

**Title:** Non-native bird species will not compensate for the loss of phylogenetic and functional diversity after the extinction of threatened species

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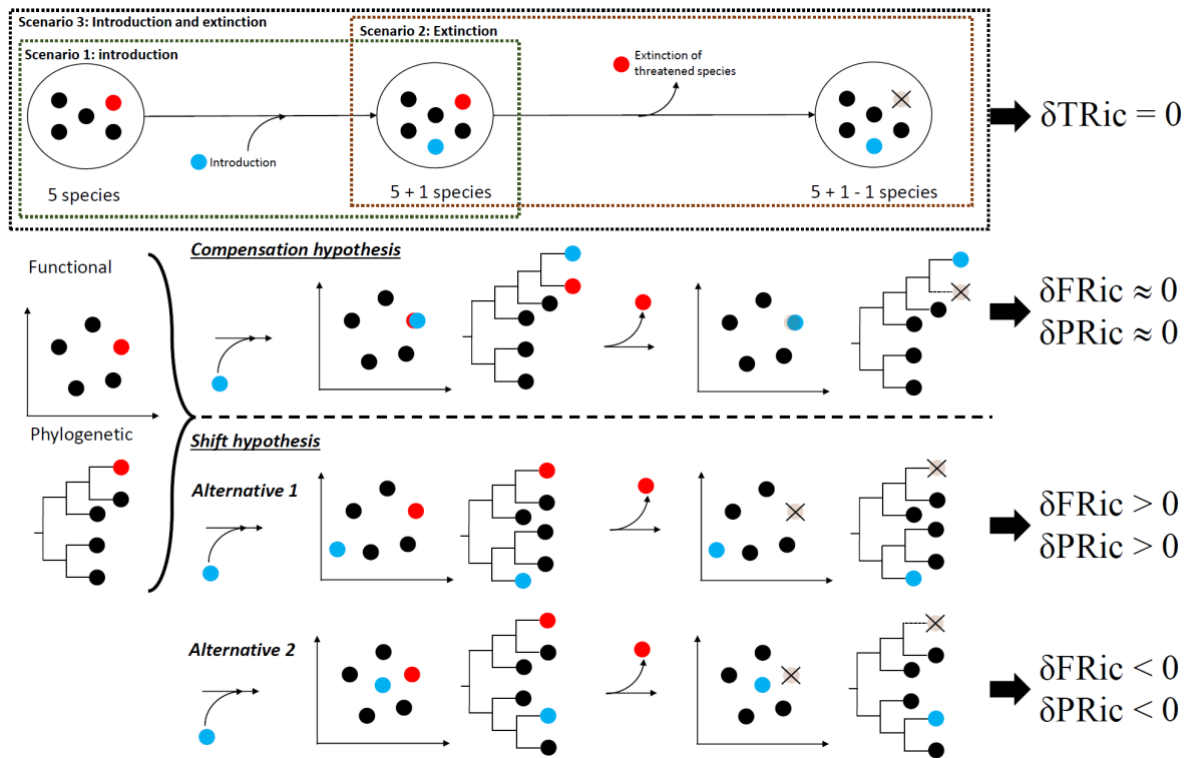
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**Abstract.** Human activities have altered the composition of species assemblages through the introduction of non-native species and the extinction of threatened species. It remains unclear whether non-native species can compensate for the loss of threatened species and thus maintain ecosystem functioning. Here we tested whether non-natives are functionally and/or phylogenetically similar (compensation hypothesis) or distinct (shift hypothesis) from native and threatened species on bird assemblages in 267 regions. Non-native species were more functionally distinct from threatened species than expected by chance but more phylogenetically related. Globally, this results in an increase in functional richness but a decrease in phylogenetic richness. Furthermore, these patterns vary across continents, revealing the role of human footprint and outlining priority areas where conservation policies should focus. In the context of the biodiversity crisis, these changes in the functional and phylogenetic structure of the bird communities might increase the vulnerability of ecosystems.

**Introduction.** Through the introduction of non-native species and the extinction of threatened species, human activities have contributed to a deep reorganization of species assemblages and triggered the sixth biodiversity crisis (Simberloff & Vitale 2014; Capinha *et al.* 2015). While many studies focused on either non-native (Gozlan *et al.* 2010; Jeschke *et al.* 2014; Martin-Albarracin *et al.* 2015) or threatened species (Pimm & Raven 2000; Jenkins *et al.* 2013; Carmona *et al.* 2021; Toussaint *et al.* 2021), the consequences of the coupled effects of introductions and extinctions are still rarely addressed (but see Daru *et al.* (2021)). It is, however, a key aspect to understanding the future composition of assemblages, its consequences for ecosystem functioning, and the potential capacity of responses of organisms. Such aspects can be apprehended by studying different facets of biodiversity such as the taxonomic, functional, and phylogenetic diversities (Jarzyna & Jetz 2016; Pollock *et al.* 2017; Su *et al.* 2020). While forecasting the future composition of assemblages under the coupled role of introductions and extinctions can be mathematically calculated as a sum of introduced and extinct species (Fig 1), predicting the changes in functional and phylogenetic diversity depend on the characteristics and the evolutionary history of the species (Sol *et al.* 2017; Su *et al.* 2019). Using a recent compilation of non-native species and threatened species of birds across the world, we evaluate the role of non-native species coupled with the potential extinction of threatened species on the native biodiversity of birds for the taxonomic, functional, and phylogenetic facets in 267 regions worldwide.

Recent evidence showed that compared to native species, non-native species tend to have distinct functional traits (Blanchet *et al.* 2010; Van Kleunen *et al.* 2010), resulting from a human selection of non-native species for specific purposes (e.g., trade, game, ornamental, pest control). Conversely, large-sized, slow-paced, and slow-reproducing species of plants and vertebrates tend to have higher risks to be threatened with extinction (Carmona *et al.* 2021; Toussaint *et al.* 2021). While non-native species belonging to some specific clades are more likely to be introduced (e.g., Anseriformes and Galliformes for bird hunting (Carpio *et al.* 2017), or Psittaciformes for bird trade (Cassey *et al.* 2004b; Strubbe & Matthysen 2009)), other clades have higher proportions of threatened species than expected (Bennett & Owens 1997; Weeks *et al.* 2022). The future composition of species assemblages will hence result from a coupled effect of both native and non-native species (Fig. 1). If non-native species have similar traits and/or belong to the same clades as threatened species, the changes in species composition will have little effect on functional and/or phylogenetic diversity and hardly impede ecosystem functioning (hereafter called the compensation hypothesis, Fig. 1). Contrastingly, if non-native and threatened species have distinct functional traits and/or belong to different clades, non-native species will introduce new ecological strategies and/or evolutionary histories susceptible to strongly disrupt the biodiversity and functioning of the invaded assemblages (hereafter called the shift hypothesis, Fig. 1). Thus, depending on the functional and phylogenetic relatedness between non-native species and threatened species, the direction of the changes in functional and phylogenetic diversity can be positive or negative (Fig. 1).



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**Figure 1. Theoretical framework of combined effects of introductions and extinctions.** Considering an assemblage of five species (in black), we study the changes in taxonomic, functional, and phylogenetic richness following three scenarios: after the introduction of non-native species (scenario 1), after the potential extinction of threatened species (scenario 2), or after coupling the effects of introductions and extinctions (scenario 3). While there are no changes in species number in scenario 3 ( $\delta TRic = 0$ ), changes in functional ( $\delta FRic$ ) and phylogenetic ( $\delta PRic$ ) can be manifold as illustrated through three theoretical situations. For the compensation hypothesis: introduced and extinct species are functionally and phylogenetically closely related and hence we expect no or few changes in FRic and PRic. For the shift hypothesis: introduced and extinct species are functionally and phylogenetically distinct. In the shift hypothesis, two alternatives can be distinguished: either non-native species is functionally and phylogenetically distinct from native species (Alternative 1) or non-native species is functionally and phylogenetically distinct from threatened species but redundant with other native species of the assemblage (Alternative 2). According to those two alternatives, the direction of the changes in FRic and PRic can be either positive (Alternative 1) or negative (Alternative 2).

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Changes in species composition are unevenly distributed across the world (Toussaint *et al.* 2014; Dyer *et al.* 2017a), with regions highly impacted by non-native species and/or threatened species (e.g., Europe, and North America) while some others are still less impacted (e.g., Africa). Beyond the different numbers of non-native and threatened species, the identity of species also depends on the human uses of non-native species and threats to native species (Cassey *et al.* 2004a; Dyer *et al.* 2017a). Thus, the changes in species composition might have

different consequences in functional and phylogenetic diversity across the world. Understanding the patterns of changes in species composition in terms of taxonomic, functional, and phylogenetic diversity will help to better identify the vulnerable ecosystems in the world and better address conservation policies.

Here, we investigate how the changes in species composition through the introduction of non-native species and the potential extinction of threatened species support the compensation or the shift hypotheses described in Fig. 1. We first test the extent to which existing non-native and threatened species are functionally and phylogenetically related by measuring the dissimilarity for taxonomic, functional, and phylogenetic facets between non-native and threatened species. Then, we quantify the effect of established non-native species and the potential extinction of threatened species on the native biodiversity of bird assemblages through three scenarios, depicting unique (scenarios 1 and 2) and coupled effects (scenario 3) of introduced and threatened species (Fig. 1). The scenarios 2 and 3 depict a snapshot of what the future of bird biodiversity might be, considering the actual knowledge in term of extinction risks and introductions of non-native species. While introductions of new non-native species are predicted for the future (Seebens *et al.* 2021), we consider only established non-native species since it is still difficult to identify exactly which species could invade and where they will be introduced but see Paganeli et al. (2022). We simulate extinctions of all threatened species currently listed by the IUCN Red List as Critically Endangered, Endangered, and Vulnerable reflecting our current knowledge of biodiversity threats. For each scenario, we measure the changes in taxonomic, functional, and phylogenetic richness. We compare each scenario to null hypotheses where the identity of introduced and threatened species is randomly sorted among the pool of species. By doing this, we test whether the changes in functional and phylogenetic richness are different from expected by chance and whether the introduced/threatened species are functionally/phylogenetically redundant with the other species of the assemblages.

## Methods.

**Spatial database.** We collected species occurrences at the country level using the IUCN spatial database “Birds of the world” (downloaded December 2020). This database allowed obtaining the species list of 328 countries (defined as political borders) across the world. We considered the names and the number of countries (including states or provinces for the United States of America, Canada, and Australia) according to the GAVIA database (see below “Non-

native species”). The country and regional designations were downloaded from the Global Administrative Areas (GADM) database ([www.gadm.org](http://www.gadm.org), downloaded March 2021). From here on, we will use the term of “region” to refer to countries, states, and provinces. The original database encompasses 10,795 species.

**Non-native species.** We collected the non-native species list in each region using the GAVIA database, which is considered the most complete and updated database for these purposes (Dyer *et al.* 2017b). GAVIA database comprises 27,723 distribution records for 971 bird species for which there is some evidence of translocation outside their native range. We used data on the first introduction records of non-native species between 1500 and 2000 AD following the recommendation of (Dyer *et al.* 2017b). We removed the records for which there is evidence that there is no established population in the country informed in the GAVIA database (i.e., occurrences listed as “Extirpated” and “DiedOut”, see (Dyer *et al.* 2017b) for details).

**Threatened species.** We collected the conservation status of species from the IUCN Red List (version 2020-3, (IUCN 2020)) using the R package ‘rredlist’ (Chamberlain 2018). Such information was available for 251 regions and 10,379 species. We used the IUCN classes: CR: critically endangered; EN: Endangered; VU: Vulnerable; NT: Near Threatened; LC: Least Concern; DD: Data Deficient.

**Functional traits.** We collected information on traits related to ecological functions for 9,683 species of birds using the AMIOTE database (Myhrvold *et al.* 2015). All the traits have been selected for their ecological relevance and gathered from published studies (Myhrvold *et al.* 2015). We selected a total of eight traits: clutch size (number of eggs), number of clutches per year, adult body mass (g), incubation time (days), longevity (years), fledging age (days), egg mass (g) and distance from the tip of the beak to the opening of the cloaca (cm).

**Phylogenetic trees.** We used the phylogeny available including 9,836 species (Jetz *et al.* 2012). Species for which we have functional traits but were not present in the phylogeny were added to the root of the genus in the phylogeny (i.e., 2,044 species), using the ‘add.species.to.genus’ from the R package ‘phytools’ (Revell 2012). By doing so, we obtained 10,471 species phylogenetically informed. We considered the phylogenetic uncertainties by calculating the dissimilarity matrix for each of the 1,000-phylogeny based on cophenetic distance and averaged those matrices in a single matrix for which we calculated the eigenvectors.

**Functional space.** The construction of the functional space of birds followed the procedure described by Carmona et al. (2021). Briefly, we identified the main axes of functional trait variation by performing principal component analyses (PCA) on the log-transformed and scaled functional traits. The space was built using all species for which we had trait information and the two first dimensions were retained based on Horn's parallel analysis from the 'paran' package (Dinno 2018). The first two axes explained 66.3% and 13.8%, respectively of the total variation of functional traits (Table S1).

Since the functional traits were not informed for all species, we imputed the missing functional traits using a machine learning approach (missForest, (Stekhoven & Bühlmann 2012)) combining the observed functional traits and the phylogenetic information. This way, we included the evolutionary relationship between species in the imputation process by including the first ten phylogenetic eigenvectors, as recommended by (Penone *et al.* 2014) (see details in the following section). While phylogenetic diversity is based on the phylogenetic distance between pairs of species, using phylogenetic information in the imputation considers the interaction between all traits and the information, so that the positions imputed in the phylogenetic space are much more accurate. However, species that are evolutionarily very far apart might be very close in the functional space.

The accuracy of the trait imputation procedure was estimated on the subset of species for which we have complete information following (Carmona *et al.* 2021). We quantified the normalized root mean square error (NRMSE) according to the number of missing values (from 1 to the number of traits). The NRMSE error increased from  $0.20 \pm 0.05\%$  for PC1 and  $0.15 \pm 0.03\%$  for PC2 (when the species has only one missing trait) to  $5.72 \pm 0.78\%$  for PC1 and  $8.71 \pm 0.56\%$  for PC2 (when the species has seven missing traits out of eight, Table S2). On average, the errors were  $2.95 \pm 0.23\%$  for PC1 and  $3.39 \pm 0.21\%$  for PC2. Imputing the position of the species based only on phylogenetic information strongly increases the error (PC1 =  $63.53 \pm 3.45\%$ , PC2 =  $18.75 \pm 1.07\%$ ), justifying the exclusion of the species for which we have only phylogenetic information (representing 2,068 species).

We estimated the probabilistic distribution of the species within the functional space using all species with spatial and functional information by performing multivariate kernel density estimations with the 'TPD' R package (Carmona *et al.* 2019). We divided the 2-dimensional spaces into 40,000 cells. The kernel for each species was a multivariate normal distribution centered in the coordinates of the species in the functional space and bandwidth chosen using unconstrained bandwidth selectors from the 'Hpi' function in the 'ks' package.

**Matching occurrences, functional traits, non-native, and IUCN Red List databases.**

Taxonomies from all the used sources were standardized using the R package ‘taxize’ (Chamberlain & Szöcs 2013) and names resolved against the GBIF Backbone Taxonomy. We had 12,507 recognized names of bird species from the four sources of data. Among those species, 10,471 species were phylogenetically informed. We had functional information (at least one functional trait) for 8,718 species. The functional space was built using this subset of species after the imputation of missing functional traits. We checked the reliability of the functional space obtained with imputed functional trait values by comparing it with the space that was based only on species with complete functional information using a Procrustes test following (Carmona *et al.* 2021). The Procrustes test was highly significant ( $P=0.0001$ , see Table S1), indicating a strong correspondence between the complete and imputed functional spaces; consequently, we used the PCA based on imputed trait data in the rest of the analyses.

Our final set of species contained 7,685 species functionally, phylogenetically, and spatially informed in 267 regions after homogenization of the country and states names. Among the 971 non-native species identified worldwide, phylogenetic, functional, and spatial information was available for 798 species (82%). Among the 1,376 species listed as threatened by IUCN, phylogenetic, functional, and spatial information was available for 897 species (65%). The proportion of species functionally and phylogenetically described varied between 63% and 100% of the country species composition (mean = 85%, 1<sup>st</sup> quartile = 83%, 3<sup>rd</sup> quartile = 88%). 267 regions (99.6%) have received at least one non-native species and 203 regions (75.5%) host at least one threatened species (Fig. S1). The proportion of introduced and threatened species that were both functionally and phylogenetically informed in the 267 regions was on average 92%, and 79%, respectively, compared to the original databases after species and region names correction (Fig. S1).

We evaluated the potential uncertainties of the results of the changes in taxonomic, functional, and phylogenetic richness by comparing the changes in taxonomic richness using the subset of species functionally, phylogenetically, and spatially informed (i.e., 7,685 species) and all spatially informed species (i.e., 9,952 species). This way, we identified the regions the most potentially affected by the lack of evaluated species. For those regions, the results should be taken with caution.

**Biodiversity indices.** Taxonomic diversity was calculated as the number of species in each region (i.e., taxonomic richness, TRic). Functional diversity was measured as the amount of functional space occupied by the species present in each country (i.e., functional richness,



FRic). Phylogenetic diversity was calculated as the sum of the branch length of species occurring in each country (i.e., phylogenetic richness, PRic).

**Comparison between non-native and threatened species.** To test the compensation/shift hypothesis between non-native and threatened species in each region (see the theoretical framework in Fig. 2A), we calculated the taxonomic, functional, and phylogenetic dissimilarity between all non-native and all threatened species in each region for which at least one species has been introduced and at least one is threatened (N=257). The dissimilarity was measured using the Jaccard dissimilarity index (Jaccard 1901) for taxonomic and phylogenetic diversities using ‘betapart’ package (Baselga & Orme 2012). For functional diversity, due to the trait probabilistic approach, we calculated the overlap-based dissimilarity (Carmona *et al.* 2019) using ‘TPD’ package (Carmona *et al.* 2019).

To test whether the functional and phylogenetic dissimilarity between all non-native and all threatened species was different than expected by chance, we performed null models where we randomized the identity of non-native and threatened species in each region within the pool of non-native and threatened species of each region, respectively. We drew 99 simulated assemblages and compared the functional and phylogenetic dissimilarity of those 99 assemblages to the observed functional and phylogenetic dissimilarity. We calculated standardized effect sizes (SES) as the difference between the observed values and the mean of the simulated ones standardized by the standard deviation of the simulated values and their associated P-values.

**Scenarios.** We built three different scenarios depicting unique (scenarios 1 and 2) and coupled effects (scenario 3) of introduced/threatened species (see Fig. 1). Scenario 1: we considered changes between assemblages with only native species and assemblages after introduction events (i.e., native + non-native species). Scenario 2: we considered changes between assemblages after introduction events (i.e., native + non-native species) and assemblages after the introduction and extinctions events (i.e., native + non-native – threatened species). Scenario 3: we considered changes between assemblages with only native species and assemblages after the introduction and extinction events (i.e., native + non-native – threatened species). For each scenario, we measured the changes in biodiversity indices (i.e., TRic, FRic, PRic) and changes in dissimilarity between all pairs of assemblages (i.e., regions) as the differences between two situations and expressed changes as a percentage of the initial situation.

For each region, we compared the changes in the three biodiversity indices for the three scenarios with a null model where the same number of species were randomly introduced from the world's pool of species (scenario 1). This null model allows us to test whether the changes in FRic and PRic observed after introductions are higher (i.e., non-native species have unique functional traits and/or evolutionary history compared to the regional pool of species) or lower (i.e., non-native species have redundant functional traits) than expected. For scenario 2, we test whether the changes in FRic and PRic observed after the extinction of threatened species are higher (i.e., threatened species have unique functional traits and/or evolutionary history compared to the regional pool of species) or lower (i.e., threatened species have redundant functional traits) than expected. For scenario 3, the null model allows us to test whether the combined effect of non-native and threatened species contributes to higher or lower changes in FRic and PRic than expected if non-native and threatened species have random functional traits and evolutionary history.

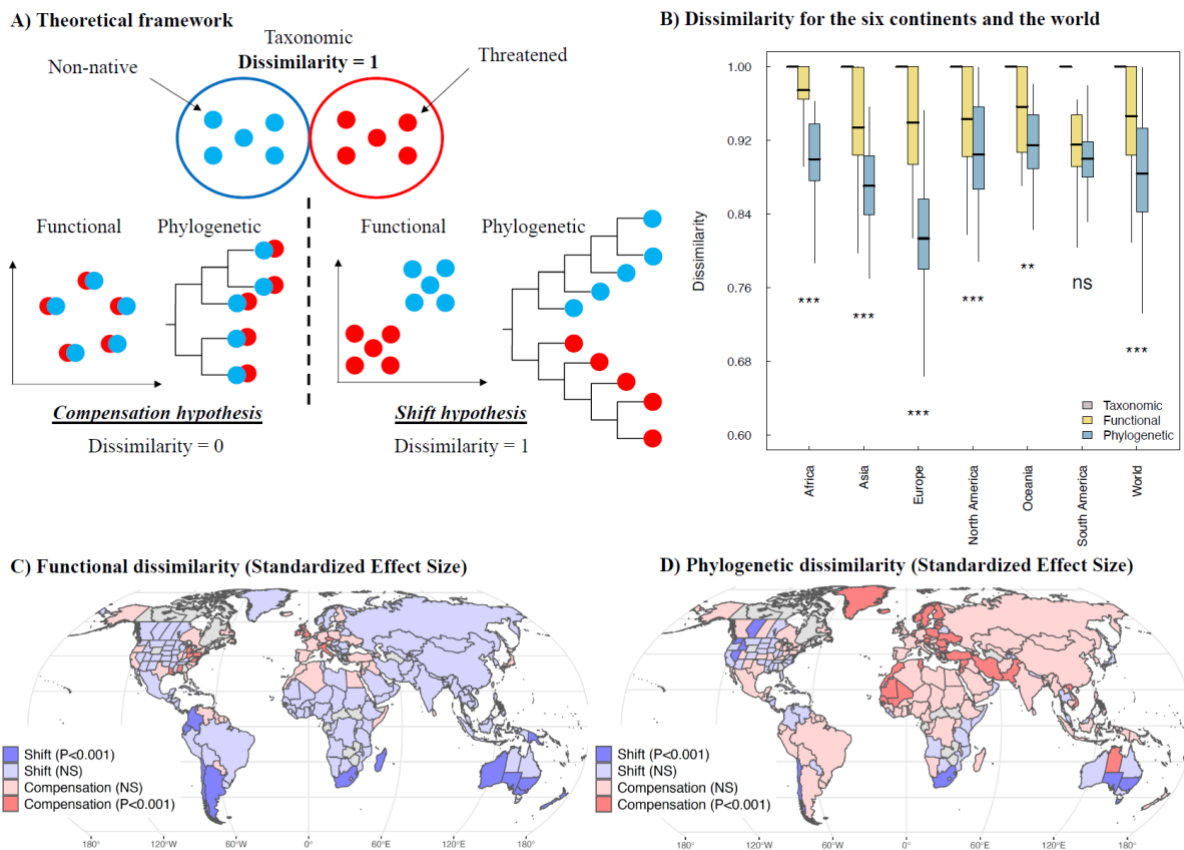
For each country, we drew 999 simulated assemblages and compared the functional and phylogenetic richness of those 999 assemblages to the observed FRic and PRic. We calculated standardized effect sizes (SES) and their associated P-values.

## **Results.**

To test whether non-native and threatened species are more functionally and/or phylogenetically similar than expected, we investigated the taxonomic, functional, and phylogenetic dissimilarity between threatened and non-native species for the regions that experienced both introduction and extinction events (N=257). Taxonomic dissimilarity can be only maximal since threatened and non-native species are completely distinct sets of species in each region (Fig. 2A). Functional, and phylogenetic dissimilarity can vary between 0 if non-native and threatened species are functionally and/or phylogenetically identical (i.e., compensation hypothesis, Fig. 2A) and 1 if non-native and threatened species are functionally and/or phylogenetically completely distinct (i.e., shift hypothesis, Fig. 2A). We found that functional dissimilarity varied between 0.73 and 1 and phylogenetic dissimilarity between 0.57 and 0.99. Functional dissimilarity was significantly higher than phylogenetic dissimilarity in all continents except South America (Student tests,  $P < 0.001$ , Fig. 2B).

Comparing observed dissimilarity to null models, where the identity of non-native and threatened species was randomized (see Methods), non-native and threatened species were more functionally distinct than expected for 183 regions (71%, Fig. 2C), supporting the shift hypothesis. For phylogenetic dissimilarity, non-native and threatened species were more

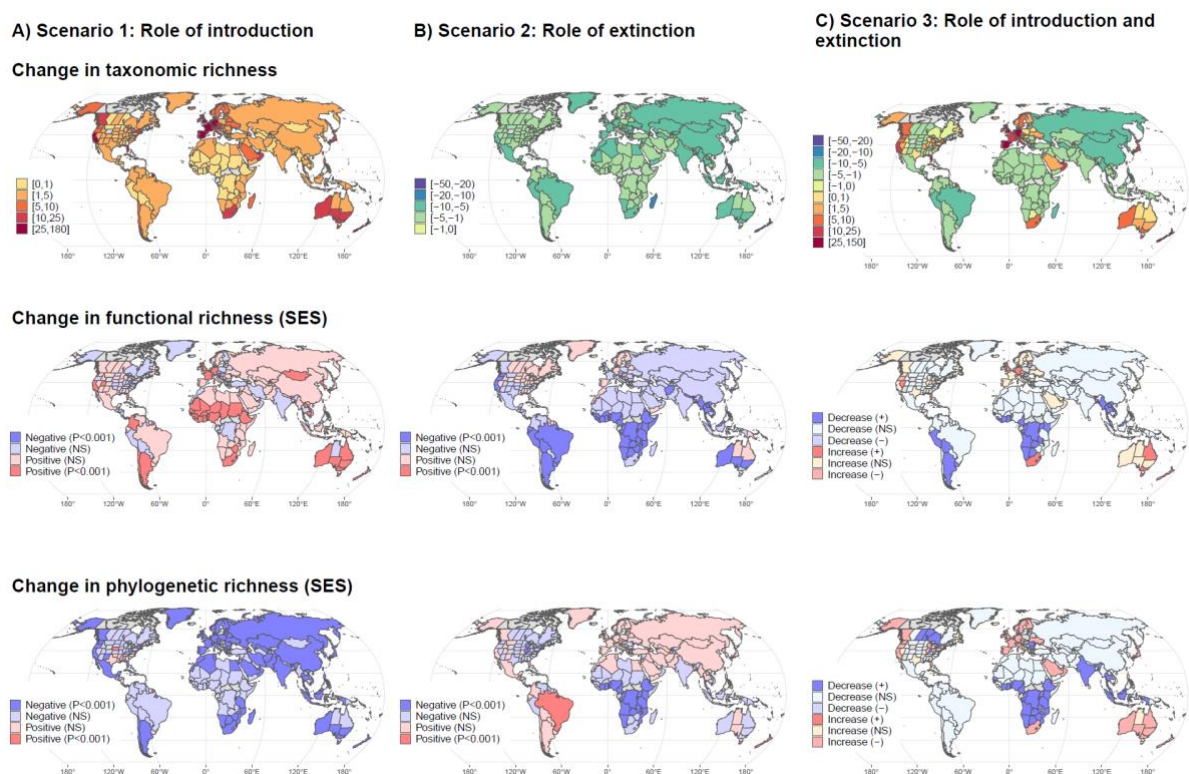
similar in 157 regions (61%, Fig. 2D), supporting the compensation hypothesis. Such pattern is globally congruent, except in some areas such as Western Europe, where non-native and threatened species are functionally more similar than expected, supporting the compensation hypothesis; or in Australia, South Africa, and some States in the USA, where non-native and threatened species are phylogenetically more distinct than expected, supporting the shift hypothesis.



**Figure 2. Taxonomic, functional, and phylogenetic dissimilarity between non-native and threatened species for each region in the six continents.** A) Theoretical framework illustrating the compensation and shift hypotheses between the non-native and threatened species. The two examples are extreme cases. B) For each region experiencing at least one introduction and hosting at least one threatened species ( $N=257$ ), we calculated the taxonomic, functional, and phylogenetic dissimilarity between non-native and threatened species. Box represents the 1<sup>st</sup> and 3<sup>rd</sup> quantiles; lines the 95% confidence interval; the horizontal lines the median. We compared the two distributions (functional dissimilarity, in yellow and phylogenetic dissimilarity, in blue) using Student tests ( $P < 0.001$ : \*\*\*,  $P < 0.01$ : \*\*,  $P > 0.05$ : ns). C and D represent the functional and phylogenetic dissimilarity, respectively, between non-native and threatened species for each region. Results are expressed in terms of Standardized effect size, where the dissimilarity was compared to a random pool of non-native and threatened species (see Methods). Blue tones mean that dissimilarity between non-native and threatened species was higher-than-expected supporting the shift hypothesis. Red tones mean that dissimilarity

between non-native and threatened species was lower-than-expected supporting the compensation hypothesis.

To quantify the consequences of non-native introductions and threatened species potential losses on the functional and phylogenetic richness in the 267 regions, we designed three scenarios, depicting unique (scenarios 1 and 2) and coupled effects (scenario 3) of introduced/threatened species (Fig. 1). We interpreted the Standardized Effect Sizes of null models to quantify the changes in functional and phylogenetic richness independently of the number of species introduced and/or threatened in each assemblage (see Methods).



**Figure 3. Changes in taxonomic, functional, and phylogenetic richness in 267 regions across the world following the three scenarios.** For each region, the changes were measured as the difference between the two periods according to the scenario (see details in Fig. 1 and Method). The changes are expressed as a percentage of taxonomic richness. For functional and phylogenetic richness, changes are shown in terms of Standardized Effect Size (SES), meaning that observed changes were compared to expected changes where the introduced species were randomized among a world pool of species. Negative values (blue tones) mean that the observed changes are lower-than-expected by chance whereas positive values (red tones) are higher-than-expected by chance. The results of the indices are available in Supplementary Fig. S2.

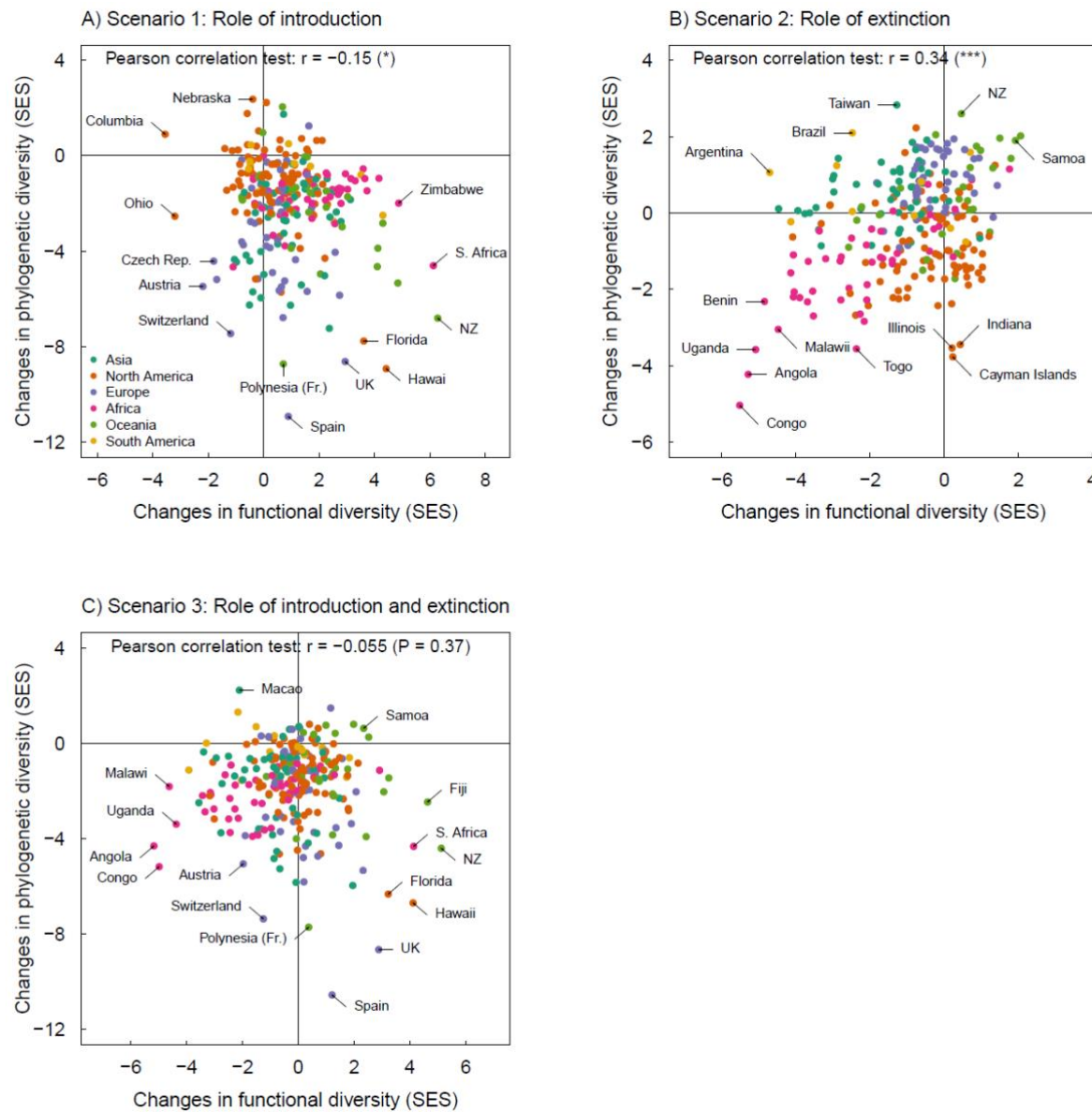
The introduction of non-native species caused a significantly higher-than-expected increase in functional richness in 20% of the regions (51 regions) and a lower-than-expected increase in phylogenetic richness in 39% of the regions (106 regions, Fig. 3A, Table S3A, Table S4A).

This result demonstrates that non-native species are more functionally distant from native species than expected (i.e., FRic SES > 0) but more phylogenetically related than expected (i.e., PRic SES < 0), as supported by a negative correlation between FRic SES and PRic SES (Pearson correlation test,  $r = -0.15$ ,  $P = 0.01$ , Fig 4A). Moreover, the 106 regions experiencing a lower-than-expected increase in phylogenetic richness were not randomly distributed between continents ( $\chi^2 = 20.5$ , d.f. = 5,  $P < 0.001$ ) but mainly distributed in Europe (30 regions), and Asia (27 regions). Similarly, the 51 regions experiencing a higher-than-expected increase in functional richness were also not randomly distributed ( $\chi^2 = 32.5$ , d.f. = 5,  $P < 0.001$ ), but they were mainly in Africa (21 regions) and Oceania (10 regions).

The potential loss of all threatened species revealed that extinction effects were not significantly different from expected in 78% of the regions (209 regions) for functional richness (Fig. 3b, Table S3B, Table S4B) and in 86% of the regions (230 regions) for phylogenetic richness. The loss of functional richness was higher-than-expected mostly in Africa (26 regions), Asia (13 regions), and South America (6 regions,  $\chi^2 = 54.1$ , d.f. = 5,  $P < 0.001$ , Table S4B). For phylogenetic richness, the loss in phylogenetic richness was higher-than-expected in Africa (N=17) and North America (N=13). Thus, the loss of threatened species has a low but similar impact on both functional and phylogenetic richness ( $r = 0.34$ ,  $P < 0.001$ , Fig. 4B).

Combining the effect of both introduction of non-native and extinction of threatened species (scenario 3) showed that, since the number of introductions exceeds the number of extinctions, dominant trends of diversity indices generally increase (Fig. 3C, Table S3C, Table S4C). At the global scale, we reported an average increase of 3.15% in taxonomic richness, and 3.63% and 2.89% in functional and phylogenetic richness, respectively. However, among the regions experiencing a net loss of species richness, functional and phylogenetic richness are decreasing more-than-expected in 18% of the regions, mainly in Africa and Asia (Fig. 3C), while decreasing less-than-expected in only 3 and 1 regions, respectively. In contrast, among the regions experiencing a net gain in species richness, functional richness is increasing more-than-expected in 14% of the regions, while none of the regions experienced a higher-increase-than expected in phylogenetic richness. Thus, combining the effect of both introduction of non-native and extinction of threatened species discards the correlation between SES FRic and SES PRic ( $r = -0.06$ ,  $P = 0.48$ , Fig. 4C). For example, regions such as Florida, England, Germany, New Zealand, or South Africa could experience higher-than-expected increases in functional richness but lower than expected in phylogenetic richness (Fig. 3C).





**Figure 4. Changes in functional and phylogenetic richness in 267 regions across the world following the three scenarios.** For each scenario (see details in Fig. 1 and Method), the changes in functional and phylogenetic richness are expressed in terms of Standardized Effect Size (SES), meaning that observed changes were compared to expected changes where the introduced species were randomized among a world pool of species. Colors represent the regions grouped by continents. We calculated the correlation between the SES of changes in functional and phylogenetic richness using Pearson's correlation tests ( $P < 0.001$ : \*\*\*,  $P < 0.01$ : \*\*,  $P < 0.05$ : \*). Some regions with the highest changes are identified. Czech Rep.: Czech Republic; NZ: New Zealand; Polynesia (Fr.): French Polynesia; UK: United Kingdom; S. Africa: South Africa.

**Discussion.** In this study, we seek to understand whether the replacement of non-native species can offset the potential loss of threatened species in terms of functional and phylogenetic diversity for bird assemblages across the world. We demonstrated that globally bird non-native species are more functionally distinct from threatened species than expected (supporting the shift hypothesis) but more phylogenetically clustered than expected (supporting the compensation hypothesis). These changes in species composition increase the functional richness of the bird assemblages due to the introduction of non-native species with distinct functional traits. They might also trigger a global loss in phylogenetic richness due to the potential extinction of phylogenetically unique species coupled with the introduction of species closely related to native fauna. Our results highlight the need to control the introduction and spread of non-native species and to protect phylogenetically unique species, which are the primary drivers of changes in the functional and phylogenetic structure of bird communities.

Ecological consequences of the replacement of threatened species by non-native species are still controversial (Wardle *et al.* 2011). Previous studies that investigated this question showed that introduced species do not compensate for the loss of extinct species but instead increase the functional and phylogenetic diversity of island bird assemblages (Sobral *et al.* 2016). Yet, other studies showed that non-native species are functionally redundant while losing functionally unique species contributing to a global loss of functional diversity (Sobral *et al.* 2016; Sayol *et al.* 2021). In fact, both studies support evidence for the shift hypothesis following the two alternatives depicted in Fig. 1. At the global scale, we also find evidence for the shift hypothesis. For functional diversity, our result supports alternative 1, indicating that non-native species have unique trait syndromes. The introduction of such species can alter ecosystem functioning since they can support unique ecological functions (Mouillot *et al.* 2013; Violle *et al.* 2017). For phylogenetic diversity, our result supports alternative 2, indicating that threatened species support unique parts of the phylogenetic diversity but are replaced by species more closely related to native fauna. The loss of unique clades can weaken the capacity for evolution and adaptation of an assemblage, in response to different kinds of environmental disturbances. This demonstrated that functional richness does not always reflect phylogenetic richness and that it is important to assess both facets of biodiversity when evaluating the ecological roles and evolutionary histories of species (Losos 2008; Gerhold *et al.* 2015).

We find disparities between continents. In Europe and North America, introductions have led to a gain of functionally distinct species that are nevertheless phylogenetically related to native fauna, while Africa and South America may experience a large loss of functional

richness due to the loss of threatened species, supporting both variants of the shift hypothesis (Fig. 1). However, increases in phylogenetic richness were mostly lower-than-expected while decreases were higher-than-expected. For example, in regions that have suffered from high introduction pressure (e.g., Spain), the decrease in phylogenetic richness results from an effect of the loss of phylogenetically unique species (e.g., great bustard, *Otis tarda*) coupled with the introduction of non-native species closely related to the native species of the recipient communities (e.g., pied crow, *Corvus albus* or house sparrow, *Passer domesticus*). The increases in functional richness should not be misinterpreted as introductions compensated for extinctions but introduced new trait syndromes reflecting the shift hypothesis (Fig. 1). Our results are in agreement with other studies on the consequences of non-native species on functional diversity (e.g., Toussaint et al. 2018, Su et al. 2019), highlighting that introductions of species with distinct functional traits might disrupt the trophic network and ecosystem functioning.

With a high number of non-native and threatened species, Oceania appears to be the most affected biogeographic zone and strongly supports the shift hypothesis, due to long-term isolation and the presence of endemic species with unique functional traits (Toussaint *et al.* 2021). For instance, New Zealand, which suffers from a high level of non-native (N=119, 43%) and threatened species (N=57, 21%), would experience strong shifts in functional space by losing large-bodies and slow-living species such as the Hutton's shearwater (*Puffinus huttoni*) or the yellow-eyed penguin (*Megadyptes antipodes*). Meanwhile, receiving small-bodied, high-reproductive species such as the common quail (*Coturnix coturnix*), or the grey partridge (*Perdix perdix*) helping to fill empty areas in the functional space (Fig. S3).

The large increases in functional richness reported in Europe and North America underscore the diversity of non-native species originating worldwide and characterized by a wide range of traits. This results in an expansion in all directions of functional space contributing to the introduction of new trait syndromes but also an increase in functional redundancy within the most densely occupied areas of functional space (>20 species, Fig. S3). The potential loss of threatened species would contribute to functional space erosion by increasing the proportion of functional space occupied by few species (e.g., < 5 species, Fig. S3). These results show that, although the effects of extinction on functional richness are still mitigated by functional redundancy of native and non-threatened species, the current biodiversity crisis and future species extinctions could trigger deeper and irreversible erosion of functional space, including the loss of specific ecological functions.



In contrast, regions less affected by non-native species (e.g., Africa, Asia, and South America) are expected to lose more functional and phylogenetic richness than expected due to species extinctions. This result implies that threatened species in these regions contribute disproportionately to functional richness by having relatively unique traits. This situation is illustrated by the introduction of non-natives that tend to be functionally redundant with native species, supporting the findings on bird island assemblages (Sayol *et al.* 2021). From a phylogenetic point of view, here we generalized a pattern observed for island bird assemblages (Sobral *et al.* 2016), where most non-native species belonged to few clades, while threatened species belonged to a diverse set of clades so that the loss of few species often leads to a loss of unique parts of the phylogenetic tree.

The coupled effect of the extinction of threatened species and the introduction of non-native species could lead to a general trend toward homogenization of the bird assemblages. We found that functional homogenization exceeds the taxonomic and phylogenetic homogenization, which is congruent with freshwater fishes in Europe (Villéger *et al.* 2014) or ants (Martello *et al.* 2018). The process of biotic homogenization is amplified by the combined effect of the loss of species with unique and distinct functional traits and phylogenetic clades between assemblages and the introduction of similar species. These results indicate that bird communities are amidst a global process of homogenization of their functional structure, which is likely to be accelerated if the introduction and extinction processes are not controlled (Devictor *et al.* 2007; Clavel *et al.* 2011; Toussaint *et al.* 2014).

Improvements in data availability will be needed to fully integrate functional and phylogenetic assessments into conservation policies. Based on an estimate of changes in taxonomic richness if all spatially described species were considered (Fig. S4), our results may underestimate the intensity of taxonomic changes, particularly in South America and Southeast Asia. In these regions, the overall decline in taxonomic richness after introduction and extinction may be higher than reported primarily due to the lack of species assessed by the IUCN Red List (Fig. S4c). These rare species are likely to have unique functional traits and belong to unique clades and highlighting the need for additional functional and phylogenetic information.

By altering species composition, the human footprint has become a major process structuring the pattern of bird biodiversity worldwide (Ellis 2015). The increasing global trade could promote an increase of non-native species across the world and mainly in countries still sparsely affected such as Africa, South America, and Asia (Dawson *et al.* 2017; Seebens *et al.*

2018). The shifts in functional and phylogenetic structure of the bird communities reported here might increase the vulnerability of ecosystems face to future changes, demonstrating the urgent need for comprehensive and ambitious policies to regulate the introduction and the conservation of threatened species across the world.

**Data availability Statement:** All data sets, as well as R codes involved in data processing, statistical analysis, and plotting of the results (including a source data file), are available in Figshare (<https://figshare.com/s/5bfe5a710cd3ea60ef2b>)

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**Conflict of interest statement.** The authors declare no competing interests.

**Supplementary Information** is available for this paper.

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