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RESEARCH PAPER

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Functional biogeography of dietary strategies in birds

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Abstract

Aim: Diet is key to understanding resource use by species, their relationships with their environment and biotic interactions. We aimed to identify the major strategies that shape the diet space of birds and to investigate their spatial distributions in association with biogeographical, bioclimatic and anthropogenic drivers.

Location: Global.

Time period: Current.

Major taxa studied: Birds.

Methods: We analysed score-based assessments of eight diet categories for 8,937 out of 10,964 extant bird species. We constructed a multivariate diet space by ordinating these data in a principal coordinates analysis and assessed its dimensionality as a balance between the representation of original diet scores and parsimony. We averaged the positions of species along each dimension for 12,705 species assemblages and used quantile regressions to infer the relative contributions of species richness, climate, primary productivity, topography and human footprint to the spatial distribution of the diet space at a global scale.

Results: The diet space of birds was structured by four dimensions ordinating species along continua ranging from insectivory to plant-based strategies, granivory to frugivory, common to rare diets, and nectarivory to carnivory and piscivory. Although orthogonal at the species level, these dimensions were correlated among species assemblages, with regional variation consistent with past climatic and tectonic events. Human footprint packed bird assemblages in the diet space, whereas warm climate, high productivity and high topographic variability were associated with high variability in the prevalence of dietary strategies among assemblages.

Main conclusions: The tremendous variability in bird diets can be explained by a few basic ecological continua sustained by morphological and ecophysiological differences among species. Strong biogeographical legacies on top of bioclimatic drivers distribute this diet space in species assemblages through environmental filtering and niche packing. However, these patterns are altered at macroecological scales by human-mediated functional homogenization, which might, in turn, affect the global distribution of bird functions and services.

KEYWORDS
biotic homogenization, birds, dietary strategies, ecological traits, functional biogeography, human footprint, multivariate analysis

1 | INTRODUCTION

How the variety of life-forms is organized in the geographical space and along environmental gradients is a long-standing question in biogeography, at the crossroads of evolutionary and functional ecology (Grinnell, 1917; MacArthur, 1972; Soberon, 2007; Violle, Reich, Pacala, Enquist, & Kattge, 2014). Trait-based strategies for growth, survival and reproduction represent a key connection between this diversity and the environment (Garnier, Navas, & Grigulis, 2016; McGill, Enquist, Weiher, & Westoby, 2006), by providing a functional explanation of species' geographical distributions and assemblages (McGill et al., 2006; Violle et al., 2014). Understanding how and why trait strategies vary in space and time should, in particular, illuminate the causes of species distributional shifts related to global changes and their vulnerability to anthropogenization (Jiguet, Gadot, Julliard, Newson, & Couvet, 2007; Purvis et al., 2000). However, inferences on trait–environment relationships have proved challenging because of the multidimensionality of the underlying niche space (Hutchinson, 1957; Laughlin, 2014), unequal contributions of traits to niche dimensions (Tucker, Davies, Cadotte, & Pearse, 2018) and data-deficient trait descriptions (Hortal et al., 2015). As a result, the macroecological distribution of trait strategies remains unknown for the vast majority of taxonomic groups (Garnier et al., 2016).

The > 10,000 avian species in the world exhibit a tremendous variability in ecological traits, which has allowed them to colonize virtually all emerged habitats on Earth (Lovette & Fitzpatrick, 2016). Owing to this diversity, birds sustain numerous ecosystem functions, including pollination, seed dispersal, pest regulation and creation of microhabitats, making them a key element of ecosystem-based conservation strategies (Şekercioğlu, Wenny, & Whelan, 2016). Diet is central to these functions and to various aspects of bird life cycle, ecosystem position and evolution (Burin, Kissling, Guimarães, Şekercioğlu, & Quental, 2016; Duffy, 2002; Lovette & Fitzpatrick, 2016). It thus forms one of the most crucial dimensions of bird life history (Hutchinson, 1959), because it determines the main lines of a species' energetic investment, survival, reproduction and, in turn, fitness (Costa, Vitt, Pianka, Mesquita, & Colli, 2008; MacArthur & Pianka, 1966; Sibly et al., 2012). Illustrating the pivotal role of diet in animal ecophysiology, herbivorous bird species exhibit lower basal metabolic rates, higher field metabolic rates and higher body temperatures than carnivores (Anderson & Jetz, 2005; Speakman, 1999), whereas energetic and water turnovers reach extreme values in nectarivorous birds (Nicolson & Fleming, 2003). As a corollary of these physiological constraints, the size and energetic value of prey are related to essential functional traits, such as body size or reproductive output, and to other ecological characteristics, such as habitat use (Janes, 1994; Sam, Koane, Jeppy, Sykorova, & Novotny, 2017; Sibly et al., 2012). Diet is under strong selection pressure because of its tight link with individual fitness, notably through competitive interactions and co-evolutionary dynamics associated with extreme morphological or ecophysiological adaptations (Grant & Grant, 2006; Nicolson & Fleming, 2003). Hence, the multiple convergences and trade-offs that have structured the evolution of traits in birds are likely to be reflected in dietary strategies that are related to biogeographical patterns of bird–environment relationships.

The highly uneven geographical distribution of bird diets could be explained by a combination of climate, primary productivity, distribution of trophic resources, and phylogenetic niche conservatism (Barnagaud et al., 2014; Kissling, Şekercioğlu, & Jetz, 2012; Lein, 1972). Dietary guild richness is strongly correlated with species richness on top of these environmental gradients, consistent with the hypothesis that long-term environmental variations have shaped dietary diversification within avian assemblages (Belmaker, Şekercioğlu, & Jetz, 2012; Burin et al., 2016; Kissling et al., 2012). High flowering and fruit plant diversities are typically sustained by climate stability and high primary productivity in the tropics, favouring the diversification of frugivores and nectarivores (Dalsgaard et al., 2011, 2017; Jetz et al., 2009; Kissling, Rahbek, & Bohning-Gaese, 2007). Inversely, at northern latitudes, carnivore and scavenger bird assemblages are composed of phylogenetically clustered species, as a consequence of past diversification events related to the physiological tolerance of the species and climatic constraints that affect prey distributions (Kissling et al., 2012; Vejrikova et al., 2016).

Previous studies on spatial patterns in bird diets have examined guild-level species richness (Burin et al., 2016; Kissling et al., 2012) or were geographically restricted (Pigot et al., 2016). One strong limitation of guild-based approaches is that they do not account for covariations among diets resulting from the evolutionary constraints of species. For instance, it is unclear whether the global congruence between high insectivore and frugivore species richness is attributable to species preying simultaneously on insects and fruits or to convergences in the distributions of species specialized on each diet (Kissling et al., 2012). Furthermore, guild approaches rely on a priori categorizations that hinder the probabilistic nature of dietary choices, more adequately quantified by continua reflecting the observation that most species rely on multiple diets in varying proportions. Covariation in the diets of birds is thus better represented within a multivariate space structured by a few continuous, orthogonal dimensions (MacArthur, 1972; Pianka, Vitt, Pelegrin, Fitzgerald, & Winemiller, 2017; Winemiller, Fitzgerald, Bower, Pianka, & Arita, 2015). The shape of this diet space is assumed to have emerged as an outcome of niche convergence and niche exclusion processes (Morowitz, 1980; Winemiller et al., 2015), providing an interface between species' diversification processes and their functions (Grime & Pierce, 2012; Wüest, Münkemüller, Lavergne, Pollock, & Thuiller, 2018), which remains, however, poorly quantified. In particular, investigating how the diet space is spread among bird assemblages at a macroecological scale might help to uncover the relative contributions of historical legacies, environmental filtering and niche convergence to the distribution of bird diets and associated functions.

Geographical variation in the diet space of a taxonomic group can be mapped by averaging the position of co-occurring species along each of its dimensions to provide a community-level attribute comparable to the widely used community-weighted mean traits approach (Ricotta & Moretti, 2011; Wüest et al., 2018). This approach resolves the double limitation of guild-based studies: first, it incorporates species-level covariations among diets in a quantitative assessment of community composition; and second, scores computed in an ordination space permit a continuous representation of gradients from assemblages dominated by opposed dietary strategies. Two patterns are likely to be identified when correlating the average positions of bird assemblages in the diet space. A systematic variation in the average diet positions of species assemblages along a well-identified environmental gradient would indicate diet-mediated environmental filtering, which is typically expected with gradual changes in climate or dominant resources along latitudinal or elevational gradients (Cadotte & Tucker, 2017). Alternatively, an increase or decrease in the range of average diet positions would reveal a differentiation or homogenization of assemblages, respectively, as a consequence of changes in resources, typically in association with productivity or high environmental heterogeneity in transition areas or mountains (Dehling et al., 2014; Pellissier, Barnagaud, Kissling, Şekercioğlu, & Svenning, 2018; Pigot et al., 2016). A packing of species assemblages in the diet space is also expected under the effect of man-mediated functional homogenization, as an outcome of the reduction in environmental turnover and simplification of the ecosystem network in highly anthropogenized areas (Baiser & Lockwood, 2011).

The aim of this study was to uncover the main dimensions of the diet space of birds and their geographical and environmental spread at a global scale. We constructed a diet space for 83% of extant bird species, mapped it and studied its distribution along climatic, topographic, productivity and anthropogenization gradients, accounting for variations in species richness. Following the prediction by MacArthur (1972), we hypothesized that no more than two to four dimensions would summarize parsimoniously the continua that structure the diets of the birds of the world. We also expected that the average positions of species assemblages along these continua would be patterned strongly in the geographical space under functional homogenization and differentiation mediated by environmental gradients and human impact.

2 | MATERIALS AND METHODS

2.1 | Data

2.1.1 | Bird diets

We compiled diet information for 9,098 out of the 10,694 extant bird species currently recognized by the International Ornithological Union, covering all 40 orders (Gill & Donsker, 2017). Among the 1,596 missing species, 1,583 were data deficient and 13 had unclassifiable diets. We also removed 161 species for which we did not have distribution or phylogenetic data, resulting in a final dataset of 8,937 species. We assessed scores of use from zero (non-use) to 10 (exclusive use) for each species and eight diet categories (fishes, vertebrates, carrion, insects, nectar, fruits, seeds and other plant material) based on the most comprehensive available information to date (Del Hoyo, Elliott, & Sargatal, 2013; Kissling et al., 2012; Şekercioğlu, Daily, & Ehrlich, 2004). Scores summed to 10 per species over all categories, thus providing a standardized, probabilistic assessment of species' diets.

2.1.2 | Species assemblages

We defined species assemblages by overlaying species' breeding extent-of-occurrence maps provided by BirdLife International (BirdLife International & Nature Serve, 2012) on a 110 km × 110 km resolution grid in cylindrical equal area projection. Extent-of-occurrence maps are not exempt from criticism, because they were built from expert opinion and incomplete observational records that are subject to error, especially at species range limits (Herkt, Skidmore, & Fahr, 2017). In spite of these limitations, these maps remain the best available description of bird distributions at the world scale. We only exploited breeding-period distributions, a limitation imposed by data deficiency on the wintering ranges of most migratory species. Diet assessments of migratory species are, however, usually conducted during the nestling period or as birds arrive on/leave breeding grounds (Del Hoyo et al., 2013), ensuring consistency between the diet and distribution datasets.

The spatial dataset encompassed 12,802 bird assemblages (grid cells), after exclusion of aquatic (> 10% of open waters in the cell) and Antarctic cells. We also removed cells with species richness < 10 species ($n = 97$ cells) because they would inflate statistical uncertainty. Furthermore, exploring species lists in these cells revealed that their extremely low species richness resulted, at least in part, from deficient assessments of species distributions in poorly surveyed areas, such as parts of North Africa or boreal Siberia. Hence, all our analyses relied on a sample size of 12,705 species assemblages (species richness from 10 to 849 species, mean ± SD = 179.6 ± 121.3 species).

2.1.3 | Environmental gradients

We retrieved rasters of mean annual temperatures (in degrees Celsius) from 1970 to 2000 at a 30″ native resolution (www.worldclim.org; Hijmans, Cameron, Parra, Jones, & Jarvis, 2005), elevational range (in metres) at a 1 km native resolution (global land cover characterization data base, https://lta.cr.usgs.gov/GLCC) and net primary productivity (NPP; in kilograms of carbon per square metre) at a 1 km native resolution (https://modis.gsfc.nasa.gov/data/dataprod/mod17.php; Zhao, Heinsch, Nemani, & Running, 2005). We also retrieved the human influence index (HII), a score-based synthetic measure of human impacts on ecosystems at a 1 km native resolution (Sanderson et al., 2002; updated for the 1995–2004 period, http://sedac.ciesin.columbia.edu/data/set/wildareas-v2-human-influence-index-geographic). We discarded precipitation, another influential predictor of bird distributions, owing to its high correlation with NPP ($R^2 = 0.6$); the other four variables were weakly correlated (maximum $R^2 = 0.21$, between NPP and temperature). We averaged all variables in each cell of the 110 km × 110 km grid for match with bird assemblage data. Correlations between bird species richness and the four bioclimatic variables peaked at $R^2 = 0.20$ (with temperature) and $R^2 = 0.24$ (with NPP).

2.2 | Building the diet space of birds

We characterized the main dimensions of the diet space of birds by the most parsimonious set of principal components of a principal coordinates analysis (PCoA; Legendre & Legendre, 2012). Principal coordinates analysis summarizes a species × species dissimilarity matrix into orthogonal components (or dimensions), and thus emphasizes relative differences among species rather than correlations among traits as a principal components analysis would do. In our analysis, these dimensions represented synthetic indices of the variation of dietary strategies among birds, clustering species with an average diet at the centre of the space and relegating the most distinct diets at its margins. Unlike principal components analysis, PCoA is robust to extreme values and double-zeros, which occurred in our data sets as a consequence of rare diets. Furthermore, PCoA is adequate to summarize non-continuous variables, such as pseudo-quantitative fuzzy scores, as in our data set.

To build the PCoA, we first calculated a species × species dissimilarity matrix from the original species × diet matrix using a modified version of Gower's distance that accommodates non-independent fuzzy variables with appropriate weighting (Pavoine, Vallet, Dufour, Gachet, & Daniel, 2009). We optimized the dimensions of the diet space by selecting a parsimonious set of PCoA components, which reflected well the pairwise distances defined in the Gower's dissimilarity matrix. For this, we calculated the mean squared deviation (mSD) between the Gower's matrix and an Euclidean matrix based on the scores of species along the PCoA dimensions, and selected the minimum dimensionality reaching an mSD of 0.01 (Maire, Grenouillet, Brosse, & Villéger, 2015). We validated the biological interpretability of the dimensions retained by projecting the original diet categories as supplementary variables on the Euclidean diet space formed by the PCoA components (Legendre & Legendre, 2012).

We computed Spearman rank correlation coefficients as a quantitative measure of the individual contribution of each diet category to each dimension of the diet space (Appendix S1). We also tested for a phylogenetic signal to measure the imprint of niche conservatism on each dimension of the diet space (Additional methods and results in Appendix S2).

2.3 | Spatial variations in the diet space of birds

We mapped the geographical spread of the diet space of birds by averaging species scores on each of its dimensions across all species occurring within each 110 km × 110 km grid cells. Similar to community-weighted mean trait values in functional ecology, this average score reflects the centroid of a species assemblage in the diet space (Newbold, Butchart, Şekercioğlu, Purves, & Scharlemann, 2012). We then regressed these assemblage-level scores on each dimension of the diet space against species richness, temperature, NPP, topographic heterogeneity and HII with quantile regressions, testing the 0.1, 0.25, 0.5, 0.75 and 0.9 quantiles (Davino, Furno, & Vistocco, 2013; Koenker, 2016). In these models, parallel regression slopes across all quantiles would indicate environmental filtering (a systematic shift from a position to another in the diet space; Cadotte & Tucker, 2017), whereas converging or diverging slopes would indicate diet homogenization or differentiation among assemblages along a bioclimatic gradient. Note that we did not account for residual spatial autocorrelation because quantile regressions do not permit the incorporation of spatial errors easily, while alternative methods do not accommodate highly heteroscedastic data.

We assessed goodness-of-fit of quantile regressions through an approximate correlation coefficient (ρ) based on a comparison of the sum of weighted deviations of each model (ρ_1) with the sum of weighted deviations of a regression without any covariate (ρ_0):$\rho = 1 - (\rho_1/\rho_0)$ (Koenker & Machado, 1999). We performed all computations and analyses in the R environment (R Core Team, 2016) with packages ade4 (Dray & Dufour, 2007) and quantreg (Koenker, 2016).

3 | RESULTS

3.1 | The structure of the diet space of birds

Four PCoA components summarized well the dissimilarity of the 8,937 bird species diets (mSD = 0.01; mSD = 0.06, 0.025 and 0.005 for two-, three- and five-dimensional spaces, respectively) and explained 42.5, 20.4, 13.4 and 9.6%, respectively, of the total variance of the Gower's dissimilarity matrix, giving rise to a strongly supported four-dimensional diet space. The ordination of species in this multidimensional space reflects dietary dissimilarities between species without relying on a priori categorical classifications: the dietary strategies of birds spread continuously from the most undifferentiated at the centroid to the most distinct at the margins of the diet space.

The highest proportion of total variance in the diet space was explained by a first dimension separating insectivory from frugivory and granivory [Figure 1; principal component 1 (PC1)]. This structure implies that species feeding on fruits and/or seeds shared similar dietary regimes, whereas species feeding on insects had distinct diet compositions. Accordingly, the negative side of PC1 was dominated by insectivore specialists (Galbuliformes, Caprimulgiformes and Cuculiformes), whereas highly positive values included a mixture of typical frugivores (Psittaciformes) and typical granivores (Pterocliformes; Appendix S2).

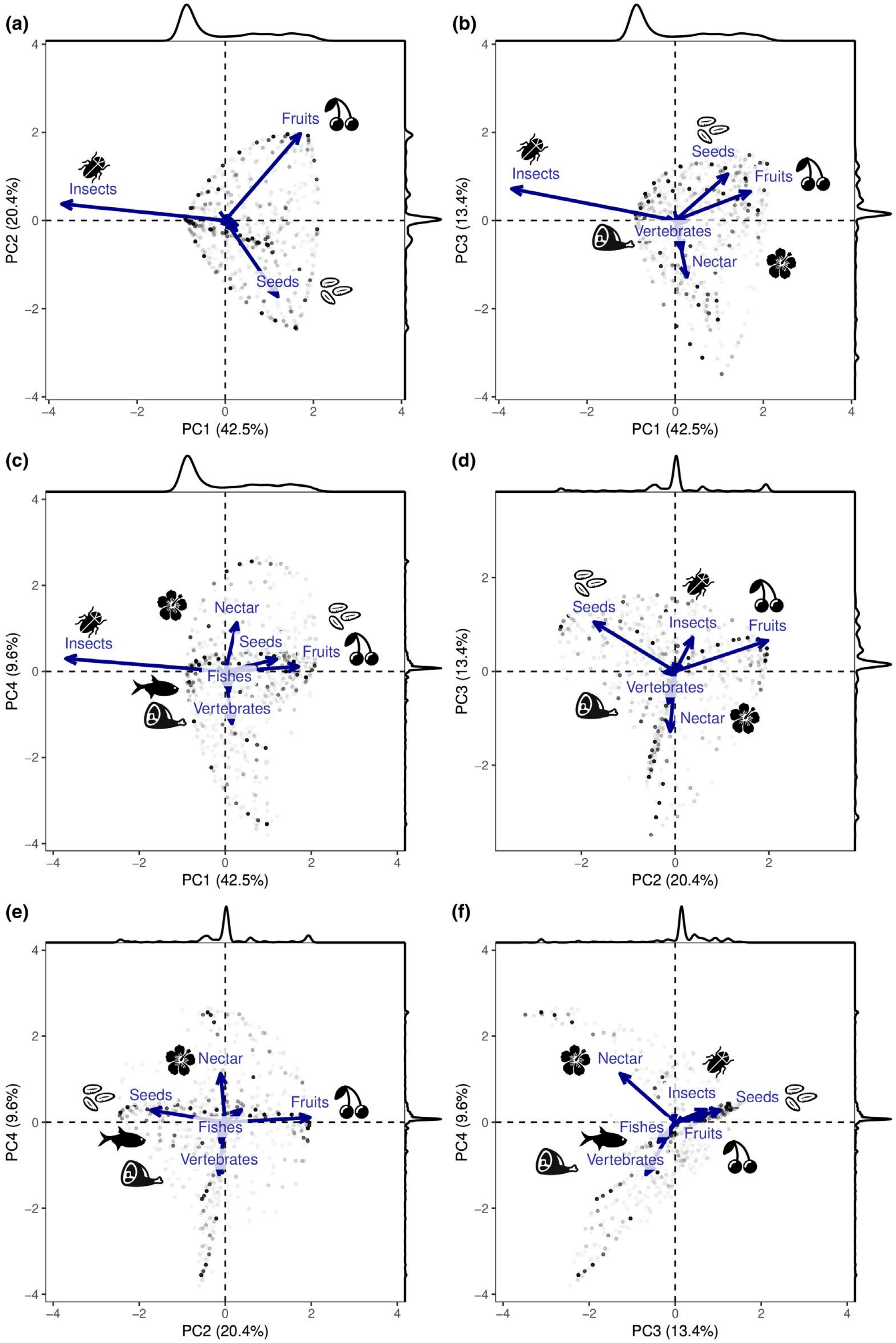

FIGURE 1 Bivariate planes representing the four dimensions of the diet space of birds and projections of the original diet categories (blue arrows). The dot cloud is shaded according to point density (one point per species, n = 8,937 species; darker shades imply that several species are superimposed). Marginal densities of species distributions along each dimension are shown on the top and the right sides of each graph [Colour figure can be viewed at wileyonlinelibrary.com]

The second dimension refined this first segregation, by opposing granivory and frugivory [Figure 1: principal component 2 (PC2)], typically separating Pterocliformes (sandgrouses) from Musophagiformes (turacos) and Bucerotiformes (hornbills; Appendix S2). Diets based on other plant materials had a negligible contribution to the diet space, being exploited by only 768 species, among which they formed a primary diet for only 181 species. Plotting these two first dimensions on a plane (Figure 1a) revealed that species spread evenly along continua from primary consumers to insectivores (PC1) and from frugivory to granivory (PC2), with representatives of all intermediate strategies along these two dimensions. The score-based structure of the original diet data resulted in species projections that form a sharp conical cloud in the first plane of the diet space (Figure 1a).

This coarse overview of dissimilarities among the diets of world bird species hinders variability associated with finer specializations that are not captured in our data. Nevertheless, it reveals that whereas insectivorous species may use seeds and fruits simultaneously as alternative prey (negative PC1 scores associated with null scores on PC2), non-insectivorous species tend to feed either on fruits or seeds, but not simultaneously on these two diets (few species associate positive PC1 scores and null scores on PC2).

The third dimension isolated nectarivory, carnivory and piscivory from all other diets [Figure 1; principal component 3 (PC3)]. Orders as different as Apodiformes, Accipitriformes and Pelecaniformes were thus grouped on its negative side (Appendix S2), suggesting high specialization levels (i.e., high scores in one or a few dietary categories). This pattern is in line with the prediction that nectarivory, carnivory and piscivory, three comparatively rare diets, involve highly energetic foods that require metabolic and morphological adaptations and restrict the use of alternative prey. Although they were grouped in negative values of PC3, no species, expectedly, combined nectarivory with carnivory or piscivory. As a result, the fourth dimension [Figure 1; principal component 4 (PC4)] ordinated species along a continuum from piscivory and carnivory (Accipitriformes and Pelecaniformes; Appendix S2) to nectarivory (Apodiformes; Appendix S2). Plotting PC4 against PC1 and PC2 (Figure 1e,f) revealed that many species used combinations of nectar and fruits or insects (e.g., Meliphagid honeyeaters), but none associated nectar and seeds, probably owing to morphological constraints. Conversely, species using carrion or fish-based diets (negative values on PC4) spread on both sides of PC1 (Figure 1c), but few expanded on positive values of PC2 (Figure 1e); these patterns reveal that strategies mixing varying levels of carnivory with reliance on insects or seeds are more common than strategies associating carnivory and frugivory.

3.2 | Spatial variations of dietary strategies of birds

Once averaged over species assemblages, all dimensions of the diet space exhibited clear and relatively congruent geographical structures matching biome boundaries or physical barriers, such as the Himalayas and Andes (Figure 2). Bird assemblages of the Western Palaearctic, Eastern Asia down to the Indo-Malayan archipelago, the Guineo-Congolian region, Madagascar and South Australia exhibited strongly negative scores along PC1, indicative of assemblages dominated by insectivory, whereas granivory and frugivory (positive scores on PC1) were more widespread, with less delineated regional patterns. Highly positive scores along PC1 in boreal regions and deserts are likely to reflect assemblages that are largely dominated by seed eaters. Supporting this interpretation, negative scores on PC1 were correlated with positive scores on PC2 in Old World bird assemblages (Figure 3a; Pearson's $R^2 = 0.42$ between the two axes, 7,880 assemblages). This pattern indicates that frugivory and insectivory were associated in species assemblages in the Old World, whereas granivory tended to be relegated to desertic and high-elevation

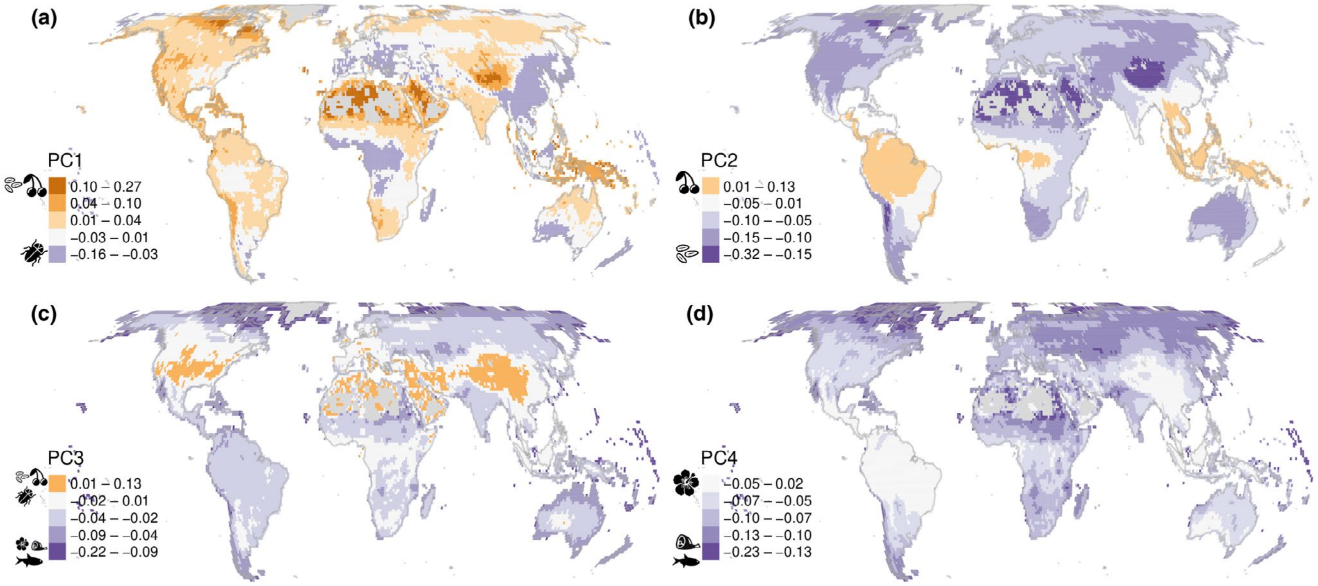

FIGURE 2 The geographical distribution of the four main dimensions (PC1–PC4) of the diet space of birds. These dimensions correspond to four continua between opposing dietary strategies, as assessed from trait covariations in 8,937 bird species. The colour gradient represents variations in the dominant dietary strategy as assessed from the average score of species along each dimension within species assemblages found in 100 km × 100 km square pixels ($n = 12,705$ assemblages). Eckert IV projection [Colour figure can be viewed at wileyonlinelibrary.com]

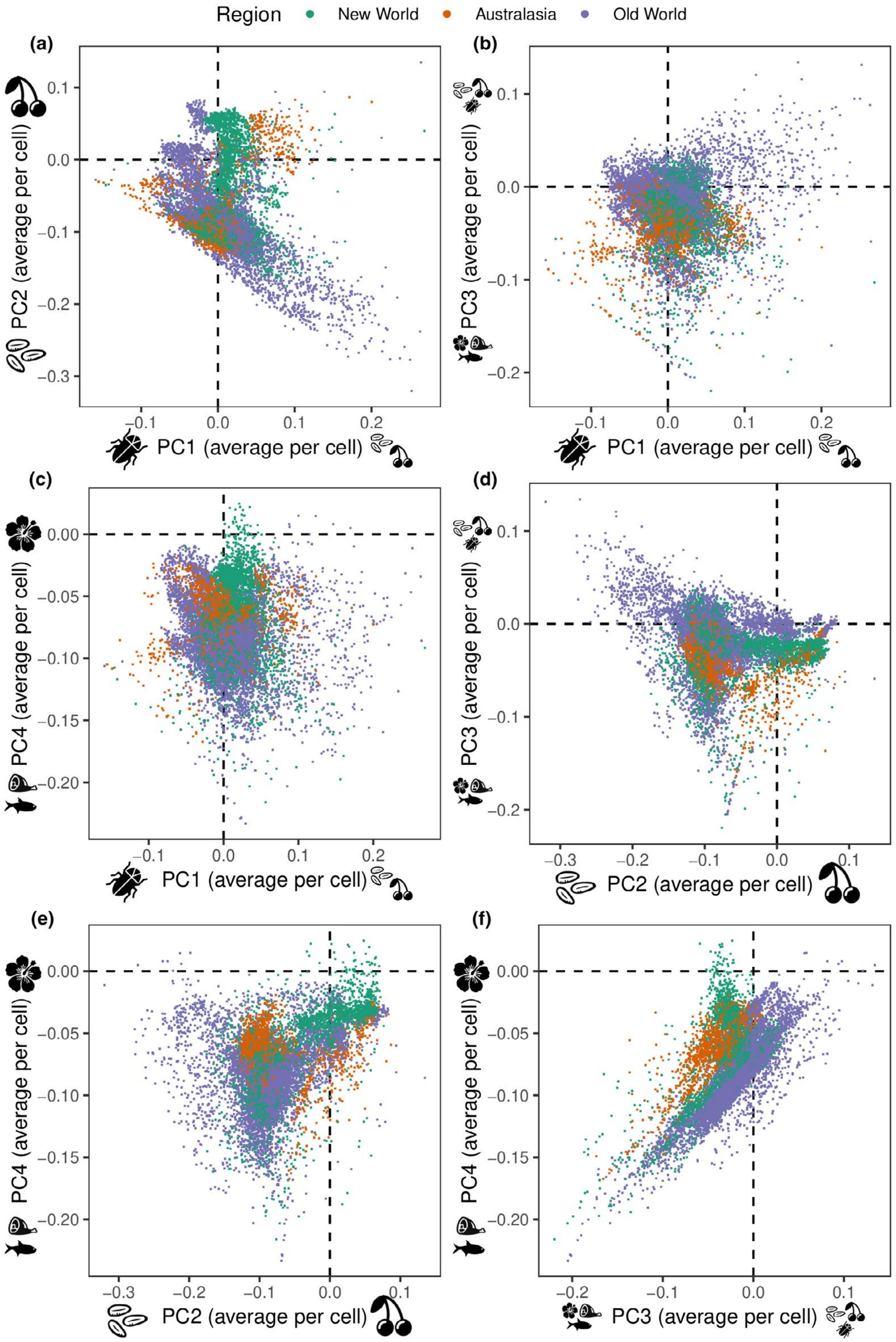

FIGURE 3 Spatial correlations among the dimensions of the diet space of birds. Each point corresponds to the average position of species found in one of 12,705 bird assemblages along each of the four dimensions of the diet space. Colours separate the correlations observed in the New World (both American continents and the Panamean region), the Old World (Eurasia, the Malay archipelago and Africa) and Australasia (encompasses Australia and New Zealand) [Colour figure can be viewed at wileyonlinelibrary.com]

regions, such as the Sahara or the Tibetan plateau, and some savannah regions (Figure 2a,b). The association between PC1 and PC2 did not hold in the New World (R^2 = 0.03, 3,711 assemblages) and was reversed in Australasia (R^2 = 0.18, 1,114 assemblages), suggesting a key role of regional biogeography in separating dietary strategies across bird assemblages.

Another striking association was the positive correlation between the average scores of bird assemblages along PC3 and PC4 in all regions (Figure 3f; $R^2 = 0.44$, 12,705 assemblages). This pattern reflected the geographical dominance of carnivory and piscivory (negative scores on PC3 and PC4) in desertic, coastal and boreal areas (Figure 2d), whereas nectarivory (positive scores on PC4) was found only in association with frugivory, granivory and insectivory (positive scores on PC3; Figure 3f), especially in southern America and southeast Asia (Figure 2c,d).

3.3 | Diet space of birds along environmental gradients

The approximate correlation coefficients of quantile regressions (used to assess the fit of the relationship between each diet space dimension and the set of environmental variables considered) ranged from .06 (PC1, .5 quantile) to 0.54 (PC2, .1 quantile), averaging 0.24 ± 0.14 (all uncertainties in standard deviation units). All variance inflation factors but two were below a threshold of five, and 87 out of 120 were below three, suggesting that regression coefficients were not affected by collinearity (Zuur, 2011). Quantile regression lines crossed in PC1, PC3 and PC4 (Figure 4a,c,d), in spite of our attempts to constrain these models at exploratory stages; correcting this artefact would lead to unnecessary complexity given the clarity of the observed patterns.

Quantile lines converged as species richness increased along all dimensions of the diet space except PC2, suggesting greater similarity of richer assemblages in terms of average diet (Figure 4a,k,p). Conversely, quantile lines diverged as the average diet composition of species assemblages became increasingly variable towards warm, productive and topographically heterogeneous environments (e.g., Figure 4b,h,d). These contradicting patterns hint that the dissimilarity of species assemblages in terms of diet increases towards tropical climates. Conversely, human influence was associated with a reduction in the range of dietary strategies along all dimensions of the diet space (Figure 4e,j,o,t), conforming to a macroecological-level signature of functional homogenization associated with anthropogenic activity.

Several quantile regressions showed a systematic shift towards undifferentiated dietary strategies along environmental gradients (assemblages with null values on a given dimension of the diet space: e.g., Figure 4,b,j,m,p), consistent with environmental filtering. However, we could not draw any general pattern from these trends because they were non-congruent across the four dimensions and the four bioclimatic variables. Although no strong evidence of filtering emerged on PC1 (Figure 4a–e), increasing NPP was associated with a marked shift from assemblages dominated by granivory to frugivory along PC2 (Figure 4h), and to a lesser extent towards rare diets along PC3 (Figure 4m). The increase in PC3 scores (lower prevalence of rare diets) towards warmer climates seemed to contradict this picture (Figure 4l), but could be driven by the negative response of carnivory and piscivory to temperature, which was more obvious along PC4 (Figure 4q). Topographic barriers imposed another strong environmental constraint, in which frugivory and carnivory were gradually replaced by granivory and nectarivory towards mountainous areas (Figure 4d–s).

4 | DISCUSSION

Our study revealed that bird species are spread inside a four-dimensional diet space, consistent with the prediction by MacArthur (1972) that the high diversity of life-forms can be summarized parsimoniously by a few basic continua bearing signs of the environmental constraints that preside to diversification. The biogeography of dietary strategies has previously been explored at regional scales (Pigot et al., 2016) or with a guild-richness approach, in which species were classified categorically according to their most prevalent diet (e.g., Kissling et al., 2012). In contrast, our study uniquely investigates the global and environmental distributions of dietary strategies in light of covariations that arise from niche convergence and exclusion (Díaz et al., 2016; Pianka et al., 2017).

The four-dimensional structure of the diet space of birds emerged from covariations among diets that species exploit either jointly or exclusively. The absence of any major discontinuities in this space shown in Figure 1 reflects the continuous, probabilistic nature of bird diets, exemplified by the tendency of passerines to feed on mixtures of fruits, seeds and insects (Herrera, Hobson, Carlos, & Méndez, 2006; Morton, 1973; Nazaro & Blendinger, 2017). In spite of this form of diet complementation, morphological differences (e.g., in bill size and shape), distinct foraging modes and digestive metabolism associated with insect or fruit-based regimes are consistent with the separation of insectivory, frugivory and granivory along the first two dimensions of the diet space (Figure 1; Hanken & Hall, 1993; Levey & Karasov, 1989; Snow & Snow, 1971). The next two dimensions (PC3 and PC4; Figure 1) corresponded to rarer diets with peculiar ecophysiological and morphological adaptations. Nectarivory implies a rapid metabolism efficient in assimilating high sugar concentrations at the cost of energetic storage, restricting this diet to the world's smallest bodied birds, hummingbirds (Trochilidae) and sunbirds (Nectariniidae), although it may also complement fruit- or insect-based diets in larger tropical species, such as honeyeaters (Meliphagidae) and *Loriculus* hanging parrots (Nicolson & Fleming, 2003; Wooller & Richardson, 2008). Nectarivory was thus logically opposed to carnivory and piscivory along the fourth dimension of the diet space (Figure 1c,e,f), with the latter two requiring large body sizes and morphological adaptations to cope with the hunting and capture of large prey (Barton & Houston, 2009; Hilton, Houston, Barton, Furness, & Ruxton, 1999). The diet space of birds is therefore likely to be sustained by a combination of behaviour, digestive physiology and morphology, which gives rise to well-identified diet-based convergences and trade-offs at the family level (see also Appendix S2; Fitzpatrick, 1985). Adaptive constraints are thus likely to provide a causal basis to our diet space, similar to the interpretation of constraints shaping plant and reptile functional spaces (Díaz et al., 2016; Pianka et al., 2017).

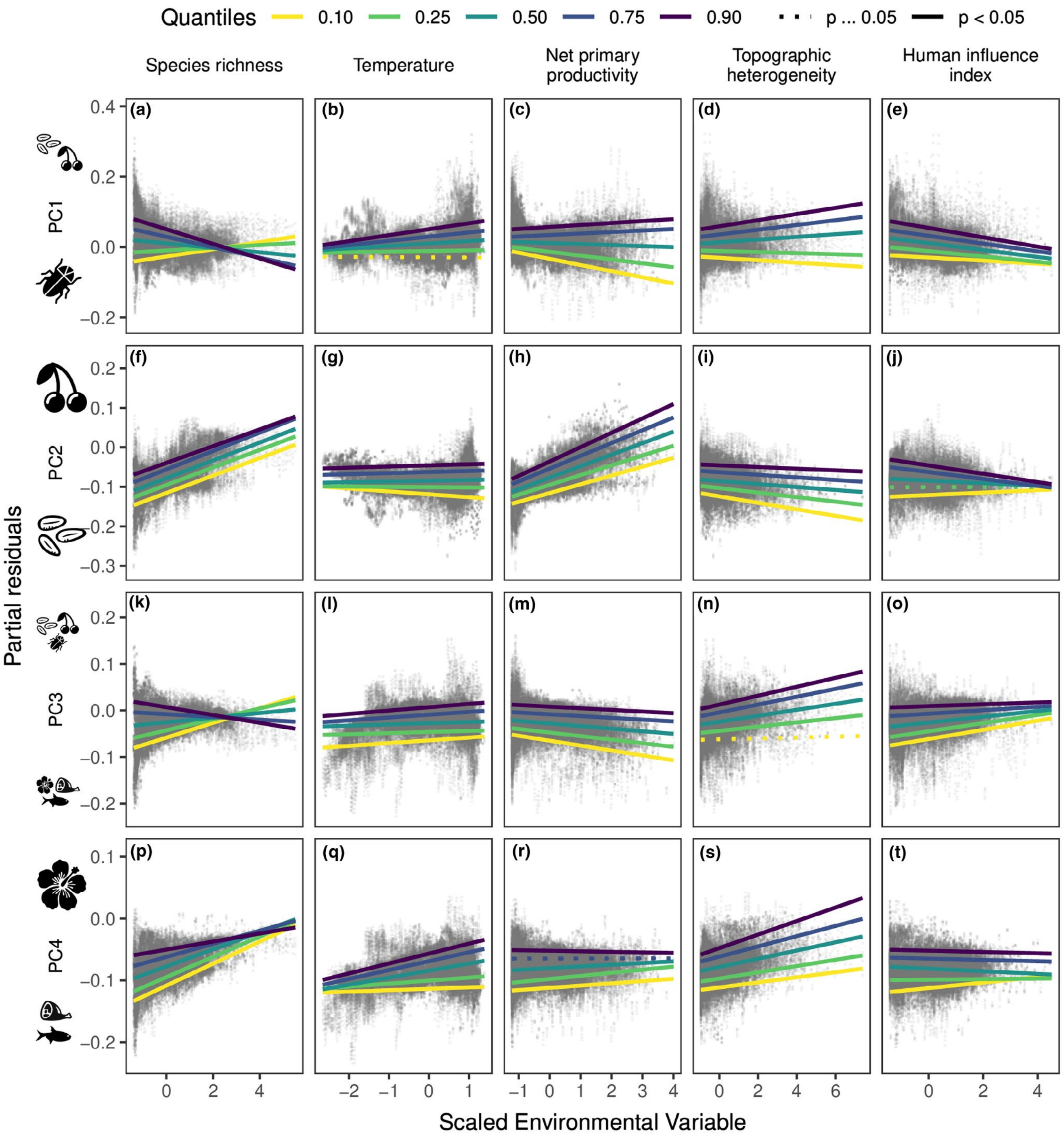

FIGURE 4 Quantile regressions of the four dimensions of the diet space of birds (PC1–PC4) against species richness, net primary productivity, temperature, topographic heterogeneity and human influence gradients. Regression lines correspond to the 0.1, 0.25, 0.5, 0.75 and 0.90 quantiles, and grey dots depict partial residuals [Colour figure can be viewed at wileyonlinelibrary.com]

We built this diet space with the most comprehensive diet assessment currently available for the birds of the world. These categories and scores form a representation of real bird diets that ignores specialization over specific prey but that are accurate at segregating major dietary groups. Given the sparsity of fine-grained data, we deliberately traded ecological resolution for an exhaustive comparative analysis unrestricted taxonomically or geographically, which comes at the cost of some coarseness in our representation of the diet space. Although diet data are likely to be more exhaustive than in most other traits (Hortal et al., 2015), they are not standardized across studies and often rely on gut contents of one to fewer than 10 individuals captured in specific locations and seasons (Del Hoyo et al., 2013). Effort on supplementary data collection would warrant a quantification of intraspecific variability in the shape of the diet space, a necessary perspective to enforce its macroevolutionary underpinnings (Violle et al., 2014). Furthermore, in addition to spatial variations across populations (Terraube & Arroyo, 2011), species may use different diets depending on age, sex, environmental constraints or resource availability (Davies, Hipfner, Hobson, & Ydenberg, 2009; León, Podos, Gardezi, Herrel, & Hendry, 2014; Murphy, 1994). In particular, numerous migratory species typically shift from insect-dominated diets to fruits at the onset of migration, whereas the diets of sedentary species follow food availability across seasons (Lovette & Fitzpatrick, 2016; Newton, 2010). This seasonality is usually aggregated or ignored in sources of species-level data, which probably leads to under-representation of the dispersion of species inside the diet space and to blurring of assemblage-level patterns, especially in temperate regions, where migratory species are most numerous. Although these limitations are unlikely to explain the whole structure of the diet space, they probably account for some (lack of) patterns, calling for increased effort into trait acquisition in poorly surveyed areas and at a finer resolution (Hortal et al., 2015).

The geographical mapping of the diet space through assemblage-averaged scores (Figure 2) supported the hypothesis that biogeographical legacies determine the distribution of bird dietary strategies on top of climatic influences and resource distributions (Belmaker et al., 2012; Ericson, 2012; Kissling et al., 2012). Increasing metabolic constraints in favour of high-order consumers promote assemblages essentially formed of carnivores and piscivores at high latitudes (Figure 2d), which accounts for the strong relationship between assemblage-averaged scores on PC3 and PC4 visible in Figure 3f (Clarke & O'Connor, 2014; Vejrikova et al., 2016; Zimmerman & Tracy, 1989). Likewise, the dominance of seed-feeding species in deserts and topographically complex regions (Figure 2b) can be related to seasonal climates and short growing seasons that restrict the availability of alternative foods for most of the year (Brown, Reichman, & Davidson, 1979; Kissling et al., 2012). Conversely, long-term climatic stability and niche conservatism confined the diversification of fruit trees and their consumers to the inter-tropical band (Jetz et al., 2009; Kissling et al., 2007, 2012), leading to a geographical association of insectivory and frugivory in the Old World (Figure 3a), although they were opposed at the species level along the first dimension of the diet space. Interestingly, however, this association was reversed in Australasia and was absent in the New World. These differences suggest that long-term climatic constraints were overcome by other processes, such as the admixture that resulted from the Great American Interchange or ancient diversification events that followed the colonization of cone-billed oscine clades from the Old-World since the late Miocene (Newton, 2003; Webb, 2006). Hence, the diet space of birds has probably been shaped largely by varying diversification rates across clades exploiting distinct dietary niches (e.g., hummingbirds, ducks and geese and various specialized passerine groups), associated with successive colonization events and recent radiations after climatic oscillations or modifications of physical barriers (Jetz, Thomas, Joy, Hartmann, & Mooers, 2012). Still consistent with a role of biogeographical legacies associated with long-term climatic variability and plate tectonics (Ficetola, Mazel, & Thuiller, 2017), assemblage-averaged scores were more variable in topographically heterogeneous regions (i.e., near mountain chains) along the four dimensions of the diet space, and clear-cut spatial structures were associated with transition areas, such as the Panamanian isthmus, the Guineo-Congolian region, the Indo-Malayan and Papua-Melanesian archipelagos. These regional patterns support the hypothesis that admixture and diversification events that have resulted from orographic or tectonic processes imprint the global distribution of the diet space and call for further studies on its diversification history using phylogenetic reconstruction methods (Burin et al., 2016; Jetz et al., 2012; Newton, 2003).

Bird assemblages tended to become more concentrated in the diet space as species richness increased, as shown by the tendency of the quantile regression line to converge towards high species richness along all dimensions but PC2 (Figure 4). This result suggests that species-rich assemblages imply the coexistence of most dietary strategies, which could be promoted by niche packing in highly productive environments (Pellissier et al., 2018; Pigot et al., 2016). In line with the interpretation that productivity enhances the coexistence of multiple dietary strategies, the variance in the positions of assemblages in the diet space increased towards warm climates, high NPP and high topographic heterogeneity (Figure 4). These patterns concur with the hypothesis that warm and productive environments in addition to endemism associated with physical barriers promote diversity in the composition of species assemblages (Ficetola et al., 2017; Hawkins et al., 2003; Jetz et al., 2009; Ruggiero & Hawkins, 2008). At the low-productive side of these gradients, environmental filters could impose constraints on the diets of species-poor assemblages facing harsh climates or low energetic input (Hawkins et al., 2003). Examples of such filtering processes typically lie in pelagic bird colonies formed almost exclusively by piscivores at boreal latitudes (Figure 4q), or in desert assemblages mainly formed by seed-eaters (Figure 4h). In line with this energetic interpretation, the 23 poorest assemblages (species richness = 10) were distinctly segregated along the first dimension of the diet space, from desert communities of the Middle East, where specialized seed-eaters such as larks (Alaudidae) and sandgrouse (Pteroclidae) account for half of the species, to coastal assemblages of eastern Russia consisting of a mixture of insectivorous or omnivorous passerines and pelagic piscivores. Inversely, the 23 richest assemblages (700–848 species), all concentrated along the Andean chain, were clustered in the diet space and held specialists of the eight dietary categories (score of 10 in a single diet). Hence, the distribution of assemblages in the diet space is consistent with a combination of regional history and environmental constraints towards the pole and deserts.

A major outcome of our study was the packing of bird assemblages close to the centroid of the diet space when the human footprint increased, in agreement with the increased risk of extinction that accompanies ecological specialization by species (Şekercioğlu, 2011). This result suggests a trophic basis to the decrease in bird trait turnover along global gradients of human influence (Barnagaud et al., 2017) and conveys a macroecological-level signal of functional homogenization in association with the loss of marginal dietary strategies and a rise in species using average diets (Baiser & Lockwood, 2011; Clavel, Julliard, & Devictor, 2011; Devictor et al., 2008). Our results thus add strong evidence that the human footprint is sufficiently pervasive to affect macroecological patterns (Šizling et al., 2016). Diets influence demographic and distributional responses of species to modifications in land use through their determinant role on offspring productivity and other aspects of energetic demands (Newbold et al., 2013; Sibly et al., 2012). The outcomes of a dietary homogenization of bird assemblages associated with the human imprint would thus deserve a more mechanistic assessment, especially with respect to the persistence and resilience of critical bird functions, such as pollination, endozoochorous dispersal and pest control (Ko, Schmitz, Barbet-Massin, & Jetz, 2013; Şekercioğlu, 2006, 2011).

4.1 | Conclusion

Our work illustrates the potential of multivariate approaches in functional biogeography analyses (Violle et al., 2014). It permits, in particular, an explicit mapping of functional strategies along continuous axes rather than using guild categorizations, and the explicit integration of covariations among traits or trait modalities. A formal test of the role of diversification processes on the diet space of birds was beyond the aims of this study, but will have to be tackled through phylogenetically informed null models (Díaz et al., 2016) or trait evolution modelling (Burin et al., 2016) for both basic and conservation-oriented aims. Our results should also draw interest on the potential alterations of macroecological-level trophic networks by anthropogenization, and their consequences for the distribution of ecosystem functions and services on earth. We hope that these outcomes, adjoined to studies on other taxa and aspects of the structure of functional spaces (Díaz et al., 2016; Pianka et al., 2017), will stimulate efforts towards bridging macroevolution and functional biogeography through the empirical exploration of global trait datasets.

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DATA ACCESSIBILITY

Data for environmental covariates and species assemblages at a 110 km × 110 km resolution, and species scores on the four dimensions of the diet space, are available through Dryad (https://doi.org/10.5061/dryad.24c3s89). Original diet data are not released, by request of their owner, but can be requested from the corresponding author.

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BIOSKETCH

The author team is broadly interested in the functional and evolutionary implications of trait distributions across species assemblages at a macroecological scale. The authors have specific expertise in functional ecology, conservation biology, biogeography and macroevolution, focusing on observational and ecoinformatics approaches.

SUPPORTING INFORMATION

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