2017; see also Appendix S3). All traits were extracted from the Elton trait database (Wilman et al., 2014) except for habitat types, which were taken from the IUCN habitat classification scheme (version 3.1). Main diet category for mammals is based on the majority of diet consumed by each species, with a 50% threshold (following Wilman et al., 2014). For instance, the mixed herbivore category represents all species whose diet consists of more than 50% of plant material, seeds, fleshy fruits, and nectar. The omnivore (mixed) category includes all species that are 50% mixed herbivore and 50% mixed animal. Foraging strata category for birds is based on the location of the different items consumed by each species with a 50% threshold (following Wilman et al., 2014). If the foraging strata include several categories, we kept the foraging strata represented by more than 50% of the whole foraging strata; and if there is no main foraging stratum represented by more 50%, it is designated as "multiple." Body mass category for birds and mammals is based on their respective quantiles with the very large category representing the largest 20% of species. Overall, we extracted trait data for 4804 mammals, including 186 invasive-threatened mammals, and 8113 birds, including 360 invasive-threatened birds (Figure S2). The two continuous variables (i.e., main diet and body size) were categorized as discrete variables following the method of Leclerc et al. (2020; see also Table 1 for details).

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

- (i) First, we grouped species as ecological entities, which represent groups of species sharing the same trait values (Table 1), methodology that has been successfully applied in functional analyses (Keyel & Wiegand, 2016; Mouillot et al., 2014). This step allowed us to calculate trait vulnerability, which is related to the number of species included in each ecological entity. Trait vulnerability is high when ecological entities have a small number of species and low when ecological entities host a high number of species, which indicates high redundancy.
- (ii) To build the trait space, we also calculated pairwise trait distances using the Gower metric, which allowed us to deal with

data of mixed types (Pavoine et al., 2009). We then used principal coordinate analysis (PCoA) on the trait distance matrix to build a multidimensional trait space, where the position of ecological entities corresponds to their differences. We selected the best functional space by choosing the number of PCoA axes that provided the most faithful representation of the initial functional trait values. In other terms, we selected the number of axes that minimized the mean squared-deviation metric (i.e., average deviation between Euclidean distance and Gower distance; Maire et al., 2015), which allowed us to compute the indices in a reasonable timeframe. In this study, we selected five axes for mammals, which represent an average error of 3.6% (average deviation between original and transformation data) and three axes for birds, which had an average error of 5.6%, indicating functional spaces of high qualities.

- (iii) Based on these trait spaces for birds and mammals, we calculated TrD (more commonly known as functional richness following the definition of Villéger et al., 2008), which represents the volume of trait space occupied by invasive-threatened species within the PCoA compared to the total pool of species. This metric is widely applied in functional studies (Leclerc et al., 2020; Mouillot et al., 2014; Toussaint et al., 2016). It has been demonstrated as the best performing index and is highly correlated to other functional diversity measures (Mouchet et al., 2010). This step was also conducted at the realm scale.
- (iv) We also performed statistical analyses to compare the trait modalities associated with invasive-threatened species and those associated with either non-invasive-threatened species worldwide and species threatened by threats other than IAS (i.e., other-threatened species). Specifically, we compared the trait distributions of invasive-threatened species with a random sample (with replacement) of an equal number of species that are not invasive-threatened within the global pool (999 repetitions). We also compared the trait distributions of invasive-threatened species with a random sample of an equal number of other-threatened species within the global pool. These two comparisons allowed us to disentangle whether the trait modalities were specific to the invasive threat or whether there were related to threatened species (Table S1).

To test the significance of the results, we applied Chi-squared tests when the number of species in each modality was ≥ 5 for all the samples. Otherwise, a Fisher's exact test was used. If at least 95% of tests had a $p < 0.05$, the two distributions were considered to significantly differ. We repeated the same analyses for both mammals and birds.

2.3 | PD analyses

To compute PD hosted by invasive-threatened species, we used the PHYLACINE 1.2 complete phylogeny by Faurby et al. (2018) for mammals. This built phylogeny relies on the morphological and

genetic data of 5831 known mammal species that have lived since the last interglacial period. It also contains 1000 trees that represent the uncertainties in topology and branch lengths. We also verified species synonyms using the `rl_synonyms()` functions in the `rredList` package (Chamberlain, 2019), and we pruned the original phylogenetic tree ($n = 5831$) to the species of the IUCN Red List included in the tree for mammals. In total, 5529 species, including 205 invasive-threatened species, were included in the phylogenetic trees (Figure S1 for the sample size of each analysis). For birds, we used the tree version (V2.iii, Ericson backbone) with the complete phylogeny of Jetz et al. (2014) and extracted 1000 trees. The built phylogeny combines the relaxed clock molecular trees of well-supported avian clades with a fossil-calibrated backbone with representatives from each clade. Similar to mammals, we also searched for synonyms and pruned the original phylogenetic tree to 8,113 birds, including 360 invasive-threatened species (Figure S1). Then, to measure PD associated with invasive-threatened species for both mammals and birds, we used the Faith Index (using the `pd()` function of the `picante` package; Kembel et al., 2010) and calculated the average PD across the 1000 trees. Ultimately, we calculated the percentage for the invasive-threatened species PD value compared to the total PD value of the sample to compare between taxa. We also conducted PD analysis for each realm.

2.4 | Null model analyses for both phylogenetic and TrD measures

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

We also randomized the phylogenetic information between the invasive-threatened species for both mammals and birds. For this purpose, we considered a constrained null model that randomizes the names of taxa to the phylogeny. Thus, it randomizes which species are most closely related to each other, although it does not alter the actual branch lengths or their distributions. The rationale for this null model is to investigate whether the species at risk of extinction due to IAS are more closely related than expected randomly given their number. The randomization was repeated 999 times over 1000 trees each time.

More specifically, we calculated the deviation from the null expectation by computing the standardized effect size (SES) and associated p value. SES represents the difference between the observed values of TrD or PD and the mean of predicted values by the null model divided by the standard deviation of predicted values. The

significance of the difference between observed values and null expectations was tested using a bilateral test at a level of 5%. In short, an observed value is considered significantly different from null expectations if the observed value is in the top or bottom 2.5% of the null expectation distribution.

2.5 | Projected extinction scenarios

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

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

3 | RESULTS

3.1 | Trait and PD hosted by invasive-threatened species worldwide and within realms

Our results showed that invasive-threatened birds occupy 40% of the total trait space (TrD) for birds worldwide. By contrast, invasive-threatened mammals represented only 14% of the total trait space for mammals (Table 2). The contribution of invasive-threatened species to the total PD worldwide was 10.2% for mammals and 11.4%

for birds. In all cases, the PD values for invasive-threatened mammals and birds were significantly lower than expected given the number of species ($SES = -7.294$ and $p > 0.99$ for mammals, and $SES = -4.542$ and $p > 0.99$ for birds). Similarly, TrD values were significantly lower than expected given the number of species ($SES = -4.177$ and $p > 0.99$ for mammals and $SES = -3.672$ and $p > 0.99$ for birds). Both diversity metrics were thus more clustered than expected under the null scenario.

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

By analyzing the diversity represented by invasive-threatened birds and mammals for each realm, we found clear spatial differences (Figure 2). The contribution of invasive-threatened birds located in the Oceanian realm to the total bird TrD worldwide is nearly 30%. The contributions of invasive-threatened birds in the Afrotropical and Neotropical realms to total bird TrD was also high with 20% and 17%, respectively, whereas the contribution of invasive-threatened mammals in the Neotropical realm to total mammal TrD was only 4%. We found that all the realms showed low PD values for invasive-threatened mammals (0.7%–4.2%) and birds (0.93%–5.4%). In addition, we found an average of 1.4 invasive-threatened species for each ecological entity (groups of species sharing the same combinations of traits) for mammals and 1.2 for birds within realms, while we estimated 6.8 species per ecological entity in the rest of the species sample for mammals and 13.7 for birds.

3.2 | Extinction scenarios of invasive-threatened species compared to random scenarios

Because all the invasive-threatened species are unlikely to go extinct in the near future, we considered extinction scenarios following the methodology of Cooke et al. (2019). On average, 6.5%–7.7% of worldwide PD associated with invasive-threatened mammals is

TABLE 2 Trait and phylogenetic diversity observed in worldwide invasive-threatened mammals and birds with their standardized effect size (SES) and p value with significant figures are indicated with ***

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

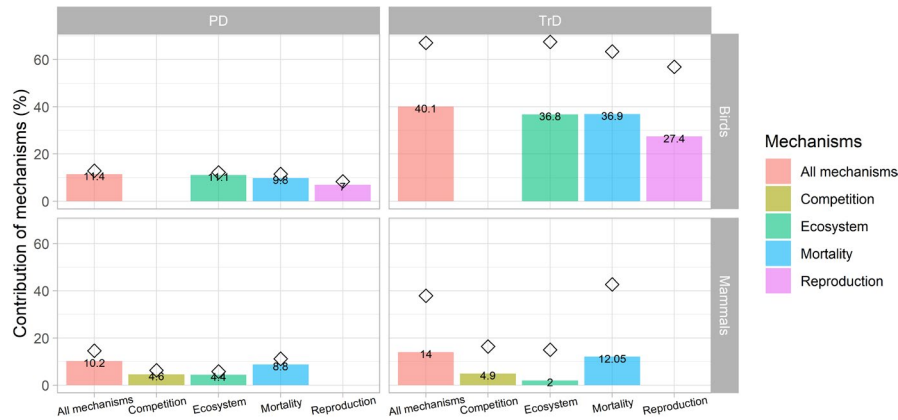


FIGURE 1 Contribution of the mechanisms (i.e., all mechanisms, competition, ecosystem degradation, mortality, and/or reduction in reproduction success) impacting invasive-threatened species to the total bird (or mammal) trait (TrD) and phylogenetic diversity (PD) in percentage. We only considered the top three mechanisms for each taxon. Bar plots represent the observed values of diversity, while the diamonds represent the null models (expected values when species identity is randomized) [Colour figure can be viewed at wileyonlinelibrary.com]

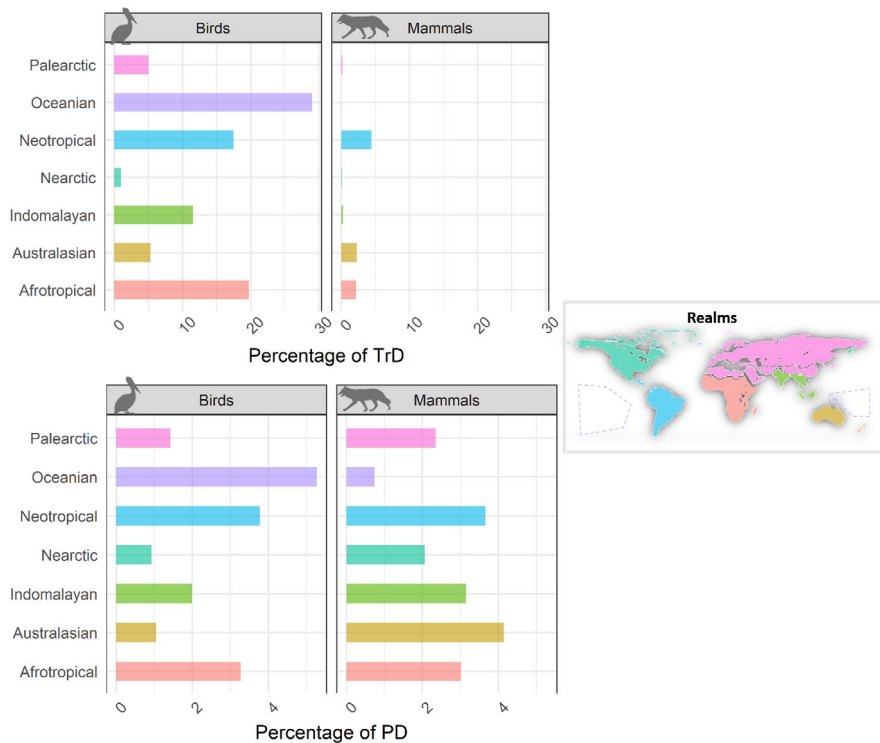


FIGURE 2 Contribution of invasive-threatened species located in each realm to the total bird (or mammal) diversity for both trait (TrD) and phylogenetic diversity (PD) [Colour figure can be viewed at wileyonlinelibrary.com]

expected to be lost over the next 50–100 years, while the percentage is slightly higher under the randomized extinction scenarios for mammals (7.7%–9.3%). Loss of PD worldwide for birds is projected to be of a similar order of magnitude with 6.1%–7.2%, which is also slightly lower compared to randomized extinction scenarios (6.5%–7.8%). The potential loss is more pronounced for TrD, which may reach 5.8%–7.8% for mammals (11.3%–15.0% under the randomized extinction scenarios) and 27.4%–30.6% for birds worldwide (32.5%–36.3% under the randomized extinction scenarios) over the next 50–100 years due to IAS. In all cases, the potential loss of both facets of diversity (PD and TrD) induced by IAS is lower than expected

given the species richness under the random extinction scenarios (Figure 3).

3.3 | Profile of species at risk of extinctions

We further analyzed the phylogenetic and ecological properties of invasive-threatened species for both mammals and birds and compared them to the characteristics of the pool of non-invasive-threatened species (hereafter, global pool) and species threatened by threats other than IAS. We found that the 186 invasive-threatened

mammals represent 109 ecological entities (groups of species sharing the same combinations of traits, with 14 ecological entities exclusively represented by invasive-threatened mammals and not found in the global pool; Table S1). Four families were comprised exclusively of species threatened by IAS, although other threats may also be involved: Solenodontidae, Myrmecobiidae, Phascolarctidae, and Thylacomyidae. Muridae and Cricetidae were the most represented families among invasive-threatened mammals as well as among the global pool of mammals. Similarly, the 360 invasive-threatened birds represented 149 ecological entities (including 10 ecological entities exclusively hosted by invasive-threatened birds), which belong to 92 families, including five families (i.e., Balaenicipitidae, Strigopidae, Rhynochetidae, Notiomystidae, and Pedionomidae) that were exclusively found in the invasive-threatened pool. The two most represented families within invasive-threatened birds were Procellariidae and Psittacidae, although they were, respectively, ranked 59th and fourth when considering the global pool of birds.

A closer investigation of the ecological profile of invasive-threatened species revealed that mammals were represented by mostly large to very large species (68%), specialists with only one or two habitats (65%), only nocturnal species (61%), those feeding on the ground (76%), and those with a primarily or exclusively herbivorous diet (62%; Figure 4; see also Table S2). We observed some significant differences with the global pool of mammals regarding foraging strata (i.e., species were mostly aerial in the global pool), diet regime (species mostly feed on invertebrates) and body size (species have a very small body size; Figure 4; see also Table S4) while significant differences were also detected for the period of activity and habitat breadth when compared to other-threatened species (see Figure 4 and Table S4). We found a significantly higher percentage of ground-foraging species within invasive-threatened mammals compared to both the global pool and the other-threatened species pool (Figure 4). By contrast, invasive-threatened mammals were significantly less represented in the arboreal foraging strata compared to the global pool and the other-threatened pool of mammals. Our results also revealed that invasive-threatened species were less likely to be diurnal and less likely to be specialized to one habitat compared to other-threatened species. In addition, it appears that invasive-threatened mammals were significantly more represented among very large species and significantly less among very small species in comparison with the global pool, although these characteristics were not specific to invasive-threatened species, as other-threatened species were also very large species. Finally, our results also revealed that invertebrate diets were less represented among invasive-threatened mammals compared to the global pool (Figure 4). This was also the case with other-threatened species, although the difference was not statistically significant.

Invasive-threatened birds were mostly large to very large species (63%) and habitat specialists with three or less habitats (81%); the majority foraged in multiple strata (57%) were active during the day (97%), and mostly fed on animals (41%; Figure 5; see also Table S3). Again, invasive-threatened species had similar ecological characteristics compared to the rest of the species pool but with a few notable

exceptions (Figure 5; see also Tables S6 and S7). For instance, a significantly higher percentage of invasive-threatened birds forages below the water surface compared to both the global pool and the other-threatened species pool while a significantly lower percentage forages in multiple strata compared to the other samples (Figure 5). Invasive-threatened species were also significantly less represented among very small species compared to both the global pool and the other-threatened species pool (Figure 4). Moreover, we also observed that invasive-threatened species mostly feed on animals. We also found that invasive-threatened birds were less likely to be habitat specialists compared to other-threatened species and more likely to live in three or four habitats, although we did not detect such differences when comparing these results to the global pool (Table S6 and S7).

4 | DISCUSSION

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

Because all the species threatened by IAS are unlikely to disappear, we also conducted 50- and 100-year extinction scenarios to provide an initial approximation of the potential cost of the current extinction debt due to biological invasions while considering only the imminent extinctions. The potential losses might be tremendous with around 7% of PD worldwide for both mammals and birds as well as

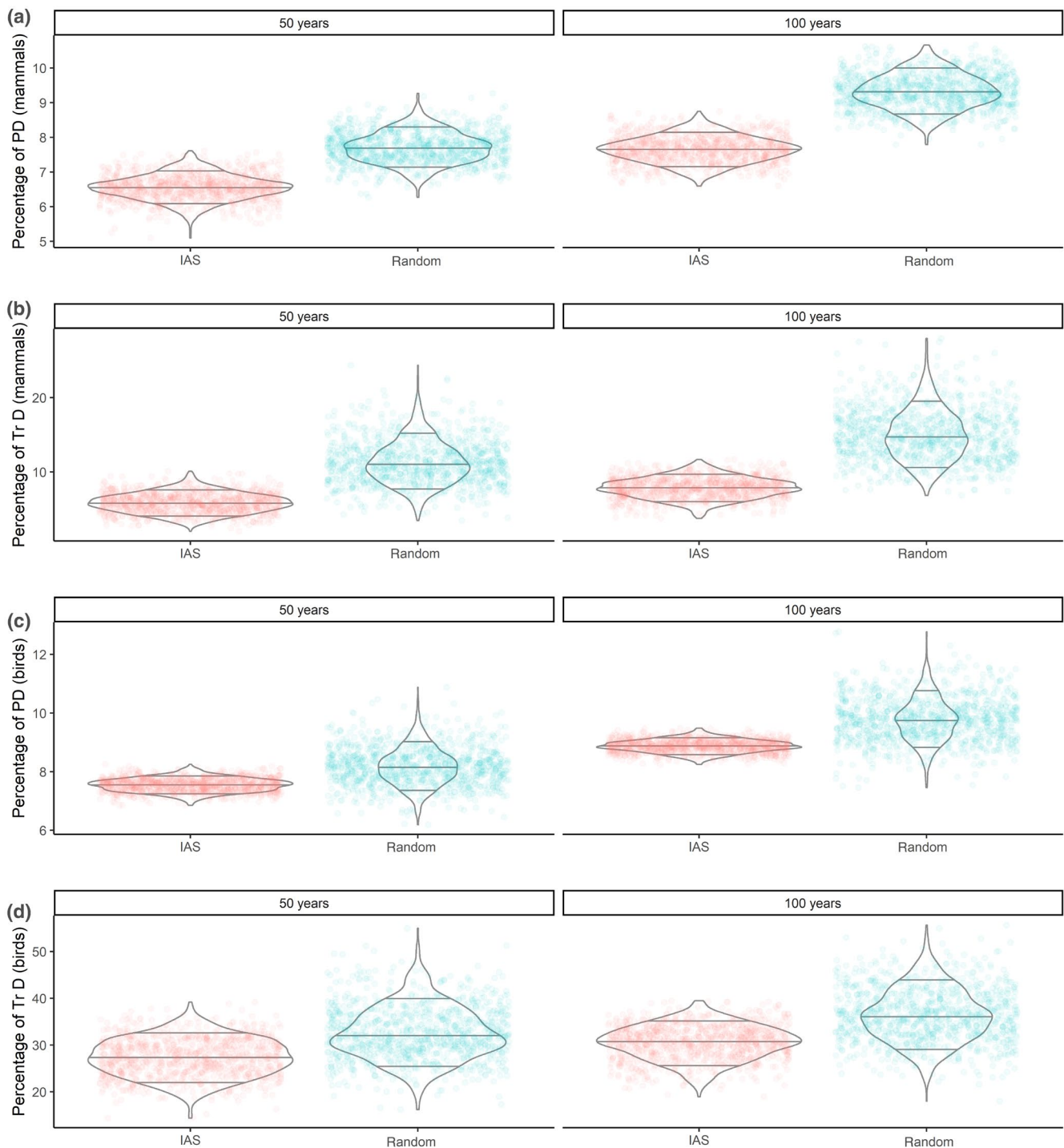


FIGURE 3 Contribution of mammals and birds to the total phylogenetic (PD) and trait diversity (TrD) expressed in percentages under 50- and 100-year extinction scenarios. These values represent potential losses of PD and TrD under different extinctions scenarios. We considered two samples of species: invasive-threatened species and random species (species taken from the total pool of mammal and bird species worldwide that are not invasive-threatened species). We included jittered points for each of the 999 repetitions; the median and quantiles (0.10 and 0.90) are also shown [Colour figure can be viewed at wileyonlinelibrary.com]

6% (mammals) and up to 27% (birds) of TrD worldwide. It is worth noting that we only considered species that are facing imminent extinction according to the IUCN Red List criteria, thus ignoring NT, LC, or data-deficient species that might be at risk of extinctions in the near future due to IAS such as the Reunion Bulbul (BirdLife International,

2021). For instance, data-deficient species represent 15% of the entire mammal dataset. Consequently, we potentially underestimated the extinction debt due to IAS in this regard. On the contrary, the potential percentage of diversity predicted to become extinct due to IAS is significantly lower than expected under the projected randomized

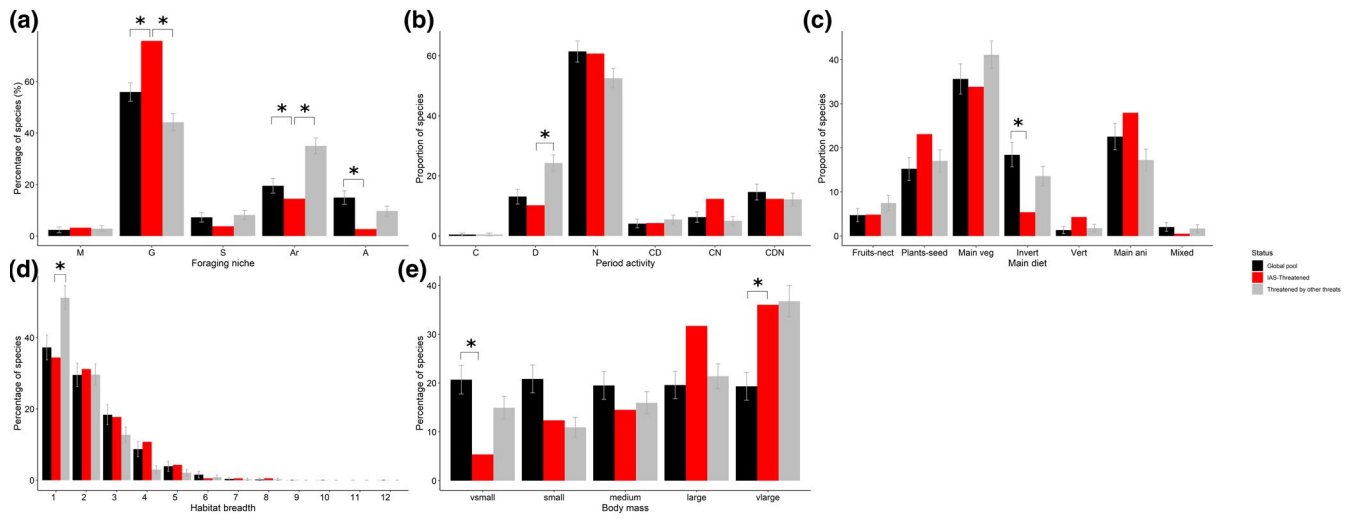


FIGURE 4 Percentage of invasive-threatened mammals (in red) for the five traits considered: (a) Foraging strata (with A, aerial, Ar, arboreal, G, ground level, M, marine, S, scansorial); (b) period of activity (with C, crepuscular; CD, crepuscular–diurnal; CDN, crepuscular–diurnal–nocturnal; CN, crepuscular–nocturnal; D, diurnal; N, nocturnal); (c) main diet; (d) habitat breadth; (e) body size. Their associated modalities are compared to the global pool (black bars with standard deviation errors bars) and other-threatened species (gray bars). See Table 1 for the modality descriptions and abbreviations. * indicates the percentage of trait modalities that are significantly different between invasive-threatened and other mammal species. A difference is significant when 95% of tests have a $p < 0.05$ (see Tables S4 and S5 for value details) [Colour figure can be viewed at wileyonlinelibrary.com]

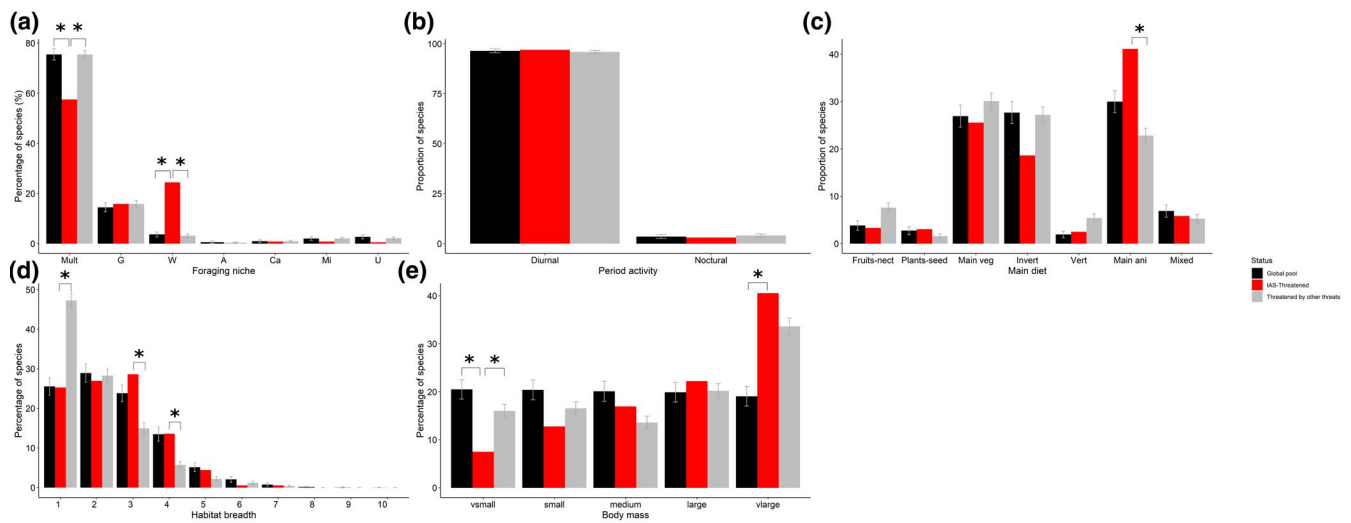


FIGURE 5 Percentage of invasive-threatened birds (in red) for the five traits considered: (a) Foraging strata (with A, aerial; Ca, canopy; G, ground level; M, multiple strata; Mi, mid-high; U, understory; W, water); (b) period of activity; (c) main diet; (d) habitat breadth; (e) body size. Their associated modalities are compared to the global pool (black bars with standard deviation errors bars) and the other-threatened species group (in gray). See Table 1 for the modality descriptions and abbreviations. * indicates the percentage of trait modalities that are significantly different between invasive-threatened and other mammal species. A difference is significant when 95% of tests have a $p < 0.05$ (see Tables S6 and S7 for value details) [Colour figure can be viewed at wileyonlinelibrary.com]

scenario given the species richness. The main explanation is that invasive-threatened species are clustered in both the phylogenetic and trait space and that the projected diversity losses associated with mammals and birds will not be random. In fact, a selective process will occur across the phylogenetic tree and the ecological strategy space (Thuiller et al., 2011; Yessoufou & Davies, 2016).

We found that both invasive-threatened mammals and birds have a significantly larger body size than the rest of the pool but not

when compared to other-threatened mammals. Large body mass has already been highlighted as a life-history trait that is strongly associated with increasing extinction risks due to the slow reproductive rate associated with large body mass (Hanna & Cardillo, 2013; Leclerc et al., 2020; Ripple et al., 2017). But note that body mass may hide the effects of other variables linked to reproduction, locomotion, or survival. Therefore, the effects of body size could not be direct but reflect the impact of other variables on species extinction risk. We

also found that invasive-threatened species were more likely to feed in the lower strata (i.e., ground level or below the water surface) and less likely to feed in the higher strata (i.e., aerial or arboreal) compared to the other-threatened species, and more generally, the global pool. This pattern has recently been highlighted for insular species (Leclerc et al., 2020). Because most invasive-threatened species are found on islands, one possible explanation could be related to the naïveté syndrome. Indeed, ground species are more exposed to the introduction of nocturnal predators and are less capable of changing their behavior to develop new defenses (Doherty et al., 2016) while higher-strata species may develop avoidance strategies with the invasive mammals. We also found that invasive-threatened species live in a limited number of habitats and are more likely to be specialist species than generalist ones (Foden et al., 2018; Gonzalez-Suarez et al., 2013; Pacifici et al., 2017), but this tendency was not significantly different compared to the rest of the species. In fact, we found that other-threatened mammals are more likely to be specialized to a single habitat than invasive-threatened mammals, which are more likely to live in four different habitats. We also found that most invasive-threatened mammals are primarily herbivorous, which confirms the results of a recent study showing that large-bodied herbivorous mammals are more at risk of extinctions due to global threats, including biological invasions (Atwood et al., 2020). However, it would appear that the vast majority of mammals are herbivorous, meaning that this characteristic is not particularly associated with threatened species. By contrast, we did not observe that invasive-threatened bird species are more likely to be herbivorous, whereas Atwood et al. (2020) detected that large-bodied herbivorous birds are more at risk of extinctions with biological invasions. In fact, we found a disproportionately higher number of invasive-threatened birds that feed on animals compared to the rest of the species. More specifically, our findings suggest that habitat specialists and species with lower-strata feeding strategies are more likely to be filtered out of the global pool of mammals and birds. This is confirmed by the higher frequency of birds that feed on multiple strata in the global pool compared to those that are threatened by IAS. Because these traits have also been identified as highly vulnerable to other components of global changes, we can expect that IAS will further affect the global composition of bird and mammal species. In the near future, we may observe a shift in the global composition of birds and mammals toward species that have a lower body mass. Indeed, the average size of invasive-threatened species is four and eight times larger than the rest of the pool of birds and mammals, respectively. Recently, Cooke et al. (2019) predicted a potential ecological downsizing within mammals and birds due to global changes (Ripple et al., 2017). Forecast shifts in ecological traits could help us to identify the potential ecological consequences of extinctions for community and ecosystem services (Mouillot et al., 2013). Moreover, the predicted loss of habitat specialists and species with restricted foraging strata may lead to a shift toward generalist species, which may result in a global process of homogenizing ecological strategies (Clavel et al., 2011; Qian & Ricklefs, 2006; Villéger et al., 2011). In other words, biological invasions have the potential to disrupt the ecosystem structure and function.

One of the most prominent findings of this study is that the evolutionary and ecological implications of the extinction debt go far beyond a simple number of lost species. Indeed, species at risk of extinctions due to IAS will impact the ecological and evolutionary composition of future communities. We observed a clear ecological and evolutionary profile of species vulnerable to invasions. While we know that IAS is one of the most important drivers of species extinctions on islands (Bellard, Genovesi, et al., 2016), this is the first time that we documented the need to further investigate the ecological and adaptive consequences of the biological invasion threat worldwide. For this reason, we investigated whether these losses might result in the disappearance of particular profiles and/or lead to a shift in the composition of mammals and birds worldwide. Our results point to the potential disappearance of specific lineages of mammals (e.g., Myrmecobiidae, Thylacomyidae) and birds (e.g., Notiomystidae, Rhynchotidae) because all species in these families are threatened by IAS. This also includes families that are currently represented by a single species. For instance, the sole member of the Myrmecobiidae family is *Myrmecobius fasciatus*, which now has fewer than 800 individuals in Australia and continues to be threatened by several IAS (Woinarski & Burbidge, 2016). Even if IAS appear to be the primary threat to these species, other threats such as habitat degradation or natural system modifications like fire regime changes are also involved in population decline; indeed, IAS is rarely the sole threat responsible for the increasing risk of extinctions (Leclerc et al., 2018 see also Appendix S1). In fact, IAS is the only threat in less than 8% of cases in our dataset.

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

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

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

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CODE AVAILABILITY

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

DATA AVAILABILITY STATEMENT

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

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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