RESEARCH PAPER

Spatial autocorrelation and red herrings in geographical ecology

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ABSTRACT

Aim Spatial autocorrelation in ecological data can inflate Type I errors in statistical analyses. There has also been a recent claim that spatial autocorrelation generates 'red herrings', such that virtually all past analyses are flawed. We consider the origins of this phenomenon, the implications of spatial autocorrelation for macro-scale patterns of species diversity and set out a clarification of the statistical problems generated by its presence.

Location To illustrate the issues involved, we analyse the species richness of the birds of western/central Europe, north Africa and the Middle East.

Methods Spatial correlograms for richness and five environmental variables were generated using Moran's I coefficients. Multiple regression, using both ordinary least-squares (OLS) and generalized least squares (GLS) assuming a spatial structure in the residuals, were used to identify the strongest predictors of richness. Autocorrelation analyses of the residuals obtained after stepwise OLS regression were undertaken, and the ranks of variables in the full OLS and GLS models were compared.

Results Bird richness is characterized by a quadratic north–south gradient. Spatial correlograms usually had positive autocorrelation up to *c*. 1600 km. Including the environmental variables successively in the OLS model reduced spatial autocorrelation in the residuals to non-detectable levels, indicating that the variables explained all spatial structure in the data. In principle, if residuals are not autocorrelated then OLS is a special case of GLS. However, our comparison between OLS and GLS models including all environmental variables revealed that GLS de-emphasized predictors with strong autocorrelation and long-distance clinal structures, giving more importance to variables acting at smaller geographical scales.

Conclusion Although spatial autocorrelation should always be investigated, it does not necessarily generate bias. Rather, it can be a useful tool to investigate mechanisms operating on richness at different spatial scales. Claims that analyses that do not take into account spatial autocorrelation are flawed are without foundation.

Key words birds, generalized least squares, latitudinal gradients, multiple regression, Palearctic, spatial autocorrelation, species richness.

INTRODUCTION

The latitudinal gradient in species richness has been known for almost 200 years (von Humboldt, 1808). Over the years, many hypotheses have been developed to explain this pattern. Many are redundant, vague or untestable, and some are simply not supported by empirical evidence. Consequently, the focus is now on a much reduced subset of hypotheses (Currie, 1991; O'Brien, 1993, 1998; Rosenzweig, 1995; Hawkins & Porter 2001; Rahbek & Graves, 2001).

Tests of mechanisms driving species diversity are usually performed using multiple regression and related statistical approaches (e.g. path analysis), in which species richness is regressed against sets of environmental variables, sometimes at different spatial scales (see Badgley & Fox, 2000; Rahbek & Graves, 2001; for recent examples). However, as is becoming widely appreciated by ecologists, patterns of spatial autocorrelation in data can create false positive results in the analyses. Autocorrelation is the lack of independence

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between pairs of observations at given distances in time or space and is found commonly in ecological data (Legendre, 1993). Recent papers have discussed the importance of measuring spatial autocorrelation when evaluating problems in geographical ecology, including latitudinal gradients in species richness (Badgley & Fox, 2000; Jetz & Rahbek, 2001; Rahbek & Graves, 2001), the relationship between local and regional richness (Bini *et al.*, 2000; Fox *et al.*, 2000), spatial patterns in community structure (Leduc *et al.*, 1992) and spatial synchrony in population dynamics (Koenig & Knops, 1998; Koenig, 1998, 1999). The problem is also potentially important in metapopulation studies and analyses of species–area relationships.

When testing statistical hypotheses using standard methods (e.g. ANOVA, correlation and regression), the standard errors are usually underestimated when positive autocorrelation is present and, consequently, Type I errors may be strongly inflated (Legendre, 1993). However, Lennon (2000) recently argued that, beyond difficulties in hypothesis testing due to inflated Type I errors, there would also be a systematic bias toward particular kinds of mechanisms associated with variables that have greater spatial autocorrelation. This is potentially a much more serious issue, and we will return to this later in this paper.

Our goal is to discuss the implications of spatial autocorrelation in geographical ecology, especially when using multiple regression models to choose between alternative mechanisms driving macro-scale patterns of species richness. We then apply spatial analysis to evaluate the role of climate in driving richness gradients, using western Palearctic birds as an example. Finally, we compare results from standard multiple regression analyses and a spatial generalized least squares approach that incorporates autocorrelation in the residuals to illustrate that changes in regression coefficients cannot be considered a 'red herring', as argued by Lennon (2000), but simply reflect the well-known scale-dependence of explanations for diversity patterns.

THEORETICAL BACKGROUND

Assessing spatial autocorrelation

Spatial autocorrelation measures the similarity between samples for a given variable as a function of spatial distance (Sokal & Oden, 1978a,b; Griffith, 1987; Legendre, 1993; Rossi & Quénéhervé, 1998). For quantitative or continuous variables, such as species richness, the Moran's *I* coefficient is the most commonly used coefficient in univariate autocorrelation analyses and is given as:

$$I = \left(\frac{n}{S}\right)\left[\frac{\sum_i\sum_j(y_i - \bar{y})(y_j - \bar{y})w_{ij}}{\sum_i(y_i - \bar{y})^2}\right]$$

where n is the number of samples (quadrats), y_i and y_j are the values of the species richness in quadrats i and j, $\bar{y}$ is the average of y and w_{ij} is an element of the matrix **W**. In this matrix, $w_{ij} = 1$ if the pair i, j of quadrats is within a given distance class interval (indicating quadrats that are 'connected' in this class), and $w_{ij} = 0$ otherwise. S indicates the number of entries (connections) in the **W** matrix. The value expected under the null hypothesis of the absence of spatial autocorrelation is $-1/(n-1)$. Detailed computations of the standard error of this coefficient are given in Griffith (1987) and Legendre & Legendre (1998).

Moran's *I* usually varies between −1.0 and 1.0 for maximum negative and positive autocorrelation, respectively. Non-zero values of Moran's *I* indicate that richness values in quadrats connected at a given geographical distance are more similar (positive autocorrelation) or less similar (negative autocorrelation) than expected for randomly associated pairs of quadrats. The geographical distances can be partitioned into discrete classes, creating then successive **W** matrices and allowing computation of different Moran's *I*-values for the same variable. This allows one to evaluate the behaviour of autocorrelation as a function of spatial distance, in a graph called a spatial correlogram, that furnishes a descriptor of the spatial pattern in the data. In this case, the correlogram as a whole can be considered significant at a given significance level α if at least one of its coefficients is significant at α/k, where k is the number of distance classes used (Bonferroni criterion — Oden, 1984).

The number and definition of the distance classes to be used in the correlograms is arbitrary, but a general methodological criterion is to try to maximize the similarity in the *S*-values (number of connections) for the different Moran's *I* coefficients, so that they are more comparable. The other possible solution is to use constant intervals, but in this case some of the Moran's *I* coefficients in the correlograms may be based on a much smaller number of connections, and this can sometimes disturb the interpretation of the entire correlogram (see van Rensburg *et al.*, 2002). The arbitrariness in the number of distance classes is not important in most cases, because the purpose of the analysis is to describe a continuous spatial process.

Three basic correlogram profiles are usually found in ecological data. The first is obtained when there is positive autocorrelation in short distance classes, coupled with negative spatial autocorrelation at large distance classes. In this case, the correlogram profile can be interpreted as a linear gradient at macro-scales. A second common type occurs when only small distance autocorrelation is found, indicating that spatial variation is structured in patches. In this case, the distance up to which spatial autocorrelation is observed can be interpreted as the average patch size in the variable (see Diniz-Filho & Telles, 2002). Thirdly, if no Moran's *I* coefficients are significant, there is no spatial pattern in the data. Of course, other correlogram profiles are possible (Legendre & Fortin,

1989; Rossi & Quénéhervé, 1998). For example, clinal patterns can reverse at large geographical distances.

Ecological interpretations and implications: the scale dependence of species richness–environmental relationships

For species richness measured in a grid system or in latitudinal bands, positive autocorrelation across short distances can originate in two ways. First, it can be a simple consequence of geographical range extension beyond the limits of a single grid cell, so that nearby cells are similar in species richness because they share most of the same species (i.e. low species turnover). Alternatively, the adjacent cells could be similar because the environmental factors that drive diversity are also spatially autocorrelated, but adjacent cells do not necessarily have the same species composition (i.e. high turnover among adjacent cells). Thus, patterns of spatial autocorrelation in species richness at small scales are linked strongly with the statistical distribution of the geographical range sizes in relation to grid cell size. For example, if most of the species have small geographical ranges (i.e. smaller than the size of a single cell), then similarity among adjacent cells must be a function of similarity of environments. In practice, the two causes of spatial pattern are expected to be found simultaneously in most datasets, and both appear as significant correlograms. However, as we will discuss below, they have completely different ecological and statistical implications.

For simplicity, let us assume that a single environmental factor is driving species richness. In the case of low turnover (large geographical range sizes relative to cell sizes), adjacent cells are pseudo-replicated units in space (*sensu* Hurlbert, 1984) and correlation or regression analyses between species richness and this environmental factor should be, in principle, tested with a reduced number of degrees of freedom. This is necessary because the adjacent cells do not represent independent realizations of the same ecological process, i.e. response of the species richness to variation in the environmental factor. This is equivalent to saying that only more distant cells furnish independent information about the relationship between richness and the driving environmental factor.

More importantly, because this environmental factor varies continuously throughout the geographical space and adjacent cells have very similar species compositions (because geographical ranges of most species extend beyond the cell size), then clearly it cannot explain variation in richness at these very small scales. So, when regressing species richness patterns that are generated under this process against this environmental factor, a positive autocorrelation is expected in the residuals of the fitted model. In contrast, if similar species richness even among adjacent cells is caused by similar responses of different groups of species to the environmental

factor studied, this indicates that even these adjacent cells are independent realizations of the same ecological processes of interest, and so the environmental factor does in fact explain species richness between adjacent cells, and no autocorrelation is expected in the residuals after fitting the environmental model. This latter process is the environmental control model recently simulated by Legendre *et al.* (2002).

We emphasize that it would be difficult to distinguish between the causes of spatial autocorrelation based only on an analysis of the original variable (species richness), even if the statistical distribution of geographical range sizes is known. Positive autocorrelation in the residuals at small distances can also be caused by not taking into account another environmental factor that would explain small-scale variation in species richness if it was included in the model. If different environmental factors act at different spatial scales (see Willis & Whittaker, 2002), the inclusion of the relevant environmental factors acting at each scale in the regression model should be sufficient to completely remove autocorrelation from the residuals at all scales. This is a spatially hierarchical version of Legendre *et al.*'s (2002) environmental control model.

Thus, this interactive modelling approach, i.e. including environmental variables to explain and evaluate the spatial autocorrelation in the residuals, allows us to treat variation in species richness at all spatial scales and, at the same time, to identify any statistical biases caused by pseudoreplication at smaller distances. By this reasoning, if no spatial autocorrelation is found in the residuals after including environmental factors in the multiple regression model, then there is no statistical bias in the overall regression analysis. Note that this is true independently of the patterns of autocorrelation in the original variables (for both species richness and the environmental factors).

However, as stressed frequently in the statistical literature (Philippi, 1993), caution is always needed when interpreting the results of any multiple regression. Even if the residuals from the model are not autocorrelated, there may still be potential problems related to multicollinearity among predictor variables, confounding correlation and cause-and-effect, and biasing model parameter estimation. In fact, macro-scale analyses are always correlative and can only suggest potential explanatory factors; they are not strict inferential tests of causality (Levin, 1992). For example, if a given environmental factor is correlated strongly with species richness across all scales (i.e. there is no autocorrelation in the residuals), this does not ensure that the actual causal factor explaining richness has been found. It is possible that the environmental factor is simply correlated with the real causal environmental factor. It must also be remembered that including many highly correlated environmental factors in a multiple regression model hoping to stumble across the ultimate causal effects will cause instability in the estimation of the partial

regression coefficients. In this case, a plausible solution would be to include in the model only variables associated with theoretical models predicting species richness. Another approach is to use multivariate techniques (such as principal components analyses) to reduce the dimensionality and, consequently, the collinearity among the predictors (Vetaas, 1997; Badgley & Fox, 2000). The main point is that these problems associated with the interpretation of multiple regression models are inherent to the technique itself and have nothing to do with spatial autocorrelation.

A slightly different problem with observational data is that it may be difficult to know if the environmental factor indeed drives species richness throughout the geographical space or if the two variables (species richness and the environmental factor) are driven independently by an unique, unmeasured spatially patterned factor created, for example, by a dynamic spatial process (e.g. the diffusion of both organisms and environmental components by vectorial processes driven by water flow in aquatic ecosystems — Legendre & Troussellier, 1988; Velho *et al.*, 2001). In this case, ecological interpretations for the spatial correlation could be completely spurious, because there is a strong possibility of no causal link between environment and richness. Thus, macro-scale spatial patterns should be controlled for, or taken into account, since explanation for the correlation between the variables occurs, in fact, at a local scale. Methods such as partial regression and trend surfaces analyses, spatial generalized least-squares (GLS) or autoregressive models (Legendre & Legendre, 1998) can then be used and will shift the explanation from macro to local scales (see below).

When modelling species richness as a function of multiple environmental factors, different combinations of the problems discussed above may appear in a single analysis. If species richness is strongly patterned in space (i.e. possess a strong pattern of spatial autocorrelation), then the relative importance of the environmental factors in the multiple regression (relative magnitude of partial regression coefficients) could, in principle, be related to the magnitude of spatial autocorrelation in these environmental factors. This could occur because some environmental factors, such as annual temperature (see 'application' below) and richness, are usually correlated mainly when dealing with macro-spatial scales (not at local scales). Standard errors of these regression coefficients could be underestimated and, consequently, there would be an increase in the significance level of the t-values associated with partial regression coefficients of these variables, as discussed previously. Therefore, their relative importance in the multiple regression model would be overestimated. This is what Lennon (2000), using a terminology derived from time-series analyses, refers to as a 'red shift' toward autocorrelated environmental effects, creating a 'red herring' in the interpretation of partial regression coefficients. He pointed out that '... the environmental factors selected by many studies as explanations for ecological patterns are "red shifted" relative to the set of potential explanatory factors: environmental factors with less spatial autocorrelation and hence bluer spectra are much more likely to be rejected'. Thus, on one hand, some environmental factors have only long-distance spatial patterns and can generate spatially autocorrelated residuals at short scales but, at the same time, statistical testing should be based on a reduced number of independent points in the grid (i.e. there is a much lower statistical power — see Dutilleul, 1993). On the other hand, other variables that affect species richness only at the local level will explain only short distance variation, and so long-distance structures will not be taken into account (thus creating spatial autocorrelation in the residuals at macro-scales).

It is difficult to predict how multiple regression deals with this combination of different spatially structured effects, because coefficients (and standard errors) are all partials. Lennon's (2000) simulations, although demonstrating this 'red shift', were based on independently generated predictors, not dealing with the complications created by strong multicollinearity of real environmental data.

Detection of the 'red shift' proposed by Lennon (2000) could be based on bias in the standard errors of partial regression coefficients (indicating a relative bias in the Type I errors of the different environmental factors), and not on changes in the standardized partial coefficients (indicating only a scale shift), after taken into account the spatial structure in data. As will be demonstrated below, if there is no autocorrelation in the residuals and no large differential underestimation of standard errors (after comparing spatial and nonspatial regression models), Lennon's (2000) 'red shift' reflects only that highly autocorrelated climatic factors may indeed be more important at the overall spatial scale of the study.

Controlling for macro-scale autocorrelation, as suggested by Lennon (2000) and others (see Selmi & Boulinier, 2001), is not necessarily the solution to the problem, because this will shift the explanation towards factors that drive species richness at smaller spatial scales. This should be performed if one has reason to believe that macro-scale correlations between environmental factors and species richness are spurious, and that other ecological processes, acting at small spatial scales, are the ultimate factors driving species richness (such as in the diffusion example mentioned previously). However, our present understanding of the mechanisms driving species richness in terrestrial ecosystems clearly indicates that different environmental factors are involved hierarchically as explanations at different spatial scales (Whittaker *et al.*, 2001; Willis & Whittaker, 2002), and no passive diffusion process could explain the high correlations between climate and species richness.

We now illustrate the ideas developed above to understand the factors influencing species richness patterns of western Palearctic birds. This represents part of a larger dataset being

used to understand the latitudinal diversity gradient for terrestrial birds (B.A. Hawkins, E.E. Porter and J.A. Diniz-Filho, unpublished).

APPLICATION: ENVIRONMENTAL GRADIENTS AND SPECIES DIVERSITY IN WESTERN PALEARCTIC BIRDS

Data

Spatial variation in bird species richness was estimated using range maps for native breeding species in the western Palearctic (Europe, North Africa and the Middle East (Cramp & Simmons, 1977, 1980, 1983; Flint *et al*., 1984; Cramp, 1985, 1988, 1992; Cramp & Perrins, 1993, 1994a,b) (Fig. 1). The region was divided into equal area cells *c*. 220 km × 220 km (2° × 2° at the equator), except for coastal cells, in which case adjacent cells were combined to obtain areas approximately equal in size to inland cells. This grid represents an intermediate scale of resolution compared to those generally used in very macro-scale studies of diversity gradients (Currie & Paquin, 1987; Currie, 1991; O'Brien *et al*., 1998; Rahbek & Graves, 2001). A species was considered present in a cell if any part of its range overlapped the cell, and only species feeding at least partially on terrestrial food were included.

Five environmental variables that are known to be associated with regional-scale diversity gradients (see Turner *et al*., 1987; Currie, 1991; Kerr *et al*., 1998; Kerr & Packer, 1999; Lennon *et al*., 2000; Rahbek & Graves, 2001) were compiled from various sources: (1) annual potential evapotranspiration (PET); (2) annual actual evapotranspiration (AET); (3) mean daily temperature in the coldest month (MINT); (4) range in elevation (RELEV); and (5) annual mean temperature (ANNT). PET (Priestley–Taylor formula) and AET (Thornthwaite's) were obtained from http://www.grid.unep.ch/data/grid (see also Ahn & Tateishi (1994) and Tateishi & Ahn (1996) for details of how these variables were modelled), while MINT and ANNT were obtained from http://www.clarklabs.org/14LINKS/14links.htm. RELEV was measured as the difference between maximum and minimum elevations, estimated to the nearest 50 m, in maps from the Polish Army Topographical Survey, 1968). The environmental data were extracted by overlaying the grid system over maps showing the distributions of the variables, including both paper and digitized maps, depending on the data source.

Data analysis

We initially estimated the spatial autocorrelation in the original data, including both the response variable (species richness) and the five environmental factors (explanatory variables). Spatial correlograms were constructed using Moran's *I* coefficients at 10 distance classes, using SAAP 4.3 (Wartenberg, 1989), as described above. Upper limits for these distance classes were 660, 1100, 1540 1760, 1980, 2420, 2860, 3080, 3740 and 5280 km.

We initially used a set of ordinary least-squares multiple regressions (OLS) to identify how spatial autocorrelation in the residuals was removed successively from the species richness data after the addition of each environmental variable. That is, we evaluated scale-specific effects of each environmental variable on spatial variation in species richness. Because the spatial autocorrelation in the data invalidated automatic procedures for variable entry into the models, we used a manual iterative forward-stepwise procedure instead (Philippi, 1993). At each step, we included each variable (as well as its quadratic term if the relationship was non-linear) sequentially, based on the improvement in the coefficient of determination in relation to the previous regression model.

We then compared the full OLS multiple regression model (using all explanatory variables and the relevant quadratic terms) with a spatial generalized least squares (GLS) model that incorporates spatial structure in the error term of the regression model (Selmi & Boulinier, 2001). Different models of spatial structure (assuming spherical, exponential, Gaussian structure — see Legendre & Legendre, 1998) were tested, and the best fitting model was defined using the Akaike information criterion (Littell *et al*., 1996; Hilborn & Mangel, 1997; Selmi & Boulinier, 2001). Parameters were estimated under restricted maximum likelihood. All these GLS procedures were implemented using the PROC MIXED routine in SAS (Littell *et al*., 1996).

We ranked the variables in each full regression model (OLS and GLS) based on their relative importance, as indicated by *t*-values for each partial regression coefficient, and associated the change in the ranks (difference in ranks between OLS and GLS) with the magnitude of spatial autocorrelation in each variable. Using other forms of evaluating the relative importance of variables in each full model (such as comparing R^2 after removing the target variable with the R^2 of the full model) produced exactly the same variable rank order.

RESULTS

Bird species richness is patterned in space (Fig. 1b), with a north–south gradient that extends throughout Europe. A reversion in the gradient occurs in North Africa and the Middle East, such that a quadratic pattern appears for the entire Western Palearctic. Indeed, the spatial correlogram for species richness (Fig. 2a) indicates that richness is positively autocorrelated up to *c*. 1600 km, followed by a continuous decrease in Moran's *I* coefficients up to *c*.
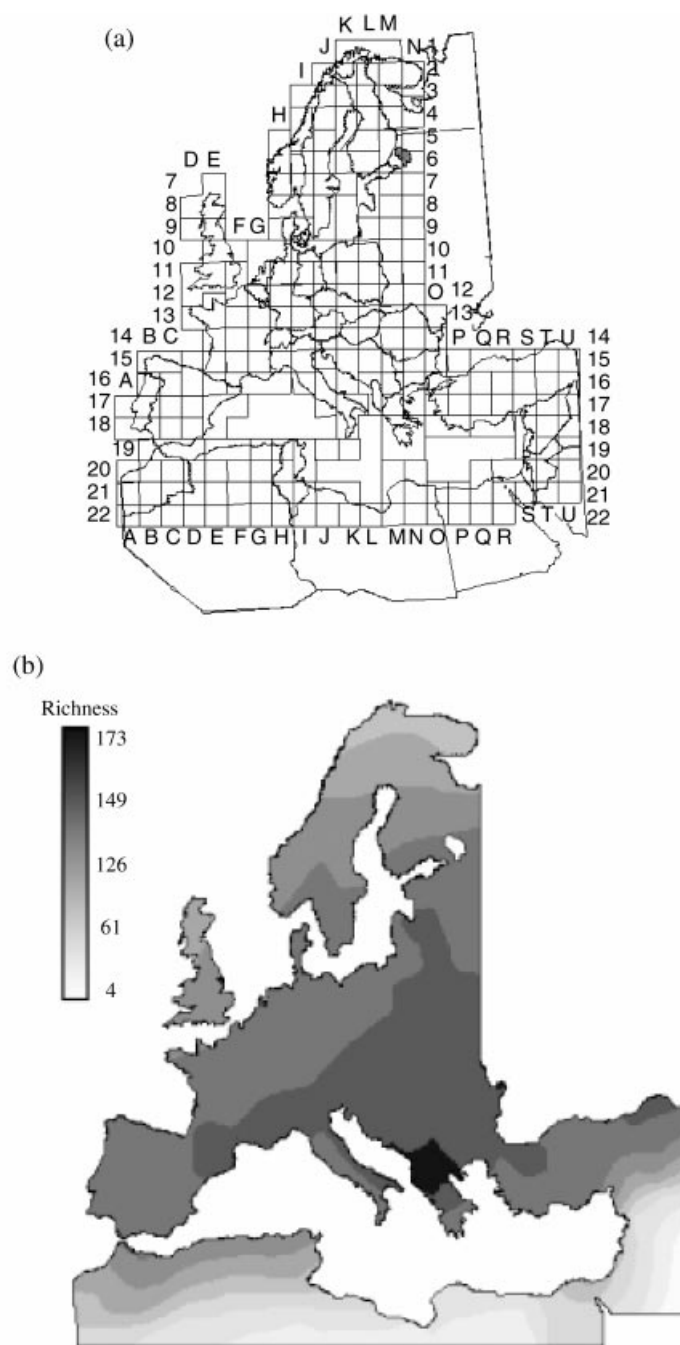
Fig. I (a) Grid covering the western Paleartic data; and (b) interpolated patterns of species richness for the entire region. Interpolation was performed using distance-weighted least-squares algorithm (DWLS).

3700 km, at which point there is a highly significant negative autocorrelation coefficient. After this distance, autocorrelation is no longer significant.

For the environmental variables, strong spatial structure in the first distance class appears for AET, MINT and ANNT.

Moderate short-distance autocorrelation coefficients were observed for RELEV and PET. MINT, ANNT and PET also show clear spatial gradients, with short-distance positive auto-correlation associated with strong negative autocorrelation at the largest distance classes. For AET, on the other hand, a
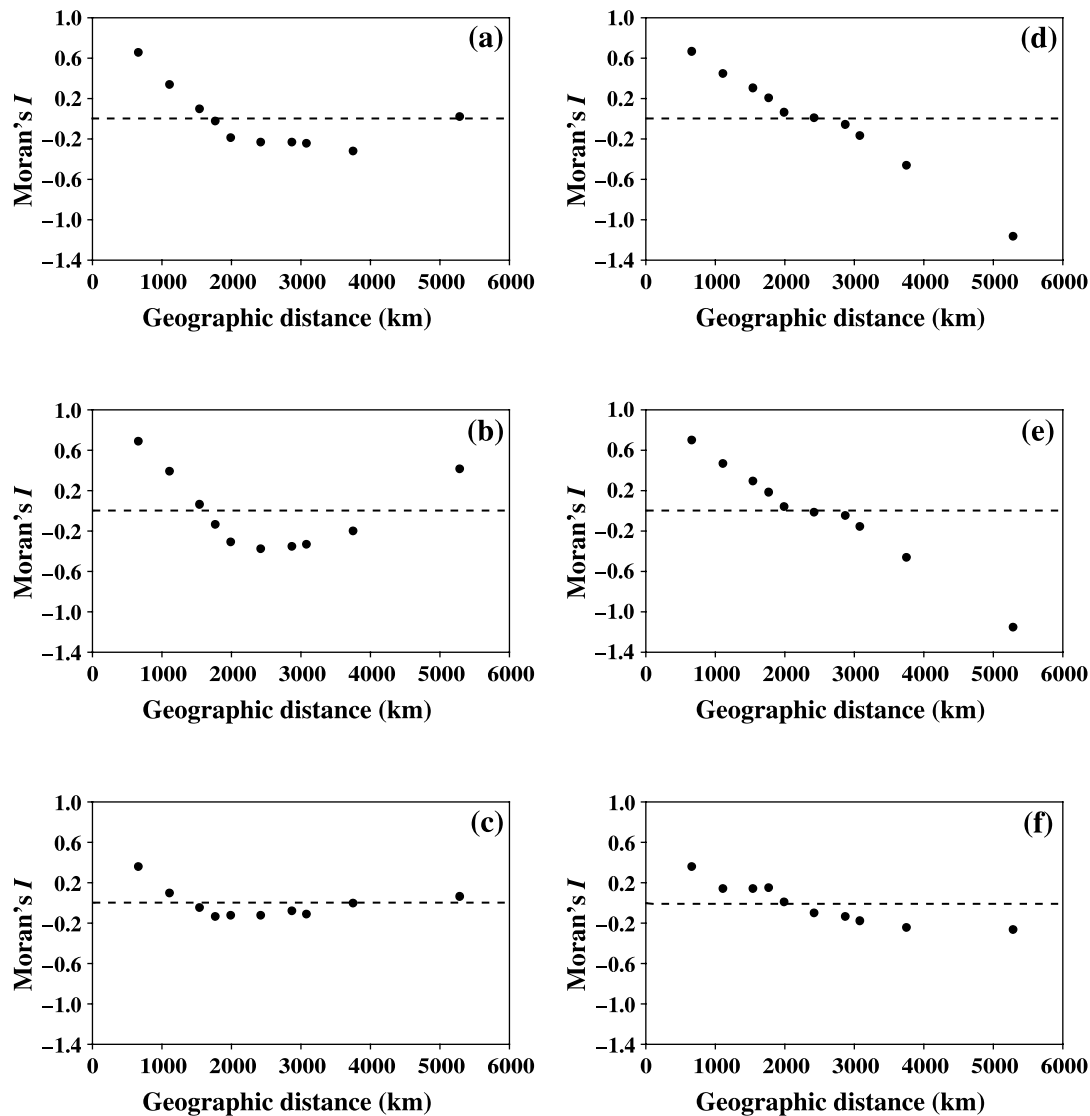
Fig. 2 Spatial correlograms for (a) species richness, (b) AET (annual actual evapotranspiration), (c) RELEV (range in elevation), (d) ANNT (annual mean temperature), (e) MINT (mean daily temperature in the coldest month) and (f) PET (annual potential evapotranspiration). All correlograms are significant at $P < 0.001$ after Bonferroni correction.

strong reversion in the gradient appears in the last distance class, with a positive autocorrelation coefficient. RELEV shows a more patchy spatial structure, with positive autocorrelation in the distance classes up to around 1000 km, followed by nonsignificant coefficients beyond this distance (Fig. 2c).

The stepwise order of inclusion of the environmental variables in the OLS regression model based on the relative improvement of the R^2 was: annual temperature (ANNT), annual actual evapotranspiration (AET), range in elevation (RELEV), mean daily temperature in the coldest month (MINT) and annual potential evapotranspiration (PET). The

first variable added to the model (ANNT plus its quadratic term) explained 76.9% of the variance in species richness, and the inclusion of all other variables improved the model to a final R^2 of 0.868 ($F = 154.6$; $P < 0.001$).

After including these environmental variables successively in the model, spatial autocorrelation in the residuals disappears (Fig. 3). When introducing only ANNT and its quadratic term, there was a strong reduction in spatial autocorrelation in the residuals. The only remaining autocorrelation occurred in the first distance class, and even at this distance the autocorrelation was reduced from 0.66 (original richness) to 0.19 (residuals). The overall correlogram, however,
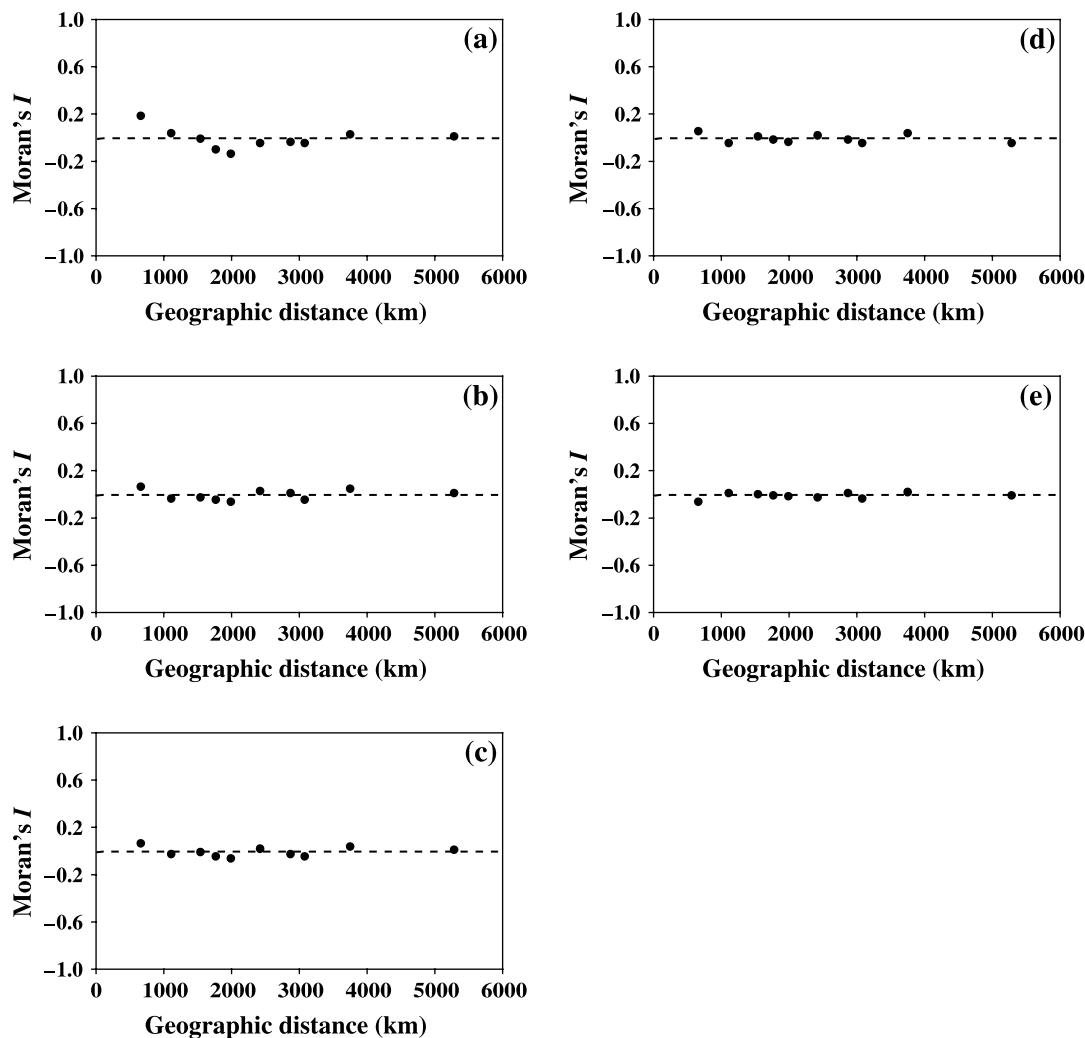
Fig. 3 Spatial correlograms for residual models, after including sequentially the following variables in the OLS regression model: (a) ANNT, (b) AET, (c) RELEV, (d) MINT and (e) PET. Significance levels of the correlograms after a Bonferroni correction were, respectively, 0.0001, 0.001, 0.003, 0.011 and 0.735.

is still significant even applying Bonferroni correction. This indicates that other variables are necessary to take fully into account variability at smaller distances (< 700 km). When AET was introduced in the model, there was an additional reduction in the Moran's I in the first distance class, from 0.19 to 0.07. In the residuals of the final full model (with all environmental variables), no Moran's I was larger than 0.055, and the overall correlogram is not significant ($P = 0.735$) according to the Bonferroni criterion (see Fig. 3). These results are not affected by number and definition of distance classes in the correlogram, and even at the smallest possible distance class (equal to cell resolution i.e. = 220 km), Moran's I coefficient is not significant ($I = 0.038$; $P = 0.223$).

We can now compare the OLS and GLS full models (Table 1). The most important variable in the full OLS model was AET, followed by the quadratic term of ANNT, by RELEV and by MINT. Linear and quadratic coefficients of PET and the quadratic coefficient of MINT were not significant (Table 1). Note that, due to the multicollinearity problems, the relative importance of the environmental variables in the full model is not the same order of entry as in the stepwise procedure previously described. For example, PET is not significant in the full model because it has a high colinearity with other macro-scale climatic variables.

The best-fitting GLS model (Akaike's information criterion equal to −821, in contrast with −858 in the OLS model) incorporated an exponential spatial relationship in the residual

Table I Coefficients of the multiple regression ($b \pm SE$) and associated *t*-tests for bird species richness regressed against environmental factors in the western Palearctic, according to ordinary least-squares (OLS) and spatial generalized least squares (GLS) models. In the GLS model, spatial structure was incorporated into the model by defining the covariance between pairs of quadrats as an exponential function of geographical distance

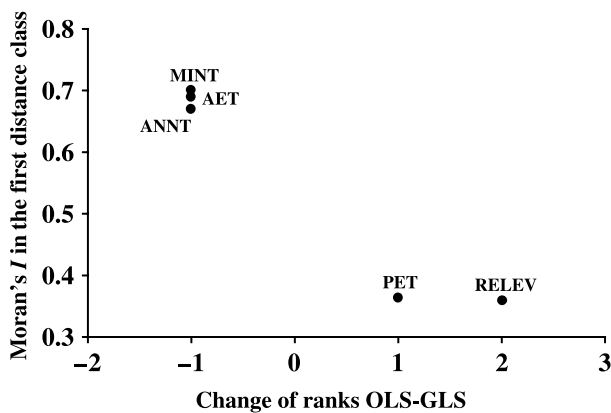| Factor	OLS		GLS	
	$b \pm SE$	*t*	$b \pm SE$	*t*
MINT	-1.574 ± 0.573	2.746**	-0.452 ± 0.865	0.522
$MINT^2$	-0.016 ± 0.041	0.390	0.007 ± 0.041	0.171
ANNT	2.822 ± 1.159	2.435*	2.290 ± 1.069	2.142*
$ANNT^2$	-0.175 ± 0.049	3.542**	-0.093 ± 0.050	1.863
RELEV	0.004 ± 0.001	3.240**	0.006 ± 0.001	4.843**
AET	0.130 ± 0.014	9.360**	0.065 ± 0.017	3.751**
PET	0.005 ± 0.016	0.344	-0.020 ± 0.012	1.719
PET^2	0.000 ± 0.000	0.042	0.000 ± 0.000	1.434

* $P < 0.05$; ** $P < 0.01$.

Fig. 4 Relationship between Moran's *I* in the first distance class and the change in rank of importance of the environmental factors between OLS and GLS regression models.

covariance matrix. A conspicuous change in the relative magnitude of regression coefficients was observed in the GLS model, and RELEV becomes the variable with the highest *t*-value, followed by AET. ANNT is still significant in the model at $P = 0.03$, but all other variables and quadratic terms become non-significant at the 5% level.

There is an association between the change in the relative rank order of importance of environmental variables and their degree of spatial autocorrelation, as measured by Moran's *I* coefficient in the first distance class (Fig. 4). RELEV has a relatively low autocorrelation and showed a great positive change in rank (i.e. gained importance in the GLS model). On the other hand, MINT, ANNT and AET all

have high autocorrelation structure, and lost relative importance in the GLS model.

DISCUSSION

Grid-based diversity datasets are almost always spatially autocorrelated (Ruggiero, 1999; Rahbek & Graves, 2001; Diniz-Filho *et al.*, 2002; van Rensburg *et al.*, 2002), as are other diversity data obtained in natural or artificial sampling units at finer spatial scales (Selmi & Boulinier, 2001). However, some ecologists ignore the inferential problems (i.e. inflated Type I errors) caused by spatial structure in their data (Legendre, 1993). Recently, Lennon (2000) called attention to the problems caused by spatial autocorrelation, focusing not only on the well-known inflation of Type I errors, but also arguing that spatial autocorrelation generates widespread 'red herrings' in the interpretation of ecological mechanisms based on geographical data. He concluded that virtually all geographical analyses had to be redone, taking into account spatial autocorrelation.

Our results for western Palearctic birds show that Lennon (2000) is 'statistically' correct, although his interpretation is not necessarily 'ecologically' correct. Range in elevation possesses a relatively low level of spatial structure (using Lennon's (2000) terminology, this variable is on the 'blue' side of the spectrum) and is not very important in the OLS model, in comparison with the other climatic variables that have strong spatial autocorrelation patterns, such as AET, ANNT and MINT. However, as will be shown below, we cannot conclude that spatial autocorrelation has biased the result against range in elevation. Rather, our analysis indicates that the climatic variables, as we would expect a priori, are better explanatory variables for bird richness at the macro-scale, across the entire region.

It is important to ask what the real statistical problem with the OLS model in our analyses is. According to Lennon (2000), the 'red-shift' occurs because predictors with strong autocorrelation would have underestimated standard errors and, consequently, acquire more importance due to 'artificially' low Type I errors (see also Ver Hoef *et al.*, 2001). In our analyses, however, standard errors of GLS and OLS are highly correlated (Spearman's rank correlation coefficient = 0.98), and shifts in the importance of predictors are due mainly to changes in partial regression coefficients themselves, not to an increase in standard errors creating reduced *t*-values (see Table 1). In short, as there is no significant autocorrelation in the residuals, there is nothing wrong with the OLS model, and the analysis does not need to be redone or 'corrected' for spatial autocorrelation. Therefore, the climatic variables have taken into account successfully all spatial structure in the original data (i.e. species richness) and thus we have strong support for the hierarchical version of the environmental control model.

We must also ask what was accomplished by using a GLS model that takes into account spatial autocorrelation in residuals, as suggested by Lennon (2000) and others (see Selmi & Boulinier, 2001; Hawkins & Diniz-Filho, 2002). In principle, if residuals are not autocorrelated, OLS becomes a special case of GLS, and both methods should converge to the same solution. However, in our analyses, there are small (although not significant) autocorrelations in the residuals of the OLS model and, probably, because of differential statistical power between GLS and spatial correlograms, slight differences between OLS and GLS appear and must be interpreted.

In principle, one explanation for the difference between OLS and GLS could be the instability of solutions under strong multicollinearity that occurs in environmental data, as previously discussed, but we would like to explore an alternative and more ecologically meaningful explanation for the difference between the two models. We found that range in elevation acquires a greater relative importance and becomes the best predictor of species richness (although annual evapotranspiration is still the second most important predictor). We advocate that the difference between the two approaches is understandable in terms of spatial scale. In the OLS model, the relationship is considered at the overall spatial scale under study (i.e. the entire western Palearctic), and so variables with strong spatial structure (i.e. climatic variables) should be considered the main candidate predictors. Note that both species richness and annual evapotranspiration (the most important predictor in the full OLS model) show similar correlogram profiles (Fig. 2), especially because of the increase in the Moran's I at the last distance class and, consequently, have higher covariance at this spatial scale.

When spatial autocorrelation is taken into account in the GLS model, the residuals are assumed to have an exponential relationship in terms of spatial distance among quadrats. Therefore, macro-scale effects were already incorporated into the error term of the model, and consequently the variation at finer scales becomes more important simply because of the larger weight in the residual covariance matrix. This will cause the increase in the relative magnitude of variables that are better explanations for diversity at small spatial scales, exactly as we would predict for range in elevation (Rahbek & Graves, 2001; van Rensburg *et al.*, 2002).

Once again, we note that GLS de-emphasizes predictors with strong autocorrelation, such as long distance clines (Ver Hoef *et al.*, 2001) so, ecologically, it tends to give more importance to mechanisms acting at local geographical scales. If higher-order correlation between predictor and response variables is created simply by long-distance diffusion (generating two long-distance correlated spatial surfaces, without a causal relationship at local scales), then the GLS estimator is clearly a more adequate model. Indeed, this seems to be the case with the simulation procedure developed by Lennon (2000), in which spatial patterns were generated as a

fractal structure, self-similar at all scales and independent of quadrat size or resolution. However, as we mentioned previously and many recent papers support (Whittaker *et al.*, 2001; Willis & Whittaker, 2002), macro-scale effects of climate on species richness are not artefacts, and no diffusion processes can be invoked to explain the relationships.

It is important to stress that our interpretation does not mean that spatial autocorrelation should be ignored. We are just clarifying that the 'red herrings' in geographical ecology, as argued by Lennon (2000), are really a question of deciding at which spatial scale one is interested in explaining diversity. Further, if residuals are still autocorrelated at small distance classes after the regression models, Type I error may indeed be inflated, because quadrats situated at short spatial distances apart do not provide independent data points for testing long distance effects. Mapping residuals of the OLS model could be used to ascertain other spatially structured environmental variables not accounted for (see Rahbek & Graves, 2001), but if autocorrelation still persists, GLS and other spatial models should be used.

A very simple strategy in this case would be to measure the average patch diameter in the correlogram of the residuals (i.e. the geographical distance at which autocorrelation becomes nonsignificant) (Diniz-Filho & Telles, 2002; see Bini *et al.*, 2000 and Diniz-Filho *et al.*, 2002; for a similar approach) and define, based on the grid map, how many data points can be found that are separated by this distance. Note that we are not proposing a re-estimation of the model using a few data points (a valid strategy, but one that loses much information — Legendre, 1993; Lennon, 2000), only that any statistical tests should use a more conservative number of degrees of freedom. A similar and more complex strategy is to define analytically the number of degrees of freedom based on the spatial autocorrelation structure in the data, as proposed by Clifford *et al.* (1989) and Dutilleul (1993) (see also Legendre *et al.*, 2002).

As Legendre (1993) pointed out, spatial autocorrelation must become a new analytical paradigm in geographical ecology, both because it allows us to understand spatial patterns, and because it can help avoid some common pitfalls in multiple regression analyses. The question of autocorrelation is not new and the message is quite simple: spatial autocorrelation in the residuals of multiple regression models must always be checked. If no autocorrelation remains in the residuals of an OLS model, interpreting a multiple regression is not affected by autocorrelation in the original variables and the best predictors usually will be those with macro-scale spatial patterns. Taking into account or removing spatial patterns created by macro-scale processes will shift the spatial scale of the analysis and, obviously, the interpretation of ecological mechanisms driving spatial variation in species richness. In short, each approach should be interpreted with awareness of spatial scale.

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Bradford A. Hawkins is interested in large-scale patterns in ecology, primarily the latitudinal diversity gradient. Recent projects involve attempts to narrow the set of the most plausible hypotheses and to reconcile points of view focusing on processes operating contemporaneously vs. those operating over evolutionary time. He also is interested in the biology and ecology of insect parasitoids.