Spatial Patterns of Terrestrial Vertebrate Species Richness in the Brazilian Cerrado

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José Alexandre F. Diniz-Filho, Luis Mauricio Bini, Cleiber Marques Vieira, Daniel Blamires, Levi Carina Terribile, Rogério Pereira Bastos, Guilherme de Oliveira, and Bruno de Souza Barreto (2008) Spatial patterns of terrestrial vertebrate species richness in the Brazilian Cerrado. *Zoological Studies* **47**(2): 146-157. In this paper, we used a "deconstruction" approach to evaluate the spatial patterns of species richness of terrestrial vertebrates in the Brazilian Cerrado. Six environmental variables as well as the human population size and number of inventories were used as predictors of species richness (the last 2 to account for variable sampling efforts). Moran's *I* coefficients revealed strong spatial autocorrelations in ordinary least-squares multiple regression residuals, and thus spatial filtering by eigenfunction maps, based on a Gabriel network for the Cerrrado grid system, was used to evaluate the influence of richness predictors, thereby minimizing statistical problems caused by spatial autocorrelations. Models generated for the species richness of each group were compared and showed that spatial patterns of richness for all groups tended to be relatively well explained by climatic variations, in terms of the energy-water balance. Effects of productivity also appeared as a secondary effect for all groups but mammals. Richness patterns in amphibians and reptiles may have been biased by a lack of precise faunal knowledge, although they were not explained by the usual surrogates of the human population size and number of inventories. http://zoolstud.sinica.edu.tw/Journals/47.2/146.pdf

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Broad-scale patterns of species richness, especially the so-called latitudinal gradients, are some of the best-documented ecological patterns and have been described since the early days of biogeography and ecology in the 19th century (Hawkins 2001). Because of this long history of research, multiple hypotheses were developed during the last 200 yr to explain these geographical patterns (Whittaker et al. 2001, Willig et al. 2003). However, at broad continental scales, there is strong evidence that climatic patterns drive species richness (reviewed by Hawkins et al. 2003b), although it is not entirely clear how macroevolutionary components generate them (Currie et al. 2004, Hawkins et al. 2005). From local to regional scales, however, spatial variations in richness tend to become much more complex and sometimes erratic, and are probably driven by more-complex interactions of past and current ecological and evolutionary processes, as well

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as by other factors such as dispersal and biotic interactions (Brown and Lomolino 1998, Willis and Whittaker 2002).

The Cerrado is the 2nd largest biome of Brazil (the 1st is the Amazon rainforest), occupying about 1,500,000 km^2, and encompasses a great amount of environmental heterogeneity at both local and regional scales. In general, it is a typical tropical savanna environment, but it actually consists of a mosaic of different vegetation types, ranging from open grasslands to dense woodlands and dry forests. The pronounced seasonality (characterized by a dry season between May and Oct.) affects water availability and produces nutritional limitations, so several plants and animals have developed elaborate adaptive mechanisms. Such adaptive pulses and the existence of ecotonal areas to all the other major Brazilian biomes make the Cerrado the richest savanna ecosystem in the world (Ratter and Dargie 1992, Ratter et al. 1996, Oliveira-Filho and Ratter 2002, Silva et al. 2006). The Cerrado was recently classified as one of the global biodiversity hotspots, because of the elevated plant endemism and high rates of habitat loss and fragmentation due to a recent expansion of soybean cultures and cattle ranching starting in the 1940s (Myers et al. 2000, Klink and Moreira 2002, Klink and Machado 2005). Satellite-based estimates of habitat conversions in the Cerrado vary from 39% to 55% (Ferreira et al. 2003, Eva et al. 2004), and regardless of whether one accepts the more-pessimistic or -optimistic figures (which actually depend on the methodologies, geographic limits, and mapping scale and scope of the study), the conversion rate in the Cerrado is still very high and far from diminishing. This is very likely to drive many endemic and rare species to high threat levels or extinction (Myers et al. 2000, Brooks et al. 2002).

Despite its importance, an evaluation of explicit spatial patterns of species richness for most groups of organisms in the Cerrado is still lacking, and most diversity analyses are conducted at local scales (but see Costa et al. 2007). Most of the studies are concentrated in well-studied regions in the core of the biome, close to the 2 main urban centers (Brasilia and Goiânia), and in the southern border in São Paulo State (Oliveira and Marques 2002). At a broad spatial scale, a few regional classifications based on vegetation types (Ratter et al. 1996, Bridgewater et al. 2004, Silva et al. 2006) suggest strong spatial patterns in both alpha and beta diversities, but spatial patterns in terrestrial vertebrates have been poorly

investigated for most groups of organisms.

Understanding spatial patterns of species richness in the Cerrado is important not only because it will foster a better understanding of ecological and evolutionary processes driving species richness, but also because it will allow the establishment of better conservation planning strategies. Although optimum conservation strategies are usually based on complementary concepts and do not necessarily rely on richness (e.g., Diniz-Filho et al. 2006 2007), understanding patterns of species richness is crucial because they can indicate potential conservation conflicts (sensu Balmford et al. 2001) and also because under emergency strategies due to high rates of habitat loss, fewer opportunities may be available and richness-based approaches will be useful as well (Meir et al. 2004, see also Possingham et al. 2007). Thus, in this paper, we use Marquet et al.'s (2004) "deconstructive" approach to analyze spatial patterns of species richness in the Brazilian Cerrado, and evaluate how species richness levels of different groups of terrestrial vertebrates (mammals, birds, reptiles, and amphibians) are explained by different combinations of environmental predictors. Since these groups of species have different ecological and physiological characteristics associated with habitat use and respond differently to climatic variations, different patterns are expected, and consequently, their comparative analysis may be useful in revealing underlying ecological and evolutionary processes driving spatial variations in species richness.

MATERIALS AND METHODS

Data

Geographic distributions, measured as extents of occurrence (Gaston 2003) of a total of 1213 species of terrestrial vertebrates that breed in the Brazilian Cerrado, including 138 mammals, 751 birds, 193 reptiles, and 131 amphibians, were mapped with a spatial resolution of 1° grid cells, using a grid with 181 cells covering the Cerrado biome as a basis (Fig. 1). Grid cell size was chosen as a compromise between omission and commission errors when dealing with geographic distributions of species (Heikkinen et al. 2006, Rondinini et al. 2006, Luck 2007).

Basic lists from Marinho-Filho et al. (2002), Macedo (2002), and Colli et al. (2002) were updated, and range maps were constructed from

many sources from the primary and secondary literature (Table 1). For mammals and birds, general maps are usually drawn as complex irregular polygons, and newer primary references of sampling records were used in some instances to update those polygons. For reptiles and amphibians, we drew our own maps using minimum convex polygons to illustrate the extents of occurrence based on all available sampling records. Distribution modeling techniques (Araújo and Guisan 2006, Elith et al. 2006) were not applied here because of the relatively few occurrence records for each species and the coarse spatial resolution of our grid system (but see Costa et al. 2007). A binary matrix was constructed by recording the species whose geographic ranges overlapped each cell, and species richness was calculated by summing the species present in cells.

We used 6 environmental variables as predictors of Cerrado richness, which can be related to the main hypotheses developed to explain richness patterns based on the current environment. One or 2 variables could be associated with each hypothesis: (i) water-energy balance (annual actual evapotranspiration, AET), (ii) ambient energy (potential evapotranspiration, PET, and average annual temperature, TEMP); (iii) productivity (enhanced vegetation index, EVI), (iv) climatic variability (coefficient of variation of monthly temperature, CVAR), and (v) habitat heterogeneity (range in elevation, RELEV) (Hawkins et al. 2003b 2005, Rodríguez et al. 2005). The EVI has been used as a reliable surrogate for plant canopy density and greenness, total standing biomass, green leaf-area index, and percent vegetation cover (Ferreira et al. 2003, Ratana et al. 2005), and was obtained as monthly averaged composites for the years 2004-2005.

We also added the effects of the human population size (POP2000) and number of inventories (INV) to the models (Bini et al. 2006, Diniz-Filho et al. 2007). These predictors were included in the models because previous papers found significant correlations between these variables and richness, presumably as indicative of processes driving species richness, mainly related to high ecological productivity and occupation of more-suitable habitats, and also driving human populations under the "more-individuals" energy hypothesis (Balmford et al. 2001, Araújo 2003, Chown et al. 2003, Gaston and Evans 2004, Diniz-Filho et al. 2005, Evans and Gaston 2005). Also, human population size may be related to the degree of knowledge about biodiversity (Dennis and Hardy 1999, Balmford et al. 2001, Bini et al. 2006), and in this case, we also used a more-explicit variable about the number of inventories carried out in each cell. Human population data were obtained from the official
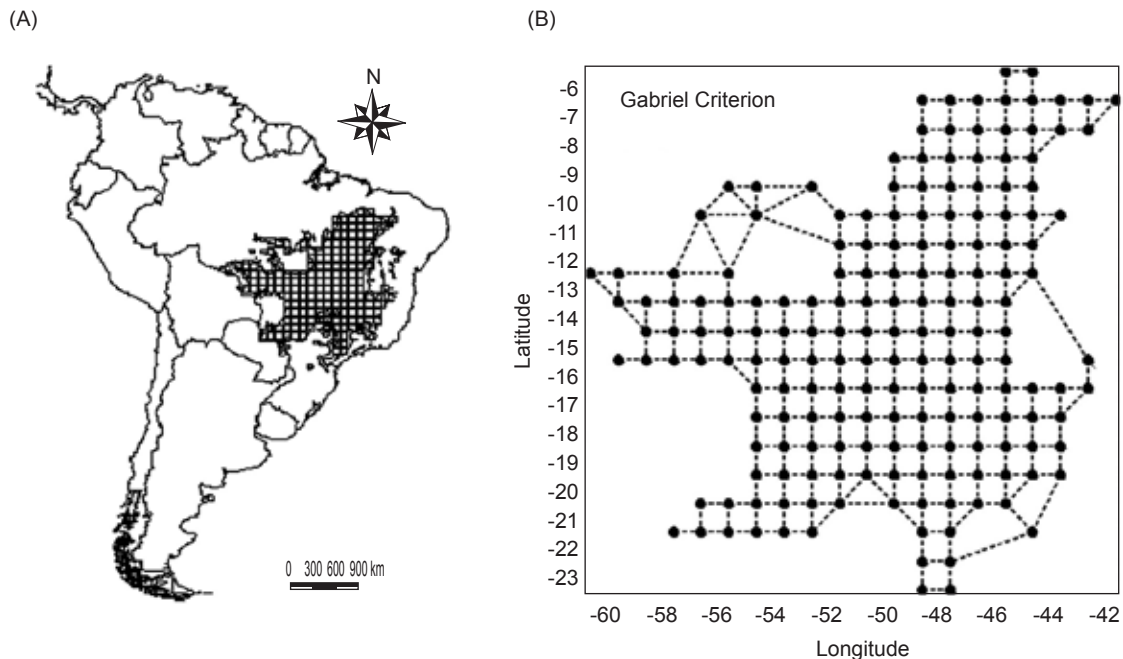

Fig. 1. (A) Distribution of 181 cells used to analyze spatial richness variations of terrestrial vertebrates in the Cerrado biome, and (B) a Gabriel network linking cell centroids.

census of the Brazilian population for the year 2000, by the Brazilian Agency of Geography and Statistics (IBGE 2000). For the 181 cells covering the Cerrado biome, the human population was obtained by summing urban and rural populations from 1054 municipalities whose geopolitical limits are within the Cerrado's borders, and data were log-transformed prior to the analysis to normalize the distribution. The number of faunal inventories in each cell was derived from maps provided by a

Table 1. Terrestrial vertebrates from Brazilian Cerrado used in the richness analyses, with the number of species per family and main sources used to generate the range maps

Class	Family (number of species)	Main sources*
Mammalia	Didelphidae (29), Bradypodidae (1), Myrmecophagidae (3), Dasypodidae (11), Callithrichidae (7), Cebidae (9), Canidae (4), Felidae (7), Mustelidae (6), Procyonidae (3), Tapiridae (1), Tayassuidae (2), Cervidae (5), Leporidae (1), Muridae (29), Erethizontidae (2), Echymyidae (8), Agoutidae (1), Hydrochaeridae (1), Caviidae (3), Ctenomyidae (1), Dasyproctidae (2), Sciuridae (2)	Marinho-Filho et al. (2002), Eisenberg and Redford (1999), Emons (1990), Fonseca et al. (1996), Wilson and Reeder (1993)
Aves	Rheidae (1), Tinamidae (16), Podicipedidae (2), Phalacrocoracidae (1), Anhingidae (1), Ardeidae (16), Ciconiidae (3), Threskiornithidae (6), Anhimidae (2), Anatidae (9), Cathartidae (4), Accipitridae (29), Falconidae (12), Cracidae (10), Aramidae (1), Rallidae (11), Heliornithidae (1), Eurypigidae (1), Cariamidae (1), Jacanidae (1), Recurvirostridae (1), Charadriidae (3), Scolopacidae (2), Laridae (3), Columbidae (18), Psittacidae (32), Opisthocomidae (1), Cuculidae (13), Tytonidae (1), Strigidae (14), Nyctibiidae (3), Caprimulgidae (13), Apodidae (5), Trochilidae (36), Trogonidae (8), Alcedinidae (5), Momotidae (3), Galbulidae (5), Bucconidae (13), Capitonidae (1), Ramphastidae (10), Picidae (24), Dendrocolaptidae (23), Furnariidae (41), Formicariidae (57), Conopophagidae (1), Rhynocryptidae (2), Tyrannidae (109), Pipridae (17), Cotingidae (6), Hirundinidae (8), Motacilidae (2), Troglotidae (9), Mimidae (2), Muscicapidae (7), Emberizidae (87), Parulidae (10), Vireonidae (7), Icteridae (16), Fringillidae (1), Corvidae (4)	Ridgely and Tudor (1989 1994), del Hoyo et al. (1992 1994 1996 1997 1999 2001 2002), Junniper and Parr (1998), Isler and Isler (1999)
Reptilia	Pelomedusidae (2), Amphisbaenidae (14), Hoplocercidae (1), Iguanidae (1), Polychrotidae (4), Tropiduridae (8), Gekkonidae (8), Teiidae (11), Gymnophthalmidae (14), Anguidae (1), Anomalepididae (2), Leptotyphlopidae (2), Typhlopidae (1), Aniliidae (1), Boidae (5), Colubridae (94), Elapidae (9), Viperidae (15)	Campbell and Lamar (1999), Colli et al. (2002), Nogueira (2001), Valdujo and Nogueira (2001), Vanzolini (1997 2002)
Amphibia	Bufonidae (8), Dendrobatidae (4), Hylidae (63), Leptodactylidae (49), Microhylidae (6), Ranidae (1)	Frost (1985), Colli et al. (2002)

*Additional references and records came from primary literature, scientific journals, and scientific collections, including reviews on *Thomson ISI Web of Science* (http://portal.isiknowledge.com), *Brazilian Journal of Zoology* (http://www.scielo.org), *Brazilian Journal of Biology* (http://www.scielo.org), and *Herpetologica Review*, and websites containing information on biodiversity, such as websites of the Brazilian Society of Herpetology (http://www2.sbherpetologia.org.br), The EMBL Reptile Database (http://www.embl-heidelberg.de/~uetz/LivingReptiles.html), Lifemapper (http://lifemapper.org), Species Analyst (http://speciesanalyst.net/index.html), Global Biodiversity Information Facility (http://www.gbif.org), IUCN (http://redlist.org), and Species Link (http://splink.cria.org.br/).

workshop on conservation priorities in the Cerrado and Pantanal, and we assumed that the number of inventories per cell represents a surrogate for biodiversity knowledge in the region (Cavalcanti and Joly 2002, Bini et al. 2006).

Analysis

We first described spatial patterns of species richness using spatial correlograms of Moran's *I* coefficients calculated at 10 geographic distance classes (Legendre and Legendre 1998, Diniz-Filho et al. 2003). We then performed a standard ordinary least-squares (OLS) multiple regression of richness against environmental predictors and the human population, and calculated correlation coefficients among richness patterns. However, since significant spatial structures were detected in model residuals using Moran's *I* correlograms, type I errors of regression parameters were biased

due to an inflation in the degrees of freedom (Legendre et al. 2002, Diniz-Filho et al. 2003), so that OLS regression models are not fully adequate for statistical purposes (but mainly for significance tests; Hawkins et al. 2007a).

We tested correlation coefficients by reducing the degrees of freedom using Duttileul's (1993) correction, based on the spatial correlograms. Many methods are currently available to take into account spatial autocorrelation problems in regression models (Diniz-Filho et al. 2003, Rangel et al. 2006). In this paper, we used a relatively new method of spatial analysis, called spatial filtering by eigenfunction mapping (Borcard and Legendre 2002, Griffith 2003, Borcard et al. 2004, Diniz-Filho and Bini 2005, Griffith and Peres-Neto 2006). More specifically, we used Griffith's (2003) method of topology-based spatial filtering, or spatial eigenvector mapping (SEVM), which extracts eigenfunctions of a binary (0/1) matrix constructed
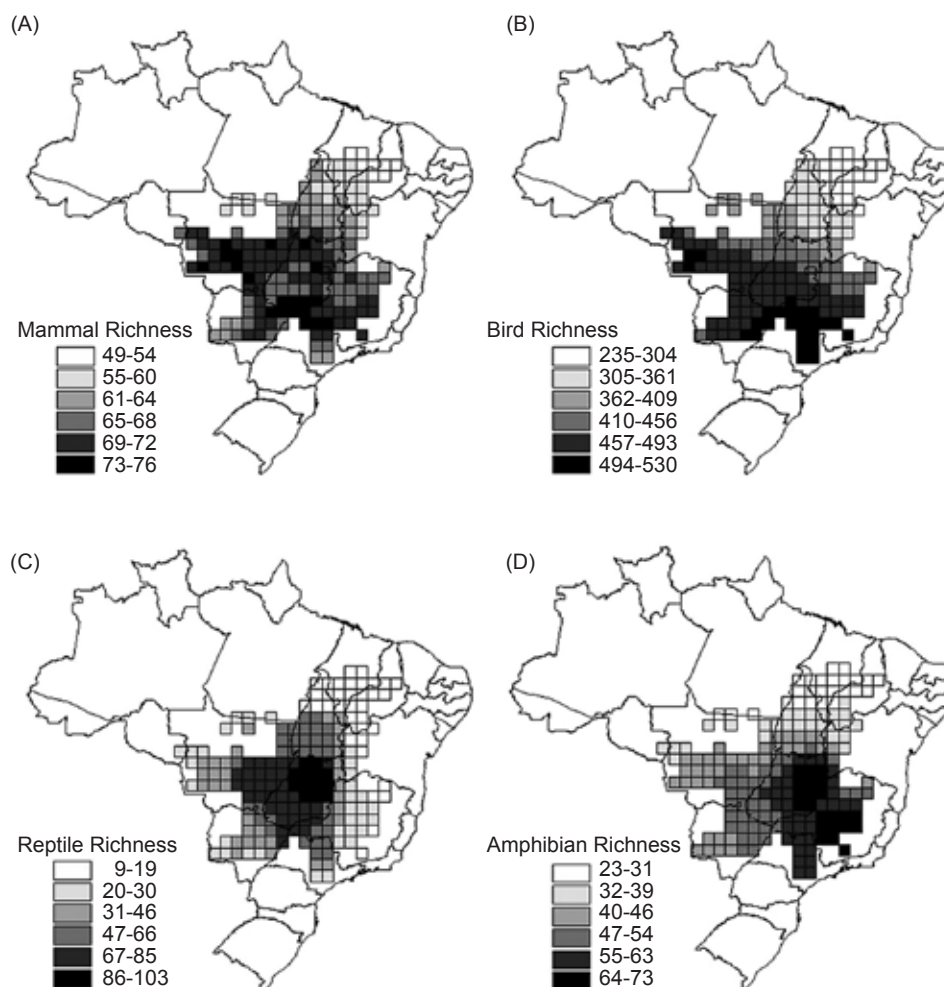

Fig. 2. Patterns of richness for mammals (A), birds (B), reptiles (C), and amphibians (D) in the Brazilian Cerrado.

based on a network linking the centroids of cells (see Dormann et al. 2007).

With SEVM, a Gabriel network (Fig. 1B) was used to link the centroids of cells covering the Brazilian Cerrado, and the spatial relationships among these cells were used to obtain a binary (0/1) connectivity matrix, **C**, in which 1 indicates that 2 cells are adjacent (i.e., are linked through their edges in the Gabriel network). In a Gabriel network, 2 centroids are considered to be linked (1) if the circle whose diameter is the distance between them does not encompass any other centroid (Fig. 1B) (Gabriel and Sokal 1969, Legendre and Legendre 1998). The eigenvectors associated with positive eigenvalues of the double-centered binary matrix **C** were extracted to describe relationships among cells covering the Cerrado at different spatial scales. These eigenvectors are new orthogonal variables (called spatial filters or eigenvector maps; Griffith 2003, Griffith and Peres-Neto 2006) that capture, at different scales, the geometry of the grid system covering the Cerrado, and they can be incorporated into a standard OLS multiple regression model in different ways. The 1st eigenvectors represent broad-scale variations, whereas eigenvectors derived from small eigenvalues represent fine-scale variations.

An important step in the SEVM protocol is selecting eigenvectors that should be retained and further used in the modeling process. In this paper, we extracted eigenvectors with Moran's *I* coefficients in the 1st distance class of > 0.1 (Griffith 2003, Diniz-Filho and Bini 2005) and then successively added these eigenvectors to the OLS model together with the other predictors until the residual spatial autocorrelation disappeared. Our final model for species richness was then obtained by combining these selected spatial filters with the environmental predictors, human population, and number of inventories.

All statistical analyses were performed in the Spatial Analysis in Macroecology (SAM) software, vers. 2.0, which is freely available at www.ecoevol.ufg.br/sam (Rangel et al. 2006).

RESULTS

Patterns of species richness in the Cerrado (Fig. 2) differed for mammals, birds, reptiles, and amphibians. Mammals and birds had quite-similar spatial patterns of richness ($r = 0.858$, $p < 0.01$ according to Duttileul's test), with more species concentrated in the southern and southwestern regions of the biome, although richness in mammals was less continuous than in birds, probably due to more-restricted ranges in the southern and western regions. On the other hand, amphibians and especially reptiles also showed some north-south gradients, but the main pattern was a peak in the middle of the biome.

These patterns were confirmed by the spatial correlograms, which showed long-distance clines for mammals and birds, characterized by positive Moran's *I* autocorrelation coefficients for the 1st distance coupled with negative long-distance Moran's *I* values (Figs. 3A, B). For reptiles and amphibians, on the other hand, a stabilization pattern in the correlograms was observed, since long-distance Moran's *I* values tended to be lower (Figs. 3C, D).

OLS residuals usually contained significant spatial autocorrelations (Table 2, Fig. 3) for all groups. Thus, a set of the 1st 25 spatial filters was added to the OLS regression together with the 6 environmental variables and human population size and number of inventories to predict patterns of species richness without biases in the significance tests generated by the latent autocorrelation structures.

The overall explanatory power of these full models was generally very high ($R^2 > 0.95$), indicating that most of the variations in species richness could be explained by the combined effects of geographical structure and environmental predictors. However, the effects of the predictors alone were much lower (when considering the R^2 of the original OLS models, Table 2), especially for reptiles.

Also, in all cases, Moran's *I* values in the 1st distance class for model residuals were usually < 0.10, and much lower than values based on the OLS regressions, in which spatial structures still appeared, and values of Moran's *I* in the 1st distance class were consistently > 0.5 (Fig. 3). This revealed that using SEVM was effective in taking into account most of the spatial autocorrelation structure in the regression residuals, and that the statistical significance of the regression coefficients could be established without problems.

For all groups, the partial regression coefficients of the AET were significant ($p < 0.05$). For mammals, an additional slightly significant effect of the RELEV was observed, whereas for birds a positive partial coefficient for the TEMP was observed. On the other hand, the effects of environmental predictors were not so clear for

reptile and amphibian richness. For amphibians, negative and significant partial regression coefficients were detected for the TEMP, whereas for reptiles a significant effect of the EVI appeared. The POP2000 and INV presented no significant effects on the spatial patterns investigated (Table 2).

DISCUSSION

Mammals and birds tended to show north-south (and to a minor extent, east-west) richness gradients, whereas reptiles and amphibians showed a concentration of richer regions in the central portion of the biome. Environmental predictors of patterns of species richness of terrestrial vertebrates were generally within the expectations for this spatial domain and scale (Hawkins et al. 2003a b). In general, richness patterns were clearly associated with the AET, reinforcing the idea that, at broad-spatial scales, richness is driven by water-energy dynamics (Hawkins et al. 2003a b, O'Brien 2006).

Patterns of mammals and birds were more similar, as found elsewhere (e.g., Grenyer et al. 2006), both in terms of mapping richness patterns (and observing the associated spatial correlograms) and of the relative magnitudes of the regression predictors. Richness patterns for these groups followed the overall pattern of South American endothermic organisms, in which the AET is the most important predictor, although the overall explanatory power of this variable can vary (Hawkins et al. 2003b, Mathias et al. 2004, Diniz-Filho and Bini 2005, but see also Jetz and Rahbek 2001). For birds, a more-complex set of explanations may be required, and this may be at least in part a consequence of combining a very large number of heterogeneous species with different ecological requirements. Blamires et al. (2008) recently used a similar deconstructive approach and showed that the habitat category (forest-dependence) affected spatial patterns of richness and, consequently, the predictors associated with these patterns.

A significant and negative effect of temperature also appeared for amphibians. Thus, after taking into account the AET (i.e., assuming that this is a more-general predictor, which acts at a higher spatial hierarchical level), more species were found in colder and drier areas. Indeed,

Table 2. Standardized partial coefficients of a multiple regression model including 8 predictors and 25 spatial filters (partial coefficients not shown) of SEVM to model spatial patterns of richness of mammals, birds, reptiles, and anurans in the Brazilian Cerrado. Spatial filters were eigenfunction maps based on a binary matrix derived from a Gabriel network linking the centroids of cells covering the Brazilian Cerrado. Coefficients of determination (R^2) for the original ordinary least-squares model and after adding the eigenvector-based spatial filters are also shown

Predictors	Mammals	Birds	Reptiles	Amphibians
AET	0.321**	0.289**	0.125*	0.079*
PET	-0.084	-0.119*	-0.074	0.036
EVI	-0.076	-0.044	-0.099*	-0.108
TEMP	-0.045	0.377**	0.064	-0.373**
CVAR	-0.039	0.003	0.016	0.023
RELEV	0.146*	-0.010	0.075	0.026
POP2000	0.031	0.018	0.014	0.037
INV	-0.049	-0.016	0.046	-0.031
R^2 (OLS + filters)	0.837	0.960	0.914	0.948
R^2 (OLS)	0.583	0.803	0.376	0.756

* $p < 0.05$; ** $p < 0.01$. AET, annual actual evapotranspiration; PET, potential evapotranspiration; EVI, enhanced vegetation index; TEMP, average annual temperature; CVAR, coefficient of variation of monthly temperatures; RELEV, range in elevation; POP2000, human population size; INV, number of inventories.

this negative effect of temperature was the most important predictor.

For reptiles and amphibians, different spatial patterns were found, in relation to the effects of temperature (and a minor effect of the AET for amphibians, perhaps because of the water requirements of this group; Rodríguez et al. 2005). However, opposite to what was recently hypothesized by the metabolic theory of ecology (Allen et al. 2002 2006, Brown et al. 2004), the negative coefficients imply that high species richness is found in colder places in the southern part of the biome. This idiosyncratic response of richness to temperature was discussed for a large number of different taxonomic groups by Hawkins et al. (2007a). Indeed, Cassemiro et al. (2007) recently showed a spatially structured variation in the response of New World amphibian richness to

temperature. When analyzing patterns in tropical regions, non-significant or negative relationships appear, whereas in temperate regions north to the US and Canada the expected values under metabolic theory are found.

For reptiles, it is clear that a peak of richness existed in the center of the biome, as recently found by Costa et al. (2007) using more-refined data and distribution models with GARP (Elith et al. 2006). Those authors explained the patterns by a simultaneous effect of habitat heterogeneity, available energy, and productivity, although the effects of sampling and human knowledge could not be discarded. Here reptile richness patterns were better explained by productivity and water-balance hypotheses, but with relatively low coefficients for the AET and EVI and much lower coefficients of determination (for the original OLS
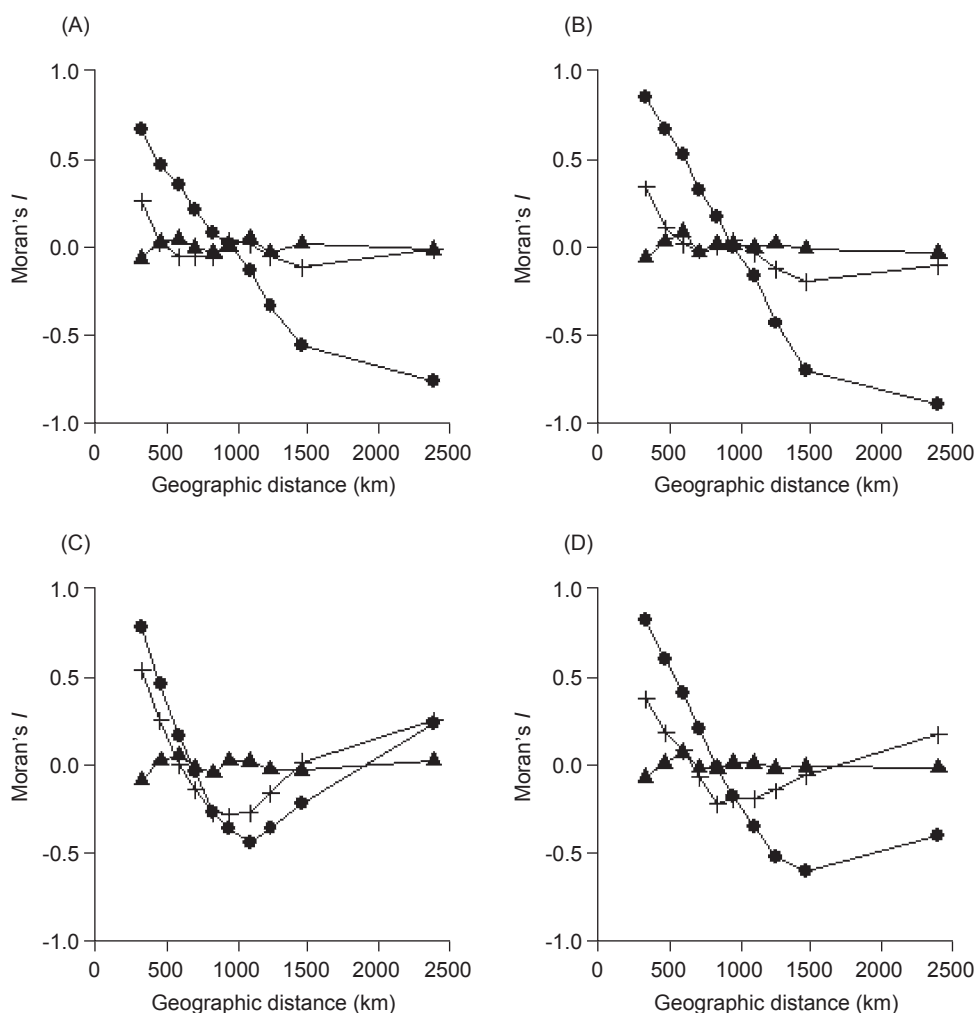

Fig. 3. Spatial correlograms of species richness in the Brazilian Cerrado, established for 10 geographic distance classes, based on original data (circles), ordinary least-squares residuals (crosses), and eigenvector filtering residuals (triangles), for mammals (A), birds (B), reptiles (C), and amphibians (D).

regression) than observed in the other groups, indicating that environmental effects were not as strong here. Also, it was not clear if the energy hypothesis was more important for reptiles than for amphibians, as expected by their thermoregulatory characteristics (Rodríguez et al. 2005). This may have been due to the idiosyncratic effects of temperature, in respect to other effects, in the tropics, as recently discussed by Hawkins et al. (2007a).

However, it is important to note that there may be an indirect effect of human colonization on species discoveries, especially for explaining patterns in amphibian and reptilian richness (Diniz-Filho et al. 2005). The lack of a clear relationship between climatic variations and variations in richness of amphibians and reptiles may have been due to the effect of the uneven distribution of biodiversity knowledge (i.e., sampling bias). However, the surrogate variables included in the models here to take this into account were not significant, although POP2000 was significantly correlated with amphibian richness ($r = 0.471$, $p = 0.047$ with Duttileul's correction) (i.e., without adding the other predictors).

Part of the difficulty in detecting these effects may be due to colinearity between ecological variations in the Cerrado (mainly forming north-south gradients) and human occupation in the biome. There is a north-south gradient in human occupation in the Cerrado, due to recent historical patterns of colonization and current patterns of development. Colonization of the region began mainly at the end of the 19th century and accelerated only after the latter half of the 20th century, with the construction of Brasilia (the current capital of the country, in the core of the biome; Klink and Moreira 2002). At the same time, agricultural and cattle ranch expansions began in the southern and southeastern regions of the country, gradually moving and occupying the Cerrado in north-south and east-west gradients (Klink and Moreira 2002). Indeed, Diniz-Filho et al. (2005) recently showed a positive correlation between average anuran description dates and the human population in Cerrado, probably more closely reflecting an indirect effect of knowledge (i.e., rates of species description) than a direct link due to more available energy (Balmford et al. 2001). Bini et al. (2006) used these macroecological patterns and showed a potential northward shift in the optimum reserve system in Cerrado if unknown hypothetical species were to be added to the system as conservation targets.

Current habitat loss and local extinctions are concentrated in the southern regions of Cerrado, and although probably strong enough to generate the observed patterns (Brooks et al. 2002), they would not be a plausible explanation in this case because our data were based on overall, broad-scale data, probably reflecting more-historical potential ranges of the species and not current real distributions (but see LaSorte 2006). Because the way geographic ranges were defined here, human effects would probably be more closely associated with knowledge effects because of undescribed endemic species in the northern part of the biome than because of the range and habitat losses in the more densely occupied southern and southeastern regions of the Cerrado.

However, it is important to note that, as expected, the explanatory power of the environmental predictors was much lower than previous analyses at continental scales, suggesting that more-complex combinations of historical and current factors are driving species richness (Hawkins et al. 2003b, Rangel and Diniz-Filho 2005). Evolutionary dynamics of these processes cannot easily be defined at the scale of the Cerrado biome, since it involves biogeographic phenomena at larger spatial and temporal hierarchical scales, as reflected in the low endemism of Cerrado vertebrates (Myers et al. 2000). Thus, a full evaluation of patterns of Cerrado richness requires, beyond measuring current ecological and climatic effects, an understanding of the broad-scale dynamics of vegetation types during the late Pleistocene and connections between the Atlantic and Amazon rainforests (Redford and Fonseca 1986, Silva 1995a b 1996 1997, Silva and Bates 2002). Despite these more-complex evolutionary processes underlying richness patterns at the biome scale, different groups of species have different requirements in terms of habitat use and response to climate, and differences in their spatial patterns may help elucidate general processes driving variations in species richness. Using the "deconstructive" approach suggested by Marquet et al. (2004), analyzing spatial patterns in mammals, birds, reptiles, and amphibians may be, as discussed above, very informative in improving our understanding of richness patterns.

Our deconstructive analysis revealed that vertebrate groups showed different spatial patterns in species richness in the Brazilian Cerrado and, consequently, may be explained by different sets of predictors. Patterns of mammals and birds tended to be relatively well explained by climatic variations,

in terms of the energy-water balance, whereas those for amphibians and reptiles may be more closely associated with current faunal knowledge. Further investigations on these issues are still required, but surely this is a 1st step towards a broad comprehension of richness patterns and their environmental drivers. Deconstruction, as shown here, may be an important component of this understanding.

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