



# Spatial patterns of woody plant and bird diversity: functional relationships or environmental effects?

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## ABSTRACT

**Aim** To understand cross-taxon spatial congruence patterns of bird and woody plant species richness. In particular, to test the relative roles of functional relationships between birds and woody plants, and the direct and indirect environmental effects on broad-scale species richness of both groups.

**Location** Kenya.

**Methods** Based on comprehensive range maps of all birds and woody plants (native species > 2.5 m in height) in Kenya, we mapped species richness of both groups. We distinguished species richness of four different avian frugivore guilds (obligate, partial, opportunistic and non-frugivores) and fleshy-fruited and non-fleshy-fruited woody plants. We used structural equation modelling and spatial regressions to test for effects of functional relationships (resource–consumer interactions and vegetation structural complexity) and environment (climate and habitat heterogeneity) on the richness patterns.

**Results** Path analyses suggested that bird and woody plant species richness are linked via functional relationships, probably driven by vegetation structural complexity rather than trophic interactions. Bird species richness was determined in our models by both environmental variables and the functional relationships with woody plants. Direct environmental effects on woody plant richness differed from those on bird richness, and different avian consumer guilds showed distinct responses to climatic factors when woody plant species richness was included in path models.

**Main conclusions** Our results imply that bird and woody plant diversity are linked at this scale via vegetation structural complexity, and that environmental factors differ in their direct effects on plants and avian trophic guilds. We conclude that climatic factors influence broad-scale tropical bird species richness in large part indirectly, via effects on plants, rather than only directly as often assumed. This could have important implications for future predictions of animal species richness in response to climate change.

## Keywords

Autoregressive model, biodiversity, community assembly, cross-taxon congruence, indirect effects, frugivory, Kenya, plant–animal interactions, species–energy theory, trophic guild.

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## INTRODUCTION

Geographic patterns of species richness are central to ecology and have gained much attention in recent years (e.g. Jetz & Rahbek, 2002; Hawkins *et al.*, 2003; Currie *et al.*, 2004; Field *et al.*, 2005). Although the precise mechanisms for the creation

and maintenance of geographic gradients in species diversity are still hotly debated (e.g. Rahbek & Graves, 2001; Currie *et al.*, 2004; Hawkins *et al.*, 2007a), there seems to be consensus that variables related to climate and habitat heterogeneity play a prominent role at broad spatial scales (Rahbek & Graves, 2001; Jetz & Rahbek, 2002; Hawkins *et al.*, 2003). Likely mechanisms

include potential effects on the physiological tolerances of individual species (Currie *et al.*, 2004), on diversification rates (Jetz *et al.*, 2004; Allen *et al.*, 2006), or on energy flow through food webs (Wright, 1983; Kissling *et al.*, 2007). If different groups of organisms show similar direct or indirect responses to environmental factors, we might expect that species richness patterns of different taxa are spatially congruent. Such patterns could have profound implications for biodiversity conservation, e.g. for global conservation planning (Lamoreux *et al.*, 2006), the selection of nature reserves (Howard *et al.*, 1998), and for assessing effects of habitat modification across taxa (Schulze *et al.*, 2004). However, the results from studies on species richness congruence have been mixed and often poor relationships between taxa have been reported (Wolters *et al.*, 2006). A better understanding of the functional relationships and mechanisms underlying richness correlations and the potential direct and indirect effects of climate and habitat heterogeneity variables is therefore urgently needed (Menéndez *et al.*, 2007).

One possibility to test for functional relationships in cross-taxon congruence patterns is to relate the species richness of animals to the species richness of plants (e.g. Currie, 1991; Hawkins & Porter, 2003; Lee & Rotenberry, 2005; Kissling *et al.*, 2007). Plants are at the base of terrestrial food webs and provide a great variety of food resources relevant for animal consumers (e.g. Hutchinson, 1959; Herrera, 1985; Shanahan *et al.*, 2001; Kissling *et al.*, 2007). A positive relationship between animal and plant species richness might therefore result from trophic relationships, with consumer diversity reflecting the diversity of the food plants (hypothesis 1, the 'food plant diversity hypothesis'; Kissling *et al.*, 2007). Plants are also key structural elements of terrestrial ecosystems and thus determine habitat configuration for many animal species, including birds (MacArthur & MacArthur, 1961). An increase in animal species richness with plant species richness might therefore result from an increase in the diversity and complexity of vegetation structure, providing more niches for animal species to coexist (hypothesis 2, the 'vegetation structure hypothesis'; MacArthur & MacArthur, 1961; Tews *et al.*, 2004; Lee & Rotenberry, 2005). This relationship has been convincingly demonstrated at local scales (MacArthur & MacArthur, 1961; Pearson, 1975; Cody, 1985) but has not yet been found at broad spatial scales, and a similar local relationship was found not to hold at the macroscale for butterflies (Hawkins & Porter, 2003). Finally, a positive correlation between animal and plant species richness could also result from both groups responding similarly to the same environmental variables. In this case, interactions between the two taxonomic groups would not be expected to affect the species richness of birds (hypothesis 3, which we call the 'similar environmental effects hypothesis'; Hawkins & Porter, 2003).

From these hypotheses, testable predictions can be derived. First, if functional (i.e. trophic or structural complexity) relationships between animals and plants shape broad-scale patterns of species richness (hypotheses 1 and 2), then a positive correlation between species richness of both taxa should persist when environmental variables have been accounted for (see Hawkins & Porter, 2003; Kissling *et al.*, 2007). Second, according

to hypothesis 1 (food plant diversity hypothesis), the plant–animal correlation should be stronger for those subgroups of animals and plants that are more specialised on each other than for subgroups with weaker trophic interactions (Kissling *et al.*, 2007). Third, hypothesis 2 (vegetation structure hypothesis) predicts a relatively strong positive plant–animal correlation regardless of whether plants are food resources for animals or not (e.g. Lee & Rotenberry, 2005). Finally, hypothesis 3 (similar environmental effects hypothesis) predicts relatively strong environment–species richness correlations that are similar for plant and animal taxa. These predictions are not mutually exclusive and may be additive. To date, however, there have been few attempts to test these predictions, or to distinguish between the three hypotheses. In particular, there have been few attempts to disentangle the relative roles of trophic relationships and vegetation structural complexity in shaping geographic patterns of animal species richness at broad spatial scales (Hawkins & Porter, 2003; Márquez *et al.*, 2004; Kissling *et al.*, 2007; Menéndez *et al.*, 2007).

Plant–frugivore interactions represent a good study system for such broad-scale analyses of animal and plant species richness. Most frugivorous animals rely heavily on fruits, particularly in the tropics (Herrera, 1985; Fleming *et al.*, 1987; Shanahan *et al.*, 2001; Kissling *et al.*, 2007). Accordingly, the food plant diversity hypothesis predicts relatively strong positive relationships between food plant and frugivore species richness (Kissling *et al.*, 2007), e.g. due to evolutionary or ecological responses of frugivores to fruit size, fruit colour, fruit biomass or vertical stratification of fruit presentation (Herrera, 2002; Kissling *et al.*, 2007). Fruit-eating vertebrate species can be classified into frugivore guilds (e.g. obligate, partial and opportunistic frugivores), and plant species into those with fleshy fruits and those without. This allows examination of trends in the strength of the relationship between different frugivore guilds and food plant species richness. Finally, habitat selection of frugivores and other birds is not only influenced by food availability but also by vegetation structure and complexity and other factors. Species richness of different feeding guilds might therefore respond differently to changes in vegetation structure and complexity across tropical ecosystems (Waltert *et al.*, 2005).

In this study, we investigate the three hypotheses using a comprehensive geographic data base at a spatial resolution of *c.* 55 km (0.5° grid cells) that includes 1005 bird species, 1417 woody plant species and six environmental variables related to climate (precipitation, temperature, potential evapotranspiration and seasonality) and habitat heterogeneity (topographic relief and land cover diversity). We classify bird species into four frugivore groups (obligate frugivores, partial frugivores, opportunistic fruit-eaters and non-fruit-eaters), and woody plant species into two resource groups (fleshy-fruited plants and non-fleshy-fruited plants). We particularly aimed to test the following five predictions. The first we call 'prediction 0' because it concerns functional relationships and therefore applies to both hypotheses 1 and 2: a significant positive correlation between bird and woody plant species richness when environmental effects have been accounted for. Secondly, hypothesis 1 (trophic relationships) predicts a stronger plant richness–animal richness correlation between

fleshy-fruited plants and frugivores than between non-fleshy-fruited plants and frugivores (prediction 1a). Hypothesis 1 also predicts that the plant–animal correlation should be successively weaker between fleshy-fruited plants and obligate frugivores, partial frugivores, opportunistic fruit-eaters and non-fruit-eaters (prediction 1b). Hypothesis 2 (vegetation structure) predicts relatively strong correlations between trophically independent groups, i.e. between frugivores and non-fleshy-fruited plants and between non-frugivores and fleshy-fruited plants (prediction 2). Finally, hypothesis 3 (similar environmental effects) predicts both very similar total effects of environmental variables on the richness variables and relatively strong direct effects of environmental variables on the richness variables, which should be similar for woody plant and bird species richness (prediction 3).

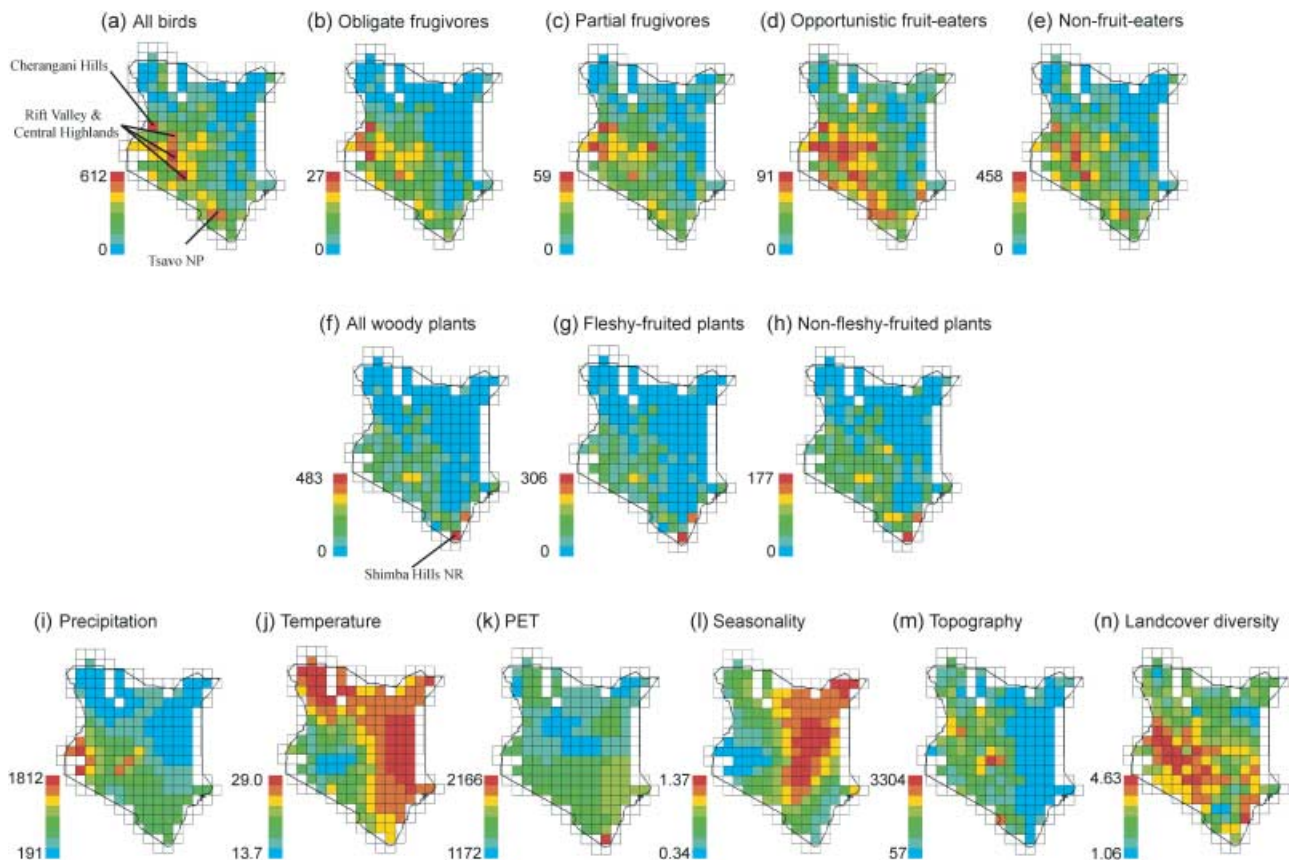
## METHODS

### Bird species richness

The *Bird Atlas of Kenya* (Lewis & Pomeroy, 1989) provides the most comprehensive information available on the distribution of birds in East Africa, with presence/absence data of species (mainly collected for the period 1970–1984) at a spatial resolution of  $0.5^\circ \times 0.5^\circ$  cells, so-called quarter square degrees (QSDs).

This spatial resolution corresponds to *c.* 55.5 km and QSD cell area is effectively constant (*c.* 3080 km<sup>2</sup>). In total, 1065 bird species are listed in the atlas, of which 871 species are presented with distribution maps; for the remaining 194 species, QSD records are only listed in the text. For our analysis, we used all available distribution information (i.e. maps and listed records, including pre-1970 records) but excluded vagrant species and those species represented only by anecdotal records (1005 bird species were thus analysed). Using the software ArcView 3.2, we transferred all presence data (i.e. maps and information on listed species records) of all included species into a digital QSD grid system (described below for the plant data).

We classified all the bird species ( $n = 1005$ ) into four frugivore guilds, depending on diet preference for fruits (see Kissling *et al.*, 2007, for details on this classification procedure): (i) obligate frugivores (species that primarily feed on fruits, i.e. the only major food items are fruits,  $n = 43$ ), (ii) partial frugivores (species that eat fruits and other major food items such as terrestrial invertebrates,  $n = 98$ ), (iii) opportunistic fruit-eaters (species only occasionally eating fruits as supplementary food,  $n = 145$ ), and (iv) non-fruit-eaters (not eating any fruits,  $n = 719$ ). These four frugivore guilds are characterized by declining degrees of specialization on fruits. For each QSD grid cell, we calculated species richness values for all birds and for the four avian guilds (Fig. 1a–e).



**Figure 1** Spatial patterns of species richness and environmental variables across Kenya. (a–e) Species richness of all birds and avian frugivore guilds. (f–h) Species richness of woody plants, fleshy-fruited plants, and non-fleshy-fruited plants. (i–n) Environmental variables (see Table 1). Equal frequency classification is shown, with colour ramps indicating minimum (blue, bottom of legend) and maximum (red, top of legend) values.

**Table 1** Environmental variables used to account for spatial variation in bird and woody plant species richness.

Abbreviation	Predictor variables (units)	Hypothesis (reference*)
<i>Climate</i>		
Prec	Mean annual precipitation (mm year <sup>-1</sup> )	Water availability (1, 2)
Temp	Mean monthly temperature (°C)	Temperature (2, 3)
PET	Mean annual potential evapotranspiration (mm year <sup>-1</sup> )	Energy (1, 2)
Seas	Seasonality, measured as coefficient of variation of monthly precipitation values (mm month <sup>-1</sup> )	Seasonality (4)
<i>Habitat heterogeneity</i>		
Topo	Topographic relief (altitudinal range in m)	Topographic heterogeneity (5, 6)
LCov	Land cover diversity (Shannon–Wiener diversity)	Habitat diversity (5, 7)

\*1, Field *et al.* (2005); 2, Hawkins *et al.* (2003); 3, Allen *et al.* (2006); 4, Hurlbert & Haskell (2003); 5, Rahbek & Graves (2001); 6, Jetz & Rahbek (2002); 7, Tews *et al.* (2004).

### Plant species richness

We estimated the species richness of woody plants for each QSD cell from a comprehensive set of distribution maps and site location data for trees and shrubs in Kenya (Beentje, 1994). We followed the same criteria as in Field *et al.* (2005) to determine which species to include, and thus retained 1417 out of 1862 species. Those eliminated were non-native species, plants  $\leq 2.5$  m in height, and plants that are not truly woody. Beentje's (1994) distribution maps use the same QSD grid system as the bird data, so we transferred the presence/absence information directly into our grid cells. Species whose distribution information is reported by Beentje in terms of collecting localities (see Field *et al.*, 2005, for details) were included in these data. Our initial grid system contained 228 QSD cells (including cells that cross the border of Kenya) from which we excluded cells that (i) lie partly outside the borders of Kenya ( $n = 52$ ), (ii) are known to be botanically undercollected ( $n = 9$ ; Beentje, 1994), or (iii) have more than 50% lake area ( $n = 7$ ). These cells were excluded because they are known to underestimate plant and bird diversity. The final data base contained 160 QSD cells and this was used for all the analyses.

We classified all woody plants ( $n = 1417$ ) into two resource groups: (i) fleshy-fruited plant species ( $n = 788$ ), and (ii) non-fleshy-fruited plant species ( $n = 629$ ). Fleshy-fruited plant species were identified according to the presence or absence of fleshy parts (information from Beentje, 1994), including species with berries, drupes, and dehiscent fruits with fleshy arils. Where fruit types were unclear, expert opinions were obtained (see Acknowledgements) and/or specimens examined. For each QSD grid cell, we calculated species richness values for all woody plants and for the two resource groups (Fig. 1f–h).

### Environmental variables

We included six environmental variables (Table 1, Fig. 1i–n) related to climate (precipitation, temperature, potential evapotranspiration [PET] and seasonality) and habitat heterogeneity (topographic relief and land cover diversity). These variables have previously been shown to be important determinants of

species richness of birds and plants at broad spatial scales (see references in Table 1).

### Climate variables

Data for precipitation and temperature were extracted from the WorldClim data base (version 1.4; Hijmans *et al.*, 2005), which yields interpolated mean monthly climatic data from the period 1950–2000 (available online at <http://www.worldclim.org/>). We used mean annual precipitation and mean monthly temperature, degraded from 1 km to c. 55 km (i.e. QSD) resolution. PET data were obtained from the United Nations Environmental Program (UNEP), available at 0.5° (i.e. QSD) resolution (<http://www.grid.unep.ch/>, see also Ahn & Tateishi, 1994). Although we have some concerns about the quality of this PET data set, it is widely used in studies of species richness (e.g. Francis & Currie, 2003) and widely accepted. Note also that, in Kenya, Thornthwaite's PET is almost completely collinear with temperature, unlike the Ahn & Tateishi (1994) data. Seasonality was calculated as the coefficient of variation of the monthly precipitation values, to quantify seasonal changes in precipitation.

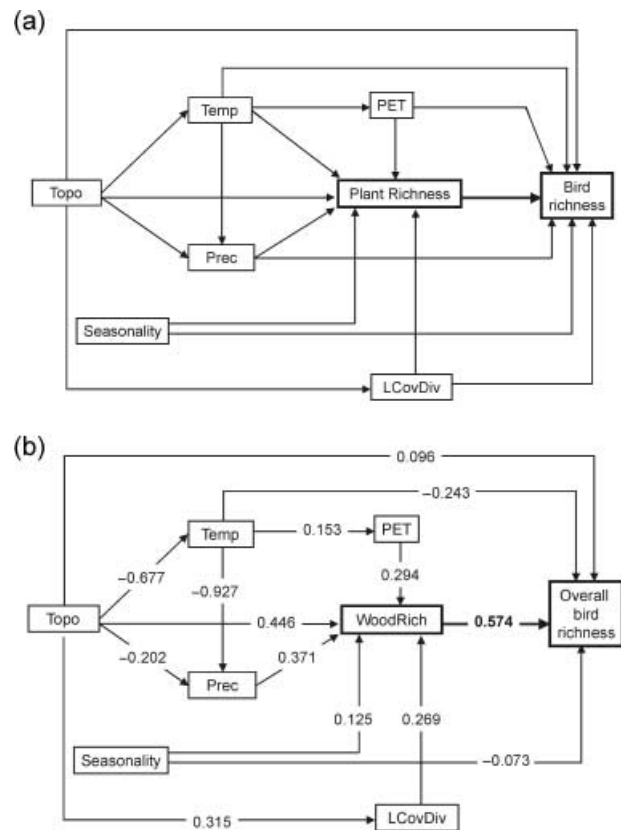
### Habitat heterogeneity

We selected two potentially relevant measures of habitat heterogeneity for our study (Table 1): (i) topographic relief, and (ii) land cover diversity. Topographic relief was quantified for each QSD cell as altitudinal range (maximum minus minimum elevation). Elevation data were extracted from the 30 arc-second SRTM-GTOPO30 data set provided by The Global Land Cover Facility (available at <http://glcf.umd.edu/data/srtm/>). Land cover diversity was calculated from the Kenya Spatially Aggregated Multipurpose Landcover data base provided by FAO-Africover (available at <http://www.africover.org/>). For each QSD cell, we calculated the proportion of each of the 101 recognized land cover types in Kenya and then computed the Shannon–Wiener function (Krebs, 1999) as an index of land cover diversity. This index varied between 0 and 4.63, with higher values indicating more (and more evenly sized) land cover types and, therefore, greater habitat diversity within a cell.

## Statistical analysis

We used path analysis and structural equation models (SEMs) (Shipley, 2000) to investigate the relative roles of environmental predictor variables and to test our five predictions. In contrast to traditional multiple regression models (which can only deal with one response variable) SEMs allow the consideration of hypothesized causal relationships in data sets with more than one dependent variable and effects of dependent variables on one another. As a consequence, SEMs allow the partitioning of correlations between predictor and response variables (so called 'total effects') into direct and indirect effects. Direct effects are measured by standardized partial regression coefficients between a predictor variable and a response variable (i.e. the direct link), whereas indirect effects can be calculated by adding the products of all standardized partial regression coefficients over all paths between a predictor and a response variable (i.e. including indirect links via other correlated predictor variables; see Shipley, 2000). Although SEMs cannot replace experimental manipulations they are one of the few methods to test ecological hypotheses at broad spatial scales (e.g. Hawkins & Porter, 2003; Hawkins *et al.*, 2005, 2007b; Menéndez *et al.*, 2007).

Based on logical and established relationships among our predictor variables (see references in Table 1) we first constructed an *a priori* theoretical SEM with bird species richness, plant species richness and all environmental variables (see Fig. 2a). This *a priori* model included all the hypothesised potential links between variables. We then constructed 15 nested SEMs, representing each plant–bird richness combination in turn: one measure of plant richness (all woody plants, fleshy-fruited plants and non-fleshy-fruited plants) and one measure of bird species richness (all birds, obligate frugivores, partial frugivores, opportunistic fruit-eaters and non-fruit-eaters). Fig. 2b is an example, showing the model for all woody plants and all birds. These nested SEMs shared the same causal structure as the *a priori* theoretical SEM but some of the paths were eliminated. Elimination of paths was guided by calculating, for each richness response variable, traditional multiple ordinary least squares (OLS) regression models with all predictor variables (including plants for birds) and then selecting the minimal adequate OLS model for each richness variable based on the Akaike Information Criterion (AIC) (Burnham & Anderson, 2002). This information theoretic approach evaluates the relative support in the observed data for a given candidate set of models and selects the most parsimonious model based on model fit and model complexity (Burnham & Anderson, 2002). Using these minimal adequate models for each richness variable we then constructed nested SEMs within our *a priori* theoretical model by removing those paths from our *a priori* model that were redundant for the most parsimonious explanation of our response variables. All nested SEMs showed high goodness of fit as indicated by a number of fit measures including high goodness-of-fit indices (all between 0.75 and 0.82) and Bentler–Bonett normed fit indices (NFI) of 0.77 to 0.84 (values close to 1 indicate a good fit). As alternatives, we also tested SEMs using the full *a priori* model structure, and these models yielded similar results to those presented here.



**Figure 2** Structural equation model (SEM) of the influence of plant species richness and environmental variables on bird species richness. (a) *A priori* theoretical SEM including all variables and the potential relationships among them. (b) Nested SEM testing the effect of woody plant species richness (WoodRich) on overall bird species richness (goodness-of-fit index = 0.75; Bentler–Bonnett NFI = 0.78). Due to the presence of spatial autocorrelation (see Tables 2 and 3) significance levels for standardized partial regression coefficients are not given. Prec: mean annual precipitation; Temp: mean monthly temperature; PET: mean annual potential evapotranspiration; Topo: topographic relief; LCovDiv: land cover diversity.

The following SEMs were used to test our five predictions. A SEM with overall bird and woody species richness (Fig. 2b) was used to test prediction 0 (the presence of any functional relationship; see also Hawkins & Porter, 2003). To test prediction 1a (a stronger correlation between food plants and frugivores than between non-food plants and frugivores) we examined SEMs with the two plant resource groups in turn (fleshy-fruited plant species and non-fleshy-fruited plant species), and the species richness of avian frugivores (obligate and partial frugivores, respectively). Similarly, to test prediction 1b (decreasing trend in the relationship between food plants and specialisation of birds on fruit eating) we used SEMs with fleshy-fruited plants and the species richness of the different avian guilds in turn (obligate frugivores, partial frugivores, opportunistic fruit-eaters and non-fruit-eaters). To test prediction 2 (vegetation structural complexity) we assessed the direct paths between plants and birds of SEMs with trophically independent groups (i.e. between frugivores and non-fleshy-fruited plants and between

non-fruit-eating birds and fleshy-fruited plants). Finally, to test prediction 3 (similar environmental effects) we examined the direct environmental effects on species richness in all SEMs, i.e. the paths between climate and habitat heterogeneity variables and plant and bird species richness, respectively. We also compared the total effects of the environmental variables on plant and bird species richness.

The presence of spatial autocorrelation violates the assumption of independently distributed errors in regression models, and, as a consequence, Type I errors of traditional tests might be inflated (Legendre, 1993). Moreover, spatial autocorrelation can affect inference from statistical models and our ability to evaluate the importance of explanatory variables (Diniz-Filho *et al.*, 2003; Dormann *et al.*, 2007). To explore the influence of spatial autocorrelation on inference from our path models, we tested for the presence of spatial autocorrelation by calculating Moran's  $I$  values (i.e. a measure of spatial autocorrelation; Legendre, 1993) on the residuals of our minimal adequate (OLS) regression models. Since most of these OLS models contained significant spatial autocorrelation in their residuals, we fitted spatial linear models (SLMs; here 'spatial simultaneous autoregressive error models'; see Kissling & Carl, 2008), which can include the spatial autocorrelation structure of a given data set. Final model assessment was based on the reduction of spatial autocorrelation in model residuals (evaluated with Moran's  $I$  values), the increase in  $r^2$ -values (for the spatial models, pseudo  $r^2$ -values were calculated as the squared Pearson correlation between predicted and observed values), and the minimization of the AIC value (see Kissling & Carl, 2008). To compare the relative importance of predictor variables from SLMs and OLS regressions, we calculated standardized partial regression coefficients from both model types. For the non-spatial (OLS) models, these standardized partial regression coefficients are equivalent to the direct effects on species richness in our SEMs.

All statistical analyses were done with the free software R (available at <http://www.R-project.org>). SEMs were calculated with the R library 'sem', v. 0.9-6, and Moran's  $I$  values and SLMs were calculated using the R library 'spdep', v. 0.3-32 (both packages are available at <http://cran.r-project.org/src/contrib/PACKAGES.html>). The spatial neighbourhood of the SLMs was defined with a distance of 57 km including the four neighbouring cells that directly join each focal cell (the rook's case). The spatial weights matrix was calculated with a row standardized coding style that scales the covariances based on the number of neighbours of each region (for details see Kissling & Carl, 2008). To improve normality and linearity in the response of richness variables to environmental predictor variables we square-root transformed all richness variables and  $\log(x + 1)$  transformed mean annual precipitation and altitudinal range.

## RESULTS

### Geographic patterns of species richness and environment

Overall bird species richness across Kenya was highest in the south-western parts of the country, with hotspots in the Cherangani

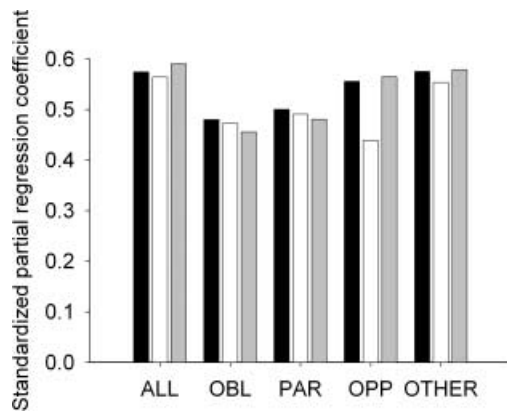
Hills, the Rift Valley, the Central Highlands, and the Tsavo National Park (Fig. 1a). In contrast, the arid bushlands and deserts of northern Kenya and the coastal plains in the East were characterized by relatively low bird diversity. The spatial patterns of species richness change somewhat when considering different avian frugivore guilds (Fig. 1b–e). Species richness of obligate and partial frugivores was highest in the West close to the border of Uganda whereas opportunistic fruit eaters were also very common much further southeast. Woody plant species richness, in contrast to bird species richness, peaked in the southernmost part of the country, which included the Shimba Hills National Reserve (Fig. 1f). Fleshy-fruited and non-fleshy-fruited plants (Fig. 1g & h) showed similar patterns to all woody plants but medium to high species richness values of non-fleshy-fruited plants appeared to be spatially spread out more than those of fleshy-fruited plants. Geographic patterns of the environmental variables revealed strong and markedly different broad-scale spatial gradients across Kenya (Fig. 1i–n).

### Functional relationships

Bivariate Pearson correlation coefficients between all variables are given in Table S1 (see Supplementary Material). The simple correlation between woody plant species richness and overall bird species richness indicated that they covary positively across Kenya ( $r = 0.81$ ). A strong correlation between the two variables remained when accounting for environmental effects with a SEM (Fig. 2b, bold coefficient), supporting prediction 0. This suggests an important role of functional relationships, either via resource–consumer interactions or vegetation structural complexity, though other explanations are possible. Dissecting the overall species richness patterns into avian guilds and plant resource groups revealed that all bird groups showed high spatial congruence ( $r \geq 0.76$ ) with the plant groups (Table S1). SEMs with species richness of the four avian guilds and the two plant resource groups supported this general trend (all standardized partial regression coefficients  $\geq 0.44$ ; see Fig. 3). In contradiction to prediction 1a, both species richness of fleshy-fruited plants and non-fleshy-fruited plants had similarly strong direct effects on obligate and partial avian frugivores (compare white with grey bars for OBL and PAR in Fig. 3). Moreover, the effect of fleshy-fruited plant species richness on species richness of avian guilds in our SEMs did not decrease from obligate frugivores, partial frugivores, opportunistic fruit-eaters to non-fruit-eaters (compare the white bars in Fig. 3), in contradiction to prediction 1b. Thus we found little support for hypothesis 1 (food plant diversity hypothesis). Consistent with prediction 2, the direct relationships between trophically independent groups of species were often strong, which can be interpreted as supporting hypothesis 2 (vegetation structural hypothesis).

### Environmental effects

Direct effects of environmental variables on the species richness of both woody plants (Fig. 4) and birds (Fig. 5) were often strong in our SEMs. The strongest direct effects of environmental variables on species richness of woody plants came from topographic



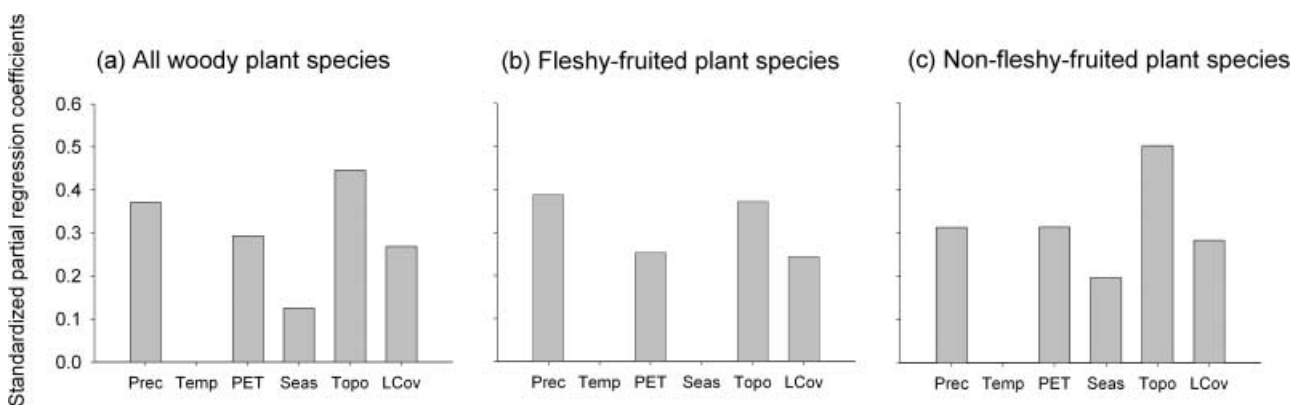
**Figure 3** Direct effects of plant species richness (black: all woody plants; white: fleshy-fruited plants; grey: non-fleshy-fruited plants) on species richness of birds (ALL: all birds; OBL: obligate frugivores; PAR: partial frugivores; OPP: opportunistic fruit-eaters; OTHER: non-fruit-eating birds). Direct effects are standardized partial regression coefficients from structural equation models similar to Fig. 2a where bird richness has been replaced by ALL, OBL, PAR, OPP and OTHER, and plant richness by richness of woody plants, fleshy-fruited plants and non-fleshy-fruited plants, respectively. See text for details on model selection.

relief, precipitation and PET, although their relative importance differed between the two plant resource groups (Fig. 4). Avian guilds differed in terms of direct effects of environmental variables on their species richness when woody plant species richness was included in SEMs (Fig. 5). For instance, precipitation showed strong direct effects on species richness of frugivores (OBL and PAR; Fig. 5a) whereas direct effects of temperature were strong for birds that are not specialized on fruit-eating (OPP and OTHER, Fig. 5b). These direct environmental effects on both bird and woody plant diversity differed from the total (i.e. direct + indirect) effects of environmental variables in our

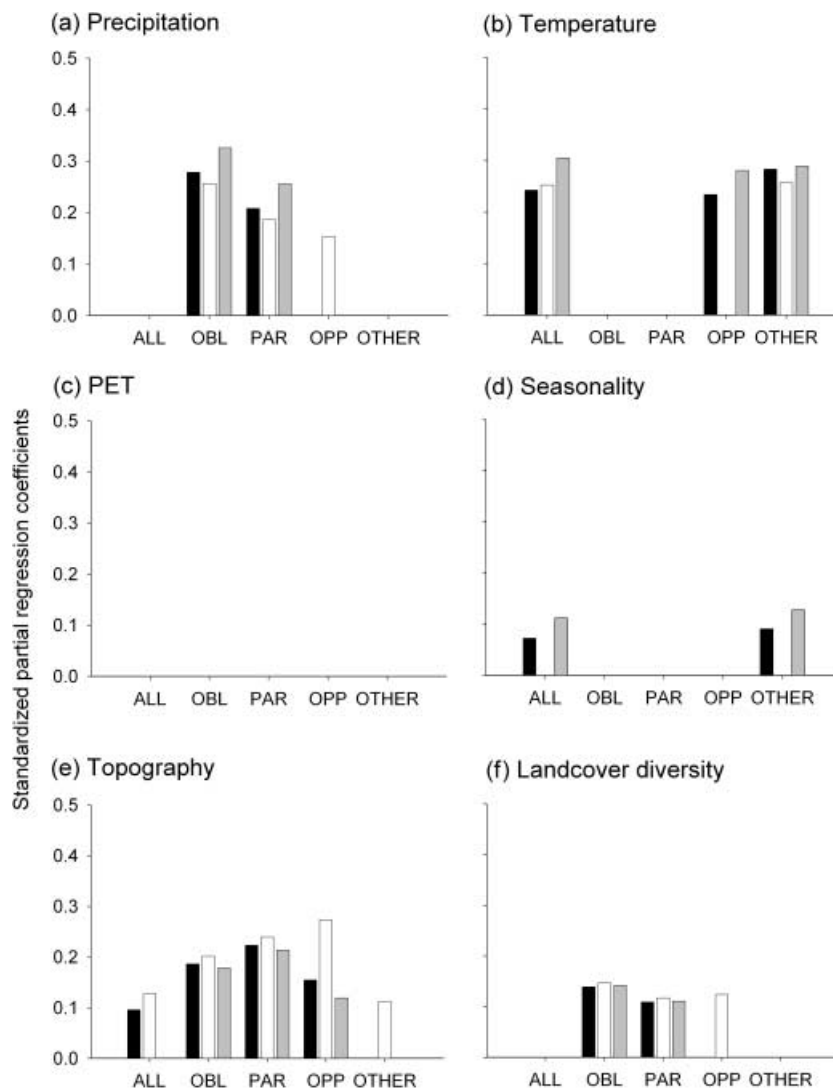
path models (see Supplementary Material, Figs S1 and S2). Total effects of some environmental variables differed a little between the plant groups (e.g. precipitation and seasonality, Fig. S1) while others were very consistent. The total effects were also relatively similar across bird groups (Fig. S2), with precipitation being the main exception as it was stronger for frugivores than non-frugivores. Strong direct and indirect environmental effects on species richness in our SEMs are consistent with prediction 3, as are broadly similar total effects of environmental variables on bird and plant species richness. However, the differences that do exist (e.g. PET and precipitation – compare Figs S1 and S2) are not consistent with hypothesis 3 (similar environmental effects hypothesis) as the sole cause of bird species richness. Nor is the important role of woody plant species richness in all the models. The contrasting nature of the direct effects of environment on richness (compare Figs 4 and 5) can be interpreted as being inconsistent with hypothesis 3.

### Effects of spatial autocorrelation

In most cases, the residuals from our minimal adequate OLS models that included avian species richness as response variable showed a spatial autocorrelation structure pattern, as indicated by significant Moran's *I* values (Table 2). Only OLS regressions with obligate frugivore richness as a response variable showed no spatial autocorrelation structure in model residuals (Table 2). When fitting SLMs with the same variables, the spatial autocorrelation structure in the OLS model residuals disappeared (i.e. non-significant Moran's *I* values around 0; see Table 2) indicating that the non-independence assumption was no longer violated. Correspondingly,  $R^2$ -values from SLMs were generally higher and AIC values lower than those of equivalent non-spatial OLS models when spatial autocorrelation was present (Table 2). Comparison of parameter estimates (i.e. standardized partial regression coefficients) from SLM and non-spatial OLS models suggested that their strengths were generally very similar (Table 2).



**Figure 4** Absolute direct effects of environmental predictor variables on species richness of plants (a: all woody plants; b: fleshy-fruited plants; c: non-fleshy-fruited plants). Values are derived from structural equation models similar to Fig. 2a, where plant richness has been replaced by species richness of woody plants, fleshy-fruited or non-fleshy-fruited plants. See text for details on model selection. Zero values indicate that the variable was not selected in the minimal adequate model. Prec: mean annual precipitation; Temp: mean monthly temperature; PET: mean annual potential evapotranspiration; Seas: seasonality in precipitation; Topo: topographic relief; LCovDiv: land cover diversity.



**Figure 5** Absolute direct effects of environmental predictor variables on species richness of birds (ALL: all birds; OBL: obligate frugivores; PAR: partial frugivores; OPP: opportunistic fruit-eaters; OTHER: non-fruit-eating birds). Values are derived from structural equation models similar to Fig. 2a, where plant richness was replaced by species richness of woody plants (black columns), fleshy-fruited plants (white) or non-fleshy-fruited plants (grey), and bird richness by ALL, OBL, PAR, OPP and OTHER. See text for details on model selection. Zero values indicate that the variable was not selected in the minimal adequate model.

Moreover, in almost all cases the relative importance of predictor variables to explain avian species richness did not change (Table 2). OLS models with woody, fleshy-fruited, or non-fleshy-fruited plant species richness as response variables and all environmental variables as predictor variables similarly indicated that differences in parameter estimates between SLM and non-spatial OLS models were unimportant (Table 3). Overall, these results suggested that inference from SLM and OLS models was very similar for our data set.

## DISCUSSION

Our analyses suggest that geographic patterns of tropical bird and woody plant diversity across Kenya are linked via functional relationships and that environmental factors differ in their direct effects on both groups. These functional relationships may be largely driven by vegetation structural effects (hypothesis 2); this is consistent with the strong correlations that we found between the species richness of trophically independent bird and plant taxa. There was no evidence for an important role of resource–

consumer interactions (hypothesis 1) since the direct effects of woody species richness on bird species richness in our SEMs were not consistent with our predictions based on trophic relationships. Our results were robust to the presence of spatial autocorrelation in our data set since both spatial and non-spatial analyses yielded very similar results (Tables 2 and 3).

It is often speculated that resource–consumer interactions play an important role in shaping geographic patterns of animal species richness (e.g. Wright, 1983; Hawkins *et al.*, 2003). However few studies have addressed this issue explicitly, and the results are contrasting. In a seminal paper, Hawkins & Porter (2003) analysed species richness of butterflies across California and found no relationship between butterfly and food plant diversity once environmental variables had been accounted for, despite strong specificity of butterflies to host plants. Across Britain, however, Menéndez *et al.* (2007) demonstrated that host-plant richness is an important determinant of butterfly diversity, even when accounting for environmental correlations. For avian consumers, Márquez *et al.* (2004) showed that the species richness of wintering birds in Europe is more dependent on



**Table 2** Standardized partial regression coefficients of traditional ordinary least squares (OLS) regressions and spatial linear models (SLM) with bird species richness (ALL, all bird species; OBL, obligate frugivores; PAR, partial frugivores; OPP, opportunistic fruit-eaters; OTHER, non-fruit-eating birds) as response variable, and plant species richness (woody plants, fleshy-fruited plants and non-fleshy-fruited plants, respectively) and six environmental variables as potential predictor variables (Prec, mean annual precipitation; Temp, mean monthly temperature; PET, mean annual potential evapotranspiration; Seas, seasonality in precipitation; Topo, topographic relief; LCovDiv, land cover diversity). Minimal adequate OLS models were chosen from the full set of explanatory variables based on the Akaike Information Criterion (AIC) (see text for details). The high spatial autocorrelation of errors in most OLS analyses (all Moran's  $I$ ,  $P < 0.05$ ) confirms the expected violation of the non-independence assumption. Coefficients from OLS analyses are identical to direct effects in structural equation models. \*\* $P < 0.01$ , \*\*\* $P < 0.001$ .

Variables	Bird species richness									
	ALL		OBL		PAR		OPP		OTHER	
	OLS	SLM	OLS	SLM	OLS	SLM	OLS	SLM	OLS	SLM
<i>Models with all woody plants (WoodRich)</i>										
WoodRich	0.574	0.533	0.480	0.477	0.500	0.489	0.555	0.504	0.575	0.545
Prec	–	–	0.278	0.273	0.208	0.164	–	–	–	–
Temp	–0.243	–0.163	–	–	–	–	–0.234	–0.212	–0.283	–0.197
PET	–	–	–	–	–	–	–	–	–	–
Seas	–0.073	–0.126	–	–	–	–	–	–	–0.091	–0.153
Topo	0.096	0.123	0.187	0.187	0.224	0.222	0.155	0.189	–	–
LCovDiv	–	–	0.139	0.142	0.109	0.144	–	–	–	–
Model $r^2$	0.73	0.76	0.82	0.82	0.76	0.79	0.69	0.71	0.70	0.74
Model AIC	835	823	294	296	432	421	554	548	804	791
Errors Moran's $I$	0.21***	0.01	0.05	0.00	0.22***	0.02	0.17**	0.00	0.23***	0.01
<i>Models with fleshy-fruited plants (FleshRich)</i>										
FleshRich	0.564	0.511	0.472	0.467	0.491	0.472	0.439	0.387	0.553	0.501
Prec	–	–	0.256	0.250	0.186	0.139	0.153	0.122	–	–
Temp	–0.253	–0.204	–	–	–	–	–	–	–0.257	–0.201
PET	–	–	–	–	–	–	–	–	–	–
Seas	–	–	–	–	–	–	–	–	–	–
Topo	0.128	0.161	0.202	0.204	0.240	0.243	0.274	0.292	0.112	0.138
LCovDiv	–	–	0.147	0.151	0.117	0.154	0.124	0.144	–	–
Model $r^2$	0.70	0.74	0.81	0.81	0.75	0.78	0.67	0.71	0.67	0.71
Model AIC	847	836	304	305	440	428	565	555	817	804
Errors Moran's $I$	0.21***	0.00	0.06	0.00	0.22***	0.01	0.21***	0.01	0.22***	0.00
<i>Models with non-fleshy-fruited plants (NonFleshRich)</i>										
NonFleshRich	0.590	0.569	0.456	0.455	0.481	0.480	0.565	0.524	0.579	0.561
Prec	–	–	0.326	0.321	0.256	0.214	–	–	–	–
Temp	–0.305	–0.241	–	–	–	–	–0.281	–0.258	–0.289	–0.204
PET	–	–	–	–	–	–	–	–	–	–
Seas	–0.112	–0.160	–	–	–	–	–	–	–0.128	–0.186
Topo	–	–	0.179	0.179	0.214	0.207	0.119	0.151	–	–
LCovDiv	–	–	0.143	0.145	0.111	0.144	–	–	–	–
Model $r^2$	0.75	0.78	0.83	0.83	0.77	0.80	0.71	0.73	0.72	0.76
Model AIC	821	809	290	292	427	415	543	538	790	776
Errors Moran's $I$	0.21***	0.01	0.05	0.00	0.22***	0.02	0.17**	0.00	0.23***	0.01

environmental factors than on food plant diversity whereas Kissling *et al.* (2007) demonstrated the opposite for avian frugivores in sub-Saharan Africa. Recently published studies indicate that generalisations about resource–consumer diversity at broad spatial scales are difficult to make, probably because the relationship between food plant diversity and animal consumers varies with geographic location (Hawkins & Porter, 2003; Márquez *et al.*, 2004; Kissling *et al.*, 2007; Menéndez *et al.*, 2007),

evolutionary history (Fleming *et al.*, 1987), spatial and temporal scales of analysis (Burns, 2004), and the metabolic ecology of animal consumers (ecto- vs. endotherms; Currie *et al.*, 2004).

For tropical frugivorous bird species, it has been shown that their species richness patterns at the continental scale of sub-Saharan Africa are very strongly linked to the species richness of fig trees (*Ficus* spp.; Kissling *et al.*, 2007) – a major fruit resource for frugivores in the tropics (Shanahan *et al.*, 2001). Such positive

**Table 3** Standardized partial regression coefficients from traditional ordinary least squares (OLS) regressions and spatial linear models (SLM) with plant species richness (all woody plants, fleshy-fruited plants and non-fleshy-fruited plants, respectively) as response variable, and six environmental variables (Prec, mean annual precipitation; Temp, mean monthly temperature; PET, mean annual potential evapotranspiration; Seas, seasonality in precipitation; Topo, topographic relief; LCovDiv, land cover diversity) as potential predictor variables. Minimal adequate OLS models were chosen from the full set of explanatory variables based on the Akaike Information Criterion (AIC) (see text for details). The high spatial autocorrelation of errors in OLS analysis (all Moran's I,  $P < 0.05$ ) confirms the expected violation of the non-independence assumption. Coefficients from OLS analyses are identical to direct effects in structural equation models. \* $P < 0.05$ , \*\* $P < 0.01$ .

Variables	Plant species richness					
	All woody		Fleshy		Non-fleshy	
	OLS	SLM	OLS	SLM	OLS	SLM
Prec	0.371	0.364	0.388	0.377	0.313	0.295
Temp	–	–	–	–	–	–
PET	0.294	0.306	0.254	0.267	0.314	0.315
Seas	0.125	0.150	–	–	0.197	0.217
Topo	0.446	0.472	0.372	0.390	0.502	0.524
LCovDiv	0.269	0.279	0.244	0.250	0.284	0.294
Model $r^2$	0.64	0.66	0.66	0.68	0.59	0.62
Model AIC	788	783	706	704	663	656
Errors Moran's I	0.16**	–0.01	0.12*	–0.01	0.18**	–0.01

relationships between species richness of animal consumers and their food plants can potentially be explained by niche assembly mechanisms, e.g. evolutionary or ecological responses to fruit size, fruit colour or vertical stratification of fruit presentation (Herrera, 2002; Kissling *et al.*, 2007). We tested the 'fig–frugivore richness hypothesis' (Kissling *et al.*, 2007) with our Kenyan data set by extracting all *Ficus* species ( $n = 32$ ) from the fleshy-fruited plants, and re-calculated all path models by interchanging woody plant species richness with *Ficus* richness (compare Fig. 2). The direct effects of *Ficus* diversity on species richness of avian guilds in our path models, however, were similar to (but weaker than) those of all fleshy-fruited plants (Table S1) providing only weak evidence for a keystone resource effect of *Ficus* richness on avian frugivore diversity at the spatial scale of Kenya. The differences at the Kenyan and African scale in the importance of *Ficus* for frugivorous birds might be explained by a lack of lowland tropical rain forest in Kenya, which is the habitat type that harbours the highest diversity of *Ficus* and frugivorous birds at the continental scale of sub-Saharan Africa (Kissling *et al.*, 2007).

A higher species richness of woody plants may also be associated with more architectural complexity (hypothesis 2) and thus more structural niches to be occupied by animal species (MacArthur & MacArthur, 1961; Cody, 1985; Tews *et al.*, 2004). Although a number of studies have demonstrated that the species richness of birds is associated with woody plant diversity at a number of spatial scales and across many habitats (e.g. MacArthur & MacArthur, 1961; Lee & Rotenberry, 2005; Rompré *et al.*, 2007), very few studies have attempted to separate the effects of resource–consumer interactions and vegetation structural complexity on bird diversity at scales comparable to our study, and none that we are aware of in the tropics. For North America, Rotenberry (1985) and Lee & Rotenberry (2005) analysed bird

diversity in relation to vegetation structure and plant species composition and concluded that plant–bird species associations are not only mediated by vegetation structural complexity but also by food resources. In contrast, our analyses suggest that functional relationships between bird and woody plant diversity across Kenya may be more associated with vegetation structural complexity than resource–consumer interactions. Vegetation structural complexity thus may be more important in shaping geographic gradients of tropical bird diversity than has previously been thought (e.g. Oindo *et al.*, 2001; Jetz & Rahbek, 2002; Hawkins *et al.*, 2003; Kissling *et al.*, 2007; but see Hawkins *et al.*, 2005, 2007b). This requires further investigation.

Although recent research has shown that diversity hotspots of a wide variety of organisms are correlated with environmental variables (see references in Table 1), few studies have tried to disentangle the relative direct and indirect effects of environmental predictor variables on plant–animal diversity (Hawkins & Porter, 2003; Kissling *et al.*, 2007; Menéndez *et al.*, 2007). Our results for woody plants are consistent with recent evidence showing that contemporary water and energy availability play a dominant role in shaping geographic patterns of plant diversity (Field *et al.*, 2005; Kreft & Jetz, 2007). However, our path models suggest that climate as well as habitat heterogeneity act in large part indirectly on bird species richness via effects on plants rather than having strong direct effects on bird species distributions (Fig. 2b). Strong direct effects of climatic factors on animal species richness are more likely for butterflies (Hawkins & Porter, 2003; Menéndez *et al.*, 2007), or other solar ectotherms such as reptiles (Hawkins *et al.*, 2003), which appear to be limited by direct effects of temperature on their physiological tolerances ('physiological tolerance hypothesis'; Currie *et al.*, 2004). For endotherms such as birds, however, it is more likely that contemporary species

diversity gradients are predominantly determined by indirect effects of climate, either mediated through trophic relationships and the production of food items (Wright, 1983; Kissling *et al.*, 2007), or via habitat composition and vegetation structural complexity (MacArthur & MacArthur, 1961; Tews *et al.*, 2004; Rompré *et al.*, 2007; this study). However, some climatic variables might be important in directly determining spatial richness patterns of certain avian trophic guilds (Fig. 5 and Table 2). Further work would be interesting to examine why there is an apparent switch from direct effects of precipitation for frugivorous birds to temperature for non-frugivorous birds.

Recent models for predicting climate change impacts on animal species richness largely rely on statistical relationships between species richness and environmental factors (e.g. Lemoine *et al.*, 2007). It is, however, unclear under which circumstances these assumptions are valid for accurately predicting future species distributions (Araújo & Rahbek, 2006). Concerns have arisen because such models assume that species interactions are of minor importance at broad geographic scales and that species assemblages are in a steady-state relationship with contemporary climate (Araújo & Rahbek, 2006). However, there is now increasing evidence that species interactions can indeed strongly influence responses to changing climates (e.g. Suttle *et al.*, 2007) and that predictions of ecological responses to climate change cannot simply be based on direct environmental effects on species (e.g. Menéndez *et al.*, 2006, 2007). Our results support this view by implying that bird species richness, at least in the tropics, is likely to respond indirectly to changing climates via direct climatic effects on plants. Our SEMs further suggest that direct environmental effects on birds and plants differ once functional relationships between birds and woody plants have been accounted for (Figs 4 & 5). This suggests that climate change could alter the spatial synchrony and reshuffle plant–animal richness, species composition and community organization in tropical ecosystems (Parmesan, 2006).

If we are to use indicator taxa for spatially explicit forecasting of changes in biodiversity, we need to know much more about what underlies richness correlations, including species interactions and direct and indirect environmental effects on species richness (Wolters *et al.*, 2006). Forecasts of changes in species richness are more likely to fail if climate is not the only factor limiting the distribution of bird species and assemblages, e.g. if functional relationships (resource–consumer interactions and vegetation structural complexity), interspecific interactions (predation, competition and mutualism) or dispersal limitation play a prominent role (Parmesan, 2006). Changes in woody plant species richness could lag behind those expected on the basis of climate-change scenarios because of dispersal limitation and longevity of the species. This in turn could affect the future distribution of bird species richness via effects on species' food and especially habitat resources. Recent research from Britain has demonstrated 'colonization lags', at least for butterflies (Menéndez *et al.*, 2006), and Svenning & Skov (2007) suggest that changes in plant species distributions may lag behind climate change by centuries. We thus conclude that direct climatic effects on plants and animals are likely to differ and that future predictions of

animal species richness in response to climate change therefore need to include indirect climatic effects, e.g. via plants.

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## SUPPLEMENTARY MATERIAL

The following supplementary material is available for this article:

**Table S1** Pearson correlations of predictor and response variables.

**Figure S1** Total effects of environmental predictor variables on species richness of plants.

**Figure S2** Total effects of environmental predictor variables on species richness of birds.

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