EDITOR'S CHOICE

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Global changes threaten functional and taxonomic diversity of insular species worldwide

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Abstract

Aim: The assessment of biodiversity patterns under global changes is currently biased towards taxonomic diversity, thus overlooking the ecological and functional aspects of species. Here, we characterized both taxonomic and functional diversity of insular biodiversity threatened by multiple threats.

Location: Worldwide islands (n = 4,348).

Methods: We analysed the relative importance of eleven major threats, including biological invasions or climate change, on 2,756 insular endemic mammals and birds. Species were functionally described using five ecological traits related to diet, habitat and body mass. We computed complementary taxonomic and functional diversity indices (richness, specialization, originality and vulnerability) of species pools affected by each threatening process to investigate relationships between diversity dimensions and threats. We also determined whether species-specific traits are associated with specific threats.

Results: On average, 8% of insular endemic species at risk of extinction are impacted by threats, while 20% of their functional richness is affected. However, a marked disparity in functional richness values associated with each threat can be highlighted. In particular, *cultivation* and *wildlife exploitation* are the greatest threats to insular endemic species. Moreover, each threat may contribute to the loss of at least 10% of functional diversity, because it affects threatened species that support unique and extreme functions. Finally, we found complex patterns of species-specific traits associated with particular threats that is not explain by the threatening processes (directly affecting survival or modifying habitat). For instance, *cultivation* threatens very large mammals, while *urbanization* threatens very small mammals.

Main conclusions: These findings reinforce the importance of exploring the vulnerability of biodiversity facets in the face of multiple threats. Anthropogenic pressures may result in a loss of unique functions within insular ecosystems, which provides important insights into the understanding of threatening processes at a global scale.

KEYWORDS
birds, functional originality, functional richness, functional specialization, islands, mammals, species traits, vulnerability

1 | INTRODUCTION

Worldwide biota is subject to an unprecedented level of rapid biodiversity loss because of human activities such as overexploitation, land modifications and pollution (Ceballos, Ehrlich, & Dirzo, 2017). At a global scale, 72% of IUCN-threatened or -near-threatened species are being overexploited (Maxwell, Fuller, Brooks, & Watson, 2016), and invasive predators have contributed to 58% of the contemporary extinctions of all birds, mammals and reptiles (Doherty, Glen, Nimmo, Ritchie, & Dickman, 2016). Among them, insular species are the first victims of these threats. Indeed, islands tend to have a high rate of endemism, making species particularly vulnerable to global changes due to both biotic and abiotic characteristics (e.g., unique species interactions, low functional redundancy, island isolation and low habitat availability) (Whittaker & Fernandez-Palacios, 2007). However, most biodiversity assessments at the global scale consider only taxonomic diversity. These assessments focusing only on species diversity assume that all species are equivalent entities, even though they are a product of complex ecological and evolutionary processes (May, 1990; Vane-Wright, Humphries, & Williams, 1991). There has thus been a growing effort over the last two decades to assess other facets of biodiversity, and more specifically, functional diversity (e.g., Brum et al., 2017; Devictor et al., 2010).

Functional diversity is a measure at the level of species' assemblages based on the value and range of organism traits that influence their performance and thus ecosystem functioning (Hooper et al., 2005; Violle et al., 2007). In the current context of global changes, declines in species populations or local extinctions are likely to be associated with a loss of particular species traits/functions (Richardson, Graham, Pratchett, Eurich, & Hoey, 2018), which could affect community structure and ecosystem functioning (Cadotte, Carscadden, & Mirotchnick, 2011). At one extreme, some threats may affect a high number of species with a similar set of traits, thus potentially resulting in the loss of a limited number of functions. At the other extreme, threats may affect only a few species, each with a unique set of traits and functions in an assemblage. Therefore, loss of functional diversity may occur regardless of changes in taxonomic diversity, revealing the importance of considering the functional dimension of biodiversity. Nevertheless, we still lack a comparative assessment of the relative importance of threats to functional diversity. Multifaceted analyses of insular biodiversity have mainly investigated the consequences of extinctions and/or introductions of species on functional diversity in communities (e.g., Boyer & Jetz, 2014; Sobral, Lees, & Cianciaruso, 2016; Whittaker et al., 2014) and are restricted to a limited number of islands and taxa. Such studies have also mainly focused on the consequences of biological invasions, regardless of the other major threatening processes on islands such as cultivation or overexploitation (Leclerc, Courchamp, & Bellard, 2018). Thus, there remains a knowledge gap about how much each facet of insular biodiversity is threatened by global changes. Better assessing the composition of species pools threatened on islands is of upmost importance for relevant conservation planning to maintain ecological processes (Brum et al., 2017; Pollock, Thuiller, & Jetz, 2017).

Moreover, specific species traits are likely to influence taxa responses to threats. For example, mammal families with small-size habitat specialists are more likely to be threatened by habitat-modifying processes (González-Suárez, Gómez, & Revilla, 2013), while mammals with a specialized diet have a greater probability of negatively responding to climate change (Pacifici et al., 2017). Although some specific trait patterns emerged for continental species, it remains unexplored whether the insular species trait response would be similar across different threats. Because some threats are more likely to disturb species resources (e.g., cultivation), while others directly affect species survival (e.g., overexploitation), we can expect that species-specific traits vary depending on the threats.

Here, we assessed how multiple threats affect the taxonomic and functional diversities of insular endemic species at the global scale. We specifically focused on the following questions: (a) What is the functional diversity harboured by insular endemic species at risk of extinction due to each threat, and how is it related to the number of species? *Overexploitation* and *cultivation* are known to be major threats to the taxonomic diversity of insular endemic species (Leclerc et al., 2018). Therefore, we hypothesize that these threats are also of major concern regarding functional diversity. However, we also expect that the relative importance of the threats to taxonomic richness (TR) may vary between the components of functional diversity. (b) Are threats associated with specific sets of ecological traits of insular endemic species at risk of extinction? We expect that species associations with particular threats be explained by some species traits. We hypothesize that habitat specialist species at risk of extinction are more likely to be associated with habitat-modifying processes such as cultivation or pollution, while species with large body mass are more likely to be associated with processes that directly affect survival such as overexploitation or competition with invasive species (González-Suárez et al., 2013). Lastly, (c) what would be the consequences on functional diversity in the event of the extinction of the threatened insular endemic species affected by each threat? Functional diversity is expected to decrease markedly when a threat affects species supporting unique and extreme functions (e.g., Mouillot, Bellwood, et al., 2013; Mouillot et al., 2014). We thus expect that threats associated with high functional diversity values will have the highest consequences on it due to the low redundancy of functions harboured by threatened species. Overall, we address these key questions using eleven categories of threats identified for 1,788 birds and 968 mammals endemic to islands (i.e., not occurring on continents). By taking into account the different threat levels, this study puts into perspective relevant conservation priorities for endemic insular species.

2 | METHODS

2.1 | Database

2.1.1 | Occurrence data

We extracted occurrence data of insular birds and mammals from polygon ranges of the IUCN Red List (IUCN, 2018) and the BirdLife International (Handbook of the Birds of the World & BirdLife International, 2016). Among all species occurring on oceanic and continental islands, only insular endemic species were considered because of their key conservation interest (Fattorini, 2017). Overall, we considered a total of 1,788 bird and 968 mammal species endemic to one or several islands (n = 4,348).

2.1.2 | Threats data

The IUCN Red List assessed the conservation status of species worldwide through a series of criteria such as population sizes and trends, geographic distribution, species' ecology and habitat preferences (Rodrigues, Pilgrim, Lamoreux, Hoffmann, & Brooks, 2006). Evaluation of species extinction risks has already been conducted exhaustively for mammals and birds (Meiri & Chapple, 2016). In total, 426 birds and 386 mammals that are insular endemic listed by the IUCN Red List as vulnerable (VU), endangered (EN) and critically endangered (CR) were considered threatened, that is, at risk of extinction in the near future due to specific threatening processes. Thus, the IUCN provides a threat classification scheme with a list of eleven direct threats relating to proximate human activities or processes that impact the status of the taxa under assessment: *biological invasions*, *climate change*, *cultivation*, *energy production/mining*, *geological events*, *habitat modifications*, *human intrusions/disturbance*, *pollution*, *transport corridors*, *urbanization* and *wildlife exploitation* (see Table S1 for definitions; Salafsky et al., 2008). Species can be affected by one or multiple threats, and association type is binary (i.e., presence/absence of the threat without any information about the threat's location on the species range). A total of 426 birds and 372 mammals considered at risk of extinction in this study are associated with at least one threatening process. Thus, the following analyses focus on pools of species at risk of extinction affected by each threat at the global scale (i.e., compared with the global pool of insular endemic species; n = 968 mammals and 1,788 birds).

2.1.3 | Functional description of species

To measure functional diversity, we selected five traits describing main diet, foraging niche, foraging period, habitat niche breadth and body mass that are available for both birds and mammals from the EltonTraits database (Wilman et al., 2014) and IUCN (2018) (Table S2). Combinations of traits govern species interactions through competition for habitat and food, for example, or species contribution

to ecosystem functioning through nutrient cycling, seed dispersal and trophic control (Hevia et al., 2017; Şekercioğlu, 2010). We transformed all trait values into a categorical nature (nominal or ordinal) for two reasons. First, this transformation allowed us to compare traits between taxonomic groups, as some variables were qualitative for one taxon, but quantitative for another (i.e., main diet and foraging niche; Table S2). Second, categorical variables reduced uncertainties relating to the accuracy of information (for further explanations, see Table S2). The set of five functional traits and their respective number of modalities yield 428 combinations of trait values for birds and 256 for mammals (Table S3, Appendix S1). We thus grouped species sharing the same trait values into functional entities (FEs; Mouillot et al., 2014) to run the functional diversity analyses. More particularly, ~34% of FEs among birds and ~46% among mammals are represented by only one species, while in other cases, many species (up to 39 birds and 42 mammals) may share the same FE.

To calculate the functional diversity of pools of insular endemic species at risk of extinction due to the different threats, we built separate functional trait spaces based, respectively, on all FEs of birds and mammals. A functional trait space summarizes the distribution of FEs, and hence the distribution of species within them according to their trait values (Villéger, Mason, & Mouillot, 2008). To this end, for each group of vertebrates, we identified the best possible functional space by comparing the distances of species in trait space with their initial functional distances, as done by Maire, Grenouillet, Brosse, and Villéger (2015). First, we computed the pairwise functional distances between each FE using the Gower dissimilarity index (Gower, 1971), which gives the same weight to each variable. Second, we computed functional dendrogram and multidimensional functional spaces from 2 to 10 dimensions based on Gower dissimilarities. We obtained the functional dendrogram through the unweighted pair group method with arithmetic mean (UPGMA) and multidimensional functional spaces using principal coordinates analysis (PCoA). We finally selected the best functional space, which provided the most faithful representation of the initial functional trait values. A functional space is of high quality when the distance between each pair of FEs in the functional space (Euclidean distance for multidimensional functional space; Cophenetic distance for UPGMA dendrogram) is congruent with the initial functional distance (Gower's distance). We computed the mean square deviation (mSD) for each functional space to assess the difference between initial and final functional distances. mSD is close to 0 when the obtained functional space faithfully represents the initial distance for all pairs of FEs. We kept the first six principal axes of the PCoAs to build separate functional spaces for birds and mammals (mSD < 0.007; Figure S1).

2.2 | Biodiversity indices

Based on the collected data, we calculated diversity indices for both taxonomic and functional dimensions associated with the eleven threats considered in this study.

2.2.1 | Taxonomic and functional diversity

Taxonomic diversity was assessed using TR. The proportion of threatened species (VU, EN and CR species) compared with the global pool of insular endemic species was thus calculated for each threat (Table S3). Functional diversity, namely the distribution of species in the multidimensional space as defined by their traits, is multifaceted (Mouillot, Graham, Villéger, Mason, & Bellwood, 2013). We used three quantitative metrics to describe the complementary components of functional diversity. First, functional richness (FRic) is computed as the volume within the minimum convex hull that wraps around the FEs of interest. This metric represents the proportion of space occupied by the FEs of threatened species (VU, EN and CR species) affected by each threat compared with the maximum volume occupied by the entire FE pool, hence all insular endemic mammals or birds (Figure 1a). This metric is driven by the few species with the most extreme trait values (Villéger et al., 2008). Second, the functional specialization (FSpe) associated with a threat category quantifies the average distinctiveness of all the threatened species. This index is measured as the mean Euclidean distance of each FE of threatened species associated with a threat category from the average position of the entire FE pool (i.e., barycenter) in the functional space (Figure 1b; Mouillot, Graham, et al., 2013). High FSpe values indicate that FEs in the studied pool are far from the barycenter and have extreme trait combinations compared with the global pool. Third, functional originality (FOri) associated with a threat category represents the uniqueness of the traits of the threatened species. This metric is computed as the mean distance between each FE of the threatened species affected by a threat category and its nearest neighbour in the functional space based on the entire FE pool (Figure 1c; Mouillot, Graham, et al., 2013). Low values indicate that FEs are on average functionally close to another FE from the global pool. All these metrics range from 0 to 1. Finally, we examined relationships between both diversities: taxonomic and functional (i.e., FRic, FSpe and FOri) of the threatened insular endemic species (i.e., VU, EN and CR) affected by each threat (n = 11) using Spearman's rank correlation test.

2.2.2 | Vulnerability of threatened species loss

We also calculated the functional vulnerability (FV) associated with each threat for birds and mammals separately. FV (Figure 1d) represents the percentage of the global FRic prone to disappear in the event of the extinction of the threatened species due to each threat, based on the metric of Toussaint, Charpin, Brosse, and Villéger (2016): $FV_{obs} = (1 - FRic_{wout\_threatened}) \times 100$, where $FRic_{wout\_threatened}$ is the proportion of FRic in the global species pool without the species that are threatened and associated with a threat category. FV reaches 100% when only the threatened species have the most extreme trait values in the functional space. Conversely, the value of the metric is null when all FEs contain at

least one species from the rest of the pool (consequently, no FE would disappear because of the threatened species' extinction) or when species from the rest of the pool have the most extreme trait values in the functional space. Indeed, species of the global pool may compensate for the loss of threatened species, as they may share the same FEs. The correlation between FV and associated FRic was tested using the Spearman's rank correlation test.

2.3 | Statistical analyses

2.3.1 | Null model

To test whether the observed functional diversity of threatened species affected by each threat was significantly different than expected by chance, we ran null models using two different FE pools. For each threat, we simulated a random sorting of threatened species from the global FE pool. We also ran a null model by randomly sorting threatened species among FEs that only occur in the biogeographical realms (based on Holt et al., 2013) where each threat occurs, as they are spatially structured. For instance, *cultivation* and *wildlife exploitation* mostly threaten insular biodiversity in the Indian Ocean and near the Asian coasts, while the Pacific and Atlantic insular regions are mostly affected by *biological invasions* (Leclerc et al., 2018). For more biological realism, we only randomized species within FEs, while keeping the number of FEs and species constant, 9,999 times. Indeed, among all possible FEs (i.e., a given number of traits and their modalities), <13% are filled. The rationale here is to explore among the possible combinations of traits (and thus FEs) that exist at the global or at the realm scale whether or not certain threats are more likely to be associated with specific traits/FEs than expected under our null model. The first null model tests whether the functional diversity associated with each threat is significantly different from the value of a random set of species of all insular endemic species across the world. By defining a specific pool of FEs for each threat, the second null model tests whether the functional diversity of threatened species significantly differs from the functional diversity of species present in the same realm. However, autocorrelation could affect the significance of our results based on null models, but to date, no method has allowed us to consider these aspects.

To identify threats that are more likely to be associated with specific traits/FEs, we investigated whether observed species pools affected by threats are functionally more or less clustered or overdispersed (i.e., are functionally more or less similar) than expected by chance. For this purpose, we measured the deviation from the null expectation by computing the standardized effect size (SES) and associated p-value. SES was calculated as the difference between the observed value of functional diversity (i.e., FRic, FSpe and FOri) and the mean of predicted values by the null model divided by the standard deviation of predicted values. The significance of the difference from null expectations was considered using a two-tailed test with a level of 5%. An observed value
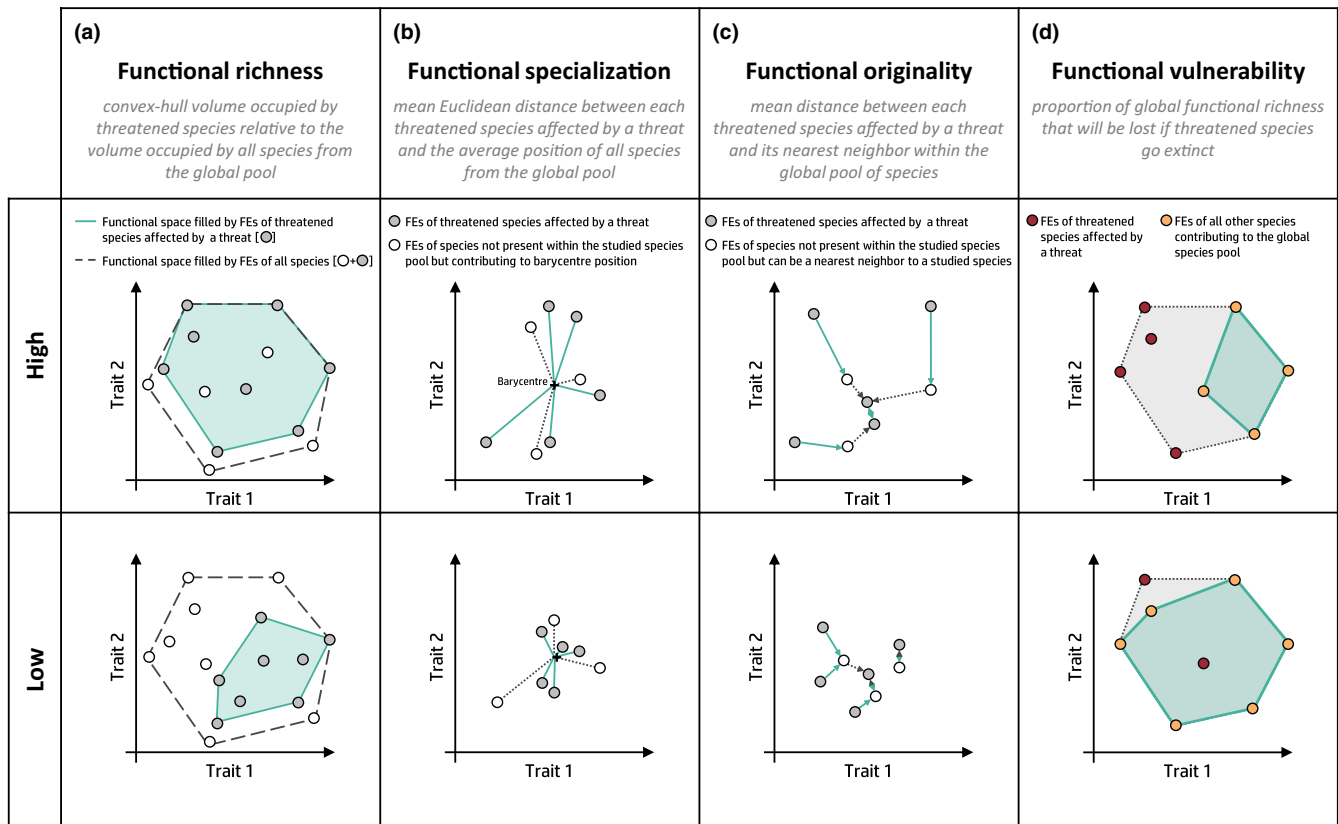
FIGURE 1　Representation of the functional diversity metrics: (a) functional richness, (b) functional specialization, (c) functional originality and (d) functional vulnerability. Species (dots) are plotted in two-dimensional functional space according to their respective trait values, where axes are synthetic traits extracted from principal coordinates analysis. The metrics do not take into account the number of species per functional entity. Threatened species comprise VU, EN and CR species identified by the IUCN

of functional diversity (i.e., FRic, FSpe and FOri) is considered significantly different from the predicted values if the observed value is in the top or bottom 2.5% of the predicted value distribution. In particular, an observed value of functional diversity (i.e., FRic, FSpe and FOri) in the bottom 2.5% of the predicted value distribution indicates that species affected by a given threat are more functionally related than expected by chance (i.e., functionally clustered). Conversely, an observed value of functional diversity (i.e., FRic, FSpe and FOri) >97.5% of predicted values indicates that species affected by a given threat are less functionally related than expected by chance (i.e., functionally overdispersed). For threats associated with a FRic value significantly different than expected under the null hypothesis, we examined the distribution of trait modalities observed and predicted to identify associations between trait modalities and threats. We also tested the significance of the observed FV values under the null model previously described. In this case, an observed FV value that was significantly higher than predicted values under the null hypothesis indicates that threatened species are functionally distinct from the global species pool. In other words, threatened species do not share the same FEs with the other species of the global pool than expected by chance. On the contrary, a FV value significantly lower than expected indicates that threatened species are functionally more

similar (i.e., share the same FEs) to other species of the global pool than expected by chance.

2.3.2 | Sensitivity analysis

Because functional diversity patterns may be affected by the set of selected traits and species, we conducted different sensitivity analyses. Specifically, we ran congruence analyses between functional diversity (i.e., FRic, FSpe and FOri) and TR using all combinations of four of the five traits to test whether a given trait drove the observed patterns (Mouillot et al., 2014). We then re-examined the relationship between functional diversity (i.e., FRic, FSpe and FOri) and TR by separating insular endemic species occurring on a single island (i.e., single-island endemics) from those occurring on several islands (i.e., multi-island endemics). We also tested the influence of the type of island (oceanic or continental) on functional and taxonomic diversity relationships.

All analyses were performed with R software (version 3.3.1, R Development Core Team, 2008) using GGPLOT2 (Wickham, 2009), GRIDEXTRA (Auguie, 2017) and MATRIXSTATS (Bengtsson, 2017) packages. Functional space analyses were performed using the R packages APE (Paradis, Claude, & Strimmer, 2004), CLUE (Hornik, 2005), CLUSTER (Maechler, Rousseeuw, Struyf, Hubert, & Hornik, 2017),

DPLYR (Wickham, Francois, Henry, & Müller, 2017), GEOMETRY (Habel, Grasman, Gramacy, Stahel, & Sterratt, 2015), GTOOLS (Warnes, Bolker, & Lumley, 2015) and STRINGR (Wickham, 2017). We also used scripts developed to compute the functional diversity indices (Villéger, 2017).

3 | RESULTS

3.1 | Taxonomic and functional diversity of species at risk of extinction due to each threat

Our results showed a marked disparity in FRic of threatened species among threats. As expected, *cultivation* and *wildlife exploitation* are

associated with the highest proportion of FRic of threatened birds and mammals. Among birds, *cultivation* was associated with 17% of TR but with a threefold higher FRic (53%). Likewise, among mammals, a lower percentage of TR (26%) was associated with *cultivation* compared with FRic (50%). Both threats are followed by *biological invasions*, *habitat modifications* and *urbanization*, which are associated with medium FRic values (~30%) but still three times higher than TR (~8%). Moreover, the remaining threats such as *geological events* and *human intrusions/disturbance* were associated with low TR values (<3.5% for both taxa), which are similar to FRic values. Among mammals, *transport corridors* threaten only 0.9% of FRic and 1.5% of TR. Overall, we found a positive relationship between threatened TR and FRic associated with each threat, but this did not follow a 1:1 ratio (Figure 2a,b; mean ± *SD*, FRic: 21.8 ± 19.7%, TR: 8.2 ± 8.4%). We did not find a
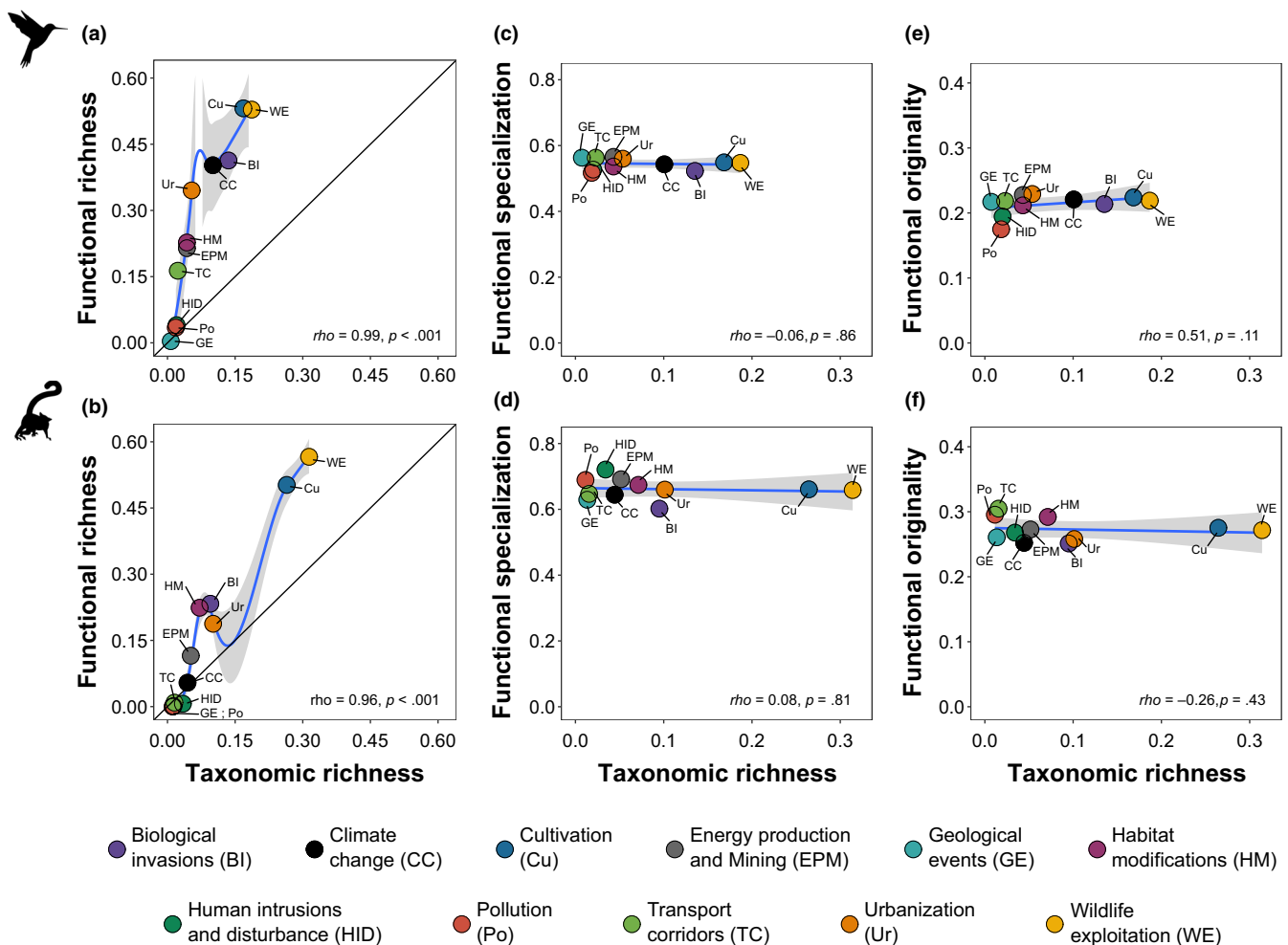

FIGURE 2 Relationships between taxonomic and functional diversity of insular endemic birds and mammals affected by each threat. Taxonomic richness is represented as the ratio of threatened species (VU, EN and CR species) affected by each threat compared with the entire species pool; functional richness is represented as the ratio of space occupied by the functional entities (FEs) of threatened species (VU, EN and CR species) affected by each threat compared with the volume occupied by the entire FE pool; functional specialization is represented as the mean Euclidean distance of each FE of threatened species affected by a threat category from the average position of the entire FE pool in the functional space; and functional originality is represented as the mean distance between each FE of threatened species affected by a threat category and its closest neighbour among all FEs in the functional space. The smooth curve was drawn with (a,b) a loess (locally weighted scatter plot smoothing) method and (c–f) a linear method. The confidence interval represents the standard error. (a,b): The black solid line represents the identity line functional richness = taxonomic richness. On each panel, Spearman's correlation coefficients and associated *p*-values are shown. See Tables S4 and S5 for complementary information about the null model results

strong relationship between threatened TR and threatened FSpe or FOri. FSpe were constantly high (~0.51–0.72), while FOri remained low (~0.17–0.30) for both low and high TR of the threatened mammals and birds regardless of the threat under consideration (Figure 2c–f).

Sensitivity analyses showed that when one trait was removed from the analyses, FRic, FSpe and FOri values were close to those observed with five traits (Figure S2). Likewise, similar patterns were obtained for relationships between functional diversity (FRic, FSpe and FOri) and TR when separately considering the single- or multi-island endemics (Figure S3), and the island types (Figure S4), except for FRic associated with threatened birds occurring on continental islands. Based on the null model analyses (simulating a random assignment of threatened species on the global FE pool without any biogeographical realm information), threats are not associated with higher or lower functional diversity than expected given TR, except in specific cases. For instance, we found that species pools at risk of extinction affected by *biological invasions* (FRic and FSpe for both taxa, and FOri for mammals), *cultivation* (FRic and FOri for mammals), *human intrusions/disturbance* (FRic for both taxa), *pollution* (FRic and FOri for birds), *urbanization* (FOri for mammals) and *wildlife exploitation* (FOri for mammals) have a functional diversity significantly lower than expected under the null hypothesis (Table S4). Nevertheless, the significance of the functional diversity results varies when considering the null model that accounted for the occurrence of FEs in biogeographical realms (Table S5). For example, only *pollution* among birds is associated with a significantly lower FRic than expected by chance.

3.2 | Associations between threats and ecological traits of threatened insular endemic species

Next, we focused on the threats associated with an observed FRic that were significantly different than expected under the first null hypothesis (Table S4 and S5). We found that threats associated with habitat-modifying processes such as *cultivation, human intrusions/disturbance, pollution* and *urbanization* are more associated with diet and/or habitat specialist species (Figure 3). We also found that these threats were associated with other specific species traits. For example, *cultivation* was more often associated than expected with threatened mammals that have arboreal foraging strategies, are diurnal, or are very large. Concerning *human intrusions/disturbance*, this threat was more associated with threatened birds that forage below the water surface or are very large. On the contrary, this threat was more often associated with threatened mammals that forage in the air, are nocturnal, or are very small. We also confirmed that processes directly affecting survival such as *biological invasions* and *wildlife exploitation* were both more often associated than expected with threatened species of large body mass, except for mammals affected by *biological invasions* (Figure 3). Both threats were also more associated than expected by chance with diet and habitat-specialized species. Further, mammals that have arboreal foraging strategies or are diurnal were more associated with *wildlife exploitation*, while *biological invasions* were more associated than expected with species with ground or below water surface foraging

strategies. Nevertheless, trait modalities significantly associated with a threat differed when the null model was controlled for species pools present in each biogeographical realm (Table S8).

3.3 | Functional vulnerability linked to threatened species loss due to each threat

Last, FV was positively correlated to the threatened FRic associated with each threat (Spearman's rank correlation, birds: ρ = 0.83, p < .01; mammals: ρ = 0.85, p < .01). The vulnerability of functional diversity due to the extinction of threatened species remains mostly very weak with birds and mammals, especially for threats that threaten small and medium amounts of FRic (Figure 4). Only *cultivation* and *wildlife exploitation* threats, which threaten a large amount of FRic, are also associated with a moderate FV of around 10%. Overall, FV associated with mammals was higher (mean ± *SD*, 3.8 ± 5.5%) than that associated with birds (2.6 ± 3.5%). Finally, only *cultivation* for birds was characterized by a FV higher than expected by chance (Table S9).

4 | DISCUSSION

Here, we assess the functional and taxonomic diversity of bird and mammal species at risk of extinction due to threatening processes at a global scale. Previous global analyses focused only on threatened taxonomic diversity according to each threat, but here, we explore both taxonomic and functional diversity for the first time. We find a disparity of threatened diversity in relation to each threat, and particularly, a higher overall amount of FRic (~20%) compared with TR (~8%). Three groups of threats can be identified based on the amount (small, medium and high) of FRic of insular endemic species at risk of extinction, despite the similarities between FSpe and FOri across threats. Moreover, complex patterns have been highlighted between species traits and threat processes (i.e., habitat-modifying processes and threats directly affecting survival). Last, according to the identified threat groups, only *cultivation* and *wildlife exploitation* associated with a large amount of FRic of threatened species (>50%) show a moderate FV (~10%).

4.1 | What is the functional diversity harboured by insular endemic species at risk of extinction due to each threat, and how is it related to the number of species?

Our investigation of how both taxonomic and functional diversity are affected by the eleven aspects of global changes revealed a positive relationship between FRic and TR but not at a 1:1 ratio. One-fifth of FRic is supported by birds and mammals at risk of extinction, which is greater than the proportion of TR (~8%). Three groups of threats could be identified based on the amount of FRic of threatened species associated with each threat. In the first group, we identified two major threats, *cultivation* and *wildlife exploitation*, in terms
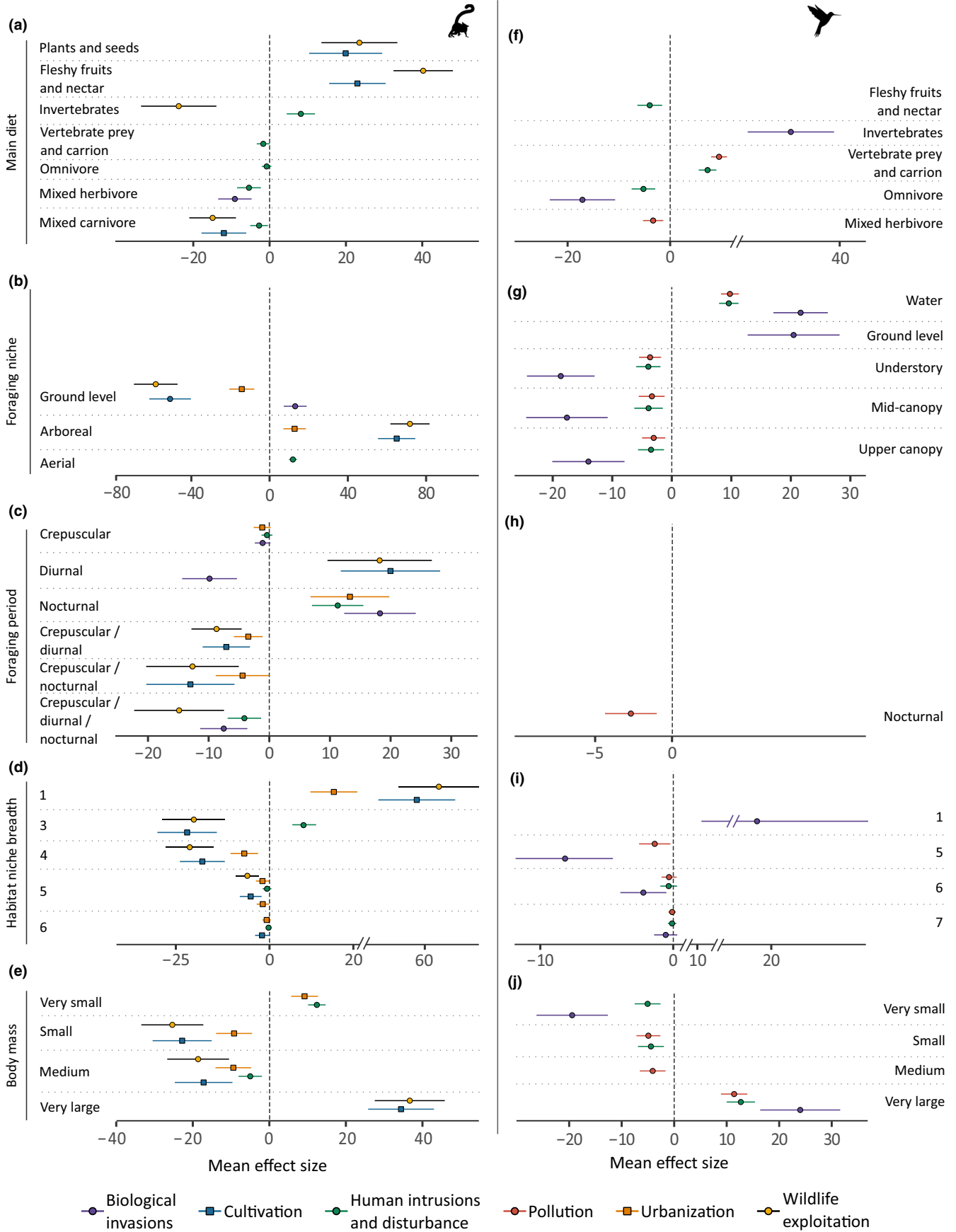
FIGURE 3 Mean effect sizes of null models for trait modalities of threatened birds and mammals (VU, EN and CR species) affected by threats: (a, f) main diet; (b, g) foraging niche; (c, h) foraging period; (d, i) habitat niche breadth; and (e, j) body mass. Only trait modalities for threats associated with an observed functional richness that is significantly different than expected under the null hypothesis based on the global FE pool are shown. Also, trait modalities that are significantly more (mean effect size; MES > 0) or less (MES < 0) associated than expected by chance with a threat are represented in the figure. Points represent the mean effect size, and bars represent the standard deviation. See Tables S4, S6 and S7 for further information
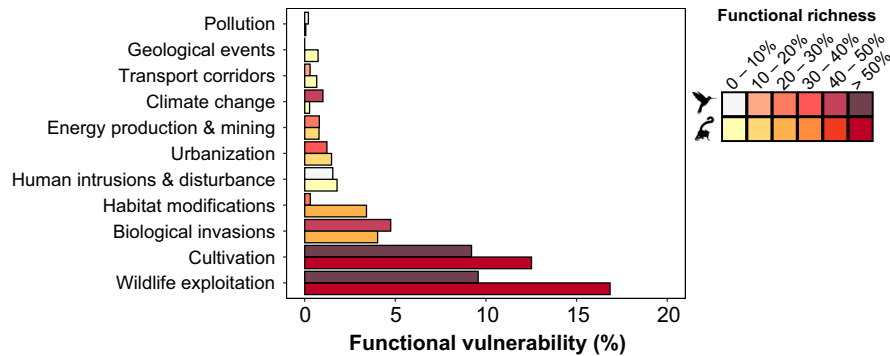

FIGURE 4 Functional vulnerability of insular endemic mammals and birds to each threat. Functional vulnerability represents the percentage of functional richness (i.e., volume of functional space filled by species) that could potentially be lost as a result of the extinction of threatened species caused by each threat. The colour gradient scale represents the proportion of functional richness supported by the threatened species compared with the functional richness of the global species pool; and the colour transparency informs about taxa studied. Threats are ranked according to the cumulated values of functional vulnerability of birds and mammals

of the FRic (~53%), and to a lesser extent, TR (~23%) of the species at risk of extinction. We confirmed our hypothesis that these threats are also of major concern regarding functional diversity facets. Indeed, their role as major drivers of insular ecosystem losses has already been described (e.g., Kingsford et al., 2009), but not for both diversity levels. Moreover, for mammals, both threats targeted species with more clustered/similar trait values in the functional space than expected by chance, which could be attributable to several different processes such as environmental filtering. Indeed, the trait space that species can occupy might be limited by abiotic factors, increasing species functional similarity within islands where threats occurred compared with a global- or realm-based null (Cooke, Bates, & Eigenbrod, 2019). The second set of identified threats was composed of *biological invasions*, *habitat modifications* and *urbanization*, which are associated with medium FRic (~30%) and always with a lower TR (~8%) of the insular endemic species at risk of extinction. Of these three threats, only *habitat modifications* were not more or less associated with species with extreme trait values in the functional space, indicating that this threat does not target specific species and associated traits. Thus, these threats should also be considered with particular attention in biodiversity assessments and conservation strategies, especially in the case of *biological invasions* where introduced species will not be able to maintain ecological roles of pre-disturbance assemblages (Sobral et al., 2016). Last, *energy production/mining*, *geological events*, *human intrusions/disturbance*, *pollution* and *transport corridors* are five threats associated with low and similar values of TR and FRic (<3.5%). These threats have little been explored in insular context, with the exception of *pollution*. Even if it has been shown that oceanic diversity can be particularly sensitive

to this threat (Caujapé-Castells et al., 2010), no study has explored the relative importance and consequences of it on functional insular diversity. Overall, these five threats can be considered to be relative minor drivers of insular ecosystem losses, owing to the very weak FRic and TR at risk of extinction. *Climate change* is also part of the second and third group of threats to birds and mammals, but it is expected to increase in the years to come (Urban, 2015). Although FRic of threatened species was disparate among threats, allowing three groups of threats to be identified, this was not the case with FSpe and FOri. Indeed, high FSpe and low FOri were observed regardless of the threat involved. This suggests that all threats are associated with specialized species (with extreme trait values), although this is redundant, because many species harboured similar traits or a close combination of them. Overall, our results illustrate that taxonomic and functional diversity indices should be studied simultaneously to better prioritize threats, and thus, the conservation of insular endemic biodiversity. Moreover, threat combinations rather than individual threats should be considered (Geary, Nimmo, Doherty, Ritchie, & Tulloch, 2019), as most islands face numerous simultaneous threats (Leclerc et al., 2018; see also Table S10).

4.2 | Are threats associated with specific sets of ecological traits of insular endemic species at risk of extinction?

Understanding which traits make species more vulnerable to which set of threats is crucial from both a fundamental and applied perspective (González-Suárez et al., 2013), but this has remained largely

underinvestigated to date (Chichorro, Juslén, & Cardoso, 2019). Here, we showed that some threats are associated with specific species traits. For example, *human intrusions/disturbance* is more likely to threaten the largest birds and smallest mammals compared with the global pool of insular endemic species. As with the probability of being threatened, drivers of extinction are mostly associated with an extreme body size in vertebrates (Ripple et al., 2017). However, based on the two null models used here, we did not observe a distinctive pattern of association between threats and species traits as previously found. Indeed, previous studies identified that habitat-modifying processes affect small-size and ecologically specialized species, while threats directly affecting survival (e.g., overexploitation, invasive species) threaten larger species with small litters (González-Suárez et al., 2013; González-Suárez & Revilla, 2014). Indeed, our results showed more complex patterns. In our insular ecosystem study, threats directly affecting survival and reducing habitat availability were more associated with both habitat and diet-specialist species. We also found that foraging niche and foraging period were important species parameters for understanding the association between threats and species traits. Nevertheless, the choice of species pool (global vs. biogeographical) used for the null models influences the modalities of species traits identified as significantly associated with a threat, because of differences in the number and variability of FEs at a global and realm scale. This result demands further investigations into the biogeographical distribution of functional diversity from the local to the realm scale, with the aim to take into account the non-random spatial distribution of threats and biodiversity (Hatfield, Orme, Tobias, & Banks-Leite, 2018). Indeed, the different threats affect portions of land in non-random spatial ways and interact with the distribution of biodiversity, which is spatially structured (Evans et al., 2011).

4.3 | What would be the consequences on functional diversity in the event of the extinction of the threatened insular endemic species affected by each threat?

Here, FV associated with the different threats is globally weak, especially for threats associated with small and medium amounts of FRic of threatened species, which reveals a strong pattern of redundancy in FEs in insular biodiversity. Only *cultivation* and *wildlife exploitation*, which threaten a large amount of FRic, are associated with FV of around 10%. More particularly, they threaten between 8% and 20% of FEs that support functionally unique species at risk of extinction (Appendix S1). Thus, threatened species affected by these threats support extreme and unique functions, and are functionally irreplaceable (Mouillot, Bellwood, et al., 2013; Mouillot et al., 2014). The risk of losing a unique function has been shown to modulate the response of species assemblages to global changes (Mouillot et al., 2014). This is especially true given that ecological disturbances diminish the number of assemblages and homogenize them (i.e., becoming functionally more similar) through the extinction of functionally unique species (e.g., Flynn et al., 2009; Richardson et al., 2018).

We explored vulnerability patterns at a global scale, although these may vary from one spatial unit to another (Toussaint et al., 2016). Further investigations should therefore be conducted to assess the vulnerability of the different insular regions, archipelagos and islands to global changes. Also, based on the null model, only *cultivation* is more associated with threatened birds than expected by chance, indicating that this threat targets functionally unique species from the global species pool, independently of species richness. Attributing a cause to species extinction and endangerment is difficult, and further investigations on the identification of biodiversity threats are thus a prerequisite to better determine diversities (taxonomic and functional) and the potential consequences of extinction of insular endemic species in the face of global changes.

4.4 | Caveats of the study

Regarding the present study, a few limitations should be acknowledged. Although we based our functional indices on five species traits, the number of traits, their relevance as well as the number of modalities were identified as important factors influencing functional diversity (Petchey & Gaston, 2006). For example, a crude categorization of trait modalities can potentially induce low FV owing to the high number of species in each FE, while a detailed categorization would lead to the opposite, that is, only a few species in each FE (Mouillot et al., 2014). However, sensitivity analyses showed that none of our traits drove the patterns of functional and taxonomic diversity associated with each threat. Moreover, ecological factors such as rarity and endemism may interfere in the IUCN assessment process. Indeed, the application of the IUCN Red List criteria generally tends to overestimate extinction risks for most island endemics, which naturally have very small areas of occupancy and extents of occurrence, even if they are common within their range (Martín, 2009; Romeiras et al., 2016). Furthermore, the true level of extinction risk for data-deficient species can lead to some uncertainty (Bland, Collen, Orme, & Bielby, 2015). Here, data-deficient species were not considered threatened, as this can lead to an underestimation of the species considered at risk of extinction. Also, the IUCN does not provide information on the occurrence of threats across species' geographic range, which prevented us from conducting analysis at the island scale. For species occurring on more than one island, it is impossible to know whether the threatening process occurs on only one or several islands, which makes the analyses by island biased. Nevertheless, to date, the IUCN Red List is the most comprehensive assessment of species at risk of extinction worldwide (Lamoreux et al., 2003).

4.5 | Conclusion

This study adds to our understanding of how global changes threaten functional and taxonomic diversity on islands, thus

providing insights for conservation purposes. Specifically, we argue that *cultivation* and *wildlife exploitation* should be taken as the top priorities to preserve both taxonomic and functional diversity for both insular endemic birds and mammals. This is supported by our vulnerability analysis, which showed a lower redundancy harboured by species affected by these two threats compared with other species. Acting on both *cultivation* and *wildlife exploitation* is therefore particularly important, since they mostly co-occur and act interactively on biodiversity. Also, conservation plans should also focus on the other threats to preserve irreplaceable species in terms of the traits/functions that may disappear, especially that the relevance of threats is depending on geographic scale, and taxa or traits considered. Finally, future studies should pay special attention to threat associations in order to improve conservation strategies.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

All data employed in the present work are public and can be downloaded from the original sources. They are also available in Appendix S1.

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BIOSKETCH

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