LETTER

Energy, range dynamics and global species richness patterns: reconciling mid-domain effects and environmental determinants of avian diversity

David Storch,[1,2]* Richard G. Davies,[3] Samuel Zajíček,[1] C. David L. Orme,[4] Valerie Olson,[5] Gavin H. Thomas,[6] Tzung-Su Ding,[7] Pamela C. Rasmussen,[8] Robert S. Ridgely,[9] Peter M. Bennett,[5] Tim M. Blackburn,[6] Ian P. F. Owens[4,10] and Kevin J. Gaston[3]

Abstract

Spatial patterns of species richness follow climatic and environmental variation, but could reflect random dynamics of species ranges (the mid-domain effect, MDE). Using data on the global distribution of birds, we compared predictions based on energy availability (actual evapotranspiration, AET, the best single correlate of avian richness) with those of range dynamics models. MDE operating within the global terrestrial area provides a poor prediction of richness variation, but if it operates separately within traditional biogeographic realms, it explains more global variation in richness than AET. The best predictions, however, are given by a model of global range dynamics modulated by AET, such that the probability of a range spreading into an area is proportional to its AET. This model also accurately predicts the latitudinal variation in species richness and variation of species richness both within and between realms, thus representing a compelling mechanism for the major trends in global biodiversity.

Keywords

Biogeography, climate–richness relationship, hotspots, latitudinal gradient of diversity, mid-domain effect, more-individuals hypothesis, mountains, productivity, spatial models, species–energy relationship.

INTRODUCTION

Species richness is not distributed equally across the Earth's surface. The most prominent pattern is its decrease from the tropics toward the poles, the latitudinal gradient of richness. There are currently several dozen hypotheses to explain this trend, but only a small minority has any empirical support (Willig *et al*. 2003). One of the most promising is the idea that the species richness of various taxa is controlled by climate (Hawkins *et al*. 2003; Currie *et al*. 2004). Indeed, climatic factors are argued to be the most widely supported predictors of species richness both within and between different regions (Francis & Currie 2003). The causal mechanisms leading from climate to species richness are still hotly debated (Currie *et al*. 2004; Evans *et al*. 2005; Clarke & Gaston 2006). In particular, two alternative forms of available energy have been recognized as being potentially important. Ambient or solar energy, usually quantified in

[1]*Center for Theoretical Study, Charles University, Jilská 1, 110 00 Praha 1, Czech Republic*
[2]*Department of Ecology, Faculty of Science, Charles University, Viničná 7, 128 44 Praha 2, Czech Republic*
[3]*Biodiversity and Macroecology Group, Department of Animal and Plant Sciences, University of Sheffield, Sheffield S10 2TN, UK*
[4]*Division of Biology, Imperial College London, Silwood Park, Ascot, Berkshire SL5 7PY, UK*
[5]*Institute of Zoology, Zoological Society of London, Regent's Park, London NW1 4RY, UK*
[6]*School of Biosciences, University of Birmingham, Edgbaston, Birmingham B15 2TT, UK*
[7]*School of Forestry & Resource Conservation, National Taiwan University, 1, Sec 4, Roosevelt Road, Taipei 106, Taiwan*
[8]*Michigan State University Museum, West Circle Drive, East Lansing, Michigan 48824–1045, USA*
[9]*Academy of Natural Sciences, 1900 Benjamin Franklin Parkway, Philadelphia, PA 19103, USA*
[10]*NERC Centre for Population Biology, Imperial College London, Silwood Park, Ascot, Berkshire SL5 7PY, UK*
Correspondence: E-mail: storch@cts.cuni.cz

terms of temperature, is thought to influence species richness distribution via its effects on the rates of biological processes including speciation (Rohde 1992, Allen *et al.* 2002). Productive energy is an estimate of energy available for use by plants in primary production of biomass, ultimately limiting the energy flowing through food-webs and hence the population growth of species (Waide *et al.* 1999; Mittelbach *et al.* 2001). According to the most recent developments of the 'species–energy theory', productivity may positively affect the total number of individuals (and consequently species) within an area, whereas temperature affects how this number of individuals is divided among species (Allen *et al.* in press). Of these two energy forms, productive energy has been argued to be the most general descriptor of broad-scale diversity gradients (Turner & Hawkins 2004).

Contemporary environmental factors do not, however, represent the only possible explanation of species richness patterns. These patterns are also the result of historical influences on the formation of the biotas of different regions, via the spatiotemporal dynamics of the geographic ranges of individual species. In an extreme case, it is even possible that such dynamics are themselves sufficient to produce the patterns observed without the need to invoke the role of environmental factors. Range dynamics are naturally constrained by the location and shape of land-masses, and thus species with large ranges will necessarily reach the central areas of respective land domains. Consequently, species richness should be higher there than in areas which are more distant from the domain centres. This so-called mid-domain effect (MDE) (Colwell & Hurtt 1994; Colwell & Lees 2000) has recently been proposed as a null explanation of spatial patterns of diversity, and in some cases has been shown to predict observed patterns quite well (Lees *et al.* 1999; Jetz & Rahbek 2001, 2002; Colwell *et al.* 2004; Bellwood *et al.* 2005). There is, however, continuing unresolved controversy concerning the extent to which this process is realistic (Koleff & Gaston 2001; Zapata *et al.* 2003, 2005; Colwell *et al.* 2005; Hawkins *et al.* 2005). Part of this controversy arises from the uncertainty in the domain definition – what is the area within which we can assume the process of random range dynamics? If we assume random range dynamics within areas delimited on the basis of prevailing ecological conditions, for instance biomes, the model would already contain quite substantial information about the environment, and the predicted species richness patterns would necessarily be a consequence both of the process itself and the climatic (or other) factors which determine the distribution of environmental conditions across the Earth's surface. The more detailed the delimitation of domains within which the process acts, the closer is the predicted pattern to the observed one, simply because the occurrence of particular species (and the

distribution of their range sizes) within the domains is always assumed *a priori*. On the other hand, very broad delimitation of domains will guarantee much weaker predictions, as it is unrealistic to assume that every species can occur and spread anywhere.

These issues are related to the ongoing discussion concerning the role of idiosyncratic regional effects on species richness. At one extreme is the claim that the total species richness within a particular region is uniquely determined by historical contingencies, and that without accounting for evolutionary history we cannot understand the difference in species richness between different regions (e.g. Latham & Ricklefs 1993; Qian & Ricklefs 1999). At the other pole of the debate is the suggestion that contemporary ecological conditions constrain local and regional species richness such that regional differences may be predicted from these conditions alone (Francis & Currie 2003). Since the former viewpoint resigns from an attempt to explain inter-regional differences on the basis of universally valid, globally consistent principles, it justifies using individual regions (biogeographic realms, continents, biomes or other biologically relevant units – note that the problem of delimitation of these units remains) as given, and trying to explain species richness differences within these units from different principles, including MDEs. On the other hand, if local ecological (e.g. climatic) constraints are essential and globally universal, we should be able to explain species richness patterns without accounting for the historical and geographic settings of different regions.

Of course, explanations of species richness patterns based on climatic and energetic environmental variables on the one hand, and on range dynamics within delimited domains on the other, are not necessarily mutually exclusive. There is a third possibility, namely that range dynamics are not completely random and constrained only by hard domain boundaries, but that the spatial dynamics of each species' range is itself also modulated by climatic factors. These dynamics then could act globally, i.e. without considering any internal domain limits based on ecological conditions, and still could produce differences among regions, simply because the modulating environmental factors themselves differ.

We have tested this idea using one of the most comprehensive data sets on the distribution of a single major taxon, that on the global distribution of all terrestrial bird species (see Orme *et al.* 2005, 2006). Global bird species richness patterns are apparently attributable to many ecological and evolutionary processes differing in their importance according to spatial scale and species properties (Rahbek & Graves 2001; Jetz & Rahbek 2002). However, since bird species richness is widely shown to be strongly associated with energy availability, we assume that this complexity could be encompassed by a simple process

comprising an important feature of species dynamics, namely that the probability of species occurrence is proportional to productivity. Clearly, speciation, as well as range dynamics and local extinction are all affected by many factors other than productivity, but if productivity influences species presence in the course of all these processes, global species richness patterns related to productivity could be reproduced by a simple range dynamics model with simplified assumptions.

We will show that the global model of range dynamics modulated by environmental productivity explains as much variance in species richness as does the pure MDE constrained by the boundaries of individual biogeographic realms, and predicts reasonably well the species richness variation both between and within individual realms. Moreover, this dynamic model generally provides better predictions of species richness variation than the pure effect of productivity, with implications for our understanding of the mechanisms underpinning the observed relationship between species richness and productivity. This process is suitable for use as a null hypothesis of species richness patterns, with the residuals being informative and important in indicating other key environmental gradients.

MATERIAL AND METHODS

Species data

The analyses presented here are based on a previously reported database (Orme *et al.* 2005) of distribution maps for 9626 extant, recognized bird species constructed using a variety of published sources (for details of sources and methodology see Orme *et al.* 2006). Briefly, breeding ranges from the published sources were mapped as vectors or 'polygons' and converted to an equal area grid for analysis. The grid used a Behrmann projection at a cell resolution of 96 486.2 m. This grid cell size is equivalent to 1° longitude and 1° latitude at 30° latitude N/S (1/360th of the width of the globe under a Behrmann projection using the WGS84 datum). The global grid therefore contains 360 by 152 cells, omitting the partial cells at latitudes higher than 87.13°. Species were scored as present in a grid cell if any of the available sources indicated that the breeding range fell within the cell boundaries. Biogeographic realms were delimited using the World Wildlife Fund ecoregions map (Nearctic, Palaearctic, Neotropical, Afrotropical, Oriental and Australasian) (Olson *et al.* 2001).

Environmental data

For each 1° grid cell, we obtained values of three measures of productive energy, namely: actual evapotranspiration (AET) (University of Delaware Global Climate Resource

Pages, available at http://climate.geog.udel.edu/~climate/html_pages/download.html); the normalized difference vegetation index (NDVI, The International Satellite Land-Surface Climatology Project (ISLSCP) Initiative II Data Archive (2004) available at http://islscp2.sesda.com/ISLSCP2_1/html_pages/groups/veg/fasir_ndvi_monthly_xdeg.html; see also Kerr & Ostrovsky 2003); and net primary productivity (NPP, Cramer *et al.* 1999). Annual measures were used in all cases. These data were resampled to the same equal-area projection and resolution as the species data (above). From the data set, we excluded land-areas falling within the Antarctic and Oceanian realms, due to lack of environmental data. However, we retained islands assigned to the six remaining biogeographic realms (see Fig. 1).

Having determined that AET was the best single correlate of bird species richness across the globe ($r = 0.714$, see Fig. 2a), and is strongly correlated to NPP ($r = 0.912$), we chose this variable as the factor modulating species range dynamics. In fact, we performed all the analyses using all three measures, but the results were not qualitatively different. Slightly worse results were obtained by using NDVI rather than AET or NPP, which is apparently related to a lower correlation of NDVI with species richness ($r = 0.650$), as well as with both AET and NPP ($r = 0.834$ and $r = 0.838$, respectively).

Models

We simulated both the random dynamics of species ranges and the dynamics modulated by productive energy using the same procedure, which is the generalized spreading dye model (Jetz & Rahbek 2001). The model assumes that species ranges are contiguous and spread from the point of origin to available neighbouring grid cells until the final number of occupied cells, hence range size, is attained (i.e. the observed distribution of range sizes in terms of number of occupied grid cells is kept). Three models were performed (for all species), and their predictions were compared with observed species richness, as well as with the prediction from a pure effect of AET.

Global MDE model
The first cell was chosen randomly from all grid cells delimiting land masses on the Earth. In subsequent steps, a species could spread to any available unoccupied cell adjacent to any already occupied, with probability of being selected $P_i = 1/N_{adj}$, where N_{adj} is the number of empty adjacent cells at each respective step (i.e. $N_{adj} \leq 8$ for a single occupied cell but is usually higher where more than one cell is occupied). Classical approaches to the MDE emerging from species range dynamics assume that the latter are strictly limited by domain boundaries, however defined. However, in our model of global range dynamics, it was
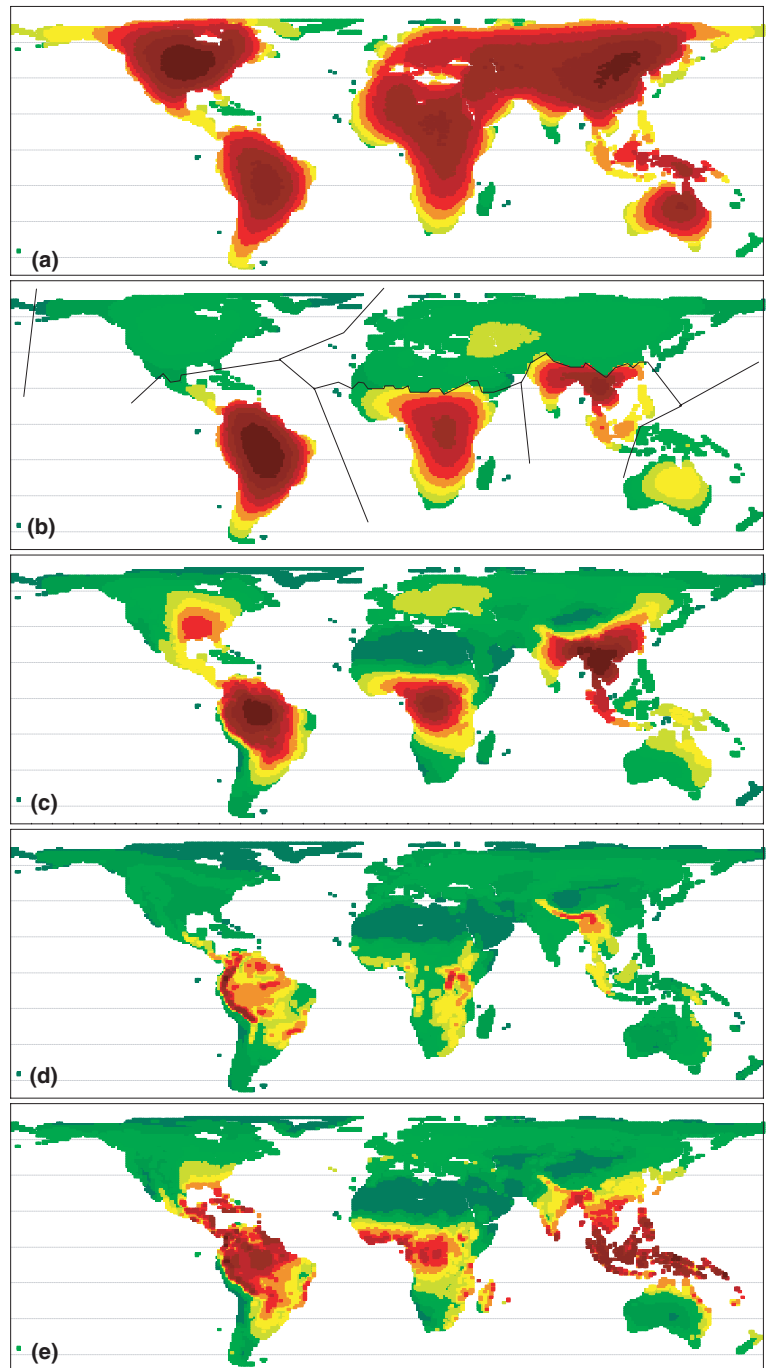
Figure 1 Equal-area maps of species richness at a resolution broadly comparable with a 1° latitude × 1° longitude grid; the gradient from dark green to dark red represents the gradient from low to high richness, (a) prediction based on the globally acting MDE (global MDE), (b) prediction of the MDE acting separately within individual biogeographic realms (within-realm MDE; realm boundaries are indicated by solid lines), (c) prediction of the globally acting AET-driven model of range dynamics and (d) observed species richness, (e) for comparison, the variation of AET values. Note that the range of species richness is rescaled in every case, i.e. a particular colour denotes different richness levels in each case; see Fig. 2 for the ranges of species richness and AET values for each situation.

possible for a species (especially those with large ranges) to spread into areas which were bounded and smaller than its range. In such cases, when a species filled the domain (island or continent) in question, it could skip to a different domain, into the cell which was the shortest distance from the last cell to be occupied within the previous domain. This simulated the rare events of long-distance dispersal, neces-sary for colonizing new and distant continents or islands. After the colonization event, the range dynamics continued within the new domain according to the rules described above; long distance jumps therefore occurred only when necessary (i.e. after complete filling of a domain), and were in fact quite rare (only about 5% of species underwent such a jump in each simulation).
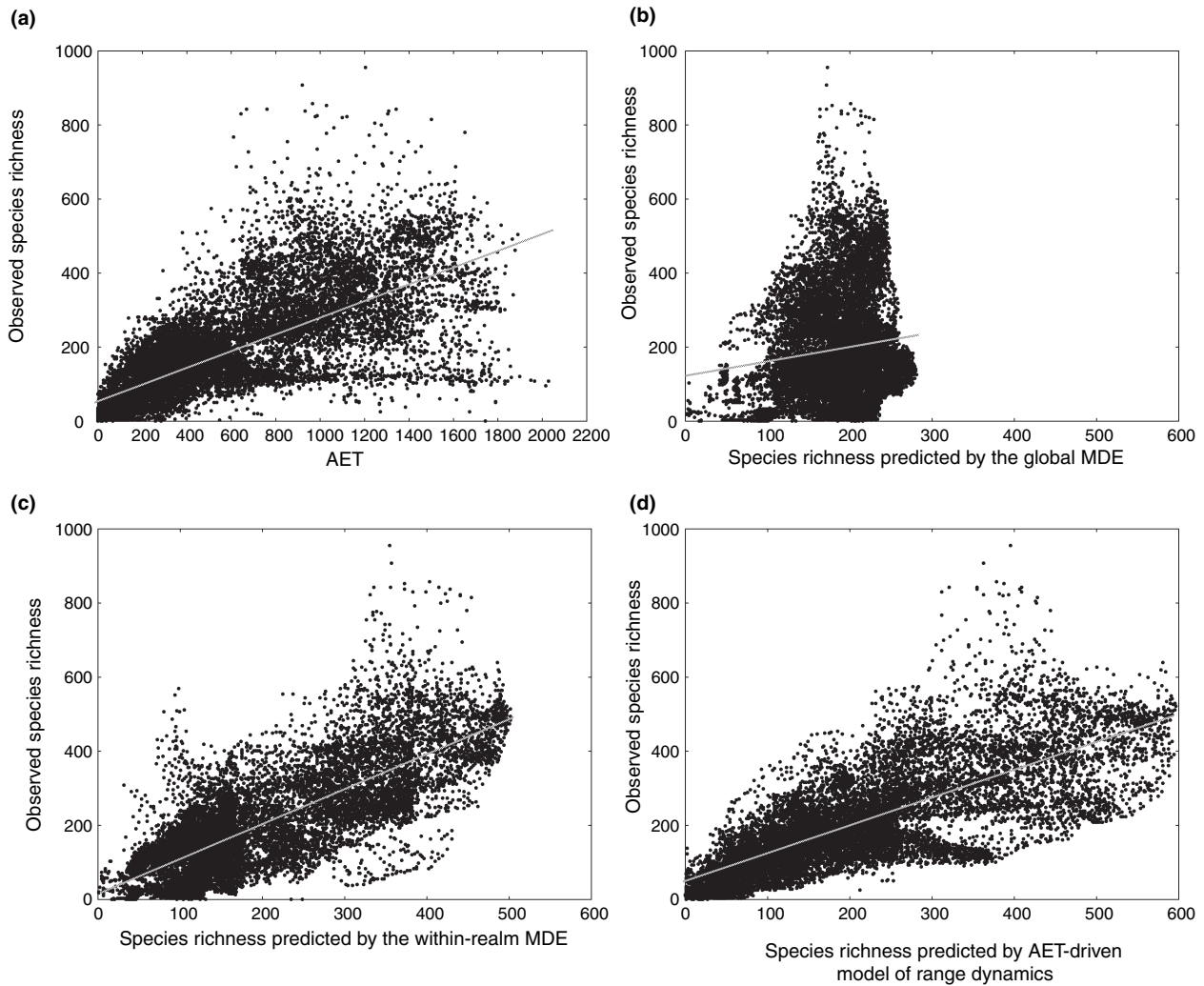
Figure 2 Species richness variation predicted by (a) the pure AET effect, (b) the global MDE, (c) the within-realm MDE, and (d) the global AET-driven model. Ordinary least-squares regression lines are provided.

Within-realm MDE model

The process was the same as in the previous case, but running within separate biogeographic realms. This is equivalent to the assumption that there are impenetrable boundaries between biogeographic realms and species can spread only within these boundaries. Total within-realm species richness was thus fixed at that actually observed, as was the distribution of species range sizes within each realm. If a species' range occurred in several realms, it was treated separately in each realm as if the parts were separate species. This is, of course, a simplification, but not unrealistic considering that very large ranges probably do not behave as coherent units, may not be contiguous if they occur on several continents, and the dynamics of their individual parts also may be affected by realm boundaries.

AET-driven model

In this model of range dynamics modulated by AET, the initial cell was not selected randomly, but with probability $P_i = \mathrm{AET}_i/\mathrm{AET}_{\mathrm{tot}}$, where AET_i was the value of AET of the particular cell, and $\mathrm{AET}_{\mathrm{tot}}$ was the sum of AET values for all cells. In all subsequent steps only empty cells adjacent to any already occupied could be selected, with probability $P_i = \mathrm{AET}_i/\mathrm{AET}_{\mathrm{adj.tot}}$, where $\mathrm{AET}_{\mathrm{adj.tot}}$ is the sum of AET values for all empty cells adjacent to those already occupied. Hence, in this model we simply assumed that the probability of species occurrence at each step is constrained by space (i.e. by continental boundaries, and by the presence of already occupied sites) and is exactly proportional to environmental productivity measured using AET. The latter assumption is justified by the fact that AET is proportional

to the total flow of energy through producers, and thus to the total abundance of resources available for consumers. When a species filled a domain, it could skip to a different domain, as in the case of the MDE models. This model necessarily generates some MDEs (as range dynamics are constrained by domain boundaries and large ranges thus necessarily reach centres of land masses). However, it is distinct from the null mid-domain model defined in previous studies, since it explicitly includes the effect of environmental productivity on these dynamics.

A total of 100 simulations were performed for each model (across all species), from which mean species richness was calculated for each grid cell.

Analyses

Correlations between mean predicted and observed species richness were compared using standard t-tests. We tested for significant differences between these correlation coefficients (Sokal & Rohlf 1995) in order to assess whether different models showed significant differences in explained variance, within each given geographical extent of consideration (i.e. globally or within realms). Such tests can give a general indication of the strength of individual predictors of species richness, but cannot evaluate the overall relative importance of each predictor across candidate model sets, including those in which the effect of the other predictors are accounted for. For this purpose, we performed model selection using multiple regressions of the effect of all predictors (pure AET, and the predictions from the MDE models and the AET-driven model) on species richness both globally and within each realm.

Use of OLS regression methods that assume independent errors may render correlation coefficients or regression slopes misleading in the case of spatially structured data (Clifford *et al.* 1989; Cressie 1991). Hence, we used generalized least squares (GLS) regression in which exponential spatial covariance structures were fitted, since these were the best-fit choice among spatial covariance options, as indicated by lowest value of Akaike's Information Criterion (AIC). Longitudinal and latitudinal cell centroid values were used as spatial variables and all models were implemented in SAS version 9.1 using the PROC MIXED procedure (Littell *et al.* 1996). Global spatial models took account of the differences among biogeographic realms in the maximum geographic distance or range parameter (ρ), measured in degrees, over which spatial autocorrelation in equivalent OLS residuals was observed to occur. This involved estimating ρ from the semi-variogram of residuals of standard OLS models that included the relevant combination of predictors, separately for each realm. All six estimates of ρ were then entered as spatial covariance parameters in the model, with spatial autocorrelation

assumed for observations within the same realm. Models for individual biogeographic realms used the corresponding spatial covariance parameters estimated for the given realm.

Globally, and within biogeographic realms, model selection procedures were performed using the results of seven GLS spatial models representing all possible combinations of our three predictors: AET; MDE model predictions; and AET-driven model predictions. Globally, the global MDE predictions were used as one predictor, while models for each biogeographic realm used the within-realm MDE predictions as the MDE model being tested. Model selection was based on the use of the AIC to compare the fit of competing models, since this approach is rapidly gaining acceptance as the preferred alternative to null hypotheses testing (Burnham & Anderson 2001; Johnson & Omland 2004; Whittingham *et al.* 2006). Following Burnham & Anderson (2001) and Johnson & Omland (2004), we calculated Δ_i, or the difference between each model's AIC value and that of the best-fitting model, the one with the smallest AIC (hence, $\Delta_i = \text{AIC}_i - \text{AIC}_{\min}$). The Akaike weight ($W$) of each model was then derived as

$$W_i = \frac{\exp(1/2\Delta_i)}{\sum_{j=i}^{R} \exp(-1/2\Delta_j)};$$

where W for each model is the model likelihood value normalised to sum to 1 across all R models being considered, and can be interpreted as the probability that each model provides the best fit among all models to explain the observed data. We then determined candidate sets of models by including only those with $W \geq 0.1$. For each of the three predictors of species richness, following Johnson & Omland (2004), we summed the Akaike weights of all the models in which the given predictor was included to estimate the relative importance of the three in predicting species richness.

We additionally compared the fit of our GLS models against OLS models that assume independent errors. In all cases OLS models were associated with higher values for -2 times the logarithm of the restricted likelihood than the equivalent GLS models (see Table S1 in Supplementary Material), indicating that adjusting for spatial autocorrelation resulted in a consistently more accurate description of variability in species richness (Littell *et al.* 1996). Hence, only the GLS model results are reported.

RESULTS

Global MDE model

Not surprisingly, the purely random model of stochastic species range dynamics constrained only by the distribution
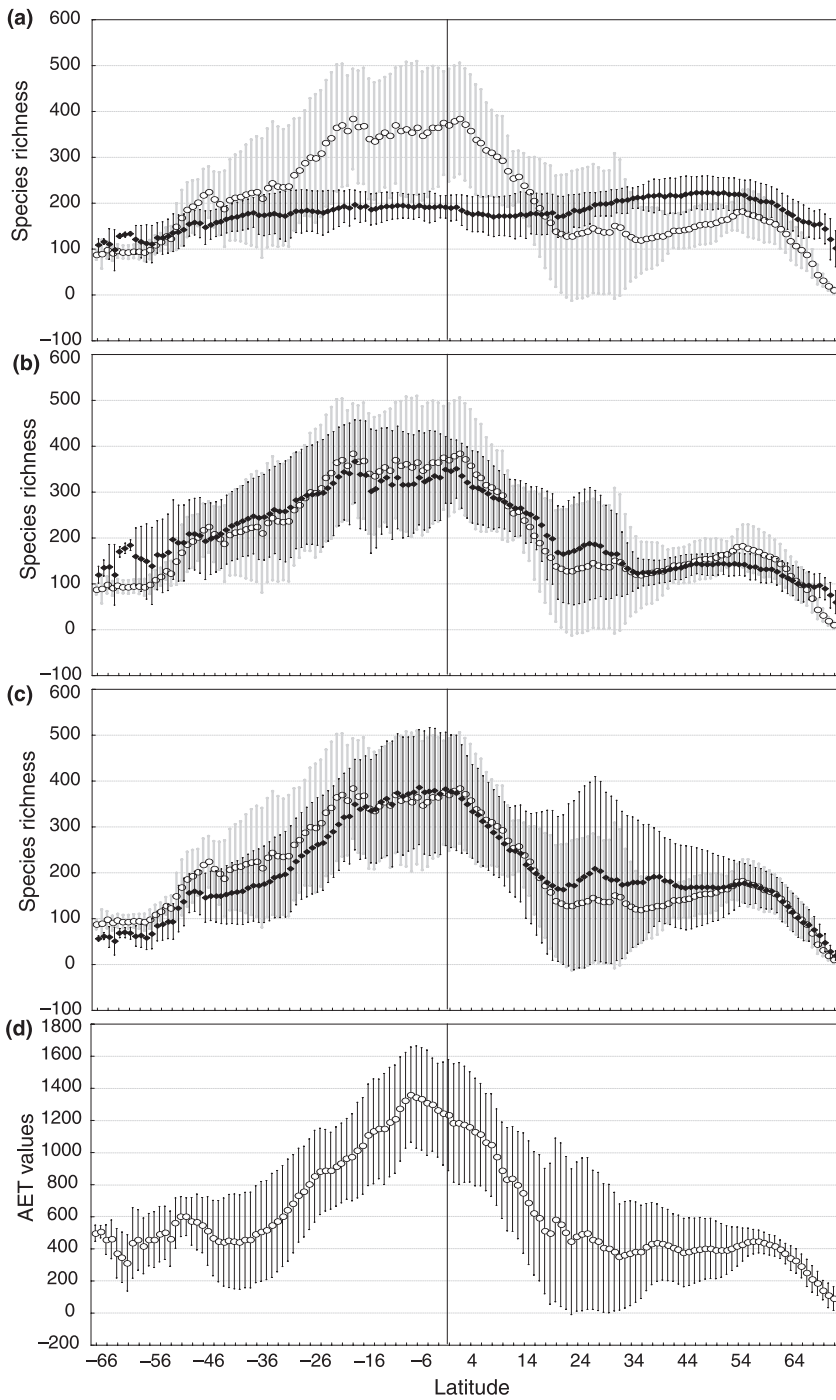
Figure 3 Latitudinal trends (species richness values in all grid cells for every 1° latitudinal band, re-sampled from the equal-area grid) in observed species richness compared with (a) the global MDE, (b) the within-realm MDE, and (c) the AET-driven model. Means and SD of observed richness values are represented by open circles and grey bars, respectively; means and standard deviations of predicted richness values are represented by black dots and solid lines, respectively; (d) the latitudinal variability (means and SD) of AET values for comparison.

of continental masses did not predict observed patterns of species richness (Fig. 1a, see Fig. 1d for comparison). Peaks of species richness predicted by this model emerged in central areas of the continents, although their exact locations were affected by the shapes of continents and their spatial relations to other landmasses. The height of a species richness peak is clearly related to the size of the continent,

since there is an equal probability that any given grid cell will be the starting point for the spread of a species' range, and thus more species will start their spreading in larger continents. The variance in predicted species richness was much lower than observed (see the scaling of axes on Fig. 2b). No latitudinal gradient in richness was predicted by the global MDE model (Fig. 3a).

Within-realm MDE model

When we ran the MDE model separately for each biogeographic realm, the picture became very different. The overall pattern of predicted distribution of global species richness roughly resembles the observed pattern (Fig. 1b, see Fig. 1d for comparison), and this model explains 60.35% of the variance in species richness (Fig. 2c), which is more than was explained by the pure effect of AET, i.e. its effect without assuming any range dynamics (Table 1). This simple model also accurately predicts the latitudinal gradient of species richness (Fig. 3b), although this finding has to be treated with caution, as the latitudinal differences were already partially accounted for by assuming the total species numbers and range sizes for individual realms (differing in latitude) to be equal to those observed. The model predicts a portion of the variation of species richness within individual realms, although the amount explained differs considerably between realms and is in most cases lower than the variation explained by the pure effect of AET (Table 1, Fig. S1).

AET-driven model

The global model of range dynamics modulated by AET explained virtually the same amount of global variance in species richness (60.00%) as did the within-realm MDE model (Figs 1c and 2d), the difference being statistically non-significant (Table 1). Moreover, although this model did not assume any initial differences between land masses in terms of their species richness, it predicted very accurately the latitudinal trends in species richness (Fig. 3c). Within realms, the AET-driven model explained greater variation than the within-realm MDE model in all cases (the difference being significant in four out of six cases), and also more than the pure effect of AET in all cases

Figure 4 Species richness for different biogeographic realms: open boxes refer to observed richness, whereas shaded boxes refer to richness predicted by the AET-driven model. Means (horizontal line), standard deviations (boxes) and non-outlier ranges are provided.

(significant in five out of six cases, Table 1, Fig. S1). The AET-driven model also predicted the major differences in mean species richness between individual realms (Fig. 4). Some biogeographic realms were evidently slightly overestimated (Oriental and Nearctic realms), some slightly underestimated (Afrotropical and Neotropical), but the general pattern is consistent with that observed. Note that the differences in mean species richness between realms are largely attributable to differences in AET (Fig. S2).

GLS comparison of species richness predictors

Both globally, and within individual biogeographic realms, the AET-driven model prediction was included in the best-fit model (lowest AIC) (Table 2; see also Table S2). Summing the Akaike weights (W) for the presence of a given predictor within models showed that the AET-driven model prediction was an essential predictor (summed $W = 1.0$) globally, and in all biogeographic realms except for Australasia where it was second in importance to the within-realm MDE model prediction (Table 3). In all cases where the AET-driven model prediction was an essential predictor, it was more important than other predictors (based on ranking the summed Akaike weights for each predictor) except in the global case, where the global MDE model prediction was equally important (Table 3; see also Table S2).

Of the seven global spatial GLS models, only the one fitting the AET-driven model prediction and the global MDE model prediction can be considered a candidate best-fit model based on the criterion of having $W \geq 0.1$

Table 1 Comparison between the models (and the pure effect of AET) in terms of the proportion of explained variance (r^2), both globally and within individual biogeographic realms

Realm	AET	Global MDE	Within-realm MDE	AET-driven
Global	0.510	0.017	0.603[a]	0.600[a]
Australasian	0.030[ab]	0.055[a]	0.018[b]	0.291
Afrotropical	0.279[a]	0.062	0.325[ab]	0.355[b]
Oriental	0.045	0.121	0.220[a]	0.284[a]
Nearctic	0.304[a]	0.317[a]	0.226	0.345[a]
Neotropical	0.436	0.255	0.384	0.619
Palearctic	0.420	0.084	0.142	0.523

The values that are not significantly different ($P < 0.05$) are indicated by shared superscript letters here; significance values were adjusted for multiple comparison using Bonferroni corrections.
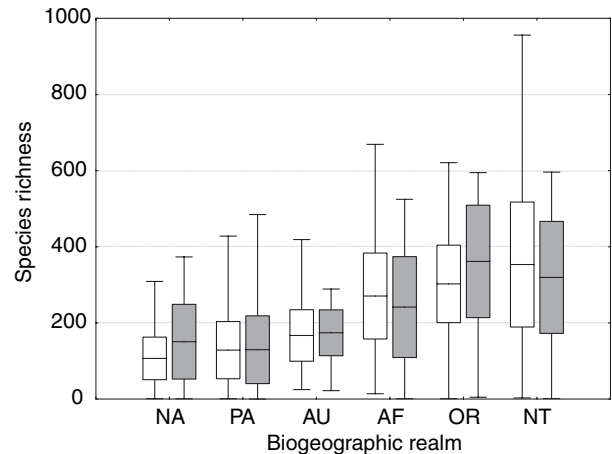
Table 2 Model selection results for spatial GLS regression models of all seven combinations of three predictors globally, and within six biogeographic realms

	Predictors			Global	
Model	AET	MDE-global	AET-driven	AIC	*W*
1			✔	140 074.7	0.000
2		✔		141 810.4	0.000
3	✔			143 428.8	0.000
4	✔		✔	140 063	0.000
5		✔	✔	**140 028.2***	**1.000**
6	✔	✔		141 256	0.000
7	✔	✔	✔	140 059.2	0.000

	Predictors			Australasia		Afrotropics		Oriental	
Model	AET	MDE-realm	AET-driven	AIC	*W*	AIC	*W*	AIC	*W*
1			✔	11 654.4	0.008	22 501.4	0.000	**10 981.9**	**0.157**
2		✔		**11 647.6**	**0.229**	22 566.9	0.000	11 008.4	0.000
3	✔			11 913	0.000	22 752.8	0.000	11 074	0.000
4	✔		✔	11 655.1	0.005	22 504.4	0.000	**10 980.7**	**0.287**
5		✔	✔	11 652.2	0.023	**22 478.6***	**0.971**	**10 980.4***	**0.333**
6	✔	✔		11 653.3	0.013	22 520.3	0.000	11 015.6	0.000
7	✔	✔	✔	**11 645.3***	**0.722**	22 485.6	0.029	**10 981.2**	**0.223**

	Predictors			Nearctic		Neotropics		Palaearctic	
Model	AET	MDE-realm	AET-driven	AIC	*W*	AIC	*W*	AIC	*W*
1			✔	20 509.9	0.000	24 067.1	0.000	50 137.7	0.000
2		✔		20 729.4	0.000	24 173.5	0.000	50 786.3	0.000
3	✔			20 556	0.000	24 393.9	0.000	50 704.6	0.000
4	✔		✔	**20 482.9**	**0.269**	**24 007.5***	**0.802**	**50 099.2***	**1.000**
5		✔	✔	20 512.2	0.000	24 052.1	0.000	50 161.7	0.000
6	✔	✔		20 532.8	0.000	24 171.9	0.000	50 699.4	0.000
7	✔	✔	✔	**20 480.9***	**0.731**	**24 010.3**	**0.198**	50 121	0.000

*The lowest value for Akaike's Information Criterion (AIC), hence the best-fitting model of the seven. Models which can be considered candidate best-fit models based on the criterion of Akaike weight $W \geq 0.1$ are high-lighted in bold.

Table 3 Summed Akaike weights (*W*) for each predictor across all models in which each occurs of the seven possible models using spatial GLS regression

Predictor	Global	Australasia	Afrotropics	Oriental	Nearctic	Neotropics	Palaearctic
AET	0.000	0.741	0.029	0.510	1.000	1.000	1.000
MDE-global	1.000	–	–	–	–	–	–
MDE-realm	–	0.987	1.000	0.556	0.731	0.198	0.000
AET-driven	1.000	0.758	1.000	1.000	1.000	1.000	1.000

(Table 2). For all biogeographic realms, candidate best-fit models (based on the same criterion) all included the AET-model prediction with the exception of Australasia where the second-best-fitting model included only the within-realm MDE model prediction (Table 2). Overall, these results indicate that the AET-driven model of range dynamics is a better predictor of species richness than both AET and MDE models, and explains a considerable amount of variance even if the effects of other predictors are accounted for.
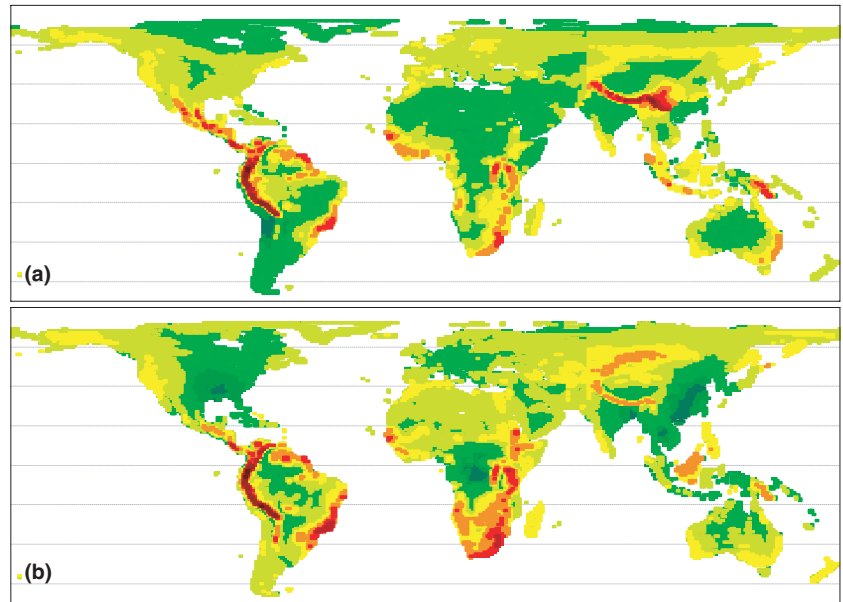
Figure 5 Residuals (observed minus predicted richness) from the within-realm MDE (a) and the AET-driven model (b). The colour gradient is the same as in Fig. 1.

Residuals from within-realm MDE and AET-driven models

The spatial distribution of the residuals, calculated as observed minus predicted richness, differs slightly between the within-realm MDE model and AET-driven models (Fig. 5), but the most pronounced pattern is common: mountain ranges, especially in the tropics, have consistently much higher observed species richness than predicted. Some biodiversity hotspots, especially Atlantic forests in Brazil, are also apparent. On the other hand, the AET-driven model apparently predicts considerably higher species richness than observed in several lowland areas, namely the south-eastern USA, the Congo basin and parts of the Amazon basin, and southeast Asia.

DISCUSSION

Although AET as a measure of productivity is a strong predictor of avian species richness at the global scale, the two models based on range dynamics predicted this richness better, both globally and within most realms. Stochastic dynamics of species ranges constrained only by the boundaries of individual biogeographic realms (within-realm MDE) showed considerable power in predicting species richness, as did the AET-driven model of range dynamics. By this criterion, then, there is little to choose between these models. However, in every other detail we consider the AET-driven model to be considerably superior.

Mid-domain effect is only a good predictor of global richness patterns if each individual realm is considered separately. The global MDE model is conspicuously poor in comparison with all others tested here (Table 1), explaining only 1.7% of global variation in avian richness. Further-

more, it predicts that peak species richness ought to be about 280 species (Fig. 2b), that this should be located in eastern Asia, and that the peak richness on any given land mass should be proportional to its area (Fig 1a). None of these predictions is upheld by the bird data. The mid-domain model generates more realistic patterns of global richness when realms are modelled separately. However, this model requires that the species richness of each realm is given *a priori*, and species cannot cross realm boundaries (or if they do that their ranges in different realms behave independently). In contrast, the AET-driven model predicts global bird richness patterns as well as does the within-realm MDE model, but without making any assumptions about how species are distributed across realms, or the permeability of realm boundaries. It produces a close fit to the latitudinal gradient in richness (Fig. 3c), which an MDE model can only match when an element of that gradient is incorporated into it via realm richness (i.e. only for the within-realm MDE model), and predicts the richness of individual realms (Fig. 4). Moreover, the AET-driven model produces richness patterns within individual realms that are a better match (often substantially) to the real patterns than those of the within-realm MDE model (Table 1), despite making no assumptions about realm richness. This productivity-driven model should therefore be considered preferable to the pure mid-domain model, as it predicts not only the within-realm variation, but also broad differences between biogeographic realms, and with more realistic dynamical assumptions.

The fact that the dynamic models provide a better fit to observed richness patterns than a simple environmental variable is significant. It suggests that species richness is not driven purely by environmental constraints, but also by the

limited ability of species to spread to favourable places. Processes that ensure some degree of range contiguity, namely spatial population dynamics driven and constrained by dispersal limitation, at the same time constrain spread to certain places even if these are suitable in terms of ecological conditions (Gaston 2003). For example, through this effect peninsular areas can be impoverished relative to their productivity, simply because species spreading across continents have a lower probability of reaching them, even if they spread preferentially into more productive areas. Indeed, this 'peninsular effect' has been widely reported (e.g. Taylor & Regal 1978; Lawlor 1983). Of course, the most extreme manifestation of the effect occurs on islands, where well-known impoverishment caused by the limiting effect of isolation upon immigration, belongs to one of the most general patterns in ecology (MacArthur & Wilson 1967; Rosenzweig 1995).

Our approach reconciles two major competing approaches to explain patterns of species richness: one combining historical thinking with the dynamics of species distribution and processes affecting species ranges (e.g. Dynesius & Jansson 2000), the other taking external environmental constraints as fundamental in determining species richness patterns (e.g. Francis & Currie 2003). We show that both range dynamics and environmental constraints contribute to species richness, that each in isolation provides only a partial explanation, and hence the two can and should be considered simultaneously. This is in broad agreement with the general notion that range dynamics and environmental effects are always tightly interconnected, as spatial patterns of species richness are necessarily proximately caused by the spatial distribution and overlap of species ranges, and, at the same time, species range dynamics, and even range contiguity, is to a large extent driven by the spatial arrangement of environmental variables perceived by individual species (Gaston 2003; Zapata *et al.* 2005).

It is possible to place our productivity-driven model of range dynamics into the context of theories which attempt to explain the observed positive relationship between energy availability and species richness, i.e. the species–energy relationship (Gaston 2000; Currie *et al.* 2004; Evans *et al.* 2005; Clarke & Gaston 2006). According to our model, the species–energy relationship emerges as a result of species range dynamics affected by the positive relationship between probability of occurrence and energy availability. Such a relationship could arise for a number of reasons. Higher resource abundance can allow potentially higher population densities, lowering the probability of extinction, in line with the more-individuals hypothesis (Wright 1983). Alternatively, a more productive environment may be more heterogeneous and consequently offer a greater number of ecological niches (Hurlbert 2004). It is even possible that the 'more individuals' effect is more important for some taxa,

while 'habitat heterogeneity' is more important for others. Indeed, there is evidence for both effects (Kerr *et al.* 2001; Bonn *et al.* 2004; Pautasso & Gaston 2005). Nevertheless, the increase in probability of species occurrence with increasing energy availability may represent a general higher-order explanation of observed species–energy relationships, even if in reality it applies only to a subset of species, namely those with larger range sizes (see Jetz & Rahbek 2002; Lennon *et al.* 2004).

No model provides perfect predictions of species richness variation, and the residuals from the predictions are as interesting as the fit of the models themselves. Some deviation of predicted from observed species richness can probably be attributed to the way in which environmental productivity is measured. It has been shown, for instance, that seasonal measures are more relevant for bird assemblages in regions with pronounced seasonality and considerable proportion of regularly migrating species (Hurlbert & Haskell 2003). Hence, it is possible that the fit of such a model could be improved by using variables more specifically associated to assemblages in question. However, in the present study, spatial distribution of the residuals of observed species richness regressed on the model predictions, clearly indicates that there are other important systematic effects on species richness. Relatively high species richness of mountain ranges, especially within the tropics, is the most pronounced pattern of deviation, and has been widely reported elsewhere (Fjeldså *et al.* 1999, Rahbek & Graves 2001; Jetz & Rahbek 2002; Orme *et al.* 2005). This has been attributed to an elevation of speciation rates due to a higher density of geographic barriers (Fjeldså & Lovett 1997), a lowering of extinction rates due to the stable persistence of various habitat types (Fjeldså *et al.* 1999), or the narrow elevational zoning of species in (especially tropical) montane areas (Janzen 1967).

More puzzling, however, is the lower observed species richness in certain lowland areas in comparison with model predictions. It is possible that in such cases the majority of ecosystem productivity is appropriated by human populations, and is hence not available to bird populations. Indeed, the deviation between prediction and observation is most pronounced in the south-eastern part of the USA and eastern areas of India and China, which are regions of very intense agricultural production. In these cases, actual evapotranspiration is apparently not the best measure of the amount of resources available to bird populations. Lower observed than predicted species richness within the Congo and, to a lesser extent, Amazon basins, indicate that other factors including idiosyncrasies of evolutionary history may affect global species richness patterns as well.

Total resource availability is but one of several key environmental drivers of species richness, and species range dynamics are certainly more complex than assumed in the models reported here. However, generally good predictions

of both within-realm and between-realm species richness variation obtained by the productivity-driven range dynamics model indicates that principles of population dynamics and environmental/energetic constraints work equally well across the whole globe, and are able to account for the majority of the spatial variation in species richness observed globally.

REFERENCES

Allen, A.P., Brown, J.H. & Gillooly, J.F. (2002). Global biodiversity, biochemical kinetics, and the energetic-equivalence rule. *Science*, 297, 1545–1548.

Allen, A.P., Gillooly, J.F. & Brown, J.H. (in press). Recasting the species-energy hypothesis: the different roles of kinetic and potential energy in regulating biodiversity. In: *Scaling Biodiversity* (eds Storch, D., Marquet, P.A. & Brown, J.H.). Cambridge University Press, Cambridge.

Bellwood, D.R., Hughes, T.P., Connolly, S.R. & Tanner, J. (2005). Environmental and geometric constraints on Indo-Pacific coral reef biodiversity. *Ecol. Lett.*, 8, 643–651.

Bonn, A., Storch, D. & Gaston, K.J. (2004). Structure of the species-energy relationship. *Proc. R. Soc. Lond. B*, 271, 1685–1691.

Burnham, K.P. & Anderson, D.R. (2001). *Model Selection and Multi-Model Inference: A Practical Information-Theoretic Approach*. Springer-Verlag, New York.

Clarke, A. & Gaston, K.J. (2006). Climate, energy and diversity. *Proc. R. Soc. Lond. B*, 273, 2257–2266.

Clifford, P., Richardson, S. & Hemon, D. (1989). Assessing the significance of the correlation between two spatial processes. *Biometrics*, 45, 123–134.

Colwell, R.K. & Hurtt, G.C. (1994). Nonbiological gradients in species richness and a spurious Rapoport effect. *Am. Nat.*, 144, 570–595.

Colwell, R.K. & Lees, D.C. (2000). The mid-domain effect: geometric constraints on the geography of species richness. *Trends Ecol. Evol.*, 15, 70–76.

Colwell, R.K., Rahbek, C. & Gotelli, N.J. (2004). The mid-domain effect and species richness patterns: what have we learned so far? *Am. Nat.*, 163, E1–E23.

Colwell, R.K., Rahbek, C. & Gotelli, N.J. (2005). The mid-domain effect: there's a baby in the bathwater. *Am. Nat.*, 166, E149–E154.

Cramer, W., Kicklighter, D.W., Bondeau, A., Moore, I.B., Churkina, G., Nemry, B. *et al.* (1999). Comparing global models of terrestrial net primary productivity (NPP): overview and key results. *Global Change Biol.*, 5(Suppl.), 1–15.

Cressie, N. (1991). *Statistics for Spatial Data*. Wiley, New York.

Currie, D.J., Mittelbach, G.G., Cornell, H.V., Field, R., Guégan, J.F., Hawkins, B.A. *et al.* (2004). Predictions and tests of climate-based hypotheses of broad-scale variation in taxonomic richness. *Ecol. Lett.*, 7, 1121–1134.

Dynesius, M. & Jansson, R. (2000). Evolutionary consequences of changes in species' geographical distributions driven by Milankovitch climate oscillations. *Proc. Natl Acad. Sci.*, 97, 9115–9120.

Evans, K.L., Warren, P.H. & Gaston, K.J. (2005). Species–energy relationships at the macroecological scale: a review of the mechanisms. *Biol. Rev.*, 80, 1–25.

Fjeldså, J. & Lovett, J.C. (1997). Geographical patterns of old and young species in African forest biota: The significance of specific montane areas as evolutionary centres. *Biodivers. Conserv.*, 6, 325–346.

Fjeldså, J., Lambin, E. & Mertens, B. (1999). Correlation between endemism and local bioclimatic stability documented by comparing Andean bird distributions and remotely sensed land surface data. *Ecography*, 22, 63–78.

Francis, A.P. & Currie, D.J. (2003). A globally-consistent richness-climate relationship for angiosperms. *Am. Nat.*, 161, 523–536.

Gaston, K.J. (2000). Global patterns in biodiversity. *Nature*, 405, 220–227.

Gaston, K.J. (2003) *The Structure and Dynamics of Geographic Ranges*. Oxford University Press, Oxford.

Hawkins, B.A., Field, R., Cornell, H.V., Currie, D.J., Guegan, J., Kaufman, D.M. *et al.* (2003). Energy, water, and broad-scale geographic patterns of species richness. *Ecology*, 84, 3105–3117.

Hawkins, B.A., Diniz-Filho, J.A.F. & Weis, A.E. (2005). The mid-domain effects and diversity gradients: is there anything to learn? *Am. Nat.*, 166, E140–E143.

Hurlbert, A.H. (2004). Species–energy relationships and habitat complexity in bird communities. *Ecol. Lett.*, 7, 714–720.

Hurlbert, A.H. & Haskell, J.P. (2003). The effect of energy and seasonality on avian species richness and community composition. *Am. Nat.*, 161, 83–97.

Janzen, D.H. (1967). Why mountain passes are higher in the tropics. *Am. Nat.*, 101, 233–249.

Jetz, W. & Rahbek, C. (2001). Geometric constraints explain much of the species richness pattern in African birds. *Proc. Natl Acad. Sci. U.S.A.*, 98, 5661–5666.

Jetz, W. & Rahbek, C. (2002). Geographic range size and determinants of avian species richness. *Science*, 297, 1548–1551.

Johnson, J.B. & Omland, K.S. (2004). Model selection in ecology and evolution. *Trends Ecol. Evol.*, 19, 101–108.

Kerr, J.T. & Ostrovsky, M. (2003). From space to species: ecological applications for remote sensing. *Trends Ecol. Evol.*, 18, 299–305.

Kerr, J.T., Southwood, T.R.E. & Cihlar, J. (2001). Remotely sensed habitat diversity predicts butterfly species richness and community similarity in Canada. *Proc. Natl Acad. Sci. U.S.A.*, 98, 11365–11370.

Koleff, P. & Gaston, K.J. (2001). Latitudinal gradients in diversity: Real patterns and random models. *Ecography*, 24, 341–351.

Latham, R.E. & Ricklefs, R.E. (1993). Continental comparisons of temperate-zone tree species diversity. In: *Species Diversity in Ecological Communities: Historical and Geographical Perspectives* (eds Ricklefs, R.E. & Schluter, D.). The University of Chicago Press, Chicago, IL, pp. 294–314.

Lawlor, T.E. (1983). The peninsular effect on mammalian diversity in Baja California. *Am. Nat.*, 121, 432–439.

Lees, D.C., Kremen, C. & Andriamampianina, L. (1999). A null model of species richness gradients: bounded range overlap of butterflies and other rainforest endemics in Madagascar. *Biol. J. Linnean Soc.*, 67, 529–584.

Lennon, J.J., Koleff, P., Greenwood, J.J.D. & Gaston, K.J. (2004). Contribution of rarity and commonness to patterns of species richness. *Ecol. Lett.*, 7, 81–87.

Littell, R.C., Milliken, G.A., Strop, W.W. & Wolfinger, R.D. (1996). *SAS System for Mixed Models*. SAS Institute, Cary, NC.

MacArthur, R.H. & Wilson, E.O. (1967). *The Theory of Island Biogeography*. Princeton University Press, Princeton, PA.

Mittelbach, G.G., Steiner, C.F., Scheiner, S.M., Gross, K.L., Reynolds, H.L., Waide, R.B. *et al.* (2001). What is the observed relationship between species richness and productivity? *Ecology*, 82, 2381–2396.

Olson, D.M., Dinerstein, E., Wikramanayake, E.D., Burgess, N.D., Powell, G.V.N., Underwood, E.C. *et al.* (2001). Terrestrial ecoregions of the worlds: a new map of life on Earth. *Bioscience*, 51, 933–938.

Orme, C.D.L., Davies, R.G., Burgess, M., Eigenbrod, F., Pickup, N., Olson, V.A. *et al.* (2005). Global hotspots of species richness are not congruent with endemism or threat. *Nature*, 436, 1016–1019.

Orme, C.D.L., Davies, R.G., Olson, V.A., Thomas, G.H., Ding, T-S., Rasmussen, P.C. *et al.* (2006). Global patterns of geographic range size in birds. *PLoS Biol.*, 4, 1276–1283.

Pautasso, M. & Gaston, K.J. (2005). Resources and global avian assemblage structure in forests. *Ecol. Lett.*, 8, 282–289.

Qian, H. & Ricklefs, R.E. (1999). A comparison of the taxonomic richness of vascular plants in China and the United States. *Am. Nat.*, 154, 160–181.

Rahbek, C. & Graves, G.R. (2001). Multiscale assessment of patterns of avian species richness. *Proc. Natl Acad. Sci. U.S.A.*, 98, 4534–4539.

Rohde, K. (1992). Latitudinal gradients in species diversity – the search for the primary cause. *Oikos*, 65, 514–527.

Rosenzweig, M.L. (1995). *Species Diversity in Space and Time*. Cambridge University Press, Cambridge.

Sokal, R.R. & Rohlf, F.J. (1995). *Biometry*. W.H. Freeman & Company, New York.

Taylor, R.L. & Regal, P.J. (1978). The peninsular effect on species diversity and the biogeography of Baja California. *Am. Nat.*, 112, 583–593.

Turner, J.R.G. & Hawkins, B.A. (2004). The global diversity gradient. In: *Frontiers of Biogeography: New Directions in the Geography of Nature* (eds Lomolino, M.V. & Heaney, L.R.). Sinauer, Sunderland, MA, pp. 171–190.

Waide, R.B., Willig, M.R., Steiner, C.F., Mittelbach, G., Gough, L., Dodson, S.I. *et al.* (1999). The relationship between productivity and species richness. *Ann. Rev. Ecol. Syst.*, 30, 257–300.

Whittingham, M.J., Stephens, P.A., Bradbury, R.B. & Freckleton, R.P. (2006). Why do we still use stepwise modelling in ecology and behaviour? *J. Anim. Ecol.*, 75, 1182–1189.

Willig, M.R., Kaufman, D.M. & Stevens, R.D. (2003). Latitudinal gradients of biodiversity: patterns, process, scale, and synthesis. *Ann. Rev. Ecol. Syst.*, 34, 273–309.

Wright, D.H. (1983). Species–energy theory: an extension of species–area theory. *Oikos*, 41, 496–506.

Zapata, F.A., Gaston, K.J. & Chown, S.L. (2003). Mid-domain models of species richness gradients: assumptions, methods, and evidence. *J. Anim. Ecol.*, 72, 677–690.

Zapata, F.A., Gaston, K.J. & Chown, S.L. (2005). The mid-domain effect revisited. *Am. Nat.*, 166, E144–E148.

SUPPLEMENTARY MATERIAL

The following supplementary material is available for this article:

Table S1 Values for −2 times the logarithm of the restricted likelihood for spatial GLS and equivalent non-spatial OLS regression models of all seven combinations of three predictors of species richness, globally, and within six biogeographic realms.

Table S2 Results for spatial GLS regression models of all seven combinations of three predictors globally, and within six biogeographic realms.

Figure S1 The relationship between AET and observed species richness, and between predicted and observed species richness within individual biogeographic realms for the within-realm MDE, and the AET-driven model.

Figure S2 Relationship between mean AET values and mean species richness per grid cell between individual biogeographic realm.

This material is available as part of the online article from: http://www.blackwell-synergy.com/doi/full/10.1111/ j.1461-0248.2006.00984.x

Please note: Blackwell Publishing are not responsible for the content or functionality of any supplementary materials supplied by the authors. Any queries (other than missing material) should be directed to the corresponding author for the article.