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Spatial patterns of species richness in New World coral snakes and the metabolic theory of ecology

Levi Carina Terribile^{a,*}, José Alexandre Felizola Diniz-Filho^b

^aDepartamento de Zoologia, ICC, Programa de Pós-Graduação em Biologia Animal, Universidade de Brasília (UnB), Brasília, DF 70910-900, Brasil

^bDepartamento de Biologia Geral, ICB, UFG, Goiânia, GO, Brazil

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ABSTRACT

The metabolic theory of ecology (MTE) has attracted great interest because it proposes an explanation for species diversity gradients based on temperature-metabolism relationships of organisms. Here we analyse the spatial richness pattern of 73 coral snake species from the New World in the context of MTE. We first analysed the association between \ln -transformed richness and environmental variables, including the inverse transformation of annual temperature ($1/kT$). We used eigenvector-based spatial filtering to remove the residual spatial autocorrelation in the data and geographically weighted regression to account for non-stationarity in data. In a model I regression (OLS), the observed slope between \ln -richness and $1/kT$ was -0.626 ($r^2 = 0.413$), but a model II regression generated a much steeper slope (-0.975). When we added additional environmental correlates and the spatial filters in the OLS model, the R^2 increased to 0.863 and the partial regression coefficient of $1/kT$ was -0.676 . The GWR detected highly significant non-stationarity, in data, and the median of local slopes of \ln -richness against $1/kT$ was -0.38 . Our results expose several problems regarding the assumptions needed to test MTE: although the slope of OLS fell within that predicted by the theory and the dataset complied with the assumption of temperature-independence of average body size, the fact that coral snakes consist of a restricted taxonomic group and the non-stationarity of slopes across geographical space makes MTE invalid to explain richness in this case. Also, it is clear that other ecological and historical factors are important drivers of species richness patterns and must be taken into account both in theoretical modeling and data analysis.

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1. Introduction

Broad scale gradients in species richness are one of the best documented ecological patterns and have been known since the early days of biogeography and ecology (Hawkins, 2001, 2004). Because of the long history of research, multiple

ecological and evolutionary hypotheses have been developed during the last 200 years to explain geographical patterns in richness. However, many hypotheses are conjectural, redundant or untestable, and efforts to reduce the number of hypotheses into a minimum set of testable and more plausible ones have accelerated in the last few years (see Jetz and

* Corresponding author. Tel.: +55 629 607 8380; fax: +55 062 521 1480.

E-mail addresses: levicarina@unb.br (L.C. Terribile), diniz@icb.ufg.br (J.A.F. Diniz-Filho).

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Rahbek, 2001; Whittaker et al., 2001; Hawkins et al., 2003a,b; Willig et al., 2003; Hawkins, 2004; Mittelbach et al., 2007). Simultaneously, workers have tried to generate specific predictions to test these hypotheses, under a more hypothetical-deductive approach (Currie et al., 2004).

More recently, in the context of the metabolic theory of ecology (MTE hereafter, see Brown et al., 2004), Allen et al. (2002) proposed that \ln -transformed species richness is a linear function of annual temperature inversely rescaled ($1/kT$, where k is Boltzman's constant and T is temperature in Kelvin), and for which the slope is between -0.6 and -0.7 (referring to the model version presented in Brown et al., 2004; see also Allen et al., 2006; Hawkins et al., 2007a). A more recent version of the theory applied to diversity gradients tries to explicitly link diversification rates and temperature variation, under Kimura's neutral theory of molecular evolution (Allen et al., 2006; Gillooly and Allen, 2007). The proponents of the theory also argue that MTE accounts for diversity gradients over a range of spatial scales, from mountains slopes to continental and global gradients, and for many groups of plants and ectothermic animals (Allen et al., 2002; Brown et al., 2004).

Metabolic theory has been criticized based on several grounds (Muller-Landau et al., 2006; van der Meer, 2006; Hawkins et al., 2007a), and its application to the study of diversity gradients has been extremely controversial as well. Algar et al. (2007) showed that for several datasets in North America (some of them previously analyzed by Allen et al., 2002) the relationship between \ln -transformed richness and temperature is actually curvilinear, so slopes vary systematically in geographic space. Cassemiro et al. (2007) expanded this approach by showing that even when the MTE prediction of a linear relationship between \ln (richness) and temperature (Allen et al., 2002) was met for New World amphibians, the slopes were spatially variable using a geographically weighted regression (GWR) approach (see Foody, 2004; Wang et al., 2005; Bickford and Laffan, 2006). This problem can appear because of non-stationarity in the data, i.e. the relationship between variables can vary systematically from one locality, or region, to another (Cassemiro et al., 2007). Thus, in GWR slopes consistent with MTE may be found in some regions but not in others, and this apparently follows the conjecture proposed by Hawkins et al. (2003b) (see also Whittaker et al., 2007) in which energy is thought to be the limiting factor in temperate regions, whereas water is more important in tropical regions. This leads to the question of incorporating other environmental variables into the analysis and evaluating the partial role of temperature in respect to these other variables.

Hawkins et al. (2007a) evaluated a large number of datasets for a wide range of organisms in different parts of the world with variable spatial extents and grain sizes and found minimal support for the model of Allen et al. (2002). Out of 46 data sets, the prediction of linear relationships between temperature and richness with a slope within the predicted range was attained in only one case using OLS regression (and in no cases using model II regression), and the slopes were widely dispersed, being both positive and negative and with a mean close to zero (see also Gillooly and Allen, 2007; Latimer, 2007; Hawkins et al., 2007b). However, neither Hawkins et al. (2007a) nor Latimer (2007) used GWR to investigate variation in

the relationship between \ln -richness and temperature expressed as $1/kT$ across geographical space.

Another criticized aspect of the metabolic theory concerns the assumptions used to test the \ln -richness vs. $1/kT$ relationship. According to Allen et al. (2002), the predicted slope would be attained for ectotherms at broad scales if the abundance and average body size are invariant along temperature gradients. However, as pointed out by Hawkins et al. (2007a), neither Allen et al. (2002) nor subsequent studies (e.g., Hunt et al., 2005; Roy et al., 2006) have tested for these two assumptions. Also, Allen et al. (2002) pointed out that model assumptions are "... not expected to hold true for groups that are narrowly defined ..." (Allen et al., 2002: 1546), but Algar et al. (2007) found support for the theory in a narrowly defined group of beetles. Indeed, given the restricted conditions for which the theory would be attained and the paucity of abundance and body size data for unrestricted taxonomic groups at large scales, it is currently unrealistic to expect a test that fulfils all assumptions of the metabolic theory.

Given the controversies around the MTE, we performed a detailed analysis of spatial patterns of species richness for New World coral snakes, with the main purpose to evaluate the relationship between richness and temperature expressed as $1/kT$. The analyses performed here present two main novelties regarding the recent discussion involving MTE. First, we empirically assessed for one of the assumptions that MTE proponents stress to be necessary for testing the -0.65 prediction, i.e., that the average body size should be independent of temperature (see Allen et al., 2002) at broad spatial scales (Gillooly and Allen, 2007). Second, by using GWR approach, we examine whether regression slopes between \ln -richness and $1/kT$ remain around the MTE prediction of -0.65 at local scales. Also, we investigate for the relative importance of $1/kT$ along with five other environmental variables to explain the richness pattern of coral snakes. Although we found a slope close to MTE predictions taking into account both the effect of other alternative hypotheses and spatial autocorrelation, a large degree of non-stationarity in the relationship between richness and temperature was also observed. Our findings allow a better understanding about the domains and data statements currently used to test MTE applied to broad scale richness gradients.

2. Materials and methods

2.1. Data

We generated the geographic distributions of 73 species of New World coral snakes (*Leptomicrurus*, *Micruroides* and *Micrurus* spp.), based on 2547 individual records. Occurrence data were compiled based on voucher specimens held in North America (American Museum of Natural History – New York, Field Museum of Natural History – Chicago, Museum of Natural History – Los Angeles, Louisiana Museum of Natural Science – Baton Rouge, Museum of Vertebrate Zoology – Berkeley, Smithsonian Institution – Washington D.C., and Texas Memorial Museum – Austin), and South American museums (Coleção Herpetológica da Universidade de Brasília – Brasília, Colección Herpetológica Corrientes – Corrientes, Colección

Herpetológica de la Fundación Miguel Lillo – Tucumán, Colección Herpetológica de Zoología de Vertebrados de la Universidad Nacional de Río Cuarto – Córdoba, Museo de Ciencias Naturales Bernardino Rivadavia – Buenos Aires, Instituto Butantan – São Paulo, Museo de História Natural Noel Kempff Mercado – Santa Cruz de la Sierra, Museo Nacional de Historia Natural del Paraguay – Asunción, Museu Paraense Emílio Goeldi – Pará, Museo de La Plata – La Plata, Museo Nacional – Rio de Janeiro, and Museu de Zoologia da Universidade de São Paulo – São Paulo). We supplemented our data sets with records that were georeferenced from Campbell and Lamar (2004). In this case, we were careful not to include pseudo-replicated records (i.e., the same record from a voucher specimen and from Campbell and Lamar, 2004). The number of records for each species varied from 1 to 217.

To test the condition that MTE can only be used to explain diversity gradients of ectotherms when average body mass is held constant across samples or communities, we obtained data of maximum total length for each species from Campbell and Lamar (2004). Considering that snakes grow indeterminate (Partridge and Coyne, 1997; Olalla-Tárraga et al., 2006) and the masses of reptiles are rarely available in the literature, maximum values of length have been considered to be a reasonable estimate of size for snakes (Reed, 2003; Olalla-Tárraga et al., 2006). Also, it has been suggested that both body length and body mass have similar results in analyses of macroecological patterns (Olalla-Tárraga et al., 2006). Maximum total lengths were log-transformed, and we calculated average body size in each cell of a geographic grid (see below).

2.2. Modeling species distributions

For species with less than 20 occurrence records (27 species), geographic distributions were established using a simple minimum convex polygon, and presence/absence of species were recorded in a grid with 4187 cells of 1° of latitude and longitude covering the New World. These species are usually very restricted and have small geographic ranges.

Geographic ranges of species for which 20 or more occurrence records were available (46 species) were modeled using GARP (genetic algorithm for rule set production) (Stockwell and Noble, 1992; Stockwell and Peters, 1999). GARP is one of the many available niche-based species distribution models, or ecological niche models (ENM) (see Segurado and Araújo, 2004; Elith et al., 2006; Pearson et al., 2007; Tsoar et al., 2007; Costa et al., 2007), which currently play a central role in many areas of ecology, conservation and evolutionary biology, both because they can fill gaps in knowledge and because they allow a better estimate of multiple components of species diversity (Guisan and Zimmermann, 2000; Araújo and Guisan, 2006; Costa et al., 2007).

We used six environmental predictors in GARP (annual mean temperature, temperature seasonality [coefficient of variation], mean temperature of the driest quarter, annual precipitation, precipitation seasonality [coefficient of variation] and precipitation of the warmest quarter), derived from the WorldClim (<http://www.worldclim.org>), and three topographic predictors (altitude, aspect and slope), derived from the Hydro-1K global digital elevation model (<http://edcdaac.usgs.gov/gtopo30/hydro>).

All predictors were reduced to a grid resolution of 0.0417° (~1 km) for the analysis.

We implemented in GARP the best-subset model selection procedure by generating 200 models, setting the convergence limit to 0.001, a 0% extrinsic omission error, 10% commission error, and 2000 maximum iterations. We then selected the 20 best models (i.e., the 20 models showing least omission error and moderate commission error, see Anderson et al., 2003) and summed them to generate a composite GARP prediction. GARP methods were evaluated using AUC and ROC curves, an approach extensively used in species' distribution modeling (see Allouche et al., 2006; Elith et al., 2006). To use this analytical approach without a sample of true absence points, Phillips et al. (2006) generated a sample of 10,000 pseudo-absence points to join to the training sample and estimated AUC derived from ROC curves of the new Maxent method. We repeated the same procedure with the GARP predictions, since true absence data were not available. We then recorded for each species the area of occurrence predicted by GARP using the threshold generated to “cut” the potential distribution and produce a presence-absence matrix (0/1) for the 4187 cells covering the New World. More than one species was present in 1784 of these cells, so these were used for further statistical analyses. Although ROC and AUC have been recently being criticized (see Lobo et al., 2008; Peterson et al., 2008), they can provide at least a preliminary indication of the usefulness of the distribution models for identifying suitable areas of occurrence for particular species (Elith et al., 2006), the overlapping of which will generate the richness patterns. Because we are actually modeling richness and not individual ranges, we expect that problems of threshold estimates do not qualitatively affect the outcomes (Wisz et al., 2007).

2.3. Environmental correlates of species richness

We used six environmental variables as correlates of coral snake richness, capturing a range of aspects of climatic and environmental variation and used in a series of papers dealing with broad scales patterns in species richness (e.g., Rodríguez et al., 2005; Hawkins et al., 2003a, 2005). We used variables related to: *ambient energy*, measured by the Priestley–Taylor equation of potential evapotranspiration (PET, see Lu et al., 2005) and mean annual temperature (TEMP); *water-energy balance*, expressed by annual actual evapotranspiration (AET) (obtained from <http://www.grid.unep.ch/data/summary.php?dataid=GNV183>) and by mean monthly annual precipitation (PREC); and *ambient productivity*, expressed by the Net Primary Productivity (NPP). We also measured *topographic heterogeneity* (RELEV) in cells, using as a surrogate the difference between minimum and maximum altitude with each cell. See Rodríguez et al. (2005) for more detailed definitions and sources for these environmental data.

It is important to note that environmental variables were used to model species' distributions, which were summed to generate richness patterns and once again modeled using environmental data to search for the main drivers in richness and allow an evaluation of MTE. This could lead to a circularity problem, but Wisz et al. (2007) recently pointed out that since multiple geographic ranges, with distinct sizes and shapes, tend to be modeled independently by different sets of

environmental variables and with different parameters, the subsequent summing to generate richness patterns will eliminate the unidirectional effects of a single variable on summed ranges. Also, recent analyses of coral snake richness for which ranges were estimated through polygons showed that more than 50% of the variance in their richness in the New World was explained by the same variables used here to explain richness patterns based on niche models for establishing species' distributions (L.C. Terribile, unpublished data). So, richness may ultimately be affected by the environmental factors acting on individual species' geographic ranges in such a way that this procedure may be viewed not as a bias (created by tautological reasoning), but instead as a more accurate way to understand environmental drivers of species richness (L.C. Terribile, unpublished data).

2.4. Spatial analysis of species richness patterns

First, we evaluated our dataset in respect to the conditions required to test MTE predictions. In the case of ectotherms, it was stated that the effect of temperature on diversity would be expressed when body size and abundance of these organisms are kept constant across temperature gradients (Allen et al., 2002). Here, we were not able to test for the abundance condition due to the absence of data on coral snake abundances, but our analyses for body size revealed that the average body size variation of this group are not constrained by the temperature gradient.

Brown et al. (2004) proposed that the relationship between \ln -transformed species richness and $1/kT$ has a slope between -0.6 and -0.7 (see also Allen et al., 2006; Hawkins et al., 2007a). Thus, annual mean temperature was expressed here as $1/kT$ and was tested alone and together with the other five variables, and 95% confidence intervals of slopes allowed us to test agreement with MTE predictions (but see Hawkins et al., 2007b for a discussion about the validity of testing MTE predictions by seeing whether 95% CI encompass the predicted slopes). For tests of temperature alone, both model I and II regressions were used (see Hawkins et al., 2007a). However, since spatial autocorrelation is usually found in this type of data, and it creates biased Type I error estimates due to inflation of degrees of freedom (see Legendre et al., 2002; Diniz-Filho et al., 2003), ordinary least squares (OLS) regression models are not entirely adequate (but see Hawkins et al., 2007c).

To examine the influences of other environmental correlates on richness patterns, we generated environmental models including multiple variables and used an AIC-based approach (see Burnham and Anderson, 2004; Diniz-Filho et al., 2008) for model selection. Specifically, besides calculating the AIC of each model, we also computed its ΔAIC_i value (i.e. $\Delta AIC_i = AIC_i - \min AIC$; where $\Delta AIC_i > 10$ represent poor fits, and $\Delta AIC_i \leq 2$ correspond to models equivalent to the best model (Burnham and Anderson, 2004)) and Akaike's weighting (w_i), an index representing the probability that model i is actually the best explanatory model among all possible models with six variables (i.e. 63 models). An average model can then be obtained by a w_i weighted average of coefficients from all tested models, and this average is usually considered more robust (Diniz-Filho et al., 2008). Finally, we can repeat

this modeling process after fixing the estimated value of richness against the spatial filters (see below) to take autocorrelation into account during the model selection procedure.

We analysed spatial autocorrelation in richness and in OLS standardized multiple regression residuals (see below) using spatial correlograms of Moran's I coefficients calculated at 20 distance classes (Legendre and Legendre, 1998; Diniz-Filho et al., 2003). To account for spatial autocorrelation in geographical data, many methods are now currently available (see Diniz-Filho et al., 2003; Rangel et al., 2006). In this paper we used two different approaches to deal more explicitly with spatial components of richness data.

First, we used eigenvector-based spatial filtering (see Borcard and Legendre, 2002; Griffith, 2003; Borcard et al., 2004; Diniz-Filho and Bini, 2005; Griffith and Peres-Neto, 2006; Blamires et al., 2008). In this approach geographical coordinates (latitude and longitude) of cells with more than one species are used to build a connectivity matrix C expressing a "queen" connection system, which can be obtained in our grid by linking neighboring cells whose centroids were situated less than 200 km away (see Legendre and Legendre, 1998). The connectivity matrix C was then submitted to a principal coordinate analysis, which consists of performing an eigenanalysis of the double-centered matrix (Legendre and Legendre, 1998).

The eigenvectors associated with positive eigenvalues of the C matrix represent the spatial relationship among cells covering the New World at different spatial scales. The first eigenvectors represent broad scale variation, whereas eigenvectors derived from small eigenvalues represent fine-scale variation. These vectors are then new orthogonal variables (called filters by Griffith, 2003) that capture, at different scales, the geometry of the grid covering the New World. They can be incorporated into an OLS multiple regression approach, taking into account spatial autocorrelation and allowing an alternative estimation of regression parameters (Diniz-Filho and Bini, 2005).

The next step of the analytical protocol includes the selection of the eigenvectors that should enter in the modeling process. Here we selected the filters (together with the other correlates) with Moran's I coefficients in the first distance class greater than 0.1 (see Griffith, 2003; Diniz-Filho and Bini, 2005) and added these eigenvectors to the multiple regression model with environmental correlates, which successfully removed all residual spatial autocorrelation.

An additional issue with respect to MTE is that the predicted slope of the relationship between \ln -richness and $1/kT$ should be found across different spatial scales of analyses (Allen et al., 2002). However, as recently pointed out by Algar et al. (2007) and Cassemiro et al. (2007), the relationships between variables can vary systematically from one locality to another (i.e., the relationships may be non-stationary). Most regression models applied to macroecological patterns assume that results apply equally to the entire study area, but they may only provide an "average" of the relationships if non-stationarity occurs in the data. Thus, the application of models that quantify non-stationarity may be useful in revealing more complex spatial structures in data and relationships between variables in multiple scales.

To account for possible non-stationarity in the relationship between richness and the environmental variables, we used geographically weighted regression (GWR), following Cassemiro et al. (2007). GWR has been recently applied in numerous macroecological analyses (Fotheringham et al., 2002; Foody, 2004, 2005; Wang et al., 2005; Bickford and Laffan, 2006; see also Jetz et al., 2005; Foody, 2005, for a discussion of the interpretation of GWR in richness data). The advantage of GWR is that instead of estimating a single slope that describes a relationship, GWR generates one regression slope for each locality, or ‘cell’ (called ‘local’ slopes) using a complex scheme of spatial weights (see Fotheringham et al., 2002). These slopes (as well as estimates for other regression parameters, such as the r^2) can then be mapped and used to investigate how the relationship between variables changes across geographic space. Also, GWR can be particularly important in relation to rare, narrow ranging species for which results are most scale-dependent, as pointed out by Foody (2004) and Jetz et al. (2005). An F -statistic can be used to test for the improvement of GWR over a standard OLS, taking into account the differences in degrees of freedom between the two models, and the spatial weightings for GWR can be defined by an adaptive kernel function, with bandwidths interactively established using the Akaike criterion (see Fotheringham et al., 2002 for details).

Finally, since the correlates used to generate the environmental model include some “compounded” variables (e.g., AET and PET), the multicollinearity among them and other “primary” explanatory variables (i.e., mean temperature, precipitation, topographic heterogeneity, and net primary productivity) could lead to a tangled interpretation of the importance of these predictors expressed on the regression coefficients (Graham, 2003) (see the correlation matrix between all environmental variables in Supplementary Material). To investigate possible effects of multicollinearity, we ran an OLS model just with ‘primary’ variables (i.e., MEAN1/kT, precipitation, topographic heterogeneity, and net primary productivity), and then compared these coefficients with those of the best AIC model including all variables.

All statistical analyses were performed in spatial analysis in macroecology (SAM), freely available at <http://www.ecoevol.ufg.br/sam> (Rangel et al., 2006).

3. Results

Coral snake species richness follows the well known latitudinal pattern in the western hemisphere (Fig. 1A), with higher richness found in northwestern South America. Overall, GARP showed good ability to predict geographic distributions of the species, with AUC values ≥ 0.92 . The good predictive performance of GARP models indicates that the generated distributions can be used to estimate regional species richness patterns.

In a simple model I regression, the observed slope between ln-richness and $1/kT$ was -0.626 ± 0.018 standard error (95% CI = 0.59–0.66), matching quite well MTE predictions (Fig. 1B). More importantly, the predicted slope of MTE was found for coral snakes in a broad spatial scale (i.e., New World) for which the average body size variation was independent of temperature across cells ($R = 0.044$; $P > 0.05$). At first this

finding implies that richness in this ectothermic group is determined by temperature following the MTE proposition. However, there is substantial heterocedasticity caused by a greater variation of richness in warm regions of Neotropics (i.e., with low $1/kT$ values), so that a ‘constraint envelope’ commonly found in macroecological studies may better describe the relationship (see also Cassemiro et al., 2007). Thus, a linear regression model is not strictly adequate to describe the richness data, and the r^2 was not very high ($=0.413$). Adding a quadratic term caused minimal improvement to the model fit ($r^2 = 0.439$). Further, using model II regression generated a slope much steeper than predicted by MTE ($b = -0.975 \pm 0.018$ standard error, CI95% = 1.011–0.939).

There was significant spatial autocorrelation in model residuals of the linear regression of ln-richness against $1/kT$ (Fig. 2), with high positive Moran’s I coefficients up to the fifth distance class (ca. 1500 km). Although confidence intervals of regression slopes presented above are underestimated because of the strong spatial autocorrelation in data, the relationship remains significant at the 5% level after correcting the degrees of freedom using Dutilleul’s procedure ($R = -0.642$; $df = 10.3$; $P = 0.022$; see also Hawkins et al., 2007a).

When adding other environmental correlates in the model I regression, the AIC multimodel selection found one good model (i.e., $\Delta \leq 2$), which included all six correlates, and the R^2 increased to 0.748. Temperature expressed as $1/kT$ was the correlate with highest rank according to the average standardized coefficients (Table 1), although RELEV and AET are also important to determine patterns of species richness and greatly improved model fit (Table 1). However, some residual autocorrelation still remained in the full OLS model, with a Moran’s I in the first distance class equal to 0.290 (Fig. 2). Adding spatial autocorrelation in the modeling process using spatial filters did not produce a qualitatively different model (i.e., all six correlates are still kept in the best model and have the same relative importance, see Table 1). After incorporating the 40 filters, most of the residual autocorrelation was taken into account (i.e., with Moran’s I in the first distance class of residuals = 0.058). In this full model (i.e., composed of six environmental correlates and 40 eigenvector filters), the R^2 increased to 0.863 and the partial regression coefficient of $1/kT$ was equal to -0.676 .

When we ran the environmental model with only ‘primary’ variables (i.e., MEAN1/kT, precipitation, topographic heterogeneity, and net primary productivity), the R^2 decreased to 0.680 in comparison with 0.748 from the full model with six variables. Even so, the slope of MEAN1/kT was still very similar (-0.640). Thus, though some multicollinearity could be affecting the full model, this did not change our interpretation that variables other than temperature alone are important drivers of coral snake richness. More important, the analyses based on AIC did not suggest removing any of the remaining variables, even considering the spatial autocorrelation.

We then applied the GWR to detect non-stationarity in the relationship between richness and other correlates and to evaluate spatial patterns in regression parameters. There was an improvement of GWR in respect to the OLS model (r^2 of GWR = 0.943 against $r^2 = -0.626$ of OLS, with an $F = 23.37$ [$P < 0.01$] for the improvement of GWR over OLS). Thus,

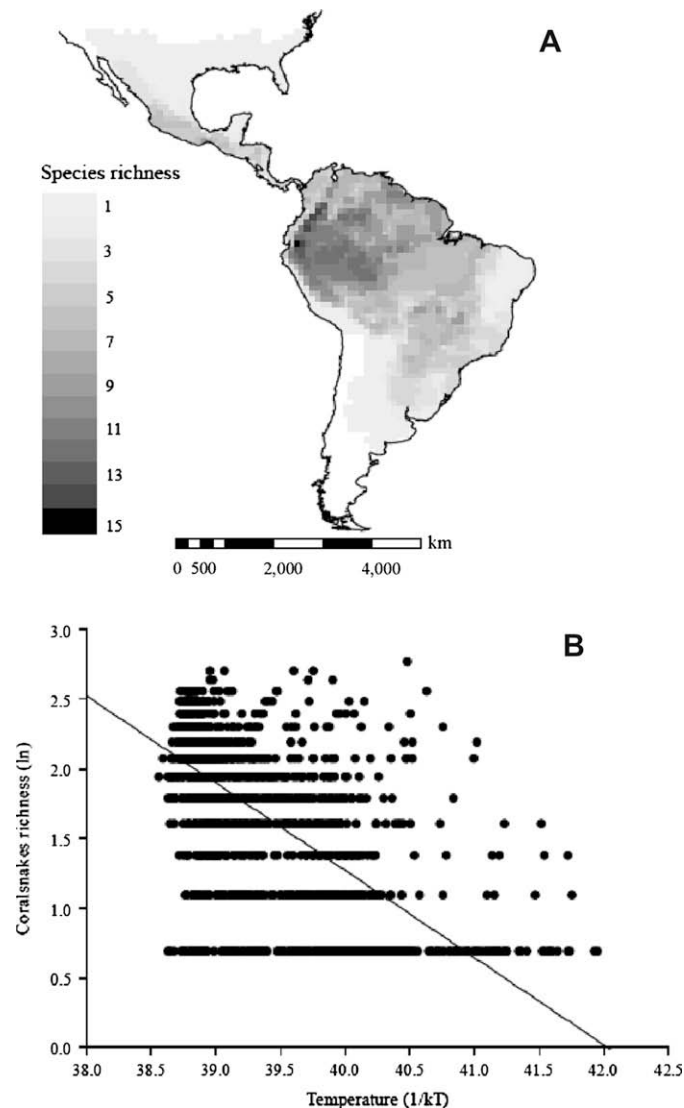


Fig. 1 – Spatial pattern of species richness for 73 species of coral snakes in the New World (A) and the relationship between ln-species richness and temperature, expressed as $1/kT$ (model I regression slope = -0.626) (B).

a highly significant non-stationarity was detected in the relationship. Indeed, local slopes of ln-richness against $1/kT$ vary between -3.084 and $+1.634$ across the New World, with a median of -0.38 (Fig. 3), and few values fell in the interval between -0.6 and -0.7 (Fig. 4). The explanatory power (r^2) is usually strong across the continent (Fig. 5), except in parts of central Brazil, but the slopes of the local regression do not have a clear spatial pattern (Fig. 3). Residuals of the GWR contained minimal spatial autocorrelation (Moran's I at the first distance class equal to -0.072).

4. Discussion

At first sight the pattern of species richness in New World coral snakes is consistent with MTE predictions, with a slope of ln-richness against $1/kT$ of -0.626 in the model I regression, within the expected range between -0.60 and -0.70 . On the other hand, model II regression generated a slope of -0.975 .

The overall explanatory power of the model I is moderate (ca. 40%), and the bivariate relationship is a constraint envelope, which generates differences between model I and II regression slopes. Recent studies have raised the question about which statistical method should be used to test MTE (whether model I or model II regression, see Hawkins et al., 2007a,b), but it is difficult to know which is the best model without knowing the true error of X (i.e., temperature), and the standard solution has been to check for both model I and II regression (Brown et al., 2004; Hawkins et al., 2007a). Furthermore, adding more environmental variables significantly improved model fit. Even so, the partial slope of $1/kT$ is also very close to the MTE prediction when using eigenvector filtering to take spatial autocorrelation into account and incorporating other correlates in the analysis. So, though our analysis is in principle consistent with MTE predictions, significant effects of AET and RELEV suggest that water-energy dynamics and habitat heterogeneity (see Hawkins et al., 2003a,b; Hawkins, 2004; O'Brien, 2006; Whittaker et al.,

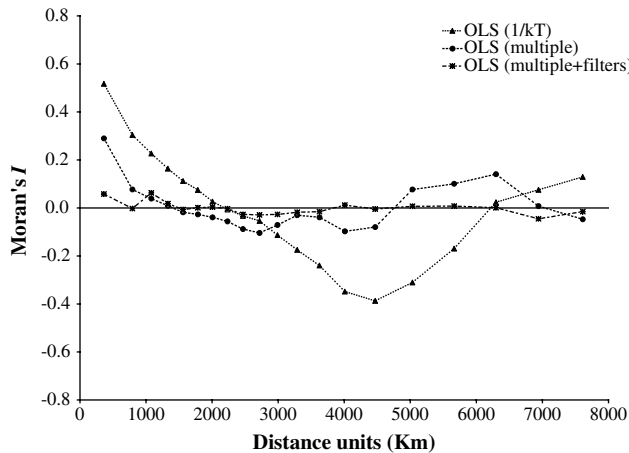


Fig. 2 – Spatial correlograms of Moran's *I* spatial autocorrelation coefficients for residual of the analyses, including the residuals from a simple regression of ln-richness against $1/kT$, from a multiple regression of ln-richness against environmental correlates, and from multiple regression of ln-richness against full model (i.e., environmental correlates more 40 filters). The Moran's *I* spatial autocorrelation coefficient was 0.739 for richness and -0.072 for GWR residuals in the first distance class.

2007) are also important drivers of New World coral snake richness patterns.

In a recent discussion about validity of MTE to explain biodiversity, Gillooly and Allen (2007) argued that Hawkins et al. (2007a) failed to support MTE for most datasets they analyzed because they tested the theory and model with data in which the assumptions were not entirely fulfilled (even though tests were performed in the same way as in Allen et al., 2002). Indeed, in some studies which the MTE prediction was not attained, *a priori* tests for body size or abundance-dependence on temperature were not performed (e.g., Hunt et al., 2005; Roy et al., 2006), so one may claim that if the empirical data do not attain the key assumptions

of a theory, it could not be expected that the predictions of this theory would be achieved. Nevertheless, the outcomes of our analyses for coral snake richness clearly show a more complex pattern in which testing the validity of assumptions of MTE is not a guarantee that theory does or does not explain richness patterns.

Regarding the assumptions of MTE, the first important result of our analyses is that average body size was not correlated with temperature across cells ($R = 0.044$; $P > 0.05$) and are not well predicted by the full set of environmental variables ($R^2 = 0.264$). Although some recent studies have evaluated interspecific body size geographical gradients in the context of Bergmann's rule for ectothermal organisms (see Olalla-Tárraga et al., 2006; Rodríguez et al., 2007), such patterns were not found in coral snakes, possible because this is a relatively homogeneous and relatively recent evolutionary group. Since body size was not correlated with $1/kT$ and only weakly with other correlates, no deviation from slopes predicted by MTE would be expected. Furthermore, the geographic extent of our dataset encompasses a broad range of temperatures across the New World, and this finding is an additional condition for which the response of richness to temperature is expected to show the predicted slope of MTE (see Brown et al., 2004; Gillooly and Allen, 2007; Hawkins et al., 2007b).

On the other hand, Allen et al. (2002) also pointed out that reptiles are not a good group to test MTE, because of the dependence between abundance and temperature, which also violates MTE assumptions. Violations of this assumption are actually very difficult to test, because of a lack of abundance data at broad geographic scales, but reptiles usually have temperature-dependent abundances.

Also, Allen et al. (2002) explicitly say that MTE predictions are not expected in restricted groups of organisms, as in a single genus or family, or in regions in which there is limited variation in temperature. Our data set comprises a very restricted group, with only three genera, though the validity of *Leptomicrurus* has been questioned (some authors consider *Leptomicrurus* a synonym of *Micrurus*, see Campbell and Lamar, 1989, 2004), and the third genus *Micruroides* has only

Table 1 – Summary of regressions analysis (OLS), including the regression slopes, standardized coefficients, and probability, using all environmental correlates, and environmental correlates and spatial filters. For the environmental model without the filters, we represent the AIC w_i -weighted averaged standardized coefficients resulting from averaging the coefficients of all possible models (i.e., 63) with six correlates. Environmental correlate codes are: AET – actual evapotranspiration; NPP – net primary productivity; PET – potential evapotranspiration; Prec – annual precipitation; Mean $1/kT$ – mean annual temperature expressed as $1/kT$ (where k is Boltzman's constant and T is temperature in Kelvin); Relev – topographic heterogeneity

Variable	Environmental model*			Environmental model + filters**		
	Slope	Stand. coefficients	Prob.	Slope	Stand. coefficients	Prob.
AET	0.009	0.452	<0.001	0.002	0.104	0.002
NPP	0.319	0.159	<0.001	0.289	0.144	<0.001
PET	-0.005	-0.208	<0.001	<0.001	-0.001	0.968
PREC	0.029	0.106	<0.001	0.015	0.045	0.026
MEAN1/kT	-0.689	-0.707	<0.001	-0.676	-0.693	<0.001
RELEV	<0.001	0.479	<0.001	<0.001	0.475	<0.001

* Model composed of six environmental correlates ($R^2 = 0.748$).

** Model composed of six environmental correlates and 40 eigenvector filters ($R^2 = 0.863$).

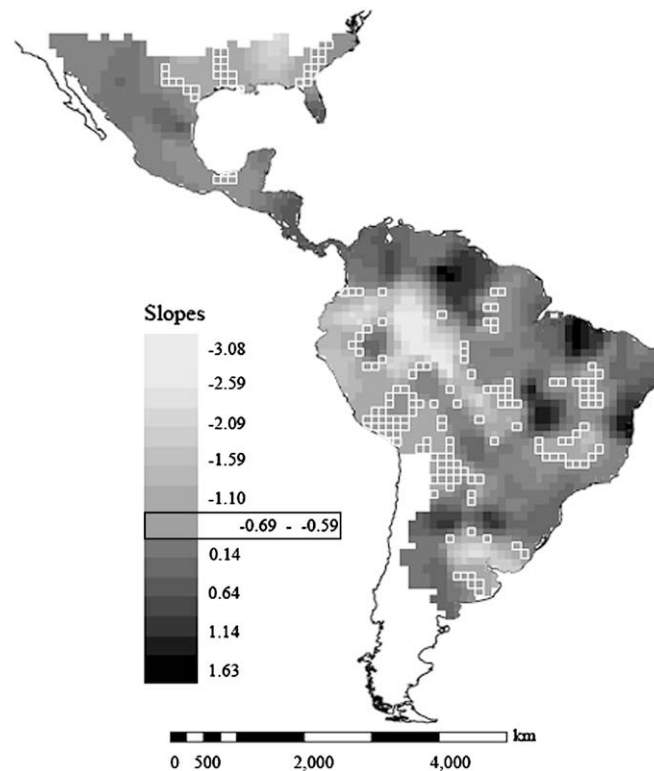


Fig. 3 – Distribution of partial regression slopes of $1/kT$ as correlate of \ln -species richness for GWR local regressions. Cells outlined in white indicate where GWR slopes match the predictions by MTE (i.e., slopes ranging between -0.6 and -0.7).

one species. This observation casts serious doubt about the validity of MTE to explain the richness pattern of these snakes. Whether, in one hand, our dataset confirms the theory (OLS slope of $1/kT = -0.626$) in agreement with some assumptions (i.e., average body size is constant across temperature gradients), on the other hand these snakes are not an ‘ideal’ group to confirm MTE, since they are a “narrowly defined” (*sensu* Allen et al., 2002) group in which abundances are regulated by temperature. This also shows that the assumptions of MTE are not compelling and that the

theory still deserves several improvements (see also Hawkins et al., 2007a).

Finally, this refined analysis with coral snakes, compared to the coarser one done by Hawkins et al. (2007a), can give some insights to the methods and data statements required to better evaluate MTE (see Ford, 2002; Hawkins et al., 2007b; del Río, 2008). The most important aspect is that GWR detected strong non-stationarity in the data, so that the slope is highly variable in space, as was recently also found for New World amphibians (Cassemiro et al., 2007). However, unlike what was found by Cassemiro et al. (2007), the range of slopes found here for $1/kT$ is much wider, ranging from -3 to 1.6 , which means that there is no support for MTE in many parts of the Neotropics. Values close to the prediction seem to be randomly scattered around the continent. Besides, the median value of GWR slopes is also far from -0.6 . Thus, the non-stationarity in coral snake richness patterns does not support clearly the idea that energy becomes more important in higher latitudes so that a better prediction of MTE is expected in regions of cool climates (see also Whittaker et al., 2007).

In addition, the relatively high explanatory power of AET (a direct measure of joint availability of energy and water in the environment and, consequently, an indirect indicator of primary productivity) and topographic heterogeneity (Table 1) suggest that effects of primary productivity (see Hawkins et al., 2003b) and habitat heterogeneity are also important drivers of coral snake richness in the New World. This finding is consistent with the proposition of Hawkins et al. (2003b, 2007a), that energy alone is not the main driver of richness in

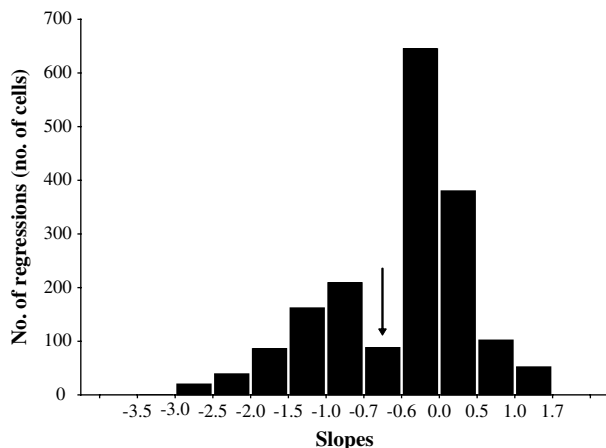


Fig. 4 – Frequency distribution of all GWR slopes across 1784 cells of New World. The arrow identifies the expected value predicted by metabolic theory.

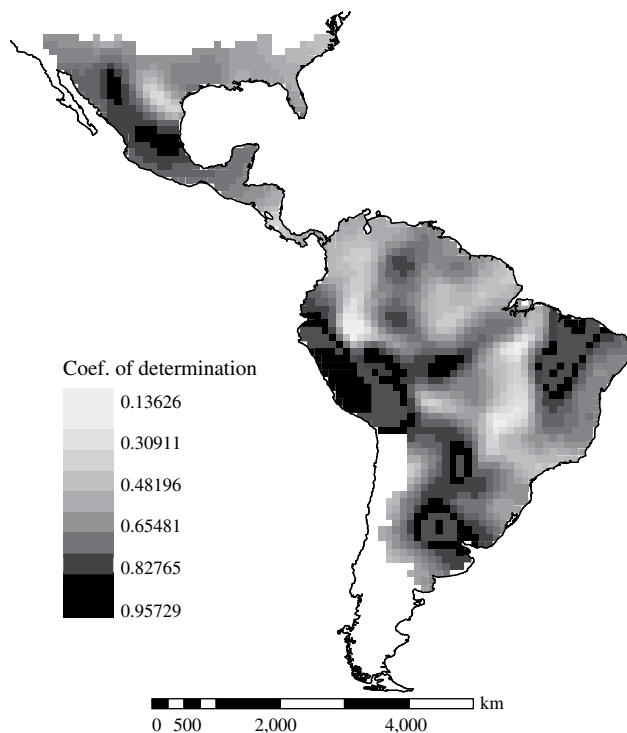


Fig. 5 – Spatial variation in coefficients of determination (r^2) obtained by GWR.

some regions, but that the interaction between water and energy provides a better explanation mainly in tropical latitudes.

Thus, although our standard spatial analysis of patterns is consistent with MTE, taking both autocorrelation and the effect of multiple variables into account, a more detailed analysis using GWR is not so supportative. In a confirmatory view of scientific knowledge, matching slopes could be important to support MTE. However, random spatial variation of these slopes in geographic space and the match of MTE for a dataset that violates some of its assumptions (i.e., the coral snake genera *Leptomicrurus*, *Micruroides* and *Micrurus* are three narrowly defined groups, and reptiles in general are able to thermoregulate and usually have temperature-dependent abundances) lead us to claim for a better evaluation of model assumptions and to better define in which domain the theory is expected to explain richness patterns (see also Hawkins et al., 2007b). Even if one takes the model I regression results to support MTE, it is clear that explanatory power of the theory is low so that other ecological and historical factors (as pointed out by Blackburn, 2004) can be important in driving species richness patterns, and they must taken into account both in theoretical modeling and data analysis.

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Appendix A. Supplemental material

Supplementary information for this manuscript can be downloaded at doi:10.1016/j.actao.2008.09.006.

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