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The global distribution of frugivory in birds

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ABSTRACT

Aim To examine patterns of avian frugivory across clades, geography and environments.

Location Global, including all six major biogeographical realms (Afrotropics, Australasia, Indo-Malaya, Nearctic, Neotropics and Palaearctic).

Methods First, we examine the taxonomic distribution of avian frugivory within orders and families. Second we evaluate, with traditional and spatial regression approaches, the geographical patterns of frugivore species richness and proportion. Third, we test the potential of contemporary climate (water–energy, productivity, seasonality), habitat heterogeneity (topography, habitat diversity) and biogeographical history (captured by realm membership) to explain geographical patterns of avian frugivory.

Results Most frugivorous birds (50%) are found within the perching birds (Passeriformes), but the woodpeckers and allies (Piciformes), parrots (Psittaciformes) and pigeons (Columbiformes) also contain a significant number of frugivorous species (9–15%). Frugivore richness is highest in the Neotropics, but peaks in overall bird diversity in the Himalayan foothills, the East African mountains and in some areas of Brazil and Bolivia are not reflected by frugivores. Current climate explains more variance in species richness and proportion of frugivores than of non-frugivores whereas it is the opposite for habitat heterogeneity. Actual evapotranspiration (AET) emerges as the best single climatic predictor variable of avian frugivory. Significant differences in frugivore richness and proportion between select biogeographical regions remain after differences in environment (i.e. AET) are accounted for.

Main conclusions We present evidence that both environmental and historical constraints influence global patterns of avian frugivory. Whereas water–energy dynamics possibly constrain frugivore distribution via indirect effects on food plants, regional differences in avian frugivory most likely reflect historical contingencies related to the evolutionary history of fleshy fruited plant taxa, niche conservatism and past climate change. Overall our results support an important role of co-diversification and environmental constraints on regional assembly over macroevolutionary time-scales.

Keywords

Biodiversity, biogeography, climate history, co-evolution, guild, historical contingency, hotspot congruence, plant–animal interactions, species–energy theory.

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INTRODUCTION

Broad-scale geographical patterns of species distributions are central to ecology and have gained much attention in recent years (e.g. Jetz & Rahbek, 2002; Hawkins *et al.*, 2003a; Currie *et al.*, 2004). Although a number of studies have shown a remarkably strong association between species richness and present-day

climate or habitat heterogeneity (Rahbek & Graves, 2001; Jetz & Rahbek, 2002; Hawkins *et al.*, 2003a) there remains much debate about the precise mechanisms of the origin and maintenance of biodiversity (Ricklefs, 1987, 2006; Mittelbach *et al.*, 2007). Ecologists recognize that ecological communities are not only constrained by current environment and ecological sorting processes but also by the evolutionary history of clades and the

biogeographical history of the region (Ricklefs, 1987; Ricklefs & Schluter, 1993; Wiens & Donoghue, 2004; Mittelbach *et al.*, 2007). Global studies and cross-continental comparisons have the greatest potential to elucidate the relative roles of environmental or historical constraints on broad-scale patterns of species distribution (Qian & Ricklefs, 2000; Ericson *et al.*, 2003; Hawkins *et al.*, 2003b, 2007; Primack & Corlett, 2005; Ricklefs, 2006; Buckley & Jetz, 2007; Davies *et al.*, 2007; Kreft & Jetz, 2007).

Here we examine global geographical patterns of frugivorous birds, an avian ecological guild composed of species that specialize in fleshy fruited plants as food resources (Fleming *et al.*, 1987). Frugivores are of great interest to ecologists because they play an important role in plant reproduction and ecosystem functioning via seed dispersal services (Karr, 1976; Fleming *et al.*, 1987; Herrera, 2002). Yet, despite decades of research on frugivores, especially at local spatial scales (e.g. Herrera, 1985, 2002; Levey, 1988; see also references in Shanahan *et al.*, 2001), little is known about the ecological and evolutionary processes that shape the broad-scale occurrence of frugivory (Fleming *et al.*, 1987; Primack & Corlett, 2005; Kissling *et al.*, 2007, 2008). For instance, it is unclear whether geographical patterns of frugivore richness at a global scale simply match those of all birds, or whether they show distinct regional differences due to the species dietary specializations and interactions with food plants (Kissling *et al.*, 2007). The unique knowledge about both the global distribution (Davies *et al.*, 2007; Jetz *et al.*, 2007) and ecology (e.g. Newton, 2003; Şekercioğlu *et al.*, 2004) of all birds now allows a first evaluation of how such dietary specializations and geographical distributions interact at the global scale for a whole clade.

Frugivorous birds may thus serve as an intriguing model system to study the relative roles of environmental, historical and biotic constraints on diversification and spatial distribution of species. On the one hand, the distribution and diversity of fleshy fruited plants, fruit biomass production and fruit phenologies are largely determined by water–energy dynamics and seasonality of the climate (Karr, 1976; Fleming *et al.*, 1987; Kreft & Jetz, 2007; Kissling *et al.*, 2007; Ting *et al.*, 2008). This suggests an important role of current climate in determining frugivore diversity at broad spatial scales. On the other hand, the diversification of frugivores might have been strongly influenced by historical factors. These include the evolutionary history and diversification of fleshy fruited plants (Snow, 1981; Gentry, 1982; Fleming *et al.*, 1987; Harrison, 2005), the presence or absence of mammalian competitors (Fleming *et al.*, 1987; Primack & Corlett, 2005) or the past climate history and the geographical position of dispersal barriers (Fleming *et al.*, 1987; Newton, 2003). This implies a strong imprint of evolutionary history on geographical patterns of avian frugivore distribution at the global scale.

Here we present a first global-scale analysis of both taxonomic and geographical patterns of avian frugivore distribution and potential environmental and historical determinants. Analysing a comprehensive database covering the distribution of all terrestrial bird species ($n = 8918$) we elucidate the taxonomic distribution of frugivory within orders and families. Using both non-spatial and spatial (controlling for spatial autocorrelation) modelling techniques, we test the potential of contemporary

climate (water–energy, productivity and seasonality), habitat heterogeneity (topography, habitat diversity) and biogeographical history (captured by realm membership) to explain avian frugivore richness and the proportion of frugivores in bird assemblages. We are particularly interested in the interplay between environment and biogeographical context in shaping patterns of frugivore distribution at the global scale.

METHODS

Species richness data

Our study is based on a comprehensive database of the breeding distributions of all bird species in the world (Jetz *et al.*, 2007). We included all 8918 terrestrial bird species (out of a total of 9753) in our analysis, excluding birds that predominantly feed in freshwater or marine habitats ($n = 835$). The maps represent the extent of occurrence during the breeding season and were compiled from the most accurate sources for a given broad geographical 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 either 110×110 or 220×220 km resolution (equivalent to c. $1^\circ \times 1^\circ$ or $2^\circ \times 2^\circ$ near the equator, respectively). A recent validation analysis confirmed satisfactory range map accuracy for this same data set at roughly 150–200-km grid cell resolution across North America, southern Africa and Australia (Hurlbert & Jetz, 2007). The classification of 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.

Frugivore classification

The diets of all species in our database were determined from a comprehensive literature survey (see Table S1 in Supporting Information) and the classification procedure follows Şekercioğlu *et al.* (2004). For all species, the dietary components mentioned in the literature were assigned to nine categories (fish, fleshy fruits, terrestrial invertebrates, nectar, aquatic invertebrates, plant material, carrion, seeds and vertebrates) and each category was ranked in importance for each individual species when it was present as a dietary component. Both the ranks and the diet breadth (i.e. number of diet categories a species has) were used to assign the relative importance of each diet category for each individual species. From this assignment we classified frugivores as those species that have fleshy fruits as their main diet. This included species where fleshy fruits were identified as the most important diet category (i.e. rank = 1) and that simultaneously had no more than three diet categories (i.e. diet breadth up to 3). With this definition of frugivory we followed other authors who define a frugivore as an animal whose diet is composed of > 50% fleshy fruits (e.g. Fleming *et al.*, 1987). To assess the sensitivity of this classification, we additionally compared geographical patterns of species richness for different levels of frugivory, including obligate frugivores (i.e. species

which exclusively feed on fleshy fruits), partial frugivores (i.e. species with fruits as main diet, but one or two other dietary components), opportunistic frugivores (i.e. species with fruits as supplementary diet and more than two other dietary components) and non-fruit eaters (i.e. species with no fruits in the diet) (cf. Kissling *et al.*, 2007). Due to lack of information we could not assess the importance of seasonal dietary shifts in our classification, but the numbers and proportions of frugivores are likely to increase at both low and high latitudes if seasonal frugivory is given more weight.

Taxonomic and geographical patterns of avian frugivore distribution

We first examined taxonomic patterns of frugivore richness by subdividing total avian frugivore richness into species richness within orders and families. For the most species-rich orders we mapped geographical patterns of frugivorous species richness to explore diversification patterns of major clades. We then analysed the overall geographical pattern of avian frugivore distribution across the world by calculating two variables for each grid cell: (1) the species richness of avian frugivores (i.e. the number of all frugivorous bird species present in each cell based on the extent of occurrence maps), and (2) the proportion of frugivores in the total bird assemblage (i.e. the species richness of frugivores divided by overall bird species richness in each cell). The first measure gives the absolute number of frugivorous species across the world, whereas the second provides a measure of the degree of frugivory in a bird assemblage correcting for overall bird species richness. To evaluate the congruence between patterns of avian frugivore richness and overall bird diversity we further identified hotspots of both categories as the richest 5% of grid cells (cf. Prendergast *et al.*, 1993). We also identified 5% frugivore richness hotspots for each of the most species-rich orders and assessed their congruence with overall bird diversity.

Putative determinants

We tested a total of 14 environmental predictor variables as potential determinants of the richness pattern of frugivorous birds. The variables belonged to three categories, i.e. water–energy and productivity (nine variables), seasonality (three variables) and habitat heterogeneity (two variables). One additional variable, realm, was used to capture historical factors related to the biogeographical history of a region. All variables have previously been shown to be strongly correlated with species richness of vertebrates and/or woody plants at continental and global scales (e.g. Rahbek & Graves, 2001; Jetz & Rahbek, 2002; Hawkins *et al.*, 2003a,b; Buckley & Jetz, 2007; Davies *et al.*, 2007; Kreft & Jetz, 2007; Kissling *et al.*, 2007).

Environmental and geographical data were assembled and extracted in ArcGIS (version 9.1, ESRI, Redlands, CA, USA) and resampled to the same resolution as the bird data. Among the variables related to water–energy and productivity, we used potential evapotranspiration (PET), mean annual temperature (TEMP) and number of frost days (FROST) to assess the effect of

temperature and energy availability on species richness. We included annual precipitation (PREC) and number of wet days (WET) to indicate water availability, and used actual evapotranspiration (AET) as an integrated measure of the water–energy balance. Additionally, we used net primary productivity (NPP), which is often thought to be a good proxy for food availability in terrestrial ecosystems (Wright, 1983; Jetz & Rahbek, 2002; Hawkins *et al.*, 2003b; Kissling *et al.*, 2007). We considered total annual aboveground productivity (NPPann) and total productivity of the least and most productive 3-month period (NPPmin, NPPmax) as estimates of energy availability. All climate variables were extracted from the mean monthly climatic database for the period 1961–90 with 10' resolution provided by New *et al.* (2002), except PET and AET which originated from the Ahn & Tateishi (1994) data set at 30' resolution, and mean monthly NPP values which were provided by Bondeau *et al.* (2007) for the time period 1961–90 at 0.5° resolution.

Seasonality in climate and productivity has been shown to strongly affect avian species richness (Hurlbert & Haskell, 2003), and this might be especially true for avian frugivores because seasonality in climate directly influences fruit production and phenologies (e.g. Karr, 1976; Ting *et al.*, 2008). We used the ratio of total productivity of the least productive 3 months and total productivity of the most productive 3 months ($NPP_{ratio} = NPP_{min}/NPP_{max}$), the seasonal pulse of production in relation to productivity of the most productive 3 months [$NPP_{pulse} = (NPP_{max} - NPP_{min})/NPP_{max}$] and the coefficient of variation of monthly NPP values (NPP_{cv}) as estimates of seasonality. Habitat heterogeneity, quantified either as topographic relief or as number of habitat types, has also been shown to determine broad-scale patterns of bird species richness (Rahbek & Graves, 2001; Jetz & Rahbek, 2002; Davies *et al.*, 2007). We used altitudinal range from the GTOPO-30 digital elevation model (TOPO; i.e. the difference between maximum and minimum elevation) and the number of vegetation classes (HABDIV) according to the Olson global land-cover classification to indicate habitat heterogeneity (both variables were derived from the Global Land Cover Characteristics Data Base available at <http://edcns17.cr.usgs.gov/glcc/>).

Finally, we investigated the potential effects of historical contingencies by partitioning the data into six biogeographical realms (REALM, including Afrotropics, Australasia, Indo-Malaya, Nearctic, Neotropics and Palearctic; see Udvardy, 1975). While the representation of evolutionary and biogeographical history as realms is relatively crude, it does capture major differences in frugivore diversification rates, such as those between the Old and New World tropics (Fleming *et al.*, 1987; Fleming, 2005). Grid cells falling within Oceania or Antarctica were omitted for statistical modelling since environmental data were lacking for these realms. Differences between realms in mean frugivore richness and mean frugivore proportion were tested with multiple pair-wise comparisons using Tukey's honestly significant difference (HSD) test which controls the group-wise type I error rate. The same tests were performed for residual frugivore richness and proportion after controlling for environmental differences (i.e. AET) between regions. To test the interplay of environmental

and historical factors on shaping global patterns of avian frugivore richness we examined whether the influence of environment on avian frugivore richness varied by realm (see below).

Statistical analysis

To analyse the potential of predictor variables in explaining global patterns of frugivore richness and proportion, we performed both non-spatial and spatial linear regression models. We compared these results with similar analyses for non-frugivorous species (including all other species, i.e. opportunistic frugivores and non-fruit-eaters, see above). We selected models based on the Akaike information criterion (AIC), an information theoretic method which evaluates the relative support in observed data based on model fit and model complexity (Burnham & Anderson, 2002). We additionally used R^2 values which provided similar results. To improve the normality and homogeneity of variance in our statistical models we log-transformed frugivore and non-frugivore richness and arcsine square root transformed proportion of frugivores and non-frugivores (note that results on untransformed variables gave qualitatively similar results). We first tested all single-predictor variables with non-spatial generalized linear models (GLMs; with Gaussian error distribution and identity link) and then used the best single environmental predictors from each category (i.e. water–energy and productivity, seasonality and habitat heterogeneity, respectively) and the historical predictor variable REALM to test combined multi-predictor models. We included squared terms in the single- and multiple-predictor regression models to account for hump-shaped relationships.

In a further step, we repeated these analyses but calculated spatial linear models (SLMs), which can account for the spatial autocorrelation structure in model residuals that affects type I error rates of non-spatial analyses (Legendre & Legendre, 1998). SLMs were calculated as 'spatial simultaneous autoregressive error models' which have been shown to perform best in terms of parameter estimation and type I error control (Kissling & Carl, 2008). The degree of spatial autocorrelation in GLM and SLM residuals was quantified with Moran's I values (Legendre & Legendre, 1998) which indicate high spatial autocorrelation with values close to 1/–1, and no autocorrelation with values close to 0. For SLMs, two R^2 values are provided which indicate the non-spatial smooth (R^2_{trend}) and the total fit between predicted and observed values (R^2_{fit} ; composed of non-spatial and spatial smooth). R^2_{trend} gives the explained variance of the SLM without including the explanatory power of the spatial weights matrix ('spatial smooth'), whereas R^2_{fit} provides the total explained variance of the SLM (including R^2_{trend} and spatial smooth). To illustrate the interaction between environment and biogeographical history in more detail we used single-predictor SLMs and analysed the relationship between the proportion of frugivores (arcsine square root transformed) and AET separately for each realm.

For the statistical analyses, we excluded cells for which environmental data were missing (i.e. Oceania, Antarctica, plus remaining island cells; see Table S2 in Supporting Information for details of frugivorous species that exclusively occur on

islands). Excluding cells with more than 50% water did not change the results of our analyses, so we included them. From these cells, we only included cells with frugivore presence in our statistical models ($n = 8563$ at resolution equivalent to 1° ; $n = 2221$ at resolution equivalent to 2°). We did the same for non-frugivorous species at a resolution equivalent to 1° ($n = 10,147$ cells). Due to memory limitations on the calculation of SLMs with global data sets we developed a bootstrapping approach where we randomly subsampled (10%, i.e. $n = 857$ cells at a resolution equivalent to 1° ; 40%, i.e. $n = 888$ cells at a resolution equivalent to 2°) the whole global data set 100 times. For each of the 100 random subsamples we calculated (single and multiple predictor) GLMs and SLMs and extracted the relevant model and test statistics (i.e. AIC, R^2 and Moran's I values). We then calculated mean values of all model and test statistics across the 100 random subsamples. Standard errors of mean values were much smaller than 10% of the mean values and are not reported. Unless otherwise stated, statistical analyses were done with R (R Development Core Team, 2007) and spatial analyses were conducted using the R library 'spdep', version 0.4–2 (2007, R. Bivand, available at <http://cran.r-project.org/web/packages/spdep/index.html>). The spatial neighbourhood of the SLMs was calculated by including the four (resolution equivalent to 1°) and two (resolution equivalent to 2°) nearest neighbouring cells, respectively, within each subsample of the data and by using a row-standardized coding scheme to calculate the spatial weights matrix (see Kissling & Carl, 2008).

RESULTS

Frugivore classification

From our 8918 terrestrial bird species a total of 1230 species (14%) were classified as frugivorous (see Table S1). To assess the sensitivity of this classification we compared geographical patterns of species richness for different levels of frugivory (see Fig. S1 in Supporting Information). Including only species which exclusively feed on fleshy fruits (obligate frugivores; $n = 365$) made frugivory a quintessential tropical phenomenon (see Fig. S1a) whereas the inclusion of frugivorous species with other dietary components (e.g. invertebrates or seeds) gradually extended frugivory to extratropical latitudes (see Fig. S1b,c). Partial frugivores (i.e. species with fruits as the main diet, but one or two other dietary components; $n = 865$) also occurred in low species numbers at temperate latitudes but showed otherwise similar geographical patterns in species richness to obligate frugivores. In contrast, both opportunistic frugivores (i.e. species with fruits as a supplementary diet and more than two other dietary components; $n = 1659$) and non-fruit eaters (species with no fruits in the diet; $n = 6029$) showed additional species-rich areas in the Himalayan foothills, the East African mountains and the Atlantic forest of Brazil (see Fig. S1c,d) which were not reflected by obligate and partial frugivores. An increase in the degree of avian specialization on fruits thus resulted in a decrease of spatial congruence between the species richness of frugivorous guilds (i.e. non-fruit eaters, opportunistic, partial and obligate

Table 1 Taxonomic distribution of frugivorous bird species ($n = 1230$) within orders and families. The expected proportion of frugivorous species within an order would be 14% based on the frequency of frugivorous species across all species.

Order	Frugivore richness	Total species richness	Proportion of frugivores in order (%)	Percentage of all frugivores ($n = 1230$)	Families (number of frugivorous species, total number of species)
Passeriformes	618	5841	11	50	Bombycillidae (8, 8), Corvidae (82, 645), Eurylaimidae (4, 15), Fringillidae (180, 1029), Hypocoliidae (1, 1), Irenidae (1, 10), Melanocharitidae (6, 10), Meliphagidae (7, 177), Muscicapidae (37, 443), Nectariniidae (6, 172), Paramythiidae (2, 2), Passeridae (1, 387), Ptilonorhynchidae (20, 20), Pycnonotidae (58, 129), Sturnidae (68, 144), Sylviidae (12, 560), Tyrannidae (124, 574), Zosteropidae (1, 97)
Columbiformes	179	308	58	15	Columbidae (179, 308)
Psittaciformes	141	351	40	11	Cacatuidae (2, 21), Psittacidae (139, 330)
Piciformes	112	349	32	9	Lybiidae (35, 41), Megalaimidae (26, 26), Picidae (3, 216), Ramphastidae (48, 49)
Craciformes	50	69	72	4	Cracidae (48, 50), Megapodiidae (2, 19)
Bucerotiformes	38	54	70	3	Bucerotidae (38, 52)
Musophagiformes	23	23	100	2	Musophagidae (23, 23)
Tinamiformes	22	47	47	2	Tinamidae (22, 47)
Trogoniformes	15	39	38	1	Trogonidae (15, 39)
Galliformes	13	211	6	1	Odontophoridae (2, 32), Phasianidae (11, 173)
Coliiformes	6	6	100	< 1	Coliidae (6, 6)
Cuculiformes	5	136	4	< 1	Cuculidae (5, 75)
Gruiformes	4	95	4	< 1	Psophiidae (3, 3), Rallidae (1, 59)
Struthioniformes	3	10	30	< 1	Casuariidae (3, 4)
Strigiformes	1	314	< 1	< 1	Steatornithidae (1, 1)

frugivores, respectively) and overall bird species richness (see Fig. S1), similar to a recent frugivore classification at the continental scale of sub-Saharan Africa (Kissling *et al.*, 2007). For all subsequent analyses we therefore included both obligate and partial frugivores as frugivorous species ($n = 1230$ species).

Taxonomic patterns of avian frugivory

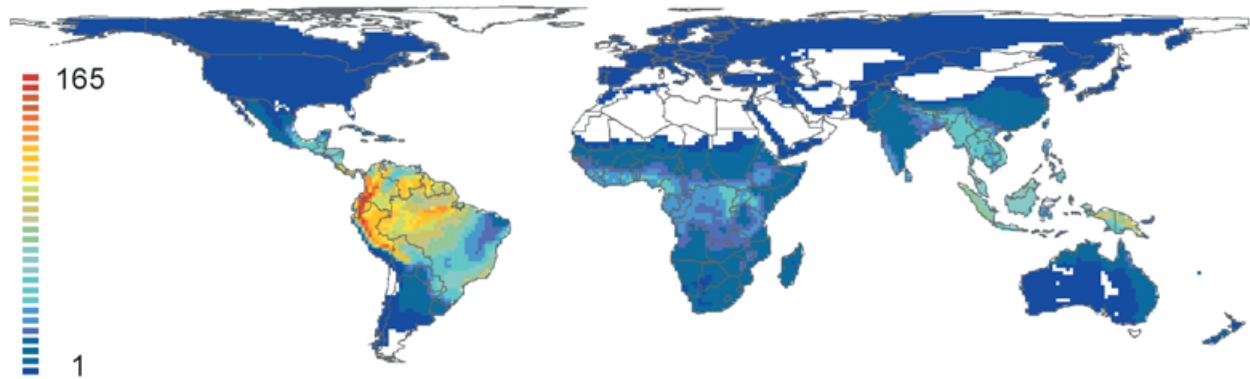
Out of a total of 1230 frugivorous bird species, most species ($n = 618$, 50%) were found within the perching birds (Passeriformes), with the family of the finches (Fringillidae) as the most species rich (Table 1). Orders that contributed a significant number of frugivorous species (> 100 species, 9–15%) included the pigeons (Columbiformes), the parrots (Psittaciformes) and the woodpeckers and allies (Piciformes). The remaining 11 orders contributed much fewer frugivorous species ($n < 50$ species, i.e. less than 4% of all frugivores; Table 1). Some orders such as the African turacos (Musophagiformes) or the African mousebirds (Coliiformes) consisted exclusively of frugivores (100%), and the pigeons (Columbiformes), the chachalacas, guans and curassows (Craciformes) and the hornbills (Bucerotiformes) had more than 50% frugivorous species (Table 1). Orders such as the Galliformes, Cuculiformes, Gruiformes and Strigiformes showed very low proportions of frugivorous species ($< 10\%$; Table 1).

Geographical patterns of avian frugivory

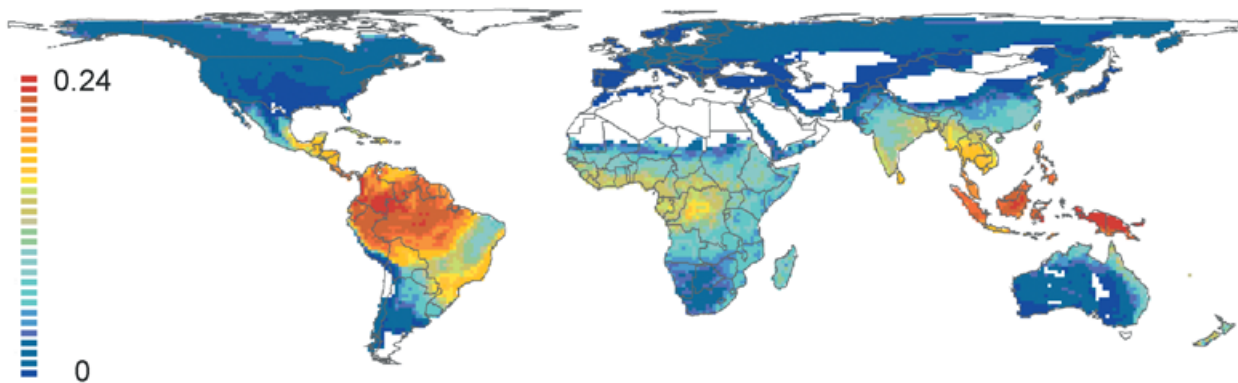
On a global scale and across all orders, the species richness of frugivorous birds was highest in the Neotropics with most species being found along the eastern slopes of the tropical Andes, the Guiana–Venezuela highlands, and along the Amazon River basin in Brazil (Fig. 1a). After accounting for overall bird diversity, the proportion of frugivores in bird assemblages had comparably high values at equatorial latitudes in the Neotropics, Indonesia and New Guinea, but not in Africa (Fig. 1b). Hotspots of frugivore richness (defined as the top 5% richest grid cells; $n = 489$ cells) were mainly concentrated in the Neotropics and to a large extent (90%; $n = 442$ cells) congruent with peaks in overall bird diversity (Fig. 1c). However, peaks in overall bird diversity in the Himalayan foothills, the East African mountains, the Atlantic forest and Parecis mountains of Brazil, and along the Rio Grande of Bolivia were not reflected by frugivores (Fig. 1c). Instead, some areas in south-east Colombia, northern Brazil and New Guinea showed peaks in frugivore richness not found for overall bird diversity (Fig. 1c).

Geographical patterns of frugivore richness of the six orders with the highest absolute number of frugivorous birds showed distinct differences in net diversification across the globe (Fig. 2a–f). Some orders such as the Passeriformes (Fig. 2a), Piciformes (Fig. 2d) and Craciformes (Fig. 2e) had their highest

(a) Frugivore richness



(b) Proportion of frugivores



(c) Hotspots of species richness

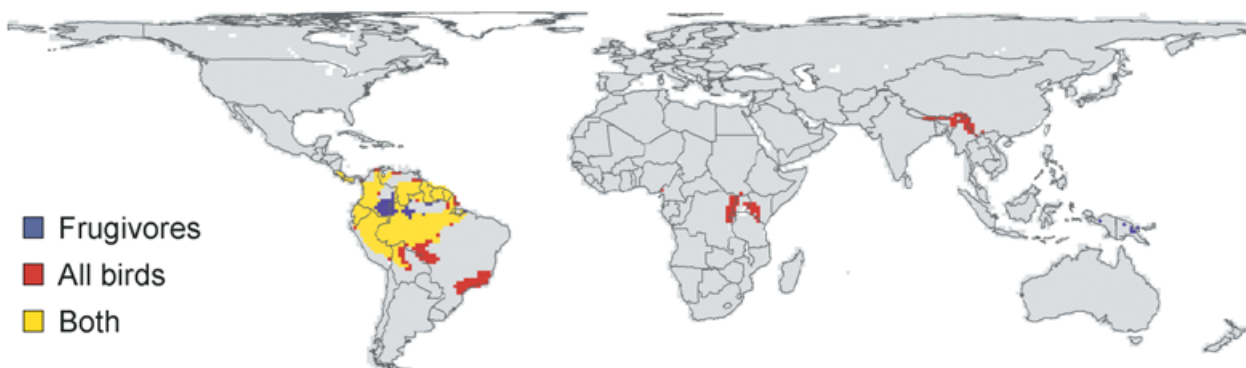


Figure 1 Global geographical patterns of avian frugivory. (a) Species richness of avian frugivores. (b) Proportion of birds that are frugivorous. (c) Hotspot congruence of avian frugivores with all birds. For (a) and (b), natural breaks classification is shown with colours varying from dark blue (lowest values) to dark red (highest values). For (c), hotspots of species richness were defined as the top 5% of grid cells richest in frugivores (deep purple and yellow) and all birds (red and yellow), respectively. Data are plotted across an equal-area grid (12,364 km², c. 1° latitude × 1° longitude near the equator).

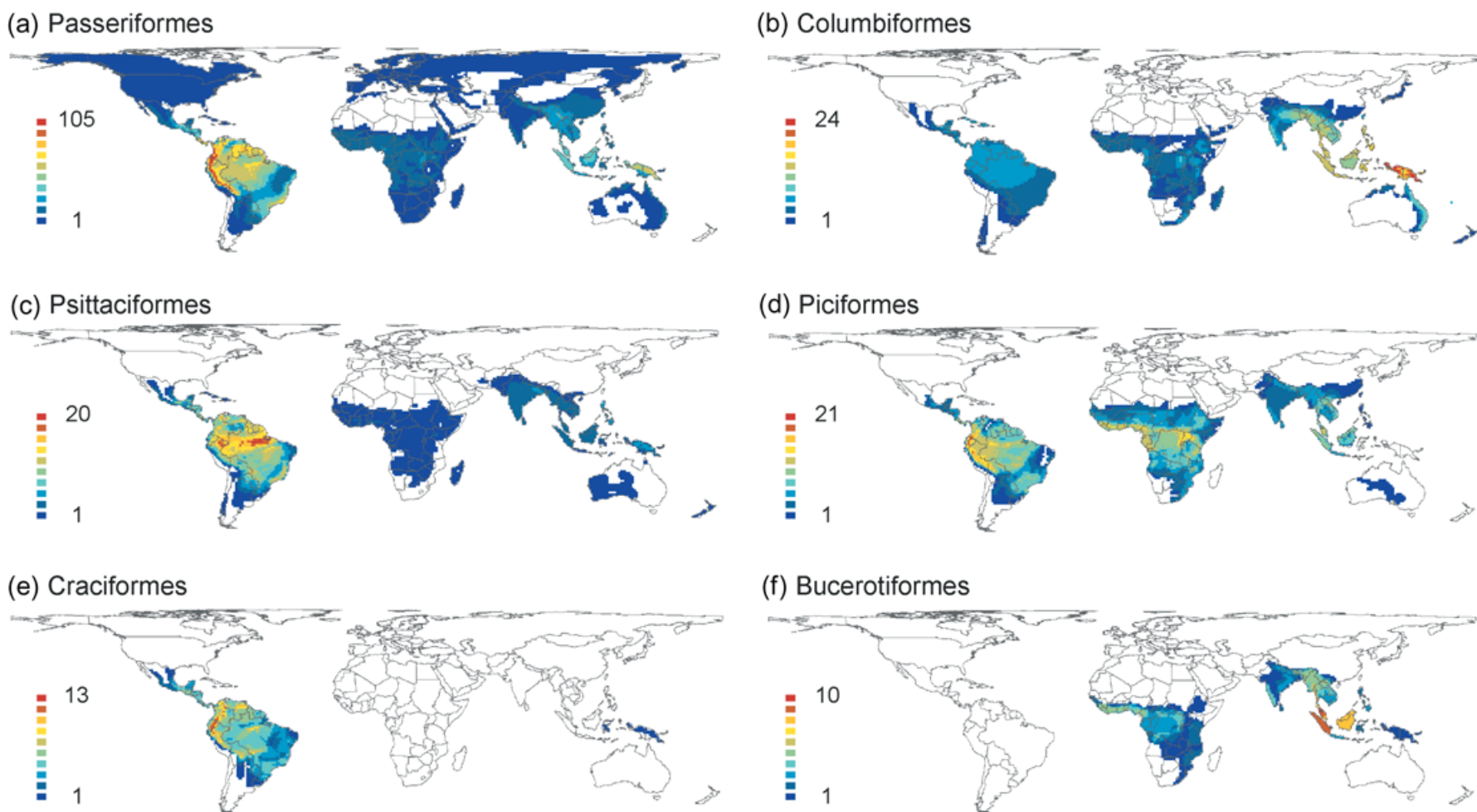


Figure 2 Global geographical patterns of frugivorous species richness within the six orders with the highest absolute numbers of frugivorous species: (a) Passeriformes ($n = 618$), (b) Columbiformes ($n = 179$), (c) Psittaciformes ($n = 141$), (d) Piciformes ($n = 112$), (e) Craciformes ($n = 50$) and (f) Bucerotiformes ($n = 38$). Natural breaks classification is shown across an equal-area grid (same as in Fig. 1).

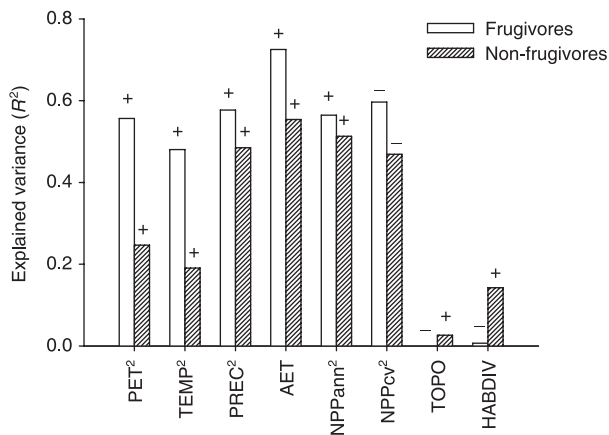


Figure 3 Variance (R^2) explained by various predictors for global species richness of frugivores (white) and non-frugivores (dashed). Values are from non-spatial regression models, but spatial models yielded similar results (for details see Supporting Information Tables S3 & S5). A + or – indicates the direction of effect. Predictors: PET, potential evapotranspiration; TEMP, mean annual temperature; PREC, annual precipitation; AET, actual evapotranspiration; NPPann, total annual above-ground productivity; NPPcv, coefficient of variation of monthly NPP values; TOPO, difference between maximum and minimum elevation; HABDIV, number of vegetation classes. A squared symbol indicates that both the linear and quadratic terms were included.

frugivore richness along the Andes in South America, whereas other orders showed their highest frugivore richness in the lowland tropical rain forests of the Amazon basin (Psittaciformes; Fig. 2c), Indonesia (Bucerotiformes; Fig. 2f) or New Guinea (Columbiformes; Fig. 2b). Hotspots of frugivore richness for the six most species-rich orders were highly congruent with overall bird diversity for the Passeriformes (91%; 372 of 409 grid cells), the Craciformes (88%; 60 of 68 grid cells), the Psittaciformes (87%; 163 of 187 grid cells) and the Piciformes (69%; 130 of 188 grid cells), but there was a lack of congruence for the Columbiformes (0%; 0 of 190 cells) and the Bucerotiformes (0%; 0 of 80 cells) (also compare Figs 1c & 2).

Environmental determinants and biogeographical variation

Among individual climatic variables, AET emerged as the strongest single climatic predictor variable explaining 71–73% of variation in global frugivore richness and proportion of frugivores (see Tables S3 and S4). No other single climatic predictor was similarly strong, although most other water–energy, productivity or seasonality variables explained around 40–60% of variation in frugivory (Fig. 3). In contrast, single climatic predictor variables generally explained much less variance in species richness and proportion of non-frugivorous species (see Table S5, Fig. 3), and measures of habitat heterogeneity (TOPO, HABDIV) had stronger effects on non-frugivores than on frugivores (Fig. 3). Non-spatial single-predictor GLMs generally contained a high amount of spatial autocorrelation in model residuals, whereas single-predictor SLMs successfully

accounted for this spatial structure (see Moran's I in Tables S3–S5). However, both regression modelling techniques showed similar results in terms of the importance of predictor variables as measured by R^2 and AIC values (see Tables S3 and S4).

Biogeographical history had a strong influence on frugivore distribution, explaining 63–70% of spatial variation in frugivore richness and proportion in single-predictor models (see Tables S3 & S4). Differences in frugivory between biogeographical realms were partly explained by different regional responses of frugivores to water–energy dynamics (Fig. 4). For instance, the proportion of frugivores increased linearly with AET in all tropical realms and the Palaearctic, but the slope of this relationship differed between regions (Fig. 4). Significant differences in frugivore richness between tropical regions disappeared for the Afrotropics, Indo-Malaya and the Neotropics once regional differences in AET had been controlled for (Fig. 5). However, Australasia, the Palaearctic and the Nearctic showed significantly lower species richness than the Afrotropics, Indo-Malaya and the Neotropics after controlling for AET (Fig. 5). There were similar, but less pronounced, trends for differences in frugivore proportion (see Fig. S2).

Multiple-predictor models that included both AET (the best environmental predictor) and REALM (i.e. biogeographical history) explained between 80% and 85% of the variation in frugivore richness and proportion (Table 2; see Table S6) indicating the importance of both environmental and historical constraints on avian frugivore distribution. These two-predictor models were improved when including an interaction term between both variables, explaining between 88% and 89% of the variation in frugivore richness and proportion (Table 2; see Table S6). The interaction term between AET and REALM is well illustrated by the different responses of frugivores to AET in different biogeographical regions (Fig. 4). Results from multiple-predictor SLMs generally supported all analyses from non-spatial GLMs (Table 2; see Table S6).

DISCUSSION

Our study constitutes the first comprehensive global-scale analysis of geographical and taxonomic patterns of avian frugivory and their potential environmental and historical determinants. On a global scale, species richness of frugivorous birds was highest in the Neotropics and significantly lower in all other realms. Peaks in overall bird diversity in the Himalayan foothills, the East African mountains and in some areas of Brazil and Bolivia were not reflected by frugivores. Measures of present-day climate and productivity generally had strong effects on frugivores, whereas habitat heterogeneity was almost unimportant. Geographical patterns of diversification between major clades, together with significant regional differences in frugivore richness and proportion once environment had been controlled for, highlighted a strong historical signal in global patterns of avian frugivory.

Our results with a wide range of environmental variables are in line with recent findings from global-scale analyses that variables related to water–energy dynamics and productivity are

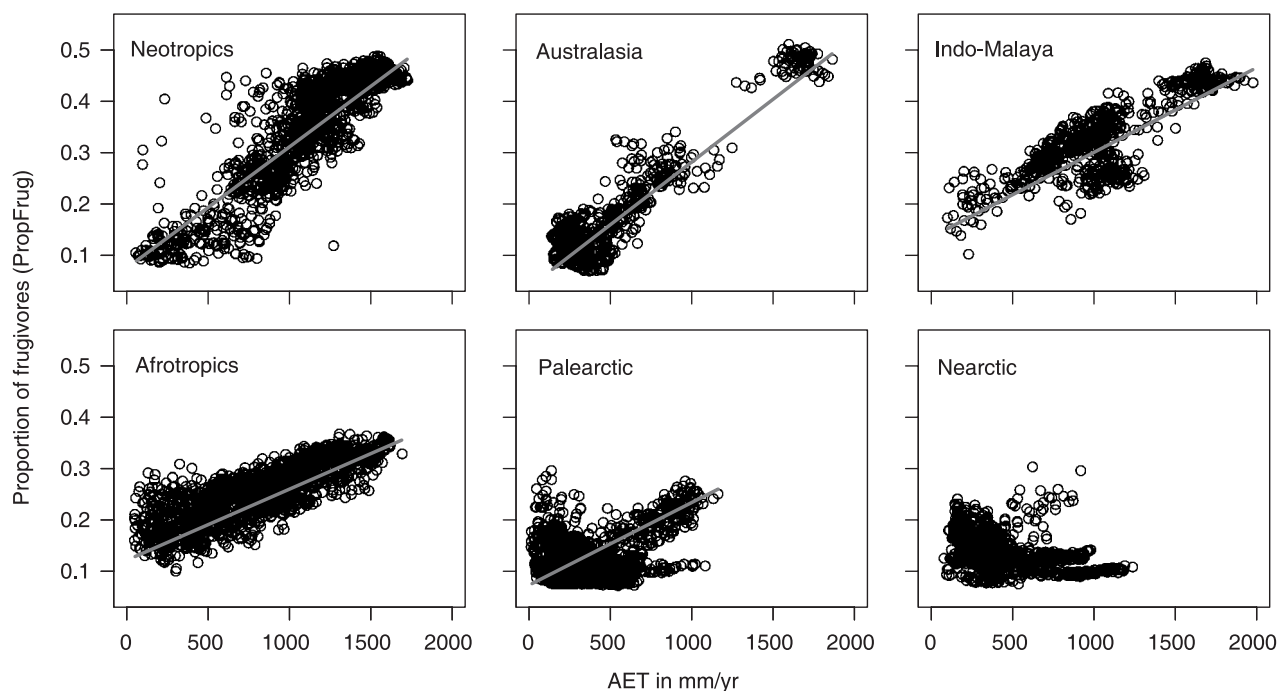


Figure 4 Relationships between the proportion of frugivores (PropFrug) and actual evapotranspiration (AET) within six biogeographical realms. Regression lines are from spatial single-predictor models with arcsine square root transformed PropFrug as the response variable across an equal-area grid equivalent to 1° grid cell size (12,364 km² area). AET was not a significant predictor variable in the Nearctic ($P = 0.09$).

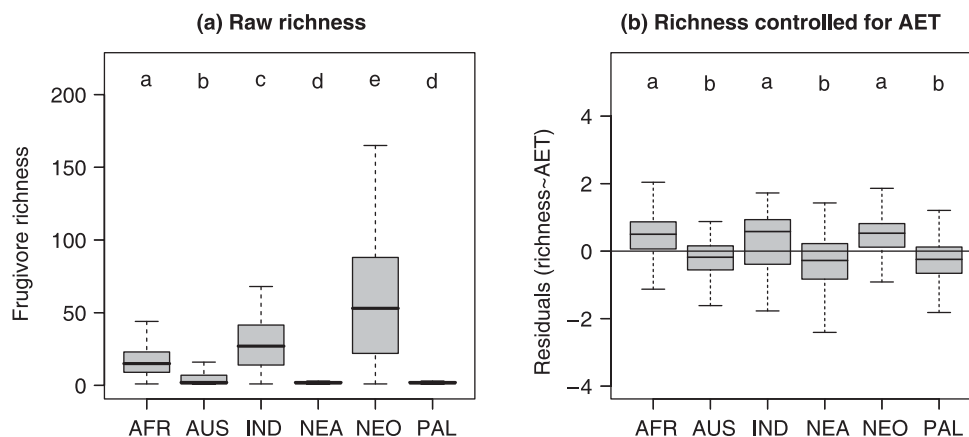


Figure 5 Variation in avian frugivory across biogeographical regions. (a) Raw frugivore richness. (b) Residual frugivore richness once controlled for actual evapotranspiration (AET). Letters indicate significant differences among biogeographical regions (multiple pair-wise comparisons with Tukey's honestly significant difference test). Biogeographical realms: AFR, Afrotropics; AUS, Australasia; IND, Indo-Malaya; NEA, Nearctic; NEO, Neotropics; PAL, Palearctic.

the core predictors of vascular plant (Kreft & Jetz, 2007) and overall bird diversity (Hawkins *et al.*, 2003b). However, our analyses additionally revealed that climate and productivity have much stronger effects on frugivores than on non-frugivores. AET and other water–energy measures may act in large part indirectly on bird species richness via effects on plants (Hawkins *et al.*, 2005), and such an effect should be particularly strong for frugivorous birds where water and energy most probably act indirectly via climatic effects on food plants (Kissling *et al.*, 2007). These indirect climatic effects on frugivore richness via plants could be

composed of water–energy effects on fruit production (e.g. Karr, 1976; Levey, 1988) and fruiting phenologies (van Schaik *et al.*, 1993; Ting *et al.*, 2008). Alternatively, there could be a 'hidden' historical and evolutionary component in the statistical relationship between AET and frugivore richness if current AET strongly co-varies with past climate history and/or the evolutionary diversification of fleshy fruited plants. Such a relationship could at least partly explain the realm-specific richness–environment relationships between frugivores and water–energy dynamics (Fig. 4). Additionally, hotspots of overall bird species richness in

Table 2 Results of multiple-predictor models examined at a resolution equivalent to 1° to explain global avian frugivore richness and the proportion of frugivores in avian assemblages. The multiple-predictor models with the highest R^2 value are highlighted in bold. The direction of effect of variables (+ or –) in multiple-predictor models was the same than in single-predictor models (cf. Table S3).

Variables	GLM			SLM			
	R^2	AIC	Moran	R^2_{trend}	R^2_{fit}	AIC	Moran
Frugivore richness							
AET + REALM	0.84	119	0.61***	0.83	0.94	–510	0.03
AET + REALM + AET:REALM	0.88	–105	0.46***	0.85	0.94	–524	0.03
AET + HABDIV	0.74	549	0.70***	0.69	0.94	–449	0.02
AET + NPPcv ²	0.73	587	0.74***	0.71	0.94	–445	0.03
AET + NPPcv ² + HABDIV	0.74	549	0.70***	0.69	0.94	–461	0.02
AET + REALM + HABDIV	0.84	120	0.60***	0.82	0.94	–525	0.03
AET + REALM + NPPcv ²	0.84	113	0.59***	0.82	0.94	–528	0.03
AET + REALM + HABDIV + NPPcv ²	0.84	114	0.59***	0.81	0.94	–541	0.03
Proportion of frugivores							
AET + REALM	0.80	–2729	0.69***	0.75	0.95	–3616	0.02
AET + REALM + AET:REALM	0.88	–3166	0.44***	0.80	0.95	–3657	0.01
AET + HABDIV	0.76	–2548	0.67***	0.71	0.95	–3581	0.01
AET + NPPcv ²	0.74	–2482	0.71***	0.70	0.95	–3596	0.01
AET + NPPcv ² + HABDIV	0.77	–2586	0.64***	0.70	0.95	–3596	0.02
AET + REALM + HABDIV	0.82	–2806	0.62***	0.75	0.95	–3615	0.02
AET + REALM + NPPcv ²	0.83	–2848	0.58***	0.74	0.95	–3628	0.02
AET + REALM + HABDIV + NPPcv ²	0.84	–2882	0.56***	0.74	0.95	–3628	0.02

Frugivore richness was log-transformed and the proportion of frugivores was arcsine square root transformed. GLM, non-spatial generalized linear model; SLM, spatial linear model (calculated as spatial autoregressive error model), Moran, Moran's I values; AIC, Akaike information criterion. A squared symbol indicates that both the linear and quadratic terms were included. R^2 values of SLM indicate the non-spatial smooth (R^2_{trend}) and the total fit (R^2_{fit} ; composed of non-spatial and spatial smooth). All values are mean values which were obtained from bootstrapping the whole data set ($n = 8563$ equal-area grid cells) 100 times with a 10% random subsample ($n = 856$). Standard errors of all mean values (not shown) were generally much smaller than 10% of the mean values. AET, actual evapotranspiration; NPPcv, coefficient of variation of monthly net primary productivity; HABDIV, number of vegetation classes; REALM, biogeographical realms.

tropical or subtropical mountain ranges outside the Neotropics (e.g. the East African mountains or the Himalayan foothills) were not reflected by frugivores (Fig. 1c) and suggest that geographical patterns of bird species richness are the result of guild-specific processes, and that understanding diversity gradients requires the identification of the guilds included.

Geographical patterns of avian frugivore richness in the Neotropics were highly congruent with overall bird species richness except for the Atlantic forest and Parecis mountains of Brazil and along the Rio Grande of Bolivia (Fig. 1c). Many bird clades have undergone extensive recent evolutionary radiations in the Neotropics (Ricklefs, 2002; Ericson *et al.*, 2003; Newton, 2003) including orders with large numbers of frugivorous species (Table 1, Fig. 2) such as the Passeriformes (Fig. 2a). For frugivores in particular, there is an exceptionally high diversity of fleshy fruited plants in the Neotropics (Snow, 1981; Gentry, 1982) which is composed of two major radiations, an Amazonian-centred radiation of canopy trees and an Andean-centred radiation of epiphytes and understorey shrubs (Gentry, 1982). This high food plant diversity in both lowland as well as mountain regions in the Neotropics could explain the high species richness of frugivores in the Andes (Fig. 1a), the relatively similar proportion of frugivores in lowland and mountain habitats at

equatorial latitudes in South America (Fig. 1b) and the comparably low frugivore richness in the Atlantic forest of Brazil (Fig. 1c). Whether mismatches in hotspots of frugivore richness and overall bird diversity in south-east Colombia, Brazil and Bolivia reflect differences in food plant diversity remains to be investigated.

The hypothesis that the geographical distribution of food plants has profoundly influenced the diversification of frugivorous birds could explain the realm-specific richness–environment relationships (Fig. 4) if AET co-varies with the evolutionary history of fleshy fruited plant diversification. A recent cross-continental comparison of 27 field studies on plant–frugivore communities supports this idea and shows that the relationship between food plant diversity and species richness of vertebrate consumers is stronger in the New World than in the Old World tropics (Fleming, 2005). In the Afrotropics, the low diversity of frugivorous bird species (Fig. 5) parallels a very low species richness of fleshy fruited plants (Snow, 1981; Fleming, 2005), and in Southeast Asia the lower species number of frugivores compared with the Neotropics could be explained by the dominance of non-fleshy fruited trees (Dipterocarpaceae) (Fleming *et al.*, 1987; Primack & Corlett, 2005). The exceptionally high diversity of fig trees (*Ficus* spp., a keystone resource for frugivores in the tropics; Shanahan *et al.*, 2001; Harrison, 2005) in the Indo-Pacific

region might explain why Indo-Malaya and New Guinea harbour higher numbers of frugivorous species than the Afrotropics (Figs 1 & 4). We recognize, however, that plant–frugivore interactions are complex because many frugivorous birds form mutualistic partnerships with plants as seed dispersers whereas others show antagonistic relationships as seed predators (e.g. many species of finches and parrots). Antagonistic (seed predation) and mutualistic (seed dispersal) interactions between birds and plants could differ between continents (Primack & Corlett, 2005) and might have very different effects on the diversification patterns of fleshy fruited plants. How these types of interaction have influenced the co-evolutionary processes in different rain forest regions remains largely unexplored (Primack & Corlett, 2005).

Even after controlling for AET (and possibly for potential co-variation with food plant diversity), Australasia and the northern temperate regions (Nearctic, Palaearctic) showed significantly lower species richness than the three remaining realms (Neotropics, Indo-Malaya, Afrotropics; Fig. 5). These differences could be explained by historical legacies related to climate change and/or niche conservatism (Wiens & Donoghue, 2004; Hawkins *et al.*, 2005, 2007; Wiens & Graham, 2005). During the Cretaceous and early Tertiary the Australian continent was warm and wet, but at the end of the Miocene it experienced increasing aridity and major decreases in precipitation. These long-term climatic shifts had profound impacts on speciation and extinction rates in Australia (Hawkins *et al.*, 2005), especially on forest birds of which many are frugivorous. Bird clades which initially evolved under wetter conditions may have failed to adapt to drier conditions or arid habitats if ancestral niches were conserved over evolutionary time (Wiens & Donoghue, 2004; Hawkins *et al.*, 2005; Wiens & Graham, 2005). We hypothesize that the extraordinary low frugivore richness and proportion in the Nearctic and Palaearctic (Fig. 5) could similarly reflect phylogenetic niche conservatism: frugivorous bird species or their food plants may have predominantly originated in tropical climates and harsh climates act as barriers to the invasion of temperate zones by tropical clades (Wiens & Donoghue, 2004; Hawkins *et al.*, 2007).

Some authors have suggested that the evolution or immigration of ecological competitors such as fruit-eating mammals might have influenced geographical patterns of avian frugivore distribution (Fleming *et al.*, 1987; Primack & Corlett, 2005). For instance, it has been hypothesized that the evolution of medium- to large-sized ground-living frugivorous birds like the Neotropical chachalacas, guans and curassows (Cracidae, Fig. 2e) could have been favoured by the absence of terrestrial frugivorous mammals, whereas the presence of terrestrial fruit-eating primates in the forests of Africa may have prevented the evolution of such ground-living frugivorous birds (Fleming *et al.*, 1987; Primack & Corlett, 2005). The Indo-Malayan region and Oceania have seen exceptional radiations of fruit-eating pigeons and doves (Columbiformes), perching birds (Passeriformes) and hornbills (Bucerotiformes) which could have been favoured by the absence of competition for fruits with primates. Similarly, the high diversity of parrots (Psittaciformes) in the

Neotropics (Fig. 2c) might be partly a result of the low number of squirrel species with which parrot diets often overlap (Primack & Corlett, 2005). We hypothesize that the lower proportion of avian frugivores in the Afrotropics compared to Indo-Malayan and Neotropical regions once AET had been accounted for (see Fig. S2b) and the lower slope in the Afrotropical relationship between AET and frugivore proportion (Fig. 4) could be due to higher competition with fruit-eating mammals.

In conclusion, our results suggest that major differences in avian frugivory between biogeographical regions are due to the diversification of food plants, niche conservatism and past climate change. Future research could benefit from using phylogenetic reconstructions to examine the diversification of fleshy fruited plants and frugivores in different biogeographical regions and from including broad-scale distribution data for other frugivorous taxa such as mammals. Frugivores, food plants and potential competitors promise to be a rewarding model system to better understand how biotic interactions and environmental constraints affect community assembly over macro-evolutionary time-scales and broad geographical scales.

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REFERENCES

- Ahn, C.H. & Tateishi, R. (1994) Development of a global 30-minute grid potential evapotranspiration data set. *Journal of the Japan Society of Photogrammetry and Remote Sensing*, **33**, 12–21.
- Barker, F.K., Cibois, A., Schikler, P., Feinstein, J. & Cracraft, J. (2004) Phylogeny and diversification of the largest avian radiation. *Proceedings of the National Academy of Sciences USA*, **101**, 11040–11045.
- Bondeau, A., Smith, P.C., Zaehle, S., Schaphoff, S., Lucht, W., Cramer, W., Gerten, D., Lotze-Campen, H., Müller, C., Reichstein, M. & Smith, B. (2007) Modelling the role of agriculture for the 20th century global terrestrial carbon balance. *Global Change Biology*, **13**, 679–706.

- Buckley, L.B. & Jetz, W. (2007) Environmental and historical constraints on global patterns of amphibian richness. *Proceedings of the Royal Society B: Biological Sciences*, **274**, 1167–1173.
- Burnham, K.P. & Anderson, D.R. (2002) *Model selection and multimodel inference*. Springer-Verlag, New York.
- Currie, D.J., Mittelbach, G.G., Cornell, H.V., Field, R., Guégan, J.-F., Hawkins, B.A., Kaufman, D.M., Kerr, J.T., Oberdorff, T., O'Brien, E. & Turner, J.R.G. (2004) Predictions and tests of climate-based hypotheses of broad-scale variation in taxonomic richness. *Ecology Letters*, **7**, 1121–1134.
- Davies, R.G., Orme, C.D.L., Storch, D., Olson, V.A., Thomas, G.H., Ross, S.G., Ding, T.-S., Rasmussen, P.C., Bennett, P.M., Owens, I.P.F., Blackburn, T.M. & Gaston, K.J. (2007) Topography, energy and the global distribution of bird species richness. *Proceedings of the Royal Society B: Biological Sciences*, **274**, 1189–1197.
- Ericson, P.G.P., Irestedt, M. & Johansson, U.S. (2003) Evolution, biogeography, and patterns of diversification in passerine birds. *Journal of Avian Biology*, **34**, 3–15.
- Fleming, T.H. (2005) The relationship between species richness of vertebrate mutualists and their food plants in tropical and subtropical communities differs among hemispheres. *Oikos*, **111**, 556–562.
- Fleming, T.H., Breitwisch, R. & Whitesides, G.H. (1987) Patterns of tropical vertebrate frugivore diversity. *Annual Review of Ecology and Systematics*, **18**, 91–109.
- Gentry, A.H. (1982) Patterns of neotropical plant species diversity. *Evolutionary Biology*, **15**, 1–84.
- Harrison, R.D. (2005) Figs and the diversity of tropical rain forests. *BioScience*, **55**, 1053–1064.
- Hawkins, B.A., Field, R., Cornell, H.V., Currie, D.J., Guegan, J.F., Kaufman, D.M., Kerr, J.T., Mittelbach, G.G., Oberdorff, T., O'Brien, E.M., Porter, E.E. & Turner, J.R.G. (2003a) Energy, water, and broad-scale geographic patterns of species richness. *Ecology*, **84**, 3105–3117.
- Hawkins, B.A., Porter, E.E. & Diniz-Filho, J.A.F. (2003b) Productivity and history as predictors of the latitudinal diversity gradient of terrestrial birds. *Ecology*, **84**, 1608–1623.
- Hawkins, B.A., Diniz-Filho, J.A.F. & Soeller, S.A. (2005) Water links the historical and contemporary components of the Australian bird diversity gradient. *Journal of Biogeography*, **32**, 1035–1042.
- Hawkins, B.A., Diniz-Filho, J.A.F., Jaramillo, C.A. & Soeller, S.A. (2007) Climate, niche conservatism, and the global bird diversity gradient. *The American Naturalist*, **170**, S16–S27.
- Herrera, C.M. (1985) Habitat–consumer interactions in frugivorous birds. *Habitat selection in birds* (ed. by M.L. Cody), pp. 341–365. Academic Press, Orlando, FL.
- Herrera, C.M. (2002) Seed dispersal by vertebrates. *Plant–animal interactions – an evolutionary approach* (ed. by C.M. Herrera and O. Pellmyr), pp. 185–208. Blackwell, Oxford.
- Hurlbert, A.H. & Haskell, J.P. (2003) The effect of energy and seasonality on avian species richness and community composition. *The American Naturalist*, **161**, 83–97.
- Hurlbert, A.H. & Jetz, W. (2007) Species richness, hotspots, and the scale dependence of range maps in ecology and conservation. *Proceedings of the National Academy of Sciences USA*, **104**, 13384–13389.
- Jetz, W. & Rahbek, C. (2002) Geographic range size and determinants of avian species richness. *Science*, **297**, 1548–1551.
- Jetz, W., Wilcove, D.S. & Dobson, A.P. (2007) Projected impacts of climate and land-use change on the global diversity of birds. *PLoS Biology*, **5**, e157.
- Karr, J.R. (1976) Seasonality, resource availability, and community diversity in tropical bird communities. *The American Naturalist*, **110**, 973–994.
- Kissling, W.D. & Carl, G. (2008) Spatial autocorrelation and the selection of simultaneous autoregressive models. *Global Ecology and Biogeography*, **17**, 59–71.
- Kissling, W.D., Rahbek, C. & Böhning-Gaese, K. (2007) Food plant diversity as broad-scale determinant of avian frugivore richness. *Proceedings of the Royal Society B: Biological Sciences*, **274**, 799–808.
- Kissling, W.D., Field, R. & Böhning-Gaese, K. (2008) Spatial patterns of woody plant and bird diversity: functional relationships or environmental effects? *Global Ecology and Biogeography*, **17**, 327–339.
- Kreft, H. & Jetz, W. (2007) Global patterns and determinants of vascular plant diversity. *Proceedings of the National Academy of Sciences USA*, **104**, 5925–5930.
- Legendre, P. & Legendre, L. (1998) *Numerical ecology*. Elsevier, Amsterdam.
- Levey, D.J. (1988) Spatial and temporal variation in Costa Rican fruit and fruit-eating bird abundance. *Ecological Monographs*, **58**, 251–269.
- Mittelbach, G.G., Schemske, D.W., Cornell, H.V., Allen, A.P., Brown, J.M., Bush, M.B., Harrison, S.P., Hurlbert, A.H., Knowlton, N., Lessios, H.A., McCain, C.M., McCune, A.R., McDade, L.A., McPeck, M.A., Near, T.J., Price, T.D., Ricklefs, R.E., Roy, K., Sax, D.F., Schluter, D., Sobel, J.M. & Turelli, M. (2007) Evolution and the latitudinal diversity gradient: speciation, extinction and biogeography. *Ecology Letters*, **10**, 315–331.
- New, M., Lister, D., Hulme, M. & Makin, I. (2002) A high-resolution data set of surface climate over global land areas. *Climate Research*, **21**, 1–25.
- Newton, I. (2003) *The speciation and biogeography of birds*. Academic Press, London.
- Prendergast, J.R., Quinn, R.M., Lawton, J.H., Eversham, B.C. & Gibbons, D.W. (1993) Rare species, the coincidence of diversity hotspots and conservation strategies. *Nature*, **365**, 335–337.
- Primack, R.B. & Corlett, R.T. (2005) *Tropical rain forests: an ecological and biogeographical comparison*. Blackwell Publishing, Malden.
- Qian, H. & Ricklefs, R.E. (2000) Large-scale processes and the Asian bias in species diversity of temperate plants. *Nature*, **407**, 180–182.
- R Development Core Team (2007) R: a language and environment for statistical computing. R foundation for Statistical Computing, Vienna (available at: <http://www.R-project.org>).

- Rahbek, C. & Graves, G.R. (2001) Multiscale assessment of patterns of avian species richness. *Proceedings of the National Academy of Sciences USA*, **98**, 4534–4539.
- Ricklefs, R.E. (1987) Community diversity: relative roles of local and regional processes. *Science*, **235**, 167–171.
- Ricklefs, R.E. (2002) Splendid isolation: historical ecology of the South American passerine fauna. *Journal of Avian Biology*, **33**, 207–211.
- Ricklefs, R.E. (2006) Evolutionary diversification and the origin of the diversity–environment relationship. *Ecology*, **87**, S3–S13.
- Ricklefs, R.E. & Schluter, D. (1993) *Species diversity in ecological communities. Historical and geographical perspectives*. University of Chicago Press, Chicago.
- Şekercioğlu, C.H., Daily, G.D. & Ehrlich, P.R. (2004) Ecosystem consequences of bird declines. *Proceedings of the National Academy of Sciences USA*, **101**, 18042–18047.
- Shanahan, M., So, S., Compton, S.G. & Corlett, R.T. (2001) Fig-eating by vertebrate frugivores: a global review. *Biological Reviews*, **76**, 529–572.
- Sibley, C.G. & Ahlquist, J.E. (1990) *Phylogeny and classification of birds: a study in molecular evolution*. Yale University Press, New Haven, CT.
- Snow, D.W. (1981) Tropical frugivorous birds and their food plants: a world survey. *Biotropica*, **13**, 1–14.
- Ting, S., Hartley, S. & Burns, K.C. (2008) Global patterns in fruiting seasons. *Global Ecology and Biogeography*, **17**, 648–657.
- Udvardy, M.D.F. (1975) *A classification of the biogeographical provinces of the world*. International Union for Conservation of Nature and Natural Resources, Morges.
- Van Schaik, C.P., Terborgh, J.W. & Wright, S.J. (1993) The phenology of tropical forests: adaptive significance and consequences for primary consumers. *Annual Review of Ecology and Systematics*, **24**, 353–377.
- Wiens, J.J. & Donoghue, M.J. (2004) Historical biogeography, ecology and species richness. *Trends in Ecology and Evolution*, **19**, 639–644.
- Wiens, J.J. & Graham, C.H. (2005) Niche conservatism: integrating evolution, ecology, and conservation biology. *Annual Review of Ecology, Evolution and Systematics*, **36**, 519–539.
- Wright, D.H. (1983) Species–energy theory: an extension of species–area theory. *Oikos*, **41**, 496–506.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Table S1 Frugivore classification and species list.

Table S2 Island frugivores.

Table S3 Frugivore richness and proportion – results of single-predictor models examined at resolution equivalent to 1°.

Table S4 Frugivore richness and proportion – results of single-predictor models examined at resolution equivalent to 2°.

Table S5 Species richness and proportion of non-frugivorous birds – results of single-predictor models examined at resolution equivalent to 1°.

Table S6 Frugivore richness and proportion – results of multiple-predictor models examined at resolution equivalent to 2°.

Figure S1 Sensitivity of frugivore classification.

Figure S2 Biogeographical differences in frugivore proportion.

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