

Contrasting impacts of non-native and threatened species on morphological, life history, and phylogenetic diversity in bird assemblages

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Abstract

Human activities have altered the species composition of assemblages through introductions and extinctions, but it remains unclear how those changes can affect the different facets of biodiversity. Here we assessed the impact of changes in species composition on taxonomic, functional, and phylogenetic diversity across 281 bird assemblages worldwide. To provide a more nuanced understanding of functional diversity, we distinguished morphological from life-history traits. We showed that shifts in species composition could trigger a global decline in avian biodiversity due to the high number of potential extinctions. Moreover, these extinctions were not random but unique in terms of function and phylogeny at the regional level. Our findings demonstrated that non-native species cannot compensate for these losses, as they are both morphologically and phylogenetically close to the native fauna. In the context of the ongoing biodiversity crisis, such alterations in the functional and phylogenetic structure of bird assemblages could heighten ecosystem vulnerability.

KEY WORDS

birds, extinction, functional, introduction, macro-ecology, phylogenetic

INTRODUCTION

Through the introduction of non-native species and the extinction of threatened species, human activities contribute to a deep reorganization of species assemblages for most of the taxonomic groups and triggered the sixth biodiversity crisis (Capinha et al., 2015; Simberloff & Vitule, 2014). While most of the studies focused on the effect of either non-native (e.g., freshwater fishes: Gozlan et al., 2010; birds: Martin-Albarracín et al., 2015) or threatened species (e.g., on vertebrates and plants: Carmona et al., 2021; Jenkins et al., 2013; Pimm & Raven, 2000; Toussaint et al., 2021), few studies have explored their combined effects (but see Daru et al., 2021) on plants. These combined effects are key 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, predicting the changes in functional and phylogenetic diversity depends on functional traits and evolutionary history of species (e.g., birds: Sol et al., 2017; freshwater fishes: Su et al., 2019). Using a recent compilation of non-native species and threatened species of birds across the world, we evaluated 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 281 regions worldwide.

On birds, previous evidence showed that non-native species often support unique traits due to human selection for specific uses like trade or pest control (Sayol et al., 2021; Sobral et al., 2016). In contrast, bird species with traits like large size and slow reproduction are more likely to be threatened (Carmona et al., 2021; Toussaint et al., 2021). Moreover, some bird clades are more prone to introduction (e.g., Anseriformes for hunting; Carpio et al., 2017) while others (e.g., Rallidae) have higher proportions of threatened species (Weeks

et al., 2022). Thus, the future composition of bird assemblages will result from the coupled effect of both native and non-native species. The net effect on biodiversity and ecosystem function depends on the functional and phylogenetic similarities between non-native and threatened species.

The ecological consequences of the replacement of threatened species by non-native species are controversial for different taxonomic groups (Wardle et al., 2011). Some studies on island bird assemblages occupy different positions than native species in the functional space and in the phylogeny (Sobral et al., 2016). By contrast, other studies have shown that non-native bird species are functionally redundant, so biotic invasions have not offset the extinction of functionally unique species on oceanic archipelagos (Sayol et al., 2021). However, those studies mainly investigated the effects of species that have already been extinct and considered only island assemblages. While island ecosystems have already experienced a significant loss of endemic bird species (approximately 8%), the extinction rate for non-island species remains relatively low (estimated at 0.002%, Matthews et al., 2022), indicating that substantial changes are likely to occur in the future. Thus, understanding how global species losses will impact ecological function remains a major challenge (Ali et al., 2023).

Here, we investigated how changes in species composition through the introduction of non-native species and the potential extinction of threatened species impact the functional and phylogenetic structure of bird assemblages across the world. To comprehensively assess functional diversity, we used two distinct sets of traits: morphological diversity from the AVONET database (Tobias et al., 2022) and life-history diversity from the AMNIOTE database (Myhrvold et al., 2015). By dissecting functional diversity in this manner, our study aimed to provide a more nuanced understanding of how different facets of biodiversity are affected by the introduction of non-native species and the loss of threatened species. This approach allowed us to identify specific ecological functions that may be disproportionately impacted, thereby offering more targeted recommendations for conservation strategies.

METHODS

Spatial resolution

Spatial entities were identified at the Biodiversity Information Standards (TDWG) level 3 according to the Global Administrative Areas (GADM) database (www.gadm.org, downloaded March 2021), resulting in 369 spatial entities worldwide. For each spatial entity, we retrieved the continental divisions also provided within the GADM database to assign the appropriate continent to each spatial entity. To mitigate the potential effects

of small islands, those with an area below 70 square kilometres, as well as islands in the “seven seas” and Antarctica, were excluded. This refinement yielded a subset of 281 entities for subsequent analyses, hereafter named as regions.

Functional traits

Functional diversity is a multi-faceted concept that encompasses a range of traits affecting species' roles in ecosystems. Traditionally, studies have aggregated traits into a single measure of functional diversity. We adopted a different approach by dissecting functional diversity into two morphological diversity and life-history diversity.

We collected 11 morphological traits from the AVONET database for 9981 species (Tobias et al., 2022) relative to beak length (Culmen and Nares), width, and depth, tarsus length, wing length, Kipps distance, hand-wing index, tail length, secondary, and body mass (Table S1). These traits influence various ecological functions like seed dispersal, predation, and resource utilization (McGill et al., 2006).

Eight life-history traits were retrieved from the AMNIOTE database for 8940 species (Myhrvold et al., 2015): clutch size, number of clutches per year, incubation time, longevity, fledging age, egg mass, and distance from the tip of the beak to the opening of the cloaca and body mass (Table S1).

Since life-history traits were not informed for all species, we imputed the missing trait values using a machine learning approach (“*missForest*,” Stekhoven & Bühlmann, 2012) combining observed life-history traits and phylogenetic information as explained in Carmona et al. (2021). This way, we included the evolutionary relationships between species in the imputation process by considering the first ten phylogenetic eigenvectors, as recommended by Penone et al. (2014). 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 (Stewart et al., 2023). We used the imputed traits to project species onto the life-history space, utilizing the complete dataset.

We assessed the accuracy of our imputation method using the Normalized Root Mean Square Error (NRMSE), which quantifies the average deviation between the “real” and imputed trait values as a fraction of the trait value range. To conduct this assessment, we intentionally removed 10% of trait values from a subset of species with complete data. We then randomly selected a species with incomplete data and applied the same pattern of missing values to it, thereby maintaining the original dataset's missing value pattern. We ran the imputation process using the full dataset, which included both species with incomplete trait data and those with

complete data (i.e., 90% of species with complete data and an additional 10% with artificially induced missing values). This approach resulted in a higher ratio of missing to complete data in the simulations compared to the original dataset, providing a conservative evaluation of our imputation quality. We repeated this procedure 100 times and found that the standard error of the NRMSE was consistently below 1%, indicating the robustness of our method (see Table S2).

After standardization of the species taxonomy and nomenclature according to BirdTree (Jetz et al., 2012) for AMNIOTE species, 8502 species were common between AVONET and AMNIOTE. To assess the impact of utilizing a subset of species (i.e., 8502 species), we performed supplementary analyses revealing strong correlations with the two sets of data (Spearman's rank correlation tests: $r>0.94$, $p<0.001$, Figure S1).

Phylogenetic information

We used a comprehensive phylogeny including 9993 bird species (Jetz et al., 2012). We extracted data from 100 individual phylogenetic trees available in the R package “*rtree*” (Li, 2023) and integrated it into a single consensus tree using the “consensus” function from the R package “*ape*” (Paradis et al., 2004). This approach allowed us to account for phylogenetic uncertainty by summarizing the topological and branch-length variations across the multiple trees. All species for which we have trait information (i.e., 9981 species) were included in the phylogeny.

Species occurrences

Species occurrences of the 9981 species were retrieved for each region from the comprehensive “Birds of The World” spatial database (Billerman et al., 2022). We considered only the species with presence categories 1 (resident), 2 (seasonal), and 3 (vagrant, or occasional) and origin of 1 (native from the region).

Conservation status

The conservation status was obtained from the IUCN Red List (version 2020-3; IUCN, 2020) using the R package “*rredlist*” (Chamberlain, 2018). We retrieved information for 9432 species with IUCN status: CR: critically endangered; EN: Endangered; VU: Vulnerable; NT: Near Threatened; LC: Least Concern; DD: Data Deficient. Since we considered current and future changes in species composition, we do not consider extinct species.

We used the regional IUCN Red List when available (167 regions, 60%); otherwise, we used the global

status. Regional assessments provide a finer resolution, accounting for localized threats, population dynamics, and ecological conditions that may vary across different regions. This approach allows for a more precise evaluation of the conservation status of species, considering region-specific factors that might not be adequately reflected in the global assessment.

Non-native species

We used the GAVIA database, the most comprehensive and updated source of non-native species for birds, to compile a list of non-native species for each region. This database included 27,723 distribution records for 970 bird species with evidence of translocation outside their native range. Only records of the first introductions between 1500 and 2000 AD were considered as recommended by Dyer et al. (2017). Records indicating no established population in the region (“Extirpated” and “DiedOut”) were excluded (Dyer et al., 2017). While introductions of new non-native species are predicted for the future (Seebens et al., 2021), we considered only established non-native species since it is still difficult to identify exactly which species could invade and where they will be introduced see Paganelli et al. (2022).

The GAVIA database, originally compiled at the country level 1, posed a spatial challenge as our analysis required data at a finer resolution. To bridge this gap, we implemented a structured framework. For the 255 regions where the spatial resolution remained consistent between country level 1 and country level 3, we used the species list of the GAVIA database. United States of America, Canada, and Australia were available at the states or provinces' spatial resolution in the GAVIA database in agreement with the spatial resolution of country level 3. For 18 regions, where country level 3 encompassed multiple regions at level 1, we combined the species list of these individual regions at level 1 to create a comprehensive list at level 3. For the nine regions where the borders are smaller in level 3 than level 1 (e.g., Argentina, Brazil, Chile, China, France, Russia, Mexico, Italy, and South Africa), we first used the species list of GAVIA at the level 1 and then used the species' ranged maps also provided by GAVIA. Since this information was available only for 362 species (Dyer et al., 2017), we completed the database by using GBIF to retrieve the occurrences of the other non-native species listed in GAVIA at a smaller spatial scale. Given the potential for misidentifications in GBIF records, we adopted a conservative approach, restricting our selection to records labelled as “HUMAN OBSERVATION” with accurate geographic coordinates to mitigate potential errors. At the global scale, 802 species were identified as non-native in at least one of the 281 regions. Among them, 789 (98%) were morphologically and phylogenetically informed.

Functional space

The construction of the morphological and life-history spaces 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 traits. The spaces were 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). For the life-history space, the first two axes explained 66.3% and 13.8%, respectively, of the total variation of the life-history traits (Table S1). For the morphological space, the first two axes explained 68.4% and 14.7%, respectively of the total variation of the morphological traits (Table S1).

We estimated the probabilistic distribution of the species within the spaces 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 centred 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.

Additional analyses indicate a positive correlation between the functional spaces constructed from both databases (PERMANOVA: $r=0.78$, $p<0.001$), suggesting that the relative position of species within each functional space is consistent. However, when we delved deeper into the correlation of each principal component (PC) axis, we observed divergent patterns. For PC1, which is influenced by body size in both functional spaces, we found a high correlation (Spearman rank correlation test: $r>0.9$, $p<0.001$). In contrast, the correlation for principal component axis 2 was not significant ($r=-0.01$, $p=0.47$). This was explained by the fact that in the life-history space, PC2 is related to reproductive strategies, while in the morphological space, PC2 is related to the shape of the bird (Table S1). This lack of correlation underscores the importance of treating the trait separately to capture the full spectrum of functional diversity impacts.

Data standardization

Taxonomies from all sources were standardized according to BirdTree, the most recent global bird phylogeny (Jetz et al., 2012). The final dataset encompassed 8143 species (82%). The proportion of species described in the subset of species (including non-native species) in each region varied between 81% and 100% of the number of species in the complete set of data (mean=93.5%, 1st quartile=92.1%, 3rd quartile=95.5%, Figure S2). The proportion of non-native species varied from 67% and 100% (mean=96.3%, 1st quartile=94.4%, 3rd

quartile=100%) and the proportion of threatened species varied from 67% and 100% (mean=94.2%, 1st quartile=90.9%, 3rd quartile=100%).

We evaluated the potential uncertainties of the results by comparing the changes in taxonomic richness using the subset of species (i.e., 8143 species) and all species (i.e., 9881 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 (Figure S3).

Scenario of species composition changes

We considered changes between assemblages with only native species and assemblages after the introduction and extinction events (i.e., native+non-native-threatened species). To reflect the varying degrees of extinction risk, we removed species classified as critically endangered (CR), representing the highest risk category, and progressively proceeded to eliminate species with lower threat statuses (i.e., endangered [EN], vulnerable [VU], and near threatened [NT]). Each step in the simulation sequentially removed species, creating a gradient of extinction risk scenarios (see Toussaint et al., 2021). For simplicity, scenarios were denoted by the least threatened category considered.

In addition, we quantified the impact of introduced non-native species and the extinction of threatened species independently considering (1) changes between assemblages with only native species and assemblages after introduction events (i.e., native+non-native species); and (2) 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).

Biodiversity indices

Taxonomic diversity was calculated as the number of species in each region (i.e., taxonomic richness). Morphological and life-history diversity was measured as the amount of morphological and life-history space, respectively, occupied by the species present in each region (i.e., functional richness). Phylogenetic diversity was calculated as the sum of the branch length of species occurring in each region (i.e., phylogenetic richness). We measured the changes in biodiversity indices as the differences between the two situations and expressed changes as a percentage of the initial situation.

Taxonomic, morphological, life history, and phylogenetic dissimilarities were assessed for each region between assemblages with only native species and assemblages after the introduction and extinction events (i.e., native+non-native-threatened species). The dissimilarity was measured using the Jaccard dissimilarity

index (Jaccard, 1901) for taxonomic and phylogenetic diversities using the “*betapart*” package (Baselga & Orme, 2012). For morphological and life-history diversity, due to the trait probabilistic approach, we calculated the overlap-based dissimilarity using the “*TPD*” package (Carmona et al., 2019).

Morphological and life-history uniqueness of non-native and threatened species were calculated in the functional spaces and for each PC axis. Uniqueness was calculated for each region and standardized to the centre of the native species of each country using the R package “*funrar*” (Grenié et al., 2017). By doing this, we were able to compare the morphological and life-history uniqueness of the two functional spaces as well as for each PC axis.

Null models

For each region, we compared the changes in morphology, life history, and phylogenetic richness and dissimilarity with null models. Null models were built to assess whether the combined influence of non-native species introductions and threatened species extinctions resulted in higher or lower changes in morphology, life history, and phylogenetic richness and dissimilarity than would be expected by chance. In the null models, we maintained the number of native species as in the community and we introduced the same number of species as observed but randomly sorted from the global pool of species. Additionally, we randomized the IUCN status among the native species pool (see Carmona et al., 2021; Toussaint et al., 2021 for similar approaches). We generated 999 simulated assemblages for each region. We then compared the changes in morphology, life-history richness, and dissimilarity values of these 999 simulated assemblages with the observed changes in morphology, life history and phylogenetic richness, and dissimilarity. To quantify the degree of deviation from random expectations, we calculated standardized effect sizes (SES), providing a measure of how observed changes compared to the null model. Additionally, we determined associated P-values to assess the statistical significance of these deviations.

RESULTS

The cumulative impact of non-native species introduction and potential extinctions of threatened species led to a net decrease of 5.53% in taxonomic (i.e., a loss of 25 species per region on average), 2.06% in morphological, 1.33% in life history, and 3.53% in phylogenetic richness on average in the 281 regions across the world (Figure 1; Figure S4, Table S3). However, this trend was not uniform across regions since Europe and Oceania experienced milder declines in biodiversity,

with occasional gains in life history and morphological richness. In contrast, Africa, Asia, and South America exhibited more substantial decreases in all aspects of biodiversity. These regional disparities can be explained by a lower introduction pressure (0.9 ± 1.4 , 3.6 ± 6.8 , and 2.0 ± 2.0 species per region on average) in Africa, Asia, and South America, respectively. This stands in contrast to Europe, North America, and Oceania, where introduction pressures were higher (9.37 ± 14.9 , 4.05 ± 8.8 , and 15.25 ± 15.9 species per region on average, respectively). Even when considering other categories of threatened species, the patterns remained consistent, suggesting that the trends identified in the most severe scenario aligned across different threat levels (Figure S5).

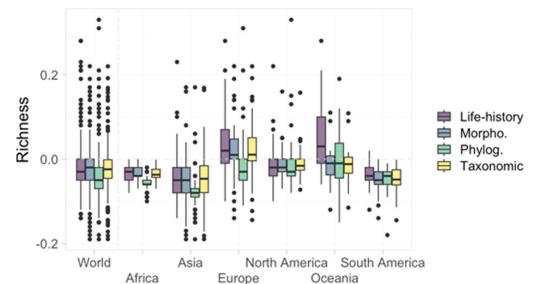
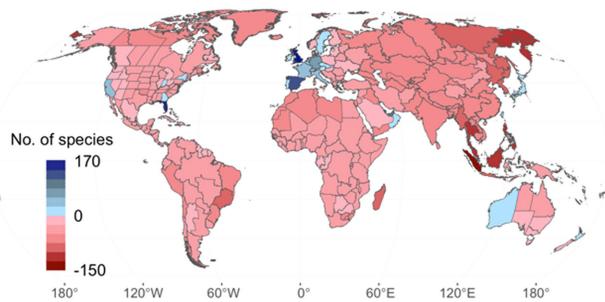
As those changes were affected by the number of non-native species and/or threatened in each assemblage, standardized effect sizes (SES) from null models were used (Figure 1). While the SES in morphological and phylogenetic richness were correlated ($r=0.65$, $p<0.001$, Figure S6), life-history traits showed a lower proportion of regions with significantly higher-than-expected losses (i.e., $\text{SES}_{\text{LH}} < 0$, $p<0.001$). Such a pattern was consistent across threat levels (Figure S5) despite differences between facets of biodiversity were even more pronounced at lower threat levels (e.g., Critically Endangered [CR] and Endangered [EN]). This indicated that the most endangered species were often more unique in morphology and phylogeny than in life-history traits.

Our analysis revealed that the higher-than-expected decrease in all facets of biodiversity was more marked in Asia, Africa, and South America (Figure 1; Figure S6) than in Europe and Oceania and, to a lesser extent, in North America. In those regions, changes in species composition resulted in higher-than-expected losses in morphological (i.e., $\text{SES}_{\text{Morpho}} < 0$, $p<0.05$) and phylogenetic richness (i.e., $\text{SES}_{\text{Phylo}} < 0$, $p<0.05$) but non-significant or even a lower-than-expected changes in life-history richness in 6 regions (i.e., $\text{SES}_{\text{LHT}} > 0$, $p<0.05$, Figure 1).

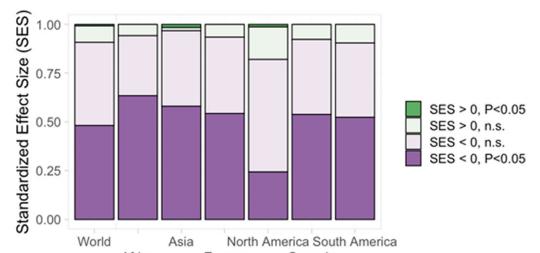
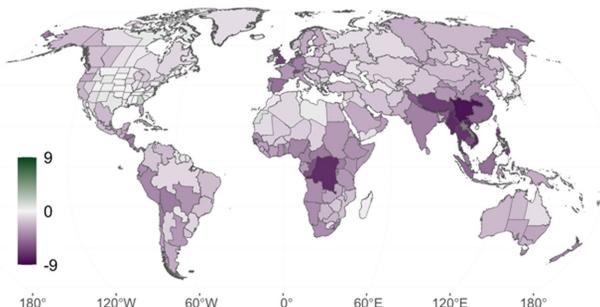
This pattern can be explained by a contrasting impact of non-native and threatened species (Figure 2). Indeed, non-native species exhibited life-history traits that diverged significantly from native fauna in 56 regions (i.e., $\text{SES}_{\text{LH}} > 0$, $p<0.05$, Figure 2b) while non-native species were more morphologically or phylogenetically closer to the native species than expected in 70 and 136 regions, respectively (i.e., $\text{SES}_{\text{Morpho}}$ and $\text{SES}_{\text{Phylo}} < 0$, $p<0.05$). Such a nuanced interplay between biodiversity facets was particularly pronounced in Oceania (78% of the regions depicted opposite patterns between $\text{SES}_{\text{Morpho}}$ and SES_{LH} , Figure 2b), underscoring the region-specific complexities in the impact of species composition changes on various facets of biodiversity.

In contrast, threatened species exhibited more consistent relationships across biodiversity facets, particularly between life history and morphological traits (Spearman rank correlation test: $r=0.64$, $p<0.001$, Figure 2c).

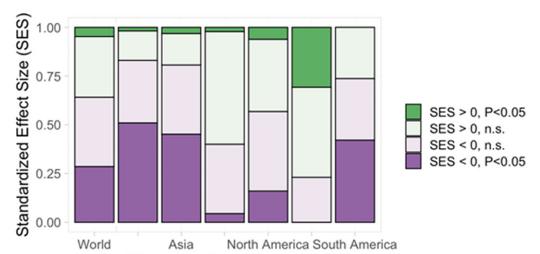
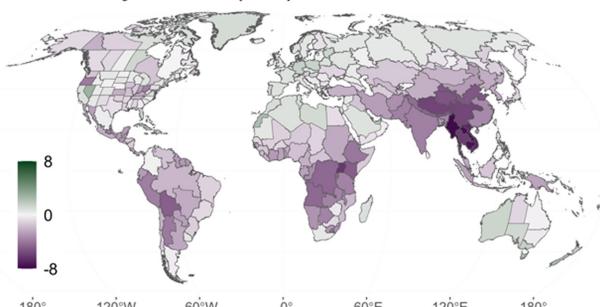
(a) Change in taxonomic richness



(b) Change in morphological richness (SES)



(c) Change in life-history richness (SES)



(d) Change in phylogenetic richness (SES)

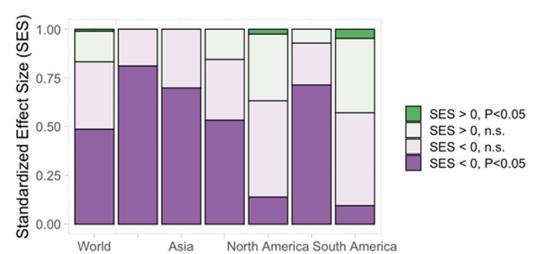
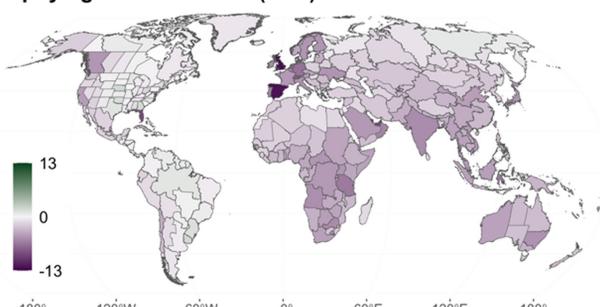
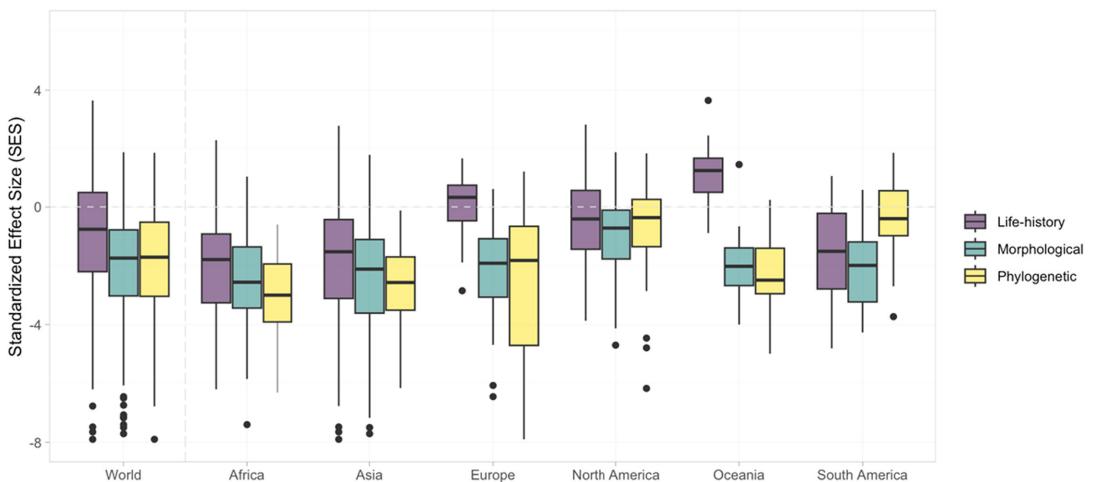


FIGURE 1 Changes in taxonomic, morphological, life history, and phylogenetic richness in 281 regions across the world. For each region, the changes were measured as the difference between native species and natives+non-natives-threatened species. Changes in richness are shown for taxonomic in map (a) and for all facets in the boxplot. Changes for morphological (b), life history (c), and phylogenetic (d) are also expressed in terms of standardized effect size (SES), meaning that observed changes were compared to 999 expected changes where the introduced species were randomized among a world pool of species. Purple tones mean that changes in morphological, life history, and phylogenetic richness were lower-than-expected. Green tones mean changes in morphological, life history, and phylogenetic richness were higher-than-expected. Threatened species are species classified as CR, EN, VU, and NT by IUCN. Maps of changes in biodiversity facets are provided in Figure S4. Scenarios with different classes of IUCN are provided in Figure S5.

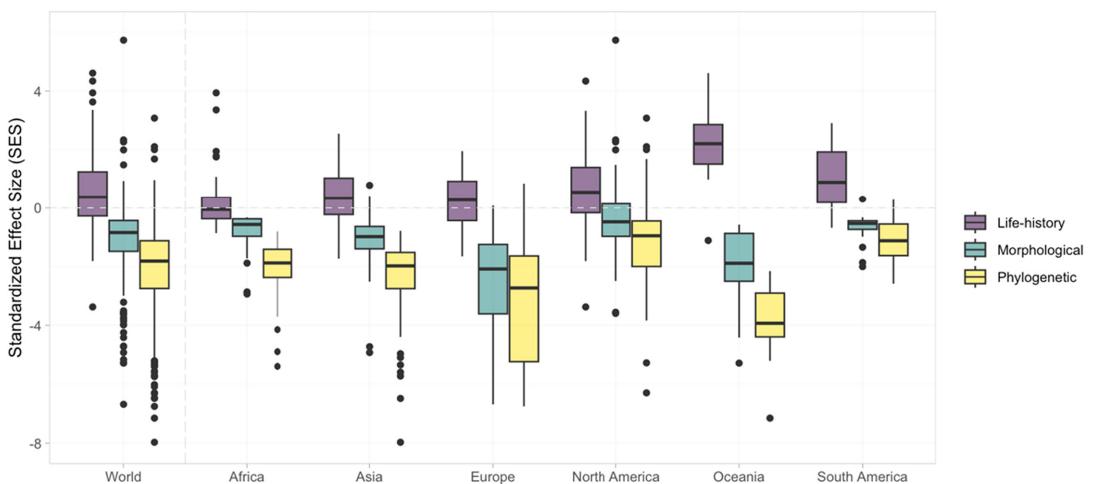
We found a dominant trend of negative Standardized Effect Sizes (SES), with 90% of regions showing negative SES in at least one biodiversity facet. In 41% of regions, the loss of threatened species correlated with a higher-than-expected decline in at least one facet, while only two regions showed the opposite trend. This

accelerated loss of biodiversity was most pronounced in Africa, Asia, and South America, underscoring the geographic variability in the impact of threatened species on biodiversity. This pattern was also evident across levels of threat (Figure S5b), especially in Africa, Asia, and South America, where even the loss of the most

(a) Combined introduction and extirpation



(b) After introduction of non-native species



(c) After extinction of threatened species

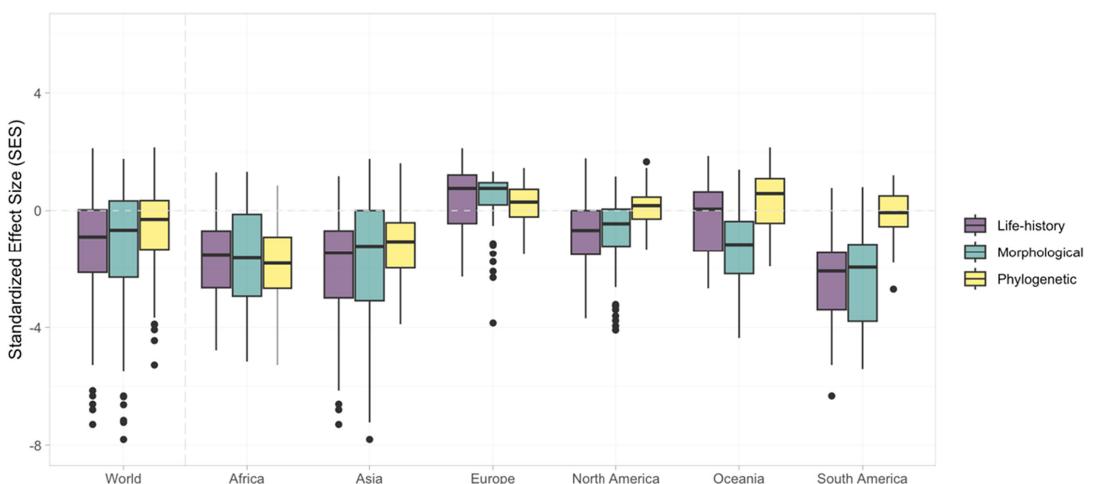


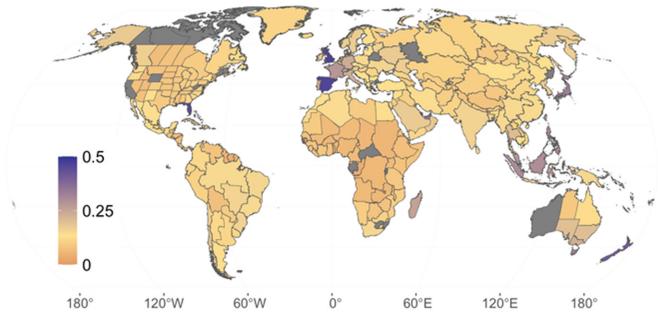
FIGURE 2 Changes in morphological, life history, and phylogenetic richness in 281 regions across the world and for the six continents. Changes are shown for three scenarios (a-c). For each scenario (see Method), the changes in morphological, life history, and phylogenetic richness are expressed in terms of standardized effect size (SES), meaning that observed changes were compared to 999 expected changes where the introduced species were randomized among a world pool of species. Threatened species are species classified as CR, EN, VU, and NT by IUCN. Scenarios with different classes of IUCN are provided in Supplementary.

critically endangered species impacted significantly avian biodiversity.

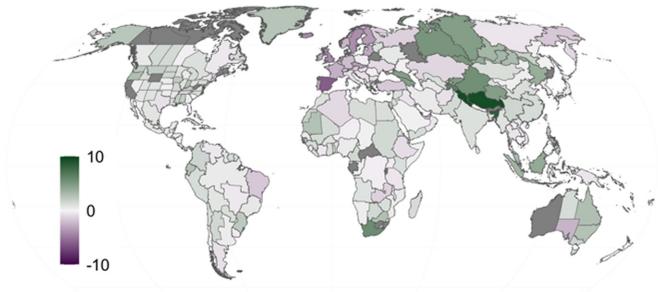
Beyond the net loss in biodiversity, changes in species composition contributed to the reorganization of biodiversity at the community level, measured as the dissimilarity between native assemblages and assemblages after

potential species composition changes (i.e., introduction and threatened species). Globally, the dissimilarity values were low as demonstrated by taxonomic dissimilarity (mean \pm SD: 13.6% \pm 8.4, Figure 3). The other facets of biodiversity were highly correlated (Spearman's rank correlation tests: $r > 0.7$, $p < 0.001$, Figure 3).

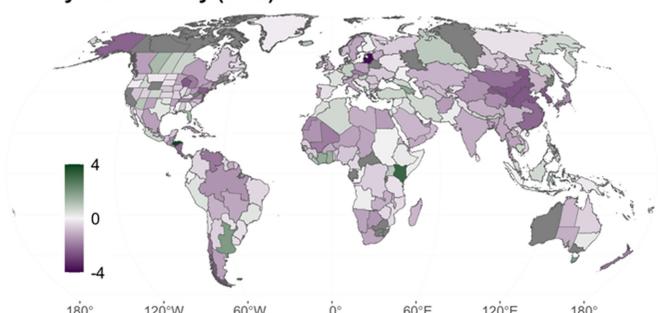
(a) Taxonomic dissimilarity



(b) Morphological dissimilarity (SES)



(c) Life-history dissimilarity (SES)



(d) Phylogenetic dissimilarity (SES)

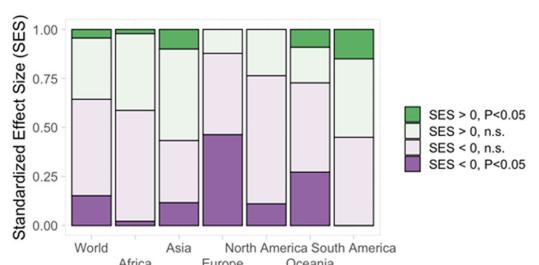
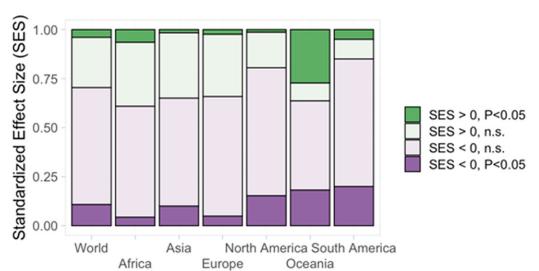
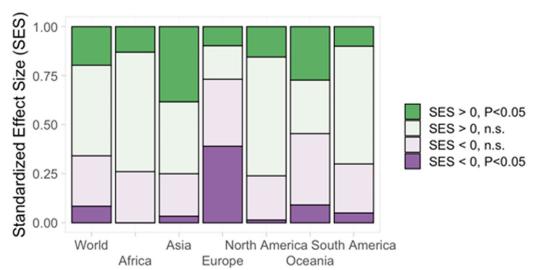
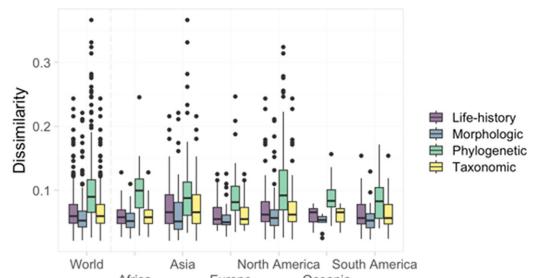
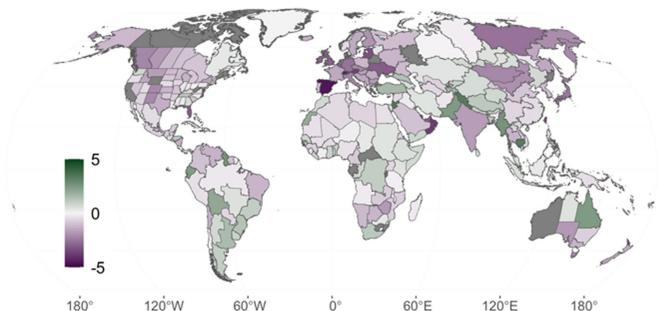


FIGURE 3 Changes in taxonomic, morphological, life history, and phylogenetic dissimilarity in 281 regions across the world. For each region, the changes were measured as the difference between native species and natives+non-natives-threatened. Changes in dissimilarity are shown for taxonomic in map (a) and for all facets in the boxplot. Changes for morphological (b), life history (c), and phylogenetic (d), are also expressed in terms of Standardized Effect Size (SES), meaning that observed changes were compared to 999 expected changes where the introduced species were randomized among a world pool of species. Purple tones mean that changes in morphological, life history, and phylogenetic dissimilarity were lower-than-expected. Green tones mean changes in morphological, life history, and phylogenetic dissimilarity were higher-than-expected. Threatened species are species classified as CR, EN, VU, and NT by IUCN.

The changes in species composition led to deeper variations in morphological dissimilarity and phylogenetic dissimilarity ($r=0.45$, $p<0.001$, Figure 4a) than in life-history dissimilarity, which showed only a weak correlation with other diversity facets ($r<0.20$, $p<0.01$, Figure 4b,c). For instance, in Asia, the decrease in morphological dissimilarity was lower-than-expected in 37% of regions while the life-history dissimilarity was not significant. In contrast, in Western Europe, 36% of the regions experienced a decrease lower-than-expected in morphological dissimilarity but not in life-history dissimilarity.

The observed discrepancies between morphological and life-history traits can be attributed to the distribution of species within the morphological and life-history spaces (Figure 5). Indeed, non-native species were more distant from native fauna in terms of life-history traits than morphological traits, with these differences being especially pronounced along the PC2 axis. This accounted for the higher-than-expected losses observed in life-history richness but also for the higher-than-expected decrease in dissimilarity for morphological traits. Conversely, for threatened species, we did not observe significant differences between the two sets of traits in the functional spaces and PC2 and even slightly higher for PC1 in morphological traits, explaining higher congruence in patterns for threatened species (Figure 2b).

DISCUSSION

Amid growing concerns about global biodiversity loss, the impacts of non-native species and the extinction of

native species on ecosystems have garnered attention on different taxonomic groups (e.g., birds: Sobral et al., 2016; freshwater fishes: Su et al., 2021). We focus on bird assemblages worldwide to evaluate whether the introduction of non-native species could potentially offset losses in morphological, life history, and phylogenetic diversity stemming from the extinction of threatened species. Our findings indicate that shifts in species composition could trigger a global decline in avian biodiversity due to the high number of threatened species. Furthermore, these losses are not random; they disproportionately involve species that are functionally and phylogenetically unique at the regional scale. Our results show that non-native species are not able to offset these changes because they are morphologically and phylogenetically close to native fauna. Consequently, our results emphasize the need for both controlling non-native species and preserving phylogenetically unique native species, which are the primary drivers of changes in the functional and phylogenetic structure of bird communities. These findings contribute to our understanding of the complex dynamics shaping global biodiversity and inform conservation strategies.

Our study reveals distinctive roles of non-native and threatened species in shaping the morphological, life history, and phylogenetic facets of avian biodiversity. Extending a pattern observed in island bird assemblages (Sobral et al., 2016), we found that non-native species often clustered within a limited number of phylogenetic clades, whereas threatened species were scattered across a diverse array of clades. Because of this, even the extinction of a few threatened species often leads to the loss of

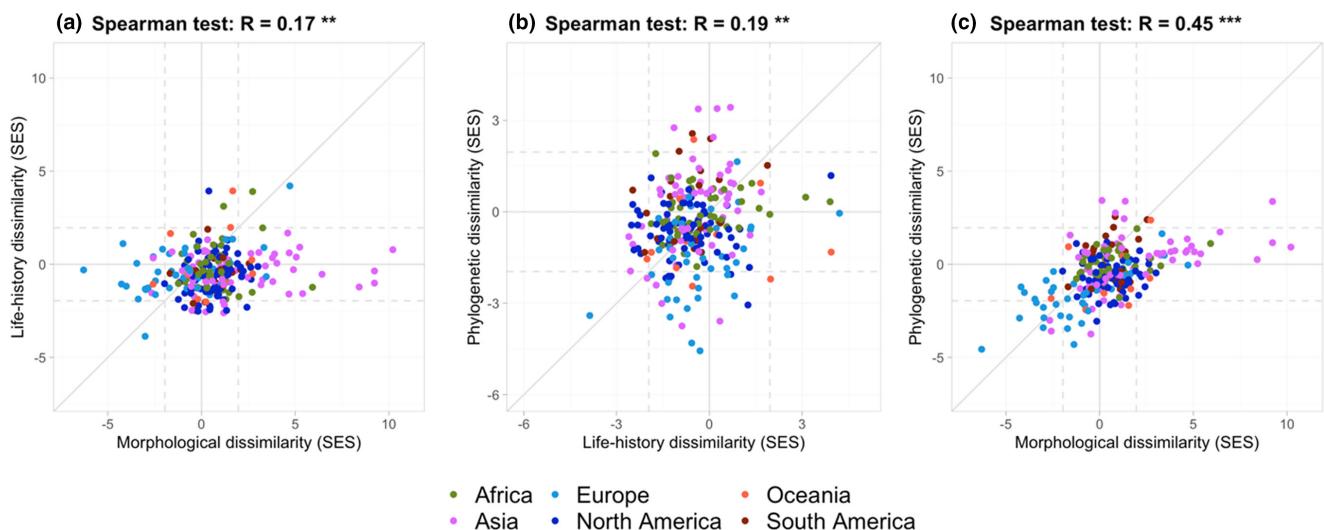


FIGURE 4 Correlation between standardized effect sizes between morphological, life history, and phylogenetic dissimilarity. Each dissimilarity metric was computed between native and native+non-native-threatened species in each country, independently. Pairs correlations are shown between morphological and life history (a), life history and phylogenetic (b), and morphological and phylogenetic dissimilarity (c). The standardized effect sizes (SES) were calculated between the observed dissimilarity and 999 expected changes if the non-native and threatened species were randomly selected (see Methods for details). Colours correspond to the continent each country belongs and are indicated in the legend. Spearman rank correlation tests were used between each standardized effect size of dissimilarity indices and indicated in the title of each panel. Threatened species are species classified as CR, EN, VU, and NT by IUCN.

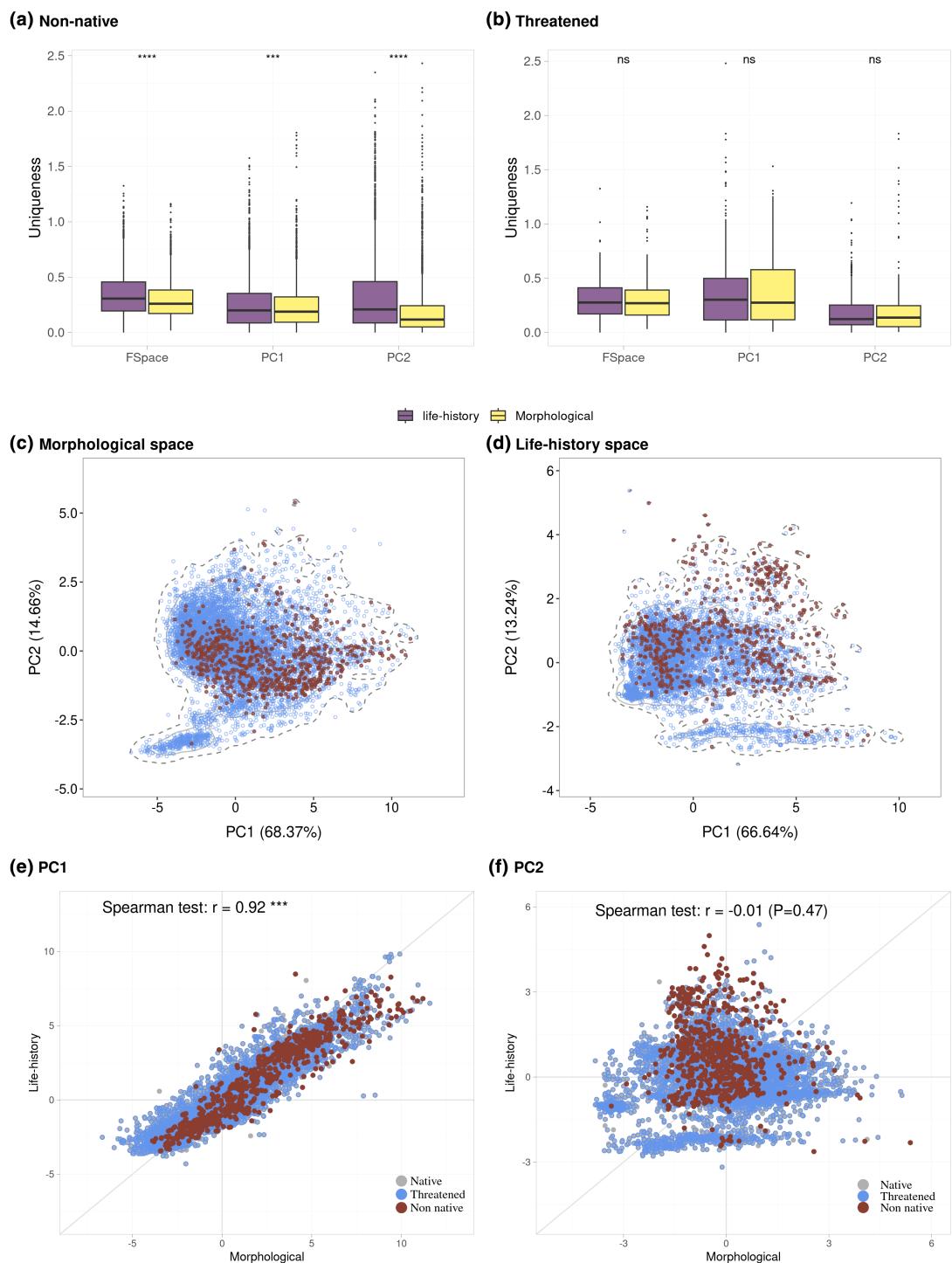


FIGURE 5 Functional uniqueness of non-native and threatened species between morphological and life-history traits. Functional uniqueness was calculated for non-native (a) and threatened species (b) in the morphological (purple) and life-history (yellow) space as well as for each PC axis. The functional uniqueness of non-native and threatened species was calculated for each region and standardized to the centre of the native species of each region. Threatened (blue) and non-native species (red) are positioned in the morphological (c) and life-history space (d). Relationships between morphological and life history are presented for each PC axis (e: PC1 and f: PC2) and tested using Spearman rank correlation tests. Threatened species are species classified as CR, EN, VU, and NT by IUCN.

unique parts of the bird phylogenetic tree. Importantly, our findings highlight that functional traits and phylogenetic richness are not always congruent. Therefore, a comprehensive understanding of species' ecological roles and evolutionary histories requires evaluating

both dimensions of biodiversity (Gerhold et al., 2015; Losos, 2008).

The choice of functional traits is critical, as it shapes our results and their ecological implications. Our data reveal a weak correlation between morphological and

life-history traits. For instance, while non-native birds displayed distinct life-history traits compared to natives, they did not necessarily introduce new morphological traits into the existing assemblages. In both functional spaces, the dominant axis was related to body size, but the secondary axes diverged significantly, each capturing different aspects of bird ecological strategies. Notably, the non-native species showed greater uniqueness in the secondary axis of the life-history space. Such distinct reproductive strategies among non-native bird species could have far-reaching implications, potentially affecting ecosystem functioning (Loiseau et al., 2020).

Furthermore, compared to changes in life-history traits, changes in morphological diversity correlated more strongly with changes in phylogenetic richness. This implies that variation in life-history traits among closely related species is larger than morphological variation which can be attributed to higher phylogenetic conservatism in morphological traits than for life-history traits. This finding deepens our understanding of the multifaceted impacts of species composition changes on biodiversity and underscores the need for nuanced conservation strategies that consider these complex relationships. This also calls for considering a large range of traits. Indeed, even if the chosen traits are known to be strongly related to the ecological strategies of species (Pigot et al., 2020), some ecological functions are not included such as the diet traits which might be also relevant to assess the ecological role of bird species (Wilman et al., 2014).

The importance of threatened species in this complex puzzle cannot be overstated. The potential loss of threatened species has a more uniform impact on all facets of biodiversity compared to the effect of non-native species. The congruence between levels of threats demonstrates that threatened species contribute significantly to both functional and evolutionary diversity, irrespective of their threat levels. The loss of endangered species not only leads to a reduction in the diversity of ecological functions but also weakens the potential for evolution and adaptation in response to different kinds of environmental disturbances. This has implications for ecosystem stability and resilience, as phylogenetic diversity often plays a crucial role in enhancing the adaptability of ecosystems to environmental changes (Cadotte & Tucker, 2018; Losos, 1996; Sobral et al., 2014; Winter et al., 2013).

Beyond the net biodiversity loss, the generally low dissimilarity values suggest that introductions or extinctions do not drastically shift the occupation of the functional spaces or the evolutionary relationships among remaining bird species. This general pattern, however, varied across the biodiversity indices. For example, Western Europe is poised for significant shifts in morphological and phylogenetic structure but not in life history. This result can be attributed to the introduction of non-natives that tend to be morphologically redundant

compared to native species, a pattern also seen in island assemblages (Sayol et al., 2021). Opposite patterns were found for several regions in central Asia depicting a turnover in the morphological and phylogenetic structure of those assemblages.

However, the full scope of this biotic reorganization may still be underestimated due to gaps in current data. Improvements in data availability are crucial for accurate functional and phylogenetic assessments in conservation policies. Particularly in regions like South America and Southeast Asia (Figure S4), our results may underestimate the intensity of taxonomic changes due to gaps in coverage of the IUCN Red List (Figure S4c). The development of a complete database such as AVONET marks a significant step forward. However, our findings indicate that certain facets of ecological functions, such as reproduction may exhibit different patterns. Therefore, it is crucial to also consider these unaddressed aspects and make further progress in characterizing species traits.

In conclusion, the human impact on the global landscape of avian biodiversity is clear and presents a pressing need for action (Ellis, 2015). The surge in global trade has the potential to significantly boost the spread of non-native species across the world, particularly 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 bird assemblages reported here might increase the vulnerability of ecosystems to future changes, demanding immediate, region-specific conservation policies. This study underscores the critical need for ambitious, comprehensive strategies to regulate both species introduction and the conservation of threatened species across the world.

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AUTHOR CONTRIBUTIONS

AT and CPC conceived the study; AT and CPC collected and processed the trait data and analyses. AT wrote the first draft of the manuscript, and all authors contributed to the interpretation of results and article writing.

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CONFLICT OF INTEREST STATEMENT

The authors declare no competing interests.

PEER REVIEW

The peer review history for this article is available at <https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/ele.14373>.

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 ([10.22541/au.169893816.69564056/v1](https://doi.org/10.22541/au.169893816.69564056/v1)).

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REFERENCES

- Ali, J.R., Blonder, B.W., Pigot, A.L. & Tobias, J.A. (2023) Bird extinctions threaten to cause disproportionate reductions of functional diversity and uniqueness. *Functional Ecology*, 37, 162–175.
- Baselga, A. & Orme, C.D.L. (2012) Betapart: an R package for the study of beta diversity. *Methods in Ecology and Evolution*, 3, 808–812.
- Billerman, S.M., Keeney, B.K., Rodewald, P.G. & Schulenberg, T.S. (2022) *Birds of the world*. Ithaca, NY, USA: Cornell Laboratory of Ornithology. Available from: <https://birdsoftheworld.org/bow/home> [Accessed 4th June 2022].
- Cadotte, M.W. & Tucker, C.M. (2018) Difficult decisions: strategies for conservation prioritization when taxonomic, phylogenetic and functional diversity are not spatially congruent. *Biological Conservation*, 225, 128–133.
- Capinha, C., Essl, F., Seebens, H., Moser, D. & Pereira, H.M. (2015) The dispersal of alien species redefines biogeography in the Anthropocene. *Science*, 348(6240), 1248–1251.
- Carmona, C.P., Bello, F., Mason, N.W.H. & Lepš, J. (2019) Trait probability density (TPD): measuring functional diversity across scales based on TPD with R. *Ecology*, 100, e02876.
- Carmona, C.P., Tamme, R., Pärte, M., de Bello, F., Brosse, S., Capdevila, P. et al. (2021) Erosion of global functional diversity across the tree of life. *Science Advances*, 7, 1–13.
- Carpio, A.J., Guerrero-Casado, J., Barasona, J.A., Tortosa, F.S., Vicente, J., Hillström, L. et al. (2017) Hunting as a source of alien species: a European review. *Biological Invasions*, 19, 1197–1211.
- Chamberlain, S.A. (2018) rredlist: "IUCN" Red List Client. Available from: <https://github.com/ropensci/rredlist> (devel) <https://docs.ropensci.org/rredlist/> (docs)
- Daru, B.H., Davies, T.J., Willis, C.G., Meineke, E.K., Ronk, A., Zobel, M. et al. (2021) Widespread homogenization of plant communities in the Anthropocene. *Nature Communications*, 12, 6983.
- Dawson, W., Moser, D., van Kleunen, M., Kreft, H., Pergl, J., Pyšek, P. et al. (2017) Global hotspots and correlates of alien species richness across taxonomic groups. *Nature Ecology & Evolution*, 1, 0186.
- Dinno, A. (2018) paran: Horn's test of principal components/factors (R package version 1.5.2) [Computer software].
- Dyer, E.E., Redding, D.W. & Blackburn, T.M. (2017) The global avian invasions atlas, a database of alien bird distributions worldwide. *Scientific Data*, 4, 170041.
- Ellis, E.C. (2015) Ecology in an anthropogenic biosphere. *Ecological Monographs*, 85, 287–331.
- Gerhold, P., Cahill, J.F., Winter, M., Bartish, I.V. & Prinzing, A. (2015) Phylogenetic patterns are not proxies of community assembly mechanisms (they are far better). *Functional Ecology*, 29, 600–614.
- Gozlan, R.E., Britton, J.R., Cowx, I. & Copp, G.H. (2010) Current knowledge on non-native freshwater fish introductions. *Journal of Fish Biology*, 76, 751–786.
- Grenié, M., Denelle, P., Tucker, C.M., Munoz, F. & Violette, C. (2017) Funrar: an R package to characterize functional rarity. *Diversity and Distributions*, 23, 1365–1371.
- IUCN. (2020) The IUCN Red List of Threatened Species. Version 2020-3. Available from: <http://www.iucnredlist.org> [Downloaded 5th January 2021].
- Jaccard, P. (1901) Étude comparative de la distribution florale dans une portion des Alpes et des Jura. *Bulletin de la Société Vaudoise des Sciences Naturelles*, 37, 547–579.
- Jarzyna, M.A. & Jetz, W. (2016) Detecting the multiple facets of biodiversity. *Trends in Ecology & Evolution*, 31, 527–538.
- Jenkins, C.N., Pimm, S.L. & Joppa, L.N. (2013) Global patterns of terrestrial vertebrate diversity and conservation. *Proceedings of the National Academy of Sciences of the United States of America*, 110, E2602–E2610.
- Jetz, W., Thomas, G.H., Joy, J.B., Hartmann, K. & Mooers, A.O. (2012) The global diversity of birds in space and time. *Nature*, 491, 444–448.
- Li, D. (2023) rtrees: an R package to assemble phylogenetic trees from megatrees. *Ecography*, 2023, e06643.
- Loiseau, N., Mouquet, N., Casajus, N., Grenié, M., Guéguen, M., Maitner, B. et al. (2020) Global distribution and conservation status of ecologically rare mammal and bird species. *Nature Communications*, 11, 5071.
- Losos, J.B. (1996) Phylogenetic perspectives on community ecology. *Ecology*, 77, 1344–1354.
- Losos, J.B. (2008) Phylogenetic niche conservatism, phylogenetic signal and the relationship between phylogenetic relatedness and ecological similarity among species. *Ecology Letters*, 11, 995–1003.
- Martin-Albarracín, V.L., Amico, G.C., Simberloff, D. & Nuñez, M.A. (2015) Impact of non-native birds on native ecosystems: a global analysis. *PLoS One*, 10, e0143070.
- Matthews, T.J., Wayman, J.P., Cardoso, P., Sayol, F., Hume, J.P., Ulrich, W. et al. (2022) Threatened and extinct Island endemic birds of the world: distribution, threats and functional diversity. *Journal of Biogeography*, 49, 1920–1940.
- McGill, B., Enquist, B., Weiher, E. & Westoby, M. (2006) Rebuilding community ecology from functional traits. *Trends in Ecology & Evolution*, 21, 178–185.
- Myhrvold, N.P., Baldridge, E., Chan, B., Sivam, D., Freeman, D.L. & Ernest, S.K.M. (2015) An amniote life-history database to perform comparative analyses with birds, mammals, and reptiles. *Ecology*, 96, 3109.
- Paganeli, B., Toussaint, A., Bueno, C.G., Fujinuma, J., Reier, Ü. & Pärte, M. (2022) Dark diversity at home describes the success of cross-continent tree invasions. *Diversity and Distributions*, 28, 1202–1213.
- Paradis, E., Claude, J. & Strimmer, K. (2004) APE: analyses of phylogenetics and evolution in R language. *Bioinformatics*, 20, 289–290.
- Penone, C., Davidson, A.D., Shoemaker, K.T., Di Marco, M., Rondinini, C., Brooks, T.M. et al. (2014) Imputation of missing data in life-history trait datasets: which approach performs the best? *Methods in Ecology and Evolution*, 5, 961–970.
- Pigot, A.L., Sheard, C., Miller, E.T., Bregman, T., Freeman, B., Seddon, N. et al. (2020) Macroevolutionary convergence connects morphological form to ecological function in birds. *Nature Ecology & Evolution*, 4(2), 230–239.
- Pimm, S.L. & Raven, P. (2000) Biodiversity. Extinction by numbers. *Nature*, 403, 843–845.
- Pollock, L.J., Thuiller, W. & Jetz, W. (2017) Large conservation gains possible for global biodiversity facets. *Nature*, 546, 141–144.

- Sayol, F., Cooke, R.S.C., Pigot, A.L., Blackburn, T.M., Tobias, J.A., Steinbauer, M.J. et al. (2021) Loss of functional diversity through anthropogenic extinctions of Island birds is not offset by biotic invasions. *Science Advances*, 7, 5790.
- Seebens, H., Bacher, S., Blackburn, T.M., Capinha, C., Dawson, W., Dullinger, S. et al. (2021) Projecting the continental accumulation of alien species through to 2050. *Global Change Biology*, 27, 970–982.
- Seebens, H., Blackburn, T.M., Dyer, E.E., Genovesi, P., Hulme, P.E., Jeschke, J.M. et al. (2018) Global rise in emerging alien species results from increased accessibility of new source pools. *Proceedings of the National Academy of Sciences of the United States of America*, 115, 201719429.
- Simberloff, D. & Vitule, J.R.S. (2014) A call for an end to calls for the end of invasion biology. *Oikos*, 123, 408–413.
- Sobral, F.L., Jardim, L., Lemes, P., Machado, N., Loyola, R. & Cianciaruso, M.V. (2014) Spatial conservation priorities for top predators reveal mismatches among taxonomic, phylogenetic and functional diversity. *Natureza e Conservacao*, 12, 150–155.
- Sobral, F.L., Lees, A.C. & Cianciaruso, M.V. (2016) Introductions do not compensate for functional and phylogenetic losses following extinctions in insular bird assemblages. *Ecology Letters*, 19, 1091–1100.
- Sol, D., Bartomeus, I., González-Lagos, C. & Pavoine, S. (2017) Urbanisation and the loss of phylogenetic diversity in birds. *Ecology Letters*, 20, 721–729.
- Stekhoven, D.J. & Bühlmann, P. (2012) MissForest—non-parametric missing value imputation for mixed-type data. *Bioinformatics*, 28, 112–118.
- Stewart, K., Carmona, C.P., Clements, C., Venditti, C., Tobias, J.A. et al. (2023) Functional diversity metrics can perform well with highly incomplete data sets. *Methods in Ecology and Evolution*, 14, 2856–2872.
- Su, G., Logez, M., Xu, J., Tao, S., Villéger, S. & Brosse, S. (2021) Human impacts on global freshwater fish biodiversity. *Science*, 371, 835–838.
- Su, G., Villéger, S. & Brosse, S. (2019) Morphological diversity of freshwater fishes differs between realms, but morphologically extreme species are widespread. *Global Ecology and Biogeography*, 28, 211–221.
- Su, G., Villéger, S. & Brosse, S. (2020) Morphological sorting of introduced freshwater fish species within and between donor realms. *Global Ecology and Biogeography*, 29, 803–813.
- Tobias, J.A., Sheard, C., Pigot, A.L., Devenish, A.J.M., Yang, J., Sayol, F. et al. (2022) AVONET: morphological, ecological and geographical data for all birds. *Ecology Letters*, 25, 581–597.
- Toussaint, A., Brosse, S., Bueno, C.G., Pärtel, M., Tamme, R. & Carmona, C.P. (2021) Extinction of threatened vertebrates will lead to idiosyncratic changes in functional diversity across the world. *Nature Communications*, 12, 1–12.
- Wardle, D.A., Bardgett, R.D., Callaway, R.M. & Van der Putten, W.H. (2011) Terrestrial ecosystem responses to species gains and losses. *Science*, 332, 1273–1277.
- Weeks, B.C., Naeem, S., Lasky, J.R. & Tobias, J.A. (2022) Diversity and extinction risk are inversely related at a global scale. *Ecology Letters*, 25, 697–707.
- Wilman, H., Belmaker, J., Simpson, J., De, C., Rosa, L.A., Rivadeneira, M.M. et al. (2014) EltonTraits 1.0: species-level foraging attributes of the world's birds and mammals. *Ecology*, 95, 2027.
- Winter, M., Devictor, V. & Schweiger, O. (2013) Phylogenetic diversity and nature conservation: where are we? *Trends in Ecology & Evolution*, 28, 199–204.

SUPPORTING INFORMATION

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