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Pink landscapes: 1/*f* spectra of spatial environmental variability and bird community composition

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Temporal and spatial environmental variability are predicted to have reddened spectra that reveal increases in variance with the period or length sampled. However, spectral analyses have seldom been performed on ecological data to determine whether these predictions hold true in the case of spatial environmental variability. For a 50 km long continuous transect of 128 point samples across a heterogeneous cultural landscape in the Czech Republic, both habitat composition and bird species composition decomposed by standard ordination techniques did indeed exhibit reddened spectra. The values of main ordination axes have relationships between log spectral density and log frequency with slopes close to −1, indicating 1/*f*, or 'pink' noise type of variability that is characterized by scale invariance. However, when habitat composition was controlled for and only residuals for bird species composition were analysed, the spectra revealed a peak at intermediate frequencies, indicating that population processes that structure bird communities but are not directly related to the structure of the environment might have some typical correlation length. Spatial variability of abundances of individual species was mostly reddened as well, but the degree was positively correlated to their total abundance and niche position (strength of species–habitat association). If 'pink' noise type of variability is as generally typical for spatial environmental variability as for temporal variability, the consequences may be profound for patterns of species diversity on different spatial scales, the form of species–area relationships and the distribution of abundances within species ranges.

Keywords: spectral analysis; fractals; species–area relationship; bird communities; heterogeneity; scaling

1. INTRODUCTION

It is common knowledge that temporal and spatial environmental variability increase with distance (Williamson 1987). The relationship between environmental variability and the scale of observation is thought to have profound consequences for population variability in space and time, as well as for community structure and dynamics (Halley 1996). It can be expressed mathematically using power spectra relating the spectral density (SD) of a variable (which can be interpreted in terms of variance) to the period or frequency. Environmental variability can then be characterized by the relative importance of different wavelengths, the pattern of which defines particular types of 'noise'. When the power spectra are dominated by long wavelengths, as is typically the case in ecological data, then they are regarded as reddened, because optical spectra that have a surplus of low-frequency light appear redder. Similarly, when all of the frequencies are equally important, the spectra are white (by analogy with white light, which contains equal amounts of all frequencies), and when shorter wavelengths/higher frequencies are more pronounced, the spectra are blue (Halley 1996).

Some types of power spectra are characterized by a relationship between SD and frequency of the form $SD \sim 1/f^{\gamma}$, where $0 \leqslant \gamma \leqslant 2$. For white noise, γ is equal to zero (SD is constant for all frequencies), whereas γ is equal to 2 when the parameter does a random walk, called brown noise (after Brownian motion). When γ is close to 1, and therefore the SD is directly inversely related to frequency, the type of variability is called 1/*f*, or 'pink' noise. Pink noise reflects scale invariance, because no frequency has a priority—the more frequent the changes, the less important they are—and it is typical of many ecological time-series. It is regarded as a natural result of a mixture of different phenomena acting impartially on different scales and should therefore be regarded as the null model for environmental fluctuation (Halley 1996).

Whereas time-series of, for example, population (Petchey 2000) and palaeontological diversity data (Solé *et al.* 1997) have been intensively studied using spectral analyses (for a review, see Gisiger 2001), spatial ecological data have largely been neglected. Perhaps the major problem is that the latter have not been systematically collected across the long transects that would be necessary to provide detailed information on variability over a wide range of different spatial scales (i.e. different wavelengths). Studying the effect of spatial scale has mostly been confined to using variograms relating some index of similarity between communities to their physical separation (e.g. Condit *et al.* 2002). Although there is a general consensus that the variability of environmental parameters, as well as community composition, increases with spatial distance (e.g. Bell *et al.* 1993), the exact scaling of the variability

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has been examined only rarely (Williamson 1987) and, moreover, mostly focused on abiotic environmental parameters. Such studies have sometimes documented two dimensional (2D) noise with $\gamma = 2$ (which actually represents pink noise for the 2D space) and this pattern has been attributed to random non-stationary processes (Sayles & Thomas 1978). However, it has not been clear whether a similar pattern also holds for factors directly influencing community composition or parameters characterizing community composition itself, although models have sometimes assumed particular types of spatial spectra for these (Lennon 2000).

The exact scaling of spatial environmental variability could have direct consequences for general patterns of species distribution and diversity. According to Williamson (1988), the slope of power spectra for environmental variability, plotted on a log–log scale (i.e. log SD versus log frequency), could be related directly to the slope of the species–area relationship, since species–area curves are thought to be affected by habitat heterogeneity that increases with space according to the spectral characteristics of an environment. Surprisingly, although the regularity of the slope of mainland species–area curves has remained a mystery (Rosenzweig 1995), the relationship between mainland species–area curves and the scaling of habitat heterogeneity has been little studied. Similarly, although macroecological models of the spatial variation of abundances within species ranges have been based on an assumption of autocorrelated spatial variability of environmental parameters (Brown 1995; Brown *et al.* 1995), no attempt, to our knowledge, has been made explicitly to test the relationship between the spatial variation of environmental parameters and of species abundances on relevant spatial scales.

In this paper, we examine power spectra exhibited by spatial environmental variability of parameters that characterize habitat and bird species composition to assess whether spatial environmental variability has the predicted spectral properties. Partialling out the contribution of environmental variables then enables us to determine whether the features of variability of bird community composition are attributable just to the variability of environment. Finally, examining power spectra of spatial variation in bird species abundances allows assessment of the importance of environmental variability for spatial variation in abundances.

2. METHODS

Habitat and bird community composition were recorded at 128 sample points arranged *ca*. 400 m apart along a 50 km linear transect in cultural landscape in southern Bohemia, traversing mixed forests, wetlands, villages and agricultural areas. At each point, habitats were mapped within a circle of diameter 300 m, during the autumn of 2001. We distinguished 34 habitat types representing different vegetation layers or other habitats (e.g. water surface) and estimated the relative proportion of each type within the census area. Naturally, the vegetation layers were not mutually exclusive, and thus they did not sum to 100%.

Bird community composition data were obtained by conducting standard point-counts (Bibby *et al.* 1992) at the sample points. Each point was visited six times, between 05.00 and 09.00 from April to June 2001, to ensure accurate estimation of species' presences and abundances; all birds perceived visually or acoustically within a 150 m distance from a point were recorded. The maximum counts recorded from all of the visits were taken as species' abundance values at a point.

The multivariate data of habitat and bird species composition were analysed by correspondence analysis (CA), which ordinates samples (sample points) and variables (habitats and species), respectively, along axes such that the differences among species and samples, respectively, are maximized (ter Braak & Šmilauer 1998). Each ordination axis represents a real or synthetic gradient along which the centroids of individual variables and/or samples are distributed so as to maximize the distances between them. The first axis represents the gradient explaining most of the variability, the second axis represents an orthogonal gradient explaining most of the residual variability, and so on. The canonical version of the correspondence analysis (CCA) ordinates species and samples such that the ordination axes represent the maximum variability that is attributable to the environmental parameters; the ordination is in this case constrained by the environmental parameters to maximize the variability accountable by them.

We also performed a univariate multiple regression (using generalized linear model (GLM)) separately for each species to obtain values predicting its abundance at a particular sample point on the basis of habitat composition, and residual values containing information on the variability in species abundance that is not attributable to this composition. Although these regression models would not be an appropriate basis for investigating the precise habitat requirements of each species (in part because of the spatial autocorrelation inherent in both habitat and species data), this does not matter here because this investigation was beyond the scope of our study.

We performed the following CAs:

(i) CCA that ordinates bird species and their assemblages (samples), respectively, such that maximum interspecific (and inter-sample) variability has been attributable to variability in habitat composition;
(ii) CA of habitat composition ordinating individual sampling points according to relative amount of individual habitats;
(iii) CA of bird species composition ordinating individual sampling points according to relative bird species abundances;
(iv) CA ordinating sampling points according to predicted values (GLM regression) of each species that represented species variability that is fully attributable to habitat;
(v) CCA ordinating bird species and their assemblages according to variability that is not accounted for by habitat composition: all habitat types were taken as covariables and only residual variability in species composition was examined; and
(vi) CA ordinating residual values of GLM regression of each species, representing species variability in abundance that is not attributable to habitat.

Spectral analyses were performed in each case on the sample scores of all the three main ordination axes representing the position of individual sampling points along the gradients. The spectra were subjected to standard Fourier analysis. Then the SD (Hamming weighting of periodogram) was plotted against the respective frequency on a log–log scale, and both the slope and coefficient of determination (r^2) of the linear regression of the power spectra were calculated. Furthermore, we also performed a spectral analysis for spatial variation in the abundance of

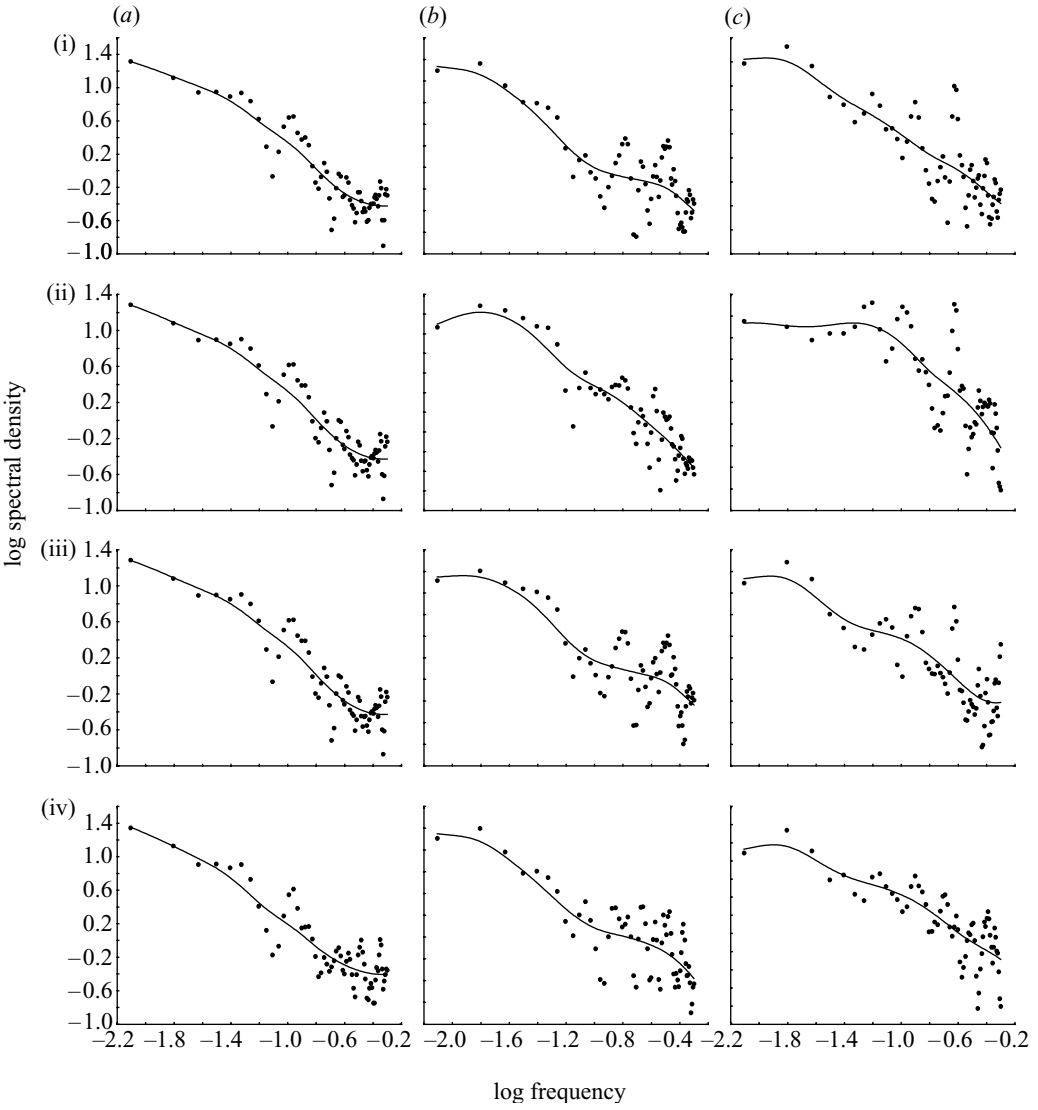

Figure 1. Spectrograms of spatial variability in scores of the first three ordination axes for the first four analyses in which the effect of habitat composition has not been controlled for ((i)–(iv), see § 2 and table 1). Columns (*a*) axis 1; (*b*) axis 2; (*c*) axis 3. Decreasing trends indicate redness, as lower frequencies (longer wavelengths) have higher spectral densities (are more important). The lines represent smoothing by distance weighted least squares.

each species. The 'redness' of the spectra of each species was characterized by γ, i.e. the inverse slope of the linear regression of power spectra, and compared with the species' abundance and with its 'niche position'. The latter quantifies the degree to which a species utilizes less common habitats and resources in the environment (Shugart & Patten 1972), species with a high value of niche position having more unusual habitat preferences. It was calculated as the Euclidean distance of a species' centroid from the centroid of the whole community within the multidimensional ordination space.

3. RESULTS AND DISCUSSION

(a) *The patterns*

The spatial variability of bird species composition was closely related to the spatial variability in habitat composition. CCA that related differences in bird species composition at individual sample points to differences in habitat composition (analysis (i)) revealed that a substantial part of the variability in species occurrence and abundance was attributable to habitat: 36.8% of overall variability in species composition was attributable to habitat variability, and the first three ordination axes together explained 44.6% of the variability related to habitat. The bird–habitat association was highly significant and this was not due to the spatial autocorrelation of both habitat and species data (Monte-Carlo permutation test performed by cyclic shifts, keeping the spatial structure of the data, $p < 0.005$). The importance of habitat spatial variability for spatial variability in bird species composition was also demonstrated by a strong correlation between CA scores for habitat (analysis (ii)) and species data (analysis (iii)): $r = 0.87$ for first axes, $r = -0.73$ for second axes, and $r = -0.5$ for third axes. The correlation between CCA scores from analysis (i) with both scores from analyses (ii) and (iii) was even stronger, but this was a direct consequence of the fact that analysis (i) correlates data entering analysis (ii) with those entering analysis (iii).

The spatial variability of the scores for all three ordination axes of those correspondence analyses where habitat composition was not controlled for (i.e. analyses (i)–(iv)) exhibited reddened spectra, with log SD decreasing

Table 1. Results of linear regression of power spectra, plotting log SD against log frequency for scores of first three ordination axes of six correspondence analyses (see § 2).
(The negative slope of the regression line indicates redness; pink noise is characterized by slope –1 ($\gamma = 1$), brown noise has a slope of –2. Zero or positive slopes indicate equal importance of all frequencies (white noise) and prevalence of short frequencies (blue noise), respectively. Parametric confidence intervals (CI) for the slopes are given, as well as standard error (s.e.), significance of linear regression (p) and coefficient of determination (r^2).)

	axis	slope ($-\gamma$)	CI −0.95	CI + 0.95	s.e.	p	r^2
analysis (i): relating species to habitats	CA1	−1.167	−1.310	−1.025	0.071	0.000	0.812
	CA2	−0.716	−0.871	−0.561	0.078	0.000	0.579
	CA3	−0.753	−0.898	−0.608	0.073	0.000	0.634
analysis (ii): habitat composition	CA1	−1.265	−1.440	−1.090	0.088	0.000	0.771
	CA2	−1.035	−1.175	−0.896	0.070	0.000	0.781
	CA3	−0.843	−1.051	−0.635	0.104	0.000	0.514
analysis (iii): bird community composition	CA1	−1.143	−1.284	−1.002	0.070	0.000	0.809
	CA2	−0.692	−0.849	−0.535	0.079	0.000	0.556
	CA3	−0.781	−0.944	−0.617	0.082	0.000	0.594
analysis (iv): ordination of values predicted by GLM regression	CA1	−1.084	−1.232	−0.936	0.074	0.000	0.775
	CA2	−0.717	−0.869	−0.565	0.076	0.000	0.590
	CA3	−0.829	−0.990	−0.668	0.081	0.000	0.631
analysis (v): ordination of CCA residuals	CA1	−0.183	−0.377	0.011	0.097	0.064	0.054
	CA2	0.313	0.180	0.445	0.066	0.000	0.264
	CA3	−0.108	−0.282	0.066	0.087	0.218	0.024
analysis (vi): ordination of GLM residuals	CA1	−0.109	−0.313	0.094	0.102	0.286	0.018
	CA2	0.075	−0.086	0.236	0.081	0.353	0.014
	CA3	−0.116	−0.296	0.065	0.090	0.206	0.026

monotonically with log frequency (figure 1). This is in accord with the suggestions of Williamson (1987, 1988) and Williamson & Lawton (1991), as well as with other notions concerning the fractal or self-similar character of natural environments (e.g. Morse *et al.* 1985; Loehle & Li 1996). All the spectra in our dataset had a slope very close to −1, indicating 'pink noise' for one-dimensional (1D) space (table 1). The slopes of linear regressions of power spectra varied from −1.26 to −0.69, being shallower for the second and third ordination axes.

When habitat composition had been controlled for, both by CCA (analysis (v)) and by multiple linear regression for each species (analysis (vi)), the spectral analyses of residual variability in species composition did not reveal reddened spectra (figure 2; table 1). Power spectra of scores of the first axes of both ordination analyses showed a peak corresponding to a log frequency of *ca.* −1, corresponding to the distance between *ca.* 10–13 sampling points (i.e. 4–5 km). The other two axes did not reveal any systematic trend, which is not surprising considering that most variability had already been accounted for. The interpretation of the peak for the first axis must be made cautiously, not least because this axis accounts for only a small proportion of overall variability. However, the peak could reflect a spatial lag that is characteristic for certain population processes, e.g. conspecific attraction or population dispersal, because processes that influence the spatial distribution of species resulting from habitat could not have a role. The lag corresponds quite well, for instance, to the mean distance of bird breeding dispersal, which is about 2–7 km for many British birds (Paradis *et al.* 1998). Unfortunately, it is not possible to test the statistical significance of this peak, so we cannot rule out a possible random effect (e.g. local population of one particular species that occurs by chance within some parts of the transect, regardless of the environment).

The slopes of power spectra for the spatial variability of individual species abundances ranged from –0.94 to 0.18 (mean of −0.35), 78% of species exhibiting a slope of less than zero, which indicates a predominance of reddened spectra. Species that were both more abundant and more extreme in their habitat requirements (those having a higher value of niche position) had more reddened spectra, although the relationship of the redness to these characteristics taken individually was masked by their strong negative correlation (figure 3). However, both factors independently influenced species redness (multiple regression, $p < 0.0001$ for both log abundance and niche position). This is not surprising, given that species strongly associated with particular habitats follow the spatial variability of habitat composition and that high species abundance is a prerequisite for revealing any measurable abundance variability. Note that abundance itself was not sufficient for revealing pink spectra: for example, the great tit *Parus major*, one of the five most abundant species, revealed white noise characteristics, with higher frequencies even slightly more pronounced (not significantly) than lower ones. Established spectra of spatial variability of bird community composition represent a by-product of spectra of variability in habitat composition.

(b) *The consequences*

If pink noise is as general for spatial environmental variability as it is for temporal environmental variability, it should have profound consequences for spatial patterns of species distribution and diversity. First, pink noise indicates scale invariance, which means that the species composition of assemblages varies spatially at all scales and no level of spatial resolution has priority. Whereas an individual species can be associated with a habitat that has some typical scale of variability (for instance, patches of forest mosaics having some typical size and consequently typical

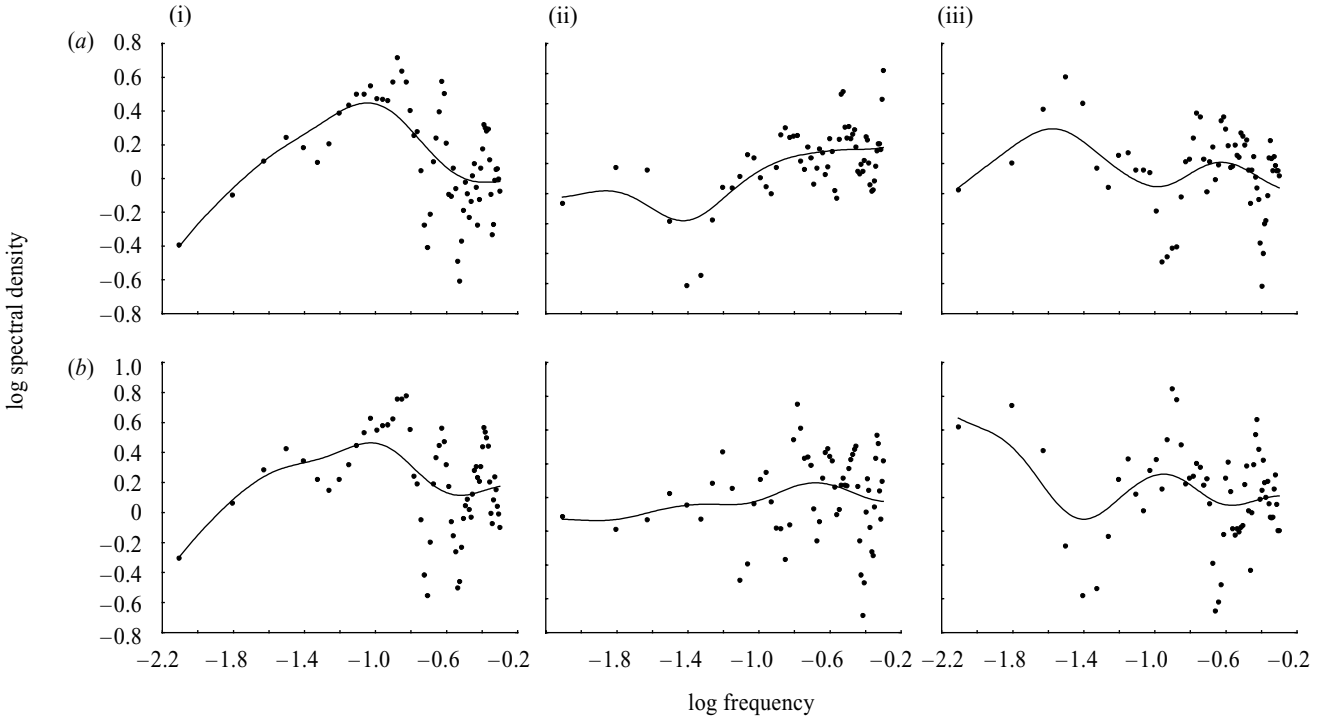

Figure 2. Spectrograms of spatial variability in scores of the first three ordination axes for those analyses where habitat composition has been controlled for by CCA ordination with habitats as (*a*) covariables (v), and (*b*) GLM regression for individual species (vi), respectively. Columns (i) axis 1, (ii) axis 2, and (iii) axis 3, respectively. The lines represent smoothing by distance-weighted least-squares.

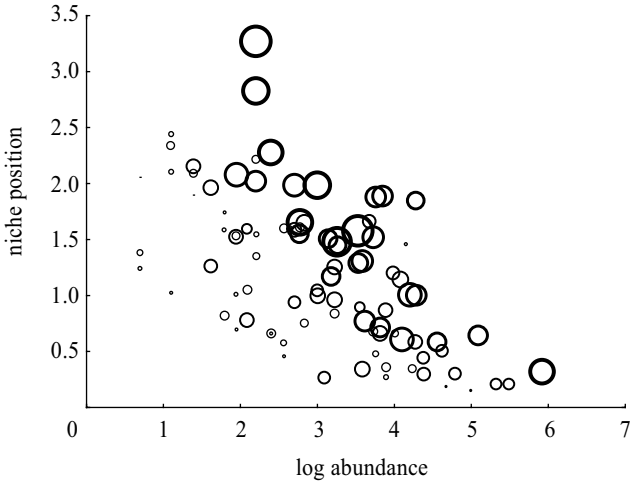

Figure 3. Redness of spatial variability in abundance of individual species, indicated by the increasing size of the circle in the plot relating species abundance to niche position.

wavelength of spatial variability), different species recognize their habitats on a large range of resolutions and consequently a sufficiently large set of species will often reveal no association with a particular spatial scale. Therefore, there is no objective guideline for how to distinguish within-habitat and between-habitat diversity (e.g. Wiens 1989), because habitat distinctions related to some spatial scale that are important for one species would be not important for another.

Second, the character of spatial environmental variability could influence patterns of spatial variability of population densities within species ranges. If population densities vary at all scales according to the environmental variation, it is probable that high population densities would occur only rarely because of the low probability that all of the frequencies would peak in the same places. This fits with the observation that the frequency distribution of population densities within the geographical range of a species is characterized by only a small proportion of sites containing dense populations (Brown *et al.* 1995; Gaston & Blackburn 2000). This pattern has been attributed to the low probability that independently fluctuating and spatially autocorrelated niche dimensions will peak in the same place (Brown *et al.* 1995), but it is possible that even spatial variability of only one niche parameter would have similar consequences if the variability follows the $1/f$ spectra.

Third, the form of power spectra can be directly related to the shape and slope of the species–area relationship. According to Williamson (1988), power spectra of environmental variability could be expressed as $\log\sigma^2 \sim \gamma \times \log L$, where σ^2 is the SD (expressed as variance of an environmental parameter) and L is the length of interval. Then the relationship between the standard deviation of an environmental parameter and the length of the interval is $2 \times \log\sigma \sim \gamma \times \log L$, and therefore $\log\sigma \sim 0.5 \times \gamma \times \log L$.

Assuming that species diversity is scaled to the standard deviation of an environmental parameter (for instance, probability of species occurrence increases linearly with an increase in the range of values of an environmental parameter), the species number, S, should be related to length in the same way as the standard deviation, σ, of the parameter. Because $\gamma = 1$ for pink noise, the relationship between species number and length of the interval should

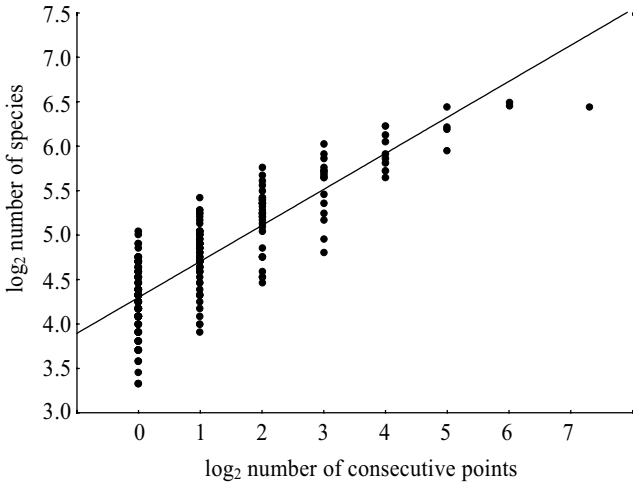

Figure 4. Species–length relationship, i.e. the relationship between the number of species and the length of spatial transect, here expressed in number of consecutive points (both axes represent logarithms with the base 2). Only non-overlapping series of points have been included for each length, each series having length of 2^N, i.e. 2, 4, 8, 16 etc. Note that the curve is slightly but significantly curvilinear; however, the parameter of the quadratic term is quite low (-0.024), and the significance value ($p = 0.0033$) is not very informative, as the data points are not independent (shorter lengths of the interval are nested within the large ones).

be, in this case, $\log S \sim 0.5 \log L$, which means that the slope Z_1 of the linear regression between log S and log L should be 0.5. This is in good agreement with our observation, where $Z_1 = 0.405$ ($r^2 = 0.712$; figure 4) for this species–length relationship, given that scaling between σ and species number cannot be perfect (because many factors, such as dispersal or different levels of habitat specialization among species, surely have a role).

It is not very clear how this species–length relationship exactly relates to the species–area relationship. Williamson (1988) assumed for a 2D area A, such that $\log A = 2 \log L$ and $\gamma = 2$, which would produce a slope equal to that of the slope of species–length relationship, $Z_2 = 0.5$. This prediction seems to be too high in comparison with published slopes of species–area curves (Connor & McCoy 1979), but the relationship between scaling on a 1D transect and over a 2D area (and between Z_1 and Z_2) may be much less straightforward than suggested by the theory of Williamson (1988). However, some relationship between the scaling of habitat heterogeneity and the shape and slope of the species–area curve is inevitable given that the patterns of species diversity and distribution are affected by habitat heterogeneity on many scales of resolution.

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