Predicting continental-scale patterns of bird species richness with spatially explicit models

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The causes of global variation in species richness have been debated for nearly two centuries with no clear resolution in sight. Competing hypotheses have typically been evaluated with correlative models that do not explicitly incorporate the mechanisms responsible for biotic diversity gradients. Here, we employ a fundamentally different approach that uses spatially explicit Monte Carlo models of the placement of cohesive geographical ranges in an environmentally heterogeneous landscape. These models predict species richness of endemic South American birds (2248 species) measured at a continental scale. We demonstrate that the principal single-factor and composite (species-energy, water-energy and temperature-kinetics) models proposed thus far fail to predict ($r^2 \leqslant 0.05$) the richness of species with small 01.8(sl35Tm[(tTJ-30.38731.83873409.8t[(smontroia)]TTD[(scip2an3rxplic7Tm[gn3r]TJfirtradl6(33425.1401505.

Digital Elevation Model (http://www.ngdc.noaa.gov/mgg/topo/globe.html). Maximum elevation was truncated at the observed snowline (1200–5700 m), which varies as a complex function of environmental variables, including latitude and precipitation. No non-marine bird species recorded in South America is known to breed on glaciers, ice or in snowfields.

(iv) Map cell surface area

Area was calculated as the land surface area within each $1° \times 1°$ latitudinal–longitudinal map cell. We retained coastal cells in the analyses because they include a significant fraction of

(iii) Temperature-kinetics model

Allen et al. (2002) derived, from first principles, a model of species richness as a function of temperature. Although their model was designed specifically for ectotherms, it may be appropriate for birds as well because the relationship between

Table 1. Explanatory models for species richness of endemic birds of South America (n = 2248). Rows represent environmental models and columns represent species range quartiles and stochastic range placement procedures (RS, range scatter model; RC, range cohesion model). In each table cell, the first entry is the simple r^2 value for the correlation between observed and predicted species richness. The second entry is the slope of the relationship, based on an appropriately fitted spatial autocorrelation model (see Rangel et al. (2006) and supplementary table 1 in the electronic supplementary material for full model details). A successful model should explain a significant proportion of the variation in species richness and have a slope that is close to 1.0. Unshaded cells indicate non-explanatory models, for which the r^2-value does not differ significantly from 0, based on the effective number of degrees of freedom using Dutilleul's method to adjust for spatial autocorrelation (Dutilleul 1993). Light grey cells indicate models for which the r^2-value was significantly different from 0, but for which the 95% confidence interval of the slope for the best-fitting spatial model did not bracket 1.0. (Note that some models in this category have negative slopes.) Dark grey cells (which have italic type) indicate models for which both the r^2

America (531 533 cell records for 2891 species). Finally, we partitioned the species pool into subsets of species based on their range size (first through fourth quartiles of ranked ranges) and repeated all analyses for each quartile. See electronic supplementary material for a detailed description of statistical analysis.

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When all species are considered together, the regressions attribute substantial explanatory power to all six climatic models (precipitation, temperature, NPP, species-energy, water-energy and temperature-kinetics; $0.24 \leqslant r^2 \leqslant 0.46$, table 1, all quartiles column). Similar correlations between climatic factors and species richness are typical of continental studies conducted at comparable spatial resolutions (1° or 2° latitude–longitude cells; Currie 1991; Rahbek & Graves 2001; Jetz & Rahbek 2002; Hawkins et al. 2003; Currie et al. 2004; Ruggiero & Kitzberger 2004; Kreft et al. 2006). At our scale of analysis, the three models related to spatial heterogeneity (surface area, ecosystem diversity and topographic relief) and the pure geometric constraints model were less successful than climate-based models in explaining aggregate species richness ($0.00 \leqslant r^2 \leqslant 0.27$, table 1, all quartiles column).

The predictive power of our climate-based models was not sustained, however, when the species pool was partitioned into quartiles of species' geographical range sizes (first quartile, smallest ranges; fourth quartile, largest ranges). For the first three range-size quartiles (all but the largest ranges), all models based on climate variables (precipitation, temperature, NPP, species-energy, water-energy and temperature-kinetics), as well as those based on geometric constraints and surface area, failed completely
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For first quartile species, the accumulation of species richness with topographic relief (as measured by elevational range) was significantly steeper than our models predicted (slope > 1.0; table 1). For second quartile species, the model based on topographic relief accurately predicted species richness, whereas, for third and fourth quartiles, the models based on topographic relief and ecosystem diversity overestimated species richness.

A previous correlative analysis of African birds also found that the effects of productivity decreased and topographic heterogeneity increased at small range sizes (Jetz & Rahbek 2002). However, our study is the first to document a complete lack of correlation between species richness and the predictions of climate-based models for all but the largest-ranged species.

4. DISCUSSION

Our results and those of some previous analyses (Jetz & Rahbek 2001, 2002; Lennon et al. 2004; Ruggiero & Kitzberger 2004; Kreft et al. 2006) suggest that statistical associations between total species richness and environmental predictor variables may be misleading owing to the dominating influence of widespread species. The geographical distribution of South American bird species with the largest geographical ranges (fourth quartile) was successfully explained only by the version of the water-energy model that incorporates geographical range cohesion as well as precipitation, temperature and NPP (table 1). In contrast, all models based on contemporary climate variables were unsuccessful in predicting species richness of taxa with smaller ranges (first to third quartiles). These results are not artefacts of sample size dilution caused by range size partitioning (tables 2 and 4 in the electronic supplementary material). Species with relatively small geographical ranges constitute the bulk of the South American avifauna, and they contribute heavily to the peaks of species richness observed in the Andes and

linear geographical ranges and disjunct habitat distributions (Vuilleumier & Simberloff 1980; Graves 1985, 1988; Fjeldså 1995; Rahbek & Graves 2001). At the continental scale, the large residual variance (more than 97% for the first three range-size quartiles) generated by our contemporary climate models (table 1) may reflect historical events associated with the Pleistocene–Holocene distribution and diversity of habitats (Haffer 1969) as well

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