For: Ecography

*Correspondence to:
Bradford A. Hawkins
email:bhawkins@uci.edu

Red herrings revisited: spatial autocorrelation and parameter estimation in geographical ecology

Bradford A. Hawkins (bhawkins@uci.edu), Dept. of Ecology & Evolutionary Biology, Univ. of California, Irvine, CA 92697, USA — José Alexandre F. Diniz-Filho, Luis Mauricio Bini, Paulo De Marco, Depto de Biologia Geral, ICB, Univ. Federal de Goiás, CP 131, 74.001-970, Goiânia, GO, Brasil — Tim M. Blackburn, School of Biosciences, University of Birmingham, Edgbaston, Birmingham B15 2TT, UK.

Emails: bhawkins@uci.edu, diniz@icb.ufg.br, bini@icb.ufg.br, pdemarco@icb.ufg.br, t.blackburn@bham.ac.uk

Keywords: Species richness, spatial autocorrelation, birds, multiple regression, ordinary least squares, red shifts, parameter estimation, macroecology

Running head: parameter estimation in geographical ecology

There have been numerous claims in the ecological literature that spatial autocorrelation in the residuals of ordinary least squares (OLS) regression models results in shifts in the partial coefficients, which bias the interpretation of factors influencing geographical patterns. We evaluate the validity of these claims using gridded species richness data for the birds of North America, South America, Europe, Africa, the ex-USSR, and Australia. We used richness in 110 x 110 km cells and environmental predictor variables to generate OLS and simultaneous autoregressive (SAR) multiple regression models for each region. Spatial correlograms of the residuals from each OLS model were then used to identify the minimum distance between cells necessary to avoid short-distance residual spatial autocorrelation in each data set. This distance was used to subsample cells to generate spatially independent data. The partial OLS coefficients estimated with the full dataset were then compared to the distributions of coefficients created with the subsamples. We found that OLS coefficients generated from data containing residual spatial autocorrelation were statistically indistinguishable from coefficients generated from the same data sets in which short-distance spatial autocorrelation was not present in all 22 coefficients tested. Consistent with the statistical literature on this subject, we conclude that coefficients estimated from OLS regression are not seriously affected by the presence of spatial autocorrelation in gridded geographical data. Further, shifts in coefficients that occurred when using SAR tended to be correlated with levels of uncertainty in the OLS coefficients. Thus, shifts in the relative importance of the predictors between OLS and SAR models are expected when small-scale patterns for these predictors create weaker and more unstable broad-scale coefficients. Our results indicate both that OLS regression

is unbiased and that differences between spatial and nonspatial regression models should be interpreted with an explicit awareness of spatial scale.

INTRODUCTION

In recent years it has become widely appreciated by ecologists that significance tests used in inferential statistics are influenced by the presence of residual spatial autocorrelation (RSA) in environmental models of spatially structured data. The problem arises because the lack of independence among residuals after model fitting generates artificially narrow standard errors, inflating Type I error. However, in addition to this almost universally recognized issue of false precision, it is also widely believed that spatial autocorrelation creates a shift in the relative importance of coefficients in simple and multiple regression models (Lennon 2000). This sometimes causes workers to abandon the results of standard ordinary least squares (OLS) regression and to interpret instead coefficients generated using one of several spatially explicit modeling procedures (Lennon 2000, Selmi and Boulinier 2001, Tognelli and Kelt 2004, Bahn 2006, Dormann 2007, Kühn 2007). Because regression models using OLS, generalized least squares (GLS), or spatial autoregression (simultaneous or conditional autoregressive models; SAR or CAR) may sometimes differ from each other, it thus becomes important to know to what extent these differences are the consequence of RSA or may be due to other structural differences among the modeling approaches that arise independently of spatial autocorrelation.

This paper is focused on the question: does spatial autocorrelation 'bias' regression coefficients (i.e., create systematic shifts) that can alter our explanations for richness patterns when using nonspatial, OLS regression? To answer this question we use geographical patterns of bird species richness, and we show that claims that OLS results are biased are without foundation, at least when the response variable is measured in a spatial grid, a widely used method in geographical ecology (e.g., Currie and Paquin

1987, Ruggiero et al. 1998, Williams et al. 1999, Lennon et al. 2000, Rahbek and Graves 2001, Blackburn and Hawkins 2004, Hawkins et al. 2005; Hawkins and Diniz-Filho 2006). We also evaluate the related claim that spatial autocorrelation generates a 'red-shift' in regression models, artefactually inflating the apparent importance of macroscale environmental variables as explanations of broad-scale ecological patterns (Lennon 2000). Given the increasing rate that spatially explicit modeling approaches are beginning to appear in the literature, we need to know how to interpret the differences that sometimes arise when using spatial and nonspatial methods on the same datasets.

It is important to note that we do not present a formal evaluation of this issue using statistical theory (see Cressie 1993, Schabenberg and Gotway 2005, Tiefelsdorf and Griffith 2007). Rather, we provide an empirical resampling analysis of spatially structured data of the type commonly found in macroecological and geographical analyses. And although further studies using simulation procedures may shed light on these issues and allow more formal evaluations of the accuracy and precision of parameter estimates under different scenarios and spatial scales, our goal is to illustrate heuristically that the often presumed bias due to spatial autocorrelation in OLS regression does not apply to real data sets.

METHODS

We analyzed the number of species in 110 x 110 km cells in equal-area girds for the birds of North America, South America, Europe, Africa, the ex-USSR, and Australia (for methods and sources of the bird data see Hawkins et al. 2007). Coastal cells containing less than 50% of the area of full cells were excluded from all grids prior to analysis. We also generated corresponding gridded environmental data for five potential explanatory variables (annual temperature, annual actual evapotranspiration, mean monthly Global Vegetation Index, range in elevation , and the interaction of annual temperature and range in elevation). All of these variables have been shown to be associated with bird richness directly or indirectly in globally extensive path models (Hawkins et al. 2007), so we expected combinations of these variables to contribute to richness to varying degrees in more regionally focused regression models (see also Hawkins et al. 2003). We divided the data into regions to provide replicate datasets to ensure that the results of our evaluation of RSA were not due to a particular data structure or a single geographical location or extent.

In the first step of the analysis we generated OLS multiple regression models for each region. Combinations of predictors were added and removed until we obtained a model with the highest coefficient of determination and simultaneously with the fewest number of variables. As the goal of the analysis was to obtain a set of models which could be used to investigate the influence of RSA, we were not concerned with generating the best possible explanatory model in each region and so we did not use probability values or information theoretic indices to select the final regional models. Rather, we generated plausible environmentally-based models which could form the basis for evaluating the extent that RSA influences model coefficients.

The second stage of the analysis generated spatial correlograms of Moran's I based on the residuals from each regional model. We used the correlograms to evaluate the ability of each model to explain the spatial structure in the data, and specifically to identify the distances at which positive spatial autocorrelation remained in the data (Haining 1990, Diniz-Filho et al. 2003). It is 'short-distance' positive RSA that is believed to generate the bias in OLS regression and which workers hope to take into account by using spatially explicit modeling (Lichstein et al. 2002).

Based on the correlograms we identified the minimum distances between cells that are necessary to avoid significant short-distance RSA in each data set. This was developed as an heuristic, intuitive, and statistically conservative way to deal with RSA, even though it causes a serious loss of power in the analyses (Legendre 1993). We then used a sampling program written in MatLab to generate samples of cells from each grid with a fixed sample size (which varied depending on the region) and in which all distances among cells were at least the minimum distance required to avoid short-distance RSA. The program starts by selecting a random cell in the grid and then randomly searches for other cells that are at least a given distance apart from all other cells. There is, therefore, a maximum number of cells that can be selected, because if a very high number of cells is chosen the program is unable to find a compromise solution between the number of samples and the minimum geographical distance. We iteratively determined the number of cells to be included in each sample by balancing statistical power in the sampling procedure (maximizing the number of cells, n_2 in Table 1) and viable computer time for each run. The sampling routine was run 500 times on each data set to generate independent samples containing no RSA. Separate OLS multiple regression models were generated from each of the 500 samples, providing a distribution of coefficients of each predictor variable in the model. We then used *t*-tests to determine if the values of the coefficients from the regression using all data (data containing RSA) were significantly different from the mean values generated by analyzing subsets of data known to contain no significant short-distance RSA. This then tested whether coefficients from resampled data differ from parameters estimated by OLS. As all other aspects of the data and modeling are identical, a significant difference between the full coefficients and the sample coefficients can be unambiguously interpreted as the 'bias' generated by RSA. In contrast, if no significant differences between the full and sample-based coefficients are found, it provides clear evidence that the presence of RSA has had no statistically detectable influence on the parameter estimates of regression models.

The next step of the analysis tested the coefficient of determination of each regional model using all cells against the distribution of adjusted R^2s from the subsampled data. We did this to evaluate the claim that RSA increases the strength of associations among variables at the macroscale in addition to causing a shift in the coefficients (Lennon 2000).

Finally, since the residuals of the full OLS regressions contained RSA at relatively short distances (see Fig. 1), we also modelled the relationship between species richness and the environmental predictors using a spatially explicit simultaneous autoregressive (SAR) model (Cressie 1993, Schabenberg and Gotway 2005, Tognelli and Kelt 2004, Kissling and Carl 2007). In the SAR error model, spatial covariance among cells (**C**) is defined as

$$\mathbf{C} = \sigma^2 \, [(\mathbf{I} - \rho\mathbf{W})^T]^{-1} \, [(\mathbf{I} - \rho\mathbf{W})]^{-1}$$

where σ^2 is the variance of the residuals, ρ is the autoregressive parameter and **I** is an n x n identity matrix. The row-standardized **W** matrix contains the spatial relationship among sampling units, with elements given by the inverse of the geographic distances (d_{ij}) among them, expressed as $1/d_{ij}^{\alpha}$, where α was chosen to minimize RSA.

Duttileul's method (see Duttileul 1993, Legendre et al. 2002) was used to correlate the estimated and observed richness for each model in order to determine the effective geographic degree of freedom for each multiple regression model and test its overall statistical significance. Since the effective degrees of freedom represents a conservative sample size that takes into account autocorrelation, they can be compared with the sample sizes used in the simulations to obtain minimum distances between cells that are necessary to avoid significant short-distance RSA in each data set.

All spatial analyses were performed using Spatial Analysis in Macroecology (SAM) software (Rangel et al. 2006), available at http://www.ecoevol.ufg.br/sam.

RESULTS

The regional regression models contained either three or four environmental predictors (Table 1). Five of the six models explained large proportions of the variance in richness (62.3% to 76.7%), indicating that even though we did not attempt to find the best possible model for richness (which in some cases would include polynomial terms), the models have strong statistical explanatory power. The exception was the European model, which explained *ca*. a third of the variance in richness. However, this was fortuitous, as it allowed us to examine the sensitivity of both strong and weak explanatory models to the presence of RSA. As would be expected, SAR models always had higher R^2s than OLS models (Table 1).

Inspection of the correlograms of the residuals from each model revealed that all contain substantial short-distance positive RSA (Fig. 1), which is typical when using richness data generated from range maps. It also indicates that all models could potentially comprise biased coefficients. However, in all cases the RSA was at or near 0 in distances ranging from 660 km (in Europe) to 1500 km (in North America and USSR), allowing us to subsample the data to eliminate significant small-scale RSA from all data sets and generate sets of regression models containing little or no potential bias. It is notable that most data sets still contain negative spatial autocorrelation at moderate to large distances. However, these structures remaining in the residuals would not produce the bias associated with RSA, because long-distance negative autocorrelation would have conservative (not liberal) effects on parameter estimates and Type I errors. The number of cells sampled in each region to generate the short-distance RSA-free data ranged from seven to 30 (Table 1). These sample sizes are very small when compared to original sample sizes and illustrate the apparent loss of statistical power of our resampling procedure. However, they are similar to the geographically effective degrees of freedom obtained using Duttileul's method.

An example of the relationships between the regression coefficients from a full model and the distributions of regression coefficients generated by resampling is presented in Fig. 2, but more generally the coefficients from the analyses of data sets containing RSA did not differ from the mean coefficients estimated in data containing no RSA in all 22 tests (Table 1). That is, coefficients generated from data containing residual spatial autocorrelation were statistically indistinguishable from coefficients generated from the same data sets in which short-distance RSA is not present. This was true in data from all parts of the world, in models with different combinations of explanatory variables of either weak or strong explanatory power, and in models with substantially different macroscale autocorrelation structures.

Although the OLS regression coefficients were not sensitive to the presence of RSA when compared to coefficients from resampling, we observed some shifts when compared to SAR coefficients (Table 1) [after standardizing them to permit direct comparisons across variables measured on different scales], indicating that spatial modeling must contain effects that are unrelated to the presence of RSA. For Africa and South America, although changes in coefficients values were observed, the relative importance (rank) of the predictors was the same in OLS and SAR, whereas in North America, Australia and Europe only the first or second most important predictors were the same. At the opposite extreme, in the USSR there is a complete shift in the ranks of predictors. We also observed that shifts in model rank are somewhat associated with the results from the resampling procedure, in that differences between model ranks based on coefficients estimated by SAR and OLS are marginally correlated with the level of uncertainty in values of the OLS coefficients derived from resampling as measured by the ratio between each estimated coefficient and its error ($r = 0.381$; $P = 0.080$).

Perhaps unexpectedly, we did find that removing short-distance spatial autocorrelation from the data improved the average explanatory power of the OLS models in all six regions, significantly so in North and South America (Table 1), and average R^2s using resampled data are more similar to those of SAR models. Thus, in contrast to the claim that spatial autocorrelation inflates the strength of associations among macroscale environmental variables and broad-scale ecological gradients (the red shift of Lennon [2000]), we found that increasing sample sizes by including spatially autocorrelated cells did the opposite.

DISCUSSION

Our analyses indicate that claims that OLS regression generates biased models and leads to incorrect interpretations of the factors influencing macroecological patterns are not necessarily true. That is, short-distance residual autocorrelation in our data, while causing inflated Type I errors, did not create problems in the interpretation of coefficients estimated by OLS. And although our examples are restricted to richness data, it should also be clear that this conclusion holds for any macroecological variables structured in space. Therefore, our general conclusion must be that the problem of autocorrelation that is beginning to dominate the geographical ecological literature is not one of parameter estimation, although it is an issue if one wants to estimate probability values associated with significance tests. We are not the first to make this claim (see e.g. Schabenberg and Gotway 2005), and methods to generate geographically effective degrees of freedom to evaluate correlations implicitly assume that the standard Pearson coefficients are unbiased in the presence of spatial autocorrelation, and it is only necessary to control the inflated Type I error (Legendre et al. 2002).

Our analysis raises a number of issues requiring further investigation. First and foremost, it remains the case that OLS and spatially explicit regression models of the same data sets sometimes differ, as we observed in our data. Ecologists often interpret this as evidence of the bias generated by spatial autocorrelation and then claim that the OLS results are not dependable (Lennon 2000, Selmi and Boulinier 2001, Tognelli and Kelt 2004, Dormann 2007, Gimona and Brewer 2006, Kühn 2007). However, spatial autocorrelation is not the source of the problem. There is no doubt that RSA inflates Type I errors, so that coefficients obtained by OLS are not minimum variance estimators.

Consequently, OLS coefficients are less precise than their spatial counterparts and may be more unstable in the analyses of particular datasets, especially if their magnitudes are low. Even so, it is well known in the statistical literature that OLS estimates are accurate, especially with large sample sizes, and coefficients are not biased in a statistical sense (see Cressie, 1993, Schabenberg and Gotway 2005, Tiefelsdorf and Griffith 2007). It should also be realized that there are sources of instability in spatial regression models as well, mainly due to the definition of spatial relationships (i.e., weightings) in the model structure or in the residual variance-covariance (see Kissling and Carl 2007). Given the confusion among ecologists concerning the effects of RSA on OLS regression modeling, we must reiterate that RSA *per se* does not cause nonspatial regression models to generate biased coefficients, even though many statisticians may wonder what the fuss is about.

We believe that the resampling procedure performed here provides some insights into the reasons for coefficient shifts sometimes found when comparing OLS and spatial regression methods. Although further studies are necessary to understand fully the reasons underlying coefficient shifts (see Dormann 2007), our resampling procedure at least partially reinforces a previous interpretation for model instability. Diniz-Filho et al. (2003) argued that coefficients change because spatially explicit models shift the effective scale of the analysis, putting stronger emphasis on local-scale patterns and processes (also see Fotheringham et al. [2002], who refer to autoregressive models as 'semi-local' approaches). Indeed, predictors having the greatest differences between OLS and SAR are also those that have large standard errors in the resampling procedure (Table 1), which indicates that these coefficients are more dependent on the particular spatial configuration of sampled points. In other words, shifts in the relative importance of the predictors between OLS and SAR models are expected when there are local or regional patterns for these predictors within the continents that, in turn, create more unstable coefficients when sampling. Thus, as observed by Lennon (2000), predictors with weak spatial patterns gain importance in SAR regression compared to predictors with strong spatial patterns (the red shift). However, this shift is not due to a bias in OLS coefficients, but instead arises because spatial regression, by adding an explicit spatial component, captures effects operating at smaller spatial scales, whereas OLS captures the overall structure at broad scales (Diniz-Filho et al. 2003). Of course, evaluating fully our interpretation for coefficient shifts requires simulation studies in which effects of predictors are known *a priori*. Kissling and Carl (2007) recently generated such simulations and compared OLS with various forms of SAR, showing that the definition of spatial relationships (i.e., weightings) in the model structure or in the residual variance-covariance generates variation among SAR methods. Indeed, they show that in some situations SAR estimates are themselves biased (although not the SAR error model we used here). Irrespective, their simulations are very simple with few predictors, and they did not examine the effects of predictors at multiple spatial scales.

A second issue that requires investigation is that shifts in coefficients when using nonspatial and spatial approaches may reflect model instability due to multicollinearity among the environmental variables usually included in macroecological analyses; it is well known that collinearity destabilizes all types of regression models (see e.g. Graham 2003). Thirdly, and potentially most seriously, virtually all biological and environmental predictors used in broad-scale macroecological analyses are spatially structured at one or more scales, so when an autoregressive parameter is added to the model complex patterns of collinearity can be generated, even if there is no collinearity among the environmental predictors themselves. If this occurs, neither OLS nor autoregressive coefficients could be interpreted unambiguously, unless one is willing to assume that the variance contained in the overlap between environment and space can be attributed solely to the effects of the modeled components of the environment or solely to the effects of space, the latter which will also contain unmodelled spatially structured environmental effects. The worst possible scenario is if coefficient shifts when using spatial models are idiosyncratic and depend on the detailed covariance structure of the particular data set being analyzed. If so, all spatially explicit models are uninterpretable, because workers will be unable to determine if coefficient shifts arise from scale shifts or effects of collinearity between space and the environment. We will address this critical issue in detail in a future paper.

Because our primary finding that residual spatial autocorrelation does not bias regression coefficients runs counter to a view widely held by ecologists and biogeographers, it is important to understand why OLS estimates will be robust in gridded data. This can be illustrated using the relationship between AET and species richness in South America (Fig. 3). The observed data cloud in the scatterplot reflects the presumed influence of AET (and collinear drivers), errors generated by inaccurate range maps and false positives in the richness values, and the effects of unmeasured driving variables. Because the data contain many cells in close proximity, the density of the data cloud is high. Now, if we only sample sites far enough apart not to contain short-distance spatial autocorrelation (22 equally spaced cells 1000 km apart in this example, see Fig. 3 insert), the density of points is lower, but all must fall within the observed data cloud.

Clearly, a regression coefficient estimated from the subsampled data represents an estimate of the relationship found among all samples. It is also clear that introducing spatial autocorrelation into a set of samples by including sites closer together will fill in gaps in the data cloud, but it cannot create a new data cloud with a different scatter, which would be required to shift the regression coefficient. The exception to this argument is if all of the added sample points were concentrated in one portion of the geographic space (e.g. all were in the Andes), but this is not an issue of spatial autocorrelation, instead reflecting that the effective extent of the data has been reduced, which can cause changes in driving forces (Willis and Whittaker 2002). This will also not occur in regularly spaced gridded data, as the short-distance spatial autocorrelation that is introduced by including additional cells will be evenly spread throughout the full extent of the study region. Of course, there is a sampling error problem in the subsampled data (extreme values are missed when few sites are sampled), but this is also unrelated to spatial autocorrelation and no one claims that increasing sample sizes generates bias. Indeed, the loss of information caused by subsampling spatially structured data is why this method is not recommended for controlling the Type I error introduced by spatial autocorrelation (Legendre 1993). We use subsampling here only to demonstrate heuristically that spatial autocorrelation does not generate a systematic bias in model estimates.

Our analytical approach can also be used to understand why OLS estimators are not those with minimum variance. When subsampling data, the loss of power creates instability in the regression slope, because slightly different configurations of points can be obtained and thus more variable slopes can be generated for different combinations of data points. However, in practice, our example is extremely conservative in the sense of using a very reduced number of points out of the all possible combinations in the continent (see below). Also, it is intuitive from Fig. 3 that instability in the coefficients will be more serious and could change the interpretation of a given regression slope only if there is a weak correlation between predictor and response variables.

The problem of power vs. error is also evident from the broad range of slopes found in the subsampled data (see Fig. 2 for South America). The wide variation around the mean values supports well-known claims that RSA inflates Type I errors. In the South American example, confidence intervals of coefficients for AET and ELEV do not include zero, whereas the CIs for temperature do (technically speaking, temperature should be removed from the model). However, again we reiterate that the purpose of sampling is to show that the average (expected) values of the coefficients are not widely different from those obtained with full OLS data. The sampling procedure used here is strongly conservative, since all information at distances smaller than the minimum distances we selected is excluded, even though actually there is a steady decrease in the potential effect of RSA as distances increase from zero to the truncation values assumed here. The point is that it is difficult to use a sampling procedure to obtain unbiased p-values for the coefficients because it is extremely difficult to balance Type I and II errors (Legendre, 1993).

An additional, counter-intuitive result of our analysis is that removing RSA from the data *increased* the explanatory power of our OLS models, and the R^2s are more similar to those from SAR models. This clearly indicates that spatial autocorrelation does not cause an overestimation of the importance of macroscale environmental drivers on broad-scale macroecological patterns. However, this is not really surprising, as the clustering of data from numerous nearby sites, as occurs in data with strong local autocorrelation, will tend to increase the local residuals associated with each datum. The accumulation of small amounts of residual variance among many spatially autocorrelated samples then decreases the apparent explanatory power of the broad-scale variables. Of course, when using spatially explicit modeling the autoregressive parameter captures these local deviations from the regression line, increasing the total coefficient of determination of the model.

In sum, we find that spatial autocorrelation is not the problem that it is sometimes claimed to be when attempting to generate and interpret regression models in geographical ecology. We reiterate that our analysis is focused on gridded data at broad spatial scales, and additional analyses are needed to evaluate the sensitivity of OLS to site-based samples that may not be uniformly distributed across the full extent of the focal region. However, when the data are gridded, claims that OLS models are necessarily wrong are false. This also means that extreme care is needed when comparing OLS and spatially explicit regression models, as using the latter methods does more than correct for RSA. Rather, coefficient shifts when applying multiple methods may reflect general model instability and be an indication that all coefficients are suspect, whether based on nonspatial or spatial methods. One result of our analysis is clear: automatically assuming that OLS generates flawed models whereas spatial methods do not is a mistake.

REFERENCES

Bahn, V., O’Connor, R. J. and Krohn, W. B. 2006. Importance of spatial autocorrelation in modeling bird distributions at a continental scale. – Ecography 29: 835-844.

Blackburn, T. M. and Hawkins, B. A. 2004. Bergmann’s rule and the mammal fauna of northern North America. — Ecography 27: 715-724.

Cressie, N. A. C. 1993. Statistics for spatial data analysis. John Wiley and Sons.

Currie, D. J. and Paquin, V. 1987. Large-scale biogeographical patterns of species richness of trees. — Nature 329: 326-327.

Diniz-Filho, J. A. F. et al. 2003. Spatial autocorrelation and red herrings in geographical ecology. — Glob. Ecol. Biogeogr. 12: 53-64.

Dormann, C. F. 2007. Effects of incorporating spatial autocorrelation into the analysis of species distribution data. — Glob. Ecol. Biogeogr. 16: 129-138.

Dutilleul, P. 1993. Modifying the t test for assessing the correlation between two spatial processes. — Biometrics 49: 305-314.

Fotheringham, A. S. et al. 2002. Geographically weighted regression: the analysis of spatially varying relationships. Wiley.

Gimona, A. and Brewer, M. J. 2006. Local environmental effects and spatial effects in macroecological studies using mapped abundance classes: the case of the rook *Corvus frugilegus* in Scotland. — J. Anim. Ecol. 75: 1140-1146.

Graham, M. H. 2003. Confronting multicollinearity in ecological multiple regression. — Ecology 84: 2809-2815.

Haining, R. 1990. Spatial data analysis in the social and environmental sciences. Cambridge Univ. Press.

Hawkins, B. A. and Diniz-Filho, J. A. F. 2006. Beyond Rapoport’s rule: evaluating range size patterns of New World birds in a two-dimensional framework. — Glob. Ecol. Biogeogr. 15: 461-469.

Hawkins, B. A. et al. 2003. Productivity and history as predictors of the latitudinal diversity gradient of terrestrial birds. — Ecology 84: 1608-1623.

Hawkins, B. A., et al. 2005. Water links the historical and contemporary components of the Australian bird diversity gradient. — J. Biogeogr. 32: 1035-1042.

Hawkins, B. A. et al. 2007. Climate, niche conservatism, and the global bird diversity gradient. —Am. Nat. (in press).

Kissling, W. D. and Carl, G. 2007. Spatial autocorrelation and the selection of simultaneous autoregressive models. — Glob. Ecol. Biogeogr. (in press).

Kühn, I. 2007. Incorporating spatial autocorrelation may invert observed patterns. — Divers. Distr. 13: 66-69.

Legendre, P. 1993. Spatial autocorrelation — trouble or new paradigm? — Ecology 74: 1659-1673.

Legendre, P. et al. 2002. The consequences of spatial structure for the design and analysis of ecological field surveys. — Ecography 25: 601-615.

Lennon, J. J. 2000. Red-shifts and red herrings in geographical ecology. — Ecography 23: 101-113.

Lennon, J. J. et al. 2000. Bird diversity and environmental gradients in Britain: a test of the species-energy hypothesis. — J. Anim. Ecol. 69: 581-598.

Lichstein, J. W. et al. 2002. Spatial autocorrelation and autoregressive models in ecology. — Ecol. Monogr. 72: 445-463.

Rahbek, C. and Graves, G. R. 2001. Multiple scale assessment of patterns of avian species richness. — Proc. Nat. Acad. Sci. USA 98: 4534-4539.

Rangel, T. F. L. V. B. et al. 2006. Towards an integrated computational tool for spatial analysis in macroecology and biogeography. — Glob. Ecol. Biogeogr. 15: 321-431.

Ruggiero, A. et al. 1998. The geographic ranges of mammalian species in South America: spatial patterns in environmental resistance and anisotropy. — J. Biogeogr. 25: 1093-1103.

Schabenberg, O. and Gotway, C. A. 2005. Statistical methods for spatial data analysis. Chapman and Hall.

Selmi, S. and Boulinier, T. 2001. Ecological biogeography of Southern Ocean islands: the importance of considering spatial issues. — Am. Nat. 158: 426-437.

Tognelli, M. F. and Kelt, D. A. 2004. Analysis of determinants of mammalian species richness in South America using spatial autoregressive models. — Ecography 27: 427-436.

Tiefelsdorf, M. and Griffith, D. A. 2007. Semi-parametric filtering of spatial autocorrelation: the eigenvector approach. — Environment and Planning A (in press).

Tognelli, M. F. and Kelt, D. A. 2004. Analysis of determinants of mammalian species richness in South America using spatial autoregressive models. — Ecography 27: 427-436.

Williams, P. H. et al. 1999. Interpreting biogeographical boundaries among Afrotropical birds: spatial patterns in richness gradients and species replacement. — J. Biogeogr. 26, 459-474.

Willis, K. J. and Whittaker, R. J. 2002. Species diversity — scale matters. — Science 295: 1245-1248.

Table 1. Unstandardized regression coefficients (b±se) and the relative importance (rank) of their standardized equivalents (not shown), adjusted coefficients of determination (R^2) from SAR models and OLS models of full data sets vs. mean coefficients of OLS models based on 500 subsamples containing no short-distance residual spatial autocorrelation. Separate models were generated for bird species richness in six geographic regions. n_1 refers to the number of cells in the full grid, v* is the geographically effective degrees of freedom of the full data sets, and n_2 is number of cells in the subsampled data. Predictor variables are Temp = annual temperature, AET = annual actual evapotranspiration, GVI = mean monthly global vegetation index, Relev = range in elevation, and Int = interaction between range in elevation and temperature. Student's *t*'s test the probability (Prob) that coefficients in models derived from data containing short-distance spatial autocorrelation differ from those generated after removing residual spatial autocorrelation by subsampling cells a minimum distance apart (see Fig. 1).

	All data							*Subsampled data (OLS)*				
		SAR		*OLS*								
Region	*Variables*	*b±se (rank)*	R^2	*b (rank)*	R^2	n_1	*v**	*b±se*	R^2	n_2	*t*	*Prob*
North America	Temp	0.242±0.337 (4)	0.911	-1.171 (3)	0.623	1634	68	-1.672±1.252	0.858±0.051	30	0.204	0.838
	AET	0.081±0.012 (2)		0.101 (2)				0.160±0.076			0.400	0.689
	GVI	0.028±0.001 (3)		0.040 (4)				0.028±0.044			0.135	0.893
	Int	0.001±0.001 (1)		0.001 (1)				0.001±0.004			0.515	0.607
South America	Temp	4.758±0.522 (3)	0.786	7.323 (3)	0.768	1456	23	3.521±4.769	0.886±0.045	20	0.797	0.426
	AET	0.194±0.010 (1)		0.284 (1)				0.286±0.086			0.018	0.986
	Relev	0.036±0.002 (2)		0.041 (2)				0.026±0.019			0.782	0.434

Europe	Temp	0.119±0.275 (2)	0.616	-0.914 (4)	0.346	445	10	-1.634±2.889	0.645±0.177	10	0.249	0.803
	AET	0.023±0.013 (1)		0.159 (1)				0.218±0.108			0.546	0.585
	GVI	0.018±0.006 (3)		-0.032 (3)				-0.051±0.068			0.279	0.780
	Relev	0.001±0.001 (4)		-0.005 (2)				-0.007±0.009			0.222	0.824
USSR	Temp	0.895±0.121 (4)	0.898	2.561 (1)	0.749	1695	19	2.616±0.848	0.817±0.075	20	0.065	0.948
	AET	0.048±0.006 (3)		0.126 (3)				0.140±0.115			0.122	0.903
	GVI	0.049±0.005 (1)		0.114 (2)				0.122±0.078			0.103	0.918
	Relev	0.005±0.001 (2)		0.009 (4)				0.008±0.010			0.100	0.920
Australia	Temp	0.094±0.351 (3)	0.806	-3.554 (2)	0.704	625	11	-3.185±5.102	0.843±0.123	7	0.072	0.943
	AET	0.031±0.004 (1)		0.125 (1)				0.128±0.115			0.026	0.979
	GVI	0.022±0.006 (2)		0.048 (3)				0.049±0.176			0.006	0.995
Africa	AET	0.143±0.007 (2)	0.852	0.162 (2)	0.741	2403	9	0.169±0.100	0.786±0.072	20	0.070	0.944
	GVI	0.073±0.010 (3)		0.159 (3)				0.153±0.157			0.038	0.970
	Temp	1.495±0.505 (4)		0.139 (4)				0.153±4.686			0.003	0.998
	Relev	0.039±0.002 (1)		0.062 (1)				0.060±0.036			0.055	0.956

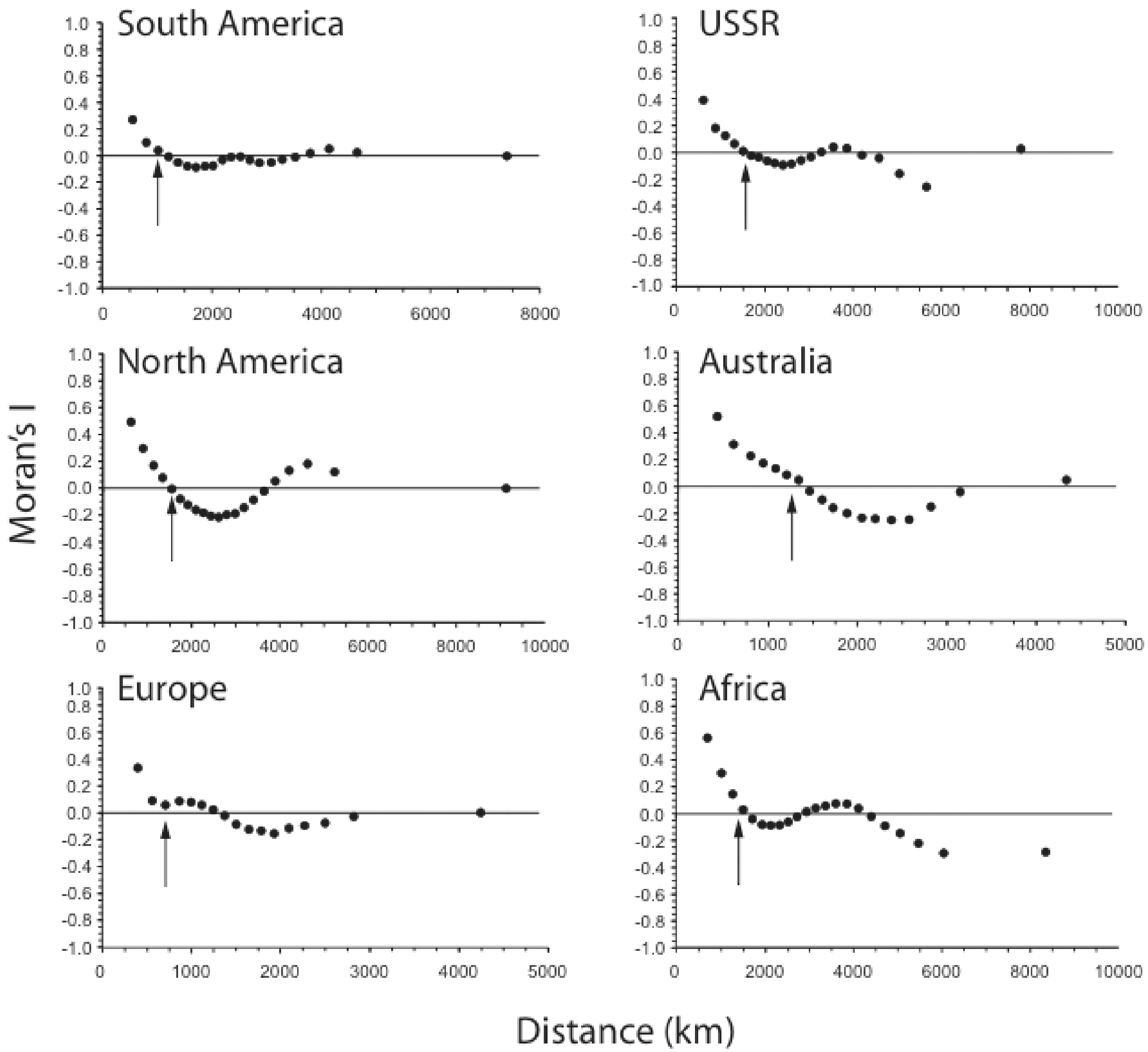
*SAR models were fitted using α =3 for all continents except Australia, for which an α of 4 was used (see text for detail)

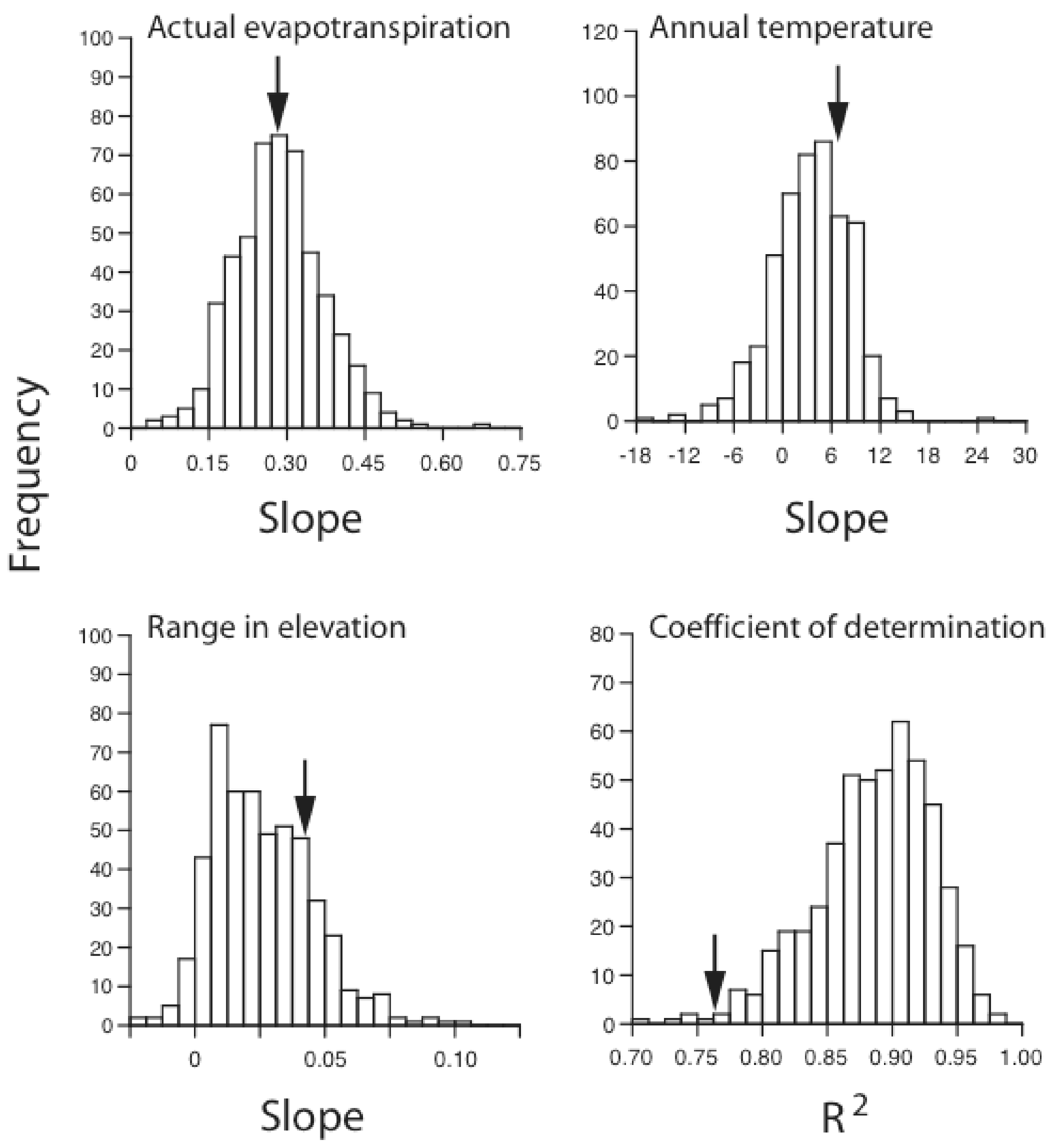
FIGURE LEGENDS

Figure 1. Correlograms of residual spatial autocorrelation for six regional OLS regression models of bird species richness (see Table 1). Arrows identify the minimum distance between cells for subsampling grids in each region used to generate regression models containing no short-distance positive autocorrelation.

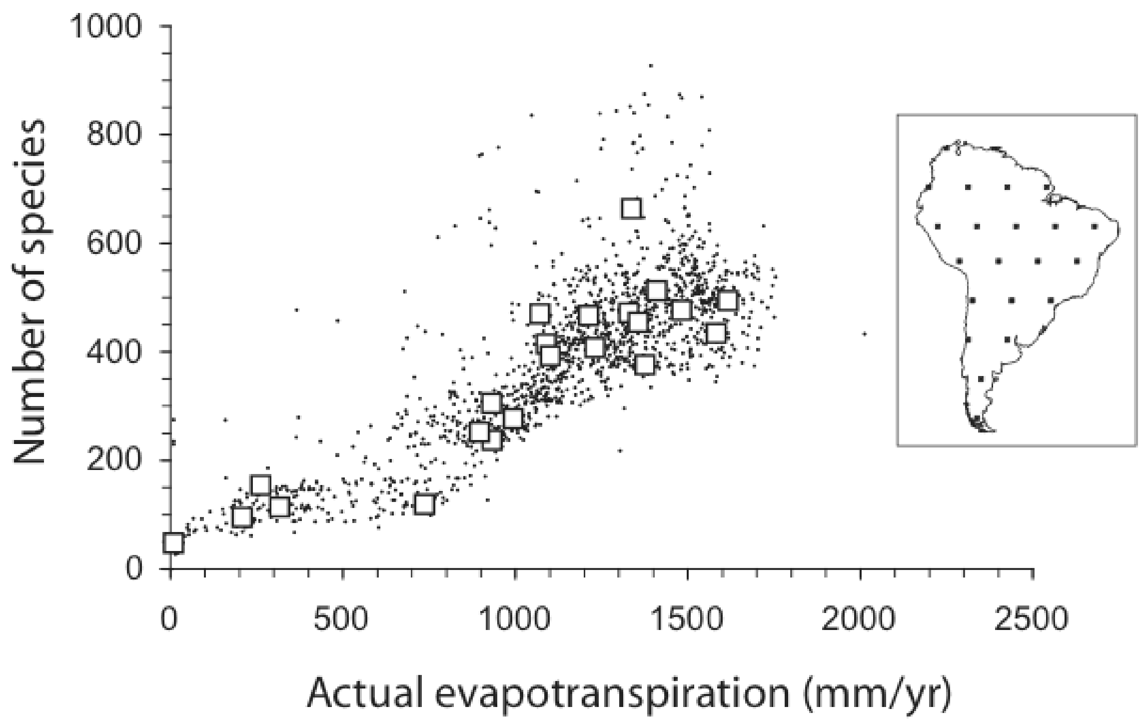
Figure 2. OLS regression coefficients of three environmental predictor variables and the coefficients of determination of 500 regression models derived from subsamples of South American grid cells at least 1000 km apart (n = 20 in all models). Arrows indicate values obtained from the model generated using all 1456 cells (see Table 1).

Figure 3. Scatterplot of bird species richness and actual evapotranspiration for all 1456 cells in the South American grid (small dots). The larger open squares identify values for a subsample of 22 cells located at least 1000 km apart. The map insert shows the location of the sampled cells (black squares).


South America
USSR
North America
Australia
Europe
Africa
Moran's I
Distance (km)



Actual evapotranspiration
Annual temperature
Range in elevation
Coefficient of determination
Frequency
Slope
Slope
Slope
R^2
100
90
80
70
60
50
40
30
20
10
0
0
0.15
0.30
0.45
0.60
0.75
120
100
80
60
40
20
0
-18
-12
-6
0
6
12
18
24
30
100
90
80
70
60
50
40
30
20
10
0
0
0.05
0.10
80
70
60
50
40
30
20
10
0
0.70
0.75
0.80
0.85
0.90
0.95
1.00



1000
800
600
400
200
0
Number of species
0
500
1000
1500
2000
2500
Actual evapotranspiration (mm/yr)