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Conservation Biology

Protected area coverage of vulnerable regions to conserve functional diversity of birds

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Abstract

Global-change drivers are increasing the rates of species extinction worldwide, posing a serious threat to ecosystem functioning. Preserving the functional diversity of species is currently a priority to mitigate abrupt biodiversity loss in the coming decades. Therefore, understanding what factors better predict functional diversity loss in bird assemblages at a global scale and how existing protected areas cover the most vulnerable regions is of key importance for conservation. We examined the environmental factors associated with the risk of functional diversity loss under 3 scenarios of bird species extinction based on species distribution range size, generation length, and International Union for the Conservation of Nature conservation status. Then, we identified regions that deserve special conservation focus. We also assessed how efficiently extant terrestrial protected areas preserve particularly vulnerable bird assemblages based on predicted scenarios of extinction risk. The vulnerability of bird functional diversity increased as net primary productivity, land-use diversity, mean annual temperature, and elevation decreased. Low values for these environmental factors were associated with a higher risk of functional diversity loss worldwide through two mechanisms: one independent of species richness that affects assemblages with low levels of niche packing and high functional dissimilarity among species, and the other that affects assemblages with low species richness and high rates of extinction. Existing protected areas ineffectively safeguarded regions with a high risk of losing functional diversity in the next decades. The global predictors and the underlying mechanisms of functional vulnerability in bird assemblages we identified can inform strategies aimed at preserving bird-driven ecological functions worldwide.

KEYWORDS
ecosystem functions, extinction risk, functional diversity, generation length, global, IUCN, protected areas, threatened species

Cobertura de áreas protegidas en regiones vulnerables para conservar la diversidad funcional de aves
Resumen: Los factores causantes del cambio global están incrementando las tasas de extinción de especies a nivel mundial, convirtiéndose en una seria amenaza para el funcionamiento de los ecosistemas. Actualmente, la preservación de la diversidad funcional de especies es una prioridad para mitigar la pérdida abrupta de biodiversidad en las próximas décadas. Por lo tanto, comprender cuáles son los factores que mejor predicen la pérdida de diversidad funcional en ensamblajes de aves a escala global y la protección de regiones vulnerables por las áreas protegidas existentes es de gran importancia para la conservación. En este estudio, examinamos los factores ambientales asociados con el riesgo de pérdida de

diversidad funcional bajo 3 escenarios de extinción de especies de aves en base a: extensión del rango de distribución de las especies, la duración generacional y el estatus de conservación según la Unión Internacional para la Conservación de la Naturaleza y las regiones identificadas que ameritan esfuerzos de conservación especiales. También evaluamos la eficiencia de las áreas protegidas terrestres para preservar ensambles de aves particularmente vulnerables con base en los escenarios de riesgo de extinción pronosticados. La vulnerabilidad de la diversidad funcional incrementó a medida que disminuyó la productividad primaria neta, la diversidad de usos del suelo, la temperatura media anual y la altitud. Los valores bajos de estos factores ambientales se asociaron con un mayor riesgo de pérdida mundial de diversidad funcional a través de 2 mecanismos, uno independiente de la riqueza de especies que afecta a ensambles con bajos niveles de empaque de nichos y elevada disimilitud funcional entre especies y el otro que afecta a ensambles con baja riqueza de especies y altas tasas de extinción. Las áreas protegidas existentes no fueron efectivas para la salvaguarda de regiones con alto riesgo de perder diversidad funcional en las próximas décadas. Los predictores globales y los mecanismos subyacentes de la vulnerabilidad funcional en los ensambles de aves que identificamos pueden proporcionar información para definir estrategias enfocadas a la preservación de funciones ecológicas llevadas a cabo por aves a nivel mundial.

INTRODUCTION

Anthropogenic impacts promote biodiversity loss, which jeopardizes the normal functioning of ecosystems (Díaz et al., 2019; Oliver et al., 2015; Schmid et al., 2009). The development of strategies aimed at efficiently preserving ecosystem functions constitutes a paramount challenge that is key to ensuring biodiversity conservation and human well-being (Díaz et al., 2019). It is widely recognized that not all species contribute equally to ecological processes (Kleijn et al., 2015; Mammola et al., 2021) and that focusing on species' roles can be a more efficient approach to preserving ecological properties and to predicting their response to environmental change (Cadotte et al., 2011). For this reason, ecologists seek to understand how global-change drivers affect communities' functional diversity (Cooke et al., 2019; García-Navas, Martínez-Núñez, Tarifa, Manzaneda et al., 2022; Loiseau et al., 2020; Toussaint et al., 2021) and their functional vulnerability (i.e., assemblage susceptibility to functional diversity loss) (Auber et al., 2022). Recent studies have addressed the functional vulnerability of plant communities to plant species loss in Mediterranean agroecosystems (Carmona et al., 2017), potential effects of climate change on avian functional diversity (Morelli et al., 2020; Stewart et al., 2022), geographic patterns in bird morphological diversity change after potential species loss (Hughes et al., 2022), expected loss of bird functional uniqueness after likely species extinction (Ali et al., 2023), and the forecasted (idiosyncratic) changes in the functional diversity of vertebrates worldwide after likely species extinctions (Toussaint et al., 2021). Yet, little is known about what environmental factors are systematically associated with bird assemblages of high functional vulnerability worldwide, which hinders the capacity to forecast these developments and

prevents a deeper mechanistic understanding of the conditions under which future ecosystem functions driven by birds are most fragile.

Several studies explore global patterns of diversity in relation to environmental factors, such as elevation (Jarzyna et al., 2021), temperature (Currie et al., 2004), precipitation (Gaston, 2000), and net primary productivity (NPP) (Cusens et al., 2012; Hughes et al., 2022). For instance, Martínez-Núñez et al. (2023) found that land-use diversity predicts bird regional taxonomic and functional richness worldwide. Thus, it is possible that environmental predictors of global diversity also affect functional vulnerability through direct mechanisms (i.e., increasing interspecific dissimilarity and determining the relative position of each species in the functional space defined by the entire assemblage), indirect mechanisms (e.g., moderating species richness), or both. Untangling the contributions of direct and indirect mechanisms is important to the understanding of the processes underlying the observed patterns.

The focus on preserving functional diversity and, thus, areas that host functionally diverse communities (Kosman et al., 2019) is a valid and significant strategy, but it may be more efficient to concentrate on safeguarding assemblages at higher risk of losing functional diversity. Hence, identifying factors that predict a heightened functional vulnerability is essential for prioritizing the preservation of biodiverse areas or threatened species, or areas and functionally vulnerable species assemblages encompassing highly threatened species that are ecologically important in that specific biotic context. Vulnerable assemblages encompass species with a high risk of extinction, and the extinction of species in these assemblages will have a large effect on the community in terms of functional diversity loss (Grenyer et al., 2006; Mouillot et al., 2013). Thus, knowing

how well extant protected areas (PAs) preserve assemblages that are functionally susceptible can help build more efficient PA networks.

We investigated the association between important environmental factors at the regional scale (elevation, mean annual temperature, annual precipitation, NPP, and land-use diversity) and the functional vulnerability of bird assemblages under 3 scenarios of likely species extinction worldwide. We also examined how well PAs around the world cover the most vulnerable assemblages. Toward this aim, we compiled a worldwide data set of bird occurrences (>15,500 bird assemblages), bird functional traits (9 traits), environmental variables, and terrestrial PAs. Then, we simulated 3 different realistic scenarios of species extinction (based on species distribution range size, generation length, and International Union for the Conservation of Nature [IUCN] conservation status) to calculate how threatened the functional diversity of present-day bird assemblages is. We asked the following questions: Is bird functional vulnerability associated with specific environmental factors worldwide; what is the mechanism driving this vulnerability (e.g., what is the role of species richness); and are these functionally vulnerable regions well covered by existing PAs? We expected assemblages with higher species richness to be less functionally vulnerable because species diversity and extinction risk are inversely related at a global scale (Weeks et al., 2022) and more diversity often leads to a higher degree of functional redundancy (Rosenfeld, 2002), which implies that functions can be relatively protected even if some species go extinct (Yachi & Loreau, 1999). Accordingly, we hypothesized that PAs do not effectively conserve particularly fragile regions.

METHODS

Bird occurrence and environmental spatial data

Bird occurrence data were retrieved from the AVONET database (Tobias et al., 2022), which provides presence–absence data on bird species in 18,710 spatially explicit terrestrial 1° grid cells (approximately 110 km^2) worldwide (gathered from BirdLife International). We used only areas corresponding to native or reintroduced breeding and resident species. Non-native species were excluded because their occurrence in a given area may depend strongly on arguably nonecological processes, such as historical commercial transactions, particular policies, or tourism. Despite that the distributional data we used were of coarse scale and limited to presence–absence data, our data set represents the best current information on global bird distributions. From the original pool of 18,710 grid cells, those cells with a small proportion of land (<10%) or <6 different species (to allow the calculation of functional spaces with 5 axes) were excluded (Hughes et al., 2022), and analyses were limited to the 6 main biogeographic realms. The following were included in the analyses: 2630 cells and 926 bird species for Nearctic, 6123 cells and 1847 bird species for Palearctic, 1087 cells and 2093 bird species for Indomalayan, 2262 cells and 4228 bird species for Neotropics, 2466 cells and 2214 bird species for Afrotrop-

ics, and 1212 cells and 1892 bird species for Australasia. Grid cells are also referred to throughout the article as regions because they cover an area corresponding to a geographic region.

In addition to bird species occurrence in each region, from which we calculated the species taxonomic richness of each assemblage, we also extracted extensive environmental information from different sources that characterized each of these spatial units. Specifically, for each grid cell, we determined the latitude, longitude, elevation, percentage of land, median mean annual temperature, median annual precipitation, biogeographic realm, normalized difference vegetation index (a proxy for NPP), and the Shannon land-use diversity index. The land-use diversity index was calculated for each grid cell based on 22 land-use types provided by the Copernicus Global Land Service Land Cover Maps (Appendix S1) at a 100-m resolution (CGLS-LC100) (Appendix S2 contains details on each environmental variable, map sources, and resolutions).

Bird traits and functional diversity

To estimate the functional diversity of bird species in each region, we extracted bird traits from the comprehensive AVONET data set (Tobias et al., 2022), which provides morphological and ecological data for all extant bird species. From this source, we selected traits of high ecological relevance (Appendix S3): body mass; 4 traits describing beak morphology (length from tip to culmen, length from the tip to nares, width, and depth); 4 traits describing body morphology (length of tarsus, wing length, tail length, and hand–wing index [HWI]); trophic niche (granivore, frugivore, nectarivore, herbivore, herbivore aquatic, invertivore, vertivore, aquatic predator, scavenger, or omnivore); and primary lifestyle (aerial, terrestrial, insessorial, aquatic, or generalist).

To synthesize trait information, we used 2 principal component analyses (PCAs). Traits were log transformed. The first PCA (PCAm) summarized highly correlated information about morphological characteristics, including length of tarsus, wing length, tail length, and body mass. The second PCA (PCAb) summarized information about beak shape. We corrected the 4 variables describing beak shape by body mass and used the obtained residuals as the input variable in the PCAb. As a result of the first PCA, 2 axes encompassed 87% of the information contained in the 4 variables. The first axis (PCA1m) was highly correlated with size (body mass), whereas the second (PCA2m) was linked to body shape. From the second PCA, a single axis encompassed 84% of the information (PCA1b) and was mainly associated with variability in beak shape. Because the HWI was not strongly correlated with any other trait and is an important morphological trait determining species dispersal capacity (Sheard et al., 2020), it was included as a raw trait. In addition to the 4 quantitative traits (PCA1m, PCA2m, PCA1b, and HWI), we included trophic niche and primary lifestyle. These 2 categorical traits are essential to defining the functional spectrum of bird life forms from a comprehensive ecological perspective (Appendix S3).

We used the 6 variables that were not significantly correlated (Appendix S4) to create a matrix of pairwise functional distances between species (Gower distance), which we used as input in a principal coordinates analysis (PCoA) (Cooke et al., 2019; García-Navas, Martínez-Núñez, Tarifa, Molina-Pardo et al., 2022). To prevent some of the possible problems that can occur when combining traits with different resolutions, we quantified the relative contribution of each set of traits and computed a functional space based on PCoA dimensions (Kohli & Jarzyna, 2021). The relative contribution of each trait to the global Gower distances was calculated using the kdist.cor function in the ade4 package (Dray & Dufour, 2007) and was relatively even across ecological facets: ~33% for quantitative traits defining physical characteristics (~12% PCA1m, ~5% PCA2m, ~5% PCA1b, and ~12% HWI), ~33% for the predominant trophic niche, and ~33% for primary lifestyle. The distance matrix between species was relatively robust to the elimination of the 2 qualitative traits (Spearman correlation coefficient = 0.67, $p < 0.001$). The PCoA's first 5 axes accounted for 72% of the total variation. Because adding more axes did not enhance the total amount of explained variance significantly (6% including the sixth axis and 4% including the seventh axis), but exponentially increased computing times, we constructed a functional space based on 5 axes. We used the package fundiversity (Gruson & Grenié, 2022) to estimate the functional richness (volume of the convex hull) from the 5-dimensional functional space for each regional assemblage corresponding to each grid cell. We focused on functional richness sensu stricto because it provides information on the net functional assets covered by a specific bird assemblage, which enabled us to study the variety of attributes represented in a certain area and the proportion that would be lost by likely species extinctions (Mammola et al., 2021).

Scenarios of realistic species loss

To assess the level of threat to functional diversity in each region and address macroecological patterns of functional vulnerability, we simulated 3 future scenarios of species extinction that are well grounded in ecological theory and empirical observations. First, we simulated species extinction probabilistically as a function of their distribution range sizes because species distribution range is an important factor in bird species vulnerability to extinction (Gaston & Fuller, 2009; Manne et al., 1999) (probability of extinction increases as species distribution area decreases) (scenario 1).

Second, we simulated species extinction based on generation length because species with long life spans are more vulnerable to extinction than species with short life spans (Bird et al., 2020) (probability of extinction increases as generation length increases) (scenario 2). Probability of species extinction was proportional to the normalized (1, maximum; 0, minimum), log-transformed distribution range and generation length in scenarios 1 and 2, respectively. Finally, we used a species' IUCN category (https://www.iucnredlist.org/) as a proxy for extinction probability (scenario 3).

In scenario 3, a certain number of species becomes extinct, the probability of which is proportional to the species' IUCN status (i.e., critically endangered, 0.95 probability; endangered, 0.8 probability; vulnerable, 0.6; near threatened, 0.4; least concern, 0.2). Thus, under this scenario, the more threatened a species is, the more likely it is to go extinct sooner than a less threatened species.

In each region, we compared the estimated functional richness value at present with values predicted under the different future scenarios (i.e., current functional richness minus predicted functional richness in each grid cell). This value represented the threat posed to functional diversity by 2 realistic probabilistic processes: species extinction and the impact extinction of a species would have in each biotic assemblage in which it occurs (Loiseau et al., 2020) (i.e., contribution to functional richness). The average risk of functional diversity loss of the 3 simulated scenarios was calculated (1, all functional richness lost; 0, no loss of functional richness under any scenario). The IUCN uses, among other variables, species distribution range as a criterion to assess species conservation status (i.e., species with small distribution ranges tend to be more vulnerable to extinction than species with large distribution ranges). Hence, as expected, at the species level, there was a negative correlation between these 2 variables (Spearman correlation = -0.41, $p < 0.001$). However, these 2 criteria provided scenarios that differed substantially at the assemblage level (Spearman correlation = 0.14, $p < 0.001$).

We used this estimated threat to functional diversity, or functional vulnerability to likely species extinctions, to build spatially explicit maps and as a response variable in subsequent models. For each scenario, we recalculated the loss of functional richness after removing 10%, 20%, 30%, 40%, and 50% of the species in each biogeographic realm, to account for different extinction intensities and time horizons (the longer the period, the more extinctions will occur). In each scenario (i.e., S1, S2, and S3), extinction intensity (i.e., 10%, 20%, 30%, 40%, and 50% species loss), and biogeographic realm (i.e., Nearctic, Palearctic, Indomalayan, Neotropical, Afrotropical, and Australasian), 1000 iterations were run to choose the most likely set of species that would go extinct. The spatial patterns of functional richness loss under different degrees of extinction intensity were similar (Appendix S5; correlation between levels of species extinctions in the 3 scenarios: mean [SD] = 0.97 [0.03], $p < 0.001$). All the maps and analyses were based on simulations of 30% species loss as representative of any degree of extinction intensity (from 10% to 50%).

Statistical analyses

We calculated and mapped the world's spatially explicit distribution of threat to bird functional richness under each scenario and the average of all of them. We ran generalized additive models to study the links between potential explanatory variables (i.e., elevation, annual precipitation, mean annual temperature, land-use diversity, NPP, and species richness) and the degree of threat to functional richness in each region. We used these

explanatory variables because they affect the structure of species assemblages worldwide and could be important factors in the functional vulnerability of bird assemblages at the same scale. The response variable was then the normalized (1, maximum; 0, minimum) threat to functional richness after realistic species extinctions, and the explanatory variables were those mentioned previously.

Models included a smoothing term for coordinates (latitude and longitude), which were used as covariates to control for spatial autocorrelation, and a smoothing term for the explanatory variable within each level of the factor biogeographic realm (specified in the model as "by = realm"). This smoothing factor captured overall patterns and helped us avoid overfitted models that were too complex, which can hamper ecological interpretability and predictability. To understand the relative contribution of each explanatory variable and its net effect without interference from other variables (some variables, such as NPP and precipitation and NPP and Shannon land-use diversity, are inherently correlated worldwide) (Appendix S6), we ran a single model for each explanatory variable (all models including coordinates). Then, we looked at the deviance explained by each model. All the models met the assumptions of normality and independence of the residuals. In particular, model residuals did not show spatial autocorrelation (Pearson correlation coefficients between model residuals and coordinates <0.001, *p* values >0.95 in all cases).

We fitted a full piecewise structural equation model because taxonomic richness is often a main driver of functional richness and is also affected by the tested environmental variables, which makes it necessary to determine what part of the effects on functional vulnerability is direct and what part arises from the influence of species richness (i.e., indirect effect) (see Appendix S7 for an explanation of why we did not use standardized effect sizes). We also used this method because linear models are less flexible than generalized additive models, but linear coefficients (e.g., slopes) improve result standardization and comparability. We used the psem function of the piecewise package (Lefcheck, 2016) in R to specify 2 linear mixed-effect models fitted with the nlme package (Pinheiro & Bates, 2000), following a similar approach used by Martínez-Núñez et al. (2020).

In the first model, species richness was the response variable. Latitude, longitude, mean annual temperature, annual precipitation, average elevation, NPP, and Shannon land-use diversity index were included as fixed factors. Biogeographic realm was a random factor. In the second model, the response variable was the calculated functional vulnerability, and the fixed and random terms were the same as in the previous model but included, in addition, species richness as fixed factor. Both models met the assumptions of residual independence (including lack of spatial autocorrelation) and normality. All variables showed a small (<2) variance inflation factor, indicating that the correlation between some of the explanatory variables was not a problem in these models.

Finally, we calculated the efficiency of currently PAs in conserving regions where functional diversity is especially threatened by likely species extinctions. To this end, we calculated the percent area in each grid cell covered by (i.e.,

overlapped with) PAs. We used the World Database on Protected Areas (https://www.protectedplanet.net/). We selected only polygons with terrestrial PAs recognized by the IUCN, including type Ia (strict nature reserve), type Ib (wilderness area), type II (national park), type III (natural monument or feature), type IV (habitat or species management area), and type V (protected landscape or seascape). Next, we calculated the percentage of area protected in each grid cell; the number of grid cells with >50% PA; and the number of grid cells with >30% PA when considering the 10% most vulnerable grid cells, 20% most vulnerable grid cells, and so on successively (from 30% to 90% more vulnerable grid cells) until all the grid cells were included (100%). A negative relationship between these rising percentages and the amount of area protected indicated highly effective selection of PAs under this criterion. All analyses were performed with R 4.0.2 (R Core Team, 2021). The data we used are available on Figshare at https://doi.org/10.6084/m9.figshare.22144082.v1.

RESULTS

Functional vulnerability to species extinction varied substantially under the different scenarios considered (Appendix S8). According to the first scenario (distribution range), the main threatened areas were New Zealand, Tasmania, Baja California peninsula (Mexico) and western Mexico, central Libya and Chad (Africa), and the southern Arabian Peninsula (Figure 1). This is very few areas relative to the widespread threat posed by the extinctions predicted under the second and third scenarios (generation length and IUCN conservation status) (Figure 2).

The main areas threatened by the loss of species with long generations were northeastern Canada (Nunavut), Saharan Africa, Borneo, New Zealand, northern Australia, northern Russia, northern Nepal, and the southernmost parts of South America and Africa (Figure 1). The third scenario, based on IUCN status, rendered similar results, with marked losses in northern Chile, Saharan Africa, Nunavut, and the Taklamakan desert in northwestern China (Figure 1). Overall, the bird functional diversity in the Australasian and Indomalayan biogeographic realms showed a more widespread and intense vulnerability to species extinction.

Despite that functional vulnerability was partly idiosyncratic to each realm (Appendix S9), some environmental factors increased the likelihood of species assemblages losing functional diversity (Figure 3). Overall, species richness was associated with low functional vulnerability, although highly diverse regions in the Nearctic and Palearctic realms were also very vulnerable. NPP (defined above) was generally associated with a decreased risk of functional diversity loss, mainly in the Nearctic, Palearctic, and Afrotropical regions (Appendix S9). High levels of NPP were linked to low bird functional vulnerability directly and indirectly via increased species richness in the assemblages (Figure 3a). Similarly, elevation, land-use diversity, and mean annual temperature were associated with increased species richness and decreased functional vulnerability at the global scale, reducing the threat of direct and indirect functional diversity
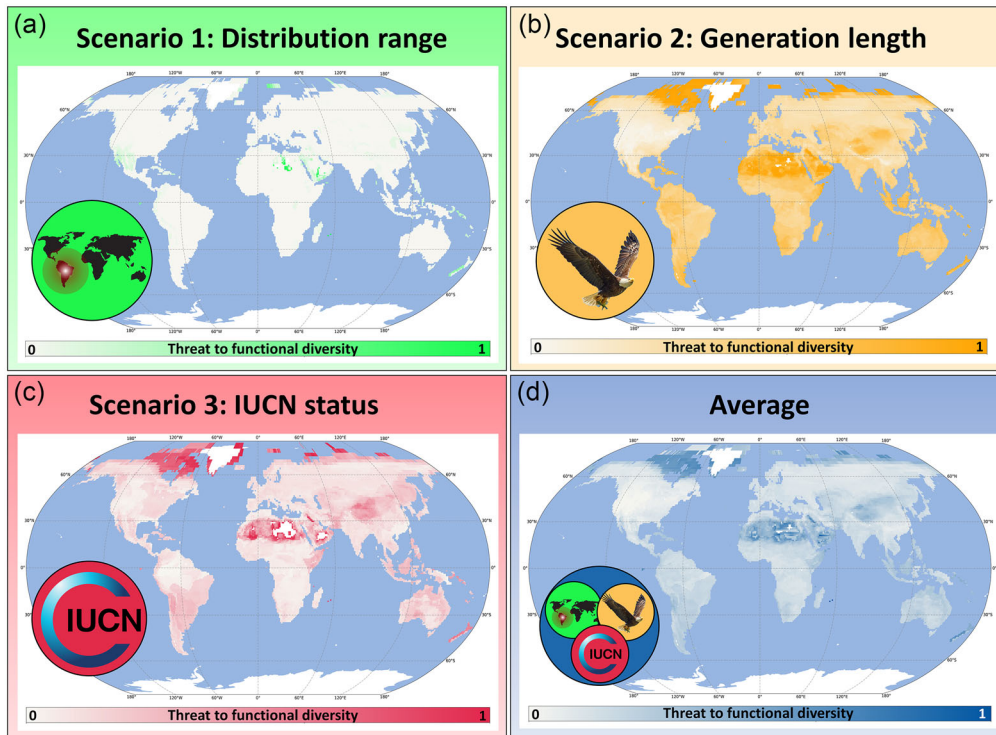
FIGURE 1 Functionally threatened regions in the world based on 4 different scenarios of realistic species extinction: (a) bird species with smaller distribution ranges are more likely to go extinct, (b) bird species with relatively long generation lengths are more likely to go extinct, (c) bird species in high International Union for the Conservation of Nature (IUCN) threat categories are more likely to go extinct, and (d) average of the previous 3 scenarios in each region (the darker the shading, the greater the risk of losing functional diversity; 0, no loss of functional diversity; 1, complete loss of functional diversity).
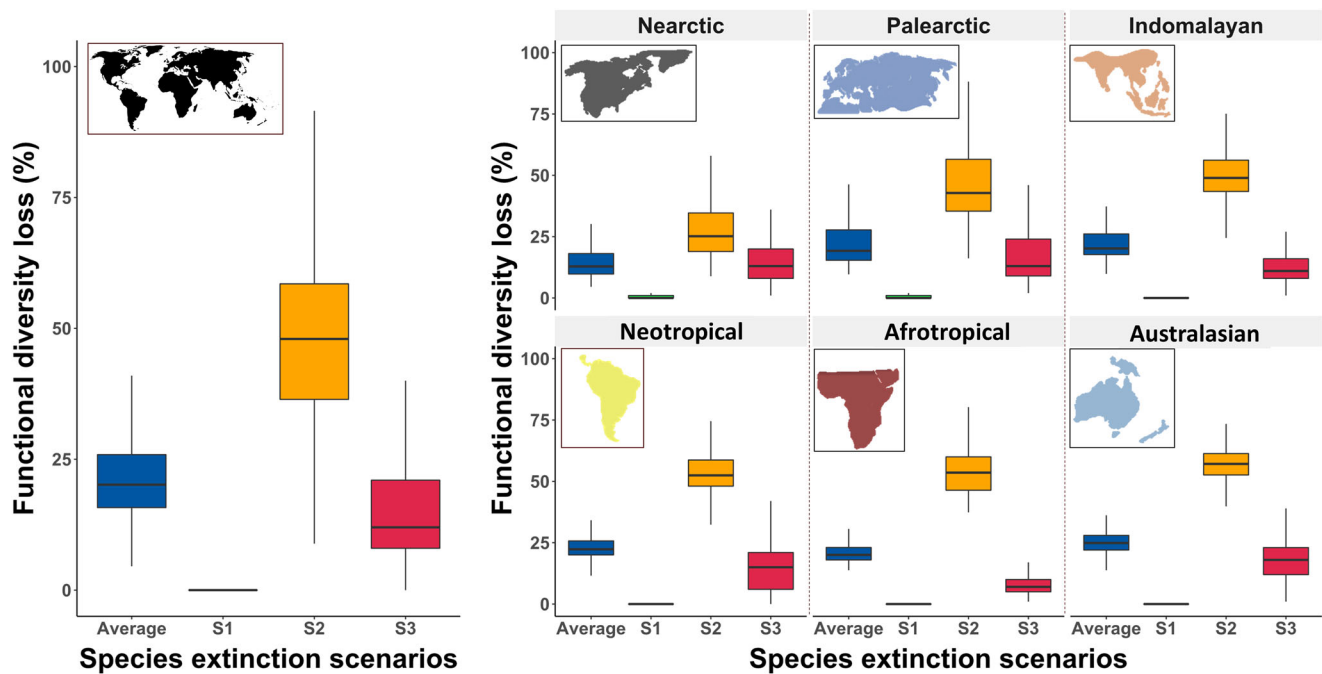
FIGURE 2 Impact of different scenarios of bird species extinction on functional diversity loss worldwide by biogeographic realm (S1, bird species with smaller distribution ranges are more likely to go extinct; S2, bird species with relatively long generation lengths are more likely to go extinct; S3, bird species in high International Union for the Conservation of Nature threat categories are more likely to go extinct; S4, average of the other 3 scenarios in each region).
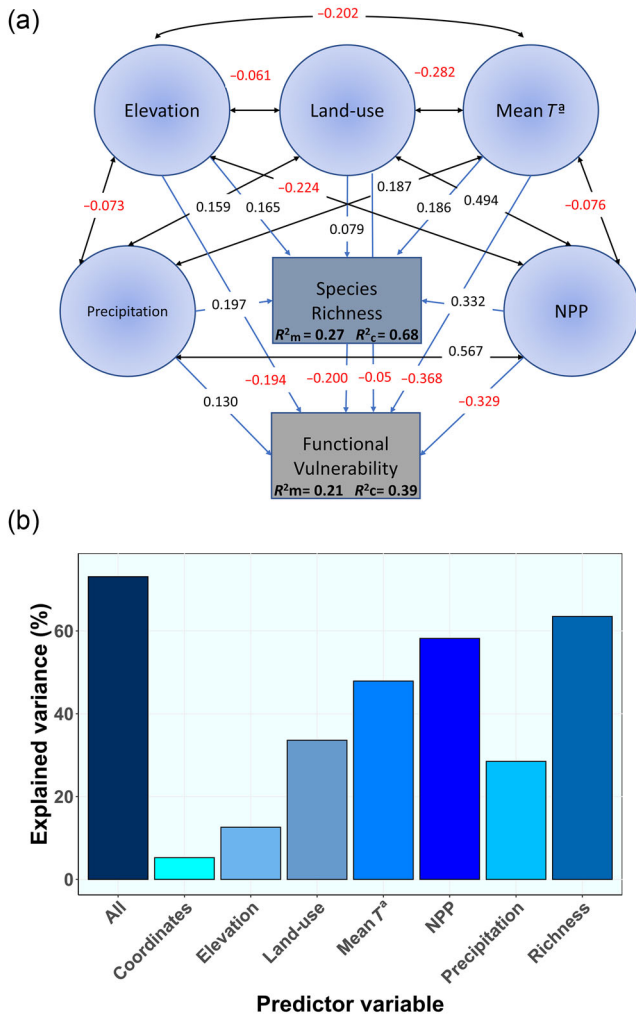
FIGURE 3 Effect size, effect direction, and relative contribution to functional vulnerability of 7 explanatory variables: (a) structural equation model showing the direct and indirect effects (through species richness) of predictors on functional vulnerability under the average scenario (defined in legend of Figure 1) (red, negative standardized coefficients; black, positive standardized coefficients; R^2_m, marginal variance explained; R^2_c, conditional variance explained; all coefficients statistically significant at $\alpha = 0.05$) and (b) explained variance of functional vulnerability for each predictor in generalized additive models (NPP, net primary productivity [normalized difference vegetation index]; land use, Shannon land-use diversity index; T^a, average annual temperature).

loss (Figure 3a). Precipitation was associated with species richness and functional vulnerability (Figure 3a), but regions with intermediate levels of precipitation were less vulnerable to likely species extinctions (Appendix S9). The most important variables in prediction of functional vulnerability were assemblage species richness (63% deviance explained), NPP (58%), and mean annual temperature (48%); the other variables were less important (Figure 3b). The model including all these predictors explained 73% of the variability in functional vulnerability to species extinction.

Extant PAs overlapped poorly with the most vulnerable regions (Figure 4; Appendix S10) (i.e., present-day PAs did not effectively protect functionally vulnerable assemblages). PAs covered ~11% of the territory we considered, but this percent-

age of PA shrank <9% when considering 20% and 10% of the territory most vulnerable to loss of bird functional richness. Protection was slightly higher for regions with a large number of PAs. The percentage of grid cells with more than 50% PA rose from ~6% (including all the grid cells) to >7% for the 10% most vulnerable grid cells (Figure 4c,d).

DISCUSSION

Extinction of threatened vertebrates leads to highly idiosyncratic changes in functional diversity (Toussaint et al., 2021). The already high extinction rates of birds will increase steeply in the future (Pimm et al., 2006), and these newly extinct species will cause a disproportionate loss of functional diversity (Ali et al., 2023). Using predictive ecology to comprehend and forecast under what environmental conditions these losses will happen is of utmost importance to inform conservation and management decisions. We found that some environmental conditions are highly associated with the risk of functional diversity loss, which is evidence that the impact of likely future bird species extinction on functional diversity across the globe can be partly predicted and follows some generalizable ecological rules.

Different scenarios of species extinctions can render different results. In our study, the second and third scenarios (based on generation length and IUCN status, respectively) were the most damaging for a generalized functional diversity loss. Other researchers found that large species with a slow life history are functionally very important (Carmona et al., 2021). This calls for the prioritization of the conservation of species with long generation lengths (e.g., penguins, parrots, flamingos) and of species that are highly threatened according to IUCN. Species with slow reproduction and growth rates (scenario 2) were important for maintaining functional diversity over large areas. In contrast, those species with small distribution ranges and high extinction risk (scenario 1) seemed associated with a relatively small and localized impact in terms of functional diversity loss. Despite that species with small distribution ranges appeared less important than species with long generation lengths, it is critical to recognize that species with small distribution ranges can be very important locally and are likely to be at greater risk of extinction (Gaston & Fuller, 2009). Also, risks segregated here in the 3 scenarios of species extinction can act additively, meaning that multiple processes can contribute simultaneously and synergistically to species extinction and functional diversity loss.

The most threatened regions were those with fewer number of species. This was expected because bird diversity and extinction risk are negatively associated at a global scale (Weeks et al., 2022) and assemblages with high species richness usually have more functional redundancy (i.e., the more species, the more likely species traits are redundant in the assemblage) (Rosenfeld, 2002; Yachi & Loreau, 1999). In the latter case, as species go extinct, others occupy part of the ecological niche of the extinct species, ensuring the maintenance of ecosystem functions (Loreau et al., 2021; Yachi & Loreau, 1999). Redundancy is associated with resilience (Walker, 1992), and some authors have used it as a proxy of low functional vulnerability (Toussaint et al.,
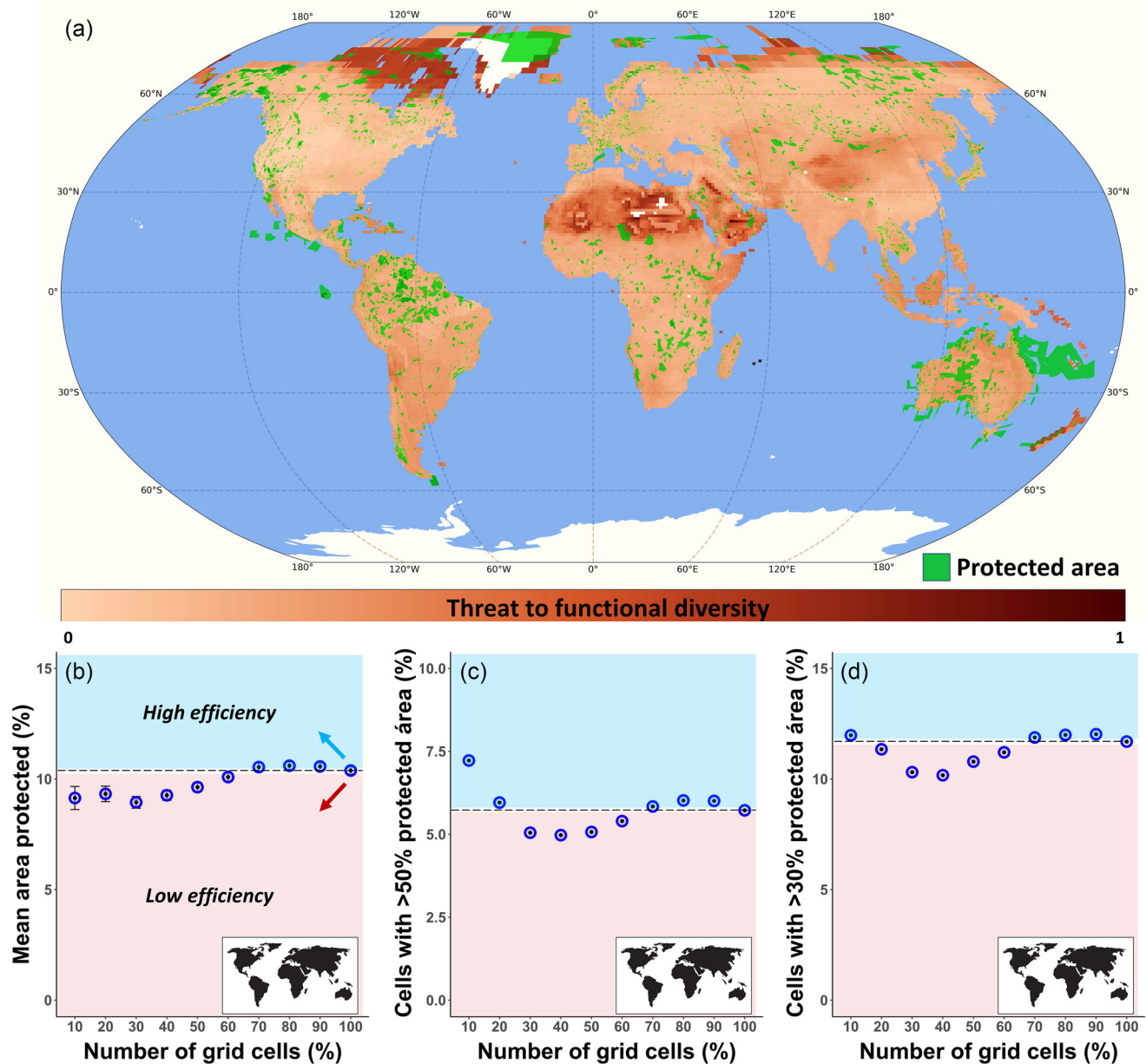
FIGURE 4 Functionally threatened regions after likely species extinction and coverage of these areas by extant protected areas: (a) gradient of functionally threatened regions in the world (orange to brown gradient) and the current network of protected areas (green), (b) coverage by extant protected areas of vulnerable regions, (c) percentage of grid cells with more than 50% of area protected, and (d) percentage of grid cells with more than 30% of area protected, for different subsets of grid cells (x-axis, gradient of functional vulnerability from the 10% most vulnerable regions to 100% of regions; effective coverage, mean area protected per region decreases as smaller subsets of increasingly vulnerable regions were considered).

2021). Thus, one would expect environmental conditions that contribute globally to increasing regional bird species richness, such as NPP (Cusens et al., 2012; Hughes et al., 2022), mean annual temperature (Currie et al., 2004), and land-use diversity (Martínez-Núñez et al., 2023), to reduce functional vulnerability to species loss. Although our results support this expectation, we additionally found that all the factors we examined were also connected with functional vulnerability at a global scale, regardless of species richness. This implies a dual positive effect of these environmental conditions on species assemblages that seems to act by increasing the number of available niches, promoting species coexistence (Weeks et al., 2022) and fostering a relatively low contribution per species to the entire functional

space (i.e., low functional dissimilarity among species, meaning more packed overlapping functional niches), a mechanism that can be relatively independent of species richness.

Our findings indicated that arid zones and high-human-impact regions with low NPP and low land-use diversity met all the conditions to be the most vulnerable to the loss of bird functional diversity. Moreover, climate change and habitat destruction driven by agricultural land-use change and urbanization are expected to aggravate this problem because they will increase desertification of extensive areas and extinction risk of species living in already extreme conditions (Iknayan & Beissinger, 2018; Ma et al., 2023). Therefore, to maintain current bird functional diversity, it is paramount to implement measures

aimed at mitigating these global-change drivers and protecting the most vulnerable areas.

Some insular regions with a large number of species and a high functional richness, such as Borneo, New Zealand, and Papua New Guinea, were also highly vulnerable to predicted bird extinctions. This pattern is associated with the large number of endemic, threatened species that are ecologically rare in these regions. The presence of large numbers of unique and threatened species on islands is common (Matthews et al., 2022). Despite that species richness can increase in islands due to species introductions, functional diversity loss caused by the extinction of rare species overrides possible gains from introductions (Sayol et al., 2021; Soares et al., 2022). We identified areas at risk of losing functional biodiversity that can be prioritized for protection to prevent disruption of the functioning of the ecosystem. Incorporating predictions of functional diversity is key to improving the effectiveness of PAs.

Our results provide evidence that regions with low bird species richness are disproportionately prone to losing functional diversity globally. This finding supports the notion that areas with low species richness are more likely to have species extinctions and are more sensitive to extinctions due to reduced functional redundancy and increased relative importance of individual species. We found that environmental factors (low elevation, low temperature, low NPP, and low land-use diversity) are associated with high functional vulnerability in bird assemblages. Thus, lowlands, cooler environments, and less productive and homogeneous regions, such as arid zones and areas highly affected by people, are the most susceptible to losing species with distinctive traits globally. Finally, our findings highlight the inadequacy of current PAs in preserving these especially vulnerable areas, underscoring the need for targeted conservation efforts in these regions.

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