HAMANDA BADONA CAVALHERI

**O PAPEL DE FATORES ECOLÓGICOS E HISTÓRICOS NA COMPOSIÇÃO E NOS
PADRÕES MORFOLÓGICOS EM TAXOCENOSES DE SERPENTES
NEOTROPICAIS**

**THE ROLE OF ECOLOGICAL AND HISTORICAL FACTORS ON THE
COMPOSITION AND MORPHOLOGICAL PATTERNS IN NEOTROPICAL SNAKE
ASSEMBLAGES**

São Paulo

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ASSEMBLAGES**

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“O homem de preto fugia pelo deserto e o pistoleiro ia atrás”.

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RESUMO

Os processos ecológicos e biogeográficos podem influenciar a composição de espécies em comunidades. A ecologia diz respeito às interações entre espécies e o ambiente enquanto que a biogeografia está relacionada à ocupação dos ambientes pelas espécies pertencentes ao pool regional. A dispersão fornece oportunidade para que as espécies ocupem diferentes ambientes, mas o modo como as espécies interagem entre si e com o ambiente é crucial para a permanência da espécie em uma taxocenose. Dentro desse contexto, este estudo busca entender qual processo, ecológico, histórico ou ambos tem influenciado na estrutura de comunidades de serpentes neotropicais com diferentes tipos de vegetação (áreas florestadas e abertas) usando métodos filogenéticos e fenotípicos. Nós detectamos diferentes padrões de estrutura filogenética nas comunidades da Amazônia (disperso) e dos Campos Sulinos (agregado). No entanto, é possível perceber que comunidades de baixas latitudes tendem a ter estrutura dispersa e comunidades de altas latitudes tendem a ter estrutura agregada. O mesmo padrão foi observado através da análise fenotípica. Além disso, dentre os atributos mensurados o tamanho do corpo é o único que está associado com o tipo de vegetação. Este resultado pode ser uma consequência da maior proporção de espécies arborícolas em taxocenoses florestadas. Essas espécies geralmente são maiores que as terrícolas e as fossoriais. Espécies que utilizam o mesmo habitat são morfologicamente similares. A influência da biogeografia nas comunidades de serpentes é um resultado da distribuição de espécies das três principais linhagens de serpentes da região Neotropical. As espécies de Colubridae e Dipsadinae contribuem mais para a riqueza de espécies em latitudes mais baixas enquanto que Xenodontinae contribui mais nas taxocenoses de altas latitudes. Isto pode explicar o padrão filogenético disperso encontrado nas comunidades de baixa latitude porque estas comunidades são compostas principalmente por espécies de duas linhagens diferentes enquanto que as comunidades de altas latitudes são basicamente compostas por uma única linhagem (o que resultaria em um padrão filogenético agregado). Isso pode explicar também a pequena diferença morfológica entre as comunidades de latitude maior devido à inércia filogenética. Nossos resultados destacam a importância da biogeografia na estruturação de comunidades, corroborando a atual hipótese de que a biogeografia é mais importante para moldar a estrutura de comunidades do que os fatores ecológicos.

Palavras-chave: taxocenoses, serpentes, biogeografia, filogenia, fenótipo

ABSTRACT

Both ecological and biogeographical process can influence assemblages' composition. Ecology may affect interactions among species and their environment while biogeography affects species' immigration from regional species' pool. Immigration provides an opportunity to arrive in different localities but the way in which species interact with their environment is a crucial factor in order for a species to thrive. This study aims to understand which processes, ecological, historical or both, have influenced the structure of Neotropical snakes' assemblages in different vegetation types (forested and open areas), using a phylogenetic and phenotypic approach. We detected different patterns of phylogenetic structure in assemblages from Amazonian rainforest (evenness) and Brazilian Campos Grasslands (clustered) but it is also possible to perceive that assemblages from lower latitudes are evenly structured and assemblages from higher latitudes are clustered, the same being true when we consider their phenotypic structure. Moreover, considering all measured traits body size is the only feature related to vegetation type (open and forested areas). This result may be a consequence of the microhabitat used by a high proportion of species - since arboreal and semi-arboreal species are primarily encountered in forested areas (when compared to open areas), and these species are normally larger than terrestrial and/or fossorial species. Furthermore, species within use the same habitat have similar morphologies. The influence of biogeography in snakes' assemblages is a result of the species' distribution from major snakes' lineages in Neotropics. The lineages Colubridae and Dipsadinae contribute more to assemblages' richness at lower latitude whereas Xenodontinae contributes more at higher latitudes. This may explain the phylogenetic evenness pattern encountered in assemblages from lower latitudes, since these assemblages are composed mainly by species from two different lineages, while assemblages from higher latitudes are basically composed by one lineage. Although the difference among species' morphology is smaller in assemblages from higher latitudes due probably to evolutionary constraints. Our results highlight the importance of biogeography in shaping assemblage structure, corroborating the current hypothesis that biogeography is more important in shaping assemblages than ecology.

Key words: assemblages, snakes, biogeography, phylogeny, phenotype

INTRODUÇÃO GERAL

Uma das questões que mais intrigam os ecólogos e chamam a atenção de muitos cientistas é como as espécies se combinam para formar uma taxocenose e quais processos tangem essa combinação. A diversidade de espécies presente em uma taxocenose é resultado de dois conjuntos de forças. O primeiro diz respeito às interações entre as espécies e aos processos abióticos, ambos os quais tendem a reduzir a diversidade (Ricklefs & Schuler, 1993). O último está relacionado à dispersão de espécies entre localidades, a qual tende a aumentar a diversidade (Ricklefs & Schuler, 1993). A diversidade de espécies tem grande influência sobre a estrutura taxocenoses. Assim, podemos concluir que a estrutura de taxocenoses é dirigida por processos ecológicos (interações) e biogeográficos (dispersão e ocupação de ambientes) (Ricklefs & Schuler, 1993).

Existem dois processos ecológicos principais que são descritos como os que mais afetam a estrutura de comunidades: a competição e o filtro ambiental. A teoria da competição afirma que as espécies, para evitarem a competição com espécies similares, tendem a se excluir mutuamente ou, se ambas coexistem, há partilha de recursos ou deslocamento de caracteres (Diamond, 1975; Gotelli & McCabe, 2002, Chao et al. 2005, Dayan & Simberloff, 2005). Por outro lado, o ambiente pode impor restrições que irão filtrar as espécies capazes de sobreviver em tal ambiente, favorecendo espécies com atributos similares (Keddy, 1992; Myers & Harms, 2009). Adicionalmente, esses dois processos, competição e filtro ambiental, atuando juntos podem influenciar a coexistência das espécies pelas interações bióticas e restrições ambientais, as quais agem em escalas de tempo ecológicas e evolutivas (Webb et al. 2002). Contudo, existe uma teoria alternativa que sugere que nenhum dos dois processos acima age na estruturação de taxocenoses. As espécies que compõem uma taxocenose e suas abundâncias seriam regidas por deriva (Hubbell, 2001). Além disso, foi sugerido que a detecção do processo (ecológico ou biogeográfico) que rege

a estruturação de uma taxocenose pode ser comprometida devido a um balanço entre interações bióticas e filtros ambientais, o que geraria um padrão de estrutura aparentemente aleatório que poderia ser interpretado como resultante de um processo neutro (Purves & Pacala, 2005).

Existem duas abordagens que são tradicionalmente usadas para determinar qual processo mais influencia na estrutura de uma taxocenose: o método fenotípico e o método filogenético (Pausas & Verdú, 2010). O método fenotípico é baseado na representação dos atributos das comunidades, enquanto que o filogenético, na relação evolutiva entre as espécies.

A estrutura fenotípica da taxocenose é inferida pela distribuição dos atributos das espécies relativa à distribuição dos atributos das espécies disponíveis no pool regional de espécies (Pausas & Verdú, 2010). O pool regional de espécies se refere às espécies que potencialmente poderiam ocupar a taxocenose. Através dessa abordagem dois padrões principais podem ser encontrados: estrutura fenotípica agregada ou dispersa uniformemente, além do randômico. A estrutura fenotípica agregada surge quando espécies co-ocorrentes são mais similares que o esperado pela distribuição dos atributos das espécies do pool. Em geral, o processo que gera este padrão fenotípico é um filtro ambiental, o qual implica que a taxocenose será composta por espécies que necessariamente possuem atributos que conferem habilidade para tolerar tal filtro (Pausas & Verdú, 2010; Weiher & Keddy, 1995). Por outro lado, quando o padrão fenotípico é disperso uniformemente, o principal processo atuando é a competição, que evidencia que as espécies co-ocorrentes são menos similares que o esperado pela distribuição dos atributos das espécies do pool (Pausas & Verdú, 2010; Weiher & Keddy, 1995).

Já o objetivo do método filogenético é inferir o processo que estrutura as comunidades a partir da relação evolutiva das espécies co-ocorrentes. Um padrão

filogenético agregado indica que as espécies co-ocorrentes são mais próximas filogeneticamente que o esperado pelo modelo nulo (Pausas & Verdú, 2010). Nesse caso, o modelo nulo corresponde à geração de comunidades randômicas, com a mesma riqueza da taxocenose estudada, a partir do pool regional de espécies. Já um padrão disperso indica que as espécies co-ocorrentes são menos relacionadas filogeneticamente do que o esperado pelo modelo nulo (Pausas & Verdú, 2010). Devido ao fato de que o filtro ambiental permite que somente as espécies portadoras de atributos particulares façam parte da taxocenose, as espécies coexistentes serão mais similares fenotipicamente que o esperado. O padrão filogenético dependerá de como foi a evolução dos atributos: se evoluíram por convergência ou resultaram de inércia filogenética (Pausas & Verdú, 2010). Se os atributos forem conservados, isto é, eles resultaram de inércia filogenética, as espécies mais próximas na filogenia terão atributos similares e, portanto, o padrão filogenético será agregado. No entanto, se espécies distantes filogeneticamente partilharem os mesmos atributos, isto é, são convergentes, então o padrão filogenético será disperso. Se o processo principal for competição, limitando a presença de fenótipos similares na taxocenose e, portanto, espécies mais relacionadas filogeneticamente, a taxocenose terá estrutura filogenética dispersa. Por outro lado, se espécies próximas forem diferentes, a estrutura filogenética será agregada.

Muitas vezes, a estrutura de uma taxocenose não pode ser explicada pelos padrões atuais de estrutura espacial ou heterogeneidade ambiental devido às restrições históricas, pois a atual estrutura de uma taxocenose está relacionada à informação histórica (Cavender-Barres et al. 2009). De fato, o processo biogeográfico tende a ser mais forte que os processos ecológicos (Ricklefs, 2007). No entanto, os padrões biogeográficos podem estar relacionados aos ecológicos, afetando a habilidade de dispersão das espécies (Ricklefs, 2004; Harisson & Cornwell, 2008).

Para a dispersão ser efetiva, as espécies devem chegar à taxocenose e serem aptas e competitivas o suficiente para sobreviver e prosperar.

Em resumo, o estudo da estrutura de comunidades deve considerar a informação filogenética, a composição de espécies e seus atributos. A análise com diferentes abordagens, tais como o método fenotípico e o método filogenético, fornece uma oportunidade para um melhor entendimento da estrutura de comunidades, pois esses métodos podem ser aplicados a diferentes organismos e escalas.

GRUPO DE ESTUDO E OBJETIVOS

Nesse trabalho usamos as serpentes como modelo de estudo. Apesar das serpentes possuírem restrições morfológicas devido à ausência dos membros, o uso do habitat influencia fortemente no tamanho do corpo e na morfologia, garantindo que o animal tenha um melhor desempenho no habitat utilizado (Guyer & Donnelly, 1990; Irshchick & Losos, 1999). São reconhecidas cinco síndromes morfológicas associadas ao uso do habitat em serpentes: criptozóica, fossorial, arborícola, aquática e terrícola (Cadle & Greene, 1993). As espécies terrícolas tendem a apresentar tamanho de moderado a grande com morfologia generalizada (Guyer & Donnelly, 1990; Cadle & Greene, 1993). Já as fossórias e criptozóicas tendem a apresentar cabeça menor e compacta, indistinta do restante do corpo, e a possuir olhos pequenos, cauda curta e boca deslocada ventralmente (Cadle & Greene, 1993). Esse dois hábitos exigem mudanças que diminuam o atrito com o solo e permitam a escavação (Savitzky, 1983). Já as serpentes aquáticas necessitam de modificações que facilitem sua locomoção na água. Assim, geralmente são mais robustas, com olhos e narinas posicionados na região dorso-anterior da cabeça e, algumas vezes, cauda em forma de remo (Greene, 1997; Scartozzoni, 2005). Serpentes arborícolas frequentemente são pouco robustas, alongadas, podendo ser achatadas lateralmente e possuir olhos (Guyer & Donnelly,

1990; Lillywhite & Henderson, 1993). O ambiente arbóreo impõe restrições quanto à descontinuidade e irregularidade do substrato (Guyer & Donnelly, 1990; Lillywhite & Henderson, 1993; Martins et al. 2001). Portanto, as serpentes compõem um grupo morfológicamente diversificado e dado que existem várias filogenias para diferentes grupos, é possível a aplicação de ambos os métodos, filogenético e fenotípico, no estudo de suas taxocenoses. Assim, foram selecionadas oito taxocenoses, sendo duas em cada bioma: Mata Atlântica, Amazônia, Campos Sulinos e Cerrado. Dentro dessa escala abrangendo vários biomas procuramos evidências de que a estrutura fenotípica e filogenética das comunidades de vegetação fechada (Amazônia e Mata Atlântica) seja diferente da estrutura de comunidades abertas (Cerrado e Campos Sulinos) devido a maior proporção de espécies arborícolas e semi-arborícolas em comunidades que ocorrem em fisionomias vegetais fechadas. Contudo, dada à escala continental escolhida, o efeito biogeográfico não pode ser descartado.

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THE ROLE OF ECOLOGICAL AND HISTORICAL FACTORS ON THE COMPOSITION AND MORPHOLOGICAL PATTERNS IN NEOTROPICAL SNAKE ASSEMBLAGES

Hamanda B. Cavalheri^{1,2} & Marcio Martins¹

¹Departamento de Ecologia, Instituto de Biociências, Universidade de São Paulo, Rua do Matão, Travessa 14, Cidade Universitária, São Paulo, SP, Brasil, CEP 05508-090

²Correspondence author: hbcavalheri@gmail.com

INTRODUCTION

One of the biggest issues in ecology is why the composition of species differs among assemblages and which processes drive these differences. Species diversity in assemblages is a result of the balance between two sets of forces: interactions between species and abiotic factors and species immigration. The first tend to reduce diversity whereas the latter tend to increase assemblage diversity (Ricklefs & Schuler, 1993). In this sense, assemblage structure is driven both by ecological (interactions between species and environment) and biogeographical (distribution of species) processes.

Competition and environmental filtering are the two main ecological processes thought to structure ecological assemblages. Competition theory predicts that in order to avoid competition one species with similar niche will exclude the other through spatial or temporal niche partitioning or character displacement due to distinct selective pressures (Diamond, 1975; Gotelli & McCabe, 2002, Chao et al. 2005, Dayan & Simberloff, 2005). Alternatively, the environment can impose ecological and evolutionary constraints that will filter the species that have the ability to survive in a given place, favoring species with similar ecological requirements (Keddy, 1992; Myers

& Harms, 2009). Furthermore, these two processes can influence species coexistence both by biotic interactions and environmental constraints, which act over ecological and evolutionary time-scales (Webb et al. 2002). However, an alternative theory suggests that neither one of the two ecological process can influence assemblage structure, suggesting that species may either drift neutrally in abundance (Hubbell, 2001) or the biotic interactions and filtering may balance each other, producing a random or neutral pattern in assemblage structure (Purves & Pacala, 2005).

If evolutionary aspects are not considered, it can be expected that all lineages can occur in any environment (Losos, 1996). However, it is known that the evolutionary history of lineages limits the geographical distribution of species and, therefore, can influence assemblage structure (Wiens et al. 2006). The pattern generated by historical constraints cannot be explained by current patterns of spatial structure or environmental heterogeneity, since current patterns are related to historical information and may reflect ancient biogeographical forces (Caverder-Barres et al. 2009). Theory suggests that the biogeographical processes are stronger than ecological ones (e.g.competition) and that environmental filtering depends on the regional species diversity (Ricklefs, 2007). Moreover, biogeographical patterns may be related to ecological processes that affect the dispersion ability of species, which is associated to speciation and extinction rates on one hand, and competition and predation on the other hand (Ricklefs 2004; Harisson & Cornwell, 2008). It is well known that factors that vary with latitude can influence richness and can be related to the distribution of species and, therefore, to their ability to occur in a given place (Ricklefs & Schulter, 1993). Hence, for dispersal to be effective, species have to arrive in an environment and be strong enough to thrive.

Trait analysis is commonly used to compare assemblages and several studies have already demonstrated the importance of environmental filtering in structuring assemblages (Kraft et al. 2008; Cornwell & Ackerly, 2009; Ingram & Shurin, 2009;

Paine et al. 2011). Considering that species experiencing similar ecological conditions also exhibit similar morphology, as a result of convergence across lineages, morphological patterns in an assemblage will be influenced by species within clades that share specific traits (Ricklefs & Travis, 1980; Ricklefs et al. 1981; Barton et al. 2011). For vertebrates, habitat use is an ecological aspect responsible for major morphological changes (Moermond, 1979; Miles & Ricklefs, 1984; Losos, 1990; Cadle; Greene, 1993; Martins et al. 2002; Pizzatto, 2006). Some common variables used to analyze these changes are related to habitat use, and involves measurements of length and mass (e. g., Martins et al. 2001; Pizzatto et al. 2007). In addition, morphological changes associated to a species' diet, such as the ingestion of different prey items, are related to stoutness and head size (Martins et al. 2002).

Many studies have investigated the structure of snakes' assemblages (Vitt & Vangilder, 1983; Martins & Oliveira, 1998; França et al. 2008). In South America the studies with snakes have been conducted mostly in Brazil, in different biomes (Amazonian Forest: Martins & Oliveira, 1998; Bernarde & Abe, 2006; Caatinga: Vitt & Vangilder, 1983; Atlantic Forest: Marques & Sazima, 2004; Pantanal: Strüssmann & Sazima, 1993). Snakes present morphological constraints due to limblessness and their body shape and morphology is highly related to habitat use (Guyer & Donnelly, 1990; Martins et al. 2001). Morphological changes in snakes are more evident when we consider, for instance, body size, stoutness, body elongation and presence and/or absence of cephalic scales (Guyer & Donnelly, 1990; Cadle & Greene, 1993; Martins et al. 2001; Pizzatto, 2006). Moreover, it has been reported that snakes occupying the same habitat are under the same selective pressures, which tends to generate similar convergent morphologies, independent of snake lineage (Klingenberg & Ekau, 1996; Irschick & Losos, 1999).

Within this context, this study aims to understand which processes – ecological, historical or both – have influenced the structure of Neotropical snake assemblages in

different vegetation types (forested and open areas), using a phylogenetic and a phenotypic approach. We explore the following questions: 1. Are assemblages inhabiting the same type of vegetation similar in terms of their composition and morphology? 2. Are these assemblages phylogenetically structured? 3. Are these assemblages phenotypically structured?

MATERIAL AND METHODS

Assemblages

We compiled a database of species composition for snake assemblages in Brazil using lists from published references in peer-reviewed journals and from unpublished data provided by other researchers. We selected data from two types of vegetation, each represented by four assemblages: open areas, with two assemblages from the Brazilian Cerrado (savanna) and two from Brazilian Campos Grasslands; and forested areas, with two assemblages from Amazonian Forest and two from Atlantic Forest. Taxonomy was updated to reflect the current version available in the Brazilian snake species list (SBH, 2011).

Data for forested areas are derived from Amazonian and Atlantic Forest studies (Amazonian 1, 3°6'S and 60°1'W, Martins & Oliveira, 1998; Amazonian 2, 11°31'S and 61°1'W, Bernarde & Abe, 2006; Atlantic 1, 14°47'S and 39°2'W, Argôlo, 2004; Atlantic 2, 24°32'S and 47°15'W, Marques, 1998) and data for open areas was compiled from studies conducted in the Brazilian Cerrado and the Brazilian Campos Grasslands (Cerrado 1, 15°48'S and 47°51'W, França et al. 2008; Cerrado 2, 22°15'S and 47°49'W, Sawaya et al. 2008; Campos 1, 29°26'S and 50°35'W, Di-Bernardo, 1998; Campos 2, 29°41'S and 53°48'W, Cechin, 1999). When one of these studies considered both open and forested areas, we considered only the species that were either seen in the open or the forested areas. Moreover, since we are looking for

processes that relate species composition and vegetation type, we chose not to include aquatic species in the analyses because they present morphological syndromes that are very characteristic of this habitat type (Greene, 1997; Scartozzoni, 2005).

Traits

Because this study considers the differences between open and forested areas, we only used traits known to be related to habitat use. We considered the following habitat categories: arboreal, semi-arboreal, terrestrial, and fossorial (cf. Martins & Oliveira, 1998). We used only female adult specimens for morphological attributes and selected specimens from locations within a latitudinal range of 5° to the north and 5° to the south of the location where the assemblage was studied. For each individual, we measured snout–vent length (SVL), tail length (TL), circumference around midbody (stoutness, CAM), head length (tip of snout to posterior edge of mandible, HL), head width (at posterior edge of mandible, HW), head height (at its highest point, HH), ventral scales count (as a surrogate for the number of body vertebrae, VS) and subcaudal scales count (as a surrogate the number of tail vertebrae, SS). We gathered data in the following scientific collections: Instituto Butantan (IB, São Paulo), Museu de Zoologia da Universidade de São Paulo (MZUSP, São Paulo, SP), Museu de Zoologia da Universidade Estadual de Campinas (ZUEC, Campinas, SP), Museu de Ciência e Tecnologia da Pontifícia Universidade Católica do Rio Grande do Sul (MCT, Porto alegre, RS), Coleção Herpetológica da Universidade Federal de Santa Maria (ZUFMS, Santa Maria, RS), Coleção Herpetológica da Universidade de Brasília (CHUNB, Brasília, DF), Museu Paraense Emílio Goeldi (MPEG, Belém, PA), Museu de Zoologia da Universidade Estadual de Santa Cruz (MZUESC, Ilhéus, BA) and Coleção Zoológica Gregório Bondar (CZGB, Ilhéus, BA). For each trait and each species with two or more individuals we calculated average values.

Phylogenies

Since the studied assemblages are far away from each other (spanning 26 degrees of latitude), species that occur in low latitude areas generally do not occur in higher latitudes, and vice-versa (Cadle & Greene, 1993). Therefore, we decided to define a species pool for each assemblage separately. Additionally, we used a different phylogeny for each assemblage using only the species present in the area, as described below.

To determine the regional species pool for each assemblage (i. e., the species that potentially composed the assemblages), we first created a buffer of 500 km around the location where the assemblage was studied. Due to differences in vegetation types within a biome (like the Amazonian forest, for instance, where patches of open formations may be found) we superimposed the species pool range on a map of the Terrestrial Ecoregions of the World (Olson et al. 2001). The ecoregions in which each Brazilian species occurred were determined by experienced researchers (M. Martins & O.A.V. Marques, pers. com.) and for Bolivian and Argentinean species, we gathered information in the literature (for Argentina: Bérnili, Giraudo & Cechin, 1990; for Bolivia: Killeen & Schulenberg, 1998; Herrera-MacBryde et al. 2000).

Phylogenetic relationships among species were inferred using published phylogenies and unpublished data from other researchers (cited below). We started by the higher level relationship (Lee & Scanlon, 2002; Zaher et al. 2009; Colston et al. 2010; Pyron et al. 2011), grouping the major lineages of snakes, and then nested the lower lineages (Boidae: Kluge, 1991; Burbrink, 2005; Colubridae: Hollis, 2006; Elapidae: Silva & Sites, 2001; Castoe et al. 2007; Viperidae: Silva & Rodrigues, 2008; Wüster et al. 2008; Fenwick et al. 2009; Castoe et al. 2009; Leptotyphlopidae: Adalsteinsson et al. 2009; Elapomorhini: Ferrarezzi, 1993; Puerto & Ferrarezzi, 1993; Giraudo & Scrocchi, 1998; Ferrarezzi et al. 2005; Cacciali et al. 2007; Lema &

Albuquerque, 2010; Dipsadini: P. Passos, pers. com.; Harvey, 2008; Passos et al. 2010; Echinantherini: Santos Jr., 2009; Philodryadini: Lobo & Scrocchi, 1994; Zaher et al. 2008a; Pseudoboini: Morato et al. 2003; Zaher et al. 2008b; Lynch, 2009). We then combined this information to construct the phylogenies by hand using the software Mesquite 2.75 (Maddison & Maddison, 2011). We were unable to find information regarding the relationship between species of the family Leptotyphlopidae and for some species of the genera *Bothrops*, *Micrurus*, *Atractus*, *Liophis*, *Apostolepis*, *Echinanthera*, *Helicops*, *Oxyrhopus* and *Phimophis*. In all these cases, politomies were used.

Statistical Analysis

We log₁₀ transformed all morphological characters prior to analyses to enhance normality and equalize variances. The dominant morphological trait among animals is body size (Peters, 1983) and we were interested in establishing patterns of morphological variation. Therefore, in order to characterize body shape in relation to the static allometry inherent in the assemblage (Ribera et al. 1999) we calculated residuals from linear regressions of morphological characters against snout-vent length for all species. We considered the residuals of linear regressions as relative variables. In addition, we explored through linear regressions the effect of latitude in assemblage composition and richness, assessed as the proportion of species of the Colubridae, Xenodontinae, and Dipsadinae lineages, since these lineages represent, in general, 80-90% of the species in snake assemblages in South America (Cadle & Greene, 1993).

To test the similarity among assemblages inhabiting the same vegetation type, we constructed matrices of the proportion of species of each genus and the proportion of species of each family. To explore the degree of similarity among assemblages according to their morphology, we constructed matrices of presence or absence of all

species that occur in each of the assemblages here considered. We then use a Mantel test to search for correlations between species distance, using Jaccard distance, and morphological distance among all pairs of species. Separate morphological distance matrices were generated for SVL and relative variables using Euclidian distances. This test computes regression coefficients and R^2 value of each correlation by using Monte Carlo permutations (we run 999 permutations). We then clustered the morphological distance matrix to create a dendrogram in order to evaluate the similarity among assemblages based on their traits.

We then tested whether or not the assemblages were phylogenetically structured. One method to determine which process (environmental filtering or competition) influences the assemblage composition is through the phylogenetic relatedness of species in an assemblage. We measured the phylogenetic structure of each assemblage using mean pairwise distance (MPD), mean nearest taxon distance (MNTD), net relatedness index (NRI) and nearest taxa index (NTI) (c.f. Webb et al. 2002). MPD is the mean pairwise distance between all species in an assemblage and MNTD is the mean distance separating each species in the assemblage from its closest relative. Therefore, MPD is more sensitive to tree-wide patterns of phylogenetic clustering or evenness, while MNTD is more sensitive to patterns of clustering or evenness closer to the tips of the phylogeny. We compared MPD and MNTD observed to the pattern expected under the null model of the phylogeny generated through assemblage randomization to obtain the standardized effect size of assemblage structure. The standardized effect size is the difference between phylogenetic distances in the observed assemblage versus null assemblages generated by randomization (we run 999 randomizations), divided by the standard deviation of phylogenetic distances in the null data.

Using the metric to calculate standardized effect size we can obtain the indexes of assemblage structure, NTI and NRI. MPD's standardized effect size is equivalent to -

1 times NRI and NTI is -1 times MNPD's standardized effect size. Thus, NRI is a standardized measure of the mean pairwise phylogenetic distance of the species in a sample relative to the phylogeny of the species pool and it quantifies overall clustering of species in a phylogeny (Webb et al. 2002). On the other hand, NRI is the standardized measure of the phylogenetic distance to the nearest species for each species in the sample and quantifies the extent of terminal clustering, independent of deep level clustering (Webb et al. 2002). Therefore, if NRI and NTI are negative and associated to a $p > 0.95$, the phylogenetic pattern is even, i. e., the phylogenetic distance among co-occurring species is larger than expected by chance. Positive NRI or NTI values (NRI or $NTI > 0$) and low p values ($p < 0.05$) indicate phylogenetic clustering, i. e., the phylogenetic distances among co-occurring species is smaller than expected by chance.

Additionally, we compared the assemblages from open and forested areas in the same latitude in order to evaluate the phylogenetic structure index in different types of vegetation subordinated to the same pool. Since the species pool of assemblages from the same latitude are very similar, we construct a pool considering species from the species pool of both assemblages. We considered Atlantic 1 and Cerrado 1, as a pair, and Atlantic 2 and Cerrado 2, as another pair, we then performed the analysis of phylogenetic assemblage structure.

Finally, we tested whether or not the assemblages were phenotypically structured. Morphological traits are commonly explored in multivariate space in order to evaluate whether species within assemblages are phenotypically structured due to their phylogeny or their ecology (snakes: França et al. 2008; beetles: Barton et al. 2011; fishes: Carlston & Wainwright, 2010; ants: Nipperess & Beattie, 2004). To construct a multivariate space we performed a principal components analysis (PCA) with the relative variables for each assemblage. We then measured the phenotypic structure for each assemblage through the measurement of the volume of the convex hull of a set of

traits of the multivariate space (Cornwell et al. 2006). This metric generate a clear signal for environmental filtering and provides a range of trait values. To detect competition from trait distribution we calculated the nearest neighbor distance for each species for each assemblage (Ricklefs & Travis, 1980) using Euclidean distance of relative variables. We took the standard deviation from the nearest neighbor distance and divided it by the volume of traits (relative variables) occupied for each assemblage (sdND/V). To evaluate these two approaches we used two indexes: trait clustering index (TCI) and trait evenness index (TEI), both described in detail by Ingram and Shurin (2009). These indexes were obtained by subtracting the value observed from that obtained by the null model and dividing the result by the standard deviation obtained by the null model. This result is then multiplied by minus one. The null model was obtained by the simulation of 999 null assemblages by sampling the number of species corresponding to the richness of the assemblage in question, without replacement, from the range of species for which morphological data were available. The p value was calculated by the proportion of 999 null assemblages with more extreme values than the observed one. Statistically significant p values were considered equal and/or lower than 0.05. Positive values of TCI indicate a lower range of trait values than expected by the null model and, consequently, a clustered pattern of phenotypic structure. The same is true for TEI, with positive values indicating a more evenly spaced traits than expected by the null model, which is a consequence of an even pattern of phenotypic structure.

All analysis described above were performed in R 2.14.2 (R Development Core Team, 2012). Specifically, NRI and NTI were calculated using *picante* package (Kembel et al. 2010). Using the *geometry* package we obtained the volume of convex hull using the *convhulln* function (Barber et al. 2012). The cluster and Mantel tests were performed using the *vegan* package, version 2.0-3 (Oksanen et al. 2012).

RESULTS

General patterns

The assemblages studied presented a great amount of variation in species richness and in the proportion of arboreal species: Amazonian 1, total of 61 species with 39% using the vegetation; Amazonian 2, total of 45 species with 57% using the vegetation; Atlantic 2, total of 28 species with 64% using the vegetation; Atlantic 1, total of 55 species with 54% using the vegetation; Campos 2, total of 18 species with 22% using the vegetation; Campos 1, total of 9 species with 25% using the vegetation; Cerrado 2, total of 30 species with 18% using the vegetation; and Cerrado 1, total of 42 species with 16% using the vegetation (Fig. 1). The majority of arboreal and semi-arboreal snakes are colubrids, dipsadids and boids (Fig. 1). Additionally, richness appears to be lower in assemblages from open areas, but richness tended to be significantly lower in higher latitudes, independent of the vegetation type ($R^2 = 0.8863$, $p < 0.01$, Fig. 2a). The proportion of colubrids and dipsadids in each assemblage decreases from lower to higher latitudes ($r^2 = 0.74$, $p = 0.006$; $r^2 = 0.64$, $p = 0.015$, respectively, Fig. 2b and Fig. 2c), whereas the proportion of xenodontines increases from higher to lower latitudes ($r^2 = 0.63$, $p = 0.017$, Fig. 2d).

The majority of terrestrial species belong to Xenodontinae (67%) and most species from Brazilian Grassland assemblages, composed mostly of xenodontines, are terrestrial (Fig. 1). Although the majority of arboreal and semi-arboreal species belongs to the Colubridae (37%) and Dipsadinae (54%), in Atlantic 2 most of the arboreal and semi-arboreal species belong to Xenodontinae, whereas arboreal and semi-arboreal species in Amazonian assemblages belong to Dipsadinae and Colubridae. On the other hand, for arboreal and semi-arboreal species, Atlantic 1 receives influence from the Colubridae, Dipsadinae, and Xenodontinae. Cerrado assemblages presented a

high proportion of terrestrial species when compared to the other assemblages, and Cerrado 1 presented a higher number of viperids than Cerrado 2.

Are assemblages inhabiting the same vegetation type similar?

Cluster analyses based on Euclidean distances of the species proportion of each genus revealed a consistent relationship between assemblages from open and forest areas and also with latitude (Fig. 3a). In addition, some assemblages presented a clustered pattern based on their biome, e.g. Amazonian assemblages appeared together and the same occurred with the Brazilian Cerrado and Brazilian Campos Grasslands assemblages. On the other hand, Atlantic 1 appeared closer to Amazonian assemblages and Atlantic 2 closer to assemblages with open vegetation, which is mainly present in higher latitudes. Regarding the proportion of species for each family the results illustrate a separation according to the vegetation type between the Amazonian forest and Brazilian Campos Grasslands assemblages (Fig. 3b). The effect of latitude acting in Atlantic forest assemblages is also evident. For example, the Atlantic assemblage 2 is clustered to the Cerrado assemblage 2. Mantel tests indicate that there is a significant correlation between composition and SVL ($r^2 = 0.5$; $p < 0.01$). On the other hand, relative TL ($r^2 = -0.12$; $p = 0.734$), relative HL ($r^2 = -0.07$; $p = 0.702$), relative HW ($r^2 = -0.006$; $p = 0.506$), relative HH ($r^2 = 0.002$; $p = 0.448$), relative CAM ($r^2 = 0.005$; $p = 0.437$), relative VS ($r^2 = -0.155$; $p = 0.914$) and relative SS ($r^2 = -0.126$; $p = 0.746$) were not correlated. Results from the dendrogram provided by cluster analysis indicate that assemblages with the same type of vegetation are similar in relation to their SVL (Fig. 4). For the other traits assemblages do not appear to be related to latitude or type of vegetation (Fig. 4).

Are assemblages phylogenetically structured?

We detected a significantly positive value of NRI, *i.e.*, a phylogenetic clustering pattern, in assemblages of Brazilian Campos Grassland and a significantly negative

value of NRI, *i.e.* phylogenetic evenness pattern, in assemblages of Amazonian Forest (Table 1). We were unable to find a pattern that appears to be influencing phylogenetic structure for the remaining assemblages (Table 1). Considering the pattern on the tips of the phylogeny (NTI) we found a phylogenetically clustered pattern for Atlantic 2 and Campos 1 and phylogenetic evenness pattern for Cerrado 1. We were unable to detect a pattern in the tips of the phylogeny for the remaining assemblages (Table 1).

Considering the assemblage pairs within the same latitudinal range, we did not detect a significantly phylogenetic structure. Although not statistically significant, phylogenetic structure in Atlantic 1 (NTI = -0.334; $p = 0.630$) seems to show more evenness than Cerrado 1 (NTI = 0.713; $p = 0.241$). Additionally, when we consider the phylogeny tips, Atlantic 1 (NRI = 1.303; $p = 0.115$) is more clustered than Cerrado 1 (NRI = -0.680; $p = 0.746$). In Atlantic 2 and Cerrado 2 both assemblages tend to be clustered across the phylogeny of the species pool (Atlantic 2: NTI = 0.189; $p = 0.423$; Cerrado 2: NTI = 0.508; $p = 0.303$). However, in the tips Atlantic 2 (NTI = 1.376; $p = 0.06$) is more clustered than Cerrado 2 (NTI = -1.008; $p = 0.843$).

Are assemblages phenotypically structured?

The two first axes extracted from the PCA for each assemblage explained most of the variance in morphology for all assemblages (Table 2). In all cases, the first axis is highly and negatively influenced by head measures and stoutness (Fig. 5). On the other hand, the second axis is influenced negatively by tail length and number of subcaudal scales and positively influenced by the number of ventral scales in Amazonian 2, Cerrado 1 and Atlantic assemblages (Table 2). However, the opposite occurs in Amazonian 1, Cerrado 2 and Brazilian Campos Grasslands assemblages: tail length and number of subcaudal scales are positive and the number of ventral scales is negative (Table 2). Finally, it is possible to note a gradient of head measures in the opposite direction to the number of ventral scales (Fig. 5). Additionally it is evident in

many communities that fossorial species are morphologically similar based on their natural history. Related these results to traits, the fossorial species in most of communities are distinguished by higher number of ventral scales and smaller values of head measurements. The majority of arboreal and semi-arboreal species are distinguished by longer tail length and higher number of subcaudal scales. On the other hand, the terrestrial species are characterized by larger head measurements and stoutness. However, it is possible perceive the effect of phylogeny. For example, species that compound the Boidae, Viperidae and Colubridae families appear closer, independently the habitat use of species.

Positive values of TCI, *i.e.* phenotypic assemblage structure is clustered, were detected in Atlantic 2, Cerrado 2, Campos1 and Campos 2 (Table 3). Assemblages that have phenotypically clustered pattern (with the exception of Cerrado 2) presented positive values for TEC, *i.e.* the species are evenly spaced in the volume occupied for all species (Table 3).

DISCUSSION

Our results indicate that the snake assemblages studied are, in most cases, phylogenetic structured. Amazonian assemblages are phylogenetically even, *i.e.*, they are composed mainly by species that came from different lineages, since species are more distantly related than would be expected if the assemblage was randomly assembled. Many of the Amazonian species are present in Atlantic 1, probably as a result of their geographical proximity (and common biogeographical history), but we were not able to detect a phylogenetic pattern. On the other hand, the difference in composition between Atlantic 1 and 2 may be related to the interruption of the Atlantic corridor in coastal Brazil during the Pleistocene (Carnaval et al. 2009), which prevented the species from Atlantic 1 to disperse to the region of Atlantic 2 and vice-versa. As a

result, Atlantic 2 is clustered phylogenetically, because of the influence of xenodontines in its composition (see below). Furthermore, Brazilian Campos Grasslands assemblages are clustered phylogenetically, *i.e.*, species are more related than expected. This pattern may occur because arboreal and semi-arboreal species are prevented to occupy these assemblages mainly due to the lack of adequate substrate for these species, indicating an environmental filtering (Pausas & Verdú, 2010). Finally, we encountered that Cerrado assemblages exhibit a phylogenetically random pattern across phylogeny. However, if we consider the tips of the phylogeny, Cerrado 1 is phylogenetic even, the same occurring in Amazonian assemblages, which indicates that, in this range of latitudes, there is an overlap of species distributions from different lineages (Cadle & Greene, 1993; see below), resulting in a phylogenetically even pattern. Although Brazilian Campos Grasslands and Atlantic 2 assemblages seem to be structured by environmental filtering, the composition of these assemblages may solely be a result of biogeographical processes.

Even though we detected a nonrandom phylogenetic assemblage structure, the biogeographical effect is evident. Assemblages located in lower latitudes tend to exhibit a pattern of phylogenetic evenness and the assemblages from higher latitudes tend to exhibit clustered patterns for phylogeny. These results may be related to biogeographical processes, which can influence the amount of species available to become members of a given assemblage. There are three main snakes lineages (Colubridae, Dipsadinae and Xenodontinae) occurring in the American continent and these lineages show distinct distribution patterns (Cadle & Greene, 1993). Cadle and Greene (1993) called attention to the fact that dipsadines are more diverse in Central America whereas xenodontines occur mainly in the southern part of South America and colubrids are more diverse in northeastern South America. As a result, Neotropical snake assemblages from different latitudes tend to present different proportions of these lineages (Cadle & Greene, 1993), with the diversity of colubrids and dipsadines

decreasing with the increase of latitude and the opposite trend occurring in xenodontines (e.g. this work, Bernarde, 2004; Sawaya et al. 2008). Hence, there is an overlap of lineage distributions in the northern part of South America, which could explain the phylogenetic evenness pattern in assemblages at lower latitudes and the phylogenetic clustered pattern in assemblages at higher latitudes.

The phenotypic structure also appears to be related to biogeographical processes. For Amazonian 1 and 2, Atlantic 1 and Cerrado 1 we were unable to detect a phenotypic pattern, neither clustered nor even. On the other hand, Atlantic 2, Brazilian Campos Grasslands 1 and 2 and Cerrado 2 appear to be phenotypically clustered and even, with the exception of Cerrado 2. Species of these assemblages occupy a limited morphological volume, indicating that they are phenotypically similar. However, a phenotypic clustered pattern may also arise due to lower richness (Cornwell et al. 2006). Because assemblages in higher latitudes have similar composition, their species are expected to be morphologically similar, which can result in similar niches (and competition, when resources are limited). On the other hand, assemblages from low latitudes are composed by species from distinct lineages and this can reflect differences in species morphology, which will result in a larger volume occupied by species. The phenotypically clustered pattern in Cerrado 2 and phenotypic randomness in Cerrado 1 may occur because Cerrado 1 has a higher number of viperids than Cerrado 2. These species are stouter and have larger head than other species, increasing the phenotypic volume occupancy. Moreover, the different proportion of each morphological type in an assemblage may influence the volume occupied by a species. For example, in assemblages at the same latitude it is possible perceive that Cerrado 1 has a smaller volume than Atlantic 1. This may be due to the presence of arboreal snakes in Atlantic 1. However, Atlantic 2 presented a smaller volume than Cerrado 2 and the cause may be the presence of fossorial snakes in Cerrado 2. Since arboreal and semi-arboreal snakes in Atlantic 2 came from the

Xenodontinae lineage, the same occurring with terrestrial species, indicating that some morphological modifications may be constrained by phylogeny, mainly body size (Cadle & Greene, 1993).

Our results indicate that species from forested areas have larger bodies than species from open areas. This may reflect the high proportion of arboreal and semi-arboreal species in forested areas. Larger body size may be advantageous to arboreal species for traversing gaps on substrate and distributing weight across several vegetation points (Lillywhite & Henderson, 1993; Jayne & Riley, 2007). In addition, morphology is influenced by shared ancestry and is affected by both ecological and evolutionary processes (Losos & Miles, 1994). Therefore, species morphology can be reflect the morphology of their ancestors or a convergence across clades, as a result of species experiencing similar ecological conditions (Cavender-Barres et al. 2009; Barton et al. 2011). In this sense, it is possible to use morphological traits as predictors of species ecology, because similar morphologies can evolve by convergence. When we consider all the species measured in this study, independently of the lineage, it is possible to detect morphological differences among terrestrial, arboreal, semi-arboreal and fossorial species. Fossorial species in all assemblages are distinguished by a higher number of ventral scales and smaller values of head measurements. Fossorial snakes tend to be smaller, with a small and compact head that is indistinct from the rest of the body in order to decrease friction with the ground (Savitzky, 1983). Contrastingly, arboreal snakes tend to be slender, to present a laterally flattened body and to have longer tails, in order to acquire greater mobility as a reflex of the discontinuity of their substrate (Vitt & Vangilder, 1983; Guyer & Donnelly, 1990; Lillywhite & Henderson, 1993; Martins et al. 2001). The majority of arboreal and semi-arboreal species here measured can be distinguished by presenting a longer tail length and a higher number of subcaudal scales. On the other hand, terrestrial species are characterized by larger head measurements and stoutness, in consonance with the

literature (Guyer & Donnelly, 1990; Cadle & Greene, 1993). These results indicate the effect of ecology in species morphology.

Species richness appears to be controlled from regional to local processes (e.g. Krasnov et al. 2006). As a result, the structure of species assemblages may be influenced by biogeography, making historical factors more important in assemblage ecology studies (Cornwell & Lawton, 1992). Higher richness in assemblages at lower latitudes can also be explained by a higher diversification rate in these areas (e.g. Mittelbach et al. 2007; Ricklefs, 2007; Wiens et al. 2007). Additionally, richness can be related to niche conservatism, which tends to confine some lineages to their original climatic or geographic zone conditions. For instance, the niche conservatism hypothesis suggests that the higher number of species at lower latitudes may be because the majority of lineages was originated in low latitudes where the environment is warm and mesic, so niche conservatism limits their adaptation to cold and dry regions (Wiens & Donoghue, 2004; Harrison & Grace, 2007; Hawkins et al. 2006; Wiens et al. 2007; Cadena et al. 2012). Alternatively, lineages can be restricted geographically because of their dispersion capacity (Ricklefs, 2004). However, these diversification hypotheses remain to be tested with snake lineages.

Finally, ecological and historical processes can affect species distribution. On one hand, ecological processes act in the interactions between species and their environment, typically in local scales (Gaston, 1998). On the other hand, historical factors related to biogeography act at more regional scales and can be more dominant in shaping species distributions (Gaston, 1998). This highlights the importance of biogeography in assemblage structure related to vegetation type (e.g. forested and open areas). Thus, this study corroborates the hypothesis that biogeographical processes are more important in shaping assemblages than ecological ones, *i.e.*, the amount of variation in assemblage composition is mostly explained by historical information, such as phylogeny (Vitt & Vangilder, 1983; Cadle & Greene, 1993; Vitt et

al. 1999, Mesquita et al. 2006, França et al. 2008). Therefore, the distribution of the major South American snake lineages contributes to the structure of assemblages. Moreover, the detection of morphological syndromes in assemblages may be a result of convergent evolution of traits across lineages, indicating that species responded to habitat in similar ways. However, as our analysis did not consider the phylogenetic effect, the inclusion of analysis phylogenetically controlled can provide a support for our conclusions. Additionally, as in the majority of the studies on assemblage structure, scale choice may influence the detection of ecological processes, even though biogeographical processes seem to be more important in structure assemblages. Furthermore, studies considering how the diversification in major lineages occurred can help clarify the question about variation in species richness in different assemblages. And finally, the inclusion of other ecological aspects, such as the relationship between diet and prey abundance, can lead to a better understanding of the differences in the composition of assemblages from forested and open areas.

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Figure 1. Number of snakes' species in each community indicated by lineage (Aniilidae (ani), Anomalepididae (ano), Boidae (b), Colubridae (c), Dipsadinae (d), Elapidae (e), Leptotyphlopidae (l), Viperidae (v) and Xenodontinae (x)) and habitat use (terrestrial (t), semi-arboreal (s), arboreal (a) and fossorial (f)).

Figure 2. Linear regression of species richness (a), proportion of Colubridae species (b), proportion of Dipsadinae species (c) and proportion of Xenodontinae species (d) against the latitude of each community.

Figure 3. Dendrogram represent proportion of species of each genus (a) and proportion of species of each family (b).

Figure 4. Dendrogram represent the proximity of assemblages based on their traits (SVL, TL, HL, HW, HH, CMC, VS and SS).

Table 1. Values of phylogenetic assemblage structure index for each assemblage. Negative values of NRI and NTI and $p > 0.95$ indicate phylogenetic evenness. Positive values of NRI and NTI and $p < 0.05$ indicate phylogenetic clustering.

Assemblage	Phylogenetic assemblage structure index			
	NRI	p	NTI	p
Amazonian 1	-1.508	0.950	-0.622	0.752
Amazonian 2	-1.994	0.981	-0.249	0.579
Atlantic 1	-0.288	0.595	1.303	0.108
Atlantic 2	0.127	0.435	1.420	0.052
Cerrado 1	0.437	0.317	-1.684	0.950
Cerrado 2	0.606	0.259	-0.945	0.825
Campos 1	2.820	0.006	1.434	0.050
Campos 2	1.440	0.050	0.717	0.246

Table 2. Factor loadings for each relative trait on the first two principal components and the proportion of the variance explained by two components. C1 is component 1 and C2, component 2.

Traits	Assemblages															
	Amazonian 1		Amazonian 2		Atlantic 1		Atlantic 2		Cerrado 1		Cerrado 2		Campos 1		Campos 2	
	C1	C2	C1	C2	C1	C2	C1	C2	C1	C2	C1	C2	C1	C2	C1	C2
Tail length	0.119	0.670	0.318	-0.564	0.129	-0.650	0.369	-0.547	-0.153	-0.641	0.017	0.671	0.370	0.555	0.213	0.667
Head length	-0.455	0.268	-0.406	-0.346	-0.465	-0.189	-0.437	-0.334	-0.467	-0.033	-0.465	0.068	-0.389	0.296	-0.417	0.273
Head width	-0.495	0.062	-0.444	-0.083	-0.472	0.059	-0.476	-0.086	-0.441	0.226	-0.467	-0.083	-0.398	-0.116	-0.432	0.134
Head height	-0.515	0.063	-0.441	-0.107	-0.481	-0.016	-0.495	-0.110	-0.458	0.148	-0.467	-0.046	-0.356	0.204	-0.433	0.167
Stoutness	-0.464	-0.099	-0.443	-0.031	-0.456	0.014	-0.108	0.223	-0.428	0.221	-0.434	-0.106	-0.390	-0.075	-0.432	-0.061
Ventral scales	0.171	-0.239	0.193	0.546	0.279	0.427	0.220	0.603	0.402	0.209	0.396	-0.292	0.345	-0.655	0.393	-0.211
Subcaudal scales	0.158	0.636	0.331	-0.495	0.162	-0.596	0.375	-0.394	-0.099	-0.650	0.045	0.663	0.394	0.338	0.255	0.622
Eigenvalue	1.876	1.435	2.221	1.249	1.999	1.479	1.936	1.207	2.097	1.459	2.098	1.479	2.445	0.766	2.199	1.313
Variables explained																
Percent	50.29	29.42	63.73	22.32	57.12	31.25	53.57	20.83	62.87	30.43	62.93	31.25	85.45	8.398	69.08	24.64
Cumulative	50.29	79.712	63.73	86.05	57.12	88.38	53.57	74.41	62.87	93.31	62.93	94.19	85.45	93.85	69.08	93.73

Figure 5. Continued.

Figure 5. Continued.

Figure 5. Continued.

Figure 5. Plots of factors scores from two principal components for snakes' species of Brazilian Cerrado. The PCA were performed with relative variables. In the first plot species are represented by habitat use: terrestrial (t), semi-arboreal (s), arboreal (a) and fossorial (f). In the second plot species are represented by lineage: Aniliidae (ani), Anomalepididae (ano), Boidae (b), Colubridae (c), Dipsadinae (d), Elapidae (e), Leptotyphlopidae (l), Viperidae (v) and Xenodontinae (x).

Table 3. Values of phenotypic assemblage structure index for each assemblage. Positive values of TCI and $p < 0.05$ indicate phenotypic clustered. Positive values TEI and $p < 0.05$ indicate phenotypic evenness.

Assemblage	Phenotypic assemblage structure index				
	TCI	p	Volume	TEI	p
Amazonian 1	-2.341	0.147	1.26e-06	-0.958	0.766
Amazonian 2	-2.341	0.969	2.37e-07	0.943	0.151
Atlantic 1	-3.628	0.990	2.73e-07	-1.761	0.939
Atlantic 2	1.066	0.001	2.13e-09	1.294	0.018
Cerrado 1	0.637	0.296	1.03e-07	0.084	0.531
Cerrado 2	1.065	0.016	6.08e-09	0.634	0.305
Campos 1	1.292	0.001	5.30e-10	1.150	0.045
Campos 2	0.946	0.002	1.05e-10	1.093	0.050

CONCLUSÃO GERAL

Apesar das diferenças na composição e nos atributos das espécies o tipo de vegetação (fechada ou aberta) não parece ser o fator que influencia na estrutura filogenética e fenotípica das comunidades de serpentes estudadas. Os fatores históricos relacionados à biogeografia agem em escalas regionais e podem ser o fator dominante na estruturação de comunidades por determinar a distribuição das espécies do pool regional (Gaston, 1998). De fato neste estudo a biogeografia se mostrou como sendo o principal fator para estruturação de comunidades de serpentes neotropicais.

Existem três linhagens principais de serpentes (Colubridae, Dipsadinae e Xenodontinae) que ocorrem na América do Sul, as quais possuem certas restrições geográficas (Cadle & Greene, 1993). Cadle e Greene (1993) estudaram várias comunidades do continente sul americano e descobriram que a espécie da subfamília Dipsadinae ocorre com maior frequência na América Central, já as espécies de Colubridae ocupam principalmente a região norte da América do Sul, enquanto que, em contraste, as espécies de Xenodontinae ocorrem na porção sul do continente americano. Dessa forma, as comunidades de serpentes Neotropicais apresentam diferentes riquezas e proporção de espécies das diferentes linhagens. Assim, como já anteriormente reportado na literatura, a riqueza de Colubridae e Dipsadinae tende a diminuir com o aumento da latitude e o oposto ocorre com Xenodontinae, que tende a contribuir com menos espécies com a diminuição da latitude (e.g. este trabalho, Bernarde, 2004; Sawaya et al. 2008).

Portanto, este estudo corrobora a hipótese que o processo biogeográfico é mais importante na estruturação das comunidades do que os ecológicos, mostrando que o fator histórico é o principal responsável pela variação de composição em comunidades (e.g. Vitt & Vangilder, 1983; Cadle & Greene, 1993; Vitt et al. 1999; Mesquita et al. 2006; França et al. 2008). Como a maioria dos estudos de estrutura de comunidades, a escolha da escala espacial pode afetar a detecção de processos

ecológicos como responsáveis pela estrutura das comunidades. Além disso, a inclusão de outros aspectos ecológicos, tais como dieta, abrangendo a relação entre dieta e abundância de presas, pode levar a um melhor entendimento das diferenças entre comunidades de tipos de vegetação distintos.

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