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Global trade-offs of functional redundancy and functional dispersion for birds and mammals

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Abstract

Aim: The diversity of birds and mammals is typically described in separate analyses, but species may play similar roles. Here, we develop a comparative trait framework for birds and mammals to provide a global quantification of the similarity of species roles (functional redundancy) and the breadth of roles across taxa (functional dispersion). We predict different contributions of birds and mammals to redundancy and dispersion, and unique geographical patterns of redundancy and dispersion by including both taxa.

Location: Global.

Time period: Contemporary.

Major taxa studied: Birds and mammals.

Methods: We systematically select, compile and impute the same six traits (i.e., a common currency of traits) across 15,485 bird and mammal species from multiple databases. We use these six traits to compute functional redundancy and functional dispersion for birds and mammals across all 825 terrestrial ecoregions. We then calculate the standardized effect size (SES) of these observed values compared with null expectations, based on a randomization of species composition (i.e., independent of differences in species richness).

Results: We find that species-rich regions, such as the Neotropics, have high functional redundancy coupled with low functional dispersion, characterizing a global trade-off. Thus, in general, as species richness increases, the similarity in species functional roles also increases. We therefore suggest that different processes generate species richness/functional redundancy and functional dispersion, leading to a novel, and generally non-tropical, distribution of hotspots of high functional dispersion across Madagascar, Eastern Asia and Western USA.

Main conclusions: We recommend consideration of both the similarity and the breadth of functional roles across species pools, including taxa that may play similar roles. We therefore suggest that functional redundancy, as a means of insurance, and functional dispersion, as an indicator of response diversity, should be evaluated further as conservation objectives.

KEYWORDS
birds, ecoregion, function, insurance, mammals, response diversity, traits

1 | INTRODUCTION

Regions of the world are exposed to multiple interacting disturbances (e.g., habitat loss, drought, disease) that are increasing in rate and intensity owing to human activities (Brook, Sodhi, & Bradshaw, 2008; Oliver, Heard, et al., 2015). At the same time, global biodiversity continues to decline, with birds and mammals being priority species of concern (Dirzo et al., 2014). These combined pressures threaten entire networks of species and thus their ecological strategies and functional roles (Cardinale et al., 2012; Dirzo et al., 2014; Oliver, Heard, et al., 2015; Oliver, Isaac, et al., 2015). In particular, birds and mammals act as crucial connecting nodes among genetic (pollinators and seed dispersers), resource (nutrient depositor) and trophic processes (primary/secondary consumers across habitats), especially across broad scales (Lundberg & Moberg, 2003; Sekercioglu, 2006). These taxa also support a variety of ecosystem functions, such as nutrient cycling, predation, herbivory, pollination and seed dispersal, across the globe (Díaz et al., 2013; Luck, Lavorel, McIntyre, & Lumb, 2012; Newbold, Butchart, Şekercioğlu, Purves, & Scharlemann, 2012; Sekercioglu, 2006). Moreover, the size and mobility of birds and mammals result in large contributions to ecological functions and processes through top-down trophic control (Lundberg & Moberg, 2003; Sekercioglu, 2006).

Birds and mammals, together, thus have the potential to influence components of biodiversity, beyond species richness. First, different species can play similar ecological and functional roles (functional redundancy; Naeem, 1998; Walker, 1992). Second, species can be dissimilar functionally, leading to a diversity of species' responses [functional dispersion (response diversity); Chapin et al., 1997; Elmqvist et al., 2003; Yachi & Loreau, 1999]. Functional redundancy and functional dispersion are determined by the ecological strategies of species via trait–environment interactions and can be quantified by functional indices (Diaz & Cabido, 2001; Laliberté et al., 2010; Luck, Carter, & Smallbone, 2013; Mouillot et al., 2013, 2014). Specifically, functional redundancy quantifies the extent to which multiple species share functional roles, thereby providing biological insurance against the loss of function owing to species extinctions (Oliver, Isaac, et al., 2015; Walker, 1992; Yachi & Loreau, 1999). In contrast, functional dispersion quantifies the breadth of functional roles across species, and, on average, systems with species pools representing higher dispersion should display greater functional dissimilarity and a broader range of responses to environmental perturbations (Elmqvist et al., 2003; Laliberté et al., 2010; Luck et al., 2013; see Supporting Information Appendix S1 for further detail on functional redundancy and functional dispersion). Thus, functional redundancy and functional dispersion may not relate directly to specific ecological functions or processes, but describe different components of biodiversity (versus species richness) related to the overlap in functional roles (redundancy) and breadth of functions (dispersion) performed by species.

Here, we look beyond species richness and offer three major advances on previous analyses of global terrestrial vertebrate functional diversity (Barbet-Massin & Jetz, 2015; Oliveira et al., 2016; Safi et al., 2011).

To date, functional metrics have generally been applied to single taxonomic groups at a time in terrestrial systems, despite the fact that different taxa can potentially fulfil similar and/or complementary ecological and functional roles (Dehling & Stouffer, 2018). Here, we recognize that birds and mammals, as mobile consumers, have the potential to be comparable ecologically, especially at broad scales and across generalizable traits, comparable to how taxonomically and ecologically diverse plants, such as large trees and small grasses, have previously been analysed together (e.g., Díaz et al., 2016). We therefore systematically selected a common currency of traits for both birds and mammals (and an increase in the number of traits previously included for either birds or mammals) with strong links to how species respond to change and their influence on ecological and biogeochemical processes (see Supporting Information Appendix S2). The selected traits are widely applicable to terrestrial vertebrates, leading to the first direct comparisons of functional redundancy and functional dispersion across and between birds and mammals.

We also account for the effects of species richness on functional metrics for multiple taxa at the global scale, which is key because richness is correlated with ecoregion area (Spearman's ρ_{823} = .27, p < .001) and functional redundancy (ρ_{823} = .94, p < .001). In addition, to compare functional metrics among ecoregions with different species richness, it is most appropriate to consider observed values relative to those expected at random (Villéger, Mason, & Mouillot, 2008).

In addition, we quantify both functional redundancy and dispersion for species pools across the terrestrial biosphere at the ecoregion scale. Ecoregions are geographical units based on delineations in taxonomic compositions, inferred evolutionary histories and shared climatic domains (Olson et al., 2001). Ecoregions are a compelling spatial unit in representing the best available global measure of coherent, spatially bounded, biologically derived systems (Olson & Dinerstein, 2002) and have close relationships with taxonomic and functional compositions (Belmaker & Jetz, 2013; González-Maya, Martínez-Meyer, Medelloín, & Ceballos, 2017). In addition, ecoregions respect spatial changes in ecosystem attributes, disturbance regimes and species interactions (González-Maya et al., 2017; Olson et al., 2001), and changes in ecoregions can propagate across the entire biosphere (Barnosky et al., 2012; Peters et al., 2009). Furthermore, ecoregions are widely used to guide global conservation investments, assessments and action (Funk & Fa, 2010; Watson, Iwamura, & Butt, 2013).

Global quantification of functional redundancy and functional dispersion remains lacking, and thus we develop a framework that allows us to quantify different taxonomic, trait and spatial signals of diversity for both birds and mammals. Our first objective is to identify a common currency of traits that allow comparisons and analyses across and between birds and mammals. Our second objective is to use our novel dataset to test two fundamental predictions: (a) functional redundancy will be coupled with species richness, owing

to expected greater overlap in species traits with greater species richness, whereas functional dispersion will be weakly related to richness, because functional dispersion has previously been shown to increase asymptotically, rather than linearly, with species richness for mammals globally (Oliveira et al., 2016); and (b) birds, as a more species-rich group, will have higher functional redundancy, whereas mammals will show higher functional dispersion, owing to greater expected ecological diversity (inferred from the greater range in body size). Our third objective is to determine the degree to which redundancy and dispersion of birds and mammals are different from the null expectation, given their species richness in a particular ecoregion, thereby identifying regions with unique patterns of redundancy and dispersion. Our third objective is exploratory, because we do not have sufficient information to make a priori predictions of the expected patterns and relationships of redundancy and dispersion for birds and mammals when accounting for species richness.

2 | METHODS

We extracted geographical range distributions, and, following a systematic trait selection process, compiled trait data from multiple databases, imputing missing values, for six traits [body mass, litter/clutch size, diel activity (diurnal/nocturnal), diet, volancy (flight ability) and habitat breadth] for 10,253 bird and 5,232 mammal species. These six traits relate to both species' functional influences on and responses to the environment (for the ecological relevance of the selected traits, see Supporting Information Appendix S2). We then calculated functional redundancy and functional dispersion for each ecoregion in addition to the standardized effect size (SES) of these observed values compared with null expectations, based on a randomization of species composition (i.e., independently of differences in species richness).

An extended version of our methods is also available, with further detail on all methodological processes and justifications (see Supporting Information Appendix S3). All analyses were performed in R (R Core Team, 2017), version 3.4.3 (for the specific functions and packages used, see Supporting Information Appendix S3).

2.1 | Spatial data

We used 825 terrestrial ecoregions (Olson & Dinerstein, 2002), excluding "Lake" and "Rock and Ice" ecoregions, because they are not coherent systems (i.e., they occur at multiple locations across the globe). We paired these ecoregions with species range maps for 15,485 species (all extant terrestrial mammals and birds): 5,232 terrestrial mammals (https://www.iucnredlist.org/resources/spatial-data-download) and 10,253 birds (http://datazone.birdlife.org/species/requestdis). We then cropped a presence–absence matrix (polygon-to-grid procedure at 0.5° resolution; *lets.presab* function; "letsR package"; Vilela & Villalobos, 2015) based on species distributions to the ecoregion boundaries (*lets.pamcrop* function; "letsR package"; Vilela & Villalobos, 2015) to generate ecoregional

composition data. The range maps used represent the best available data, and although they are susceptible to commission errors, the coarse resolution (ecoregion scale) of our analyses reduces pseudo-replication (Belmaker & Jetz, 2015; Buschke, De Meester, Brendonck, & Vanschoenwinkel, 2015; Jetz & Fine, 2012; see Supporting Information Appendix S3). Range maps also reduce the effects of differences in detectability between species and over- or undersampling (see Supporting Information Appendix S3).

2.2 | Trait data

We followed a systematic three-step trait selection process: (a) compiled an extensive list of potential traits that may relate birds and mammals to their environment (17 traits; Supporting Information Appendix S4, Table S4.1); (b) filtered to those that had > 50% species coverage (Laliberté et al., 2010) for our species list (seven traits); and (c) had low multicollinearity (based on variance inflation factors, leading to the exclusion of generation length; Luck et al., 2012; Zuur, Ieno, & Elphick, 2010). Our trait selection process resulted in six traits that summarize both the effect of a species on ecological and biogeochemical processes and its response to environmental change: body mass, diel activity, diet, habitat breadth, litter/clutch size and volancy (see Supporting Information Appendix S2; Appendix S4, Table S4.2). These traits reflect the spatio-temporal distribution of resource capture, utilization and release by species and are commonly used in assessments of mammal and bird functional diversity (Chillo & Ojeda, 2012; Flynn et al., 2009; Leitão et al., 2016; Luck et al., 2013, 2012; Newbold et al., 2012, 2013; Safi et al., 2011).

We extracted trait data from a number of available databases (Jones et al., 2009; Myhrvold, Baldridge, Chan, Freeman, & Ernest, 2015; Pacifici et al., 2013; Wilman et al., 2014), taking the median value across estimates when applicable (for details on the data compilation process, see Supporting Information Appendix S3). To ensure that species were matched across the geographical data and the available trait data, which often use different taxonomic frameworks, we sourced species synonyms from the Integrated Taxonomic Information System and the International Union for Conservation of Nature databases via their application programming interfaces (see Supporting Information Appendix S3).

Trait data were transformed where it improved normality, as recommended by Villéger et al., (2008): $\log_{10}$ for body mass and litter/clutch size, square root for habitat breadth, and all traits were standardized to zero mean and unit variance (z-transformation).

To achieve complete species trait coverage, we imputed missing data using multivariate imputation with chained equations (MICE), based on functional (the transformed traits) and phylogenetic [the first 10 phylogenetic eigenvectors extracted from trees for birds (Prum et al., 2015) and mammals (Fritz, Bininda-Emonds, & Purvis, 2009)] relationships between species. MICE has been shown to have improved sample size and smaller error and bias than the data deletion approach and other multiple imputation approaches (Kim, Blomberg, & Pandolfi, 2018; Penone et al., 2014; Taugourdeau, Villerd, Plantureux, Huguenin-Elie, & Amiaud, 2014).

The data deletion approach was performed for comparative purposes (Supporting Information Appendix S4, Figure S4.1, Table S4.3). We also evaluated the effect of the imputation procedure by analysing the 25 imputed datasets separately and found very strong agreement between the datasets (Supporting Information Appendix S4, Figure S4.2). Thus, for all analyses we used a single, randomly selected, imputation dataset, owing to the high computational costs associated with running the null models for all the imputed datasets. For completeness, we also present the mean results (correlation between single, randomly selected, imputation dataset and mean imputation values: functional redundancy ρ_{823} = .99, p < .001; functional dispersion ρ_{823} > .99, p < .001) across the 25 imputed datasets (Supporting Information Appendix S4, Figure S4.3).

To test the sensitivity of the results to the inclusion of the number and the identity of traits, we reran all analyses with all combinations of five out of six traits. We did not reduce the number of traits lower than five because we might have missed important dimensions of the functional space (Mouillot et al., 2014). The results were robust to this procedure (Supporting Information Appendix S4, Figure S4.1, Table S4.3).

2.3 | Functional metrics

Functional redundancy was computed using the unique trait combination (UTC) approach (Keyel, Wiegand, & Orme, 2016), where the continuous traits (body mass, litter/clutch size and habitat breadth) were binned using the Sturges algorithm (Sturges, 1926). The Sturges algorithm breaks the data into classes based on the sample size and distribution of values across each trait (Sturges, 1926). Our characterization of functional redundancy has a broad resolution, and we therefore do not expect species in the same UTC to compensate fully for the loss of group members. Instead, we propose that species with similar traits have similar ecological strategies, hence they can be considered as functionally redundant (Carmona, de Bello, Mason, & Lepš, 2016; Laliberté et al., 2010). Our broad resolution also avoids a potential pitfall, where including too many traits or too many fine-scale features leads to a metric that simply reflects taxonomy (every species is unique) and thus is equivalent to species richness. We calculated functional dispersion from a Gower dissimilarity matrix produced from the transformed traits.

2.4 | Null model

To test whether observed functional values differed from the expected distribution of functional values given the observed species richness of an ecoregion, we used a null model based on global randomization of species composition (Oliveira et al., 2016; Villéger et al., 2008). We also implemented a null model based on biome-scale randomization of species composition (i.e., using biome species pools), with the potential to account better for the spatial filtering of trait combinations owing to biogeographical and historical processes. Results were qualitatively similar when using a global or biome null model (Supporting Information Appendix S4, Figures S4.1, S4.4,

Table S4.3); here, we present the global null model to allow functional contributions across biomes to be assessed. To implement the null model, for each ecoregion, we constructed 999 randomized assemblages drawn from a global species pool, while holding species richness constant [the R and bash scripts to run the null models on a high-performance computer (we used the IRIDIS High Performance Computing Facility and associated support services at the University of Southampton) are available from the author upon request]. To assess the magnitude of the difference for functional redundancy and functional dispersion between the observed (F_{obs}) and null (F_{null}) results, we calculated the standardized effect size: SES = [F_{obs} − mean(F_{null})]/$SD(F_{null})$. We also carried out one-tailed permutation tests, where the null hypothesis was that the observed and null functional values were equivalent and the alternative hypothesis was that observed functional values were greater (or less) than the expected value under the null model assumptions. If the alternative hypothesis (H_1) was greater, a p-value was estimated as: (number of F_{null} ≥ F_{obs} + 1)/(999 + 1). If the alternative hypothesis was less, a p-value was estimated as: (number of F_{null} ≤ F_{obs} + 1)/(999 + 1). Our rarefied analysis therefore maps functional patterns independently of differences in species richness, allowing us to assess the degree to which the observed functional values differ from the null distribution of functional values, revealing regions with higher [positive SES; permutation test (H_1 = greater)] or lower [negative SES; permutation test (H_1 = less)] functional values than expected at random (Maire, Grenouillet, Brosse, & Villéger, 2015; Villéger et al., 2008). Moreover, the use of SES, which represents the magnitude of the difference between the observed and null results, allows us to compare values across functional dispersion and functional redundancy, and across taxonomic groups with greatly different species richness, such as birds and mammals. Thus, we also performed the functional analyses for birds and mammals independently (Supporting Information Appendix S4, Figures S4.5, S4.6) and assessed the differences in the functional metrics between birds and mammals using two-tailed Kolmogorov–Smirnov tests.

Overall, our results and conclusions were similar: (a) with and without imputed data (compare Figure 1 and Supporting Information Appendix S4, Figures S4.1, S4.2, S4.3, Table S4.3); (b) with all combinations of five of six traits (Supporting Information Appendix S4, Figure S4.1, Table S4.3); and (c) with a null model based on a global or biome species pool (Supporting Information Appendix S4, Figures S4.1, S4.4, Table S4.3).

To facilitate reproducibility and encourage open science, the code (R script), data and results are available in a figshare repository at: https://figshare.com/articles/Global_trade-offs_of_functional_redundancy_and_functional_dispersion_for_birds_and_mammals/5616424.

3 | RESULTS

We classify 2,991 ecological strategies, quantified here as unique trait combinations (UTCs), across 15,485 species of birds and mammals. The mean number of species per UTC is 5.2 at the global scale
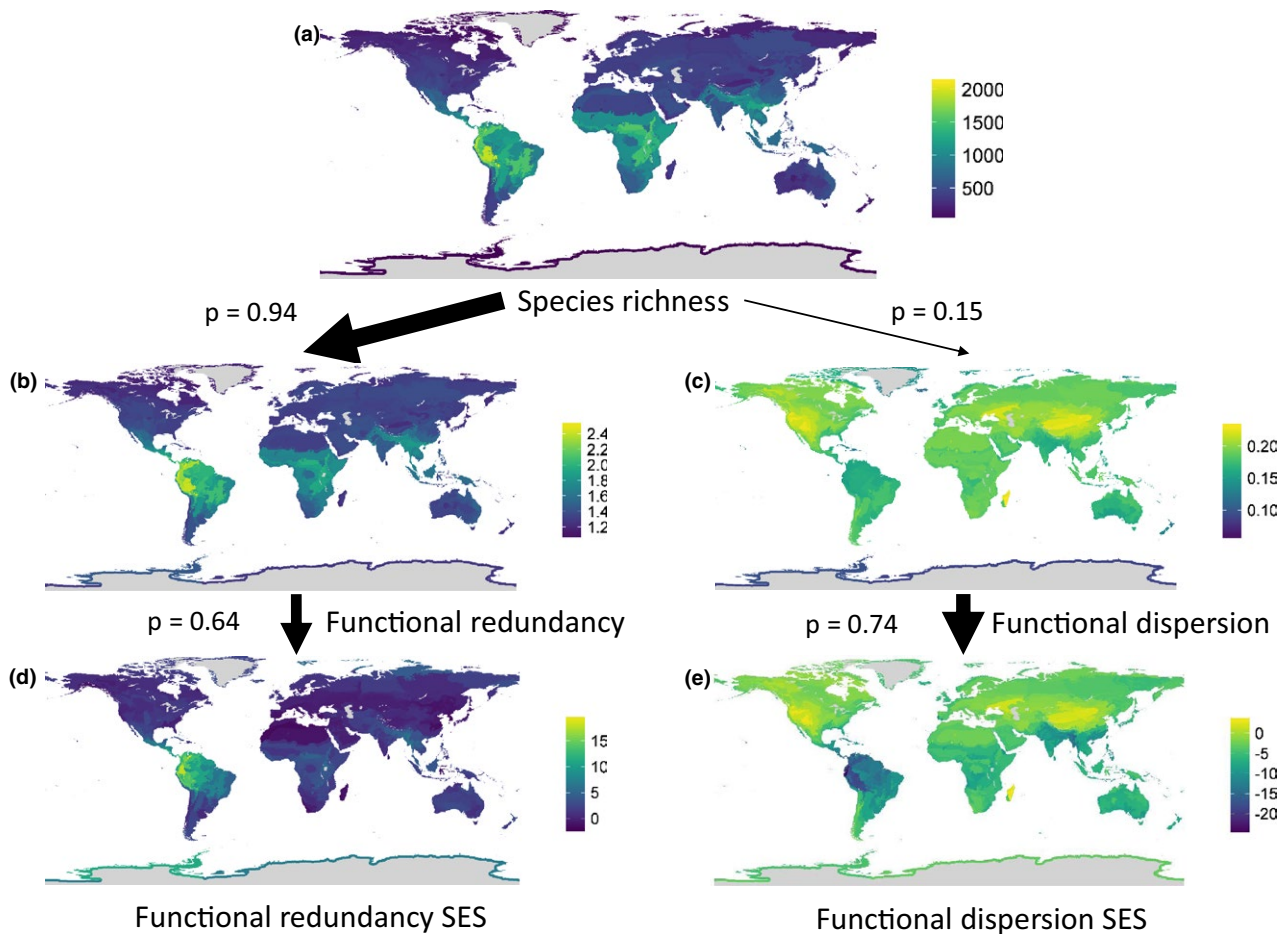
FIGURE 1 Functional dispersion and functional redundancy across 825 terrestrial ecoregions for 15,485 species (all extant terrestrial birds and mammals). (a) Species richness. (b) Functional redundancy. (c) Functional dispersion. (d) Functional redundancy standardized effect size (SES; calibrating against species richness, positive SES values indicate higher functional values than expected at random given their species richness and negative values vice versa). (e) Functional dispersion SES. Arrows are proportional to Spearman's ρ correlation coefficients (all correlations are significant; ρ_{823}, $p < .001$). Ecoregions in grey were not considered in the analyses ("lake" and "rock and ice" ecoregions, because they are not coherent systems, i.e., they occur at multiple locations across the globe)

(Supporting Information Appendix S4, Figure S4.7) and 1.5 within ecoregions. The most species-rich UTC contains 327 species and is characterized by ecologically similar species that are 10–32 g, have 2.0–2.5 offspring per litter/clutch, are diurnal, can fly, exist across two to four habitats and are invertivores. In contrast, 43% of UTCs are composed of only one species, and of these ecologically unique species, 55% are mammals (719 mammal species) and 45% birds (578 bird species) (Supporting Information Appendix S4, Figure S4.7).

We also identify a common currency of traits (body mass, diel activity, diet, habitat breadth, litter/clutch size and volancy) across birds and mammals. We find cross-taxa redundancy for the traits included here, with 31 cross-taxa UTCs (335 species: 175 bird and 160 mammal species). For example, we identify a UTC composed of four bird species and five mammal species: spangled owlet-nightjar, *Aegotheles tatei*; Sri Lankan frogmouth, *Batrachostomus moniliger*; cinnamon dog-faced bat, *Cynomops abrasus*; Archbold's nightjar, *Eurostopodus archboldi*; cyclops roundleaf bat, *Hipposideros cyclops*; Pratt's roundleaf bat, *Hipposideros pratti*; rufous-bellied nighthawk,

Lurocalis rufiventris; Medje free-tailed bat, *Mops congicus*; and Pel's pouched bat, *Saccolaimus peli*. These nine species thus have similar ecological strategies and play similar roles, such as nocturnal insect predation.

Patterns of functional redundancy and functional dispersion are geographically structured. Tropical ecoregions display the highest functional redundancy, conforming to previously described patterns of taxonomic diversity (Gaston, 2000; Hillebrand, 2004; Figure 1a,b; correlation between species richness and functional redundancy: $\rho_{823} = .94$, $p < .001$). Conversely, we observe a weak relationship between species richness and functional dispersion (Figure 1a,c; $\rho_{823} = .15$, $p < .001$), although the relationship is stronger and contrasting for birds (Supporting Information Appendix S4, Figure S4.5; $\rho_{823} = -.51$, $p < .001$) and mammals (Supporting Information Appendix S4, Figure S4.6; $\rho_{823} = .56$, $p < .001$). Ecoregions with the highest functional dispersion are primarily located outside the tropics; 95% of the top 10% of ecoregions are non-tropical, based on functional dispersion. Specifically, ecoregions with the highest functional

dispersion are located across Madagascar, Eastern Asia (especially the Gobi and Taklimakan deserts and the Tibetan and Mongolian plateaus), Western USA and the Pontic steppe (Russia, Kazakhstan and Ukraine; Figure 1c). Thus, we find, as predicted, that functional redundancy is coupled with species richness, resulting in high functional redundancy across the tropics, whereas functional dispersion is largely decoupled from richness (Figure 1).

However, we find a different geographical signal after accounting for species richness. Standardized effect size reveals that, on average, ecoregions are more redundant (global mean functional redundancy SES = 2.9; 47% of ecoregions have greater functional redundancy than expected at random, $p \leq .05$) and are less dispersed (global mean functional dispersion SES = −6.2; 84% of ecoregions have less functional dispersion than expected at random, $p \leq .05$) than expected under null model assumptions (Figure 1d,e; for SES values and permutation test p-values per ecoregion, see https://figshare.com/articles/Global_trade-offs_of_functional_redundancy_and_functional_dispersion_for_birds_and_mammals/5616424). The Neotropics, especially the Andean region, present an extreme example of this pattern, with functional redundancy $\sim 10 SD$ higher and functional dispersion $\sim 15 SD$ lower than expected at random (Figure 1d,e). Thus, ecoregions in the Neotropics are composed of many species with similar ecological strategies and functional roles.

Ecoregions with the highest functional redundancy SES are concentrated within the Neotropics (Figure 1d); 92% of the top 10% of ecoregions were Neotropical, based on functional redundancy SES, which differs from the broader inclusion of tropical ecoregions as hotspots of functional redundancy (Figure 1b,d; $\rho_{823} = .64$, $p < .001$). Functional dispersion SES shows similar patterns to functional dispersion (Figure 1c,e; $\rho_{823} = .74$, $p < .001$).

Our functional lens therefore identifies ecoregions that have equal species richness, such as the Patagonian steppe (Argentina

and Chile) and Northern short grasslands (USA and Canada) (419 species each) but very different functional values: Patagonian steppe functional redundancy SES = 2.5, functional dispersion SES = −4.8; Northern short grasslands functional redundancy SES = 0.7, functional dispersion SES = 0.1.

We also identify a spatial disconnect between functional redundancy SES and functional dispersion SES ($\rho_{823} = −.64$, $p < .001$; Figure 2). For example, ecoregions generally have either: (a) high functional redundancy SES coupled with low functional dispersion SES, characterized by much of the area south of the Tropic of Cancer (Figure 2a; dark red areas); or (b) high functional dispersion SES and low functional redundancy SES, such as across Madagascar, Eastern and Central Asia and Western USA (Figure 2a; yellow areas). Some ecoregions, such as across the Sahara and North America, show a more balanced relationship between functional redundancy SES and functional dispersion SES (Figure 2a; orange areas), although there are few ecoregions with both high redundancy and dispersion (Figure 2b). We thus reveal a global trade-off between functional redundancy SES and functional dispersion SES.

Finally, our results highlight that birds and mammals do not contribute equally to redundancy and dispersion (Figure 3). Before accounting for species richness, birds have greater functional redundancy than mammals (Figure 3a; Kolmogorov-Smirnov D statistic = .53, $p < .001$), whereas mammals show greater functional dispersion than birds (Figure 3b; $D = .97$, $p < .001$), confirming our predictions. However, when accounting for species richness we find the reverse, with greater functional redundancy SES for mammals (Figure 3c; $D = .51$, $p < .001$) and greater functional dispersion SES for birds (Figure 3d; $D = .25$, $p < .001$).

The greater contribution to functional redundancy SES for mammals is particularly strong across tropical biomes, such as mangroves;
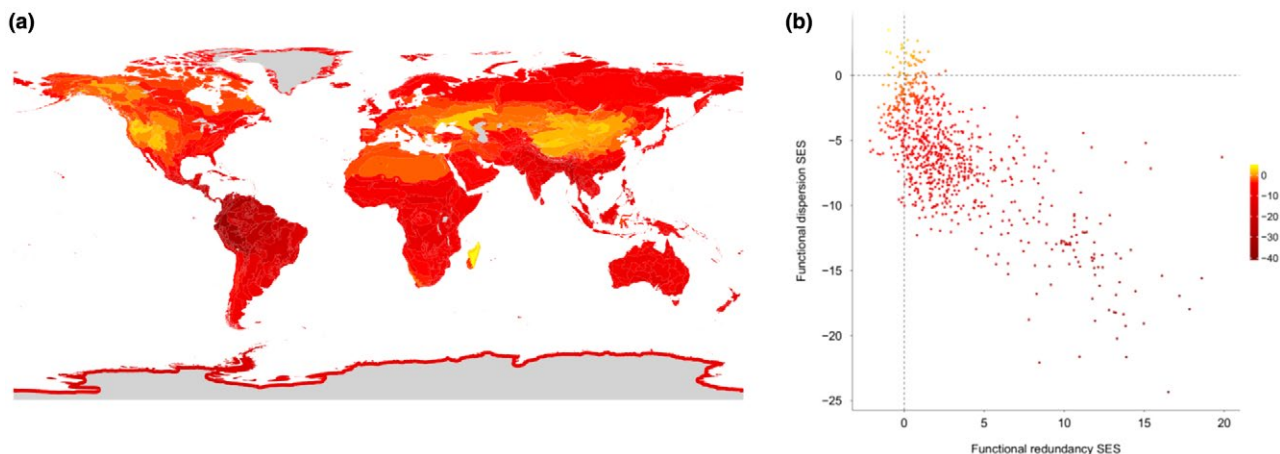

FIGURE 2 The trade-off between functional redundancy and functional dispersion across 825 terrestrial ecoregions for 15,485 species (all extant terrestrial birds and mammals). (a) Mapped spatially. (b) Plotted. The trade-off is calculated as functional dispersion standardized effect size (SES) minus functional redundancy SES. Thus, negative values (dark red) demonstrate greater redundancy than dispersion based on null expectations, positive values (yellow) indicate the dominance of dispersion, and zero values (orange) highlight a balance between the two. The SES represents the magnitude of the difference between the observed and null results and is therefore scaled relative to the null and is directly comparable between the two metrics. The same colour/transparency scheme is applied to the map and scatter plot. Ecoregions in grey were not considered in the analyses ("lake" and "rock and ice" ecoregions, because they are not coherent systems, i.e., they occur at multiple locations across the globe)
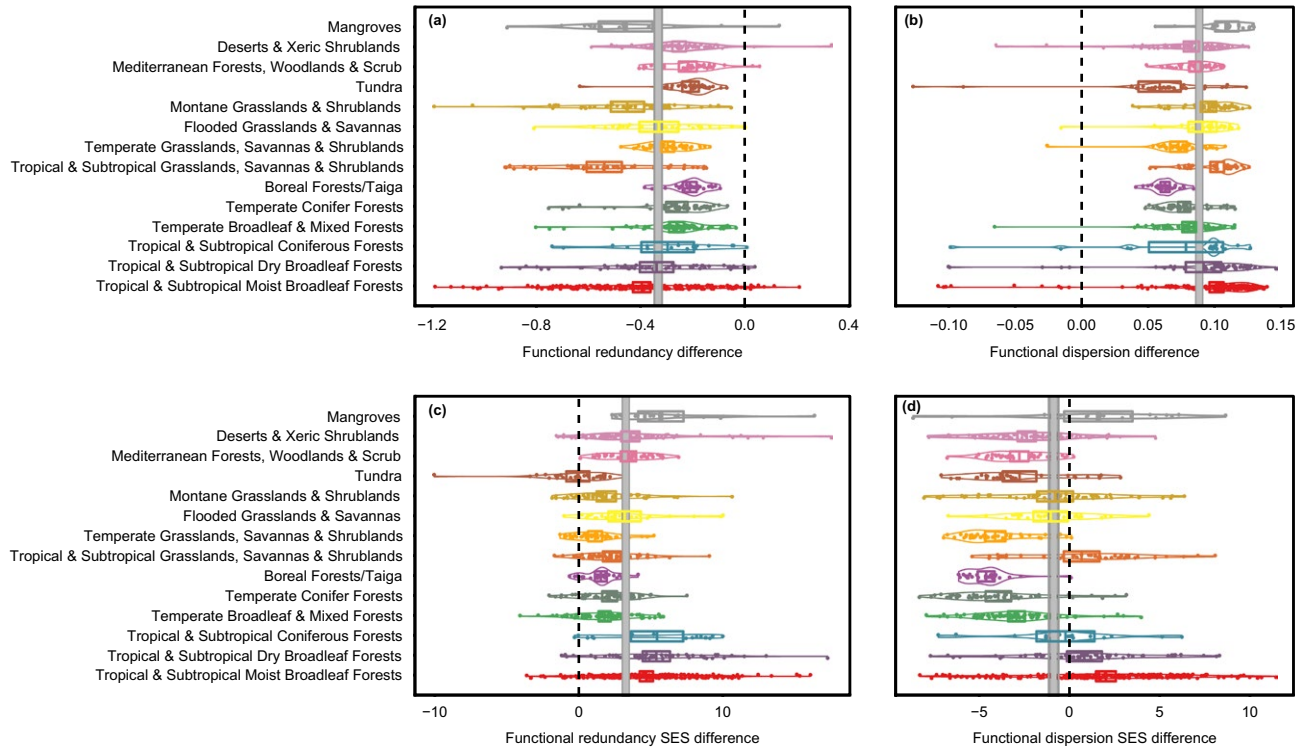
FIGURE 3 Functional differences (functional value for mammals minus functional value for birds) between birds and mammals across the world's biomes. Differences for: (a) functional redundancy; (b) functional dispersion; (c) functional redundancy standardized effect size (SES; calibrating against species richness); and (d) functional dispersion SES. Negative values indicate greater functional values for birds compared with mammals, whereas positive values represent greater contributions from mammals. Included for each panel is a dashed line with an intercept of zero (i.e., the null hypothesis of no difference between birds and mammals) and a line for the global average across all ecoregions (light grey line) with 95% confidence intervals (dark grey envelope). Also included are the values for each ecoregion per biome as jittered points, violins of data density and boxplots where the central thick line is the mean and the edges of the rectangle are the 95% confidence intervals around the mean

tropical and subtropical coniferous forests; and tropical and subtropical dry broadleaf forests (Figure 3c). Conversely, the greater contribution to functional dispersion SES for birds is strongest across temperate and polar biomes, such as boreal forests/taiga; temperate grasslands, savannas and shrublands; and temperate conifer forests (Figure 3d). The difference in functional dispersion SES for birds and mammals is also reflected spatially, where birds have high functional dispersion SES across temperate ecoregions, and mammals show high functional dispersion SES across tropical ecoregions (Supporting Information Appendix S4, Figures S4.5e, S4.6e).

Our findings were robust to the imputation of missing trait data, the traits selected and the scale at which the randomized pool was constructed (see Supporting Information Appendix S4, Figures S4.1, S4.2, S4.4 and Table S4.3).

4 | DISCUSSION

Here, we quantify functional redundancy and functional dispersion globally for 15,485 bird and mammal species, using a systematic approach. Previous global analyses have focused on either functional redundancy (sensu Huang, Stephens, & Gittleman, 2012) or functional dispersion (Oliveira et al., 2016) for mammals only, but here

we summarize both redundancy and dispersion across birds and mammals for the first time. We also establish a common currency of traits that allow comparisons and analyses to be made across and between birds and mammals, broadening current single-taxon approaches (Barbet-Massin & Jetz, 2015; Oliveira et al., 2016; Safi et al., 2011). We find overlap in the roles played by birds and mammals, even when including flight ability and diel activity (two major differentiators between birds and mammals), indicating cases where birds and mammals have converged on similar ecological strategies. Thus, single-taxon analyses testing for functional redundancy and functional dispersion offer limited insights, because an unknown number of roles fulfilled by other taxa is ignored (Dehling & Stouffer, 2018). These results therefore demonstrate the importance of considering ecological comparability between birds and mammals in conservation strategies.

Species richness has dominated our view of global biodiversity patterns for centuries (Gaston, 2000; Hillebrand, 2004); however, functional redundancy and functional dispersion are increasingly recognized as essential biodiversity components (Elmqvist et al., 2003; Laliberté et al., 2010; Luck et al., 2013; Oliver, Isaac, et al., 2015). Although high species richness, functional redundancy and functional dispersion are all predicted to increase the capacity of communities to adapt, reassemble, retain biotic interactions and

maintain ecosystem functions with disturbance events (Holling, 1973; Hooper et al., 2005; Laliberté et al., 2010; Luck et al., 2013; Oliver, Heard, et al., 2015; Oliver, Isaac, et al., 2015; see Supporting Information Appendix S1), our results show that all three do not generally coexist in the ecoregional species pools of birds and mammals. Instead, we observe that the overall breadth of functional roles for bird and mammal species combined does not increase proportionally with richness, leading to a global trade-off between functional redundancy and functional dispersion (Figure 2). We therefore suggest that different processes generate species richness/functional redundancy and functional dispersion, leading to a novel, and generally non-tropical, distribution of hotspots of high functional breadth for birds and mammals, across Madagascar, Eastern Asia, Western USA and the Pontic steppe. A potential explanation is that these predominantly steppe and desert regions are highly dynamic and environmentally variable, resulting in high levels of competition, strong spatio-temporal resource partitioning, and therefore high ecological dissimilarity.

We also find strong spatial differences in the contributions of birds and mammals to functional redundancy and dispersion (Figure 3). Before accounting for species richness, birds have greater functional redundancy than mammals, simply because birds are more species rich compared with mammals (almost double the number of species of birds). As species richness increases, the similarity in species functional roles also increases (Safi et al., 2011). However, after accounting for species richness, mammals show greater similarity in their functional roles, whereas birds support greater breadth of functional roles. This is particularly apparent in the tropics, where mammals have relatively higher functional redundancy SES. Birds, in comparison, have higher functional dispersion SES, predominantly across temperate and polar biomes. We propose that this latitudinal trade-off between birds and mammals could be underpinned by the pronounced mobility of birds, which could allow them to exploit transient mid/high-latitude resources (Kirby et al., 2008). For instance, one of the most common patterns for migratory birds is to breed in northern temperate or polar biomes, before spending the non-breeding season in tropical biomes (Kirby et al., 2008). Birds may therefore provide ecological and functional links (Lundberg & Moberg, 2003) between tropical and temperate biomes. Alternatively, the latitudinal trade-off between birds and mammals could be the consequence of the late Quaternary extinctions and extirpations, which reshaped patterns of mammalian species richness and functional diversity (Faurby & Svenning, 2015). In particular, the late Quaternary extinctions led to reduced functional diversity of mammals outside sub-Saharan Africa (Faurby & Svenning, 2015). We therefore suggest that the late Quaternary extinction filter could have resulted in the higher functional dispersion SES for birds compared with mammals across temperate and polar biomes.

The greater functional dispersion SES of birds at high latitudes has the potential to stabilize ecosystem functions (e.g., process rates) through compensatory dynamics between species (i.e., the portfolio effect), where a diversity of responses should lead to some bird species successfully responding to a specific disturbance

(Elmqvist et al., 2003; Luck et al., 2013; Mori, Furukawa, & Sasaki, 2013; see Supporting Information Appendix S1). In contrats, the higher functional redundancy SES of mammals than birds across the tropics could insure these regions against species loss and declines (Carmona et al., 2016; Fonseca & Ganade, 2001; Luck et al., 2013); the loss of species from ecoregions with high redundancy should not result in a substantial decrease in function, because other species with similar traits are likely to remain (Carmona et al., 2016; Flynn et al., 2009).

Under null model assumptions, on average, ecoregional species pools are functionally more redundant and less dispersed than expected. Therefore, species within ecoregions are more clustered (had more similar trait values) than expected at random, which could be attributable to several different processes. A plausible candidate for this finding of over-redundancy and underdispersion is environmental filtering. Environmental filtering theory states that abiotic factors, such as climatic stress, increasingly constrain the trait combinations expressed in environments (Lamanna et al., 2014). Thus, environmental filtering at the ecoregion scale might limit the trait space that species can occupy, increasing functional similarity within ecoregions compared with a global- or biome-based null, especially across the Neotropics and for mammals. For instance, the higher functional redundancy SES for mammals compared with birds could be attributable to stronger environmental filtering, leading to greater ecological similarity for mammals within ecoregions, whereby ecoregional scale selection favours a restricted set of mammalian traits. Consequently, we suggest that weaker environmental filtering for birds might allow a greater breath of functional roles to coexist within the species pool.

The highest functional redundancy SES is across the Neotropics. Neotropical ecoregions are, therefore, composed of many species with similar functional roles and ecological strategies. There are a number of potential, non-mutually exclusive mechanisms for the finding of greater redundancy than expected across the Neotropics, such as high environmental stability, relaxed competition, low environmental heterogeneity, strong environmental filtering, high productivity and/or slow trait evolution (Belmaker & Jetz, 2015; Lamanna et al., 2014; Oliveira et al., 2016; Safi et al., 2011). For instance, low seasonality and high resource availability, as observed across the Neotropics, might together facilitate the coexistence of functionally redundant species (Oliveira et al., 2016; Safi et al., 2011); the "more individuals" hypothesis (Currie et al., 2004). Alternatively, or in addition to resource availability, we suggest that the high species richness observed in the Neotropics could result from a fast accumulation of species, owing to higher rates of speciation (via increased opportunities for the evolution of reproductive isolation, or faster molecular evolution, or the increased importance of biotic interactions) and/or low extinction rates (Belmaker & Jetz, 2015; Currie et al., 2004; Mittelbach et al., 2007; Rolland, Condamine, Jiguet, & Morlon, 2014). This high Neotropical richness might then promote stabilizing selection on traits, inhibiting evolutionary responses within species (de Mazancourt, Johnson, & Barraclough, 2008) and ultimately lead to strong ecological similarities, highly

conserved trait combinations and high functional redundancy SES. The high functional redundancy SES across the Neotropics could therefore be simply the result of rapid accumulation of species with little time for ecological divergence. In addition, our results add further evidence that the high species richness in the Neotropics is associated with a denser occupation of trait space ("niche packing"), which could arise through finer specialization or greater overlap in resource use, rather than a consequence of more ecological opportunities ("niche expansion"; Belmaker & Jetz, 2015; Klopfer & MacArthur, 1961; MacArthur, 1965; Pigot, Trisos, & Tobias, 2016).

It is possible that the interrelationship between redundancy and dispersion, such as hotspots of each, could be used to identify the mechanisms by which environmental change might impact ecoregional species pools. For example, a given disturbance might result in greater species loss from an ecoregion with low dispersion, but if functional redundancy is high this perturbation might have little impact on functioning overall (Luck et al., 2013). Conversely, if dispersion is high, an assemblage overall might respond successfully to environmental changes, but the loss of even a few species could have major implications if redundancy is low (Luck et al., 2013). Ecoregions can, therefore, generally be divided into those potentially more vulnerable to disturbance events (high redundancy, low dispersion, e.g., the Neotropics) and those potentially more vulnerable to species loss (low redundancy, high dispersion, e.g., Madagascar).

Thus, overall our results illustrate that focusing conservation efforts in regions with high species richness, as is traditionally done (Olson & Dinerstein, 2002; Reid, 1998), will simultaneously benefit species richness and functional redundancy, but will not maintain functional dispersion. However, the relationship between species richness and functional dispersion differs for birds and mammals when analysed separately. For birds, the prioritization of species richness will have undesirable consequences for functional dispersion, owing to a negative relationship between richness and dispersion, whereas for mammals the conservation of species richness will provide some support of functional dispersion. In addition, phylogenetic diversity, which is often used to guide conservation management, has been found to capture functional diversity unreliably (Mazel et al., 2018), thus functional indices provide a complementary and distinct dimension of biodiversity, in combination with taxonomic and phylogenetic diversity. Hence, we suggest that functional dispersion should be evaluated further as a conservation objective. For instance, ecoregions with high functional dispersion should have greater capacity to respond successfully to multiple disturbances, because greater functional dispersion is predicted to lead to asynchrony between the population sizes of species and enhanced compensatory responses after environmental change, and therefore, greater ecological recovery and stability (Mori et al., 2013; Oliver, Heard, et al., 2015). Furthermore, the importance of functional dispersion is predicted to become increasingly evident in an ever-changing world (Elmqvist et al., 2003; Laliberté et al., 2010; Luck et al., 2013), especially in relationship to disturbances that span the globe and are difficult to manage directly, such as climate change (Barbet-Massin & Jetz, 2015). We therefore recommend further

study of the identified regions of high and low functional dispersion for birds and mammals combined and separately, which could elucidate the mechanisms and temporal impacts of high functional breadth for these taxa.

The traits used were selected to reflect the spatio-temporal distribution of resource capture, utilization and release by birds and mammals. However, the ecological importance of any particular trait might vary across and between bird and mammal taxa, and the selection of ecologically relevant traits is always somewhat subjective and dependent on data availability (Belmaker & Jetz, 2015; Mouillot et al., 2014; Oliveira et al., 2016). To tackle this, we implemented a transparent and systematic trait selection process (Supporting Information Appendix S3; Luck et al., 2012), within the constraints of data availability and data resolution, to construct the most complete and inclusive database of bird and mammal traits to date. The patterns and relationships we outline here reflect a complex history of speciation, extinction, anagenesis and dispersal, with each factor probably shaped by species traits (Davies et al., 2008) and dynamically driven by both natural (e.g., environmental filtering, biogeography, competition) and human pressures (e.g., habitat loss, invasive species). Here, we analyse only the resultant outcome of these two types of drivers on species composition, because disentangling these processes is beyond the scope of our study. We also accounted explicitly for only two of the major components of the functional roles of species: species distributions and species ecological strategies (traits). We did not, however, account for the direct interactions between species and their effects on each other, known as the "Eltonian shortfall" (Peterson et al., 2011), although information on species interactions is contained indirectly within our analysis through species diets (Dehling & Stouffer, 2018). Thus, future work that explicitly accounts for the interactions between species within the regional species pool, for instance, by using network analysis (Dehling & Stouffer, 2018), could reveal further insights into how species roles and functional contributions summate across the regional pools.

In conclusion, we show that the analysis of functional redundancy and functional dispersion at the global scale can provide new insights into taxonomic, trait and spatial signals of bird and mammal diversity. We recommend consideration of both the similarity and the breadth of functional roles across multi-taxa species pools, in order to accommodate the global trade-off between functional redundancy and functional dispersion and to support the maintenance of insurance and response diversity between and within ecoregions.

AUTHOR CONTRIBUTION

R.S.C.C., A.E.B. and F.E. formulated the study; R.S.C.C. developed and implemented the analyses and wrote the first draft. All authors contributed to interpreting the results and the editing of manuscript drafts.

DATA ACCESSIBILITY

Distribution data are available via the IUCN (https://www.iucn-redlist.org/resources/spatial-data-download) and BirdLife (http://datazone.birdlife.org/species/requestdis). An ecoregion-scale species-by-site matrix is available from figshare: https://figshare.com/articles/Global_trade-offs_of_functional_redundancy_and_functional_dispersion_for_birds_and_mammals/5616424.

The raw trait data are available from multiple sources (Jones et al., 2009; Myhrvold et al., 2015; Pacifici et al., 2013; Wilman et al., 2014); generation length for birds was supplied by BirdLife, but restrictions apply to the availability of these data, which were used under licence for the present study, and so are not publicly available. Bird generation length data are, however, available directly from BirdLife (birdlife@birdlife.org) upon reasonable request. The compiled (untransformed) trait data (see Supporting Information Appendix S3 for details on the data compilation process) are available from figshare: https://figshare.com/articles/Global_trade-offs_of_functional_redundancy_and_functional_dispersion_for_birds_and_mammals/5616424, including the single, randomly selected, imputed dataset.

The empirical and null values for functional dispersion and functional redundancy per ecoregion are also available from figshare.

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BIOSKETCHES

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.