

LETTER

The species-area-energy relationship

Abstract

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INTRODUCTION

Two patterns in species richness have been documented sufficiently frequently, and across such a wide range of taxonomic groups, biogeographic regions and spatial scales, that they may be considered universal. First, species richness increases with area – the species-area relationship (SAR; Arrhenius 1921; Gleason 1922; Williamson 1988; Rosenzweig 1995). Second, the energy available to an assemblage (i.e. that which it can turn into biomass) at a particular spatial resolution influences its species richness – the species-energy relationship (SER; e.g. Wright 1983; Currie 1991; Rosenzweig 1995; Gaston 2000; Hawkins *et al.* 2003).

These two fundamental ecological patterns may be closely interrelated. Indeed, Wright (1983) used one of the mechanisms contributing to the SAR to derive a potential explanation of the SER. He suggested that larger areas may contain more species as they have more resources that enable species populations to be larger, buffering them from extinction and promoting species richness (the ‘area *per se*’ hypothesis, according to Connor & McCoy 1979). Similarly, sites with more available energy may host more species because population densities are larger; this is often termed the more individuals hypothesis (Gaston 2000). However,

whilst the importance of determining whether energy availability influences the form of the SAR and vice versa has been recognized (Scheiner *et al.* 2000), unequivocal empirical evidence that addresses these issues is lacking. Much research has been devoted to the scale-dependency of the form of the SER (Waide *et al.* 1999; Mittelbach *et al.* 2001, 2003; Chase & Leibold 2002; Whittaker & Heegaard 2003), but with two notable exceptions (Pastor *et al.* 1996; Weiher 1999), to our knowledge no study has systematically and simultaneously considered the interaction between these two patterns, i.e. how area affects the slope and strength of the SER and how energy availability affects the slope of the SAR.

Both the SER and SAR can be related to patterns of species abundance and occupancy. Although conclusive evidence that supports the more individuals hypothesis of the SER is not yet available (Currie *et al.* 2004; Evans *et al.* 2005), there is evidence that areas with higher energy availability host not only higher numbers of species, but also more individuals (Kaspari *et al.* 2003; Hurlbert 2004). Moreover, Bonn *et al.* (2004) reported that areas with higher energy availability have on average higher species occupancies (i.e. proportion of sites occupied by each species).

The SAR is linked to species abundance patterns as well (Chave *et al.* 2002; He & Legendre 2002) and its slope varies

with mean species occupancy. Indeed, the exponent γ of the power-law form of the SAR (i.e. the slope of the linear regression in a log–log bivariate plot of area and species richness; Rosenzweig 1995) measured on a grid can be derived from mean species occupancy and the number of grid cells considered. According to Šízling & Storch (2004), it can be estimated from the largest and smallest areas analysed, i.e. the total number of grid cells A_{tot} and total species richness S_{tot} , and the minimum area considered, that of the base grid cell ($A = 1$), and mean species richness within the base grid cell, which is equal to the sum of species relative occupancies. The slope of the line defined by these two extreme points in a log–log space is then

$$Z = \frac{\ln(S_{\text{tot}}/\sum \pi_i)}{\ln(A_{\text{tot}})},$$

where π_i is the proportion of grid cells occupied by species i . And since mean species relative occupancy $\bar{\pi} = \sum \pi_i/S_{\text{tot}}$, then $\gamma = -\ln(\bar{\pi})/\ln(A_{\text{tot}})$. Therefore, if species' occupancies are higher in areas with higher energy availability, this should simultaneously reduce the slope of the SAR. Here we test this theory using some of the most comprehensive quadrat-based distributional data, that of avian distributions in southern Africa and Britain. For both assemblages positive SERs have previously been documented (Turner *et al.* 1988; Lennon *et al.* 2000; van Rensburg *et al.* 2002; Chown *et al.* 2003; Bonn *et al.* 2004).

METHODS

We used two data sets on species numbers, areas and energy availability as follows:

- (1) Avian species distribution data for South Africa and Lesotho, obtained from the South African Bird Atlas Project (Harrison *et al.* 1997) at the resolution of quarter degree cells on a latitude/longitude grid (the area of each grid cell is $\approx 676 \text{ km}^2$). We considered presences and absences of 651 native species excluding marine, vagrant and marginal species. Within the area covered by the atlas, we delimited 21 non-overlapping squares, each of 8×8 quarter degree grid cells (Fig. 1a). Then, we extracted species numbers for all non-overlapping quadrats within these 8×8 squares, ranging from 1 grid cell (i.e. $n = 64$), 2×2 cells ($n = 16$), 4×4 cells ($n = 4$) and the whole 8×8 square. For these quadrats we also calculated the mean Normalized Difference Vegetation Index (NDVI) as a measure of energy available to an assemblage. NDVI is strongly and positively correlated with net primary productivity in South Africa (Woodward *et al.* 2001) and elsewhere (Kerr & Ostrovsky 2003), and thus is a suitable measure of the energy available to consumers. We used mean January

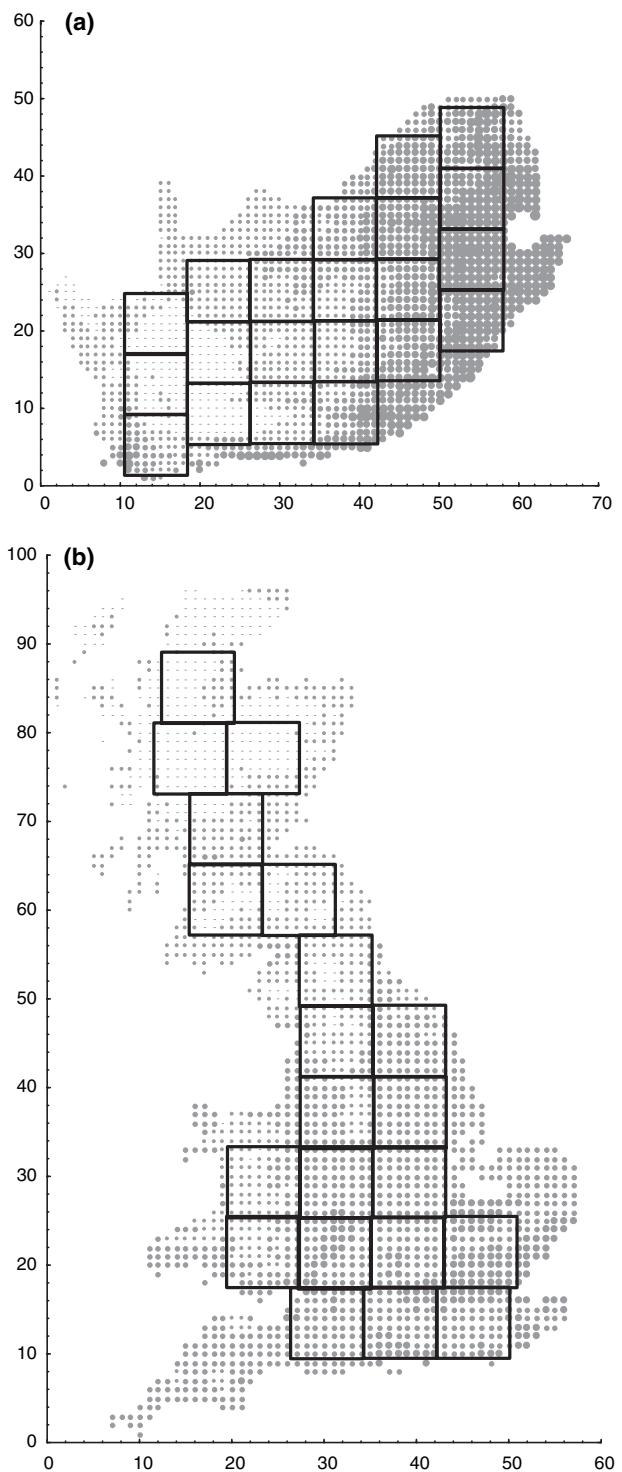


Figure 1 Map of the grids of atlases of (a) South Africa and (b) Great Britain. The size of grey dots correspond to NDVI values in January (for South Africa) and May (Great Britain). Solid lines delineate squares within which the analyses were performed (see Methods).

NDVI values averaged between 1982 and 1999 (see Bonn *et al.* 2004 for details) because (i) spatial variation in NDVI values was most pronounced during January, and (ii) these data have previously been used to describe the SER in South African birds (Bonn *et al.* 2004). Moreover, the majority of the South African avifauna is breeding in January, and, as has been shown by Hurlbert & Haskell (2003) and Hawkins (2004), seasonal productivity is more important for bird assemblages than annual productivity and correlates better with bird species richness than an annual measure.

- (2) Data on the breeding distribution of the British avifauna recorded in 1988–1991 at a resolution of 10×10 km grid cells in the British Trust for Ornithology/Scottish Ornithologists' Club/Irish Wildbird Conservancy atlas (Gibbons *et al.* 1993). We excluded marine species, vagrants and introduced species whose populations were not self-sustaining, leaving a total of 189 breeding species. Quadrats containing less than 50% land were also excluded. We delimited 21 non-overlapping squares of 8×8 grid cells (Fig. 1b), and calculated species richness for the non-overlapping quadrats of different areas. We obtained NDVI data from the NOAA/NASA Pathfinder AVHRR Land Data Set (see <http://ciesin.columbia.org/TG/RS/landpath.html>). These data were collected between 1981 and 2001 at a spatial resolution of a 0.1° latitude/longitude grid, approximately equivalent to an 8 km quadrat in the UK. Daily readings are converted to maximum values for each ten day period, which markedly reduces the effects of cloud cover. From these we calculated mean monthly NDVI values and then used GIS to re-project these data at a 10 km resolution which was compatible with our avian distribution data. We used mean May NDVI as a measure of available energy because (i) this corresponds to the breeding season; and (ii) spatial variation in NDVI values was most pronounced during this period. Following other work on the SER in British birds we also used the mean summer temperature (averaged across May, June and July) as a measure of energy availability (Turner *et al.* 1988; Lennon *et al.* 2000; Evans & Gaston 2005).

Using SAS (vs 8.2) we constructed General Linear Models of log species richness that used $\log(\text{area})$, $\log(\text{NDVI})$ and their interaction as predictors (natural logarithms were used in all cases). In such spatially structured data, spatial autocorrelation may invalidate the assumption of independent errors, invalidating estimates of correlation coefficients, regression slopes and statistical significance (Clifford *et al.* 1989; Cressie 1991; Legendre 1993; Lennon 2000; Legendre *et al.* 2002). To avoid this, a

second set of analyses was conducted using the PROC MIXED procedure to implement spatial correlation models that fit a spatial covariance matrix to the data and use this to adjust test statistics accordingly (Littell *et al.* 1996). Spatial null models which assumed exponential spatial covariance structures fit the logarithmically transformed species richness data significantly better than null models which assumed independent errors (likelihood ratio test: South Africa $\chi^2 = 948$, Great Britain $\chi^2 = 42.8$; $P < 0.0001$) and also gave a better fit than spatial models that specified alternative covariance structures (spherical, Gaussian, linear, linear log and power). Littell *et al.* (1996) provide technical details of these spatial models. As is increasingly recommended, the fit of all spatial models was assessed using Akaike's Information Criteria (AIC); we constructed all possible models (i.e. all combinations of area, NDVI and the

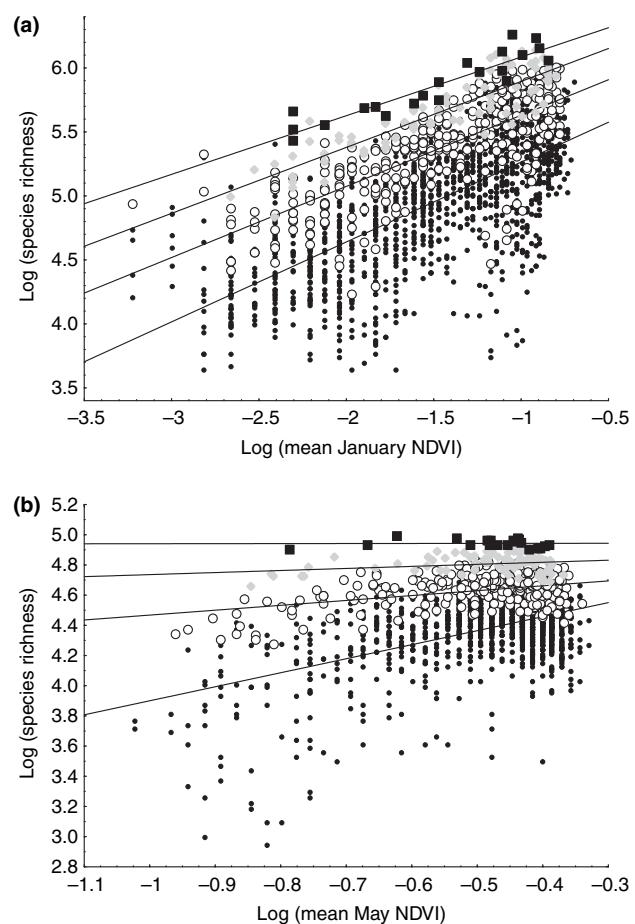


Figure 2 Relationship between logarithmically transformed NDVI and species richness in (a) South Africa and (b) Great Britain, for non-overlapping squares differing in size. Black dots, basic grid cells; white circles, squares of 2×2 (4) grid cells; grey diamonds, squares of 4×4 (16) grid cells; black squares, squares of 16×16 (64) grid cells.

interaction term NDVI \times area) and used AIC values to determine each model's weight, i.e. the probability that it provides the best fit to the data (Ginzburg & Jensen 2004; Johnson & Omland 2004).

RESULTS AND DISCUSSION

As expected, logarithmically transformed species richness was positively related both to log area and log NDVI for both avifaunas. The SER was more pronounced in South Africa, which is apparently related to low spatial variation in NDVI values in Britain compared with South Africa (Fig. 2). The interaction between log area and log NDVI was stronger in Britain than in South Africa, but was negative and significant in both cases, even when spatial autocorrelation was taken into account (Table 1). Therefore, the slope of the SER is lower for larger areas, and the slope of the SAR is lower in areas with high energy availability (Fig. 3).

Previous investigations of SERs in the British avifauna have used temperature as a measure of energy availability (Turner *et al.* 1988; Lennon *et al.* 2000; Evans & Gaston 2005). Using this metric (which was not log transformed as it is measured on an interval scale instead of a ratio scale) gave almost identical results with a highly significant negative interaction term. All of our results thus provide evidence in support of our theory that high levels of energy availability depress the slope of the SAR by elevating species' occupancies.

Our results appear to disagree with some previous findings. Weiher (1999) reported the opposite pattern, i.e. a positive relationship between productivity and the slope of the SAR so that the SAR had a higher slope in more

productive areas. However, in this study (of plants at a very local scale, 0.25–150 m²) species richness decreased monotonically with increasing productivity. In this case higher productivity is likely to be associated with lower mean species occupancies, thus increasing the slope of the SAR and actually confirming our theory relating the interaction between the SER and SAR to the effect of species occupancies. Indeed, in a study in which plant species richness increased with productivity, Pastor *et al.* (1996) documented the decrease of γ with increasing productivity.

At very large spatial scales, the latitudinal gradient in species richness has been reported to be stronger for larger areas (Stevens & Willig 2002; Hillebrand 2004). As energy availability is often higher in tropical regions this may also appear to contradict our findings. However, latitudinal gradients in species richness may arise through many factors other than energy availability, including topography and habitat diversity, and thus latitude is not an appropriate surrogate for energy availability (Rahbek & Graves 2001; Hawkins & Diniz-Filho 2004). Southern parts of North America, for example, are considerably drier and have accordingly lower NDVI than more northern areas (see Hurlbert & Haskell 2003). It is then not surprising that the slope of the SAR has been reported to be higher at low latitudes in North American non-volant mammals (Rodríguez & Arita 2004), but when humid Central and South America were also included the opposite pattern was found (i.e. γ decreasing towards the tropics; Lyons & Willig 2002). As such, these findings are actually all in accord with our theory.

In summary, our theory should apply in all situations where available energy increases species richness by

Table 1 Relationships between species richness of South African and British avian assemblages and area, NDVI, and the interaction between area and NDVI

(a) Independent error models

Region	Log area	Log NDVI	Log area \times log NDVI	r^2
South Africa	$F_{1,1769}$ 45.3****	$F_{1,1769}$ 1473.6****	$F_{1,1769}$ 6.0††	0.591
UK	$F_{1,1775}$ 74.8****	$F_{1,1775}$ 572.3****	$F_{1,1775}$ 66.2††††	0.488

(b) Models that take spatial autocorrelation into account

Region	Log area	Log NDVI	Log area \times log NDVI	Model weight
South Africa	$F_{1,1769}$ 98.3****	$F_{1,1769}$ 257.3****	$F_{1,1769}$ 13.4†††	0.969
UK	$F_{1,1775}$ 165.7****	$F_{1,1775}$ 178.2****	$F_{1,1775}$ 133.2††††	>0.999

Model weight is calculated following Johnson & Omland (2004) and gives the probability that the model presented provides the best fit to the data out of all models that could be constructed given the predictor variables.

Positive effects: * P < 0.05; ** P < 0.01; *** P < 0.001; **** P < 0.0001.

Negative effects: † P < 0.05; ‡ P < 0.01; ‡‡ P < 0.001; ‡‡‡ P < 0.0001.

The multiple regression equations are as follows:

South Africa – independent error model: $\log(\text{richness}) = 5.895 + 0.189\log(\text{area}) + 0.624\log(\text{NDVI}) - 0.043\log(\text{area}) \times \log(\text{NDVI})$; spatial model: $\log(\text{richness}) = 5.635 + 0.195\log(\text{area}) + 0.452\log(\text{NDVI}) - 0.045\log(\text{area}) \times \log(\text{NDVI})$.

UK – independent error model: $\log(\text{richness}) = 0.626 + 1.554\log(\text{area}) + 0.912\log(\text{NDVI}) - 0.338\log(\text{area}) \times \log(\text{NDVI})$; spatial model: $\log(\text{richness}) = 0.715 + 1.588\log(\text{area}) + 0.890\log(\text{NDVI}) - 0.345\log(\text{area}) \times \log(\text{NDVI})$.

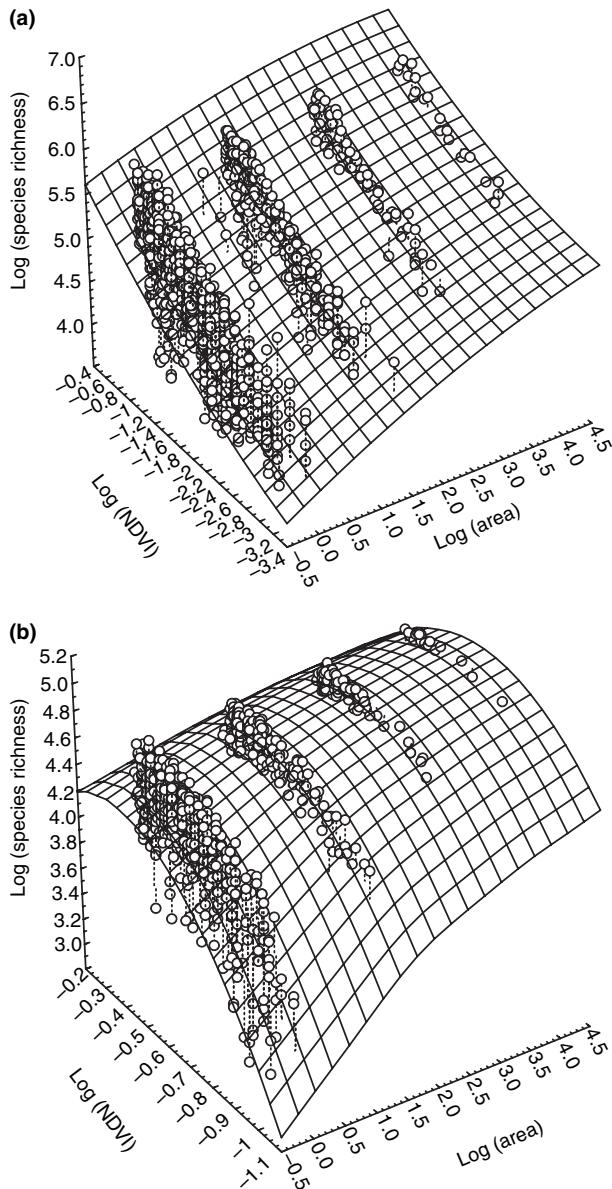


Figure 3 The three-dimensional species-area-energy relationship for (a) South Africa and (b) Great Britain. The surface is fitted by a spline.

increasing species occupancies. These situations appear to be sufficiently common to promote frequent three-dimensional species-area-energy relationships characterized by a negative interaction between area and energy.

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REFERENCES

- Arrhenius, O. (1921). Species and area. *J. Ecol.*, 9, 95–99.
- Bonn, A., Storch, D. & Gaston, K.J. (2004). Structure of the species-energy relationship. *Proc. R. Soc. Lond. B*, 271, 1685–1691.
- Chase, J.M. & Leibold, M.A. (2002). Spatial scale dictates the productivity–biodiversity relationship. *Nature*, 416, 427–429.
- Chave, J., Muller-Landau, H.C. & Levin, S.A. (2002). Comparing classical community models: theoretical consequences for patterns of diversity. *Am. Nat.*, 159, 1–23.
- Chown, S.L., van Rensburg, B.J., Gaston, K.J., Rodrigues, A.S.L. & van Jaarsveld, A.S. (2003). Species richness, human population size and energy: conservation implications at a national scale. *Ecol. Appl.*, 13, 1233–1241.
- Clifford, P., Richardson, S. & Hemon, D. (1989). Assessing the significance of the correlation between two spatial processes. *Biometrics*, 45, 123–134.
- Connor, E.F. & McCoy, E.D. (1979). The statistics and biology of the species-area relationship. *Am. Nat.*, 113, 791–833.
- Cressie, N. (1991). *Statistics for Spatial Data*. Wiley, New York.
- Currie, D. (1991). Energy and large-scale patterns of animal- and plant-species richness. *Am. Nat.*, 137, 27–49.
- 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.
- Evans, K.L. & Gaston, K.J. (in press). People, energy and avian species richness. *Glob. Ecol. Biogeogr.*, 14, 187–196.
- Evans, K.L., Warren, P.H. & Gaston, K.J. (in press). Species-energy relationships at the macroecological scale: a review of the mechanisms. *Biol. Rev.*, 80, 1–25.
- Gaston, K.J. (2000). Global patterns in biodiversity. *Nature*, 405, 220–227.
- Gibbons, D.W., Reid, J.B. & Chapman, R.A. (1993). *The New Atlas of Breeding Birds in Britain and Ireland: 1988–91*. T & AD Poyser, London.
- Ginzburg, L.R. & Jensen, C.X.J. (2004). Rules of thumb for judging ecological theories. *Trends Ecol. Evol.*, 19, 121–126.
- Gleason, H.A. (1922). On the relation between species and area. *Ecology*, 3, 158–162.
- Harrison, J.A., Allan, D.G., Underhill, L.G., Herremans, M., Tree, A.J., Parker, V. *et al.* (1997). *The Atlas of Southern African Birds*, Vol. I & II. Bird Life South Africa, Johannesburg.
- Hawkins, B.A. (2004). Summer vegetation, deglaciation and the anomalous bird diversity gradient in eastern North America. *Global Ecol. Biogeogr.*, 13, 321–325.
- Hawkins, B.A. & Diniz-Filho, J.A.F. (2004). ‘Latitude’ and geographic patterns in species richness. *Ecography*, 27, 268–272.
- 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.

- He, F.L. & Legendre, P. (2002). Species diversity patterns derived from species-area models. *Ecology*, 85, 1185–1198.
- Hillebrand, H. (2004). On the generality of the latitudinal diversity gradient. *Am. Nat.*, 163, 192–211.
- 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.
- Johnson, J.B. & Omland, K.S. (2004). Model selection in ecology and evolution. *Trends Ecol. Evol.*, 19, 101–108.
- Kaspari, M., Yuan, M. & Alonso, L. (2003). Spatial grain and the causes of regional diversity gradients in ants. *Am. Nat.*, 161, 459–477.
- Kerr, J.T. & Ostrovsky, M. (2003). From space to species: ecological applications for remote sensing. *Trends Ecol. Evol.*, 18, 299–305.
- Legendre, P. (1993). Spatial autocorrelation: trouble or new paradigm? *Ecology*, 74, 1659–1673.
- Legendre, P., Dale, M.R.T., Fortin, M.J., Gurevitch, J., Hohn, M. & Myers, D. (2002). The consequences of spatial structure for design and analysis of ecological field surveys. *Ecography*, 25, 601–615.
- Lennon, J.J. (2000). Red shifts and red herrings in geographical ecology. *Ecography*, 23, 101–113.
- Lennon, J.J., Greenwood, J.J.D. & Turner, J.R.G. (2000). Bird diversity and environmental gradients in Britain: a test of species energy hypothesis. *J. Anim. Ecol.*, 96, 581–598.
- Littell, R.C., Milliken, G.A., Stroup, W.W. & Wolfinger, R.D. (1996). *SAS® System for Mixed Models*. SAS Institute Inc., Cary, NC.
- Lyons, S.K. & Willig, M.R. (2002). Species richness, latitude, and scale-sensitivity. *Ecology*, 83, 47–58.
- 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.
- Mittelbach, G.G., Scheiner, S.M. & Steiner, C.F. (2003). What is the observed relationship between species richness and productivity? *reply*. *Ecology*, 84, 3390–3395.
- Pastor, J., Downing, A. & Erickson, H.E. (1996). Species-area curves and diversity-productivity relationships in beaver meadows of Voyageurs National Park, Minnesota, USA. *Oikos*, 77, 399–406.
- Rahbek, C. & Graves, G.R. (2001). Multiscale assessment of patterns of avian species richness. *Proc. Natl. Acad. Sci. U.S.A.*, 98, 4534–4539.
- van Rensburg, B.J., Chown, S.L. & Gaston, K.J. (2002). Species richness, environmental correlates, and spatial scale: a test using South African birds. *Am. Nat.*, 159, 566–577.
- Rodríguez, P. & Arita, H.T. (2004). Beta diversity and latitude in North American mammals: testing the hypothesis of covariation. *Ecography*, 27, 547–556.
- Rosenzweig, M.L. (1995). *Species Diversity in Space and Time*. Cambridge University Press, Cambridge.
- Scheiner, S.M., Cox, S.B., Willig, M., Mittelbach, G.G., Osenberg, C. & Kaspari, M. (2000). Species richness, species-area curves and Simpson's paradox. *Evol. Ecol. Res.*, 2, 791–802.
- Šízling, A.L. & Storch, D. (2004). Power-law species-area relationships and self-similar species distributions within finite areas. *Ecol. Lett.*, 7, 60–68.
- Stevens, R.D. & Willig, M.R. (2002). Geographical ecology at the community level: perspectives on the diversity of new world bats. *Ecology*, 83, 545–560.
- Turner, J.R.G., Lennon, J.J. & Lawrenson, J.A. (1988). British bird species distributions and the energy theory. *Nature*, 335, 539–541.
- 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.
- Weiher, E. (1999). The combined effects of scale and productivity on species richness. *J. Ecol.*, 87, 1005–1011.
- Whittaker, H. I. & Heegaard, E. (2003). What is the observed relationship between species richness and productivity? *Comment*. *Ecology*, 84, 3384–3390.
- Williamson, M.H. (1988). Relationship of species number to area, distance and other variables. In: *Analytical Biogeography* (eds. Myers, A.A. & Giller, P.S.). Chapman & Hall, London, pp. 91–115.
- Woodward, F.I., Lomas, M.R. & Lee, S.E. (2001). Predicting the future production and distribution of global terrestrial vegetation. In: *Terrestrial Global Productivity* (eds. Roy, J., Saugier, B. & Mooney, H.). Academic Press, San Diego, CA, pp. 519–539.
- Wright, D.H. (1983). Species-energy theory: an extension of species-area theory. *Oikos*, 41, 496–506.

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