

Spatial scale, abundance and the species–energy relationship in British birds

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Summary

1. The spatial scale of analysis may influence the nature, strength and underlying drivers of macroecological patterns, one of the most frequently discussed of which is the relationship between species richness and environmental energy availability.

2. It has been suggested that species–energy relationships are hump-shaped at fine spatial grains and consistently positive at larger regional grains. The exact nature of this scale dependency is, however, the subject of much debate as relatively few studies have investigated species–energy relationships for the same assemblage across a range of spatial grains. Here, we contrast species–energy relationships for the British breeding avifauna at spatial grains of 1 km × 1 km, 2 km × 2 km and 10 km × 10 km plots, while maintaining a constant spatial extent.

3. Analyses were principally conducted using data on observed species richness. While survey work may fail to detect some species, observed species richness and that estimated using nonparametric techniques were strongly positively correlated with each other, and thus exhibit very similar spatial patterns. Moreover, the forms of species–energy relationships using observed and estimated species richness were statistically indistinguishable from each other.

4. Positive decelerating species–energy relationships arise at all three spatial grains. There is little evidence that the explanatory power of these relationships varies with spatial scale. However, ratios of regional (large-scale) to local (small-scale) species richness decrease with increasing energy availability, indicating that local richness responds to energy with a steeper gradient than does regional richness. Local assemblages thus sample a greater proportion of regional richness at higher energy levels, suggesting that spatial turnover of species richness is lower in high-energy regions. Similarly, a crude measure of temporal turnover, the ratio of cumulative species richness over a 4-year period to species richness in a single year, is lower in high-energy regions. These negative relationships between turnover and energy appear to be causal as both total and mean occupancy per species increases with energy.

5. While total density in 1 km × 1 km plots correlates positively with energy availability, such relationships are very weak for mean density per species. This suggests that the observed association between total abundance and species richness may not be mediated by population extinction rates, as predicted by the more individuals hypothesis.

6. The sampling mechanism suggests that species–energy relationships arise as high-energy areas support a greater number of individuals, and that random allocation of these individuals to local areas from a regional assemblage will generate species–energy relationships. While randomized local species–energy relationships are linear and positive, predicted richness is consistently greater than that observed. The mismatch between the observed and randomized species–energy relationships probably arises as a consequence of the aggregated nature of species distributions. The sampling mechanism, together with species spatial aggregation driven by limited habitat availability, may thus explain the species–energy relationship observed at this spatial scale.

Key-words: energy availability, sampling effects, spatial turnover, species richness, temperature, temporal turnover.

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Introduction

Describing spatial patterns in species richness, and identifying their underlying drivers, is of fundamental importance in ecology. Such patterns, like many of those in ecology, are scale-dependent; that is, their form, strength and the nature of their underlying causal mechanisms vary with the extent of the study area and the size of the unit of investigation, i.e. spatial grain (Wright, Currie & Maurer 1993; Blackburn & Gaston 2002; McGeoch & Gaston 2002; Rahbek 2005). The strong association between species richness and environmental energy, the species–energy relationship (Hawkins *et al.* 2003; Pimm & Brown 2004), is a prime example of an apparently scale-dependent pattern. As spatial grain increases, unimodal relationships typically decline in frequency, and positive monotonic ones become more common (Waide *et al.* 1999; Mittelbach *et al.* 2001). However, the exact nature of the species–energy relationship that predominates at any particular spatial scale remains strongly contested (Mittelbach, Steiner & Scheiner 2003; Whittaker & Heegaard 2003; Gillman & Wright 2006). This is partly because relatively few of the numerous studies that have described the form of the species–energy relationship have done so across a range of spatial scales for a single assemblage. Among those that have, the finest spatial grains have typically remained rather coarse (Rahbek & Graves 2001; van Rensburg, Chown & Gaston 2002; Hurlbert & Haskell 2003; Storch, Evans & Gaston 2005).

This lack of studies conducted across multiple scales also contributes to a lack of detail in most discussions of the factors contributing to scale dependency in the species–energy relationship. It is commonly simply stated that scale dependency is an inevitable outcome of the nonlinear relationship between species richness and area, or that it arises because the mechanisms influencing species richness vary with spatial scale (Rosenzweig 1995). For example, the species interactions that are often thought to structure local assemblages, such as competition, predation and parasitism, operate at a fine spatial grain and their effects may thus be more noticeable at such a scale, contrasting with the influence of regional processes that may be more detectable at coarser scales (Shurin & Allen 2001; Kneitel & Chase 2004; Srivastava 2005). Therefore, while detailed investigations of the relative roles that different mechanisms play in generating species–energy relationships at different spatial scales are currently rare, they are central to understanding scale dependency.

A crucial question related to the species–energy relationship is whether the increase of species richness with energy availability is accompanied by an increase in abundance. This is a key prediction of the more individuals hypothesis (MIH), which suggests that in high-energy regions species populations are larger, buffering them from extinction and elevating species richness (Wright 1983). While an increase in total abundance with available energy has been documented in many cases (Kaspari, Yuan & Alonso 2003; Hurlbert 2004; Pautasso & Gaston 2005; Evans, James & Gaston 2006), such patterns could be generated by a number of alternative mechanisms, most notably through a sampling effect (Evans,

Warren & Gaston 2005a). Moreover, evidence for other predictions derived from the MIH, such as an increase in mean species abundance with energy availability, is limited and species richness has been observed to increase with energy availability without an increase in total abundance (Currie *et al.* 2004; Evans *et al.* 2005a, 2006; Evans, Greenwood & Gaston 2005b).

An alternative to abundance-focused mechanisms for the species–energy relationship is that greater species richness in high-energy areas is a consequence of a positive association between energy availability and habitat heterogeneity, with the latter promoting greater spatial turnover and thus higher species richness (Hurlbert 2004). Indeed, positive associations between spatial turnover and energy have been documented in a number of, largely botanical, assemblages (Chase *et al.* 2000; Chase & Leibold 2002; Chalcraft *et al.* 2004). While such patterns have been shown to be negative within some avian assemblages, they have only been observed at relatively large scales and the direction of the relationship may be reversed at finer scales (Bonn, Storch & Gaston 2004; Storch *et al.* 2005; Evans, Lennon & Gaston, in press). Crucially, empirical evidence indicates that positive relationships between spatial turnover and energy may be associated with a switch from unimodal to linear species–energy relationships as spatial grain increases (Chase & Leibold 2002). To understand scale dependency in species–energy relationships it is thus necessary not just to describe such patterns for a single assemblage across a range of scales, but to explore simultaneously the relationship between energy availability, abundance, species richness, and species turnover on multiple spatial scales. Doing so enables one to assess how the relative contributions of different putative drivers of the species–energy relationship vary with spatial scale.

Here we explore scale dependency in the influence of environmental energy availability on assemblage structure. We use the British breeding avifauna as a case study and focus on three spatial grains: 1 km × 1 km, 2 km × 2 km and 10 km × 10 km. We conduct analyses using both observed species richness and that estimated using jackknife and bootstrapping procedures. We first describe the nature of the species–energy relationship at these contrasting spatial scales. Second, we assess how ratios of regional (large-scale) to local (small-scale) species richness vary with increasing energy availability. We also conduct equivalent analyses assessing the influence of energy availability on spatial variation in the ratio of species richness measured over a large number of years to that measured in a single year, which represents a crude measure of temporal turnover. Third, we assess how spatial scale influences how occupancy and abundance, measured both across all species and as per species means, respond to energy. We thus provide one of the few studies that simultaneously investigates scale dependency in the species–energy and abundance–energy relationships for the same assemblage. Finally, we use abundance data to contrast observed and randomized species–energy relationships as a means of assessing the extent to which sampling effects may drive species–energy relationships.

Methods

AVIAN SURVEY METHODS

Data at the 10 km × 10 km and 2 km × 2 km spatial grains were obtained from the second BTO/SOC/IW breeding bird atlas (Gibbons, Reid & Chapman 1993). These record the summer (breeding) distribution of the British avifauna as presence/absence during April–July 1988–91. Data are based on timed visits, of 2 h duration (split into two 1 h counts during the early and late parts of the breeding season), to at least eight 2 km × 2 km plots within each 10 km × 10 km plot and supplemented with additional records collated haphazardly by members of the public during the four survey years. The vast majority of the data for a 10 km × 10 km square were collated within three survey years, with the additional fourth year being used to fill in gaps in coverage. These constitute one of the best sets of distributional data for any assemblage and have been successfully used in numerous macroecological studies.

Data at the 1 km × 1 km spatial grain were obtained from the BTO/JNCC/RSPB Breeding Bird Survey (BBS; see Raven, Noble & Baillie 2005 for full details). BBS squares are selected from a random stratified sample according to 83 BTO organizational regions, roughly counties, across the UK. Data from Northern Ireland are not included here. Avian data are collected twice (early April to mid-May, and mid-May to late June). Adult birds are recorded within 200 m sections along two 1 km transects in one of three distance bands (0–25 m, 25–100 m, > 100 m) within each 1 km × 1 km square. Habitat within each 200 m transect section was recorded according to a four level hierarchical coding system that documents the main habitat, such as farmland or woodland, together with finer level habitat features (Crick 1992). For resident species breeding population density was estimated using data from the early visit in order to minimize the possibility of inflating density estimates due to the inclusion of juveniles. For migrants only late visits were used to avoid underestimating population size if some individuals had not arrived when the early visit was conducted. The one exception was corn bunting *Miliaria calandra*, a late breeding resident species for which we have used data from the late BBS visit only.

SPECIES RICHNESS DATA

We calculated five species richness measures from these data: (1) total 10 km × 10 km species richness (collected over a maximum of 4 years); (2) standardized 10 km × 10 km species richness based on cumulative data from eight 2 km × 2 km squares selected randomly from those that were visited in each 10 km × 10 km square (typically collected in a single year); (3) 2 km × 2 km species richness for a single year (some squares were visited more than once either by different observers and/or in different years, and in these cases we randomly selected one set of observations); (4) 1 km × 1 km species richness in a single year (2000); and (5) cumulative 1 km × 1 km species richness (1998–2000), which matches the number of years spent collating total richness data for the majority of 10 km × 10 km squares. In all analyses we excluded marine species and vagrants, but retained the more naturalized introductions, giving a total of 189 species. We excluded data from all 10 km × 10 km squares that contained less than 50% land, and also excluded data from smaller units located within such squares.

Survey work may fail to detect all of the species present in a given area, and this may bias our interpretation of spatial patterns in species richness. Here, we investigate this possibility. There are a plethora of species richness estimators available, and a number of

papers have attempted to assess which are the most reliable. Nonparametric estimators are almost invariably recommended as providing the best estimates, with jackknife estimators being particularly recommended when there is variation in spatial grain and for use with presence/absence data (Palmer 1991; Boulinier *et al.* 2001; Hortal, Borges & Gaspar 2006; Walther & Moore 2005; Kéry & Schmid 2006). We used the R program (R Development Core Team 2005) to calculate jackknife estimates of species richness (specifically the specpool option in the Vegan package), and also calculated the bootstrap estimator for further comparison. We did so at the 1 km × 1 km spatial grain, using data from 2000, by treating each of the 10 transect sections as repeated samples of the same assemblage. Similarly, we used eight randomly selected 2 km × 2 km cells (those used to estimate standardized species richness) as repeated samples of the 10 km × 10 km cells. Analysis indicated that using estimated rather than observed species richness data did not alter our results or conclusions (see below).

Using the observed species richness data and a nested design we calculated four measures of the ratios of regional and mean component local species richness as metrics of spatial turnover: (1) total 10 km × 10 km and mean cumulative 1 km × 1 km richness; (2) standardized 10 km × 10 km and mean single year 1 km × 1 km richness; (3) standardized 10 km × 10 km and mean 2 km × 2 km richness; and (4) 2 km × 2 km and mean single year 1 km × 1 km richness. We consider these pairs of species richness estimates to be comparable because each member of a pair is collated over the same number of years. Similarly we measure the ratio of cumulative species richness estimated over a number of years to species richness in a single year. This metric provides a useful first approximation of temporal turnover. An equivalent measure of temporal turnover could not be constructed at the 10 km × 10 km spatial grain as at this grain, single and multiple year measures of species richness differ in factors other than the number of years over which species richness data were collated. These metrics can be considered broad sense measures of turnover (Koleff, Gaston & Lennon 2003).

OCCUPANCY AND ABUNDANCE

We used the total number of occupied 2 km × 2 km plots, summed across all species and based only on the eight randomly selected plots as a standardized measure of total occupancy at the resolution of 10 km × 10 km plots. We calculated equivalent data on mean occupancy per species. Empirical data indicate that occupancy and abundance are positively correlated in British birds (Gaston, Blackburn & Gregory 1997) and thus this measure of occupancy provides some indication of avian abundance in a 10 km × 10 km plot.

We used distance sampling software (DISTANCE, version 4.1 Release 2; Buckland *et al.* 2001; Thomas *et al.* 2004) to calculate total avian density within each 1 km × 1 km plot surveyed in 2000 (the year with the most data). We modelled the decline in detectability with distance from the transect line and took the heterogeneity in detectability between species, habitats and regions into account. We calculated detectability functions for each species with 40 or more observations; for other species we used the detectability function for a commoner surrogate species, which was as similar to the rare species in its conspicuousness and habitat type as possible (Table S1). Detectability functions were constructed using nine main habitat types (broad-leaved woodland, coniferous woodland, mixed woodland, scrub, seminatural grassland, heath and bog, farmland, humans and water bodies, based on Crick 1992) and 11 regions (nine English Government Office Regions, Wales and Scotland) as factors. We fitted half-normal and hazard-rate key functions and

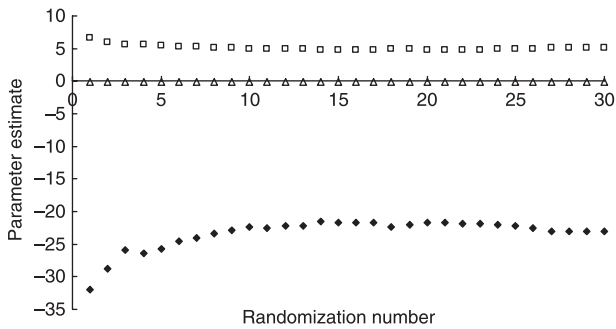


Fig. 1. Parameter estimates from regression of randomized species richness in 1 km × 1 km squares on summer temperature. Parameter estimate values have stabilized after 30 randomizations, and also did so when other measures of environmental energy were used. Species richness data were obtained from 30 random draws, from the regional species pool, of the number of individuals observed in each square. Symbols represent the running mean of the parameter estimates for temperature (open squares), temperature² (open triangles), and the intercept (solid black diamonds).

selected the detectability function that provided the best fit to the data as judged by Akaike Information Criteria (AIC) values. Once this best fitting model had been chosen for a species, it was applied to the encounters from surveyed squares to produce an estimate of the number of individuals of that species within each square; these were summed to estimate total avian density. We also calculated mean density per species present in the local assemblage.

RANDOMIZED SPECIES RICHNESS

We used the summed observed numbers of each species in 1 km × 1 km squares as a regional species pool from which individuals were drawn at random, without replacement, and allocated to each square according to the observed total number of individual birds in that square. Using the R package we conducted 30 randomization runs; for each run we calculated the randomized species richness for each 1 km × 1 km square and the consequent parameters of the species–energy relationship. These parameter estimates had stabilized after 30 randomizations (Fig. 1) and we used the mean data in comparisons of randomized and observed patterns in species richness. Constructing the regional species pool using the observed number of individuals provides a more conservative test of differences from observed patterns than using the estimated densities obtained from distance sampling. While we only present the former method here, both led to identical conclusions.

ENERGY METRICS

Environmental productivity limits the amount of energy available to consumers. In high northern latitudes, such as Britain, plant productivity is not markedly influenced by water availability, and temperature is a good measure of plant productivity in such regions (Hawkins *et al.* 2003). High temperatures may also reduce the energetic requirements of endotherms by enabling them to divert resources away from maintaining their body temperature (the thermoregulatory load hypothesis, Lennon, Greenwood & Turner 2000). An alternative surrogate measure of plant productivity is the Normalized Difference Vegetation Index (NDVI), which is a satellite derived measure of the greenness of vegetation that is strongly and

positively correlated with plant productivity (Kerr & Ostrovsky 2003). We used both NDVI and temperature as metrics of energy availability.

We used gridded mean monthly temperature data at the resolution of 10 km × 10 km squares that were derived from meteorological recording station readings for the period 1961–90 using surface interpolation techniques (Barrow, Hulme & Jiang 1993). From these data we calculated mean monthly summer (May, June and July) and mean monthly annual temperature. The measure of summer temperature used is strongly positively and linearly correlated ($r^2 = 0.97$, $P < 0.0001$) with that used in previous investigations of the species–energy relationship in British birds (e.g. Lennon *et al.* 2000; Evans *et al.* 2005b; Evans, Greenwood & Gaston 2005c) although the latter concerned the mean temperature in June, July and August.

NDVI data were obtained from the NOAA/NASA Pathfinder AVHRR Land Data Set (see <http://www.ciesin.org/>). These data were collected between 1981 and 2001 at a spatial resolution of a 0.1° latitude/longitude grid. We calculated mean monthly summer (May, June and July) and mean monthly annual NDVI values and then used GIS to re-project these data at the resolution of 10 km × 10 km squares.

We use data relating to long-term averages of both energy metrics for four reasons. First, pragmatically, due to issues of data availability. Second, with NDVI data the use of a long-term average smoothes out anomalies created by heavy cloud cover over a given region in any one year. Third, the use of long-term averages reduces the influence of extreme annual fluctuations in environmental conditions. Finally, and related to the last point, species distributions do not respond instantaneously when environmental conditions change but can take some years to adjust to new conditions.

ANALYSES

In order to meet the assumptions of normality, avian density data were square root transformed and the ratios of regional to local richness were logarithmically transformed to base 10. We first regressed each of the species richness measures against the four measures of energy availability (summer and annual measures of temperature and NDVI), with square terms of the latter used to detect simple nonlinear relationships. We assessed which energy metric provided the best fit to the data using an information theoretic approach (Johnson & Omland 2004). The model with the smallest AIC value was considered to provide the best fit to the data and we calculated each model's weight, i.e. the probability that it provides the best fit to the data. We then regressed the ratio of regional to local richness, and multiple to single year species richness against the energy metric that was the best predictor of species richness (see above). Finally, we regressed the abundance measures against each of our energy metrics.

We first constructed General Linear Models (GLMs) that assumed independent errors between the data points. Spatial autocorrelation may, however, invalidate the assumption of independent errors distorting classical tests of association and rendering correlation coefficients, regression slopes and associated significance tests misleading (Cressie 1991; Lennon 2000; Legendre *et al.* 2002). To avoid this, analyses were also 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, i.e. ones that lacked predictor variables, which assumed exponential spatial covariance structures generally fitted the data significantly better

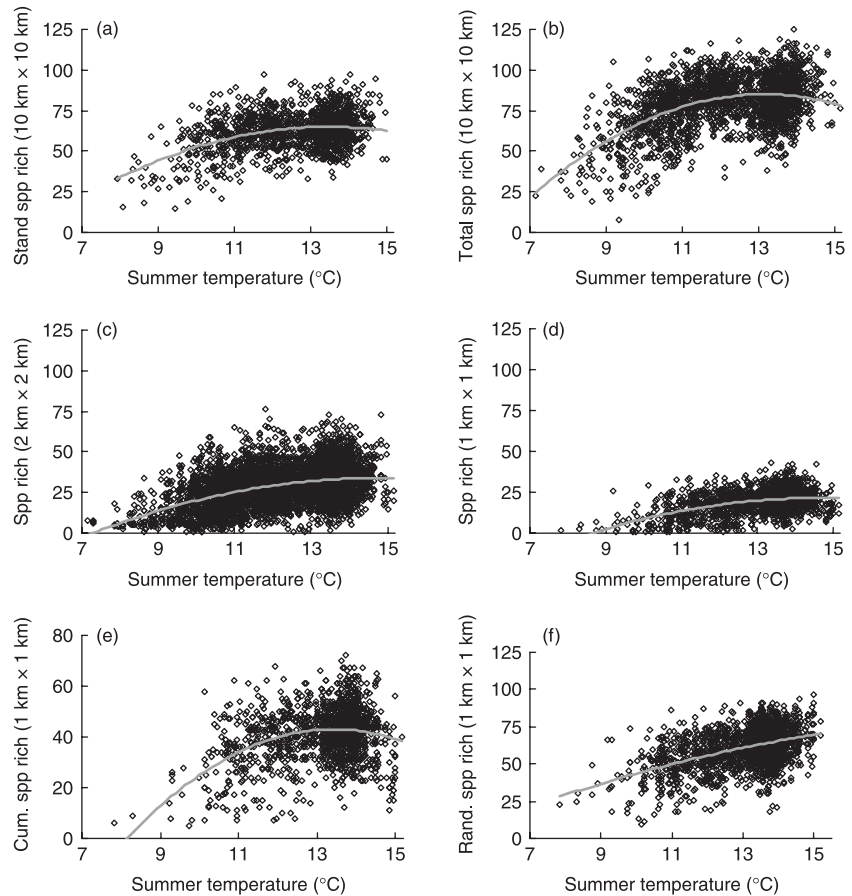


Fig. 2. Relationships between mean summer temperature and species richness for: (a) standardized species richness in 10 km × 10 km squares; (b) total species richness in all 10 km × 10 km squares; (c) species richness in 2 km × 2 km squares; (d) 1 km × 1 km squares in a single year; (e) cumulative species richness in 1 km × 1 km squares; and (f) mean species richness across 30 randomized draws of individuals from a regional species pool in 1 km × 1 km squares. Grey lines indicate relationships fitted in nonspatial models (Table 1a). To facilitate illustration data points in panel c are from a maximum of three randomly selected 2 km × 2 km plots per 10 km × 10 km plot.

than independent error null models (likelihood ratio tests $P < 0.0001$) and also gave a better fit than spatial models that specified alternative covariance structures (spherical, Gaussian, linear, linear log and power). The two exceptions to this were avian density and the ratio of 2 km × 2 km and 1 km × 1 km richness measures; these did not exhibit significant spatial autocorrelation ($P > 0.05$) and we thus only fitted nonspatial models to these variables.

Results

Observed and estimated species richness are strongly positively correlated (minimum $r = 0.85$; maximum $r = 0.99$; Table S2), suggesting that using observed species richness does not generate major biases in spatial patterns in species richness. However, the slope of the relationship between estimated and observed species richness is steeper than 1, particularly at the 1 km × 1 km grain, so there is greater underestimation of species richness in the most species rich areas. To check if this was sufficiently marked to influence the nature of the species–energy relationship we compared the parameter estimates of such relationships constructed using observed and estimated species richness. At both the 1 km × 1 km and the 10 km × 10 km spatial grain these parameter estimates were statistically indistinguishable (Table S3). We thus conclude that the use of observed rather than estimated species richness estimates will not have altered our conclusions regarding the spatial dependency of the species–energy relationship.

Regardless of spatial grain, summer temperature was consistently the strongest predictor of observed species richness; observed species–energy relationships consistently followed positive decelerating curves at all spatial grains (Table 1; Fig. 2a–e). In contrast, the randomized species–energy relationship was linear (Fig. 2f). At any given temperature randomized species richness was always higher than that observed, and the absolute increase in randomized richness relative to observed richness increases at higher levels of the latter (upper and lower 95% confidence intervals of the slope of a reduced major axis regression of observed and randomized richness are 1.31 and 1.39, respectively; Fig. 3). At both the smallest and largest spatial grains the nature of species–energy relationships is similar whether species richness is calculated in a single year or over a number of years, although species richness is naturally higher in the latter case. The explanatory power of observed species–energy relationships does not vary in a consistent systematic manner with spatial grain.

The log-transformed ratio of regional to local richness is negatively related to summer temperature when regional richness is measured at a spatial grain of 10 km × 10 km, regardless of the grain at which local richness is measured (Table 2a; Fig. 4a–c). A less clear pattern between the log-transformed ratio of regional to local richness and summer temperature emerges when the former are measured at respective grains of 2 km × 2 km and 1 km × 1 km, although there is still

Table 1. Species–energy relationships at different spatial scales for (a) independent error models and (b) spatial models (randomized species richness does not exhibit significant spatial autocorrelation, so spatial models are not presented for this response variable). For each combination of species richness measure and predictor variable we present the best fitting model as assessed by Akaike Information Criterion (AIC); lower values indicate a better fit. In addition, for each species richness measure we provide the model weight for the overall best fitting model, i.e. the probability that the model provides the best fit to the data out of all those constructed. Note that r^2 values cannot be provided for the spatial models

Species richness measure	Predictor	x	x^2	AIC	Model weight	r^2
(a)						
Single year 1 km × 1 km	sum temp	$F_{1,1982} = 70.5+ + + +$	$F_{1,1982} = 51.5- - - -$	12883.1	> 0.999	19.5%
	ann temp	$F_{1,1982} = 60.6+ + + +$	$F_{1,1982} = 36.0- - - -$	12940.9		17.1%
	sum NDVI	$F_{1,1982} = 26.0+ + + +$	$F_{1,1982} = 24.1- - - -$	13261.0		1.6%
	ann NDVI	$F_{1,1982} = 6.2+$	$F_{1,1982} = 5.5-$	13283.4		0.5%
Randomized single year 1 km × 1 km	sum temp	$F_{1,1982} = 452.2+ + + +$		14066.8	0.754	18.6%
	ann temp	$F_{1,1982} = 381.44+ + + +$		14125.1		16.1%
	sum NDVI	$F_{1,1981} = 12.4+ + +$	$F_{1,1981} = 14.3- - -$	14430.0		1.4%
	ann NDVI	$F_{1,1981} = 0.03 \text{ NS } -$	$F_{1,1981} = 0.01 \text{ NS } +$	14455.8		1.1%
Cumulative 1 km × 1 km	sum temp	$F_{1,1507} = 109.3+ + + +$	$F_{1,1507} = 95.4- - - -$	11072.8	> 0.999	14.1%
	ann temp	$F_{1,1507} = 88.4+ + + +$	$F_{1,1507} = 70.7- - - -$	11106.0		12.2%
	sum NDVI	$F_{1,1507} = 25.7+ + + +$	$F_{1,1507} = 21.6- - - -$	11224.5		3.9%
	ann NDVI	$F_{1,1507} = 13.8+ + +$	$F_{1,1507} = 12.0- - -$	11258.1		1.7%
2 km × 2 km	sum temp	$F_{1,23076} = 323.6+ + + +$	$F_{1,23076} = 204.2- - - -$	173015.6	> 0.999	15.0%
	ann temp	$F_{1,23076} = 365.0+ + + +$	$F_{1,23076} = 185.5- - - -$	173608.1		12.8%
	sum NDVI	$F_{1,23076} = 197.8+ + + +$	$F_{1,23076} = 159.2- - - -$	176188.9		2.4%
	ann NDVI	$F_{1,23076} = 141.6+ + + +$	$F_{1,23076} = 124.4- - - -$	176523.7		1.0%
Standardized 10 km × 10 km	sum temp	$F_{1,1500} = 68.6+ + + +$	$F_{1,1500} = 55.4- - - -$	11307.3	> 0.999	14.4%
	ann temp	$F_{1,1500} = 87.1+ + + +$	$F_{1,1500} = 66.8- - - -$	11341.0		12.5%
	sum NDVI	$F_{1,1500} = 20.3+ + + +$	$F_{1,1500} = 16.9- - - -$	11474.2		3.1%
	ann NDVI	$F_{1,1500} = 26.4+ + + +$	$F_{1,1500} = 24.5- - - -$	11490.8		2.1%
Total 10 km × 10 km same cells as above	sum temp	$F_{1,1500} = 76.7+ + + +$	$F_{1,1500} = 65.7- - - -$	11939.4	> 0.999	11.1%
	ann temp	$F_{1,1500} = 106.3+ + + +$	$F_{1,1500} = 90.3- - - -$	11960.5		9.9%
	sum NDVI	$F_{1,1500} = 16.7+ + + +$	$F_{1,1500} = 14.0- - - -$	12058.9		2.5%
	ann NDVI	$F_{1,1500} = 53.4+ + + +$	$F_{1,1500} = 50.6- - - -$	12040.4		3.7%
Total 10 km × 10 km all cells	sum temp	$F_{1,2263} = 219.9+ + + +$	$F_{1,2263} = 179.4- - - -$	18331.5	> 0.999	23.4%
	ann temp	$F_{1,2263} = 185.9+ + + +$	$F_{1,2263} = 136.9- - - -$	18502.7		17.4%
	sum NDVI	$F_{1,2263} = 62.2+ + + +$	$F_{1,2263} = 45.0- - - -$	18581.9		13.7%
	ann NDVI	$F_{1,2263} = 176.5+ + + +$	$F_{1,2263} = 151.1- - - -$	18602.9		12.9%
(b)						
Single year 1 km × 1 km	sum temp	$F_{1,1982} = 70.5+ + + +$	$F_{1,1982} = 51.5- - - -$	12883.4	> 0.999	
	ann temp	$F_{1,1982} = 60.3+ + + +$	$F_{1,1982} = 36.0- - - -$	12940.9		
	sum NDVI	$F_{1,1982} = 10.5+ +$	$F_{1,1982} = 9.2- -$	13183.9		
	ann NDVI	$F_{1,1982} = 1.3 \text{ NS } +$	$F_{1,1982} = 1.0 \text{ NS } -$	13196.6		
Cumulative 1 km × 1 km	sum temp	$F_{1,1507} = 109.3+ + + +$	$F_{1,1507} = 95.4- - - -$	11072.8	> 0.999	
	ann temp	$F_{1,1507} = 88.4+ + + +$	$F_{1,1507} = 70.7- - - -$	11106.0		
	sum NDVI	$F_{1,1507} = 339.7+ + + +$	$F_{1,1507} = 257.4- - - -$	11174.1		
	ann NDVI	$F_{1,1507} = 212.3+ + + +$	$F_{1,1507} = 187.7- - - -$	11195.2		
2 km × 2 km*	sum temp	$F_{1,5955} = 82.5+ + + +$	$F_{1,5955} = 54.7- - - -$	43997.9	> 0.999	
	ann temp	$F_{1,5955} = 68.9+ + + +$	$F_{1,5955} = 34.1- - - -$	44114.3		
	sum NDVI	$F_{1,5955} = 6.0+$	$F_{1,5955} = 2.7 \text{ NS } -$	44409.7		
	ann NDVI	$F_{1,5955} = 17.5+ + + +$	$F_{1,5955} = 12.4- - -$	44442.2		
Standardized 10 km × 10 km	sum temp	$F_{1,1500} = 73.3+ + + +$	$F_{1,1500} = 60.4- - - -$	11199.9	> 0.999	
	ann temp	$F_{1,1500} = 77.5+ + + +$	$F_{1,1500} = 58.9- - - -$	11229.1		
	sum NDVI	$F_{1,1500} = 5.4+$	$F_{1,1500} = 3.6 \text{ NS } -$	11333.2		
	ann NDVI	$F_{1,1500} = 9.2+ +$	$F_{1,1500} = 7.1- -$	11342.4		
Total 10 km × 10 km same cells as above	sum temp	$F_{1,1500} = 51.4+ + + +$	$F_{1,1500} = 57.6- - - -$	11443.3	> 0.999	
	ann temp	$F_{1,1500} = 73.1+ + + +$	$F_{1,1500} = 54.8- - - -$	11463.4		
	sum NDVI	$F_{1,1500} = 3.2 \text{ NS } +$	$F_{1,1500} = 2.2 \text{ NS } -$	11566.1		
	ann NDVI	$F_{1,1500} = 7.7+ +$	$F_{1,1500} = 5.8-$	11553.0		
Total 10 km × 10 km all cells	sum temp	$F_{1,2263} = 161.6+ + + +$	$F_{1,2263} = 126.4- - - -$	17413.4	> 0.999	
	ann temp	$F_{1,2263} = 155.5+ + + +$	$F_{1,2263} = 105.4- - - -$	17460.0		
	sum NDVI	$F_{1,2263} = 5.1+$	$F_{1,2263} = 2.7 \text{ NS } -$	17686.1		
	ann NDVI	$F_{1,2263} = 15.7+ + + +$	$F_{1,2263} = 10.6- -$	17674.8		

Positive effects: + + + $P < 0.0001$, + + + $P < 0.001$, + + $P < 0.01$, + $P < 0.05$, NS + $P > 0.05$; negative effects: - - - - $P < 0.0001$, - - - $P < 0.001$, - - $P < 0.01$, - $P < 0.05$, NS - $P > 0.05$.

*The spatial model for 2 km × 2 km squares is based on randomly selected squares (maximum of three per 10 km × 10 km square) in order to reduce the sample size below the threshold (approximately $n = 6000$) at which spatial models require more than the available computer memory to run.

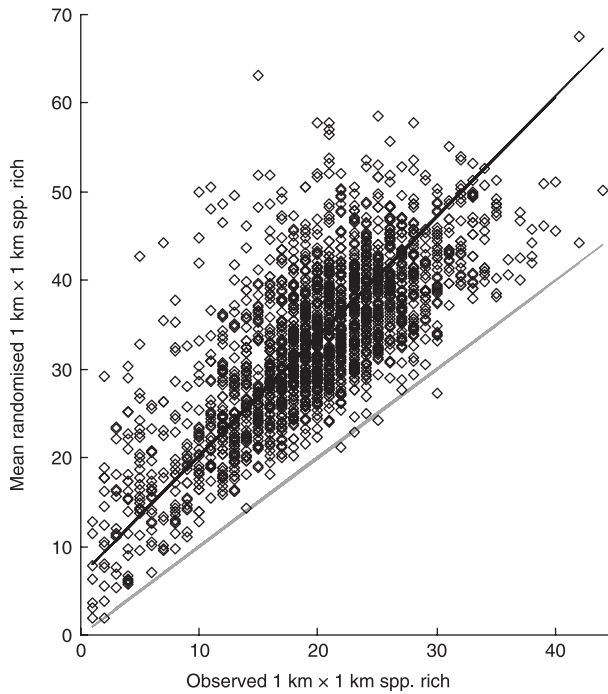


Fig. 3. Relationships between observed and randomized species richness. The black open points represent the raw data, the solid black line represents the relationship calculated by reduced major axis regression, and the grey line the line of equivalence.

evidence for a negative relationship (Table 2a; Fig. 4d). The log-transformed ratio of multiple to single year species richness is also negatively related to summer temperature (Table 2b; Fig. 4e).

Spatial variation in density and occupancy is also associated with summer temperature more closely than other energy metrics. Square root transformed total density is positively correlated with summer temperature ($r^2 = 20\%$; Fig. 5a,

Table 3), which contrasts with the weak u-shaped relationship between square root transformed mean density per species and summer temperature ($r^2 = 7\%$; Fig. 5b, Table 3). Total and mean occupancy respond to summer temperature along a positive decelerating curve and the two relationships have similar explanatory power (respective r^2 values of 30% and 34%; Fig. 5c,d, Table 3).

Discussion

There is intense theoretical and empirical debate regarding the performance of different species richness estimators. However, it is rare for studies to document whether spatial variation in species richness is markedly different when estimated rather than observed species richness data are used. There is no doubt that a failure to take species detectability into account when estimating species richness can result in biased results and misguided conclusions regarding its spatial variation, particularly in diverse tropical regions. However, in our case study the correlation between spatial variation in species richness and a major determinant of such variation, i.e. energy availability, is statistically indistinguishable whether one uses observed or estimated species richness. Thus at least in some cases it is possible to design sampling strategies that can adequately describe spatial variation in species richness without the need to use species richness estimators.

Summer temperature is consistently the best predictor of species richness across each of the spatial grains that we analyse. We use energy metrics that are calculated over a larger spatial grain, 10 km \times 10 km, than some of our avian data. However, the temperature at these finer spatial scales will be strongly positively correlated with temperature in 10 km \times 10 km plots, as the latter exhibits strong spatial autocorrelation (log-likelihood ratio test, $P < 0.0001$). Spatial variation in NDVI exhibits a more heterogeneous pattern

Table 2. Relationships between summer temperature and (a) spatial and (b) temporal turnover in species richness. Model fit is assessed using AIC values, and for each response variable we present the 95% confidence set of models, i.e. those whose weights sum to 0.95. Spatial and temporal turnover are measured as the \log_{10} transformed ratios of regional and mean local richness, and multiple year and single year richness, respectively. Data are only sufficient to calculate temporal turnover at the 1 km \times 1 km spatial grain. Spatial autocorrelation in the ratio of 2 km \times 2 km and 1 km \times 1 km richness, and temporal turnover is not significant (log likelihood ratio test $P > 0.05$) so spatial models are not provided for these response variables

Regional richness	Local richness	Model type	Summer temperature	Summer temperature ²	AIC	Model weight	r^2
(a)							
Total 10 km \times 10 km	cum 1 km \times 1 km	GLM spatial	$F_{1,888} = 64.9$ ----	$F_{1,888} = 56.1$ ++++	-1126.3	> 0.999	15.2%
			$F_{1,888} = 55.7$ ----	$F_{1,888} = 47.6$ ++++	-1139.5	> 0.999	n/a
Standard 10 km \times 10 km	single year 1 km \times 1 km	GLM spatial	$F_{1,817} = 38.7$ ----	$F_{1,817} = 30.3$ ++++	-524.0	> 0.999	21.2%
			$F_{1,817} = 35.5$ ----	$F_{1,817} = 27.8$ ++++	-539.7	> 0.999	n/a
Standard 10 km \times 10 km	2 km \times 2 km	GLM spatial	$F_{1,1500} = 67.2$ ++++	$F_{1,1500} = 41.7$ ++++	-3972.7	0.999	36.9%
			$F_{1,1500} = 56.8$ ++++	$F_{1,1500} = 36.7$ ----	-4026.5	0.999	n/a
2 km \times 2 km	single year 1 km \times 1 km	GLM	$F_{1,972} = 19.9$ ----		-317.4	0.952	2.0%
(b)							
cum 1 km \times 1 km	single year 1 km \times 1 km	GLM	$F_{1,508} = 349.5$ ----		-2325.4	0.33	18.8%
			$F_{1,507} = 20.7$ ----	$F_{1,507} = 12.2$ +++	-2326.8	0.67	19.5%

Positive effects: + + + + $P < 0.0001$; + + + $P < 0.001$; negative effects: ---- $P < 0.0001$. Note that r^2 values cannot be provided for the spatial models.

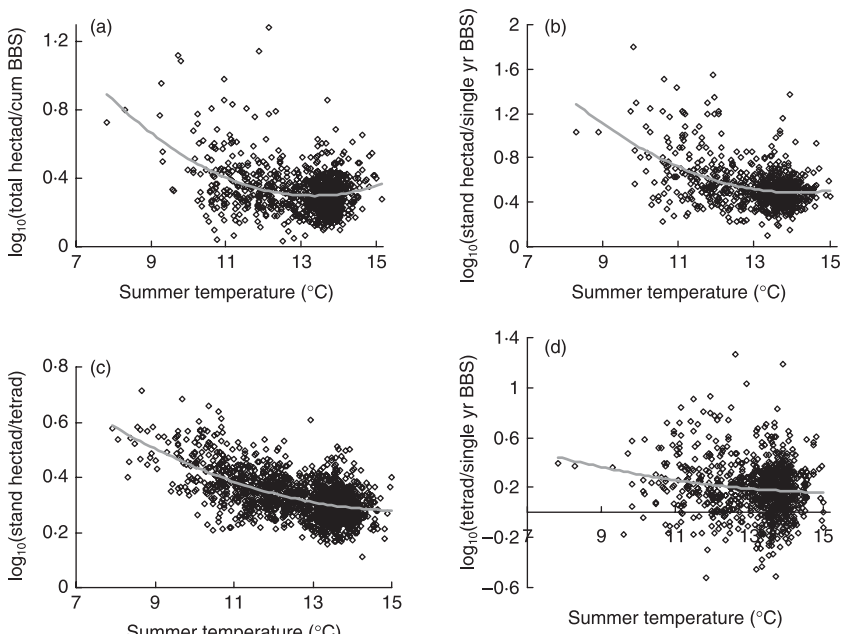


Fig. 4. Relationships between summer temperature and spatial and temporal turnover, measured as the ratio of regional to local species richness for (a) total 10 km \times 10 km and cumulative 1 km \times 1 km species richness (b) standardized 10 km \times 10 km and single year 1 km \times 1 km richness (c) standardized 10 km \times 10 km and 2 km \times 2 km richness (d) 2 km \times 2 km richness and single year 1 km \times 1 km richness, and (e) multiple year and single year 1 km \times 1 km richness. Grey lines indicate the relationship fitted in non-spatial models, see Table 2.

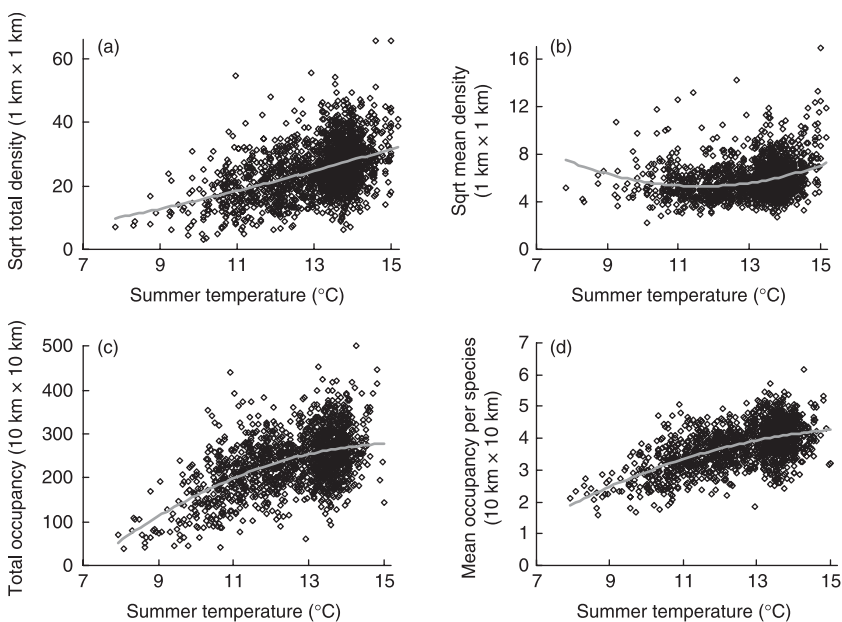


Fig. 5. Relationships between summer temperature and (a) total density in 1 km \times 1 km squares (square root transformed); (b) as in panel a but for mean density per species; (c) total occupancy across all species measured as number of occupied 2 km \times 2 km squares (out of eight) in 10 km \times 10 km squares; and (d) as c, but for mean occupancy per species. Grey lines indicate the relationship fitted in nonspatial models, see Table 3.

than that of temperature and although we use NDVI data at the finest resolution available, the relationship between NDVI values at different spatial grains will contain more noise than is the case for temperature. This may contribute to the finding

that summer temperature is a stronger predictor of species richness and abundance at the finer spatial scales than NDVI metrics, but cannot explain why temperature is a stronger predictor at the 10 km \times 10 km spatial grain. We consider it likely

Table 3. Density–energy and occupancy–energy relationships at contrasting spatial scales. Square root transformed densities in 1 km × 1 km plots do not exhibit significant spatial autocorrelation ($P > 0.05$) so spatial models are not provided for this response variable. For further details see legend for Table 2

Abundance measure	Model type	Predictor	x	x^2	AIC	Model weight	r^2
sqrt total density 1 km × 1 km	GLM	sum temp	$F_{1,1983} = 479.0+ + + +$ $F_{1,1982} = 0.3 \text{ NS} +$	$F_{1,1982} = 0.7 \text{ NS} +$	13519.1	0.714	19.5%
sqrt mean density 1 km × 1 km	GLM	sum temp	$F_{1,1982} = 57.9- - - -$	$F_{1,1982} = 66.6+ + + +$	6918.0	> 0.999	19.5% 6.9%
total occup. 10 km × 10 km	GLM	sum temp	$F_{1,1500} = 46.5+ + + +$	$F_{1,1500} = 28.5- - - -$	16330.9	> 0.999	29.6%
	spatial	sum temp	$F_{1,1500} = 50.1+ + + +$	$F_{1,1500} = 33.8- - - -$	16260.1	> 0.999	N/A
Mean occup. 10 km × 10 km	GLM	sum temp	$F_{1,1500} = 39.6+ + + +$	$F_{1,1500} = 21.5- - - -$	2425.8	0.999	34.1%
	spatial	sum temp	$F_{1,1500} = 37.0+ + + +$	$F_{1,1500} = 22.2- - - -$	2355.9	> 0.999	N/A

that the nature of the energy predictor that can best explain the structure of avian assemblages is independent of the spatial grain of analysis.

The explanatory power of the species–energy relationship does not markedly covary with the spatial grain of the analysis. A similar lack of scale dependency has been found in an analysis of species richness in South American avian assemblages in relation to climatic variables across a wide range of grid cell sizes ($1^\circ \times 1^\circ$ to $10^\circ \times 10^\circ$; Rahbek & Graves 2001). Conversely, avian species richness in North America becomes less strongly correlated with NDVI as spatial grain increases from 20 000 to 80 000 km² (Hurlbert & Haskell 2003). Turning to more local scales, net primary productivity explained less of the variance in ant species richness as spatial grain increased from 1 m² plots to estimates of species richness at a larger, but unspecified, ‘habitat level’ spatial scale (Kaspari *et al.* 2003). Thus, and while the number of available studies is somewhat limited, there does not seem to be a consistent pattern between the strength of the species–energy relationship and spatial grain.

The broad form of the species–energy relationship also appears to be stable across the range of spatial scales that we investigate; as environmental energy increases species richness consistently increases along a decelerating curve. The lack of a hump-shaped relationship at small spatial grains, at a regional spatial extent, is consistent with patterns found in a re-analysis of a large number of studies compiled from the literature (Gilman & Wright 2006), but contrasts with the conclusions of the original analysis of those data (Mittelbach *et al.* 2001). The precise nature of the species–energy relationship does, however, exhibit scale dependency. Ratios of regional to mean local richness decrease with increasing energy availability. Thus local richness increases more rapidly with increasing energy than does regional richness and the slope of the species–energy relationship is steeper at local scales. While this pattern is particularly strong when comparing standardized 10 km × 10 km richness with that in 2 km × 2 km plots, this is probably a consequence of the survey methods being identical at these two spatial scales rather than an inherent characteristic of the scale of analysis.

Ratios of regional to local richness may be used as one measure of spatial turnover or beta diversity (β_w , Whittaker 1960). While these arguably are not true measures of turnover

as they do not consider species identity, and thus relative species gains and losses, they may be viewed as broad sense measures of turnover (Koleff *et al.* 2003). Similar relationships between environmental energy availability and beta diversity metrics, including ones that take species identity into account, have been found at larger spatial scales in British (Gaston, Evans & Lennon 2007a) and South African avifaunas (Bonn *et al.* 2004). It is also noteworthy that at a global extent beta diversity of avian assemblages is high in regions of both extremely high and low energy availability and species richness (Davies *et al.* 2007; Gaston *et al.* 2007b).

Some measures of beta diversity, such as β_w , are formally related to the slope (z) of the power law form of the species–area relationship (SAR, Harte & Kinzig 1997). Thus our observation is also consistent with the lower z -values of nested SARs in areas of higher energy availability (Storch *et al.* 2005; Evans *et al.*, in press). While a positive correlation between the slope of SARs and energy availability has been reported for non-nested SARs (Kalmar & Currie 2007) the latter have different properties to nested SARs thus limiting their comparability (Scheiner 2003). It is, however, noteworthy that the slope of SARs generally decreases with latitude, which is a very crude surrogate measure of energy availability (Drakare, Lennon & Hillebrand 2006).

We find that both total and mean per species occupancy in 10 km × 10 km squares increases with energy availability. This concurs with larger scale studies of the South African avifauna (Bonn *et al.* 2004), and is expected given that high occupancy reduces spatial turnover in species composition (Leitner & Rosenzweig 1997). High occupancy reduces extinction risk and may thus lower temporal turnover. It is thus noteworthy that a crude measure of the latter, the ratio of multiple to single year species richness at the 1 km × 1 km spatial grain, is negatively correlated with summer temperature. This finding concurs with empirical demonstration of negative relationships between energy availability and extinction rates (Evans *et al.* 2005c).

The negative relationships that we find between measures of turnover and energy availability contrast with the suggestion that species–energy relationships may be driven by an association between high-energy availability and greater habitat heterogeneity promoting greater spatial turnover and thus higher species richness (Hurlbert 2004). Our results also

contrast with studies reporting positive relationships between beta diversity and environmental energy availability (Chase *et al.* 2000; Chase & Leibold 2002; Chalcraft *et al.* 2004). Such investigations typically concern plants studied at very fine spatial grains, and whether these contrasting results have a simple explanation is an open question. However, plants strongly compete for space and thus, above a certain threshold of energy availability, higher species richness cannot be associated with higher abundances. In such a system individual species densities and occupancies will decline with increasing energy and the latter and beta diversity must thus be positively correlated.

In our data total avian density and energy availability are positively correlated, which is compatible with both the MIH and the sampling hypothesis. However, the MIH also predicts that mean species density will increase with environmental energy availability, which is not the case. This concurs with analyses of global avian assemblages in forests (Pautasso & Gaston 2005) and the North American avifauna (Evans *et al.* 2006). Investigations of other predictions derived from the MIH concerning the relative responses of the numbers of common and rare species and their extinction risk to energy availability in British breeding birds find little support for the hypothesis (Evans *et al.* 2005b,c). Therefore, although our investigations support the role of the total number of individuals in generating species richness patterns, this role appears unlikely to be driven by a reduction in species extinction rates.

The positive relationship between total density and energy is also compatible with the sampling hypothesis. However, the randomized species–energy relationship predicted by the sampling hypothesis differs from the observed relationship in two important and interrelated ways. First, randomized and observed relationships, respectively, exhibit linear and decelerating curves. Second, at any given temperature observed species richness is lower than that predicted by the sampling mechanism, and this discrepancy increases at high levels of species richness. The predominant reason why randomization will overestimate species richness, and generate a linear rather than curvilinear species–energy relationship, is that the model assumes a homogeneous spatial distribution of individuals, while observed species distributions are more aggregated. This aggregation is principally driven by the nonrandom distribution of habitat types in combination with habitat selection, although other factors can also contribute to aggregation (Storch, Šizling & Gaston 2003). Consequently, some of the species allocated to a cell by randomization will not be able to occur there, because the cell lacks the appropriate habitat type. Thus, at least at the 1 km × 1 km spatial grain, the sampling mechanism, together with species spatial aggregation may explain the observed species–energy relationship.

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Supplementary material

The following supplementary material is available for this article.

Table S1 Rare species for which the detectability function of a commoner surrogate species was used when calculating densities in 1 km × 1 km quadrats.

Table S2 Correlation coefficients and slopes (\pm one standard error) for relationships between estimated and observed species richness.

Table S3 Using estimated rather than observed species richness does not significantly alter the parameter estimates of the species–energy relationship.

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