Title

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

Permalink

https://escholarship.org/uc/item/5x97369z

Journal

Ecography, 30

ISSN

0906-7590

Authors

Hawkins, Bradford A.
Diniz-Filho, Jose Alexandre F.
Bini, Luis Mauricio
et al.

Publication Date

2007-06-01

Peer reviewed

*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

25   There have been numerous claims in the ecological literature that spatial autocorrelation

26   in the residuals of ordinary least squares (OLS) regression models results in shifts in the

27   partial coefficients, which bias the interpretation of factors influencing geographical

28   patterns. We evaluate the validity of these claims using gridded species richness data for

29   the birds of North America, South America, Europe, Africa, the ex-USSR, and Australia.

30   We used richness in 110 x 110 km cells and environmental predictor variables to generate

31   OLS and simultaneous autoregressive (SAR) multiple regression models for each region.

32   Spatial correlograms of the residuals from each OLS model were then used to identify the

33   minimum distance between cells necessary to avoid short-distance residual spatial

34   autocorrelation in each data set. This distance was used to subsample cells to generate

35   spatially independent data. The partial OLS coefficients estimated with the full dataset

36   were then compared to the distributions of coefficients created with the subsamples. We

37   found that OLS coefficients generated from data containing residual spatial

38   autocorrelation were statistically indistinguishable from coefficients generated from the

39   same data sets in which short-distance spatial autocorrelation was not present in all 22

40   coefficients tested. Consistent with the statistical literature on this subject, we conclude

41   that coefficients estimated from OLS regression are not seriously affected by the presence

42   of spatial autocorrelation in gridded geographical data. Further, shifts in coefficients that

43   occurred when using SAR tended to be correlated with levels of uncertainty in the OLS

44   coefficients. Thus, shifts in the relative importance of the predictors between OLS and

45   SAR models are expected when small-scale patterns for these predictors create weaker

46   and more unstable broad-scale coefficients. Our results indicate both that OLS regression

2

47   is unbiased and that differences between spatial and nonspatial regression models should

48   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

4

72 1987, Ruggiero et al. 1998, Williams et al. 1999, Lennon et al. 2000, Rahbek and Graves

73 2001, Blackburn and Hawkins 2004, Hawkins et al. 2005; Hawkins and Diniz-Filho

74 2006). We also evaluate the related claim that spatial autocorrelation generates a 'red-

75 shift' in regression models, artefactually inflating the apparent importance of macroscale

76 environmental variables as explanations of broad-scale ecological patterns (Lennon

77 2000). Given the increasing rate that spatially explicit modeling approaches are

78 beginning to appear in the literature, we need to know how to interpret the differences

79 that sometimes arise when using spatial and nonspatial methods on the same datasets.

80   It is important to note that we do not present a formal evaluation of this issue

81 using statistical theory (see Cressie 1993, Schabenberg and Gotway 2005, Tiefelsdorf and

82 Griffith 2007). Rather, we provide an empirical resampling analysis of spatially

83 structured data of the type commonly found in macroecological and geographical

84 analyses. And although further studies using simulation procedures may shed light on

85 these issues and allow more formal evaluations of the accuracy and precision of

86 parameter estimates under different scenarios and spatial scales, our goal is to illustrate

87 heuristically that the often presumed bias due to spatial autocorrelation in OLS regression

88 does not apply to real data sets.

89 METHODS

90   We analyzed the number of species in 110 x 110 km cells in equal-area girds for

91 the birds of North America, South America, Europe, Africa, the ex-USSR, and Australia

92 (for methods and sources of the bird data see Hawkins et al. 2007). Coastal cells

93 containing less than 50% of the area of full cells were excluded from all grids prior to

94 analysis. We also generated corresponding gridded environmental data for five potential

95   explanatory variables (annual temperature, annual actual evapotranspiration, mean

96   monthly Global Vegetation Index, range in elevation , and the interaction of annual

97   temperature and range in elevation). All of these variables have been shown to be

98   associated with bird richness directly or indirectly in globally extensive path models

99   (Hawkins et al. 2007), so we expected combinations of these variables to contribute to

100   richness to varying degrees in more regionally focused regression models (see also

101   Hawkins et al. 2003). We divided the data into regions to provide replicate datasets to

102   ensure that the results of our evaluation of RSA were not due to a particular data structure

103   or a single geographical location or extent.

104   In the first step of the analysis we generated OLS multiple regression models for

105   each region. Combinations of predictors were added and removed until we obtained a

106   model with the highest coefficient of determination and simultaneously with the fewest

107   number of variables. As the goal of the analysis was to obtain a set of models which

108   could be used to investigate the influence of RSA, we were not concerned with

109   generating the best possible explanatory model in each region and so we did not use

110   probability values or information theoretic indices to select the final regional models.

111   Rather, we generated plausible environmentally-based models which could form the basis

112   for evaluating the extent that RSA influences model coefficients.

113   The second stage of the analysis generated spatial correlograms of Moran's I

114   based on the residuals from each regional model. We used the correlograms to evaluate

115   the ability of each model to explain the spatial structure in the data, and specifically to

116   identify the distances at which positive spatial autocorrelation remained in the data

117   (Haining 1990, Diniz-Filho et al. 2003). It is 'short-distance' positive RSA that is

118   believed to generate the bias in OLS regression and which workers hope to take into

119   account by using spatially explicit modeling (Lichstein et al. 2002).

120   Based on the correlograms we identified the minimum distances between cells

121   that are necessary to avoid significant short-distance RSA in each data set. This was

122   developed as an heuristic, intuitive, and statistically conservative way to deal with RSA,

123   even though it causes a serious loss of power in the analyses (Legendre 1993). We then

124   used a sampling program written in MatLab to generate samples of cells from each grid

125   with a fixed sample size (which varied depending on the region) and in which all

126   distances among cells were at least the minimum distance required to avoid short-

127   distance RSA. The program starts by selecting a random cell in the grid and then

128   randomly searches for other cells that are at least a given distance apart from all other

129   cells. There is, therefore, a maximum number of cells that can be selected, because if a

130   very high number of cells is chosen the program is unable to find a compromise solution

131   between the number of samples and the minimum geographical distance. We iteratively

132   determined the number of cells to be included in each sample by balancing statistical

133   power in the sampling procedure (maximizing the number of cells, n_2 in Table 1) and

134   viable computer time for each run. The sampling routine was run 500 times on each data

135   set to generate independent samples containing no RSA. Separate OLS multiple

136   regression models were generated from each of the 500 samples, providing a distribution

137   of coefficients of each predictor variable in the model. We then used t-tests to determine

138   if the values of the coefficients from the regression using all data (data containing RSA)

139   were significantly different from the mean values generated by analyzing subsets of data

140   known to contain no significant short-distance RSA. This then tested whether

7

141   coefficients from resampled data differ from parameters estimated by OLS. As all other

142   aspects of the data and modeling are identical, a significant difference between the full

143   coefficients and the sample coefficients can be unambiguously interpreted as the 'bias'

144   generated by RSA. In contrast, if no significant differences between the full and sample-

145   based coefficients are found, it provides clear evidence that the presence of RSA has had

146   no statistically detectable influence on the parameter estimates of regression models.

147   The next step of the analysis tested the coefficient of determination of each

148   regional model using all cells against the distribution of adjusted R^2s from the

149   subsampled data. We did this to evaluate the claim that RSA increases the strength of

150   associations among variables at the macroscale in addition to causing a shift in the

151   coefficients (Lennon 2000).

152   Finally, since the residuals of the full OLS regressions contained RSA at

153   relatively short distances (see Fig. 1), we also modelled the relationship between species

154   richness and the environmental predictors using a spatially explicit simultaneous

155   autoregressive (SAR) model (Cressie 1993, Schabenberg and Gotway 2005, Tognelli and

156   Kelt 2004, Kissling and Carl 2007). In the SAR error model, spatial covariance among

157   cells (**C**) is defined as

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

159   where σ^2 is the variance of the residuals, ρ is the autoregressive parameter and **I** is an n x

160   n identity matrix. The row-standardized **W** matrix contains the spatial relationship

161   among sampling units, with elements given by the inverse of the geographic distances

162   (d_{ij}) among them, expressed as $1/d_{ij}^{\alpha}$, where α was chosen to minimize RSA.

163   Duttileul's method (see Duttileul 1993, Legendre et al. 2002) was used to

164   correlate the estimated and observed richness for each model in order to determine the

165   effective geographic degree of freedom for each multiple regression model and test its

166   overall statistical significance. Since the effective degrees of freedom represents a

167   conservative sample size that takes into account autocorrelation, they can be compared

168   with the sample sizes used in the simulations to obtain minimum distances between cells

169   that are necessary to avoid significant short-distance RSA in each data set.

170   All spatial analyses were performed using Spatial Analysis in Macroecology

171   (SAM) software (Rangel et al. 2006), available at http://www.ecoevol.ufg.br/sam.

172   RESULTS

173   The regional regression models contained either three or four environmental predictors

174   (Table 1). Five of the six models explained large proportions of the variance in richness

175   (62.3% to 76.7%), indicating that even though we did not attempt to find the best possible

176   model for richness (which in some cases would include polynomial terms), the models

177   have strong statistical explanatory power. The exception was the European model, which

178   explained *ca*. a third of the variance in richness. However, this was fortuitous, as it

179   allowed us to examine the sensitivity of both strong and weak explanatory models to the

180   presence of RSA. As would be expected, SAR models always had higher R^2s than OLS

181   models (Table 1).

182   Inspection of the correlograms of the residuals from each model revealed that all

183   contain substantial short-distance positive RSA (Fig. 1), which is typical when using

184   richness data generated from range maps. It also indicates that all models could

185   potentially comprise biased coefficients. However, in all cases the RSA was at or near 0

186   in distances ranging from 660 km (in Europe) to 1500 km (in North America and USSR),

187   allowing us to subsample the data to eliminate significant small-scale RSA from all data

188   sets and generate sets of regression models containing little or no potential bias. It is

189   notable that most data sets still contain negative spatial autocorrelation at moderate to

190   large distances. However, these structures remaining in the residuals would not produce

191   the bias associated with RSA, because long-distance negative autocorrelation would have

192   conservative (not liberal) effects on parameter estimates and Type I errors. The number

193   of cells sampled in each region to generate the short-distance RSA-free data ranged from

194   seven to 30 (Table 1). These sample sizes are very small when compared to original

195   sample sizes and illustrate the apparent loss of statistical power of our resampling

196   procedure. However, they are similar to the geographically effective degrees of freedom

197   obtained using Duttileul's method.

198   An example of the relationships between the regression coefficients from a full

199   model and the distributions of regression coefficients generated by resampling is

200   presented in Fig. 2, but more generally the coefficients from the analyses of data sets

201   containing RSA did not differ from the mean coefficients estimated in data containing no

202   RSA in all 22 tests (Table 1). That is, coefficients generated from data containing

203   residual spatial autocorrelation were statistically indistinguishable from coefficients

204   generated from the same data sets in which short-distance RSA is not present. This was

205   true in data from all parts of the world, in models with different combinations of

206   explanatory variables of either weak or strong explanatory power, and in models with

207   substantially different macroscale autocorrelation structures.

208   Although the OLS regression coefficients were not sensitive to the presence of

209   RSA when compared to coefficients from resampling, we observed some shifts when

210   compared to SAR coefficients (Table 1) [after standardizing them to permit direct

211   comparisons across variables measured on different scales], indicating that spatial

212   modeling must contain effects that are unrelated to the presence of RSA. For Africa and

213   South America, although changes in coefficients values were observed, the relative

214   importance (rank) of the predictors was the same in OLS and SAR, whereas in North

215   America, Australia and Europe only the first or second most important predictors were

216   the same. At the opposite extreme, in the USSR there is a complete shift in the ranks of

217   predictors. We also observed that shifts in model rank are somewhat associated with the

218   results from the resampling procedure, in that differences between model ranks based on

219   coefficients estimated by SAR and OLS are marginally correlated with the level of

220   uncertainty in values of the OLS coefficients derived from resampling as measured by the

221   ratio between each estimated coefficient and its error ($r = 0.381$; $P = 0.080$).

222   Perhaps unexpectedly, we did find that removing short-distance spatial

223   autocorrelation from the data improved the average explanatory power of the OLS

224   models in all six regions, significantly so in North and South America (Table 1), and

225   average R^2s using resampled data are more similar to those of SAR models. Thus, in

226   contrast to the claim that spatial autocorrelation inflates the strength of associations

227   among macroscale environmental variables and broad-scale ecological gradients (the red

228   shift of Lennon [2000]), we found that increasing sample sizes by including spatially

229   autocorrelated cells did the opposite.

230 DISCUSSION

231 Our analyses indicate that claims that OLS regression generates biased models and leads

232 to incorrect interpretations of the factors influencing macroecological patterns are not

233 necessarily true. That is, short-distance residual autocorrelation in our data, while

234 causing inflated Type I errors, did not create problems in the interpretation of coefficients

235 estimated by OLS. And although our examples are restricted to richness data, it should

236 also be clear that this conclusion holds for any macroecological variables structured in

237 space. Therefore, our general conclusion must be that the problem of autocorrelation that

238 is beginning to dominate the geographical ecological literature is not one of parameter

239 estimation, although it is an issue if one wants to estimate probability values associated

240 with significance tests. We are not the first to make this claim (see e.g. Schabenberg and

241 Gotway 2005), and methods to generate geographically effective degrees of freedom to

242 evaluate correlations implicitly assume that the standard Pearson coefficients are

243 unbiased in the presence of spatial autocorrelation, and it is only necessary to control the

244 inflated Type I error (Legendre et al. 2002).

245 　　　Our analysis raises a number of issues requiring further investigation. First and

246 foremost, it remains the case that OLS and spatially explicit regression models of the

247 same data sets sometimes differ, as we observed in our data. Ecologists often interpret

248 this as evidence of the bias generated by spatial autocorrelation and then claim that the

249 OLS results are not dependable (Lennon 2000, Selmi and Boulinier 2001, Tognelli and

250 Kelt 2004, Dormann 2007, Gimona and Brewer 2006, Kühn 2007). However, spatial

251 autocorrelation is not the source of the problem. There is no doubt that RSA inflates

252 Type I errors, so that coefficients obtained by OLS are not minimum variance estimators.

253   Consequently, OLS coefficients are less precise than their spatial counterparts and may

254   be more unstable in the analyses of particular datasets, especially if their magnitudes are

255   low. Even so, it is well known in the statistical literature that OLS estimates are accurate,

256   especially with large sample sizes, and coefficients are not biased in a statistical sense

257   (see Cressie, 1993, Schabenberg and Gotway 2005, Tiefelsdorf and Griffith 2007). It

258   should also be realized that there are sources of instability in spatial regression models as

259   well, mainly due to the definition of spatial relationships (i.e., weightings) in the model

260   structure or in the residual variance-covariance (see Kissling and Carl 2007). Given the

261   confusion among ecologists concerning the effects of RSA on OLS regression modeling,

262   we must reiterate that RSA *per se* does not cause nonspatial regression models to

263   generate biased coefficients, even though many statisticians may wonder what the fuss is

264   about.

265   We believe that the resampling procedure performed here provides some insights

266   into the reasons for coefficient shifts sometimes found when comparing OLS and spatial

267   regression methods. Although further studies are necessary to understand fully the

268   reasons underlying coefficient shifts (see Dormann 2007), our resampling procedure at

269   least partially reinforces a previous interpretation for model instability. Diniz-Filho et al.

270   (2003) argued that coefficients change because spatially explicit models shift the

271   effective scale of the analysis, putting stronger emphasis on local-scale patterns and

272   processes (also see Fotheringham et al. [2002], who refer to autoregressive models as

273   'semi-local' approaches). Indeed, predictors having the greatest differences between OLS

274   and SAR are also those that have large standard errors in the resampling procedure (Table

275   1), which indicates that these coefficients are more dependent on the particular spatial

276   configuration of sampled points. In other words, shifts in the relative importance of the

277   predictors between OLS and SAR models are expected when there are local or regional

278   patterns for these predictors within the continents that, in turn, create more unstable

279   coefficients when sampling. Thus, as observed by Lennon (2000), predictors with weak

280   spatial patterns gain importance in SAR regression compared to predictors with strong

281   spatial patterns (the red shift). However, this shift is not due to a bias in OLS

282   coefficients, but instead arises because spatial regression, by adding an explicit spatial

283   component, captures effects operating at smaller spatial scales, whereas OLS captures the

284   overall structure at broad scales (Diniz-Filho et al. 2003). Of course, evaluating fully our

285   interpretation for coefficient shifts requires simulation studies in which effects of

286   predictors are known *a priori*. Kissling and Carl (2007) recently generated such

287   simulations and compared OLS with various forms of SAR, showing that the definition

288   of spatial relationships (i.e., weightings) in the model structure or in the residual

289   variance-covariance generates variation among SAR methods. Indeed, they show that in

290   some situations SAR estimates are themselves biased (although not the SAR error model

291   we used here). Irrespective, their simulations are very simple with few predictors, and

292   they did not examine the effects of predictors at multiple spatial scales.

293   A second issue that requires investigation is that shifts in coefficients when using

294   nonspatial and spatial approaches may reflect model instability due to multicollinearity

295   among the environmental variables usually included in macroecological analyses; it is

296   well known that collinearity destabilizes all types of regression models (see e.g. Graham

297   2003). Thirdly, and potentially most seriously, virtually all biological and environmental

298   predictors used in broad-scale macroecological analyses are spatially structured at one or

299   more scales, so when an autoregressive parameter is added to the model complex patterns

300   of collinearity can be generated, even if there is no collinearity among the environmental

301   predictors themselves. If this occurs, neither OLS nor autoregressive coefficients could

302   be interpreted unambiguously, unless one is willing to assume that the variance contained

303   in the overlap between environment and space can be attributed solely to the effects of

304   the modeled components of the environment or solely to the effects of space, the latter

305   which will also contain unmodelled spatially structured environmental effects. The worst

306   possible scenario is if coefficient shifts when using spatial models are idiosyncratic and

307   depend on the detailed covariance structure of the particular data set being analyzed. If

308   so, all spatially explicit models are uninterpretable, because workers will be unable to

309   determine if coefficient shifts arise from scale shifts or effects of collinearity between

310   space and the environment. We will address this critical issue in detail in a future paper.

311   Because our primary finding that residual spatial autocorrelation does not bias

312   regression coefficients runs counter to a view widely held by ecologists and

313   biogeographers, it is important to understand why OLS estimates will be robust in

314   gridded data. This can be illustrated using the relationship between AET and species

315   richness in South America (Fig. 3). The observed data cloud in the scatterplot reflects the

316   presumed influence of AET (and collinear drivers), errors generated by inaccurate range

317   maps and false positives in the richness values, and the effects of unmeasured driving

318   variables. Because the data contain many cells in close proximity, the density of the data

319   cloud is high. Now, if we only sample sites far enough apart not to contain short-distance

320   spatial autocorrelation (22 equally spaced cells 1000 km apart in this example, see Fig. 3

321   insert), the density of points is lower, but all must fall within the observed data cloud.

15

322   Clearly, a regression coefficient estimated from the subsampled data represents an

323   estimate of the relationship found among all samples. It is also clear that introducing

324   spatial autocorrelation into a set of samples by including sites closer together will fill in

325   gaps in the data cloud, but it cannot create a new data cloud with a different scatter,

326   which would be required to shift the regression coefficient. The exception to this

327   argument is if all of the added sample points were concentrated in one portion of the

328   geographic space (e.g. all were in the Andes), but this is not an issue of spatial

329   autocorrelation, instead reflecting that the effective extent of the data has been reduced,

330   which can cause changes in driving forces (Willis and Whittaker 2002). This will also

331   not occur in regularly spaced gridded data, as the short-distance spatial autocorrelation

332   that is introduced by including additional cells will be evenly spread throughout the full

333   extent of the study region. Of course, there is a sampling error problem in the

334   subsampled data (extreme values are missed when few sites are sampled), but this is also

335   unrelated to spatial autocorrelation and no one claims that increasing sample sizes

336   generates bias. Indeed, the loss of information caused by subsampling spatially

337   structured data is why this method is not recommended for controlling the Type I error

338   introduced by spatial autocorrelation (Legendre 1993). We use subsampling here only to

339   demonstrate heuristically that spatial autocorrelation does not generate a systematic bias

340   in model estimates.

341   Our analytical approach can also be used to understand why OLS estimators are

342   not those with minimum variance. When subsampling data, the loss of power creates

343   instability in the regression slope, because slightly different configurations of points can

344   be obtained and thus more variable slopes can be generated for different combinations of

16

345   data points. However, in practice, our example is extremely conservative in the sense of

346   using a very reduced number of points out of the all possible combinations in the

347   continent (see below). Also, it is intuitive from Fig. 3 that instability in the coefficients

348   will be more serious and could change the interpretation of a given regression slope only

349   if there is a weak correlation between predictor and response variables.

350   The problem of power vs. error is also evident from the broad range of slopes

351   found in the subsampled data (see Fig. 2 for South America). The wide variation around

352   the mean values supports well-known claims that RSA inflates Type I errors. In the

353   South American example, confidence intervals of coefficients for AET and ELEV do not

354   include zero, whereas the CIs for temperature do (technically speaking, temperature

355   should be removed from the model). However, again we reiterate that the purpose of

356   sampling is to show that the average (expected) values of the coefficients are not widely

357   different from those obtained with full OLS data. The sampling procedure used here is

358   strongly conservative, since all information at distances smaller than the minimum

359   distances we selected is excluded, even though actually there is a steady decrease in the

360   potential effect of RSA as distances increase from zero to the truncation values assumed

361   here. The point is that it is difficult to use a sampling procedure to obtain unbiased p-

362   values for the coefficients because it is extremely difficult to balance Type I and II errors

363   (Legendre, 1993).

364   An additional, counter-intuitive result of our analysis is that removing RSA from

365   the data *increased* the explanatory power of our OLS models, and the R^2s are more

366   similar to those from SAR models. This clearly indicates that spatial autocorrelation does

367   not cause an overestimation of the importance of macroscale environmental drivers on

368 broad-scale macroecological patterns. However, this is not really surprising, as the

369 clustering of data from numerous nearby sites, as occurs in data with strong local

370 autocorrelation, will tend to increase the local residuals associated with each datum. The

371 accumulation of small amounts of residual variance among many spatially autocorrelated

372 samples then decreases the apparent explanatory power of the broad-scale variables. Of

373 course, when using spatially explicit modeling the autoregressive parameter captures

374 these local deviations from the regression line, increasing the total coefficient of

375 determination of the model.

376   In sum, we find that spatial autocorrelation is not the problem that it is sometimes

377 claimed to be when attempting to generate and interpret regression models in

378 geographical ecology. We reiterate that our analysis is focused on gridded data at broad

379 spatial scales, and additional analyses are needed to evaluate the sensitivity of OLS to

380 site-based samples that may not be uniformly distributed across the full extent of the

381 focal region. However, when the data are gridded, claims that OLS models are

382 necessarily wrong are false. This also means that extreme care is needed when

383 comparing OLS and spatially explicit regression models, as using the latter methods does

384 more than correct for RSA. Rather, coefficient shifts when applying multiple methods

385 may reflect general model instability and be an indication that all coefficients are suspect,

386 whether based on nonspatial or spatial methods. One result of our analysis is clear:

387 automatically assuming that OLS generates flawed models whereas spatial methods do

388 not is a mistake.

REFERENCES

389   REFERENCES

390   Bahn, V., O'Connor, R. J. and Krohn, W. B. 2006. Importance of spatial autocorrelation

391   in modeling bird distributions at a continental scale. – Ecography 29: 835-844.

392   Blackburn, T. M. and Hawkins, B. A. 2004. Bergmann's rule and the mammal fauna of

393   northern North America. — Ecography 27: 715-724.

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

395   Currie, D. J. and Paquin, V. 1987. Large-scale biogeographical patterns of species

396   richness of trees. — Nature 329: 326-327.

397   Diniz-Filho, J. A. F. et al. 2003. Spatial autocorrelation and red herrings in geographical

398   ecology. — Glob. Ecol. Biogeogr. 12: 53-64.

399   Dormann, C. F. 2007. Effects of incorporating spatial autocorrelation into the analysis of

400   species distribution data. — Glob. Ecol. Biogeogr. 16: 129-138.

401   Dutilleul, P. 1993. Modifying the t test for assessing the correlation between two spatial

402   processes. — Biometrics 49: 305-314.

403   Fotheringham, A. S. et al. 2002. Geographically weighted regression: the analysis of

404   spatially varying relationships. Wiley.

405   Gimona, A. and Brewer, M. J. 2006. Local environmental effects and spatial effects in

406   macroecological studies using mapped abundance classes: the case of the rook

407   *Corvus frugilegus* in Scotland. — J. Anim. Ecol. 75: 1140-1146.

408   Graham, M. H. 2003. Confronting multicollinearity in ecological multiple regression. —

409   Ecology 84: 2809-2815.

410   Haining, R. 1990. Spatial data analysis in the social and environmental sciences.

411   Cambridge Univ. Press.

412 Hawkins, B. A. and Diniz-Filho, J. A. F. 2006. Beyond Rapoport's rule: evaluating range

413   size patterns of New World birds in a two-dimensional framework. — Glob. Ecol.

414   Biogeogr. 15: 461-469.

415 Hawkins, B. A. et al. 2003. Productivity and history as predictors of the latitudinal

416   diversity gradient of terrestrial birds. — Ecology 84: 1608-1623.

417 Hawkins, B. A., et al. 2005. Water links the historical and contemporary components of

418   the Australian bird diversity gradient. — J. Biogeogr. 32: 1035-1042.

419 Hawkins, B. A. et al. 2007. Climate, niche conservatism, and the global bird diversity

420   gradient. —Am. Nat. (in press).

421 Kissling, W. D. and Carl, G. 2007. Spatial autocorrelation and the selection of

422   simultaneous autoregressive models. — Glob. Ecol. Biogeogr. (in press).

423 Kühn, I. 2007. Incorporating spatial autocorrelation may invert observed patterns. —

424   Divers. Distr. 13: 66-69.

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

426   1659-1673.

427 Legendre, P. et al. 2002. The consequences of spatial structure for the design and analysis

428   of ecological field surveys. — Ecography 25: 601-615.

429 Lennon, J. J. 2000. Red-shifts and red herrings in geographical ecology. — Ecography

430   23: 101-113.

431 Lennon, J. J. et al. 2000. Bird diversity and environmental gradients in Britain: a test of

432   the species-energy hypothesis. — J. Anim. Ecol. 69: 581-598.

433 Lichstein, J. W. et al. 2002. Spatial autocorrelation and autoregressive models in ecology.

434   — Ecol. Monogr. 72: 445-463.

435   Rahbek, C. and Graves, G. R. 2001. Multiple scale assessment of patterns of avian

436   species richness. — Proc. Nat. Acad. Sci. USA 98: 4534-4539.

437   Rangel, T. F. L. V. B. et al. 2006. Towards an integrated computational tool for spatial

438   analysis in macroecology and biogeography. — Glob. Ecol. Biogeogr. 15: 321-431.

439   Ruggiero, A. et al. 1998. The geographic ranges of mammalian species in South

440   America: spatial patterns in environmental resistance and anisotropy. — J.

441   Biogeogr. 25: 1093-1103.

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

443   Chapman and Hall.

444   Selmi, S. and Boulinier, T. 2001. Ecological biogeography of Southern Ocean islands:

445   the importance of considering spatial issues. — Am. Nat. 158: 426-437.

446   Tognelli, M. F. and Kelt, D. A. 2004. Analysis of determinants of mammalian species

447   richness in South America using spatial autoregressive models. — Ecography 27:

448   427-436.

449   Tiefelsdorf, M. and Griffith, D. A. 2007. Semi-parametric filtering of spatial

450   autocorrelation: the eigenvector approach. — Environment and Planning A (in

451   press).

452   Tognelli, M. F. and Kelt, D. A. 2004. Analysis of determinants of mammalian species

453   richness in South America using spatial autoregressive models. — Ecography 27:

454   427-436.

455   Williams, P. H. et al. 1999. Interpreting biogeographical boundaries among Afrotropical

456   birds: spatial patterns in richness gradients and species replacement. — J.

457   Biogeogr. 26, 459-474.

458   Willis, K. J. and Whittaker, R. J. 2002. Species diversity — scale matters. — Science

459   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

23

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

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

469

470 FIGURE LEGENDS

471 Figure 1. Correlograms of residual spatial autocorrelation for six regional OLS

472   regression models of bird species richness (see Table 1). Arrows identify the

473   minimum distance between cells for subsampling grids in each region used to

474   generate regression models containing no short-distance positive autocorrelation.

475

476 Figure 2. OLS regression coefficients of three environmental predictor variables and the

477   coefficients of determination of 500 regression models derived from subsamples

478   of South American grid cells at least 1000 km apart (n = 20 in all models).

479   Arrows indicate values obtained from the model generated using all 1456 cells

480   (see Table 1).

481

482 Figure 3. Scatterplot of bird species richness and actual evapotranspiration for all 1456

483   cells in the South American grid (small dots). The larger open squares identify

484   values for a subsample of 22 cells located at least 1000 km apart. The map insert

485   shows the location of the sampled cells (black squares).