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RESEARCH PAPER

Food resources and vegetation structure mediate climatic effects on species richness of birds

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ABSTRACT

Aim Climate is widely recognized as a major predictor of species richness patterns along large-scale environmental gradients. Nevertheless, the mechanisms by which climate influences species richness are still a matter of debate. We disentangle whether climate influences species richness of birds *directly* via physiological limitations or *indirectly* via vegetation structure or the availability of food resources.

Location Mount Kilimanjaro, Tanzania.

Methods We recorded bird species richness along an elevational gradient from 870 to 4550 m a.s.l. We quantified local climatic conditions, vegetation structure and the availability of food resources, and applied path analysis to disentangle their direct and indirect effects on species richness of all birds, frugivores and insectivores.

Results Overall, we recorded 2945 individuals from 114 bird species. Species richness of all birds was closely correlated with temperature, vegetation structure and invertebrate biomass and both direct and indirect (via vegetation structure and availability of food resources) climatic effects were important for the diversity of the whole, trophically heterogeneous bird community. The species richness of insectivorous birds was linked to vegetation structure and invertebrate biomass, while the richness of frugivores was strongly associated with fruit abundance. Climatic factors influenced bird species richness of both avian feeding guilds exclusively *indirectly* via vegetation structure and availability of food resources.

Main conclusions We reveal the importance of trophic interactions for generating species richness patterns along large-scale environmental gradients. Our results challenge the general assumption that temperature and water availability influence species richness mostly directly, and underscore the importance of vegetation structure and the availability of food resources as principal mediators of climatic effects on species richness patterns on macroecological scales.

Keywords
Ambient energy hypothesis, elevational gradient, energy–richness hypothesis, habitat heterogeneity hypothesis, path analysis, physiological tolerance hypothesis, productivity hypothesis, resource availability hypothesis, species–energy hypothesis, vegetation structure hypothesis.

INTRODUCTION

Changes in species richness along large-scale environmental gradients, such as latitude and elevation, are among the longest known and most intensively studied patterns in ecology and biogeography (Gaston, 2000). Although a wealth of hypotheses have been formulated to explain species richness gradients, it is widely recognized that current climatic conditions, especially

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energy and water availability, are strongly correlated with species richness (Hawkins *et al.*, 2003; Currie *et al.*, 2004; Turner, 2004). Nevertheless, the mechanisms by which climate influences species richness are still a matter of debate (Currie *et al.*, 2004; Evans *et al.*, 2005; Clarke & Gaston, 2006). The 'physiological tolerance hypothesis' proposes a *direct* effect of climate on species richness via physiological constraints (Currie *et al.*, 2004; Buckley *et al.*, 2012). It predicts higher species richness under warmer and wetter conditions than under colder and drier conditions, because more species can tolerate more favourable environmental conditions. The 'vegetation structure hypothesis' proposes an *indirect* effect of climate on species richness via the structural complexity of habitats (Hurlbert, 2004; Tews *et al.*, 2004). It predicts higher species richness in more complex habitats that offer more diverse ways to exploit resources (instead of more resources per se) and can therefore sustain more specialists. The 'resource availability hypothesis' proposes an *indirect* effect of climate on species richness via trophic relationships, mediated by the effect of climate on plant productivity and the subsequent availability of food resources (Davies *et al.*, 2007; Jetz *et al.*, 2009). It assumes that the species richness of a specific trophic level is limited by the amount of energy provided by the next lower trophic level and thus predicts higher species richness in areas with higher food resource availability.

All three hypotheses are supported by empirical studies (Hurlbert, 2004; Kissling *et al.*, 2007; Menéndez *et al.*, 2007; Mulwa *et al.*, 2013), suggesting that climate–richness relationships cannot be explained by a single hypothesis but that several direct and indirect effects act in concert (Clarke & Gaston, 2006). Path analysis allows us to test for such direct and indirect effects simultaneously and has successfully been applied to study the effects of climate and vegetation structure on species richness at large-scale environmental gradients (Kissling *et al.*, 2008; Zhang *et al.*, 2013). However, due to the difficulties in quantifying the availability of food resources over large spatial scales, its effect has so far only been tested indirectly by using species richness of food plants as a proxy (Kissling *et al.*, 2007, 2008; Menéndez *et al.*, 2007).

Tropical mountains provide the opportunity to test all three hypotheses (physiological tolerance, vegetation structure and availability of food resources) simultaneously because they constitute large-scale environmental gradients over relatively small spatial distances and thus allow a field-based quantification of food resources. Birds are an excellent model system for testing the three hypotheses as they occur in nearly all the climatic zones and habitat types of tropical mountains (McCain, 2009). Because birds occupy a wide range of trophic positions (Kissling *et al.*, 2012), they offer the opportunity to also test the three hypotheses with functional subsets of the bird community. For example, testing the effect of fruit abundance on frugivorous bird richness yields an additional, more specific way of testing the 'resource availability hypothesis'. A recent meta-analysis found that a combination of temperature and water availability well explains the elevational patterns in bird species richness (McCain, 2009). There is also growing evidence that the distribution of vegetation structure along a mountain contributes to the elevational pattern in bird species richness (Acharya *et al.*, 2011; Dainese & Poldini, 2012; Jankowski *et al.*, 2013). By contrast, there is little and only indirect evidence for an influence of the availability of food resources on the elevational distribution of bird species richness (Loiselle & Blake, 1991; Carrascal *et al.*, 2012).

Here, we used path analysis to simultaneously disentangle the *direct* and *indirect* effects of climate, vegetation structure and availability of food resources on macroecological bird species richness patterns. Along a 3700-m elevational gradient on Mount Kilimanjaro, Tanzania, we tested the following three predictions.

1. If physiological limitations influence patterns of bird species richness we expect a positive *direct* relationship between climatic factors and bird species richness when accounting for the effects of vegetation structure and food resources ('physiological tolerance hypothesis').

2. If vegetation structure influences patterns of bird species richness we expect a positive *direct* relationship between vegetation structure and bird species richness when accounting for effects of climatic factors and food resources ('vegetation structure hypothesis').

3. If food resource availability influences patterns of bird species richness we expect a positive *direct* relationship between food resources and bird species richness when accounting for effects of climatic factors and vegetation structure ('resource availability hypothesis').

To analyse the role of guild-specific food resources, we tested how the availability of different food types (insects, flowers, fruits) influences the species richness patterns of the entire bird community and of two feeding guilds (insectivores and frugivores).

METHODS

Study area

We conducted this study on Mount Kilimanjaro (2°45′–3°25′ S, 37°0′–37°43′ E), Tanzania, the highest free-standing mountain on earth, which rises from 700 m a.s.l. at the mountain base to 5891 m a.s.l. at Uhuru Peak (Fernandes *et al.*, 2009). Rainfall is seasonally distributed with long rains from March to May and short rains around November. While temperature decreases linearly with elevation, mean annual precipitation peaks around 2200 m a.s.l and decreases towards lower and higher elevations (Hemp, 2006; Appendix S1 in Supporting Information).

Plot selection was based on the study plots of the DFG-Research Unit 'KiLi – Kilimanjaro ecosystems under global change: linking biodiversity, biotic interactions and biogeochemical ecosystem processes'. The 60 0.25-ha study plots of the KiLi project cover six near-natural and six disturbed habitat types. Each habitat type is covered by five replicate plots, which are distributed over five transects on the southern slope of Mount Kilimanjaro. The minimum distance between transects is 12.2 km on the foothills and 4.6 km in the alpine zone, and the minimum distance between plots is 300 m. We conducted this study on the 30 KiLi plots that are located within the six near-natural habitat types, covering an elevational gradient of about 3700 m, a temperature gradient of about 21K°C and a precipitation gradient of about 2100 mm year^{-1} (Appendices S1 & S2). Thus, our research plots cover a large-scale environmental gradient ranging from warm tropical lowland to cold Afro-alpine temperature regimes and from semi-arid to perhumid conditions. Habitat types were savanna (870–1150 m a.s.l.), lower montane forest (1560–2020 m a.s.l.), *Ocotea* forest (2120–2750 m a.s.l.), *Podocarpus* forest (2720–2970 m a.s.l.), *Erica* forest (3500–3880 m a.s.l.) and *Helichrysum* scrub (3880–4550 m a.s.l.). All plots were sampled twice between March 2011 and October 2012, once during the warm dry season (December to March) and once during the cold dry season (July to October).

Birds

We used audiovisual point counts on eight subplots per plot to record birds. We established circles with a 20-m radius in densely vegetated habitats (savanna and all forest habitats) and 35.5 m × 35.5 m squares at *Helichrysum* plots, covering the same sampling area in all habitat types. All birds heard or seen in one subplot were counted for 10 min and identified to species level (Zimmerman *et al.*, 1999). Point counts started 15 min before sunrise and were completed before 09:00. All 480 point counts (30 plots × 8 subplots × 2 seasons) were conducted by the same observer (S.W.F.) to reduce inter-observer variability (Campbell & Francis, 2011). We calculated bird species richness as the cumulative sum of species across all eight subplots per plot, but excluded birds that were recorded at higher than maximum canopy height within the respective subplots. We used a database of the diet of all sub-Saharan breeding bird species compiled from a detailed literature survey (Kissling *et al.*, 2007) to classify bird species into feeding guilds according to their major food items (Appendix S3).

Climatic factors, vegetation structure and food resources

Mean annual temperature and mean annual precipitation were interpolated for every plot using a 15-year dataset from a network of about 70 temperature loggers and rain gauges on Mount Kilimanjaro (Hemp, 2006). To test the effects of vegetation structure, we quantified vertical vegetation heterogeneity, canopy height and canopy closure on every subplot in both seasons. To obtain vertical vegetation heterogeneity, we first estimated the vegetation cover in layers at 0, 1, 2, 4, 8, 16, 32 and 64 m above ground and then calculated the Shannon–Wiener diversity index across these eight strata (Bibby *et al.*, 2000). Canopy height was measured with a laser rangefinder as maximum canopy height above ground. Canopy closure was measured as the mean percentage of closed cells from four spherical canopy densitometer readings taken at the centre of each subplot in the four cardinal directions. We used the average vegetation heterogeneity, the average canopy closure and the maximum canopy height across the eight subplots per plot and season for analyses. We recorded food resources by estimating the number of ripe fleshy fruits and open flowers for every individual fruiting/flowering plant within all subplots on a logarithmic scale, considering woody plant species only, and summed them per plot and season for analyses. We did not consider fruits and flowers of herbaceous plants due to their low abundance and because they are mostly pollinated and dispersed by invertebrates (Cain *et al.*, 1998). In addition, we used 100 sweeps with a 30-cm diameter sweep net along two parallel, permanently marked 50-m transects on the KiLi plots to sample invertebrate biomass per plot in both seasons. All invertebrates ≥ 1 mm were lumped to one sample per plot and season, which was immediately weighed to obtain fresh biomass.

Statistical analyses

We conducted all analyses for species richness of all birds and separately for species richness of frugivorous and insectivorous birds. To reduce the influence of outliers and to improve normality of residuals, we log-transformed the richness measures and food resources, square root-transformed canopy height and logit-transformed canopy closure. Prior to analyses, all variables were standardized (mean = 0, SD = 0.5) to obtain standardized parameter estimates.

To examine how bird species richness was distributed along the elevational gradient, we compared the fit of linear mixed effect models (LMMs) with a linear (monotonous increase/decrease with elevation), a quadratic (accelerating increase/decrease) and a linear plus a quadratic (unimodal or accelerating increase/decrease) term of elevation. In all models, we included plot as a random factor to control for the two repeated measures at each plot.

We used path analysis to investigate which factors influence the observed elevational bird species richness pattern. We based the a priori structure of the path model (Fig. 2a) on the hypotheses that climate influences vegetation structure, that both jointly influence food resources for birds and that all three factors are associated with bird species richness. To avoid collinearity and to increase the sample/parameter ratio of the path models, we pre-selected predictor variables within groups (climatic factors, vegetation structure, food resources). Pre-selection was based on our ecological understanding of the study system and the strength of the relationship between predictor variables and overall bird species richness, as estimated by marginal R^2 values (Nakagawa & Schielzeth, 2013) from simple LMMs with plot as random factor (Appendix S4). We pre-selected temperature and precipitation as climatic variables because both were significantly positively related to overall bird species richness. We did not consider season because only 5% of the observed bird species were migrants (Appendix S3) and species richness did not differ between seasons (Appendix S4). We chose vertical vegetation heterogeneity as a measure of vegetation structure as it explained more variance in bird species richness than canopy closure and canopy height and because the three variables were highly collinear. We pre-selected the number of fruits and the biomass of invertebrates as measures of food resources and modelled them with correlated errors in the path model as we assumed the same causal ancestors for both variables (Fig. 2a). We did not consider the number of flowers due to its low explanatory power (Appendix S4) and the lack of strictly nectarivorous bird species in our dataset (Appendix S3). Within the set of pre-selected predictor variables all variance inflation factors (VIFs) were below the critical value of 10 (Appendix S4), indicating that collinearity was not a problem (Dormann *et al.*, 2013).

Based on the a priori structure of the path model (Fig. 2a), we tested all possible combinations of paths leading to a specific endogenous variable with LMMs. We fitted LMMs with maximum likelihood and included plot as a random factor. We ranked LMMs by the Akaike information criterion with a correction for small sample size (AICc). We then recalculated the best-fit LMM (i.e. the one with the lowest AICc value) for each endogenous variable with restricted maximum likelihood and checked for multivariate normality using histograms of the residuals and for spatial autocorrelation by calculating Moran's *I*-values using a permutation approach with 1000 permutations. We combined the best-fit LMMs according to the a priori structure of the path model. Paths that were omitted by best-fit LMMs were not included in the resulting path model. We tested the overall fit of the path model with Shipley's generalized d-sep test for path models with correlated errors (Shipley, 2003, 2009). If there was no single best-fit LMM (i.e. at least one alternative LMM with ΔAICc < 2), we used competing LMMs to construct alternative path models according to the procedure described above and compared them with the best-fit path model with an AICc approach for whole path models (Shipley, 2013). All statistical analysis were performed with R 2.15.2 (R Core Team, 2012). We used the lme4 package to calculate LMMs (Bates *et al.*, 2012), the MuMIn package to select best-fit LMMs (Barton, 2012), the car package to calculate VIFs (Fox & Weisberg, 2011) and the spdep package to calculate Moran's *I*-values (Bivand, 2013).

RESULTS

We recorded 2945 individuals from 114 bird species across all plots and seasons. Among these were 510 individuals from 19 frugivorous species and 1178 individuals from 55 insectivorous species. The best-fit models for the elevational richness pattern included both a positive linear and a negative quadratic elevation term for all three bird groups, but this hump-shaped model predicted only a slight increase in overall and frugivorous bird species from low to mid elevations (Fig. 1a–c) and for insectivores it could not be separated from a model with a single negative quadratic term (ΔAICc = 1.09).

The best-fit path models yielded a very good fit to the data (overall richness, $\chi^2 = 5.76$, d.f. = 8, $P = 0.674$; frugivore richness, $\chi^2 = 10.57$, d.f. = 12, $P = 0.566$; insectivore richness, $\chi^2 = 8.28$, d.f. = 10, $P = 0.602$) and explained 83, 83 and 62% of the variance in overall, frugivore and insectivore species richness, respectively (Fig. 2b–d). There was no spatial autocorrelation in the residuals of any of the best-fit LMMs (Appendix S5).

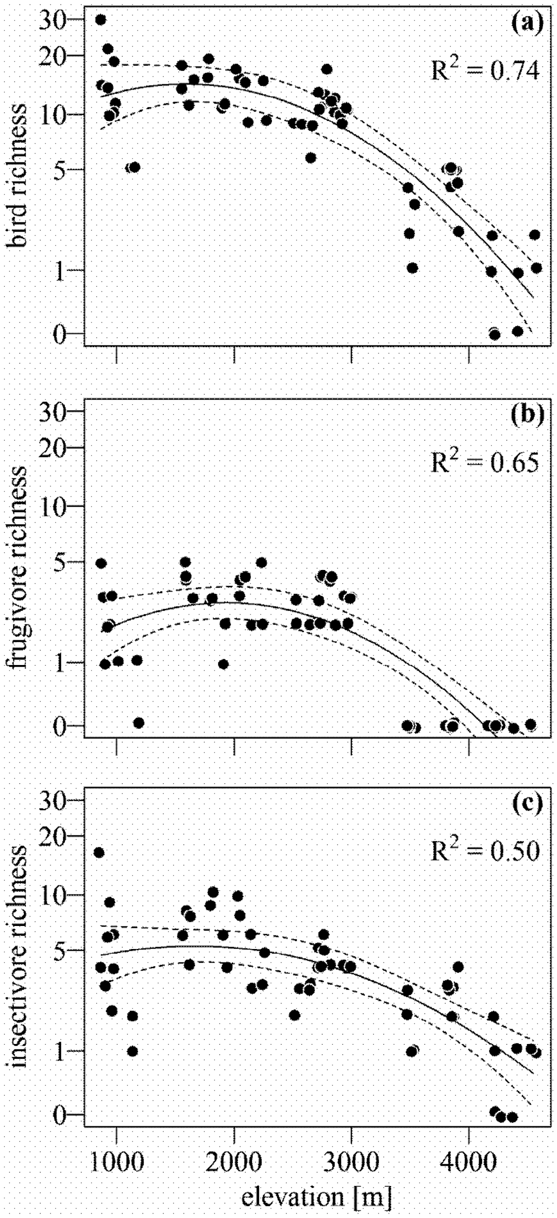

Figure 1 Species richness of all birds (a), frugivorous birds (b) and insectivorous birds (c) on 30 plots along an elevational gradient on Mount Kilimanjaro. Each plot was sampled in two seasons. The solid line represents the model prediction and the dashed lines the upper and lower 95% confidence limits, respectively. Note that the *y*-axis is log-transformed and that slight noise (1/100 of the axis length) has been introduced into the data to avoid completely overlapping points.

The climatic factors, both temperature and precipitation, strongly influenced species richness of all birds, frugivores and

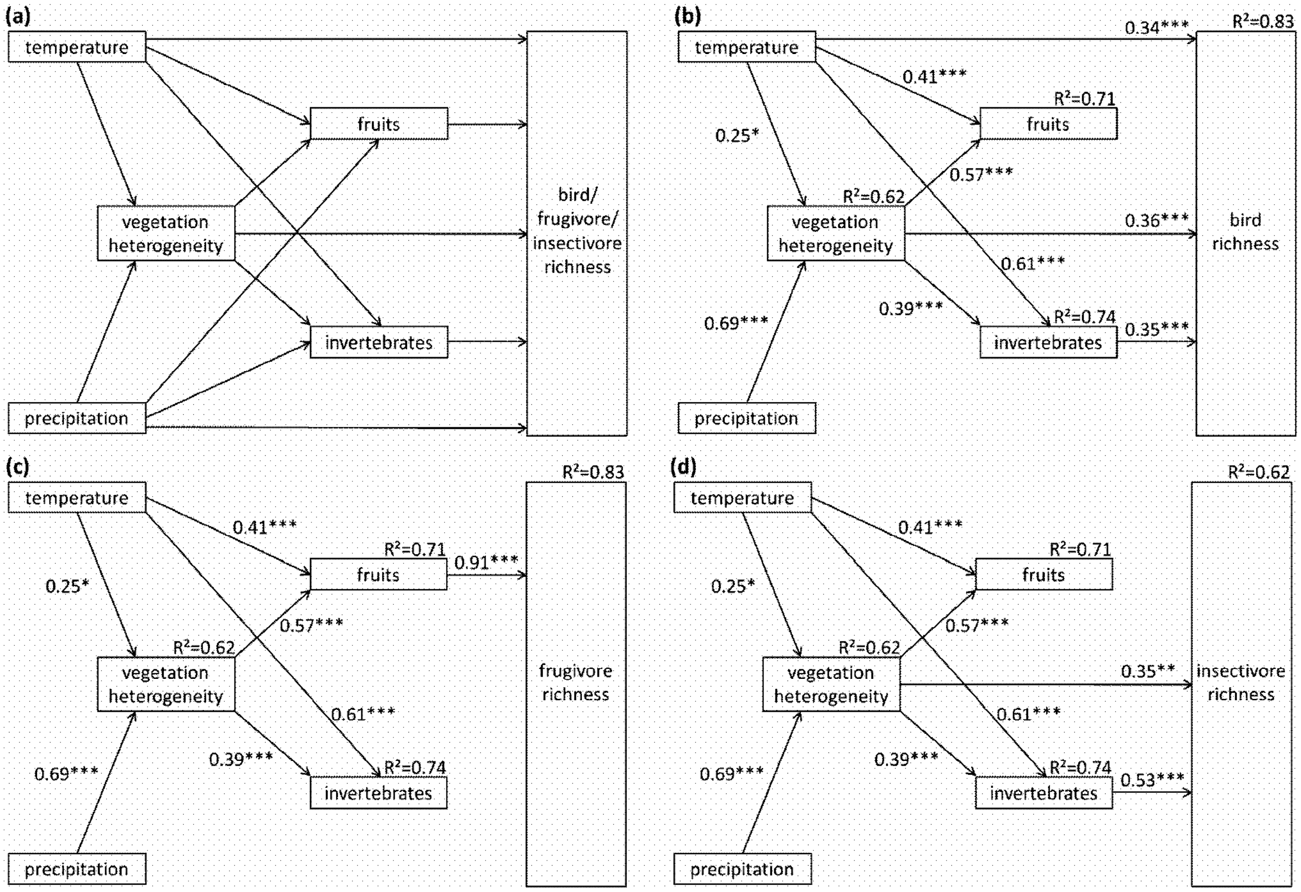

Figure 2 A priori hypothesized causal structure (a) of the relationships among climatic factors (temperature and precipitation), vegetation heterogeneity, food resources (fruits and invertebrates, both log-transformed) and bird species richness (log-transformed); and the best-fit path models (based on the Akaike information criterion with a correction for small sample sizes, AICc) for all birds (b), frugivorous birds (c) and insectivorous birds (d). The standardized path coefficients, their statistical significance ($^{+}P < 0.1$, $^{*}P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$) and the marginal coefficients of determination (R^2) are given. Paths that did not contribute to the best-fit models have been deleted in (b), (c) and (d). For clarity, error terms and the correlation of errors of fruits and invertebrates are not shown. Note that alternative models, which include the single, but non-significant, link from precipitation to fruit abundance in (b), (c) and (d), all have a ΔAICc < 2 (Appendix S6) and can therefore not be distinguished statistically from the models presented here, but that all alternative models that affect bird species richness as response variable have a significantly worse fit to the data (ΔAICc > 2; Appendix S6).

insectivores, and temperature had the strongest overall effect on species richness of all birds (Table 1). However, both climate variables acted predominantly indirectly through vegetation heterogeneity, fruit abundance and invertebrate biomass, except for a significant direct effect of temperature on overall species richness (Fig. 2b). Vertical vegetation heterogeneity influenced species richness of all birds and insectivores directly and indirectly through invertebrate biomass, and richness of frugivores only indirectly through fruit abundance (Table 1, Fig. 2b–d). The availability of food resources influenced richness in a guild-specific way. While invertebrate biomass was correlated with richness of all birds and insectivores, fruit abundance had a strong, direct effect on frugivore richness (Fig. 2b–d).

We identified one alternative path model for overall bird species richness, five alternative models for frugivorous bird species richness and three alternative models for insectivorous bird species richness (Appendix S6). None of the additional paths in the alternative path models was significant and all alternative models that affected bird species richness as a response variable had a significantly worse fit to the data (Appendix S6) than the best-fit models presented in Fig. 2. Path models that included only the climatic variables, i.e. annual mean temperature and precipitation, as sole predictors for overall, frugivore and insectivore species richness, explained considerably less variance (68, 60 and 49%, respectively) and had a significantly worse fit to the data (ΔAICc > 15 in all cases) than the respective best-fit path models in Fig. 2.

DISCUSSION

The present analysis is the first simultaneous test of the ‘physiological tolerance hypothesis’, the ‘vegetation structure hypothesis’ and the ‘resource availability hypothesis’ in a coherent analytical framework. By using path analysis, we show that climate influences overall bird species richness on the one hand *directly* and on the other hand *indirectly* via vegetation

Table 1 Standardized direct, indirect and total effects of predictor variables on species richness of all, frugivorous and insectivorous birds as derived from the models given in Fig. 2(b)–(d). Species richness, number of fruits and invertebrate biomass were log-transformed prior to analyses.

	Bird richness			Frugivore richness			Insectivore richness		
Predictor	Direct	Indirect	Overall	Direct	Indirect	Overall	Direct	Indirect	Overall
Temperature	0.34	0.33	0.67	n.s.	0.50	0.50	n.s.	0.46	0.46
Precipitation	n.s.	0.34	0.34	n.s.	0.36	0.36	n.s.	0.38	0.38
Vertical vegetation heterogeneity	0.36	0.14	0.49	n.s.	0.52	0.52	0.35	0.20	0.56
Number of fruits	n.s.	n.a.	n.s.	0.91	n.a.	0.91	n.s.	n.a.	n.s.
Biomass invertebrates	0.35	n.a.	0.35	n.s.	n.a.	n.s.	0.53	n.a.	0.53

n.s., not significant; n.a., not applicable.

heterogeneity and food resource availability, supporting all three hypotheses. The high predictive power of food resources for the species richness of specific feeding guilds reveals the importance of trophic interactions for generating species richness patterns along large-scale environmental gradients, supporting the 'resource availability hypothesis'.

On Mount Kilimanjaro, bird species richness was high between 1500 and 2000 m (Fig. 1), in the elevational band that provides the most benign combination of high temperature (15–17°C) and high water availability (1800–2700 mm year^{-1}; Appendix S1). While climate has been shown to be an important predictor of species richness for many taxa (Evans *et al.*, 2005; Clarke & Gaston, 2006; Field *et al.*, 2009), *direct* effects of temperature and water availability on species richness, as proposed by the 'physiological tolerance hypothesis', are more likely for plants and ectothermic animals and directly influence endotherms such as birds mostly under rather extreme climatic conditions (Hawkins *et al.*, 2003; McCain, 2007, 2009; McKechnie & Wolf, 2010; Buckley *et al.*, 2012). Both ambient temperature and water availability directly limit growth, spatial distribution and species richness of plants (Francis & Currie, 2003; Kluge *et al.*, 2006; Kreft & Jetz, 2007). Correspondingly, energy-related variables like temperature and potential evapotranspiration explain richness patterns of ectothermic animals such as invertebrates or reptiles (Rodríguez *et al.*, 2005; Menéndez *et al.*, 2007). By contrast, active control of their body temperature enables endotherms to survive in a wider range of climatic conditions than ectotherms (Porter & Kearney, 2009; Buckley *et al.*, 2012). As opposed to these theory-based arguments and empirical studies, we actually found a significant direct effect of temperature (but not of precipitation) on overall bird species richness. We stress, however, that this direct effect was not significant when analysing subsets of the bird community (frugivores and insectivores) for which we sampled food resources appropriately. This suggests that climate influences the species richness patterns of specialized feeding guilds primarily indirectly, whereas both direct and indirect climatic effects are important for the diversity of whole, trophically heterogeneous bird communities. An extension of our study to more extreme climatic conditions may increase the strength of the direct climatic effects, as endothermic vertebrates become more sensitive to changes in temperature and precipitation under extreme climates, especially in very arid environments (McKechnie & Wolf, 2010; McCain & Colwell, 2011; Buckley *et al.*, 2012). Hence, under benign climatic conditions a more thorough sampling of a broader spectrum of food resources may replace the direct link of temperature to overall bird species richness by stronger indirect climatic effects via the availability of food resources (Hawkins *et al.*, 2003; McCain, 2007, 2009).

Vegetation structure had the strongest overall effect on species richness of insectivorous birds on Mount Kilimanjaro, but was less important for frugivore richness. While vegetation provides a crucial structural element for birds in terrestrial ecosystems through the provision of shelter, nesting sites and foraging substrate (MacArthur & MacArthur, 1961), several studies have recorded a stronger dependence on vegetation structure for insectivorous than for frugivorous birds (Waltert *et al.*, 2005; Mulwa *et al.*, 2012; Ferger *et al.*, 2013). In a global analysis of species richness within different avian feeding guilds, habitat heterogeneity (measured as the number of vegetation classes per area) was closely correlated with species richness of all birds and insectivores, but not with that of frugivores (Kissling *et al.*, 2012). Similarly, increasing vegetation structure was positively related to regional bird species richness in the central United States primarily through the addition of new foraging guilds rather than by a higher richness of the guilds that were already present (Willson, 1974). These new guilds mostly comprised insectivorous species with specialized foraging techniques; for example, the development of a tree layer added up to eight insectivorous guilds like bark drillers or high-canopy foliage gleaners (Willson, 1974). In contrast, species richness of frugivorous birds has previously been associated rather with the species richness of food plants (Kissling *et al.*, 2007) or mere fruit abundance (Loiselle & Blake, 1991) than with the structural composition of habitats (but see Kissling *et al.*, 2008). This highlights the variation in the relative importance of factors driving species richness patterns among avian feeding guilds, and warns against simplified macroecological analysis pooling different functional groups of organisms in a single species pool (Kissling *et al.*, 2012).

The availability of food resources was the most important *direct* predictor of species richness on Mount Kilimanjaro for both feeding guilds, insectivores and frugivores. The importance of the availability of food resources for bird species richness has been demonstrated in local studies, which have shown that species richness of avian feeding guilds responds positively to seasonal increases in their food resources (Loiselle & Blake, 1991; Mulwa *et al*., 2013). However, it is difficult to test the 'resource availability hypothesis' on large spatial scales due to the difficulty in quantifying food resources. Our sampling of food resources also had some caveats, for example sweep netting samples invertebrates only up to a height of about 2 m above ground and the accuracy of estimates of fruit and flower abundance decreases with the number of vegetation strata and the height of the canopy. However, the large environmental gradient that we covered made our analyses quite robust to habitat-specific sampling biases, which is supported by the strong effects that fruit abundance and invertebrate biomass exhibited on their respective consumer communities. Many large-scale studies have used plant species richness as a proxy for the availability of food resources (Kissling *et al*., 2007, 2008; Menéndez *et al*., 2007) assuming that higher plant richness is linked to higher food biomass (the 'resource availability hypothesis') or to a higher diversity of resources (the 'resource specialization hypothesis'; Abrams, 1995). However, high plant species richness has been shown to be positively related not only to species richness of avian primary consumers (e.g. frugivores), but also to bird species richness across multiple trophic levels (Jetz *et al*., 2009). This suggests that positive relationships between plant and bird species richness are influenced more generally by a higher availability of food resources and vegetation structure than by species-specific resource–consumer relationships (Kissling *et al*., 2008; Jetz *et al*., 2009). We tested whether plant species richness would have been a sufficient proxy for resource availability in our study system and recalculated the path models, incorporating the species richness of woody plants instead of vertical vegetation structure (Appendix S7). Across all three analysed bird groups, food resources were more important than woody plant species richness as direct predictors of bird species richness, showing that woody plant richness was insufficient to explain bird species richness in our study system. Our study thus demonstrates that the availability of food resources is the most important direct predictor of species richness of avian feeding guilds along a large-scale environmental gradient on Mount Kilimanjaro.

CONCLUSIONS

Our results confirm the general importance of temperature and water availability for bird species richness patterns. However, while both direct and indirect climatic effects were important for the diversity of the whole, trophically heterogeneous, bird community, climatic factors influenced bird species richness of specific avian feeding guilds exclusively *indirectly*. This contradicts the 'physiological tolerance hypothesis', at least for those feeding guilds. Our analyses show that climate is closely correlated with vegetation structure and the availability of food resources, and that joint *direct* effects of vegetation structure and guild-specific food resources influence patterns of bird species richness within feeding guilds. This result supports the 'vegetation structure hypothesis' and the 'resource availability hypothesis' and points against explanations of species richness patterns that neglect trophic interactions. While we are aware that path analyses are correlational analyses, this finding is a step towards a more mechanistic understanding of the processes that generate species richness patterns along large-scale environmental gradients.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's web-site.

Appendix S1 Scatter plots of predictor variables used in the path models against the elevational gradient.
Appendix S2 Map of the study region.
Appendix S3 List of observed bird species.
Appendix S4 Variable pre-selection and variance inflation factors.
Appendix S5 Test for spatial autocorrelation.
Appendix S6 Alternative path models and their test statistics.
Appendix S7 Path models with woody plant species richness instead of vertical vegetation heterogeneity.

BIOSKETCH

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Author contributions: K.B.G., M.S. and S.W.F. designed the study. S.W.F. conducted the field work, assembled the data, performed the analyses and wrote the first draft of the manuscript. A.H. contributed climate and plant richness data. S.W.F., M.S., A.H., K.M.H. and K.B.G. contributed to the final version of the manuscript.

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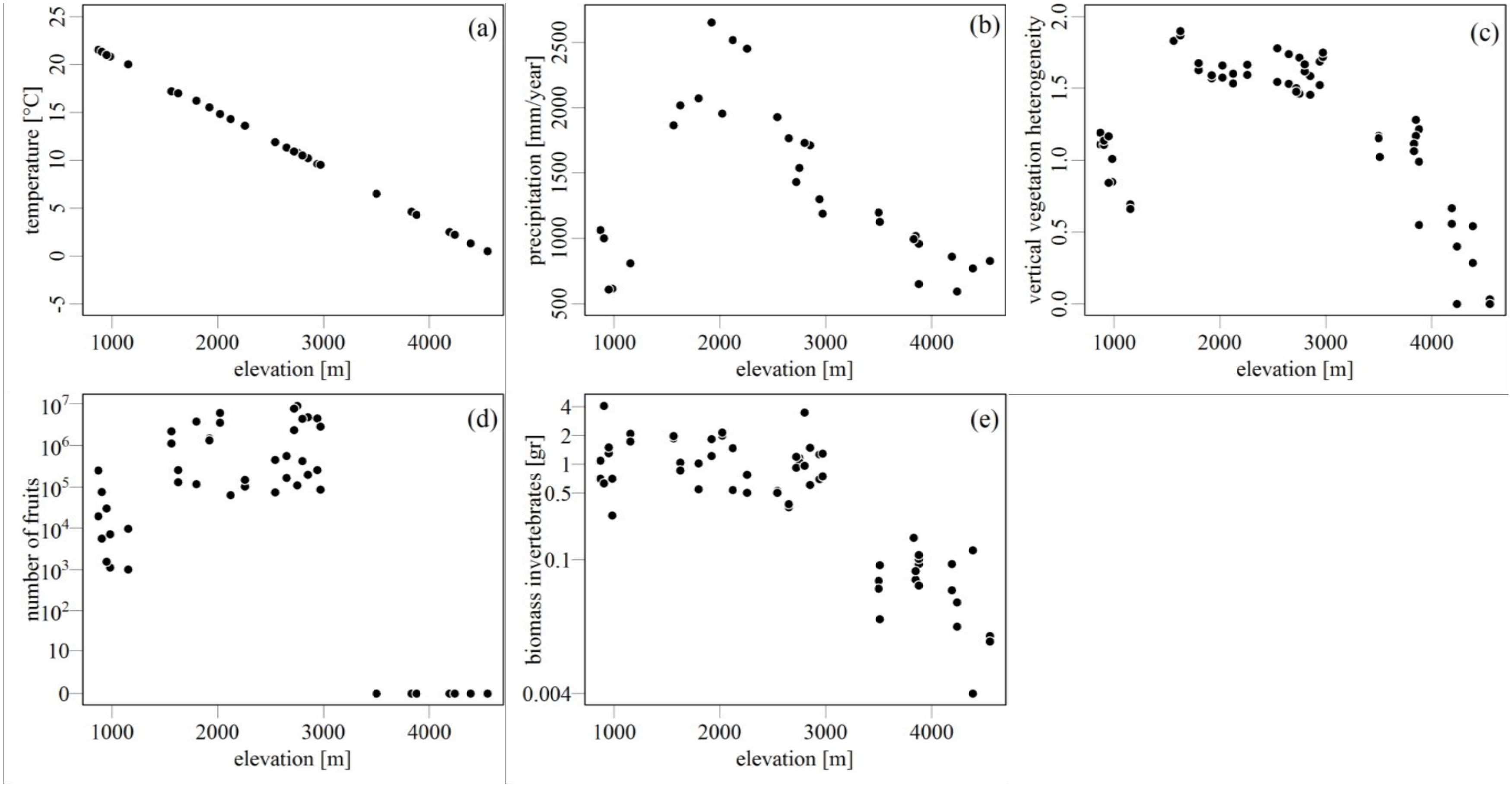
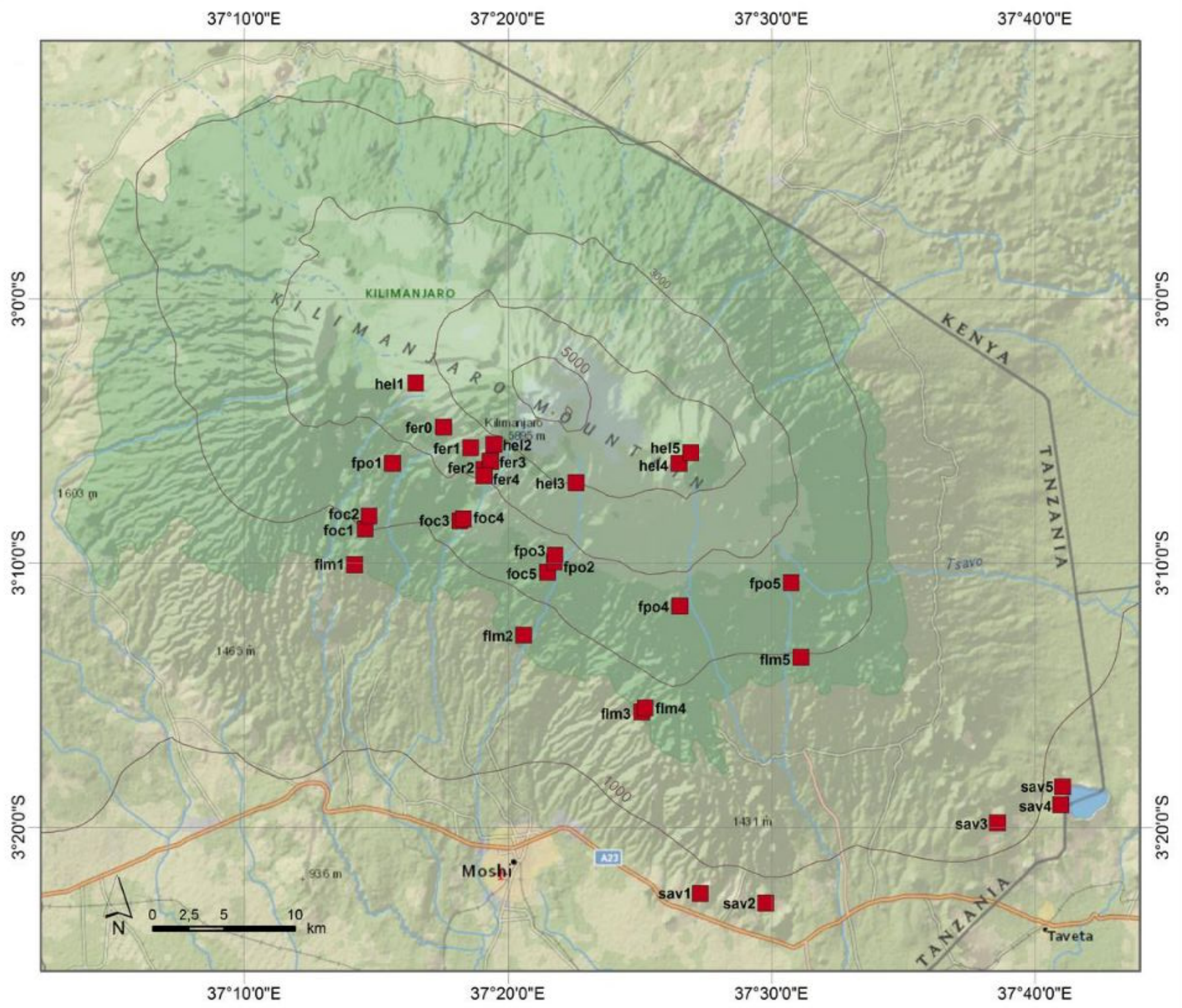
SUPPORTING INFORMATION

Appendix S1: Mean annual temperature (a), mean annual precipitation (b), vertical vegetation heterogeneity (c), number of fruits ((d), y-axis log-transformed) and biomass of invertebrates ((e), y-axis log-transformed) on thirty plots along an elevational gradient on Mt. Kilimanjaro. Each plot was sampled in two seasons. Note that slight noise (1/100 of axis length) has been introduced into the data to avoid completely overlapping points. See the methods for detailed description of sampling procedures.



Appendix S2: Map of Mount Kilimanjaro showing the location of the 30 study plots (sav = savannah, flm = lower montane forest, foc = *Ocotea* forest, fpo = *Podocarpus* forest, fer = *Erica* forest, hel = *Helichrysum* scrub). As background map, we used the National Geographic World Map developed by National Geographic and Esri (http://goto.arcgisonline.com/maps/NatGeo_World_Map).



Appendix S3: List of all 114 observed bird species, their migratory status (r = resident, p = Palearctic migrant, a = intra-African migrant), feeding guild (c = carnivorous [major food items consist of invertebrates + other animal material], f = frugivorous [major food items fruits; fruits + other plant material], g = granivorous [major food items only seeds; non-fruit plant material + seeds], i = insectivorous [major food item only invertebrates], o = omnivorous [major food items any animal material + any plant material], v = vertebrates [major food items only vertebrates and/or carrion], note that no species could be assigned as nectarivorous [major food item only nectar]) and the elevations of the lowest and highest plot at which the respective species was observed during the point counts. Species are ordered by feeding guilds first and taxonomy second.

					Elevation	
Common name	Scientific name	Family	Migrant	Food	min.	max.
Spotted Eagle-Owl	*Bubo africanus*	Strigidae	r	c	871	871
Von der Decken's Hornbill	*Tockus deckeni*	Bucerotidae	r	c	951	984
Scaly Francolin	*Francolinus squamatus*	Phasianidae	r	f	1800	1800
Eastern Bronze-naped Pigeon	*Columba delegorguei*	Columbidae	r	f	2020	2020
Olive Pigeon	*Columba arquatrix*	Columbidae	r	f	1560	2970
Tambourine Dove	*Turtur tympanistria*	Columbidae	r	f	1560	1560
Lemon Dove	*Aplopelia larvata*	Columbidae	r	f	1800	2020
Red-fronted Parrot	*Poicephalus gulielmi*	Psittacidae	r	f	2260	2260
Hartlaub's Turaco	*Tauraco hartlaubi*	Musophagidae	r	f	1560	2970
White-bellied Go-away-bird	*Corythaixoides leucogaster*	Musophagidae	r	f	951	951
Moustached Green Tinkerbird	*Pogoniulus leucomystax*	Capitonidae	r	f	1560	2020
Red-fronted Tinkerbird	*Pogoniulus pusillus*	Capitonidae	r	f	871	871
Spot-flanked Barbet	*Tricholaema lacrymosa*	Capitonidae	r	f	951	951
Common Bulbul	*Pycnonotus barbatus*	Pycnonotidae	r	f	871	1560
Mountain Greenbul	*Andropadus nigriceps*	Pycnonotidae	r	f	1623	2970
Stripe-cheeked Greenbul	*Andropadus milanjensis*	Pycnonotidae	r	f	1560	1920
Zanzibar Sombre Greenbul	*Andropadus importunus*	Pycnonotidae	r	f	871	871
Kenrick's Starling	*Poeoptera kenricki*	Sturnidae	r	f	1560	2260
Violet-backed Starling	*Cinnyricinclus leucogaster*	Sturnidae	a	f	871	906
Abbott's Starling	*Cinnyricinclus femoralis*	Sturnidae	r	f	2120	2970

Yellow-spotted Petronia	*Petronia pyrgita*	Passeridae	r	f	871	984
Emerald-spotted Wood-Dove	*Turtur chalcospilos*	Columbidae	r	g	871	984
Ring-necked Dove	*Streptopelia capicola*	Columbidae	r	g	951	951
Red-eyed Dove	*Streptopelia semitorquata*	Columbidae	r	g	951	951
Laughing Dove	*Streptopelia senegalensis*	Columbidae	r	g	871	951
Dusky Turtle Dove	*Streptopelia lugens*	Columbidae	r	g	2800	3880
Red-billed Quelea	*Quelea quelea*	Ploceidae	r	g	951	984
Abyssinian Crimsonwing	*Cryptospiza salvadorii*	Estrildidae	r	g	1920	1920
Red-cheeked Cordon-bleu	*Uraeginthus bengalus*	Estrildidae	r	g	871	1153
Red-billed Firefinch	*Lagonosticta senegala*	Estrildidae	r	g	871	951
Jameson's Firefinch	*Lagonosticta rhodopareia*	Estrildidae	r	g	906	906
Bronze Mannikin	*Lonchura cucullata*	Estrildidae	r	g	871	906
Yellow-fronted Canary	*Serinus mozambicus*	Fringillidae	r	g	906	1153
Yellow-crowned Canary	*Serinus canicollis*	Fringillidae	r	g	4550	4550
Yellow-rumped Seedeater	*Serinus reichenowi*	Fringillidae	r	g	871	1153
Oriole-Finch	*Linurgus olivaceus*	Fringillidae	r	g	2800	2850
Cinnamon-breasted Rock Bunting	*Emberiza tahapisi*	Emberizidae	r	g	871	1153
African Wood Owl	*Strix woodfordii*	Strigidae	r	i	2020	2020
Alpine Swift	*Apus melba*	Apodidae	r	i	3880	3880
Scarce Swift	*Schoutedenapus myoptilus*	Apodidae	r	i	2120	2120
Bar-tailed Trogon	*Apaloderma vittatum*	Trogonidae	r	i	1800	2970
Little Bee-eater	*Merops pusillus*	Meropidae	r	i	871	871
Red-billed Hornbill	*Tockus erythrorhynchus*	Bucerotidae	r	i	951	951
African Grey Hornbill	*Tockus nasutus*	Bucerotidae	r	i	871	1153
Greater Honeyguide	*Indicator indicator*	Indicatoridae	r	i	1560	1560
Nubian Woodpecker	*Campethera nubica*	Picidae	r	i	871	984
Olive Woodpecker	*Dendropicos griseocephalus*	Picidae	r	i	1560	1800
Rock Martin	*Hirundo fuligula*	Hirundinidae	r	i	906	906
Barn Swallow	*Hirundo rustica*	Hirundinidae	p	i	951	951

Black Saw-wing	*Psalidoprocne holomelas*	Hirundinidae	r	i	1560	2120
Mountain Wagtail	*Motacilla clara*	Motacillidae	r	i	1560	1623
Grassland Pipit	*Anthus cinnamomeus*	Motacillidae	r	i	906	906
Long-billed Pipit	*Anthus similis*	Motacillidae	r	i	906	1153
Cabanis's Greenbul	*Phyllastrephus cabanisi*	Pycnonotidae	r	i	1623	2800
Rüppell's Robin-Chat	*Cossypha semirufa*	Turdidae	r	i	2020	2020
Common Rock-Thrush	*Monticola saxatilis*	Turdidae	p	i	984	984
Spotted Morning-Thrush	*Cichladusa guttata*	Turdidae	r	i	871	906
Alpine Chat	*Cercomela sordida*	Turdidae	r	i	3510	4550
Mountain Yellow Warbler	*Chloropeta similis*	Sylviidae	r	i	2720	2800
Cinnamon Bracken Warbler	*Bradypterus cinnamomeus*	Sylviidae	r	i	1623	2970
Evergreen Forest Warbler	*Bradypterus lopezi*	Sylviidae	r	i	1560	2970
Willow Warbler	*Phylloscopus trochilus*	Sylviidae	p	i	1920	1920
Brown Woodland Warbler	*Phylloscopus umbrovirens*	Sylviidae	r	i	1560	3880
Red-faced Crombec	*Sylvietta whytii*	Sylviidae	r	i	871	984
Winding Cisticola	*Cisticola galactotes*	Sylviidae	r	i	984	984
Hunter's Cisticola	*Cisticola hunteri*	Sylviidae	r	i	3510	4190
Tawny-flanked Prinia	*Prinia subflava*	Sylviidae	r	i	871	871
Grey-backed Camaroptera	*Camaroptera brachyura*	Sylviidae	r	i	1560	1560
Grey Wren-Warbler	*Calamonastes simplex*	Sylviidae	r	i	871	984
Yellow-breasted Apalis	*Apalis flavida*	Sylviidae	r	i	871	906
Black-headed Apalis	*Apalis melanocephala*	Sylviidae	r	i	1560	2020
Bar-throated Apalis	*Apalis thoracica*	Sylviidae	r	i	2020	2020
White-eyed Slaty Flycatcher	*Melaenornis fischeri*	Muscicapidae	r	i	1623	1623
African Grey Flycatcher	*Bradornis microrhynchus*	Muscicapidae	r	i	951	984
African Dusky Flycatcher	*Muscicapa adusta*	Muscicapidae	r	i	1560	2970
Chin-spot Batis	*Batis molitor*	Platysteiridae	r	i	871	1623
Forest Batis	*Batis mixta*	Platysteiridae	r	i	1560	1800
African Paradise-flycatcher	*Terpsiphone viridis*	Monarchidae	r	i	871	2020

Blue-mantled Crested-flycatcher	*Trochocercus cyanomelas*	Monarchidae	r	i	1800	2020
African Hill-Babbler	*Pseudoalcippe abyssinica*	Timaliidae	r	i	1800	2020
Arrow-marked Babbler	*Turdoides jardineii*	Timaliidae	r	i	906	906
Abyssinian White-eye	*Zosterops abyssinicus*	Zosteropidae	r	i	871	906
Common Fiscal	*Lanius collaris*	Laniidae	r	i	871	871
Black-crowned Tchagra	*Tchagra senegala*	Malaconotidae	r	i	871	984
Brown-crowned Tchagra	*Tchagra australis*	Malaconotidae	r	i	871	871
Sulphur-breasted Bush-shrike	*Malaconotus sulfureopectus*	Malaconotidae	r	i	871	871
Black-fronted Bush-shrike	*Malaconotus nigrifrons*	Malaconotidae	r	i	1560	2020
Northern White-crowned Shrike	*Eurocephalus rueppelli*	Prionopidae	r	i	951	984
White-crested Helmet-shrike	*Prionops plumatus*	Prionopidae	r	i	951	951
Fork-tailed Drongo	*Dicrurus adsimilis*	Dicruridae	r	i	871	871
Red-billed Buffalo-Weaver	*Bubalornis niger*	Ploceidae	r	i	951	951
Baglafecht Weaver	*Ploceus baglafecht*	Ploceidae	r	i	871	871
Crested Francolin	*Francolinus sephaena*	Phasianidae	r	o	951	951
Flappet Lark	*Mirafra rufocinnamomea*	Alaudidae	r	o	984	1153
Northern Brownbul	*Phyllastrephus strepitans*	Pycnonotidae	r	o	1920	2020
White-starred Robin	*Pogonocichla stellata*	Turdidae	r	o	1560	2970
Olive Thrush	*Turdus olivaceus*	Turdidae	r	o	1560	2970
Common Whitethroat	*Sylvia communis*	Sylviidae	p	o	871	871
Blackcap	*Sylvia atricapilla*	Sylviidae	p	o	1800	2720
Montane White-eye	*Zosterops poliogaster*	Zosteropidae	r	o	1560	3849
Scarlet-tufted Malachite Sunbird	*Nectarinia johnstoni*	Nectariniidae	r	o	3830	3880
Eastern Double-collared Sunbird	*Nectarinia mediocris*	Nectariniidae	r	o	2540	2970
Amethyst Sunbird	*Nectarinia amethystina*	Nectariniidae	r	o	871	906
Olive Sunbird	*Nectarinia olivacea*	Nectariniidae	r	o	1560	2850
Scarlet-chested Sunbird	*Chalcomitra senegalensis*	Nectariniidae	r	o	871	906
Hunter's Sunbird	*Chalcomitra hunteri*	Nectariniidae	r	o	871	984
Variable Sunbird	*Cinnyris venusta*	Nectariniidae	r	o	871	906

Waller's Starling	*Onychognathus walleri*	Sturnidae	r	o	1560	2750
Lesser Masked Weaver	*Ploceus intermedius*	Ploceidae	r	o	906	906
Grey-headed Negrofinch	*Nigrita canicapilla*	Estrildidae	r	o	1560	1800
Village Indigobird	*Vidua chalybeata*	Estrildidae	r	o	906	906
Somali Golden-breasted Bunting	*Emberiza poliopleura*	Emberizidae	r	o	906	906
Mountain Buzzard	*Buteo oreophilus*	Accipitridae	r	v	1920	2970
Long-crested Eagle	*Lophaetus occipitalis*	Accipitridae	r	v	1800	1800

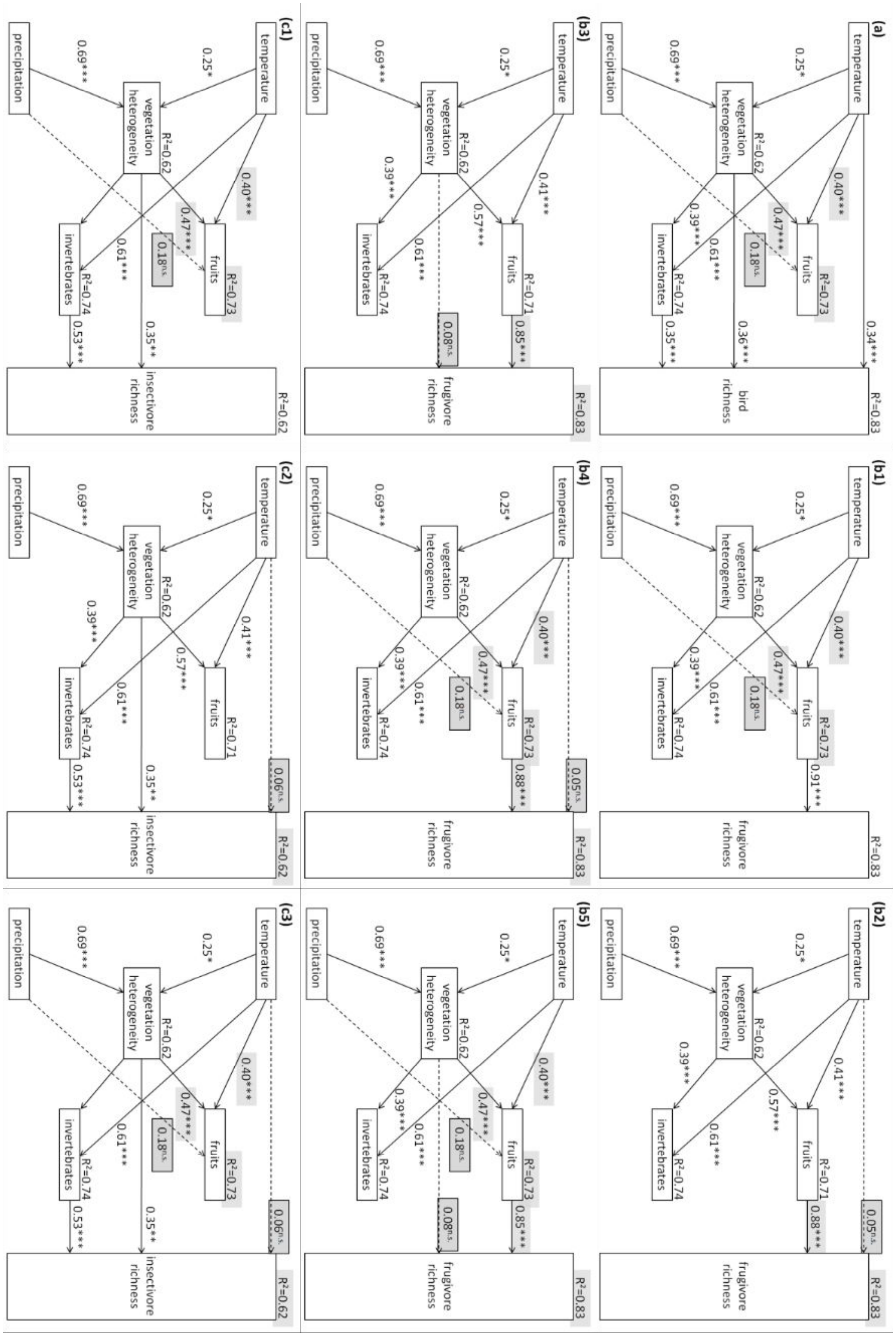
Appendix S4: Variable pre-selection within groups (climatic factors, vegetation structure, food resources), based on our ecological understanding of the study system and the strength of the relationship between predictor variables and overall bird species richness, as estimated by marginal R^2 values (Nakagawa & Schielzeth, 2013) from simple linear mixed effect models (LMMs) with plot as random factor. Given are the standardized effects of all predictor variables on overall bird species richness (log-transformed) as derived from simple linear mixed effect models with plot as random effect, p-values (corrected for multiple testing (Holm, 1979)), the coefficient of determination (R^2) and the variance inflation factors in the set of all (VIFall) and in the subset of pre-selected (VIFselect) predictor variables.

predictor	standardized estimate	standardized se	t	p	marginal R^2	VIF_{all}	VIF_{select}
climatic factors							
season	0.03	0.04	0.95	0.345	<0.01	1.17	
temperature	0.78	0.11	6.88	<0.001	0.59	4.35	2.75
precipitation	0.53	0.16	3.43	0.003	0.27	4.69	2.62
vegetation structure							
vegetation heterogeneity	0.66	0.11	6.12	<0.001	0.49	11.83	3.66
logit(canopy closure)	0.52	0.14	3.73	0.002	0.29	13.73	
sqrt(canopy height)	0.65	0.13	5.12	<0.001	0.44	9.67	
food resources							
log(fruits)	0.76	0.09	8.06	<0.001	0.63	7.09	6.17
log(flowers)	0.04	0.07	0.66	0.690	<0.01	1.59	
log(biomass invertebrates)	0.74	0.08	9.60	<0.001	0.67	6.77	6.24

Appendix S5: Moran’s I values based on the residuals of the best-fit LMMs and a spatial weights matrix from the four nearest neighbors of each study plot. P-values are based on a permutation test with 1000 permutations. Results are qualitatively the same when using only the one, two or three nearest neighbors.

response	Moran's I	p
vegetation heterogeneity	0.021	0.653
log(fruits)	0.027	0.584
log(biomass invertebrates)	0.067	0.316
log(all birds)	-0.009	0.878
log(frugivores)	-0.035	0.974
log(insectivores)	0.013	0.712

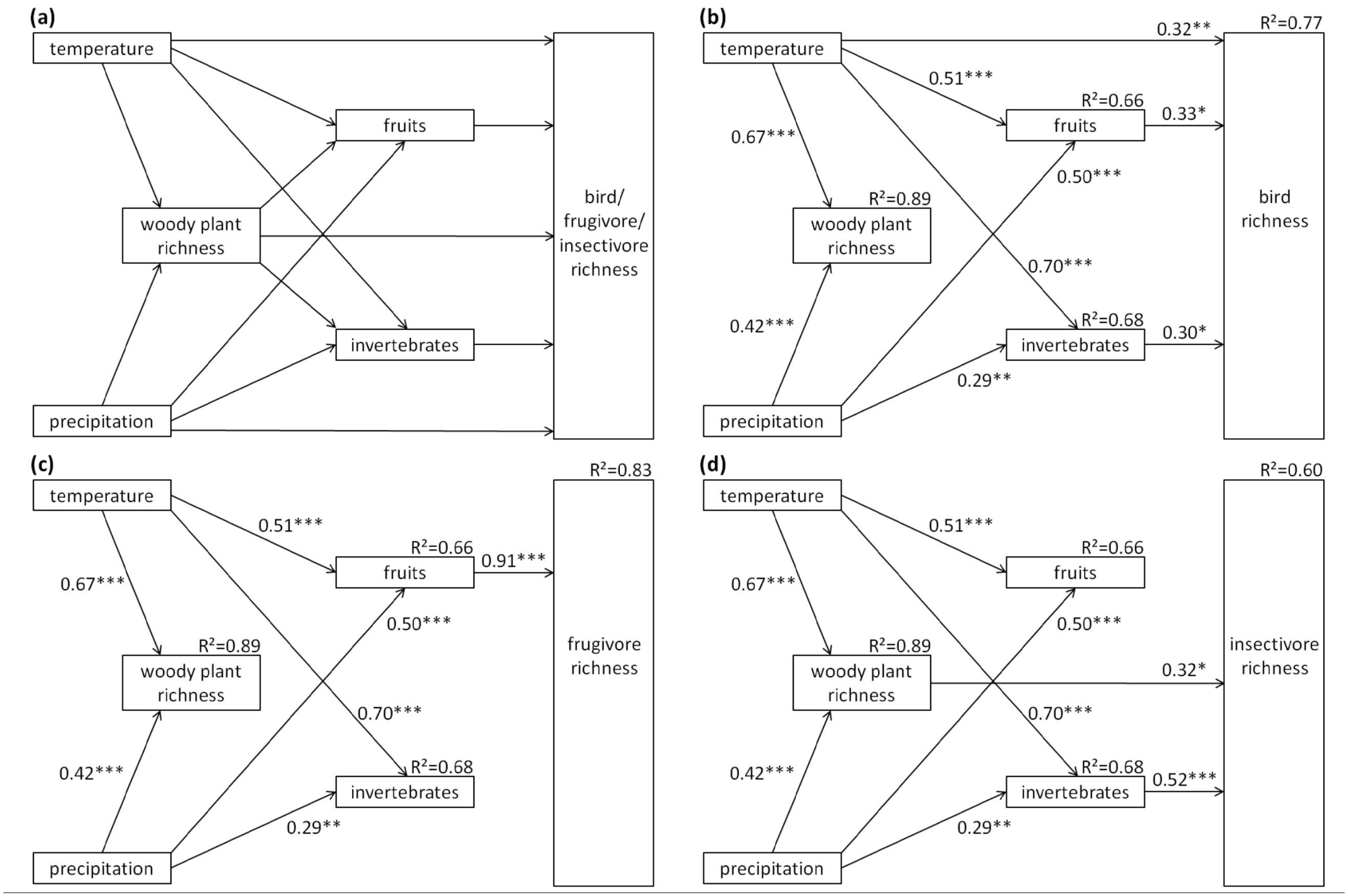
Appendix S6.1: Alternative path models for all birds (a), frugivorous birds (b) and insectivorous birds (c) that consist of LMMs with a Δ AICc < 2 compared to the best-fit LMMs presented in Fig. 2. Given are standardized path coefficients, their statistical significance ($^{+}$ $p < 0.1$, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$) and the coefficients of determination (R^2). For clarity, error terms and the correlation of errors of fruits and invertebrates are not shown. Additional paths (compared to the path models in Fig. 2) are dashed and their path coefficients are presented in a black-framed box with grey shading. Path coefficients and R^2-values that have been altered due to the inclusion of additional paths are presented with grey shading (but no black box). Note that all additional paths of the alternative models are non-significant and that the explained variance in bird species richness is not higher than in the more parsimonious models in Fig. 2 (changes in R^2 are in the 3rd or 4th decimal place). All alternative models that affect bird species richness have a significantly worse fit to the data than the best-fit models in Fig. 2, i.e. the models b2-b5, c2 and c3 (see Appendix S6.2).


(a)
temperature
precipitation
vegetation heterogeneity
R^2=0.62
fruits
R^2=0.73
invertebrates
R^2=0.74
bird richness
R^2=0.83
0.25*
0.69***
0.40***
0.47***
$0.18^{n.s.}$
0.39***
0.61***
0.36***
0.34***
0.35***
(b1)
temperature
precipitation
vegetation heterogeneity
R^2=0.62
fruits
R^2=0.73
invertebrates
R^2=0.74
frugivore richness
R^2=0.83
0.25*
0.69***
0.40***
0.47***
$0.18^{n.s.}$
0.39***
0.61***
0.91***
(b2)
temperature
precipitation
vegetation heterogeneity
R^2=0.62
fruits
R^2=0.71
invertebrates
R^2=0.74
frugivore richness
R^2=0.83
0.25*
0.69***
0.41***
0.57***
0.39***
0.61***
0.88***
$0.05^{n.s.}$
(b3)
temperature
precipitation
vegetation heterogeneity
R^2=0.62
fruits
R^2=0.71
invertebrates
R^2=0.74
frugivore richness
R^2=0.83
0.25*
0.69***
0.41***
0.57***
0.39***
0.61***
0.85***
$0.08^{n.s.}$
(b4)
temperature
precipitation
vegetation heterogeneity
R^2=0.62
fruits
R^2=0.73
invertebrates
R^2=0.74
frugivore richness
R^2=0.83
0.25*
0.69***
0.40***
0.47***
$0.18^{n.s.}$
0.39***
0.61***
0.88***
$0.05^{n.s.}$
(b5)
temperature
precipitation
vegetation heterogeneity
R^2=0.62
fruits
R^2=0.73
invertebrates
R^2=0.74
frugivore richness
R^2=0.83
0.25*
0.69***
0.40***
0.47***
$0.18^{n.s.}$
0.39***
0.61***
0.85***
$0.08^{n.s.}$
(c1)
temperature
precipitation
vegetation heterogeneity
R^2=0.62
fruits
R^2=0.73
invertebrates
R^2=0.74
insectivore richness
R^2=0.62
0.25*
0.69***
0.40***
0.47***
$0.18^{n.s.}$
0.61***
0.35**
0.53***
(c2)
temperature
precipitation
vegetation heterogeneity
R^2=0.62
fruits
R^2=0.71
invertebrates
R^2=0.74
insectivore richness
R^2=0.62
0.25*
0.69***
0.41***
0.57***
0.39***
0.61***
0.35**
0.53***
$0.06^{n.s.}$
(c3)
temperature
precipitation
vegetation heterogeneity
R^2=0.62
fruits
R^2=0.73
invertebrates
R^2=0.74
insectivore richness
R^2=0.62
0.25*
0.69***
0.40***
0.47***
$0.18^{n.s.}$
0.61***
0.35**
0.53***
$0.06^{n.s.}$

Appendix S6.2: Overall fit of the best-fit path models (Fig. 2 in the manuscript) and the alternative path models (see Appendix S6.1) based on Shipley's generalized d-sep test for path models with correlated errors (χ^2 test statistic, degrees of freedom, p-values; (Shipley, 2003, 2009)) and AICc values (Shipley, 2013). Note that the structure of all alternative path models does not deviate significantly from the structure in the data (non-significant p-values), but that they fit the data consistently worse than the more parsimonious best-fit models (larger AICc for all alternative models). All alternative models that affect bird species richness as response variable have a significantly worse fit to the data than the best-fit models in Fig. 2, i.e. the models b2-b5, c2 and c3 (see Appendix S6.1). Models are ordered by Δ AICc.

Additional paths compared to the best fit models in Fig. 2	figure	χ^2	df	p	AICc	Δ AICc
All birds						
best-fit model	2b	5.76	8	0.674	72.08	0.00
precipitation-fruits	S5a	2.00	6	0.920	73.35	1.28
Frugivorous birds						
best-fit model	2c	10.57	12	0.566	67.57	0.00
precipitation-fruits	S5b1	6.81	10	0.743	68.35	0.78
temperature-frugivore richness	S5b2	8.10	10	0.618	69.64	2.07
vegetation heterogeneity-frugivore richness	S5b3	8.42	10	0.587	69.96	2.39
precipitation-fruits, temperature-frugivore richness	S5b4	4.35	8	0.825	70.66	3.09
precipitation-fruits, vegetation heterogeneity-frugivore richness	S5b5	4.66	8	0.793	70.98	3.41
Insectivorous birds						
best-fit model	2d	8.28	10	0.602	69.82	0.00
precipitation-fruits	S5c1	4.51	8	0.808	70.83	1.01
temperature-insectivore richness	S5c2	6.47	8	0.595	72.79	2.97
precipitation-fruits, temperature-insectivore richness	S5c3	2.71	6	0.845	74.06	4.24

Appendix S7: *A priori* hypothesized causal structure (a) of the relationships among climatic factors (temperature and precipitation), woody plant species richness (log-transformed; recorded on the 30 0.25-ha study plots of the KiLi project described in the methods), food resources (fruits and invertebrates, both log-transformed) and bird species richness (log-transformed); and the best-fit path models (based on AICc) for all birds (b), frugivorous birds (c) and insectivorous birds (d). Given are standardized path coefficients, their statistical significance ($^{+}$ $p < 0.1$, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$) and the coefficients of determination (R^2). Paths that did not contribute to the best-fit models have been deleted in (b), (c) and (d). For clarity, error terms and the correlation of errors of fruits and invertebrates are not shown. All path models yield a good fit to the data (overall richness: $\chi^2 = 7.38$, df = 8, p = 0.496; frugivore richness: $\chi^2 = 7.64$, df = 12, p = 0.813; insectivore richness: $\chi^2 = 4.51$, df = 10, p = 0.921).


(a)
temperature
woody plant richness
fruits
invertebrates
precipitation
bird/ frugivore/ insectivore richness
(b)
temperature
0.32**
R²=0.77
0.51***
R²=0.66
0.33*
0.67***
0.50***
R²=0.89
woody plant richness
fruits
bird richness
0.70***
R²=0.68
0.42***
invertebrates
0.30*
0.29**
precipitation
(c)
temperature
R²=0.83
0.51***
R²=0.66
0.91***
fruits
0.67***
0.50***
R²=0.89
woody plant richness
frugivore richness
0.70***
0.42***
R²=0.68
invertebrates
0.29**
precipitation
(d)
temperature
R²=0.60
0.51***
R²=0.66
fruits
0.67***
0.50***
R²=0.89
woody plant richness
0.32*
insectivore richness
0.70***
0.42***
R²=0.68
invertebrates
0.52***
0.29**
precipitation

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