

Environmental correlates of anuran beta diversity in the Brazilian Cerrado

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Evolutionary processes are known to influence contemporary patterns of biological diversity, yet disentangling the effects of current and historical drivers of biodiversity patterns remain challenging. We use spatial analyses of community dissimilarity to generate hypotheses about the current and historical processes underlying patterns of beta diversity in anuran species in the Brazilian Cerrado. Specifically, we use a generalized dissimilarity modeling (GDM) approach to model compositional dissimilarity of anuran species and endemics as a function of geographic separation and local (within-Cerrado) environmental conditions. To gain insight about potential historical processes, we incorporate information from biomes adjacent to the Cerrado to investigate whether environmental conditions in neighboring areas can help explain patterns of beta diversity within the Cerrado. Patterns of anuran beta diversity of both endemics and all species in the Cerrado appear to be strongly influenced by local environmental gradients, with elevation as one of the most important variables in all models. However, in models using endemic species only, environmental conditions of adjacent biomes were related to beta-diversity patterns, and more strongly so, than to total species models. These results suggest that phylogenetic niche conservatism within species groups that invaded the Cerrado from adjacent biomes may cause these species to be restricted to environmental conditions within the Cerrado that are most similar to the conditions in the adjacent biome where they originated. Time-calibrated phylogenies of Cerrado endemics and studies of ancestral and current ranges of Cerrado species are needed to test this hypothesis.

Studies of beta diversity, the dissimilarity in species composition across sites (Whittaker 1960), can reveal evolutionary and ecological processes underlying patterns of species richness and distribution. Recent research programs have addressed how species dissimilarity is influenced by the interplay between physiological requirements of species and environmental conditions such as climate (Azeria et al. 2009, Overton et al. 2009, Ashcroft et al. 2010), topography (Jankowski et al. 2009, Qian 2009), and microhabitat availability (Ellwood et al. 2009, Vasconcelos et al. 2009). Patterns of beta diversity can also be influenced by processes acting at broader spatial and temporal scales (Wiens and Donoghue 2004, Ricklefs 2006), a topic not fully explored to date. Building on recent advances in beta diversity studies afforded by generalized dissimilarity modeling (GDM, Ferrier et al. 2007), we explore how the consideration of environmental conditions in areas adjacent to a target region (i.e. the regional environmental conditions) can be used to further our understanding of historical biogeographic processes and their impacts on patterns of dissimilarity within a region of interest.

Regional environmental conditions and the biogeographic history of the regional species pool are expected to play a crucial role in beta diversity patterns, especially along large-scale environmental gradients (Wiens and Donoghue 2004, Kraft et al. 2011). Due to common ancestry, related species are more likely to have similar environmental requirements (Brooks and McLennan 1991). If eco-physiological requirements are phylogenetically determined and constrain taxa to a portion of an environmental gradient, then niche conservatism can influence patterns of community dissimilarity (Wiens and Graham 2005, Wiens et al. 2010). When this is true, a historical imprint on within-region beta diversity patterns will be evident, not only in recently dispersed species, but also in ancient endemic species that are closely related to lineages present in neighboring regions. If physiological and life history constraints are phylogenetically conserved, the interplay between the biogeographic history of the regional species pool and the environmental conditions within a study region will ultimately define and limit ranges of local species, and hence species assemblages.

Generalized dissimilarity modeling was developed to model species compositional dissimilarity as a function of local environmental conditions and geographical separation; this is achieved by maximizing the correlation between environmental and biological dissimilarities (Ferrier et al. 2007). The resulting function can be used to subdivide a large study area into a pre-defined number of homogeneous landscapes (Ferrier et al. 2002). GDM has been increasingly applied in conservation-related studies to direct future sampling efforts and improve survey efficiency (Ashcroft et al. 2010), or to assess the representativeness of reserve networks (Overton et al. 2009, Thomassen et al. 2010). It also has been applied to model intra-specific phenotypic and genetic variation as a function of environmental gradients, distance, and geographic barriers, in order to evaluate the evolutionary processes underlying generation and maintenance of biodiversity (Thomassen et al. 2010, 2011). These recent studies demonstrate that GDM may be useful in both applied conservation and evolutionary frameworks. Here we extend to use of GDM to evaluate how local and regional environmental descriptors influence compositional change of the anurofauna of the complex and biodiverse Brazilian Cerrado.

The anurofauna of the Brazilian Cerrado represents an ideal system to evaluate the influence of local environmental gradients and regional imprints on beta diversity. Distributed in central Brazil, the Cerrado is a savanna phytogeographical domain adjacent to two South American forest domains (Amazon and the Atlantic Forest) and three open vegetation domains (Caatinga, Pantanal and Chaco) through wide ecotones that favor biological interchange. More than 200 amphibian species are known to be distributed in the Cerrado, half of which are endemic (Valdujo et al. 2012). Amphibian distribution within the Cerrado is strongly influenced by contemporary climatic conditions (Eterovick and Fernandes 2002, Diniz-Filho et al. 2008), and hence environmental gradients are expected to influence species distribution and compositional dissimilarity. Not surprisingly, however, assemblages within the Cerrado are structured as a mosaic, combining species from multiple adjoining regional species pools, as evidenced by the distribution patterns of woody plants (Oliveira-Filho and Ratter 1995, Klink and Machado 2005), birds (Silva 1996), mammals (Costa 2003), squamate reptiles (Nogueira et al. 2011) and amphibians (Valdujo et al. 2012). Moreover, the open interfluvial habitats within the Cerrado, especially the headwaters, may act as barriers to dispersal and preserve signatures of the regional biogeographical history (Silva 1996, Valdujo et al. 2012). Existing phylogenetic data, albeit limited, suggest that the sister-groups of several Cerrado endemic anurans occupy adjoining biomes (Faivovich et al. 2005, Hedges et al. 2008), making this system ideal to investigate whether descriptors of the environmental conditions experienced by neighboring areas, which may be ancestral to many Cerrado groups, provide useful insight about in current beta diversity patterns within the Cerrado.

To shed light on this issue, we use the following framework. First, we compare whether and how environmental gradients within the Cerrado are correlated with dissimilarity in anuran endemic and total species composition. Then, we expand the geographical extent of our analysis to neighboring biomes, where several sister-taxa of Cerrado endemic amphibians are distributed (Faivovich et al. 2005, Hedges et al. 2008). Our ultimate goal is to test whether the inclusion of regional information in a GDM analysis of Cerrado anurans improves explanation of within-biome beta diversity patterns, hence guiding follow-up work to detect signatures of historical constraints caused by environmental niche conservatism on beta diversity. Based on existing knowledge of Cerrado diversity patterns (Oliveira-Filho and Ratter 1995, Silva 1996, Eterovick and Fernandes 2002, Costa 2003, Diniz-Filho et al. 2008, Valdujo et al. 2012), we predict that our GDM analysis will demonstrate that 1) dissimilarities in assemblage composition among localities within the Cerrado correlate with changes in climate and topography across the Cerrado (the local effect), 2) the degree of environmental overlap between the Cerrado habitats and adjoining biomes will further influence species compositional dissimilarity (the regional effect), and 3) this regional influence will be particularly strong for endemic, narrowly distributed Cerrado species, since most species belong to lineages distributed in adjoining biomes, especially in the Atlantic Forest.

Methods

Study area

The Cerrado is a mosaic of savannas, grasslands, woodlands and gallery forests that covers the Brazilian central plateau (Fig. 1). It contacts all other major biomes in Brazil, including



Figure 1. Map depicting the extent of Cerrado in Brazil and the location of sampling sites. Black dots represent sites included in GDM1 and GDM2, where all species were taken into account. White circles represent sites included in GDM3 and GDM4, where only endemic species were taken into account. Crosses represent sites where we performed field work to complement existing data.

the wet forests of the Amazon and Atlantic Forest, high elevation grasslands of the Atlantic Forest, and the semiarid Catinga and Chaco, yet is unique because of its low fertility soils and distinct fire regime (Oliveira-Filho and Ratter 2002). The Cerrado also holds the headwaters of three important South American river basins: the Paraná, the São Francisco and the Araguaia-Tocantins (Eiten 1972). The local relief is an important source of habitat heterogeneity, ranging from mountains (with numerous temporary streams) to plateaus and lowlands (with temporary flooded grasses and veredas, i.e. clusters of buriti palm trees along the headwaters). There are two marked seasons; a dry season from April to September and a wet season from October to March. The seasonal rainfall favors the occurrence of seasonal aquatic environments. Mean temperatures range from 22 to 27°C (additional physical characteristics of the Cerrado are reviewed by Werneck 2011).

For the purposes of this study, we delimited the Cerrado extent as per Brazil's official vegetation classification (Veloso et al. 1991). This includes the following components found in the digitized map of terrestrial ecoregions of the world (Olson et al. 2001): the savanna ecoregion in central Brazil, the Alto Paraná Atlantic Forest patches within the savanna boundaries, and the patches of Mato Grosso Seasonal Forests on the east bank of Araguaia River. To account for the wide and patchy transition zones between the Cerrado and its neighbor biomes (Amazon, Atlantic Forest, Caatinga, Chaco, and Pantanal), we included a 50 km buffer around the aforementioned region to arrive at a final study area.

Species data

We examined 31024 specimens deposited in 11 Brazilian zoological collections (Museu de Zoologia da Univ. de São Paulo, MZUSP; Coleção Herpetológica da Univ. de Brasília, CHUNB; Museu Nacional do Rio de Janeiro, MNRJ; Museu de Ciencias Naturais da Pontifícia Univ. Católica de Minas Gerais, MCN PUC-MG; Museu Paraense Emílio Goeldi, MPEG; Coleção da Univ. Federal de Goiás, ZUFG; Coleção da Univ. Federal do Mato Grosso, ZUFMT; Coleção da Univ. Federal do Mato Grosso do Sul, ZUFMS; Museu de Zoologia da Univ. Estadual de Campinas, ZUEC; Coleção Célio Haddad da Univ. Estadual Paulista, CFBH; Coleção da Univ. Estadual Paulista Campus de São José do Rio Preto, UNESP-RP) and performed additional fieldwork in 13 Cerrado localities to fill main survey gaps (Fig. 1). Species identities were assessed through comparison with type specimens, species descriptions, and taxonomic revisions. When coordinates were not available in museum databases, precise locations were obtained directly from collectors. Because all specimens with imprecise location were discarded for the purpose of analysis, our actual working database became reduced to 2662 individuals. To reduce bias due to uneven sampling in microhabitats across localities, and to enhance sample representativeness, we defined a site as the totality of sampled habitats within an 8.33×8.33 km area, which matches the 5 arc-minutes resolution of the environmental data. To reduce bias from omission errors, our analyses were restricted to sites from which at least 10 species were recorded. This data-cleaning process resulted in 64 wellsampled, precisely located sites within the study area (Fig. 1). We also generated a second dataset, containing only presence data for Cerrado endemic species. We then removed all localities with zero or one endemic species, reducing our dataset to 23 sites that had two or more endemic species.

Environmental data

We analyzed environmental correlates of beta diversity using two sets of environmental data that account for local and regional influences on species composition dissimilarity (Table 1). The local dataset included local climatic and topographic features expected to limit species distribution within the Cerrado and is referred to as the 'within Cerrado descriptors'. These were chosen considering species-specific physiological and microhabitat requirements. The second dataset comprised regional scale variables, which were based on the environmental conditions of the neighboring biomes, and represent the historical component in our analysis, referred to as the 'regional descriptors'. All raster and vector files were degraded to the resolution to 8.33 km to meet the resolution of species data.

Table 1. Environmental predictors included in the GDM, with biological justification.

Predictor	Justification for predictor		
Local (within Cerrado) predictors			
Elevation	Lower elevations have wider gallery forests, which provide breeding habitat for forest species		
Slope	Steeper slope areas have narrow temporary streams, with a series of small pools and falls, which are important breeding habitats for some species		
Minimum temperature of coldest month	Low temperatures affect the activity of nocturnal species		
Temperature annual range	A high temperature range affects the metabolism rate of ectotherms throughout the year		
Annual precipitation	Rainfall affects availability of sites for breeding and tadpole development throughout the year		
Precipitation of coldest quarter	Dry season rainfall affects availability of sites especially for prolonged breeders and tadpoles with slow developmental rates		
Soil moisture	More saturated soils have a higher tendency to fill and longer persistence of ponds		
Regional (outside of Cerrado) predictors			
Environmental overlap with each of the six adjoining biomes	More similar environmental conditions between the Cerrado and adjoining biomes favor the occurrence of lineages that originated in these biomes		

Within Cerrado descriptors

Moderately high-resolution (1 km) bioclimatic variables based on 50-yr climate data (1950-2000) were downloaded from WorldClim (Hijmans et al. 2005; < www.worldclim. org/>). This dataset provides maps of annual means, seasonal extremes, and seasonality in temperature and precipitation. Among the WorldClim variables, we discarded highly correlated variables (r > 75%), as well as variables that would lead to similar interpretations about anuran biology. We then selected biologically meaningful predictor variables related to climate, topography, or soil moisture, which could potentially explain amphibian distribution in the Cerrado, as well as variables that had the highest range in the study region (to maximize variation across environmental gradients). The final climate variables were minimum temperature of coldest month, annual temperature range, annual precipitation, and precipitation of coldest quarter. We also incorporated topographical variables, namely elevation and slope, from EROS-USGS (U.S. Geological Survey Center for Earth Resources Observation and Science; < http://eros.usgs.gov/products/ elevation/hydro1k.html>). Soil moisture data, which quantify the amount of water available to the vegetation per each grid cell, were downloaded from the Atlas of the Biosfere (Willmott and Matsuura 2001).

Regional (outside of Cerrado) descriptors

To test the impact of regional factors on beta diversity, we produced six new environmental variables, each representing the climatic similarity between the Cerrado and one adjoining biome where sister-taxa to Cerrado species are known to occur. First, we drew a 200 km buffer around the Cerrado and overlapped this zone with the map of terrestrial ecoregions (Olson et al. 2001). We chose 200 km as it represents the range of environmental conditions in a given adjacent biome, yet is not so large as to include very distinct environmental conditions. Using this buffered region we delimited six areas, representing the neighboring area in each adjoining biome: Amazon, Atlantic Forest, high elevation grasslands in the Atlantic Forest, Caatinga, Pantanal, and Chaco. The Atlantic Forest was split in two parts due to significant differences observed in the flora and fauna of forested areas vs open, mountaintop landscapes (Oliveira-Filho and Fontes 2000, Vasconcelos 2011). To obtain a measure of environmental similarity between the Cerrado and each adjoining biome, we selected 200 random points within each biome region present within the 200 km buffer and modeled the environmental conditions of this region with the distributional modeling tool MAXENT (Phillips et al. 2006). The probability of occurrence of each neighboring region when projected onto the Cerrado map was used as new variable, representing the degree of environmental similarity between every pixel within the Cerrado and each one of the six adjoining regions. For this modeling we used the same topography and soil data included in the GDM. However, because MAXENT obtains the best distribution model by letting its algorithm fit the distribution of maximum entropy to the data (Elith et al. 2011), we used all WorldClim bioclimatic variables to develop the models of the six adjacent climatic spaces. We used the following climatic variables in MAXENT: annual precipitation, isothermality, maximum temperature of warmest month, mean diurnal range, mean temperature of warmest quarter, mean temperature of wettest quarter, minimum temperature of coldest month, precipitation of coldest quarter, precipitation of driest month, precipitation of warmest quarter, precipitation of wettest month, precipitation seasonality, temperature annual range, and temperature seasonality.

Quantification of beta diversity

To investigate environmental correlates of species dissimilarity, we developed a generalized dissimilarity model (GDM) using a downloadable package for R environment (<www.biomaps.net.au/gdm/>). The GDM package is a matrix-regression tool that models compositional dissimilarity as a function of environmental dissimilarity and geographic distance (Ferrier et al. 2007). GDM is a reformulation of the Mantel approach as a generalized linear model, in which a single response matrix can be modeled as a function of distance matrices of a number of explanatory variables (Manly 1986, Ferrier et al. 2007). Composition dissimilarity between each pair of sampled sites is calculated using the Bray-Curtis index, and weighted by the number of sampled species. Then, for each environmental variable, the GDM derives a series of I-spline basis functions, and calculates the difference between each pair of sites. The same procedure is applied to geographic distance between pairs of sites. Finally, GDM uses a maximum likelihood estimator to fit coefficients to the I-spline basis functions, with composition dissimilarity as the response variable and the series of differences in the I-spline functions as predictors (Ferrier et al. 2007). Monte-Carlo permutations are used to assess the extent to which each predictor variable explains the observed response variable (Ferrier et al. 2004). Environmental variables that fail to significantly affect the dissimilarity in species composition are removed from the model. Further, the function describing the association between compositional dissimilarity and environmental dissimilarity is used to predict compositional dissimilarity across the area from which the assemblages were sampled. The number of landscapes (k) in the predicted dissimilarity map is attributed by the user and the resulting subdivisions are labeled 1 to k, in which more similar areas have closer numbers.

Using GDM to investigate the influence of local and regional environmental descriptors in beta diversity patterns within the Cerrado

To evaluate the importance of within-Cerrado and outside of Cerrado (regional) environmental descriptors in influencing beta diversity patterns, we produced and compared four generalized dissimilarity models: 1) GDM1 was based on an environmental dataset composed of local (within Cerrado) environmental predictors and excluding measures of environmental similarity with neighboring regions; species composition data included all amphibian species observed in 64 sampled sites (herein called the 'total species' dataset); 2) GDM2 described the combined effects of local and regional environmental variables, thus including measures of environmental similarity with neighboring regions; like GDM1, it used the total species sample; 3) GDM3 described the effects of local environmental factors on Cerrado endemics only; and 4) GDM4 described the combined effects of local and regional variables on endemics only.

From each GDM, we obtained the environmental variables that explained the most variation in species and endemic beta diversity. We also produced a map of predicted differences in assemblage composition for any two locations, based on the relationship between environmental conditions and species dissimilarity. Multidimensional scaling techniques were then applied to this map to classify the Cerrado into a pre-defined number of environmental landscapes (Ferrier et al. 2007), easing a comparison of our results to classification schemes based on other taxonomic groups. Because the Cerrado contacts six main South American biomes, we set the number of landscapes to six, for visualization purposes only. The use of a greater number of landscapes would have resulted in too much missing data, precluding accurate models and making interpretation of results difficult.

Results

The 64 localities assessed by our analyses included 85% of the 209 species and 69% of 108 endemics known from the Cerrado region. These species represented 93% of the 15 families of amphibians known from the Cerrado region. Detailed description of the distribution of individual species can be found in Valdujo et al. (2012).

Compositional dissimilarity across Cerrado amphibian assemblages is partially explained by contemporary environmental conditions. A GDM using contemporary predictors and total species datasets (GDM1) identified six out of seven environmental variables as significantly correlated with species dissimilarity, and explained 42.35% of the variance in compositional dissimilarity. The inclusion of geographical distance increased the explained variance to 44.40%. Minimum temperature of coldest month, elevation, annual precipitation, and precipitation of the coldest quarter were the most important variables contributing to the model (Table 2). The inclusion of regional environmental surrogates in the GDM of the total species datasets (GDM2) slightly improved prediction of beta diversity to 43.83%. The inclusion of geographic distance increased this explained variance to 45.05%. While regional variables were selected in this model, the same variables identified by GDM1 explained most of the variation in GDM2 (Table 2).

Model performance improved considerably when only Cerrado endemics were analyzed. GDM3, a model developed for endemic species based on within Cerrado factors alone, selected all seven environmental variables and explained 52.62% of the variance in compositional dissimilarity. Explained variance increased only slightly (52.84%) with the inclusion of geographical distance. The most important variables contributing to the model were soil

Table 2. Environmental predictors used to produce the generalized dissimilarity models (GDM) where GDM1 and GDM2 had all species as response variable and GDM3 and GDM4 had only endemic species. GDM1 and GDM3 were built with local, within-Cerrado variables only; GDM2 and GDM4 also included regional (outside of Cerrado) variables. Local variables are local-scale climatic, topographic and soil variables related to amphibian eco-physiological requirements. Regional variables represent the similarity in environmental envelope of the Cerrado and its neighboring phytogeographical biomes. Values indicate the y-axis range for each partial response curve. Higher ranges indicate greater influence on the predicted beta diversity.

	Partial contribution			
Predictor	GDM1	GDM2	GDM3	GDM4
Contemporary				
Elevation	0.55	0.52	1.86	1.73
Slope	0.12	0.10	1.79	1.87
Minimum temperature of coldest month	0.76	0.70	0.24	n/s
Temperature annual range	n/s	0.03	0.60	1.31
Annual precipitation	0.30	0.22	0.01	n/s
Precipitation of coldest quarter	0.28	0.23	2.02	n/s
Soil moisture	0.09	0.08	3.51	1.99
Historical				
Pantanal	_	0.17	_	2.38
Chaco	_	0.04	_	n/s
Amazonia	_	0.02	_	0.58
Atlantic forest	-	0.07	-	1.42
Caatinga	_	0.15	_	2.10
High elevation grasslands in Atlantic forest	-	0.08	-	0.58

moisture, precipitation of the coldest quarter, elevation, and slope (Table 2). GDM4, developed for endemic species and based on within-Cerrado (local) and outside of Cerrado (regional) factors, selected nine out of thirteen environmental variables, and explained 55.30% of the variance in compositional dissimilarity. Explained variance was similar (55.32%) after the inclusion of geographical distance. The most important variables contributing to the model were environmental overlap with Pantanal, Caatinga and Atlantic Forest, as well as slope, elevation, and soil moisture (Table 2). Two variables, minimum temperature of the coldest month and precipitation of the coldest quarter, were chosen in GDM3 but not in GDM4. These variables were somewhat correlated with the regional similarity descriptors (absolute values of r range from 0.04 to 0.73); however, the regional similarity variables that were most highly correlated to within-Cerrado variables (Amazon and high elevation grasslands in Atlantic Forest) had relatively low partial contributions to the model (Supplementary material Appendix 1).

Models produced from the different combinations of predictor and response datasets resulted in four different predictive maps, subdividing the study area into six landscapes (Fig. 2). Landscapes resulting from GDM1 and GDM2, both based on total species datasets, showed similar patterns. Landscapes from GDM3 and GDM4, based on endemics, were more distinct from each other. Furthermore, landscapes were more continuous in maps resulting from GDM1 and GDM2, whereas GDM3 and GDM4 had more scattered and disjunct landscapes. Both GDM1 and



Figure 2. Maps depicting landscapes based on expected compositional dissimilarity in the Cerrado which resulted from four different combinations of environmental predictors and anuran assemblages. (A) Total assemblage dissimilarity predicted by local scale variables (GDM1); (B) total assemblage dissimilarity predicted by local and regional scale environmental variables (GDM2); (C) endemic species dissimilarity predicted by local scale environmental variables (GDM3); and (D) endemic species dissimilarity predicted by local and regional scale environmental variables (GDM4). Color differences depict the amount of turnover among landscapes and are proportional to the level of divergence in terms of shared species.

GDM2 identified the same three landscapes: the transition between Cerrado and Caatinga, western Cerrado, and central Cerrado. However, the northernmost landscape of GDM1 is divided in two landscapes in GDM2, whereas the southeastern Cerrado consists of two landscapes in GDM1 and one landscape in GDM2. Although elevation had a high partial contribution in all four models, it clearly has a greater influence in landscape subdivision for endemic species models (GDM3 and GDM4) then for total species. The landscape 4 in GDM3 represents the mountain ranges, and landscape 2 represents lowlands. Similarly, in GDM4, landscape 3 represents lowlands, whereas there is no distinction between mountain ranges and plateaus (all represented by landscape 4).

Discussion

Relative roles of local and regional environmental variables in beta diversity patterns of Cerrado endemics vs total species assemblies

Patterns of anuran beta diversity appear to be strongly influenced by local environmental gradients: half of the dissimilarity in total species and endemic species datasets can be explained by contemporary environmental factors related to anuran eco-physiological constraints. However, variables that describe environmental conditions in the Pantanal, Caatinga, and Atlantic Forest were selected by the GDM4 model, suggesting that historical contingencies may have also influenced beta diversity patterns of Cerrado endemic anurans. This association may be due to the fact that many of these species are representatives of clades that diversified, and probably originated, in one neighboring biome - especially Atlantic Forest. For instance, Crossodactylus, Hylodes, and Phasmahyla species that inhabit the Cerrado are restricted to its easternmost region, in the Espinhaço mountain range, which borders western areas of the Atlantic Forest (IUCN 2010). This relationship between anuran species in the Espinhaço and Atlantic Forest has been similarly documented by Heyer (1999). In several other vertebrates, biogeographical links have also been made between the Cerrado and the neighboring Caatinga and the Chaco (reviewed by Werneck 2011, Werneck et al. 2012a). Because sister species often share morphological, behavioral, and eco-physiological characteristics with their closest relatives (Felsenstein 1985), niche conservatism may limit the movement of some Cerrado endemics originating in neighboring biomes into regions with novel environments in the Cerrado (Ricklefs 2006).

Based on these GDM results, we predict that three historical factors influence patterns of anuran beta diversity within Cerrado endemic anurans: 1) the similarity of environmental conditions between landscapes and their adjoining biomes; 2) the close relationship between Cerrado endemics and lineages distributed in neighbor biomes (especially the Atlantic Forest, given preliminary data in Faivovich et al. 2005, Hedges et al. 2008) and 3) the tendency for species to retain ancestral features, resulting in the conservatism of climatic niches (Brooks and McLennan 1991). Our analyses demonstrate that prediction i above is true and lend support to predictions ii and iii; however, additional phylogenetic sampling within and around the Cerrado, tied to studies of climatic niches of the lineages encountered, are needed to confirm these latter predictions.

In contrast to the endemics-focused analyses, environmental similarity with neighboring biomes explained very little of the variation in total-species models. In the later, local environmental predictors, principally minimum temperature of the coldest month, elevation, annual precipitation, and precipitation of the coldest quarter, explained beta diversity for total species datasets. These variables are directly related to physiological constraints and the availability of breeding habitats for different reproductive modes. Minimum temperature of the coldest month, the most important selected factor, can limit the geographic distribution of species because activity of nocturnal ectotherms is strongly influenced by lower temperatures faced by individuals (Hillman et al. 2009). The second most important variable, elevation, broadly captures differences in habitat type and water availability in the Cerrado. Dense riverine forests cover warmer lowlands on the northern and western parts of the Cerrado, temporary streams are present in highlands and mountains in its southeastern portion, while plateaus offer a lower range of habitat types. This microhabitat turnover, associated with the elevational gradient, may explain the importance of elevation in GDMs. Future GDM-based studies of Cerrado amphibians may hence profit from the direct inclusion of hydrological datasets to pinpoint the specific role of water sources (besides soil moisture) in community dissimilarity. Finally, annual precipitation and precipitation of the coldest quarter directly relate to breeding habitat availability for the great majority of Cerrado anuran species, which breed in temporary water bodies (Brasileiro et al. 2005, 2008, Valdujo et al. 2009). Anuran breeding sites vary in terms of pond size and hydroperiod: small rain puddles may be sufficient for fast developing species such as *Dendropsophus rubicundulus* (Barreto and Moreira 1996), while species that take more than a year to complete tadpole development (e.g. *Pseudis* spp., Fabrezi et al. 2009) need larger permanent or semipermanent ponds and may require a greater amount of rain to breed.

Different local environmental variables were important in endemic-species GDMs (GDM3 and GDM4) than in total-species GDMs, including soil moisture, slope, and precipitation of the coldest quarter. These variables also make biological sense. A steeper relief (represented by higher slope), together with higher elevation and higher precipitation, enable the presence of temporary mountain streams, allowing for the occurrence of stream-breeder species. Soil moisture facilitates breeding habitat availability, especially for species that depend upon semi-permanent ponds. These breeding habitats are more common when soil is saturated. Since the coldest season in the Cerrado is also the dry season, precipitation of the coldest quarter may affect the availability of breeding sites for species that reproduce during the winter time, in temporary water bodies.

Contrasts between GDMs and previous Cerrado studies

Total species GDMs identified regions that roughly correspond to previously proposed subdivisions of the Cerrado based on the distribution of woody-plants (Ratter et al. 2003) and, although weakly, vegetation physiognomy (Silva et al. 2006, Fig. 3). This similarity is encouraging, especially given that our GDM analysis did not take anthropogenic land use change into account – which is naturally expected to impact amphibian species richness and can hence affect models of species dissimilarity across sites.

Because the two maps based on total species dissimilarity (GDM1 and GDM2) were comparable, we only describe the results with the complete set of variables here (GDM2). There is a fair correspondence between the configuration of the six landscapes obtained by the GDM and Ratter et al.'s (2003) woody-plant province subdivision: landscape 3 corresponds to Ratter et al.'s (2003) southern and to central and southeastern provinces, landscape 2 and landscape 1 subdivides the north and northeastern provinces, and landscape 4, landscape 5, and landscape 6 subdivides the central-western woody-plant province (Fig. 3). Subdivisions obtained with total datasets GDMs are also roughly consistent with the distribution of anuran species in the Cerrado and neighboring biomes (Valdujo et al. 2012). For instance, Cerrado species that are related to Atlantic lineages are distributed in landscape 3, and those that are related to Amazonian lineages are distributed in landscape 6 and partially in landscape 4. Species shared with Caatinga are distributed in landscapes 1 and 2, and those shared with the Chaco and Pantanal occur in



Figure 3. Subdivision of Cerrado. (A) Land systems (adapted from Silva et al. 2006). (B) Floristic regions (adapted from Ratter et al. 2003).

landscape 5 (Valdujo et al. 2012). The correspondence of our GDM results to the ecological units presented by Silva et al. (2006), who proposed a hierarchical classification of environmental diversity of the Cerrado based on ecological units nested within landscapes, is less evident (Fig. 2, 3). In Silva et al. (2006), landscapes were based on landform and vegetation types, and ecological units were based on physiognomy, phenology, topography, and drainage. Our landscapes 1, 2, and 3 overlap to some extent with their ecological units 3D, 1D, and, 1A; respectively. However, landscapes 4, 5, and 6 partially overlap with several ecological units. The fact that the vegetation physiognomy map show only moderate correspondence with anuran beta diversity, suggests that there is a complex relationship between them, which could be partly the result of historical contingency on species distributions.

Maps depicting the results of GDMs for endemic species (GDM3 and GDM4) differed from each other, and the landscapes generated by these models have weaker correspondence with published Cerrado subdivisions. The map resulting from GDM3 shows a strong influence of elevation and slope, and subdivides the Cerrado according to the topography. Landscape 3 corresponds to plateau areas, landscape 2 represents the highlands and landscape 4 represents lowlands. The map resulting from GDM4 shows all lowlands combined in landscape 3, while plateaus and highlands are in landscape 4. GDM4 landscapes are influenced by the environmental similarity with adjoining biomes: landscape 6 overlaps with Atlantic Forest environmental envelope, landscape 5 overlaps with Chaco environmental envelope and landscape 1 overlaps with Amazon environmental envelope. Maps depicting landscape subdivision based on endemic species reinforce the importance of historical factors combined with environmental heterogeneity in influencing beta diversity in the Cerrado, a pattern obscured by the distribution patterns of widespread taxa in the total species models.

Apart from revealing the importance of faunal interchange in species assemblages, GDMs can be central to

conservation by integrating taxonomic and environmental data in a single predictive model of species dissimilarity (Overton et al. 2009, Thomassen et al. 2010). In the Cerrado, where amphibian diversity is known to be underestimated (Bastos 2007), this integration is fundamental to pinpoint areas where environmental change may be accompanied by changes in assemblage composition. Less than 3% of the Cerrado region is under legal protection, yet threats to its flora and fauna abound - including human occupation, invasive species (e.g. African grasses), uncontrolled fires, and the advance of mechanized agriculture (Klink and Machado 2005). A recent study of Werneck et al. (2012b) suggested that historical climatic stability predicts Cerrado species (squamate) richness better than present-day climatic variables, and proposed that historical climate stability maps be used as biodiversity surrogates for conservation planning. Yet, our results demonstrate that several Cerrado lineages are restricted to specific parts of the environmental gradient indicating that distinct habitats that span the gradient should be protected even if only as small, scattered reserves. Diniz-Filho et al. (2004) once proposed that Cerrado reserve selection should account for environmental dissimilarity; our analyses support this strategy and demonstrate why it is key for this system.

Concluding remarks

In this paper, we propose a method to detect potential effects of historical factors in beta diversity analyses by explicitly incorporating the impact of neighboring environments on local assemblages. Proof of the importance of these historical factors in the Cerrado will depend on follow-up studies that demonstrate that local species are closely related to lineages distributed in these adjoining areas, and that niche conservatism is prevalent. Because beta diversity patterns are likely generated by a combined effect of environmental and biotic filtering and location where a lineage originated (Graham and Fine 2008, Vamosi et al. 2009), the approach we develop will be useful to evaluate possible mechanisms or generate new hypotheses relating to patterns of beta diversity in the Cerrado as well as other biomes worldwide.

Lineage history may restrict species ranges to a portion of the environmental gradient in a given region, and this ought to be incorporated into conservation planning. Thus, we expect to find high beta diversity in regions where coexisting species belong to lineages with different biogeographical histories. This interplay of environmental and historical constraints on anuran richness patterns was previously detected at a global scale (Buckley and Jetz 2007), and our results reinforce that taking biogeographical history into account when analyzing spatial patterns of species diversity at a smaller scale can also be insightful. Detailed phylogenetic and phylogeographic studies of Cerrado species and their sister-taxa will provide further insight about the interplay between historical and contemporary factors and their impact on biodiversity patterns in this global hotspot.

Acknowledgements - We thank the curators and staff of the many herpetological collections visited during the course of this work. We also thank C. Araújo, C. Brasileiro, C. Cândido, K. Kopp, F. Leite, R. K. Ribeiro, M. Teixeira-Jr, and V. Verdade for providing precisely located occurrence records and J. Parra for his help with the GDM command lines. G. Manion generously provided R-code for analyses. We thank J. Knowlton, M. Martins, C. Nogueira, P. I. Prado, C. Prado, G. Costa, P. Guimarães Jr, and J. Ladau for thoughtful comments on the manuscript. This study was conducted at Dept of Ecology and Evolution of Stony Brook Univ., which hosted PHV as a visiting PhD student. PHV acknowledges fellowship from FAPESP (2007/51956-6), and funding from Conservation International (CP-FY 08/017 and CP-FY 08/018), Neotropical Grassland Conservancy, FAPESP (06/58011-4) and Fundação O Boticario de Proteção à Natureza (0747_20071 and 0798_20082). ACC acknowledges funding from NSF (DEB-1035184 and DEB-1120487). CHG acknowledges funding from NSF (DEB-082049).

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Supplementary material (Appendix E7374 at <www. oikosoffice.lu.se/appendix >). Appendix 1.

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