



Squamate richness in the Brazilian Cerrado and its environmental–climatic associations

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ABSTRACT

We investigate patterns of species richness of squamates (lizards, snakes, and amphisbaenians) in the Brazilian Cerrado, identifying areas of particularly high richness, and testing predictions of large-scale richness hypotheses by analysing the relationship between species richness and environmental climatic variables. We used point localities from museum collections to produce maps of the predicted distributions for 237 Cerrado squamate species, using niche-modelling techniques. We superimposed distributions of all species on a composite map, depicting richness across the ecosystem. Then, we performed a multiple regression analysis using eigenvector-based spatial filtering (Principal Coordinate of Neighbour Matrices) to assess environmental–climatic variables that are best predictors of species richness. We found that the environmental–climatic and spatial filters multiple regression model explained 78% of the variation in Cerrado squamate richness ($r^2 = 0.78$; $F = 32.66$; $P < 0.01$). Best predictors of species richness were: annual precipitation, precipitation seasonality, altitude, net primary productivity, and precipitation during the driest quarter. A model selection approach revealed that several mechanisms related to the different diversity hypothesis might work together to explain richness variation in the Cerrado. Areas of higher species richness in Cerrado were located mainly in the south-west, north, extreme east, and scattered areas in the north-west portions of the biome. Partitioning of energy among species, habitat differentiation, and tolerance to variable environments may be the primary ecological factors determining variation in squamate richness across the Cerrado. High richness areas in northern Cerrado, predicted by our models, are still poorly sampled, and biological surveys are warranted in that region. The south-western region of the Cerrado exhibits high species richness and is also undergoing high levels of deforestation. Therefore, maintenance of existing reserves, establishment of ecological corridors among reserves, and creation of new reserves are urgently needed to ensure conservation of species in these areas.

Keywords

Conservation, niche modelling, reptiles, richness gradients, spatial statistics, species distribution.

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INTRODUCTION

The Cerrado is the second largest biome in South America, originally occupying about 20% of Brazil's land surface (Ab'Saber, 1977; Ratter *et al.*, 1997; Silva & Bates, 2002). It is located mainly in central Brazil and shares contact zones with almost all other Brazilian biomes. The Cerrado consists of savanna vegetation distributed in a gradient from open grassland to forested sites with closed canopy (Eiten, 1972). A recent overview of the Cerrado fauna and flora is available in Oliveira & Marquis (2002).

Along with 34 other ecosystems, the Cerrado is considered a global biodiversity 'hotspot', as defined by diversity, endemism, and human threats (Myers, 2003; Mittermeier *et al.*, 2005). A recent estimate based on satellite remote sensing shows that approximately 55% of the Cerrado's original vegetation has been removed, and the annual deforestation rate is higher than that in the Amazon (Machado *et al.*, 2004b). If the current destruction rate is not reversed, no natural areas will remain in the Cerrado by 2030 (Machado *et al.*, 2004b). Agriculture and cattle farming, the major economic activities in Brazil, are the main threats to

Table 1 General hypotheses explaining species richness patterns, environmental characteristics traditionally used to test these hypotheses, and variables used in this paper in the regression models to assess the importance of each hypothesis for Cerrado squamates. Adapted from: (Moser *et al.*, 2005).

Hypothesis	Argument	Factor used to test	In this paper
Available energy*	Partitioning of energy among species limits richness	Temperature, potential evapotranspiration, and precipitation	Annual precipitation, net primary productivity
Environmental stress†	Fewer species are physiologically equipped to tolerate harsh environments	Minimum values of temperature and potential evapotranspiration	Precipitation of driest quarter, mean temperature of driest quarter
Environmental favourableness‡	Better life conditions promote higher species numbers	Maximum values of temperature and potential evapotranspiration	Mean temperature of warmest quarter, precipitation of warmest quarter
Environmental stability§	Fewer species are physiologically equipped to tolerate variable environments	Annual variation in temperature	Temperature seasonality, temperature annual range, precipitation seasonality
Environmental heterogeneity¶	Habitat differentiation and resource partitioning facilitate coexistence and enhance species richness	Topographical, spatial climatic, edaphic, and land-use heterogeneity	Altitude, terrain declivity

*(Wright, 1983).

†(Fraser & Currie, 1996).

‡(Pianka, 1966; Richerson & Lum, 1980).

§(Pianka, 1966; Fraser & Currie, 1996).

¶(Richerson & Lum, 1980).

Cerrado, and the pace of deforestation is not likely to change in the near future (Klink & Moreira, 2002; Klink & Machado, 2005). Hence, Cerrado conservationists face the challenge of preserving the maximum amount of biodiversity using an ever-decreasing available space. Immediate action is needed because every year vast areas of the Cerrado are lost (Machado *et al.*, 2004b).

Despite its great diversity, endemism, and level of deforestation, less than 3% of the Cerrado's land area is protected in reserves (Machado *et al.*, 2004a; Rylands *et al.*, 2007). To identify priority areas for conservation, detailed information on species distributions is necessary. Vast areas of Cerrado are still poorly sampled (Silva, 1995; Ratter *et al.*, 1997; Aguiar, 2000; Felfili *et al.*, 2004), and biological surveys require significant investments of both time and money. Unfortunately, the speed at which the Cerrado is being destroyed does not allow sufficient time to adequately survey the entire region.

Recently, new advances in geographical information systems (GIS) allow modelling of species distributions based on attributes of the environment that should be correlated with species niche requirements (Peterson, 2001; Guisan & Thuiller, 2005). These models identify previously unsampled locations where the species have a high probability of occurrence because the environment is similar to conditions at known occurrence localities. These techniques do not account for species interactions or historical factors, they combine spatially explicit factors to yield potential geographical distributions of species (Araujo & Guisan, 2006). These methods have been successfully applied to several animal groups in different ecosystems, including butterflies in Finland (Luoto *et al.*, 2002), birds in North America (Peterson, 2001), and lizards in Madagascar (Raxworthy *et al.*, 2003). A recent study comparing different methods for predicting species distributions using presence-only data concluded that overall, these techniques produce good results (Elith *et al.*, 2006).

Additionally, niche modelling can be used to generate distribution maps for several species, which can be superimposed to generate maps showing gradients in species richness. The occurrence and determinants of large-scale patterns of species richness are fundamental questions in ecology that are still far from being resolved (Ricklefs, 2004). Several hypotheses exist to explain such patterns, some of which relate richness to particular environmental-climatic parameters (see Table 1 for a list of current hypotheses and how they relate to environmental-climatic variables). For example, the 'available energy hypothesis' states that energy partitioning among species is the most important factor limiting species richness (Wright, 1983). According to the predictions of this hypothesis, richness should be highly correlated with temperature, precipitation, and potential evapotranspiration because higher available energy can support more species (Fraser & Currie, 1996; Moser *et al.*, 2005).

The goal of our study is twofold. First, we use niche-modelling techniques along a large data set on Cerrado squamate (lizards, snakes, and amphisbaenians) occurrences to produce distribution maps for all Cerrado species. Then, we superimpose these maps to make a single map, depicting patterns of squamate species richness across the biome. After that, we analysed the richness map generated using multiple regression and spatial analysis techniques to determine which environmental-climatic variables exert a greater influence on species richness, and use model selection to evaluate which hypothesis best explains species richness gradients in the Brazilian Cerrado.

Second, we provide biological information to support conservation decisions. Using the richness map produced, we identify areas of high richness within the Cerrado. Although we used only squamate reptiles, previous works have shown that richness across large geographical scales is correlated among several different animal groups (Lamoreux *et al.*, 2006); thus, patterns that

emerge from this analysis can be extrapolated for other animal groups in Cerrado. This analysis will provide substantial data for further studies on identifying priority areas for conservation.

METHODS

Data collection

We collected locality data for squamate species occurring in the Cerrado from museums, literature, and fieldwork, and created a database with species names, localities, and geographical coordinates. The database consists of records from the major collections for Cerrado squamates: Coleção Herpetológica da Universidade de Brasília (CHUNB), Museu de Zoologia da Universidade de São Paulo (MZUSP), and Instituto Butantan (IB). When available, we used geographical coordinates from museum databases or published studies, and in other instances, we approximated point localities from locality descriptions using georeferencing techniques and gazetteers (NGA, 2005).

In the analysis, we used only those species that had at least one data point within the Cerrado biome. However, for species whose distributions spanned multiple biomes, we also included data points outside the Cerrado, because characteristics of these points can help identify suitable regions for species occurrence within Cerrado. At the time of the analysis the database showed a total of 237 species as occurring in the Cerrado (Appendix A).

Niche modelling

For each of the 237 species, we produced predicted distribution maps, using the software *DESKTOPGARP*[®]. This software uses the GARP algorithm (Genetic Algorithm for Rule-set Prediction), which includes several distinct algorithms in an iterative, artificial intelligence approach based on species presence data points (Stockwell & Peters, 1999). *DESKTOPGARP*[®] software generates each species' predicted distribution based on characteristics of environmental–climatic variables for localities in which a given species has been previously collected. We used a total of 22 variables (see Appendix S1 in Supplementary Material). Variables were downloaded from the Worldclim project (Hijmans *et al.*, 2005). Details, descriptions, and files for download are available free on-line at: <http://www.worldclim.org/>.

We used the following options while running the software: optimization parameters — 20 runs, 0.001 convergence limit, and 1000 maximum interactions; rule types — atomic, range, negated range, and logistic regression; best subset active, 5% omission error, 40% commission error, and 50% of points for training; omission measure = extrinsic, and omission threshold = hard; 10 models under hard omission threshold.

The output of *DESKTOPGARP*[®] consists of Arc/Info grid maps with 'zeros', where the species do not occur, and 'ones', where the species are predicted to occur. We used as the estimation of the distribution of each species, the area covered by the coincidence of at least seven out of the 10 models in the best subset selection (optimum models considering omission/commission relationships; Anderson *et al.*, 2003). This approach is called ensemble

forecasting and has been recently reviewed by Araujo & New (2007). By doing that and by setting the commission error to 40%, we believe we added a component of conservatism in the predictions of GARP that otherwise could extrapolate too much in the direction of areas too far from where the species have previously been collected. After producing such maps using the same criteria for all 237 species, we overlaid the distributions of all species into a composite map using the software *ARCGIS*[™]. This final map consisted of a grid where the value of each cell was the predicted number of species (species richness), calculated by summing the number of overlaid corresponding cells with positive occurrence results.

Multiple regression

We performed a multiple regression analysis to evaluate which environmental–climatic variables are the best predictors of squamate richness. We selected 300 random points in the Cerrado region using a filter option in the software *IDRISI KILIMANJARO* (Eastman, 2003). Values of richness (dependent variable) and environmental variables (independent variables) for the selected points were used to build a matrix. We did not use all environmental variables used to run GARP, because including many highly correlated variables in a multiple regression creates several theoretical and statistical problems, especially in the estimation of partial regression coefficients (Tabachnick & Fidell, 2000). We selected variables that were previously identified as influencing species richness patterns and were not highly correlated ($r < 0.9$) (Table 1, Appendix B). We added to the regression the variable net primary productivity downloaded from the Atlas of Biosphere website: <http://www.sage.wisc.edu/atlas>. This variable has been previously suggested to have influence in species richness (Table 1). We performed an exploratory analysis of the data matrix where we identified and eliminated univariate and multivariate outliers. The spatial distribution of points used in the analysis can be seen in Fig. 1.

Ecologists have long recognized that macroecological and biodiversity data show strong spatial patterns, which are driven by structured biological processes and therefore are usually spatially autocorrelated (Legendre, 1993; Diniz-Filho *et al.*, 2003). Spatial autocorrelation occurs when variable values at a certain distance apart are more (positive autocorrelation) or less similar (negative autocorrelation) than expected by chance (Legendre, 1993). Failure to account for spatial autocorrelation in multiple regression analysis results in inflation of type I error (Legendre, 1993; Diniz-Filho *et al.*, 2003). To alleviate this problem, we used spatial filters obtained by Principal Coordinates Neighbour Matrices (PCNM). This method partitions variation between spatial and environmental components, and works well at different spatial scales (Borcard & Legendre, 2002; Borcard *et al.*, 2004; Diniz-Filho & Bini, 2005). In the analysis, we treated the filters as candidate predictor variables, along with other environmental predictors. Using this approach, the effects of environmental predictors are evaluated as partial effects, taking space into account explicitly (Rangel *et al.*, 2006). We selected filters in an iterative process, by examining the pattern of spatial autocorrelation of regression

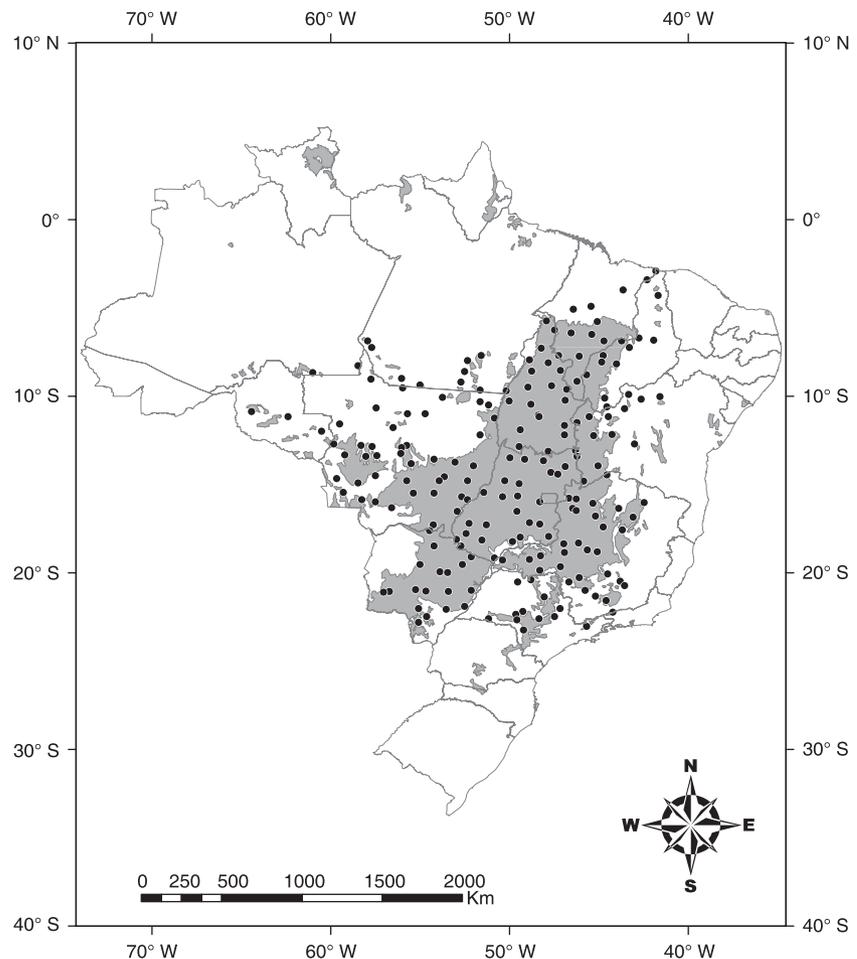


Figure 1 Spatial distribution within Cerrado of points used in the multiple regression analysis. The area in grey corresponds to the Cerrado limits and transition areas with other biomes.

residuals. Filters were selected to minimize both the autocorrelation among residuals and the number of filters used in regression. To investigate the presence of spatial autocorrelation, we used Moran's coefficient, the most commonly used statistic for autocorrelation analysis in macroecology and biogeography (Diniz-Filho *et al.*, 2003).

In addition, based on r^2 values for partial regressions made with filters alone, and environmental predictors alone, we divided the total variation explained by the model into: explained by space only, explained by the environmental variables only, and shared explained variance. All spatial analyses were performed in SAM — Spatial Analysis in Macroecology (Rangel *et al.*, 2006), which is freely available at: www.ecoevol.ufg.br/sam.

In order to determine which hypotheses best explained variation in species richness in the Cerrado squamates, we conducted separate regressions to fit each of the hypothesis presented in Table 1 (with the addition of two mixed models, one incorporating all variables related to each hypothesis, and other using only the variables pointed out as significant by the multiple regression). We used model selection based on the sample corrected Akaike Information Criteria (AICc). We used AIC because information-theoretic approaches are strongly recommended alternatives to traditional hypothesis testing. Particularly, AIC is more tolerant

to violations of the assumptions of parametric statistics that are commonly encountered in ecological data (e.g. normality), it is specially useful when comparing multiple working hypotheses, and does not rely solely on the use of random P -values for determining significance (Anderson *et al.*, 2000; Burnham & Anderson, 2004).

Finally, to compare the pattern predicted by niche modelling with the actual available data, we mapped species locality points and determined species richness for a Cerrado grid consisting of 100,000 ha cell size (Fig. 2). This approach allowed us to identify whether a spatial bias in sampling effort was present in the final modelling map (i.e. areas that have more species collected coincide with the areas the model pointed out as having higher richness).

RESULTS

The composite map summing all 237 species individual maps is shown in Fig. 3. In this map, areas with greater species richness are located mainly in the south-west portion of the Cerrado biome, in areas corresponding to the southern portion of Goiás state (GO), northern portion of Mato Grosso do Sul state (MS), and the very southern part of Mato Grosso state (MT). An interesting pattern is the presence of an area with high richness in

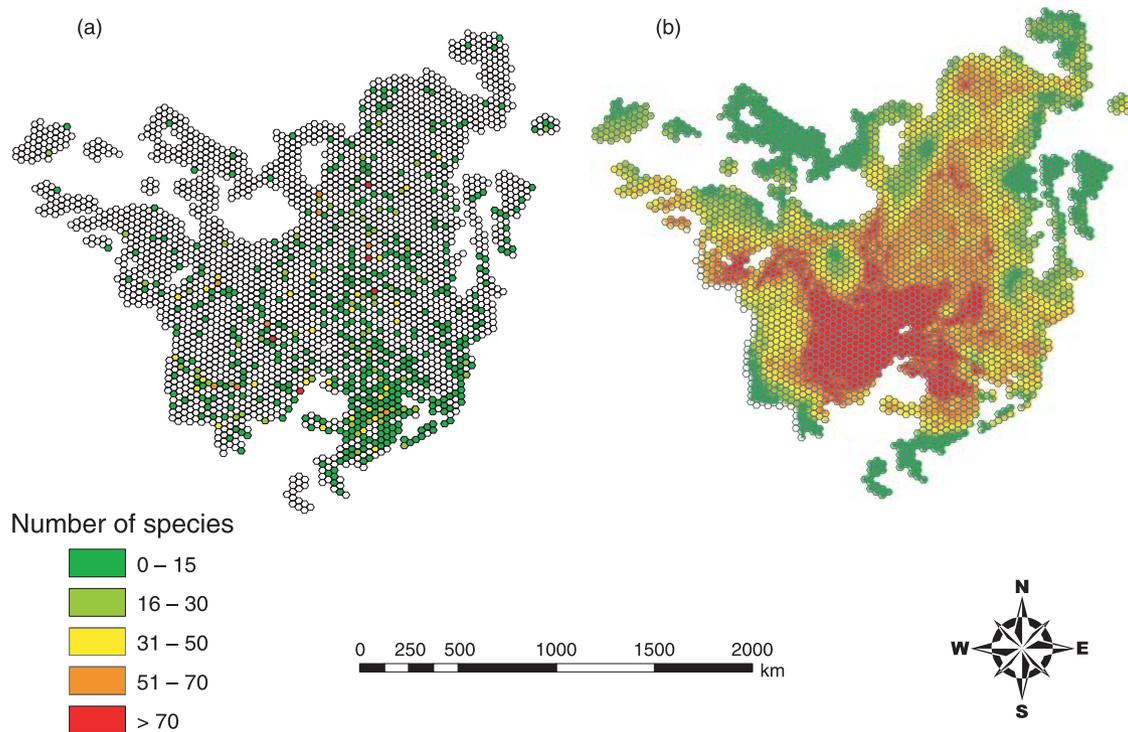


Figure 2 Number of species per unit area (cell) based on museum collections. The grid corresponds to the approximate area of the Cerrado biome. The area of each cell is 100,000 ha (a) Number of species based on the raw data. Blank cells have no specimen based on the major Cerrado collections; (b) Number of species based on the niche modelling of 237 species.

northern Cerrado, corresponding to the border between the states of Tocantins (TO) and Maranhão (MA). In addition, areas of high richness exist in the extreme west portion of Cerrado in Minas Gerais state (MG) and scattered areas in Mato Grosso and Rondônia (RO) states (Fig. 3).

Mapping of raw data shows a slight sampling bias towards the south-eastern portion of Cerrado, where the largest biological collections (MZUSP and IB) are located (Fig. 2a). However, the results of our modelling are not highly influenced by this bias, since areas with the greatest diversity in Cerrado do not overlap completely with this pattern. In addition, high richness areas were found by the modelling in regions where the sampling effort was extremely poor, such as the northern portion of Cerrado (Fig. 2b).

In the iterative process of filter selection for the multiple regression analysis, nine eigenvector spatial filters (PCNM) were sufficient to remove most spatial autocorrelation in regression residuals (Fig. 4). An examination of the spatial correlogram based on Moran's coefficient of the dependent variable (species richness) and regression residuals confirmed this pattern (Fig. 4). Addition of more filters did not significantly reduce autocorrelation in the residuals; therefore, we used only the best nine filters to minimize the number of independent variables.

The climatic–environmental and spatial filters (PCNM) multiple regression model explained 78% of the variation in Cerrado squamate richness ($r^2 = 0.78$; $F = 32.66$; $P < 0.01$). The partial regression approach revealed that the variance explained by space alone was 37%, the variance explained by the environmen-

Table 2 Partial regression coefficients of the multiple regression model (b), *t* statistics, and associated *P*-values for species richness of Brazilian Cerrado squamates regressed against environmental variables. Spatial structure was accounted for in the multiple regression by adding nine eigenvector filters produced with the method of Principal Coordinates of Neighbour Matrices (PCNM). Filters were omitted from table.

Variables	<i>b</i>	<i>t</i>	<i>P</i>
Annual precipitation	−0.04	−5.08	< 0.01
Precipitation seasonality	−1.23	−4.75	< 0.01
Altitude	0.03	3.28	< 0.01
Precipitation of driest quarter	−0.28	−2.93	< 0.01
Net primary productivity	23.6	2.52	0.01
Mean temperature of driest quarter	0.92	2.39	0.02
Temperature annual range	0.21	2.04	0.04
Precipitation of warmest quarter	0.02	1.87	0.06
Terrain declivity	0.11	1.32	0.20
Mean temperature of warmest quarter	−0.20	−0.45	0.65
Temperature seasonality	0.004	0.425	0.67

tal variables alone was 12%, and the shared explained variance was 28%.

Based on the analysis including both the climatic–environmental variables and the PCNM spatial filters, annual precipitation, precipitation seasonality, altitude, net primary productivity, and precipitation of the driest quarter were the best predictors of species richness (Table 2). Using spatial filters in this analysis

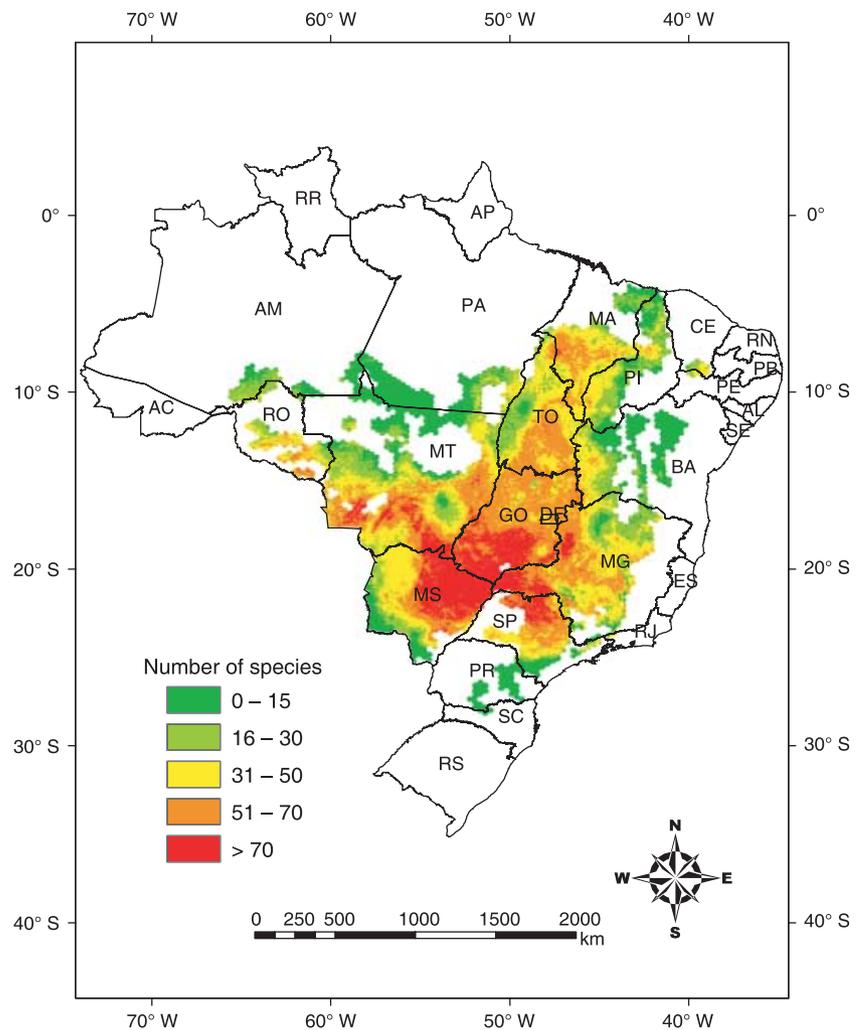


Figure 3 Raster grid of Cerrado squamate species richness based on the sum of 237 individual species maps.

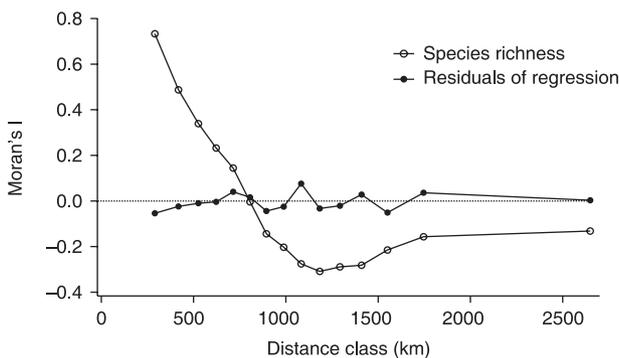


Figure 4 Moran's index correlogram for squamate species richness and the residuals of multiple regression with environmental predictors.

ensured that environmental variables were evaluated while taking into account spatial autocorrelation.

The model with the lowest AICc was the mixed model contained all variables related to several different hypotheses (Table 3). All other models had considerable less support (ΔAICc

Table 3 Summary of the model selection procedure. The model with the lowest corrected Akaike Information Criterion (AICc) value is the most parsimonious one among the fitted models and is selected (marked in bold). ΔAICc is the difference in AICc to the selected model. W_i is the Akaike weight and it indicates the relative support a given model has when compared with the other models. K is the number of parameters of the model (no. of variables + intercept).

Model	AICc	ΔAICc	K	W_i
Available energy	1290.74	65.56	3	0.00
Environmental favourableness	1301.10	75.92	3	0.00
Environmental heterogeneity	1289.53	64.35	3	0.00
Environmental stability	1256.76	31.58	3	0.00
Environmental stress	1293.06	67.88	3	0.00
*Mixed model	1225.18	0.00	12	1.00
†Only significant	1262.44	37.26	8	0.00

*All 11 variables used in the multiple regression.

†Only the significant variables ($P < 0.05$) from the multiple regression.

> 10 and low values of Akaike weight, see Burnham & Anderson (2004)). These results suggest that an interaction of factors related to the different hypotheses may be the best explanation for the variation on squamates species richness in the Cerrado.

DISCUSSION

Our results based on the multiple regression, and the model selection suggest that several mechanisms related to the different diversity hypothesis might work together to explain richness variation in the Cerrado. Annual precipitation was the most important climatic variable predicting Cerrado squamate richness supporting the species–energy hypothesis. Several studies on different organisms and at different geographical scales have found that species richness was correlated with available energy (Hawkins *et al.*, 2003; Currie *et al.*, 2004). Results of our study join the body of literature that corroborates the species–energy hypothesis.

The species–energy hypothesis posits that the amount of energy available and energy partitioning among species limit species richness (Wright, 1983). A mechanism explaining how diversity gradients are produced based on energy is lacking but several hypotheses exist (Clarke & Gaston, 2006). Exciting recent studies suggest that variation in temperature results in variation in DNA substitution rates and, may influence rates of evolution (Wright *et al.*, 2003; Allen & Gillooly, 2006; Allen *et al.*, 2006). Although this mechanism may be operating on a global scale, whether it is important at smaller geographical scales such as the Cerrado region remains undetermined.

The environmental stability hypothesis posits that physiological tolerances of species to variable environments may limit species richness leading to higher diversity in more stable environments (Pianka, 1966; Currie, 1991). Although the rationale behind the hypothesis seems reasonable, recent studies failed to support this hypothesis (Velho *et al.*, 2004; Mora & Robertson, 2005). We found supporting evidence for the environmental stability hypothesis in that precipitation seasonality was the second best climatic variable in predicting squamate richness. The Cerrado is a highly seasonal environment with two well-defined seasons, one dry and cold, and the other wet and warm. This seasonality may influence variation in species richness because some species may not be able to physiologically tolerate the harsh dry season, and/or areas with less severe conditions may be colonized by species that primarily occur in other biomes, such as the Amazon forest.

Altitude was important in predicting Cerrado squamate species richness. Correlations of species richness with altitude suggest that the environmental heterogeneity hypothesis, which posits that habitat differentiation and resource partitioning facilitate coexistence and enhance species richness (Richerson & Lum, 1980), may play a role in large-scale patterns of species richness. Relationships of species richness to topographical and environmental heterogeneity have been shown previously, especially at smaller spatial scales (Bohning-Gaese, 1997; Cleary *et al.*, 2005; Triantis *et al.*, 2005). In addition, some studies supporting the species–energy hypothesis have also found a significant effect of topography or landscape heterogeneity as in South American

birds (Diniz-Filho & Bini, 2005) and plants (Lavers & Field, 2006).

Altitude may have had an historical influence on the distribution and composition of Cerrado fauna and flora (da Silva, 1996; Meio *et al.*, 2003; Colli, 2005). In birds Amazonian elements are restricted to gallery forests at lower altitude, whereas Atlantic elements are found in higher altitudes (Silva, 1996). The same pattern is repeated for trees and shrubs species (Meio *et al.*, 2003). A crucial event responsible for current patterns of species distribution of Cerrado squamates was the uplift of the Central Brazilian Plateau in the Tertiary (Colli, 2005), again evidencing the importance of altitude and topography.

The above hypotheses are not mutually exclusive and, based on results of the model selection, which pointed out that the best model to explain species richness is a combination of the different hypothesis, we advance the idea that partitioning of energy among species, habitat differentiation, and tolerance to variable environments are the primary ecological factors determining variation in squamate richness across Cerrado. Other studies in the literature also suggested that a combination of different hypotheses may best explain species richness patterns (Bohning-Gaese, 1997; Hurlbert, 2004; Diniz-Filho & Bini, 2005). Additional studies that examine richness at different spatial scales are necessary, as well as studies that explore other factors known to affect species richness, such as historical factors (e.g. geographical barrier and/or effect of regional pool of species) and ecological interactions such as competition and predation. The Cerrado is a highly heterogeneous landscape, composed of a mosaic of edaphic conditions and different vegetation types, and it would be constructive to investigate how finer-scale environmental and landscape variables affect species richness. For instance, Nogueira *et al.* (2005) studied a lizard assemblage in the central Cerrado and found that richness is higher in the open landscape when compared with forested habitats.

Deforestation of Cerrado has accelerated during the past 20 years, and landcover has shifted greatly towards planted pastures and agriculture (Klink & Moreira, 2002; Klink & Machado, 2005). The central portion of Cerrado and areas of the southern portion of Goiás state (GO) and northern portion of Mato Grosso do Sul state (MS), all of which coincide with large patches of high squamate richness (Fig. 3), are of particular concern because these areas have been largely converted into pasture and agriculture (Silva *et al.*, 2006). Due to its fragmentation, maintenance and protection of current reserves, establishment of ecological corridors among existing reserves, and creation of new reserves, are urgently needed to ensure the conservation of squamate richness in these regions.

The northern portion of Cerrado also exhibited high richness of squamate species. Luckily, most of the remaining pristine native Cerrado areas are located in this region. Recent infrastructure development is changing this situation, and large portions of native vegetation are being replaced by soybean plantation. However, these areas remain poorly sampled (Fig. 2a). Lack of sampling is a major issue in the Neotropics and particularly in the Cerrado. Bini *et al.* (2006) modelled range distributions of Cerrado amphibian species based on habitat suitability and

number of inventories, and reached similar conclusions to this study regarding the importance for conservation of the northern areas of the Cerrado. Consequently, priorities for this region should begin with biological surveys, followed by the creation of new reserves where deemed necessary.

Overall, the level of deforestation and threats to Cerrado biodiversity are so alarming that any action towards conservation is important. Because both time and monetary resources are limited, decisions often must be based on available data. Thus it is crucial to maximize utility of these data. However, results of species niche modelling studies cannot be considered unequivocally true, and repeated verification based on fieldwork is necessary to ensure that proper decisions are being made. Biodiversity data, in the form of compilations of revised point-localities, are crucial for interpreting richness patterns and are highly informative to conservation. In addition, niche-based models cannot account for factors that may have limited species distributions historically, such as geographical barriers, resulting in speciation events. In Madagascar, niche models predicted occurrence of known species, but fieldwork revealed that closely related and ecologically similar undescribed species lived in the predicted areas (Raxworthy *et al.*, 2003).

To complement and add utility of the information provided by our study, additional studies on the geographical patterns of endemism in Cerrado species and the temporal and spatial pattern of deforestation are needed. Analysing patterns of species richness and endemism and correlating them with patterns of deforestation and human occupation can help define conservation strategies and minimize conflicts between development and conservation (Whittaker *et al.*, 2005; Diniz-Filho *et al.*, 2006). Our results are an initial step towards the development of a large comprehensive data set on richness, endemism, and patterns of deforestation that will provide the necessary information to support conservation decisions for the Cerrado.

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SUPPLEMENTARY MATERIAL

The following supplementary material is available for this article:

Appendix S1 List of variables used in the desktopGarp environmental data base.

This material is available as part of the online article from:

<http://www.blackwell-synergy.com/doi/abs/10.1111/j.1472-4642.2007.00369.x>

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Appendix A

List of the 237 species used in the analysis.

Ameiva ameiva, *Amphisbaena alba*, *A. anaemariae*, *A. camura*, *A. crisaie*, *A. fuliginosa*, *A. leeseri*, *A. mensae*, *A. mertensi*, *A. miringoera*, *A. neglecta*, *A. sanctaeritae*, *A. silvestrii*, *A. talisiae*, *A. vermicularis*, *Anilius scytale*, *Anisolepis grillii*, *Anolis chrysolepis*, *Anolis meridionalis*, *Anops bilabialatus*, *A. albicollaris*, *Apostolepis ammodytes*, *A. assimilis*, *A. cearensis*, *A. cerradoensis*, *A. cf. longicaudata*, *A. christineae*, *A. dimidiata*, *A. flavotorquata*, *A. goiasensis*, *A. intermedia*, *A. lineata*, *A. longicaudata*, *A. nigroterminata*, *A. sp.*, *A. polylepis*, *A. vittata*, *Atractus albuquerquei*, *A. latifrons*, *A. pantostictus*, *Bachia bresslaui*, *B. cacerensis*, *Boa constrictor*, *Boiruna maculata*, *Bothrops alternatus*, *B. itapetiningae*, *B. lutzii*, *B. mattogrossensis*, *B. moojeni*, *B. neuwiedi*, *B. pauloensis*, *Bothrops sp.*, *Briba brasiliana*, *Bromia bedai*, *B. kraoh*, *B. saxosa*, *Cercolophia roberti*, *C. steindachneri*, *Cercosaura albostrigatus*, *C. ocellata*, *C. parkeri*, *C. schreibersii*, *Chironius bicarinatus*, *C. exoletus*, *C. flavolineatus*, *C. laurenti*, *C. quadricarinatus*, *C. scurrulus*, *C. laeivcollis*, *C. multiventris*, *Clelia bicolor*, *C. clelia*, *C. plumbea*, *C. quimi*, *C. rustica*, *Cnemidophorus aff. parecis*, *C. mumbuca*, *C. gr. ocellifer*, *C. parecis*, *Coleodactylus brachystoma*, *C. meridionalis*, *Colobosaura modesta*, *Corallus hortulanus*, *Crotalus durissus*, *Dipsas indica*, *Dracaena paraguayensis*, *Drymarchon corais*, *Drymoluber brazilii*, *Taeniophallus occipitalis*, *Enyalius bilineatus*, *E. brasiliensis*, *E. catenatus*, *Epicrates cenchria*, *Erythrolamprus aesculapii*, *Eunectes murinus*, *E. notaeus*, *Gomesophis brasiliensis*, *Gonatodes humeralis*, *Gymnodactylus amarali*, *G. guttulatus*, *Helicops angulatus*, *H. gomesi*, *H. infrataeniatus*, *H. leopardinus*, *H. modestus*, *H. polylepis*, *H. trivittatus*, *Hemidactylus mabouya*, *Heterodactylus lundii*, *Hoplocercus spinosus*, *Hydrodynastes bicinctus*, *H. gigas*, *Iguana iguana*, *Imantodes cenchoa*, *Kentropyx aff. paulensis*, *K. calcarata*, *K. paulensis*, *K. vanzoi*, *K. viridistriga*, *Leposternon infraorbitale*, *L. microcephalum*, *L. polystegum*, *Leptodeira annulata*, *Leptophis ahaetulla*, *Leptotyphlops brasiliensis*, *L. dimidiatus*, *L. kopessi*, *Liophis almadensis*, *L. dilepis*, *L. frenatus*, *L. jaegeri*, *L. maryellenae*, *L. meridionalis*, *L. miliaris*, *L. paucidens*, *L. poecilogyrus*, *L. reginae*, *L. taeniogaster*, *L. typhlus*, *Liotyphlops beui*, *L. schubarti*, *L. ternetzii*, *Lygodactylus wetzeli*, *Lystrophis matogrossensis*, *L. nattereri*, *Mabuya dorsivittata*, *M. frenata*, *M. guaporicola*, *M. heathi*, *M. nigropunctata*, *Mastigodryas bifossatus*, *M. boddaerti*, *Micrablepharus atticolus*, *M. maximiliani*, *Micrurus brasiliensis*, *M. aff. ibiboboca*, *M. frontalis*, *M. lemmiscatus*, *M. spixii*, *M. surinamensis*, *M. tricolor*, *Ophiodes fragilis*, *O. 'striatus'*, *Ophiodes sp. 1*, *Ophiodes sp. 2*, *Oxybelis aeneus*, *O. fulgidus*, *Oxyrhopus guibei*, *O. petola*, *O. rhombifer*, *O. trigeminus*, *Phalotris concolor*, *P. labiomaculatus*, *P. lativittatus*, *P. mertensi*, *P. multipunctatus*, *P. nasutus*, *P. tricolor*, *Philodryas aestiva*, *P. livida*, *P. mattogrossensis*, *P. nattereri*, *P. olfersii*, *P. patagoniensis*, *P. psammophidea*, *P. viridissima*, *Phimophis guerini*, *P. iglesiasi*, *Phyllopezus pollicaris*, *Polychrus acutirostris*, *P. marmoratus*, *Pseudablabes agassizii*, *Pseudoboa coronata*, *P. neuwiedii*, *P. nigra*, *Pseudoeryx plicatilis*, *Pseustes sulphureus*, *Psomophis genimaculatus*, *P. joberti*, *Rhachidelus brazilii*, *Sibynomorphus mikanii*, *S. turgidus*, *S. ventrimaculatus*, *Simophis rhinostoma*, *S. leucocephalus*, *S. longicaudatus*, *S. worontzowi*, *Spilotes pullatus*, *Stenocercus quinarius*, *Stenocercus aff. tricristatus*, *Stenocercus caducus*, *S. dumerilii*, *Tantilla boipiranga*, *T. melanocephala*, *Teius teyou*, *Thamnodynastes chaquensis*, *T. hypoconia*, *T. rutilus*, *Tropidurus etheridgei*, *T. guarani*, *T. hispidus*, *T. insulanus*, *T. itambere*, *T. montanus*, *T. oreadicus*, *T. semitaeniatus*, *T. torquatus*, *Tupinambis duseni*, *T. merianae*, *T. quadrilineatus*, *T. teguixin*, *Typhlops brongersmianus*, *Vanzosaura rubricauda*, *Waglerophis merremii*, *Xenodon rhabdocephalus*, *X. severus*, *Xenopholis undulatus*.

Appendix B

Correlation matrix of the variables selected for the multiple regression analysis. The variables were selected in a way to minimize the correlation among each other and to relate to different hypothesis to explain patterns of species richness.

Variables	ALT	BIO4	BIO7	BIO9	BIO10	BIO12	BIO15	BIO17	BIO18	DECL	NPP
ALT	—	0.44**	0.18*	-0.72**	-0.84**	-0.28**	0.19**	-0.10	0.37**	0.21**	0.22**
BIO4		—	0.40**	-0.86**	-0.56**	-0.40**	-0.38**	0.57**	0.60**	0.11	0.29**
BIO7			—	-0.49**	-0.38**	0.08	-0.17*	0.14*	0.52**	0.01	0.30**
BIO9				—	0.89**	0.24**	0.25**	-0.41**	-0.71**	-0.15*	-0.48**
BIO10					—	0.07	0.05	-0.18*	-0.61**	-0.17*	-0.52**
BIO12						—	-0.28**	0.16*	0.23**	-0.18**	0.44**
BIO15							—	-0.90**	-0.37**	0.01	-0.28**
BIO17								—	0.43**	0.00	0.34**
BIO18									—	-0.09	0.55**
DECL										—	0.05
NPP											—

**Correlation is significant at the 0.01 level.

*Correlation is significant at the 0.05 level.