# Spatial autocorrelation, model selection and hypothesis testing in geographical ecology: Implications for testing metabolic theory in New World amphibians

## Autocorrelação espacial, seleção de modelos e teste de hipóteses em ecologia geográfica: implicações para testar a teoria metabólica em anfíbios do Novo Mundo

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## Abstract

In this paper, we stressed that avoiding significance tests under an alternative model selection framework does not mean that spatial autocorrelation no longer matters, since Akaike information criterion (AIC) is sensitive to the presence of spatial autocorrelation. We exemplify our discussion by analysing species richness patterns of American amphibians, in the context of metabolic theory, to understand how the presence of spatial autocorrelation in data affects data analysis under alternative frameworks of hypothesis testing and model selection. In general, temperature was found to be an important predictor of species richness in both frameworks, although particular predictions of metabolic theory were not fully satisfied when taking spatial autocorrelation into account.

**Key words:** hypothesis testing; spatial autocorrelation; model selection; Akaike information criterion; macroecology; richness gradients; metabolic theory

## Resumo

Neste artigo, enfatiza-se que evitar os testes de significância baseados na seleção de modelos alternativos não significa que a autocorrelação espacial não ocorra, pois o critério de informação de Akaike (AIC) é sensível à presença de autocorrelação espacial. A discussão é exemplificada pela análise de padrões de riqueza de espécies de anfíbios americanos, no contexto da teoria metabólica, de forma a entender como a presença da

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autocorrelação afeta a análise dos dados com base em uma abordagem alternativa de teste de hipótese e seleção de modelos. Em geral, a temperatura foi uma importante preditora da riqueza de espécies em ambas as abordagens, embora predições específicas da teoria metabólica não foram completamente alcançadas quando consideramos a autocorrelação espacial.

**Palavras-chave:** teste de hipóteses; autocorrelação espacial; seleção de modelos; critério de infomação de Akaike; macroecologia; gradiente de riqueza; teoria metabólica

## Introduction

In recent years there has been increasing interest in the application of spatial analysis techniques to problems in ecology and biogeography (see Fortin and Dale, 2005 for a recent review). This has been motivated by several advances, including a resurgence of interest in broad-scale diversity gradients and other macroecological patterns, the ability to deal with large databases on biodiversity, climate and geography, and the application of more sophisticated statistical techniques that take into account the spatial dimension of data (Keitt *et al.*, 2002). This final point arises from the recognition that spatially distributed ecological phenomena usually generate spatial autocorrelation in biological data, an issue that can be viewed either as a 'problem' that must be solved or as an opportunity to understand the spatial context of these phenomena (Legendre, 1993; Legendre and Legendre, 1998). It is now widely recognized that spatial autocorrelation affects significance tests in geographical ecology analyses, since error variances are underestimated (Legendre, 1993; Legendre and Legendre, 1998; Diniz-Filho *et al.*, 2003; Dormann, 2007). For example, when spatial structure appears in regression residuals, this is an indicative of a potential misspecification in the regression models, which usually assume normally distributed and independent errors with constant variance (see Lennon, 2000 and Diniz-Filho *et al.*, 2003 for a discussion on the origins of autocorrelation structures in richness data). Formally, the covariance matrix among residuals is equal to $\sigma^2\mathbf{I}$,

where $\mathbf{I}$ is an identity matrix (Cressie, 1993; Haining, 1990, 2002; Griffith, 2003). This is why spatial statistics, and specifically spatial regression models, are used to 'correct for' or to 'take into account' the presence of spatial structure in data or model residuals. As pointed out by Cressie (1993), "…if it appears that [spatial covariance among residuals] > 0, there may be a missing variable (varying spatially) that is causing it. By (unknowingly) modelling its presence through spatial dependence parameters, the spatial model is more resistant to misspecification errors".
Despite the ever increasing range of spatial statistics that can be applied to macroecological and biogeographical data (Lennon, 2000; Lichstein *et al.*, 2002; Liebhold and Gurevitch, 2002; Legendre *et al.*, 2002; Diniz-Filho *et al.*, 2003; Hawkins and Porter, 2003; Borcard *et al.*, 2004; Diniz-Filho and Bini, 2005; Bahn and MacGill, 2007; Kuhn, 2007; Dormann, 2007; for recent examples), many ecologists still have problems dealing with the phenomenon of spatial autocorrelation. Simultaneously, there has been a reaction growing for quite some time against the standard statistical testing approach when applied to non-experimental, usually broad-scale spatial data in ecology and evolution, especially with respect to model selection procedures (e.g., Quinn and Dunham, 1983; Hilborne and Mangel, 1997; Hobbs and Hilborne, 2006; Stephens *et al.*, 2007; see also Cohen, 1994). As a consequence of this latter movement, an increasing number of ecologists now advocate alternative approaches to data analysis, including Bayesian methods and model selection pro-

cedures based on information theory (mainly Akaike Information Criterion, AIC), thereby completely avoiding the classical hypothesis-testing approach (see Burham and Anderson, 2002, 2004; Ellison, 2004; Johnson and Omland, 2004; Richards, 2005; Stephens *et al.*, 2007).
For ecologists working with broad-scale geographic distribution data and derived measures, such as species richness, it is tempting to link these two discussions (i.e., problems in estimating true Type I errors in the presence of spatial autocorrelation and conceptual problems with hypothesis testing) and justify a paradigm shift from hypothesis testing to model selection under information theory at least in part as a way to deal with inferential problems caused by spatial autocorrelation (e.g., Stohlgren *et al.*, 2005; Segurado *et al.*, 2006). However, we would like to stress here that avoiding significance tests under an alternative model selection framework in fact does not necessarily mean that spatial autocorrelation no longer matters, although this has not yet been explicitly tested in geographical ecology (but see Hoeting *et al.*, 2006). In this paper, we discuss how geographical data analysis can be understood with respect to the alternative frameworks of hypothesis testing and model selection, especially considering the presence of spatial autocorrelation in data. To illustrate our point, we analysed spatial patterns of species richness of American amphibians, showing how data fits the predictions from metabolic theory of ecology (see Allen *et al.*, 2002; Brown *et al.*, 2004; Hawkins *et al.*, 2007a,b) under the two alternative data analysis frameworks.

## Material and methods

### Data

To illustrate the use of hypothesis testing and model selection frameworks we analysed data of 3,019 amphibians species of New World, obtained from Global Amphibian Assessment (see Stuart *et al.*, 2004), available at http://www.natureserve.org, using grid with 4,187 cells of 1° of latitude and longitude. We selected seven predictors for further analysis: annual actual evapotranspiration (AET), elevation (ELEV), mean annual temperature (TEMP), annual potential evapotranspiration (PET), mean annual precipitation (PREC), averaged relative humidity (HUM), net primary productivity (NPP) (New *et al.*, 1999).

### Hypothesis testing

We first analysed the effect of temperature on species richness, following recent work on the metabolic theory of ecology (MTE, see Allen *et al.*, 2002; Brown *et al.*, 2004). The idea of applying MTE to evaluate richness gradients is that regressing the logarithm of species richness of ectotherms organisms against temperature will give a specific slope (see below), which was derived based on the first principles of termodynamics and on biochemical kinetics at cellular level. Thus, testing this particular prediction of metabolic theory represents the classical application of hypothesis testing in geographical ecology. Temperature is given as $1/kT$, were temperature $T$ is expressed in Kelvin and $k$ is Boltzmann's constant (in eV, equal to $8.62 \times 10^{-5}$) and the predicted slope should be between -0.6 and -0.7 (Brown *et al.*, 2004; see also Evans and Gaston, 2005 for definitions). The observed slope $b$ can be statistically compared with a parametric value of b using, for example, the classical *t*-distribution, in which $t = (b - \beta)/s_b$, were $s_b$ is the standard error of slope.

However, it is important to realize that this simple test of the theory suffers from a potential problem, because there is usually a strong autocorrelation in model residuals. This can be tested using Moran's *I* coefficients (see Diniz-Filho *et al.*, 2003; Rangel *et al.*, 2006). Thus, hypothesis testing from OLS model may be biased and it is necessary to adopt an explicit spatial regression approach to better test a hypothesis about a regression slope. The statistical theory underlying spatial data is now well developed (Haining 1990, 2002; Cressie, 1993), although new issues and methods continue to arise (see Anselin, 2002; Fotheringham *et al.*, 2002; Griffith, 2003; Diniz-Filho and Bini, 2005; Kuhn *et al.*, 2006; Carl and Kuhn, 2007; Kuhn, 2007). A way to incorporate spatial autocorrelation structure in data analysis is better understood in a generalized least squares (GLS) regression framework. The standardized regression slopes (given in the vector β) are used to evaluate the relative importance of the predictors (matrix X) in explaining a given response variable (the vector Y), and are obtained by

$$\beta = (X^T \Sigma^{-1} X)^{-1} X \Sigma^{-1} Y$$

where $\Sigma^{-1}$ is a matrix containing the spatial structure in the residuals. The residuals can be obtained from a standard, non-spatial multiple regression (OLS), and spatial structures in these residuals can be modelled using different forms of correlograms and variograms (spherical, exponential, Gaussian, etc.), and then these parameters can be used to estimate $\Sigma$ (see Cressie 1993). Simultaneous autoregressive (SAR) and conditional autoregressive (CAR) spatial regression models can also be generated by using specific definitions of $\Sigma$ as a function of residual autocorrelation (see Lichstein *et al.*, 2002; Tognelli and Kelt, 2004; for recent applications in Ecology). For example, in the SAR model, the covariance matrix $\Sigma$ is given by

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

where r is the first-order autoregressive parameter and W is the row-standardized connectivity matrix among spatial units (Cressie, 1993; Haining, 2002). Notice that when $\Sigma = \sigma^2 I$ (i.e., the residuals are independent, with zero covariance, and they have constant variance $\sigma^2$), the GLS estimation of the β vector will reduce to the standard OLS estimator of the regression coefficients. We fitted a SAR model building the matrix W based on the distance among cells ($W = 1/d^3$, where $d$ is distance between a pair of sample size).

All spatial analyses were performed in SAM 2.0 (Rangel *et al.*, 2006), freely available at www.ecoevol.ufg.br/sam.

### Model selection and information theory

In the absence of a formal mathematical model to deal with colinearity among temperature and other predictors (i.e., that can generate a different theoretical partial slope b to be formally tested, as previously described – see Hawkins *et al.*, 2007b), the alternative to understand patterns of species richness is to identify the best predictive model and then link this model with the available theories to explain geographic patterns in richness (e.g., Hawkins *et al.*, 2003). Within the context of metabolic theory, we can at least verify if temperature is one of the predictors retained in the best environmental model, providing support for a formal modelling strategy to understand how collinearity could be incorporated into metabolic theory. It is also possible to verify that the partial coefficient of temperature (i.e., taking into account all other predictors) is still close to MTE predictions. In this case, it might appropriate to abandon the idea of a formal hypothesis testing and shift to a model selection framework under information theory (i.e., we are not interested in simply rejecting the null hypothesis of b = 0 for all predictors; rather, it is more interest to compare multiple potential alternative models and to verify the parameter estimated.

The likelihood of data given multiple possible models has been recently evaluated under information theory, a com-

pletely different framework from classical hypothesis testing (Burham and Anderson, 2002). Akaike information criterion (AIC) is the most widely used metrics for model selection under this new framework and is computed as

$$AIC = -2 \, Ln \, [L(x \mid M_i)] + 2K$$

where $Ln[L(x|M_i)]$ is the log-likelihood of data $x$ given the model $M_i$, as previously defined, and $K$ is the number of parameters in the model. A small-sample correction, which must always be used when $n/K > 40$, is easily obtained by adding the term $[2K(K+1)/(n-K-1)]$ to the AIC formula. When computing an ordinary least squares (OLS) regression, an approximate AIC value can be given by

$$AIC = n \, Ln(\sigma^2) + 2K$$

where $\sigma^2$ is the variance of the residuals of each regression model, and $K$ is the number of parameters, including the intercept and the residual variance $\sigma^2$. The value of $\sigma^2$ is used as a proxy for the likelihood of the model given the data, and is given by

$$\sigma^2 = \mathbf{e}^T\mathbf{e}/n$$

where $\mathbf{e}$ is the vector with regression residuals (see Burham and Anderson, 2002, 2004 for details).

After calculating AIC values for various models, one can use the standard model selection protocol (Burham and Anderson, 2002; Johnson and Omland, 2004; Richards, 2005). The AIC of each model is transformed to DAIC, which is the difference between AIC of each model and the minimum AIC found for the set of models compared. A value of DAIC higher than 7 indicates that a model has a poor fit relative to the best model, whereas a value less than 2 indicates that a model is equivalent to the minimum AIC model (Burham and Anderson, 2002, 2004). The DAIC values can also be used to compute Akaike's weighting of each model ($w_i$), which provides evidence that the model is actually the best explanatory model. These values of $w_i$ are usually standardized by their sum across all models evaluated, so they are dependent on the set of models used, and are given then by

$$w_i = e^{(-1/2 \, \Delta AIC)} / \Sigma_i [e^{(-1/2 \, \Delta AICi)}]$$

Finally, $w_i$ values can also be used to define the relative importance of each predictor across the full set of models evaluated by summing $w_i$ values of all models that include the predictor of interest, taking into account the number of models in which each predictor appears (Burham and Anderson, 2002). Thus, since AIC is dependent on $\sigma^2$, even in the absence of a specific statistical hypothesis to be tested it is still important to know how autocorrelation in data perturbs model selection procedures. Of course, model selection based on statistical criterion (such as in stepwise procedures) will be strongly affected by autocorrelation, since they are based on $P$-values that are biased in the presence of autocorrelation, tending to result in the inclusion of all variables in the model (since they all tend to be statistically significant). However, since spatial autocorrelation biases residual variance estimates and affects the likelihood of the OLS model given the data (due to probable misspecifications), it will affect model selection procedures too, as well as in SAR analysis, which create another residual variance. Thus, we compared OLS and SAR results for 22 models to understand how explicitly incorporating spatial structure into regression model affects model selection procedure based on AIC.

## Results

For the New World amphibians data, we found a slope of -0.686 ($CI_{95\%}$ = -0.63, -0.742) according to an OLS regression (Figure 1A). The confidence interval does not include zero, so the slope is significant at 5% level (i.e., differs from zero, the expectation under the null hypothesis, $H_0$: $\beta = 0$). The temperature (1/kT) explains 83.5% of the variation in the logarithm of species richness (Figures 1A, B), although a heterocedastic distribution can be observed, forming a constraint envelope common in macroecological data (see Brown, 1995; Gaston and Blackburn,

2000). Confidence interval includes the expected value of -0.60 or -0.70, so this dataset support metabolic theory. However, for the first geographic distance class (0 – 463 km), a Moran's $I$ coefficient equal to 0.427 ($P < 0.001$, based on a randomization test) was found, so that a spatially explicit regression model can be fitted to better estimate slope and confidence interval. The SAR model got worse model fit, with an $R^2 = 0.087$ due to pure effect of temperature, although $R^2$ of the fitted model (including both predictor and space) was higher than OLS ($R^2 = 0.928$) (see Rangel *et al.*, 2006). The slope of temperature was reduced to -0.354 ($CI_{95\%}$ = -0.331, -0.377), less consistent with metabolic theory than the original OLS model. The SAR model is in principle more adequate than OLS, since the residuals are much less spatially autocorrelated (Moran's $I$ at the first distance class $I = 0.167$, $P = 0.206$) (but see Hawkins *et al.*, 2007c). Other forms of spatial regression (CAR) and spatial filtering (Rangel *et al.*, 2006; not shown to conserve space) provided equivalent results (although some of them showed no significant correlation between the two variables).

The comparison between OLS and SAR results for the 23 models incorporating multiple combinations of environmental predictors is shown in Table 1. The correlation between ΔAIC values of SAR and OLS models is high (r = 0.907), which suggests a very similar sequence of ranking between alternative models generated by non-spatial and spatial models. However, this correlation is mainly due to the models with high ΔAIC values (the poor models) found in both SAR and OLS regressions.

In both SAR and OLS, the full models (i.e., with all predictors, TEMP, NPP, PET, AET, PREC, ELEV and HUM) were retained as the best models (i.e., ΔAIC = 0) (Table 1). The other models showed very high ΔAIC values, so they are not parsimonious explanations for richness patterns, suggesting that variations in temperature alone are not a good explanation for richness patterns.

Notice also that regression coefficient for temperature in the best model selected using AIC was equal to -0.496 to SAR and -0.668 to OLS, whereas the standardized regression coefficient was equal to -0.66 in SAR and -0.889 in OLS (Table 2). Temperature was the predictor with highest standardized coefficient, followed by AET and RELEV, despite best estimated coefficient by SAR is a bit lower than expected by MTE.

## Discussion

### Spatial autocorrelation, model selection and hypothesis testing

Under a classical hypothesis testing framework, OLS analysis strongly supports MTE, since the observed slope is not statistically different from the predicted one. However, after taking spatial autocorrelation into account using spatial regression (SAR), we found even less support for metabolic

theory. Thus, using spatial models qualitatively changed our conclusions, although this is probably not so simple (Hawkins *et al.*, 2007c). Most of the statistical literature suggests that spatial regression is more robust than OLS when there is strong, and since Allen *et al.* (2002) did not consider these issues, we can say that MTE is not quite well supported when using a more adequate model that takes residual autocorrelation into account. However, Hawkins *et al.* (2007c; see also Diniz-Filho *et al.*, 2003) recently warned that adding spatial components may also add scale issues to the modeling process that may disturb parameter estimation and, more importantly, interpretation of the parameter.

Thus, tests of metabolic theory that do not incorporate spatial structure may not be robust. The difference in slopes obtained from OLS and SAR models also suggests that most of regression of logarithm of richness against tem-

perature found using OLS might be due to spatial covariance structure in both variables (as well as non-stationarity issues, see Cassemiro *et al.*, 2007). This leads to a more complicated issue of how to evaluate simultaneously the effect of temperature and other predictors (including the effects of unknown 'latent' predictors that are 'captured' by spatial structure), under metabolic theory, leading to issues of comparison of multiple models, incorporating different sets of predictors.

When we compare the ΔAIC values between SAR and OLS alternative models, we verified that the lower values were found in OLS regression, as found in many other studies (see Kuhn, 2007). These lower values of OLS when compared to SAR are due to the fact that OLS regression does not take spatial structure into account. Indeed, all OLS models contain significant spatial autocorrelation in the first distance class (Table 1), so they are not maximum likelihood models

**Table 1.** Results of model selection based on AIC values calculated from Ordinary Least-Squares (OLS) and Simultaneous AutoRegressive (SAR) models, including the ΔAIC values and the standardized Akaike's weightings (*w*). The best model under each approach is in bold. The *I*-value refers to the Moran's *I* autocorrelation coefficient in OLS residuals in the first geographic distance class (0-463 km).

| | SAR | | OLS | | |
| --- | --- | --- | --- | --- | --- |
| | ΔAIC | w | ΔAIC | w | I |
| AET,PET | 3577.641 | 0.00 | 3567.873 | 0.00 | 0.57 |
| AET,PREC | 3 577.641 | 0.00 | 4319.985 | 0.00 | 0.657 |
| PET,PREC | 3618.091 | 0.00 | 3571.938 | 0.00 | 0.58 |
| AET,PET,PREC | 3618.091 | 0.00 | 3465.549 | 0.00 | 0.593 |
| AET,NPP | 3335.788 | 0.00 | 4305.343 | 0.00 | 0.666 |
| NPP,PET | 3776.86 | 0.00 | 3278.093 | 0.00 | 0.565 |
| NPP,PREC | 3752.266 | 0.00 | 5516.111 | 0.00 | 0.681 |
| AET,PET,NPP | 3312.15 | 0.00 | 3242.638 | 0.00 | 0.586 |
| AET,PET,NPP,PREC | 3148.682 | 0.00 | 3200.8 | 0.00 | 0.601 |
| TEMP,AET | 2190.009 | 0.00 | 856.033 | 0.00 | 0.452 |
| TEMP,PET | 2382.434 | 0.00 | 1985.884 | 0.00 | 0.451 |
| TEMP,AET,PET | 1193.59 | 0.00 | 135.422 | 0.00 | 0.403 |
| TEMP,PREC | 2070.23 | 0.00 | 880.629 | 0.00 | 0.443 |
| TEMP,AET,PET,PREC | 1130.787 | 0.00 | 82.592 | 0.00 | 0.405 |
| TEMP,NPP | 2179.02 | 0.00 | 752.755 | 0.00 | 0.418 |
| TEMP,NPP,PET,AET | 1060.516 | 0.00 | 74.412 | 0.00 | 0.416 |
| TEMP,NPP,PET,AET,PREC | 1003.775 | 0.00 | 40.941 | 0.00 | 0.417 |
| **TEMP,NPP,PET,AET,PREC,ELEV,HUM** | **0** | **1** | **0** | **1** | **0.431** |
| TEMP,HUM | 2496.984 | 0.00 | 1472.458 | 0.00 | 0.402 |
| TEMP,HUM,AET,PET | 1192.57 | 0.00 | 136.677 | 0.00 | 0.402 |
| TEMP,ELEV | 1521.546 | 0.00 | 1975.022 | 0.00 | 0.444 |
| HUM,ELEV | 4739.809 | 0.00 | 9133.797 | 0.00 | 0.801 |
| ELEV,PREC | 4010.902 | 0.00 | 5685.369 | 0.00 | 0.616 |

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**Table 2.** Linear coefficients of OLS and SAR regressions of log-transformed species richness in New World on seven environmental variables.

| | SAR | | | | | OLS | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | Standardized $b$ | $b$ | Standard Error | $t$ | $P$ | Standardized $b$ | $b$ | Standard Error | $t$ | $P$ |
| AET | 0.204 | 0.009 | <0.001 | 12.874 | <0.001 | 0.36 | 0.015 | <0.001 | 19.005 | <0.001 |
| PET | -0.018 | -0.004 | <0.001 | -6.162 | <0.001 | -0.364 | -0.014 | <0.001 | -19.256 | <0.001 |
| PREC | 0.073 | 0.05 | 0.007 | 7.466 | <0.001 | 0.06 | 0.041 | 0.008 | 5.082 | <0.001 |
| HUM | 0.093 | 0.009 | 0.001 | 7.821 | <0.001 | 0.019 | 0.002 | 0.001 | 1.946 | 0.052 |
| ELEV | 0.165 | <0.001 | <0.001 | 18.088 | <0.001 | 0.044 | <0.001 | <0.001 | 6.331 | <0.001 |
| NPP | 0.041 | 0.199 | 0.028 | 7.073 | <0.001 | 0.072 | 0.345 | 0.047 | 7.286 | <0.001 |
| TEMP | -0.66 | -0.496 | 0.017 | -28.232 | <0.001 | -0.889 | -0.668 | 0.013 | -50.335 | <0.001 |

A)



B)



Amphibian Richness
- 0 - 0.693
- 0.693 - 1.609
- 1.609 - 2.485
- 2.485 - 3.135
- 3.135 - 3.714
- 3.714 - 4.19
- 4.19 - 5.106
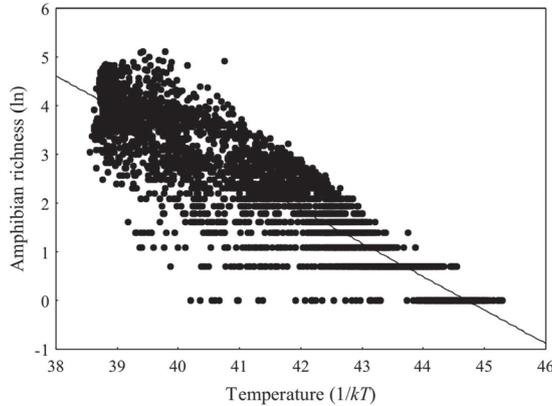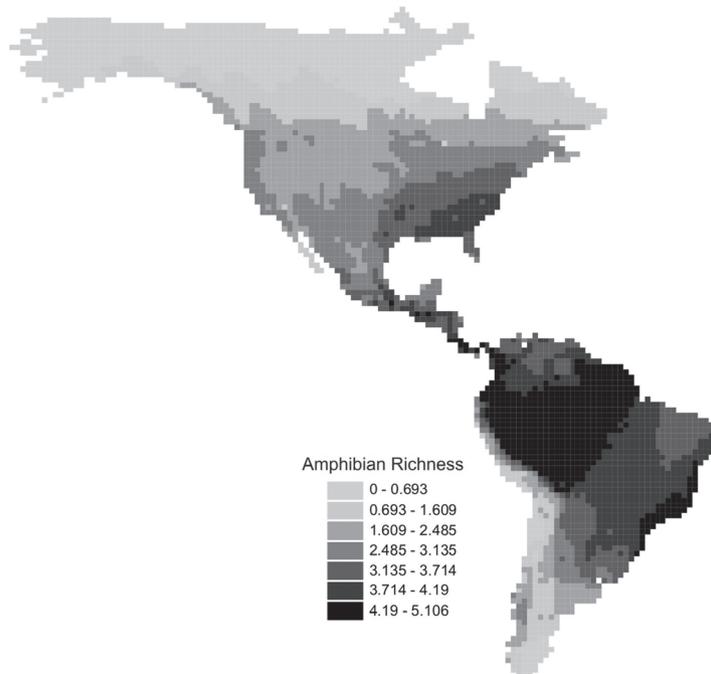
**Figure 1. A.** Relationship between ln-transformed species richness of amphibians and temperature for 4187 cells (1° x 1° latitude-longitude), covering the American continent. Temperature is expressed as $1/kT$, where $k$ is Boltzmann's constant and $T$ is average annual temperature in degrees Kelvin. **B.** Spatial patterns of Amphian richness in the New World.

because residuals are not independent. Thus, this apparently lower uncertainly should not be viewed as an advantage of OLS over spatial model.

In fact, it is equivalent to find a very low Type I error for a given predictor that, as we already discussed, may be artificially caused by spatial autocorrelation. In this case, one should be 'certain' about the effect of a given predictor but, when taking into account spatial autocorrelation, its influence may be smaller than previously assumed (Lichstein *et al.*, 2002), as occurred with the effect of temperature on species richness, as previously described.

Because of the high ΔAIC in the models, the Akaike weights $w_i$ are not dispersed among them, suggesting a considerable certainty in deciding the best model. Certainly the model with ΔAIC equal zero is the best model in SAR and OLS. This absence of variation in the ΔAIC and Akaike weights values might be due to great amount of our data. According to Richards (2005), AIC ranks models depends on the amount type of data, and simpler models often rank highly when data are scarce. On the other hand, more complex models usually improve the ranking as more data is collected. The same author also points out that, the more data collected, the less likely a useful simple model will be judged best according to AIC.

## What is the support for metabolic theory under alternative data analysis frameworks?

Our analyses of American amphibians under the two alternative data analysis

frameworks may be useful to define further developments in both methodological and theoretical issues on MTE. Classical hypothesis testing does not provide strong support to the theory when taking into account autocorrelation in data, probably, because part of the correlation between richness and temperature may be due to intrinsic spatial components. This suggests that further developments may be necessary to establish data statements for analysis (see Hawkins *et al.*, 2007b) and to establish expected slopes for temperature taking into account its correlation with other predictors, including latent spatial structure and productivity variables (see Brown *et al.*, 2004) in a multivariate context.

Cassemiro *et al.* (2007) showed that part of this correlation may also be due to spatially structured variations, which can be the cause of the non-stationarity in the relationship between richness and temperature, showed by Geographically Weighted Regression analysis (GWR). Another potential explanation of non-stationarity is that the effects of temperature on other variables that are assumed to be constant in Allen *et al.*'s (2002) model (i.e., average body mass and abundance) also vary in space, generating then a systematic lack of agreement with the MTE prediction in some regions, but not in others.

Until further developments for understanding the predictions of metabolic theory in a multivariate context, a model selection framework seems to be the best way to evaluate the role of multiple predictors on species richness. Analyses based both on OLS and SAR suggest that temperature is of great importance to species richness in New World amphibians, although SAR coefficients in the multiple regression model also do not represent direct support for metabolic theory. This may be due to several reasons, especially break with model assumptions such as spatial variation in abundance and body size (see Hawkins *et al.*, 2007b). Also, it is important to note that many am-

phibians species may thermorregulate (Hutchinson and Dupré, 1992), thereby not all species in this study can be true ectothermics, as required for a good test of metabolic theory. Thus, this study provides the basis for further refinements in the theory taking into account the species physiology as well as multivariate and multi-scale nature of causal explanations for species richness.

## Concluding remarks

There is no doubt that understanding the origins of spatial autocorrelation in geographical data is important both to investigate the processes underlying spatial patterns and to estimate parameters correctly. In this context, it is important to realize that model selection procedures based on AIC values may be also sensitive to the presence of residual autocorrelation and, thus, shifting from a classical hypothesis testing to information theory or Bayesian approaches will not necessarily 'eliminate the problem' of spatial autocorrelation in data. Despite this, our analyses suggest that model selection procedure using AIC based on OLS and SAR models tend to find the same models with a high number of predictors, and with high certainty in model choice. This may be due to great amount of structure in our data, which consequently leads to an easily in establishing a rank of predictor importance. In general, temperature was found to be an important predictor of species richness in both frameworks, although particular predictions of MTE were not fully satisfied when taking spatial autocorrelation into account.

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