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Bird dietary guild richness across latitudes, environments and biogeographic regions

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ABSTRACT

Aim To integrate dietary knowledge and species distributions in order to examine the latitudinal, environmental, and biogeographical variation in the species richness of avian dietary guilds (herbivores, granivores, frugivores, nectarivores, aerial insectivores, terrestrial/arboreal insectivores, carnivores, scavengers, and omnivores).

Location Global.

Methods We used global breeding range maps and a comprehensive dietary database of all terrestrial bird species to calculate guild species richness for grid cells at 110 × 110 km resolution. We assessed congruence of guild species richness, quantified the steepness of latitudinal gradients and examined the covariation between species richness and climate, topography, habitat diversity and biogeographic history. We evaluated the potential of current environment and biogeographic history to explain global guild distribution and compare observed richness–environment relationships with those derived from random subsets of the global species pool.

Results While most guilds (except herbivores and scavengers) showed strong congruence with overall bird richness, covariation in richness between guilds varied markedly. Guilds exhibited different peaks in species richness in geographical and multivariate environmental space, and observed richness–environment relationships mostly differed from random expectations. Latitudinal gradients in species richness were steepest for terrestrial/arboreal insectivores, intermediate for frugivores, granivores and carnivores, and shallower for all other guilds. Actual evapotranspiration emerged as the strongest climatic predictor for frugivores and insectivores, seasonality for nectarivores, and temperature for herbivores and scavengers (with opposite direction of temperature effect). Differences in species richness between biogeographic regions were strongest for frugivores and nectarivores and were evident for nectarivores, omnivores and scavengers when present-day environment was statistically controlled for. Guild richness–environment relationships also varied between regions.

Main conclusions Global associations of bird species richness with environmental and biogeographic variables show pronounced differences between guilds. Geographic patterns of bird diversity might thus result from several processes including evolutionary innovations in dietary preferences and environmental constraints on the distribution and diversification of food resources.

Keywords

Aves, biogeography, birds, ecology, food, guild assembly, niche, species diversity, species–energy theory, tropics.

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INTRODUCTION

The latitudinal gradient of increasing species richness from polar and temperate to tropical regions is probably the longest recognized, albeit not completely understood, pattern in biogeography and ecology (Willig *et al.*, 2003; Hillebrand, 2004). On the one hand, geographical variation in species richness varies considerably along environmental gradients of temperature, water availability, productivity, seasonality and/or habitat heterogeneity (Jetz & Rahbek, 2002; Hawkins *et al.*, 2003; Hurlbert & Haskell, 2003; Currie *et al.*, 2004). On the other hand, latitudinal gradients of species richness are products of evolutionary history (Ricklefs & Schluter, 1993; Wiens & Donoghue, 2004; Mittelbach *et al.*, 2007), and differences in net diversification rates provide alternative explanations for the uneven spatial distribution of biodiversity across the world (Cardillo *et al.*, 2005; Mittelbach *et al.*, 2007). Specific traits such as dietary preference, body size, morphology or life history are often thought to facilitate the diversification of clades ('key innovations'; Simpson, 1953; de Queiroz, 2002), but to date the latitudinal and geographical variation of such key functional traits has only been rarely quantified across species-rich clades (Jetz *et al.*, 2008; Olson *et al.*, 2009).

Birds are an excellent model system for global analyses because species distributions are well known (Davies *et al.*, 2007; Jetz *et al.*, 2007; Qian, 2008; Kissling *et al.*, 2009) and their dietary preferences can be broadly quantified across the whole clade (Sekercioglu *et al.*, 2004). The diet of a bird species represents a fundamental aspect of its ecological niche (Root, 1967; Simberloff & Dayan, 1991) and dietary adaptations have played an important role in understanding the ecology and evolution of communities (Hutchinson, 1959; Cody & Diamond, 1975). A species' functional role in an ecosystem considerably depends on its dietary preference, and taxonomically unrelated species can exhibit similar ecological functions in different parts of the world (Lein, 1972; Duffy, 2002). Dietary strategies are also crucial for understanding species formation because interspecific competition for similar food resources can explain character displacement and the evolutionary divergence of species (Brown & Wilson, 1956; Grant & Grant, 2006). However, despite a long interest in diet and foraging ecology we still have little quantitative knowledge about the determinants of latitudinal, environmental and biogeographic variation in dietary preferences at a global scale (Lein, 1972; Hillebrand, 2004; Primack & Corlett, 2005; Carnicer & Díaz-Delgado, 2008).

Given the variation in feeding strategies and their association with specific food resources, we can expect differences in the latitudinal, environmental and biogeographic distribution of dietary guilds. For instance, the availability of insects, fleshy fruits and vertebrate prey peaks at tropical latitudes (Primack & Corlett, 2005) which should result in steep latitudinal gradients in species richness of their consumers (i.e. insectivores, frugivores and carnivores) and in strong covariation with environmental productivity or other measures of the water–energy balance (Hawkins *et al.*, 2003). Other dietary guilds, however, might show stronger associations with seasonality or tempera-

ture, e.g. if metabolism and temperature regulation is linked to small body sizes (e.g. nectarivores; Brown *et al.*, 1978) or if food resources are predominantly available in dry, open and hot habitats (e.g. carrion for scavengers; Morrison *et al.*, 2007). We further expect historical imprints in the geographical distribution of consumer richness if immigration, speciation and extinction rates of resources (e.g. prey or food plants) or opportunities for niche separation differ between biogeographic regions (Hutchinson, 1959; Primack & Corlett, 2005; Kissling *et al.*, 2009).

Here, we provide a novel view on the world's avifauna by linking dietary strategies of all terrestrial bird species and their breeding distributions at the global scale. We separate the world's landbirds into herbivores, granivores, frugivores, nectarivores, aerial insectivores, terrestrial/arboreal insectivores, carnivores, scavengers and omnivores, and examine how avian dietary guild species richness differs in latitudinal, environmental and biogeographic space. With our analyses, we demonstrate that species richness peaks, richness congruence, latitudinal gradients, environmental associations and biogeographic differences are often guild-specific, suggesting that species dietary strategies play an important role in determining the global bird diversity gradient.

MATERIALS AND METHODS

Species distribution data

We used a comprehensive database of the breeding distributions of all bird species in the world (Jetz *et al.*, 2007). We included 8919 terrestrial bird species (out of a total of 9754) in our analysis, excluding birds that predominantly feed in freshwater or marine habitats ($n = 835$). The classification of the species follows Sibley & Ahlquist (1990) for non-passerines and Barker *et al.* (2004) for passerines and was updated for newly described species and recent splits and lumps. Distribution maps of species represent a conservative extent-of-occurrence extrapolation of the breeding range and were compiled from the best available sources for a given broad geographic region or taxonomic group (see Fig. S4 of Jetz *et al.*, 2007, and references therein). Originally in polygon format, the maps of all species were overlaid onto a grid in cylindrical equal area projection with 110×110 km resolution (equivalent to $c. 1^\circ \times 1^\circ$ near the equator). A recent validation analysis confirmed satisfactory range map accuracy for this same dataset at roughly 150–200 km grid cell resolution across Australia and southern Africa (Hurlbert & Jetz, 2007). We repeated all statistical analyses at 220×220 km resolution, but results were similar to those derived from the 110×110 km grid, so we only report results from the latter grid resolution.

Diet classification

The diets of all bird species in our database were determined from a comprehensive literature survey (Sekercioglu *et al.*, 2004). We used an updated version (31 January 2009) of this database

where, for each species, the dietary components mentioned in the literature were assigned to seven categories (plant material, seeds, fleshy fruits, nectar, invertebrates, carrion and vertebrates) and each category was ranked in importance for each individual species when it was present as a dietary component (for sources of diet data see Appendix S1 in Supporting Information). Diet ranks of a species add up to a score of 10, and from this assignment we classified species into dietary guilds based on their primary (i.e. predominant) diet and foraging type (score > 5): (1) herbivores (i.e. predominantly feeding on plant material such as leaves, roots and shoots), (2) granivores (i.e. predominantly feeding on seeds), (3) frugivores (i.e. predominantly feeding on fleshy fruits), (4) nectarivores (i.e. predominantly feeding on nectar), (5) aerial insectivores (i.e. predominantly feeding on insects in the air, e.g. swifts and swallows), (6) terrestrial/arboreal insectivores (i.e. predominantly feeding on insects, excluding guild 5), (7) carnivores (i.e. predominantly feeding on vertebrates), and (8) scavengers (i.e. predominantly feeding on carrion). All remaining species with diet ranks ≤ 5 (e.g. fruit 5, insect 2, nectar 2, seed 1) were classified as omnivores (9). This classification characterizes the dominant diet type of a species and represents a robust way to examine the geographic distribution of dietary guilds at a global scale (compare the sensitivity analysis in Kissling *et al.*, 2009, for an example with frugivores). For 625 species (7%), there was no dietary information available from the literature, and for these species expert guesses of diet were obtained. Excluding these species from the analyses had only a minor impact on the results (see the sensitivity analysis in Appendix S2), so we included them in all analyses below. Our dietary classification does not account for seasonal shifts in dietary preferences (due to lack of information) and instead summarizes the overall importance of food types in the diet of a species during its life cycle and across its geographic range. This reflects the average ecological role of birds in their environments and their broad contributions to the functioning of ecosystems (Sekercioglu *et al.*, 2004; Sekercioglu, 2006; Wenny *et al.*, 2011).

Global geographical patterns and species richness congruence

We examined geographical patterns of avian dietary guild species richness across the world by mapping species richness of each guild at 110×110 km resolution (see Species distribution data). To assess the extent of richness congruence among guilds and between guilds and overall bird richness we calculated cross-correlations between richness patterns on log-transformed data. To avoid bias due to different guild sample sizes (ranging from 5357 to 10,147 occupied grid cells), we resampled 1000 random grid cells from each species richness map 100 times to calculate Pearson correlations of log-transformed richness patterns. To assess the extent of richness congruence among guilds and between guild species richness and overall bird richness we provide average Pearson correlations (mean \pm SD) over the 100 runs. We ran similar analyses to assess the extent of richness congruence among a given guild and all other guilds taken together.

We further examined latitudinal gradients in avian guild species richness by summarizing the grid-based species richness values per 10° latitudinal band. Following Hillebrand (2004) we quantified the steepness of latitudinal gradients by calculating the slope b of the linear regression of median untransformed species richness (per 10° latitudinal band) versus latitude, for both southern (-50° to 0°) and northern (70° to 0°) bands. Positive values for b indicate an increase of species richness towards the equator.

Environmental associations

We selected four climatic and two habitat heterogeneity variables to examine environmental associations of guild species richness: (1) mean annual temperature (TEMP) to assess the effect of temperature and kinetic energy (Allen *et al.*, 2002); (2) annual precipitation (PREC) to indicate water availability (Hawkins *et al.*, 2003); (3) actual evapotranspiration (AET) as an integrated measure of the water–energy balance and net primary productivity (Hawkins *et al.*, 2003); (4) the coefficient of variation of monthly net primary productivity values as an estimate of seasonality (SEAS; Hurlbert & Haskell, 2003; Kissling *et al.*, 2009); (5) altitudinal range (TOPO, i.e. the difference between maximum and minimum elevation) as a measure of topographic heterogeneity (Jetz & Rahbek, 2002); and (6) the number of vegetation classes (i.e. habitat diversity, HAB) as an indicator of habitat heterogeneity (Olson *et al.*, 2001). All variables have previously been shown to be strongly correlated with species richness of birds at continental and global spatial scales (e.g. Jetz & Rahbek, 2002; Hawkins *et al.*, 2003; Hurlbert & Haskell, 2003; Davies *et al.*, 2007; Kissling *et al.*, 2007, 2009).

Basic climatic variables (TEMP, PREC) were extracted from the mean monthly climatic database for the period 1961–1990 with $10'$ resolution provided by New *et al.* (2002), AET originated from the Ahn & Tateishi (1994) dataset at $30'$ resolution, and mean monthly net primary productivity values (for seasonality) were provided by Bondeau *et al.* (2007) for the time period 1961–90 at 0.5° resolution. Altitudinal range (TOPO) was obtained from the GTOPO-30 digital elevation model at a spatial resolution of 30 arcsec and the number of vegetation classes (HAB) from the Olson global land-cover classification (both variables were downloaded from the Global Land Cover Characterization Data Base available at <http://edc2.usgs.gov/glcc/>).

We took a three-step process for analysing environmental associations of guild species richness. In the first step, we calculated single-predictor regression models to test the individual potential of climate (TEMP, PREC, AET, SEAS) and habitat heterogeneity (TOPO, HAB) as predictors of guild species richness. We used spatial linear models (SLM) of the simultaneous autoregressive error type to account for spatial autocorrelation in model residuals (Kissling & Carl, 2008). We ran similar non-spatial models for comparison (see Fig. S5 in Appendix S2). Due to the computational intractability of applying SLMs to large datasets we developed a bootstrapping approach (cf. Kissling *et al.*, 2009) where we randomly

subsampled the dataset for each dietary guild 100 times. We tested 2–10% of the grid cells as subsamples for each guild dataset and used the smallest possible percentage of grid cells that allowed reduction of spatial autocorrelation to a non-significant level (i.e. mean Moran's I -values with $P \geq 0.05$). Spatial weight matrices were calculated with two to eight nearest neighbours and a row-standardized coding scheme (Kissling & Carl, 2008), and Moran's I -values with a fixed spatial lag of 600 km. Final grid cell percentages ranged from 6–10% between guilds because different dietary guilds have (1) different global sample sizes and (2) different spatial autocorrelation structures in their richness distributions. For each of the 100 random subsamples we calculated single-predictor SLMs with log-transformed response variables and extracted the Akaike information criterion (AIC), model fit (i.e. R^2_{env} or R^2_{realm} measuring the pure fit of the predictor variable, and R^2_{full} measuring the full fit of the SLM including the explained variance of the spatial weight matrix, calculated as the squared Pearson correlation between fitted and observed species richness), Moran's I -values (a measure of residual spatial autocorrelation) and P -values of Moran's I . The subsampling procedure provided robust results as indicated by comprehensive validation tests (see Fig. S4 and text in Appendix S2). We report mean values of all model and test statistics across the 100 random subsamples and use AIC and R^2_{env} to compare models among predictor variables and guilds. We additionally added squared terms to our linear predictors if model fit was improved (i.e. AIC reduced) to account for hump-shaped relationships. We also developed multiple-predictor SLMs for each guild, mainly to examine regional effects after accounting for environment and to test whether richness–environment relationships vary between regions (see Biogeographic variation).

In a second step, we used all six environmental variables (TEMP, PREC, AET, SEAS, TOPO, HAB) and combined them in a principal components analysis (PCA) to examine the overall distribution and peaks of guild species richness in multivariate environmental space. The first two components (PC1 and PC2) produced by the PCA accounted for 77% of the variance in the six environmental variables (see Table S1 and Fig. S6 in Appendix S2) and were used in this study. PC1 largely represents climatic variables and shows highly positive Pearson correlations with AET ($r = 0.95$), PREC ($r = 0.89$) and TEMP ($r = 0.69$), and a highly negative correlation with SEAS ($r = -0.94$). PC2 instead correlates strongly with both measures of habitat heterogeneity, i.e. TOPO ($r = 0.78$) and HAB ($r = 0.83$). We plotted the species richness values (of grid cells) of a given dietary guild (with the same colour scheme as in the maps) along the first two axes (PC1, PC2) from this PCA to visualize whether peaks in species richness of different dietary guilds cluster in similar or different environmental space.

In a third step, we evaluated whether the observed richness–environment relationships might depend on the number of species per guild (ranging from 28 species of scavengers to 4903 species of terrestrial/arboreal insectivores). For instance, for any small set of species (e.g. scavengers) the richness–environment relationship might not differ from a random expectation. We

therefore compared the observed explained variance (R^2_{env}) of single-predictor guild richness–environment relationships with the variability in R^2_{env} as obtained from random subsamples of the global species pool. For each guild, we randomly drew the guild-specific number of species (e.g. 28 species for scavengers and 4903 species for terrestrial/arboreal insectivores) 100 times from the global species list, overlaid the occurrences in each run to obtain a richness map, and then calculated the richness–environment relationships (i.e. 100 relationships for each environmental variable, TEMP, PREC, AET, SEAS, TOPO, and HAB). This provided the variability in richness–environment relationships (R^2_{env}) for a specific guild size as obtained from random draws of the species pool. Due to the computational demand of SLMs we used non-spatial regression models for calculating the richness–environment relationships. However, we note that the observed R^2_{env} of SLMs was similar to the R^2_{env} from non-spatial models (see Fig. 3a and Fig. S5 in Appendix S2).

Biogeographic variation

To test for biogeographic differences in species richness and environmental correlates we assigned each grid cell to one of the six biogeographic realms (including Afrotropics, Australasia, Indo-Malaya, Nearctic, Neotropics and Palaearctic) according to the classification of the biogeographical provinces of the world (Udvardy, 1975). We first used single-predictor SLMs (as above) with realm membership (REALM, a categorical variable) as predictor variable and compared its explained variance (R^2_{realm}) for the species richness of different dietary guilds. We then assessed the effect of REALM on guild species richness after accounting for environmental variables. For this, we quantified the uniquely explained variance of REALM by subtracting the explained variance (i.e. pure fit of predictor variables) of multiple predictor SLMs using all six environmental variables without REALM from the explained variance (i.e. pure fit) of multiple predictor SLMs using all six environmental variables plus REALM. This allowed us to compare the explained variance of REALM (R^2_{realm}) between guilds after the differences in environment between regions were statistically removed.

In a second step, we developed multiple-predictor models to examine whether the effect of environment (climate and habitat heterogeneity, see above) on guild species richness varies between regions. We used the best predictor variable (in terms of AIC and R^2_{env}) from our single-predictor SLMs out of two categories 'climate' (TEMP, PREC, AET, SEAS) and 'habitat heterogeneity' (TOPO, HAB) and combined the climate and habitat heterogeneity variable, respectively, with REALM in multiple-predictor SLMs. We specifically tested for the region effect by including an interaction term between REALM and the respective climate or habitat heterogeneity variable to examine whether richness–environment relationships vary between biogeographic regions. We also fitted a model with all three variables (climate, habitat heterogeneity and REALM) for comparison. All statistical analyses were done with R (R Development Core Team, 2009, version 2.9.0). PCA analyses were

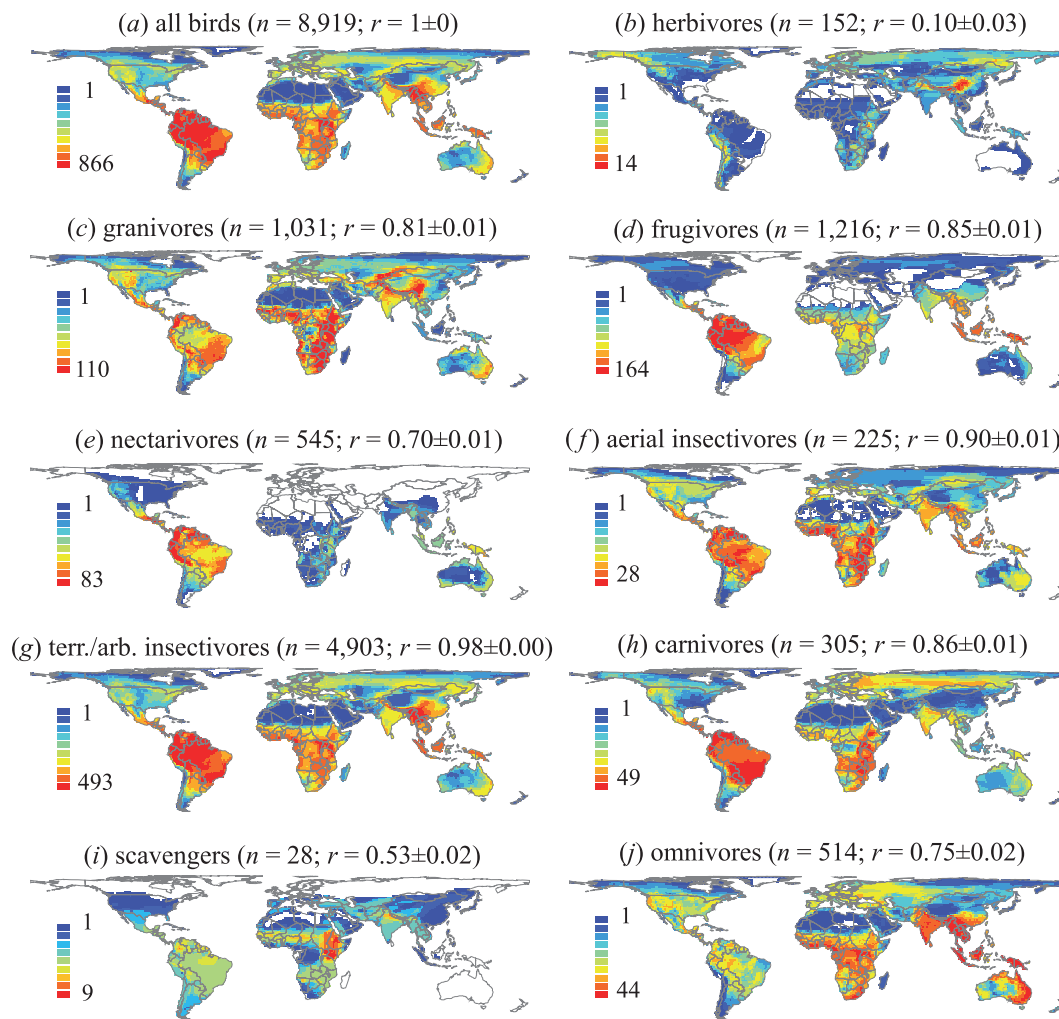


Figure 1 Geographic patterns of (a) overall and (b)–(j) guild species richness across an equal-area grid of 110×110 km resolution (quantile classification, world cylindrical equal area projection). Total species richness of each guild (n) and cross-correlations with overall bird richness (Pearson correlations r , mean \pm SD from randomly sampling 1000 grid cells for each guild over 100 runs) are given in brackets. For taxonomic composition of each guild see Table S4 in Appendix S2.

conducted using the R library ‘vegan’, version 1.15–2, and spatial analyses were conducted using the R library ‘spdep’, version 0.4–34. Both packages are available at <http://cran.r-project.org/web/packages/>.

RESULTS

Global geographical patterns and species richness congruence

The species richness of all terrestrial birds in the world peaks in (sub)tropical America, Africa, the Himalayas and the Indo-Pacific region (Fig. 1a). The highest congruence with overall bird diversity ($r = 0.98 \pm 0.00$) was found for terrestrial/arboreal insectivores (55% of all species) which show almost identical spatial patterns of species richness at the global scale (Fig. 1g). Instead, herbivore richness peaks in the Himalayas, granivores in the East African mountain ranges, frugivores at tropical latitudes

in South America, nectarivores along the Neotropical Andes, aerial insectivores and carnivores in the eastern parts of Africa and in South America, scavengers in East Africa and omnivores in the Himalayas and Southeast Asia (Fig. 1). Some of these guilds (i.e. granivores, frugivores, aerial insectivores and carnivores) also showed a high congruence ($r > 0.80$) with overall bird species richness (Fig. 1, Table 1) but richness of herbivores and scavengers overlapped little with total bird species richness (Fig. 1). Additionally, frugivores, granivores, insectivores and carnivores showed high levels ($r \geq 0.70$) of species richness congruence amongst each other while other guilds showed mostly intermediate ($0.30 < r < 0.70$; nectarivores and scavengers) or low levels ($r < 0.30$; herbivores) of congruence with other guilds (Table 1). The congruence of species richness of a given guild with that of all other guilds is given in Table S2 in Appendix S2.

Latitudinal gradients in species richness were observed for most dietary guilds, but gradient steepness differed between guilds (Fig. 2). The steepest increases (i.e. largest slopes, b , in

Table 1 Correlations among global patterns of species richness of avian dietary guilds.

	Herb	Gran	Frug	Nect	Ins _{Aer}	Ins _{Terr}	Carn	Scav	Omni	All
Herb	1.00 (± 0.00)									
Gran	0.12 (± 0.03)	1.00 (± 0.00)								
Frug	-0.07 (± 0.03)	0.54 (± 0.02)	1.00 (± 0.00)							
Nect	-0.23 (± 0.03)	0.46 (± 0.02)	0.79 (± 0.01)	1.00 (± 0.00)						
Ins _{Aer}	0.04 (± 0.03)	0.80 (± 0.01)	0.71 (± 0.01)	0.57 (± 0.01)	1.00 (± 0.00)					
Ins _{Terr}	0.13 (± 0.03)	0.75 (± 0.01)	0.82 (± 0.01)	0.65 (± 0.01)	0.88 (± 0.01)	1.00 (± 0.00)				
Carn	0.11 (± 0.03)	0.71 (± 0.02)	0.71 (± 0.01)	0.60 (± 0.02)	0.77 (± 0.01)	0.83 (± 0.01)	1.00 (± 0.00)			
Scav	-0.09 (± 0.03)	0.58 (± 0.02)	0.53 (± 0.02)	0.51 (± 0.02)	0.51 (± 0.02)	0.47 (± 0.02)	0.38 (± 0.02)	1.00 (± 0.00)		
Omni	0.02 (± 0.03)	0.64 (± 0.02)	0.62 (± 0.02)	0.37 (± 0.02)	0.73 (± 0.01)	0.73 (± 0.02)	0.62 (± 0.02)	0.26 (± 0.03)	1.00 (± 0.00)	
All	0.10 (± 0.03)	0.81 (± 0.01)	0.85 (± 0.01)	0.70 (± 0.01)	0.90 (± 0.01)	0.98 (± 0.00)	0.86 (± 0.01)	0.53 (± 0.02)	0.75 (± 0.02)	1.00 (± 0.00)

Random samples of 1000 grid cells were taken for each guild over 100 runs to avoid bias due to different guild sample sizes. In each run, Pearson correlations between the richness patterns were calculated on log-transformed data. Given are mean values (bold) and standard deviations (brackets) as derived from these resampling tests.

Abbreviations of guilds: Herb, herbivores; Gran, granivores; Frug, frugivores; Nect, nectarivores; Ins_{Aer}, aerial insectivores; Ins_{Terr}, terrestrial/arboreal insectivores; Carn, carnivores; Scav, scavengers; Omni, omnivorous species; All, all terrestrial species.

guild species richness towards the equator, calculated with untransformed richness as response) were observed for terrestrial/arboreal insectivores (Fig. 2g). Frugivores, granivores and carnivores also showed steep latitudinal gradients (Fig. 2c, d, h), whereas herbivores and scavengers did not show any pronounced peak at tropical latitudes (slopes $b \leq 0.06$). The remaining guilds had intermediate gradient slopes.

Environmental associations

Across guilds, climatic predictor variables usually showed stronger effects on guild species richness than topographic heterogeneity and habitat diversity (with $R^2_{\text{env}} \leq 0.23$), and multiple-predictor climate-REALM models generally showed a better fit (i.e. lower AIC, higher R^2_{env}) than habitat heterogeneity-REALM models for the same guild (Table 2). Nevertheless, the richness–environment associations markedly differed between guilds (Fig. 3). For instance, richness of frugivores and insectivores (both aerial and terrestrial/arboreal) was best explained by AET ($R^2_{\text{env}} \geq 0.53$) whereas herbivores and scavengers showed only weak climatic associations ($R^2_{\text{env}} \leq 0.27$). Temperature was the most important climatic correlate of the two latter guilds, but notably with opposite direction of effect (Fig. 3a). In contrast to other guilds, seasonality (having a negative effect) was the strongest climatic predictor for the species richness of nectarivores (Fig. 3a). Overall, the results from spatial autoregressive models were broadly similar to those from non-spatial models (see Fig. S5 in Appendix S2) and supported strong differences in richness–environment relationships between guilds.

Within two-dimensional, multivariate environmental (PCA) space, peaks in species richness of different dietary guilds sometimes showed distinct environmental associations (Fig. 3b). Overall bird species richness peaked in climatically benign areas (high PC1 scores, i.e. low SEAS, high AET, PREC, and TEMP), including grid cells with both high and low levels of habitat heterogeneity, i.e. PC2 scores (orange and red points, Fig. 3b). Terrestrial/arboreal insectivores, aerial insectivores and omnivores showed a similar pattern. In contrast, herbivore richness only peaked in areas with high habitat heterogeneity at medium levels of climatic suitability, frugivore and nectarivore richness abounded in areas with the highest climate (i.e. PC1) scores and granivore richness had an equal distribution of high richness across environmental space (Fig. 3b).

Richness–environment relationships as obtained from randomly sampling the global species pool indicated that variability in the explained variance (R^2_{env}) from random richness patterns decreased with an increasing number of species per guild (Fig. 4). Except for scavengers (the smallest guild, $n = 28$ species), observed richness–environment relationships deviated from random expectations in most cases (Fig. 4). For instance, most guilds showed a higher observed effect of precipitation, AET and seasonality on richness than expected by chance. The observed habitat diversity effect on richness was usually smaller, but the observed effect of topographic heterogeneity mostly similar, to a random pattern. Overall, the observed guild richness–environment relationships deviated from random in

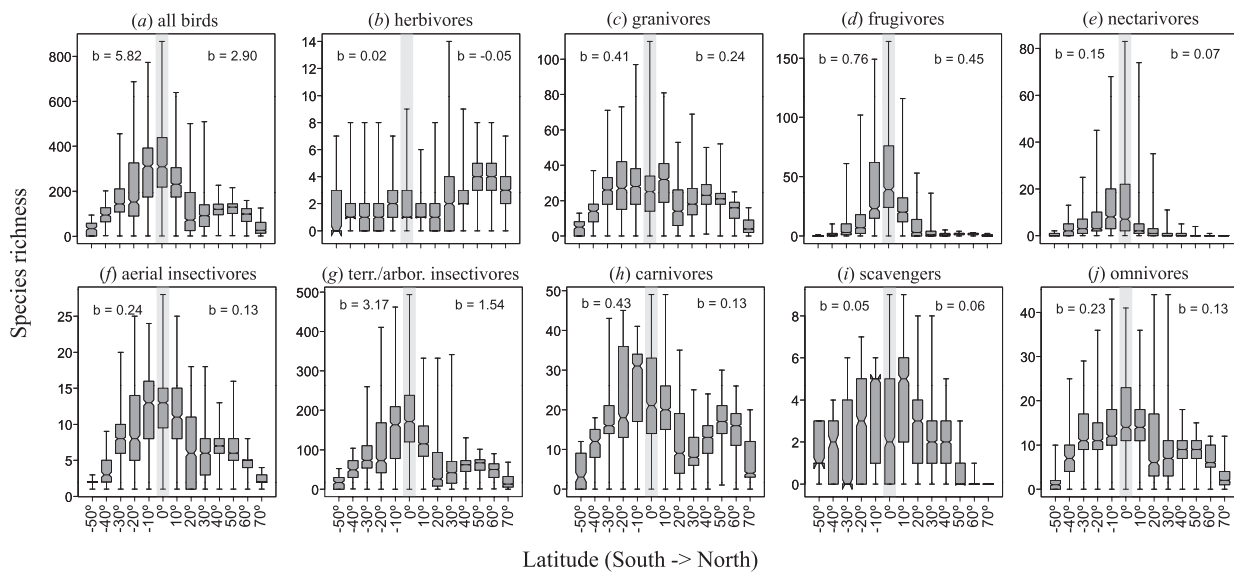


Figure 2 Latitudinal gradients of 110 km grid cell guild species richness per 10° latitudinal band. Boxes of boxplots represent the inter-quartile range (IQR) and whiskers extend to the data extremes. The tropical latitudinal band (from -5° to 5° latitude) is highlighted in light grey. For both southern and northern bands (including the tropical band in each), the slope (b) indicates gradient steepness (calculated using untransformed median band richness as response).

most cases except for topographic heterogeneity as a predictor and for guilds with very small species numbers (i.e. < 50 species, e.g. scavengers).

Biogeographic variation

Biogeographic region had a strong effect on avian guild species richness ($R^2_{\text{realm}} \geq 0.24$; Fig. 5a, Table S3 in Appendix S2) indicating that species richness patterns differ largely between regions. The strongest regional differences in species richness between regions were found for frugivores and nectarivores ($R^2_{\text{realm}} = 0.64$ and 0.60 , respectively). In contrast, biogeographic differences in species richness were small for herbivores ($R^2_{\text{realm}} = 0.14$) and intermediate for all other dietary guilds (Fig. 5a). Notably, for nectarivores and scavengers the effect of biogeographic realm membership was stronger than any environmental effects (compare Figs 3a & 5a). After accounting for present-day environment, guild richness differed less strongly between regions (Fig. 5b). The strongest REALM effects after accounting for environment were observed for nectarivores ($R^2_{\text{realm}} = 0.33$), scavengers ($R^2_{\text{realm}} = 0.23$) and omnivores ($R^2_{\text{realm}} = 0.17$). All other guilds showed clearly weaker differences between biogeographic regions when the effect of current environment was statistically removed ($R^2_{\text{realm}} < 0.10$; Fig. 5b).

In multiple-predictor SLMs, REALM and either climatic or habitat heterogeneity variables together often explained > 50% of variation in guild species richness on a global scale (see R^2_{env} in Table 2). The inclusion of an interaction term in both climate–REALM and habitat heterogeneity–REALM models often improved model fit, indicating that the richness–environment relationship of many dietary guilds varies between biogeographic regions (Table 2). For some guilds (e.g. herbivores, granivores

and scavengers) there was no evidence of a realm-specific response to environmental conditions because interaction terms did not improve model performance (Table 2). For most guilds (except frugivores), multiple-predictor models including all three types of predictor variables (i.e. climate, habitat heterogeneity and REALM) had the highest explanatory power (Table 2).

DISCUSSION

By linking world-wide species distributions with dietary knowledge of all terrestrial birds we were able to document that peaks in species richness of avian dietary guilds show pronounced differences in global geographical and environmental space. Furthermore, we found marked guild-specific variation in richness congruence and differences in the steepness of latitudinal gradients among guilds. Environmental drivers of species richness as well as historical (i.e. biogeographic) imprints in spatial patterns of species richness also differ between guilds, and richness–environment relationships differ from those obtained from random patterns in most cases. We therefore suggest that global patterns of bird species diversity result from several divergent processes including evolutionary innovations in dietary preferences and environmental constraints on the distribution and diversification of food resources.

For most (but not all) guilds, a measure of net primary productivity (i.e. AET) explained a large proportion of spatial variation in species richness which supports the idea that environmental productivity is a major determinant of taxonomic richness over broad geographic extents (Jetz & Rahbek, 2002; Hawkins *et al.*, 2003). The importance of AET was most pronounced for frugivores and insectivores, guilds that show also high levels of richness congruence. For these guilds,

Table 2 Multiple-predictor spatial linear models (SLMs) to explain global guild species richness.

Models	AIC	R^2_{env}	R^2_{full}	Moran's I	P	Models	AIC	R^2_{env}	R^2_{full}	Moran's I	P
All birds						Aerial insectivores					
AET ² + REALM	-737	0.66	0.91	0.09	0.05	AET ² + REALM	-695	0.54	0.82	0.07	0.10
AET ² + REALM + AET : REALM	-743	0.68	0.92	0.08	0.07	AET ² + REALM + AET : REALM	-696	0.55	0.82	0.07	0.10
HAB ² + REALM	-637	0.57	0.91	0.07	0.09	HAB ² + REALM	-620	0.45	0.81	0.06	0.13
HAB ² + REALM + HAB : REALM	-641	0.60	0.91	0.07	0.09	HAB ² + REALM + HAB : REALM	-625	0.47	0.81	0.06	0.14
AET² + HAB² + REALM	-794	0.72	0.92	0.09	0.05	AET² + HAB² + REALM	-731	0.58	0.83	0.07	0.09
Herbivores						Terr.-arb. insectivores					
TEMP ² + REALM	-404	0.34	0.68	0.05	0.13	AET ² + REALM	-500	0.64	0.88	0.07	0.17
TEMP ² + REALM + TEMP : REALM	-405	0.36	0.69	0.05	0.14	AET ² + REALM + AET : REALM	-510	0.66	0.89	0.06	0.18
HAB + REALM	-356	0.18	0.68	0.06	0.12	HAB ² + REALM	-416	0.58	0.88	0.06	0.20
HAB + REALM + HAB : REALM	-356	0.20	0.69	0.05	0.13	HAB ² + REALM + HAB : REALM	-422	0.61	0.88	0.05	0.21
TEMP² + HAB + REALM	-414	0.36	0.69	0.05	0.13	AET² + HAB² + REALM	-565	0.71	0.89	0.06	0.16
Granivores						Carnivores					
AET ² + REALM	-800	0.41	0.81	0.07	0.10	AET ² + REALM	-786	0.45	0.84	0.10	0.06
AET ² + REALM + AET : REALM	-798	0.42	0.81	0.07	0.10	AET ² + REALM + AET : REALM	-794	0.48	0.84	0.09	0.07
HAB ² + REALM	-773	0.38	0.81	0.07	0.10	HAB ² + REALM	-734	0.45	0.82	0.09	0.08
HAB ² + REALM + HAB : REALM	-774	0.39	0.81	0.07	0.10	HAB ² + REALM + HAB : REALM	-739	0.48	0.82	0.09	0.09
AET² + HAB² + REALM	-837	0.46	0.82	0.07	0.11	AET² + HAB² + REALM	-801	0.50	0.84	0.09	0.07
Frugivores						Scavengers					
AET + REALM	-332	0.83	0.94	0.06	0.08	TEMP + REALM	-668	0.38	0.81	0.06	0.07
AET + REALM + AET : REALM	-357	0.86	0.94	0.06	0.09	TEMP + REALM + TEMP : REALM	-668	0.41	0.81	0.06	0.07
HAB + REALM	-93	0.64	0.93	0.05	0.15	HAB ² + REALM	-668	0.37	0.82	0.06	0.08
HAB + REALM + HAB : REALM	-106	0.66	0.93	0.05	0.15	HAB ² + REALM + HAB : REALM	-667	0.34	0.82	0.06	0.09
AET + HAB + REALM	-339	0.83	0.94	0.06	0.08	TEMP + HAB² + REALM	-671	0.39	0.81	0.06	0.08
Nectarivores						Omnivores					
SEAS + REALM	-304	0.62	0.90	0.04	0.23	AET ² + REALM	-624	0.60	0.83	0.06	0.18
SEAS + REALM + SEAS : REALM	-310	0.64	0.90	0.04	0.24	AET ² + REALM + AET : REALM	-631	0.61	0.83	0.06	0.19
HAB ² + REALM	-313	0.53	0.91	0.02	0.36	HAB ² + REALM	-527	0.50	0.82	0.06	0.21
HAB ² + REALM + HAB : REALM	-320	0.54	0.91	0.02	0.37	HAB ² + REALM + HAB : REALM	-531	0.52	0.82	0.05	0.23
SEAS + HAB² + REALM	-334	0.61	0.91	0.03	0.28	AET² + HAB² + REALM	-652	0.64	0.83	0.06	0.19

The best-fit predictors from single-predictor SLMs (see Fig. 3a and Table S3 in Appendix S2) out of two categories 'climate' (TEMP, temperature; PREC, annual precipitation; AET, actual evapotranspiration; SEAS, seasonality) and 'habitat heterogeneity' (TOPO, altitudinal range; HAB, number of vegetation classes) were combined with REALM to develop multiple-predictor SLMs. An interaction term between REALM and the respective climate or habitat heterogeneity variable was included to test for realm-specific richness–environment relationships. Models with all three types of variables (climate, habitat heterogeneity, REALM) are given for comparison. AIC, Akaike information criterion; R^2_{env} , non-spatial model fit; R^2_{full} , full fit of SLM including spatial weight matrix; Moran's I , a measure of residual spatial autocorrelation; P , significance value of Moran's I value. The squared term indicates that both the linear and quadratic terms were included if model fit was improved (i.e. AIC reduced) to account for hump-shaped relationships. Moran's I values with $P \geq 0.05$ indicate non-significant residual spatial autocorrelation. AIC values are only comparable between models of the same guild. The model with the lowest AIC value is given in bold.

resource availability (i.e. abundance and diversity of fruits and insects) is strongly associated with the high productivity of tropical ecosystems. Interestingly, for nectarivores a relatively high effect of seasonality on species richness was found which could reflect their strong dependence on the seasonal availability of flower resources (Abrahamczyk & Kessler, 2010). This effect

could be further enforced by the small body sizes and high metabolic rates of species in this guild (Brown *et al.*, 1978). The positive effect of temperature on scavenger richness was the only environmental effect that deviated from random, and coincides with the availability of food resources for these consumers (i.e. carrion) in open, hot and savanna-like habitats (Morrison *et al.*,

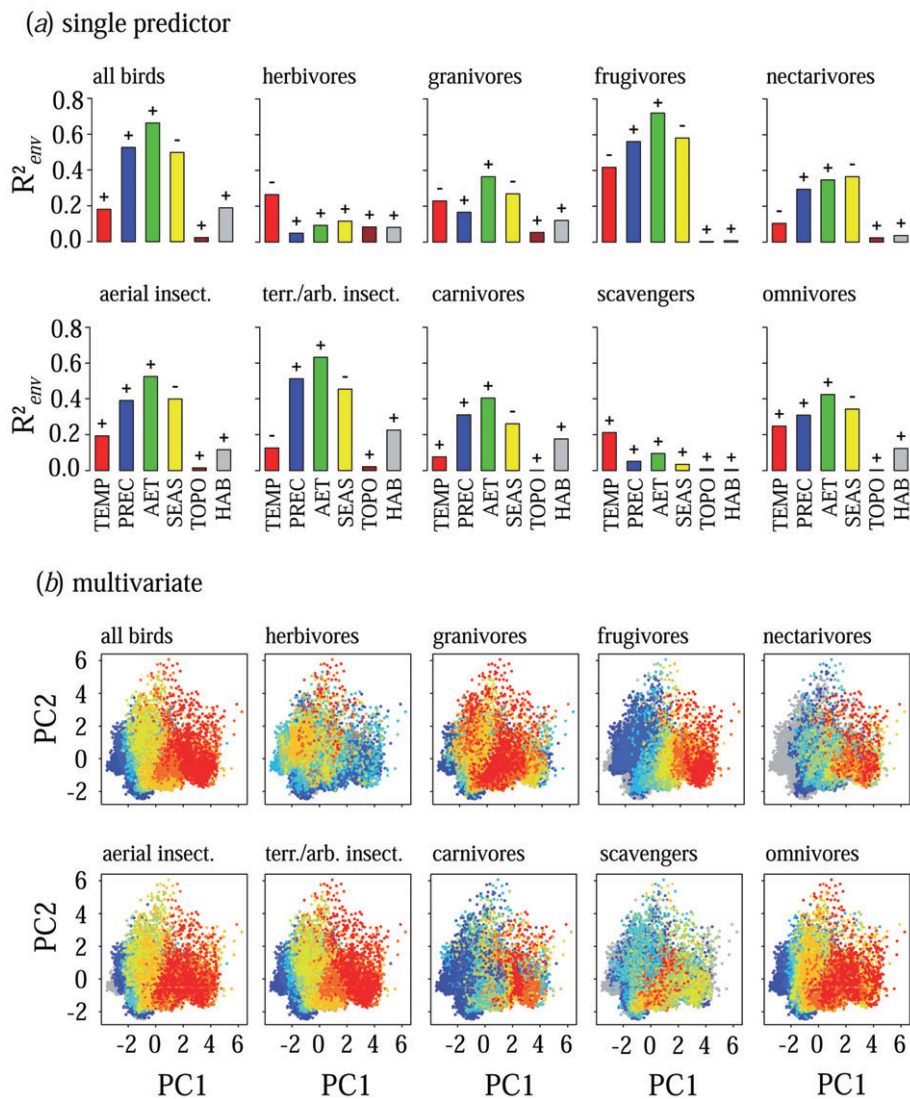


Figure 3 Environmental associations of global guild species richness with (a) single environmental predictors and (b) multivariate environmental space. In (a) the explained variance (R^2_{env} , coloured bars) from single-predictor spatial autoregressive models is given for individual predictor variables: TEMP, temperature (red); PREC, precipitation (blue); AET, actual evapotranspiration (green); SEAS, seasonality (yellow); TOPO, topographic heterogeneity (brown); HAB, habitat heterogeneity (grey). Quadratic terms of predictor variables were included when appropriate (see Table S3 in Appendix S2). + or – indicates the direction of effect. In (b) each coloured dot represents the species richness of one grid cell [colour ramps from blue (low richness) to red high (richness) correspond with panels in Fig. 1 except for grey dots representing unoccupied cells] along two axes (PC1: increasing AET, PREC, and TEMP, and decreasing SEAS; PC2: increasing HAB and TOPO) of a principal components analysis.

2007). Topographic heterogeneity was a rather poor predictor of guild species richness at this spatial scale, and its effect did not differ from random expectations. These findings are supported by most other broad-scale studies (birds, e.g. Jetz & Rahbek, 2002; Qian, 2008; across taxa, Hawkins *et al.*, 2003) which show that measures of climate explain spatial variation in overall species richness better than non-climatic variables at continental and global spatial scales (Field *et al.*, 2009). However, a recent analysis by Davies *et al.* (2007) showed that elevational range is the strongest predictor of bird diversity at the global scale, but differences in spatial model choice, unknown levels of residual spatial autocorrelation (e.g. Moran's I -values) and a strong dis-

crepancy between results of non-spatial and spatial models (compare Table 2 and Table S2 from Davies *et al.*, 2007) impede a direct comparison with our results.

In a recent meta-analysis, Hillebrand (2004) found no consistent differences in the slopes of latitudinal gradients between seven trophic levels across a variety of taxa (autotrophs, herbivores, carnivores, omnivores, suspension feeders, microbivores, parasites). In birds, however, marked differences in gradient slope exist between major functional groups which could (at least partly) be attributed to evolutionary innovations in dietary strategies and environmental constraints on the distribution of food resources. For instance, the steepest richness increase

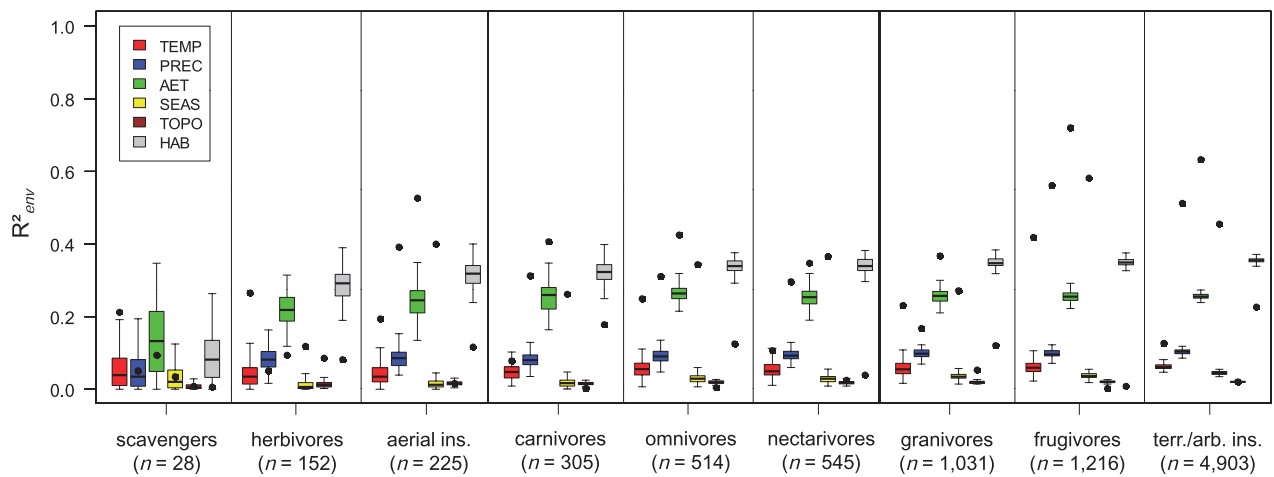


Figure 4 Explained variance (R^2_{env}) of richness–environment relationships as obtained from random richness patterns ($n = 100$ simulated richness maps per guild obtained from subsampling the global species pool with the guild-specific number of species; box-and-whisker plots) compared with those from observed richness patterns (black dots). For colours and abbreviations of environmental predictors see Fig. 3(a). Guilds are ordered by increasing species richness (given in brackets). Boxes represent the inter-quartile range (IQR), horizontal lines within the boxes represent medians, and whiskers extend to 1.5 times the IQR. Note that the variability in random guild richness–environment relationships decreases with increasing species richness of guilds (from left to right). TEMP, temperature; PREC, annual precipitation; AET, actual evapotranspiration, SEAS, coefficient of variation of monthly net primary productivity; TOPO, altitudinal range; HAB, number of vegetation classes.

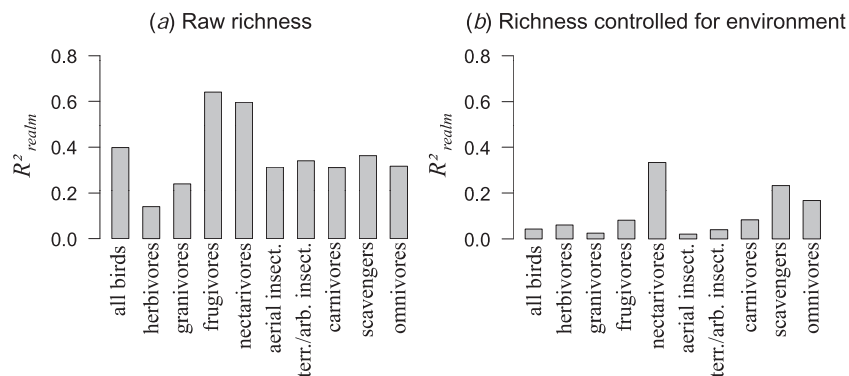


Figure 5 Effect of biogeographic context on (a) raw guild species richness and (b) guild richness after accounting for environment. In (a), R^2_{realm} is the explained variance of realm membership (including Afrotropics, Australasia, Indo-Malaya, Nearctic, Neotropics, and Palearctic) from single-predictor spatial autoregressive models (SLMs; see Table S3 in Appendix S2). In (b), R^2_{realm} is the uniquely explained variance of realm membership calculated as the explained variance (pure fit of predictor variables) of multiple predictor SLMs using all six environmental variables and REALM minus the explained variance (pure fit) of multiple predictor SLMs using all six environmental variables without REALM. Note that (b) statistically accounts for present-day environment although some historical (i.e. biogeographic) effects could also be removed if they covary with present-day environment.

towards the tropics was observed for terrestrial/arboreal insectivores, a guild including the diversification of > 400 species of New World flycatchers (Tyrannidae) and an exceptional radiation of more than 560 species of Neotropical woodcreepers, ovenbirds and antbirds (superfamily Furnarioidea) (order Passeriformes; Table S4 in Appendix S2). For frugivores, the steep richness gradient towards the tropics can be explained by the year-round availability of fruits in tropical lowland regions (Kissling *et al.*, 2007, 2009) and the resulting opportunities for dietary niche separation over ecological and evolutionary time (Snow, 1981; Primack & Corlett, 2005). The shallow gradient

slopes for herbivores and scavengers indicate that these dietary guilds do not predominate at tropical latitudes. Peaks in scavenger richness (i.e. species belonging mainly to the Falconiformes; Table S4 in Appendix S2) are found in East Africa where the diversity and abundance of large ungulates is exceptionally high (Morrison *et al.*, 2007), whereas herbivores abound in the Himalayas, mainly due to the radiation of ground-living Galliformes (including the grouse, quails and pheasants; see Table S4 in Appendix S2), many of which preferably feed on vegetable matter. Our results suggest that the spatio-temporal availability of food resources, especially in (sub)tropical regions, plays an

important role in shaping the steepness of the latitudinal gradient and the biogeographical patterns of species richness we observe.

We observed strong differences in species richness between biogeographic regions, and for some guilds (e.g. nectarivores, scavengers and omnivores) this biogeographic effect was retained even after environment was statistically accounted for. However, it is important to note that accounting for the current environment can also remove some historical effects, e.g. if current climate is highly correlated with past climate or if current environment covaries with the diversification and diversity of food resources. For instance, the spatial distribution of species richness of frugivores covaries with the diversity of fleshy fruited plants (Snow, 1981; Gentry, 1982; Kissling *et al.*, 2007). Given that fleshy fruited plant diversity also strongly covaries with water–energy availability (Kissling *et al.*, 2007), accounting for current environment might remove historical and evolutionary effects due to past climate history and/or the evolutionary diversification of fleshy fruited plants (Kissling *et al.*, 2009). Interestingly, for nectarivores a strong biogeographic effect is retained even when accounting for environment, suggesting that historical and evolutionary factors might have played an extraordinary role in the diversification of this guild. The global richness pattern of nectarivores is mainly driven by the spectacular Neotropical radiation of hummingbirds (Bleiweiss, 1998) which make up about 60% of all nectarivores on earth (see Table S4 in Appendix S2). The species richness and nectar dependence of hummingbirds is larger than in other clades with nectarivorous species (Nicolson & Fleming, 2003), and this could at least partly explain the biogeographically uneven distribution of nectarivore richness. Similarly, the strong environmentally independent biogeographic effect on scavenger richness and their peak in East Africa corresponds to the peak in the abundance and species richness of large mammals (Morrison *et al.*, 2007). Thus, for scavengers, frugivores and nectarivores, the apparent regional covariation with the richness of food items supports the idea that the diversification and immigration of food resources has strongly influenced the biogeographic distribution of global consumer richness.

Our analyses finally showed that richness–environment relationships are often guild- and region-specific. Such results argue against a universal (global) richness–environment relationship within and across dietary and taxonomic levels. Given the often strong phylogenetic conservatism of traits (Wiens & Graham, 2005), we hypothesize that much of the broadly recognized conservatism of broad-scale climatic niches (cf. Wiens & Donoghue, 2004) may actually arise via constraints imposed by species ecological attributes and functional traits such as dietary preference. The relative importance of dietary versus environmental (e.g. climatic) niches in interaction with phylogenetic constraints clearly deserves further study, but our study already highlights that ecological specialization such as dietary preferences within and across lineages needs to be included to fully understand the global bird diversity gradient. We suggest that future studies will greatly benefit from better linking the knowledge of ecological adaptations and functional traits with

species distributions in the context of abiotic environmental gradients.

ACKNOWLEDGEMENTS

We thank Jonathan Belmaker, Frank La Sorte, Holger Kreft, Trevor Price, David Currie and anonymous referees for comments on various versions of the manuscript. W.J. acknowledges the support by National Science Foundation grant BCS-0648733 and C.H.S. acknowledges Christensen Fund's support. C.H.S. is grateful to Sherron Bullens, Debbie Fisher, David Hayes, Beth Karpas and especially Kathleen McMullen for their dedicated help with the world bird ecology database.

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Appendix S1 References for diet data.

Appendix S2 Additional results.

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Editor: Tim Blackburn