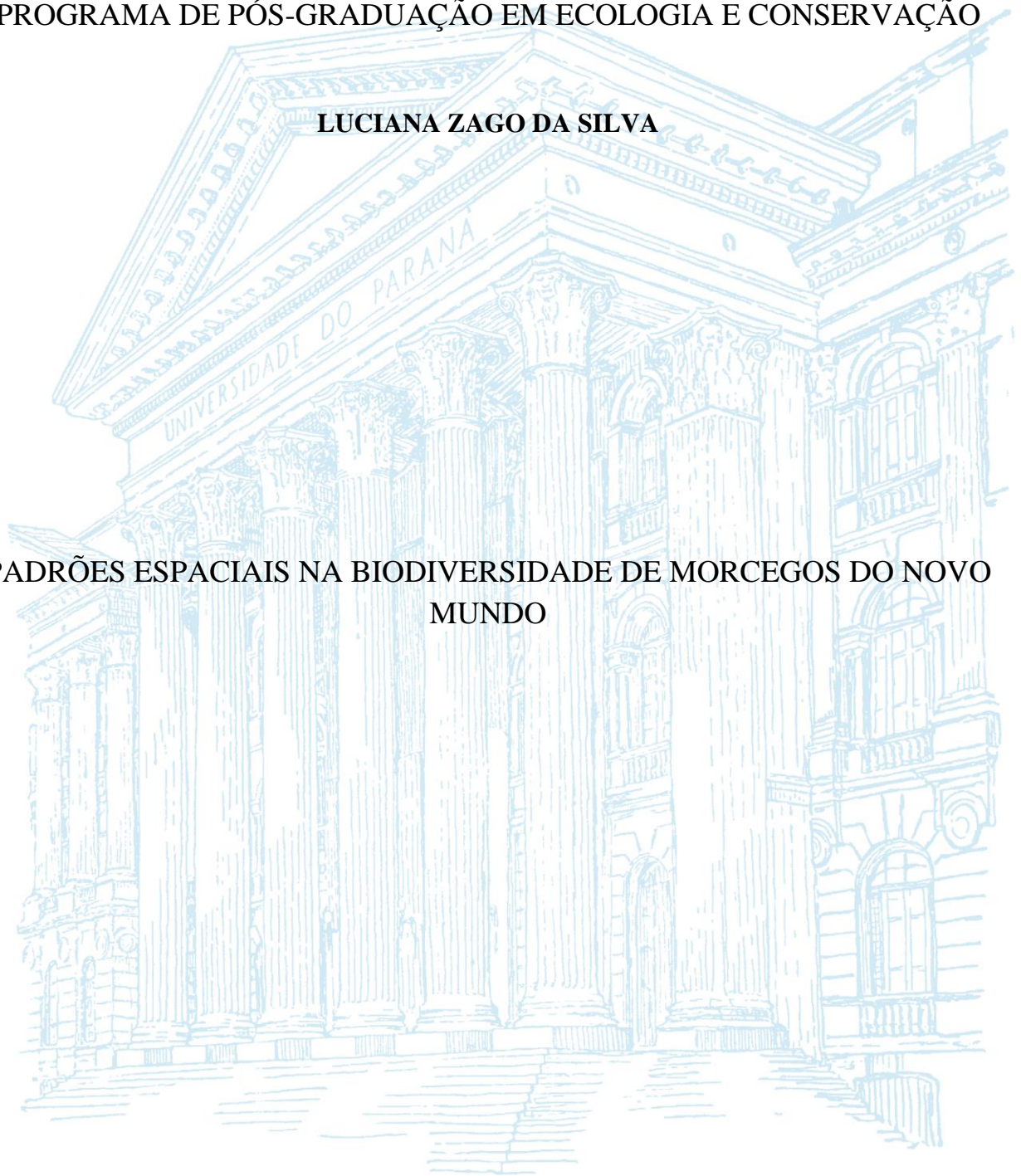


UNIVERSIDADE FEDERAL DO PARANÁ  
PROGRAMA DE PÓS-GRADUAÇÃO EM ECOLOGIA E CONSERVAÇÃO

**LUCIANA ZAGO DA SILVA**

PADRÕES ESPACIAIS NA BIODIVERSIDADE DE MORCEGOS DO NOVO  
MUNDO



CURITIBA  
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Tese apresentada ao Programa de Pós-Graduação em Ecologia e Conservação, Setor de Ciências Biológicas da Universidade Federal do Paraná, como requisito parcial a obtenção do título de Doutora em Ecologia.

Orientador: Prof. Dr. Fernando C. Passos

Coorientador: Prof. Dr. Mauricio O. Moura

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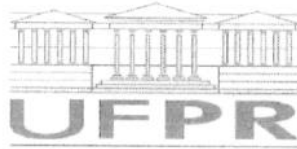
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## RESUMO

A compreensão dos padrões espaciais da biodiversidade e os processos que os modulam estão entre os objetivos mais antigos dos estudos ecológicos. Entretanto, a maioria dos estudos que tentam compreender estes padrões e processos são feitos apenas com uma medida de diversidade: a riqueza de espécies. A riqueza de espécies representa apenas uma dimensão da biodiversidade, sendo uma abordagem incompleta para se compreender os processos evolutivos e ecológicos que modulam esses padrões. O presente trabalho tem o objetivo de elucidar os possíveis processos envolvidos na determinação dos padrões espaciais da diversidade de morcegos do Novo Mundo sob abordagens com diferentes dimensões da biodiversidade. No primeiro capítulo, as dimensões taxonômica, filogenética e funcional da biodiversidade são abordadas simultaneamente. Com essa abordagem, nossos resultados apontaram a existência de regiões com diversidade funcional abaixo e acima do esperado pela diversidade filogenética e apresentaram padrões diferentes para as diferentes famílias de morcegos. Esses resultados estão relacionados principalmente a fatores espaciais e à variável ambiental temperatura média anual. Assim, estruturas geográficas, filtros ambientais e a conservação ou evolução de nicho parecem modelar sinergicamente os padrões de diversidade encontrados. No segundo capítulo abordamos a partição da beta diversidade filogenética em componentes de aninhamento e substituição de linhagens para os diferentes biomas do Novo Mundo. Essa abordagem apontou o aninhamento filogenético como principal fenômeno modelador da betadiversidade filogenética de morcegos do Novo Mundo. O agrupamento de biomas de acordo com suas dissimilaridades filogenéticas apontou a existência de três grandes grupos com mais de 50% de dissimilaridade. Um dos grupos é composto por biomas tropicais e subtropicais, um segundo grupo é composto por biomas temperados e mediterrâneos e um terceiro grupo é formado pelos biomas temperados mais frios. Assim, filtros ambientais parecem ser as principais forças atuantes na modulação das assembleias destes biomas. Além disso, esses resultados reforçam que limitações fisiológicas provavelmente são mais importantes que a habilidade de dispersão para a formação de assembleias de morcegos.

Palavras-chave: Chiroptera; Macroecologia; Diversidade Funcional; Diversidade Filogenética; Betadiversidade.

## **ABSTRACT**

The understanding of spatial patterns of biodiversity and the process that module this patterns are between the oldest goals of ecological studies. However, most studies that try to understand these patterns and process are made only with one metric of diversity: the species richness. The species richness presents only one dimension of biodiversity and is an incomplete approach to the understand of evolutionary and ecological process that module these patterns. The present study aims to elucidate the possible patterns involved in the spatial patterns of New World bat diversity with different biodiversity dimensions approaches. At the first chapter the taxonomic, phylogenetic and functional biodiversity dimensions are addressed simultaneously. With this approach, our results pointed to the existence of regions with functional diversity lower and above the expected by phylogenetic diversity and the different bat families present different patterns. These results are related mainly to spatial factors and to the environmental variable annual mean temperature. Therefore, geographical structures, environmental filtering and the niche conservation or evolution seems to drive synergistically the diversity patterns we found. At the second chapter we addressed the phylogenetic beta diversity partition in nestedness and turnover components to the different New World biomes. This approach pointed the phylogenetic nestedness as the mainly driver of New World phylobetadiversity. The grouping of biomes according to their phylogenetic dissimilarities pointed the existence of three large groups with more than 50% dissimilarity. One of the groups is composed by tropical and subtropical biomes, a second group is composed by temperate and mediterranean biomes, and a third group is composed by the coldest temperate biomes. Therefore, environmental filters seem to be the mainly forces driving these biomes assemblages. Besides, these results reinforce that physiological constraint probably are more important than the dispersion ability to bat community assembly.

Keywords: Chiroptera; Macroecology; Functional Diversity; Phylogenetic Diversity; Beta diversity.

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## **INTRODUÇÃO GERAL**

## **Padrões e processos ecológicos e medidas de biodiversidade**

A compreensão dos padrões espaciais da biodiversidade e os processos que os modulam estão entre os objetivos mais antigos dos estudos ecológicos (Hawkins, 2001). Com as expedições de historiadores naturais europeus, nos séculos XVIII e XIX, a compreensão de padrões na biodiversidade tornou-se ainda mais desafiadora, passando a ser investigada em escalas globais (Ricklefs, 2004). Alexander von Humboldt em 1808, por exemplo, publicou o seu reconhecimento da presença de um padrão latitudinal na diversidade biológica (Hawkins, 2001).

Contudo, foi no só no século XX, a partir de eventos como a Rio 92, que os impactos humanos sobre a biodiversidade passaram a não ser preocupações só científicas. O conhecimento da biodiversidade passou a ser também uma preocupação pública e política (Magurran, 2004). Diante deste contexto, para se avaliar quais ações devem ser prioritárias para a conservação da biodiversidade, é fundamental que se tenha medidas mais completas da biodiversidade. Entretanto, não há um consenso quanto ao conceito de biodiversidade e muitos estudos utilizam apenas a riqueza de espécies para sua medida (Magurran, 2004).

Embora a riqueza de espécies possa revelar padrões biogeográficos, ela considera apenas alguns aspectos da dimensão taxonômica desta diversidade (Wilsey *et al.*, 2005). Assim como a riqueza, outras medidas taxonômicas da diversidade que consideram apenas nomes e números de espécies pouco revelam sobre as funções ecológicas e histórias evolutivas destas espécies na comunidade (Swenson, 2014). Por exemplo, um ecossistema marinho polar pode ter exatamente o mesmo número ou diversidade de espécies (por índices que consideram apenas riqueza e abundância) de um ecossistema terrestre desértico tropical, e assim, se parecerem sob estas perspectivas taxonômicas da biodiversidade. Entretanto, claramente esses são ambientes que possuem organismos funcionalmente e filogeneticamente muito diferentes. Assim, utilizando-se apenas essa abordagem taxonômica da biodiversidade, será muito difícil se compreender os processos envolvidos na formação das comunidades destes ecossistemas tão diferentes.

A necessidade de se expandir a compreensão da diversidade incorporando aspectos evolutivos levou a criação de diferentes medidas desta diversidade. Abordagens com dimensões taxonômicas mais completas passaram a considerar as

relações evolutivas por meio da inserção de informações cladísticas das espécies. Com essa nova abordagem, novas perspectivas foram dadas para ecologia como um todo, sendo destacada a sua utilização para a seleção de áreas prioritárias para a conservação. Passamos a ter uma medida mais completa da biodiversidade, que considera não só riqueza e abundância de espécies, mas também as relações evolutivas das mesmas (Vane-Wright *et al.*, 1991).

Embora as análises de dimensões taxonômicas da biodiversidade tenham sido muito aprimoradas ao longo do tempo, elas permanecem incompletas, já que desconsideram as diversidades de funções ecológicas e não abordam todas as informações de relações evolutivas que ferramentas atuais nos permitem ter hoje. Em função disto, novas abordagens com medidas de outras dimensões da biodiversidade foram desenvolvidas. Com o desenvolvimento de melhores técnicas para se inferir relações filogenéticas, novas medidas de diversidade puderam considerar o comprimento de ramos de filogenias, permitindo a interpretação não só de dimensões taxonômicas, mas também filogenéticas das comunidades (Faith, 1992).

Dimensões funcionais também foram desenvolvidas, primeiramente considerando o número de grupos funcionais existentes em uma assembleia. Entretanto, essas abordagens estavam expostas a uma subjetividade quanto à forma como estes grupos funcionais seriam delineados e as espécies que neles deveriam ser incluídas (Magurran, 2004). Posteriormente, novas abordagens passaram a medir a diversidade funcional a partir do comprimento de ramos de um dendrograma construído a partir das características funcionais das espécies (Petchey & Gaston, 2002), tendo-se uma abordagem mais semelhante a utilizada para se mensurar a diversidade filogenética.

O desenvolvimento dessas novas abordagens incluindo mais dimensões da biodiversidade possibilitou uma melhor compreensão de processos ecológicos e evolutivos e novas abordagens para seleção de áreas prioritárias para a conservação (Faith, 1992; Petchey & Gaston, 2002). Entretanto, os padrões globais de biodiversidade não resultam apenas de processos ecológicos e evolutivos isolados, mas sim de efeitos sinérgicos destes processos (Wiens & Donoghue, 2004). Assim, nenhuma destas dimensões sozinhas é capaz de representar toda a complexidade de uma comunidade. Se trabalhadas de maneira isolada, essas dimensões são insuficientes para compreendermos os processos que resultam nos padrões de diversidade medidos nestas abordagens.

Abordagens com o estudo simultâneo de padrões filogenéticos e ecológicos e cooperação de áreas como biogeografia e ecologia podem ser mais esclarecedoras

quanto a ação sinérgica de diferentes processos (Wiens & Donoghue, 2004; Kluge & Kesser, 2011; Safi *et al.*, 2011). Portanto, estes trabalhos devem considerar a análise conjunta das diferentes dimensões da biodiversidade. Além disso, compreender como estas dimensões de diversidade diferenciam-se de ambiente para ambiente é fundamental para se determinar a importância de fenômenos como a substituição ou a perda de espécies, linhagens ou funções ecológicas entre ambientes. Diferentes abordagens com medidas de beta diversidade podem ser utilizadas para este fim, fazendo-se a partição de diferentes dimensões da beta diversidade nos componentes de aninhamento e substituição de espécies, ou *turnover* (Baselga, 2010; Leprieur *et al.*, 2012).

### **Quirópteros como modelos para estudos de padrões e processos ecológicos**

Os morcegos pertencem à ordem Chiroptera, a segunda maior ordem dentre os mamíferos (Wilson & Reeder, 1993), e possuem uma grande variedade de tamanhos, formas, dietas, formas de forrageio e tipos de abrigos (Simmons & Conway, 2003; Patterson *et al.*, 2003). Estes mamíferos são responsáveis pela regulação de processos ecológicos complexos através de ações como a polinização e a dispersão de sementes (Fleming & Heithaus, 1981) e o controle populacional de insetos (Cleveland *et al.*, 2006). Além disso, a ordem Chiroptera é a única ordem dentre os mamíferos com indivíduos capazes de efetuarem voo verdadeiro (Simmons, 2005) e, portanto, de dispersarem até mesmo sobre a água (Morgan & Czaplewski, 2012).

No Novo Mundo há mais de 300 espécies de morcegos (Wilson & Reeder, 1993) que, de maneira geral, seguem o padrão de aumento da diversidade com a aproximação da região tropical (Stevens & Willig, 2002; Willig *et al.*, 2003b; Stevens, 2004; Willig & Bloch, 2006). Estes morcegos são de nove diferentes famílias (Phyllostomidae, Vespertilionidae, Molossidae, Mormoopidae, Emballonuridae, Noctilionidae, Furipteridae, Thyropteridae, Natalidae), sendo que seis delas são endêmicas da região Neotropical (Phyllostomidae, Mormoopidae, Noctilionidae, Furipteridae, Thyropteridae, Natalidae), com apenas poucas espécies de Phyllostomidae e Mormoopidae atingindo o Neártico na península da Flórida ou no Sudeste dos Estados Unidos.

Diante de sua grande diversidade de espécies, famílias e funções ecológicas, os morcegos são bons modelos para se estudar processos ecológicos sob abordagens com diferentes dimensões. Cisneros *et al.* (2014), por exemplo, utilizaram uma abordagem com o estudo simultâneo das dimensões taxonômica, filogenética e funcional de morcegos em um gradiente altitudinal neotropical para compreender os mecanismos que podem estar atuando sobre a biodiversidade neste gradiente. Em um importante contexto de alterações antrópicas na paisagem, Cisneros *et al.* (2015) utilizaram uma semelhante abordagem com as mesmas três dimensões de diversidade para entender os processos ambientais e espaciais que podem levar a alterações nas assembleias de morcegos. Já Peixoto *et al.* (2014), em uma abordagem global, utilizaram uma medida de beta diversidade filogenética para entender os processos evolutivos que levaram aos padrões filogenéticos de morcegos encontrados atualmente.

Diante do contexto atual de utilização de abordagens multidimensionais da biodiversidade para compreendermos os diferentes processos atuantes em diferentes escalas espaciais, o presente estudo almeja a ampliação do conhecimento de padrões e processos evolutivos e ecológicos na diversidade de morcegos sob duas abordagens ainda não realizadas para este táxon. A primeira, presente no primeiro capítulo deste trabalho, discorre sobre padrões multidimensionais na diversidade de morcegos do Novo Mundo e os processos bióticos e abióticos que podem os modular. As dimensões taxonômica, funcional e filogenética da diversidade de morcegos são trabalhadas em conjunto para se determinar estes possíveis processos. Já em uma segunda abordagem, referente ao segundo capítulo, estudamos os padrões existentes na beta-diversidade filogenética de morcegos nos biomas do Novo Mundo para entender os processos biológicos atuantes na determinação de fenômenos de substituição ou aninhamento de linhagens de morcegos entre diferentes ambientes.

CAPÍTULO 1

**MULTIDIMENSIONAL PATTERNS OF NEW WORLD BAT  
DIVERSITY**

## 1.1 INTRODUCTION

Effective conservation strategies and policies depend on the knowledge of spatial biodiversity patterns and the processes that drive them. One of the most known and studied spatial biodiversity patterns is the increase of species diversity from the poles to the Equator (Hawkins, 2001) or the latitudinal diversity gradient (LDG). Although there are few studies that account for LDG exceptions (Willig *et al.*, 2003a; Morinière *et al.*, 2016), most taxa follow this pattern (Willig *et al.*, 2003a) even at different ecological scales (Stevens & Willig, 2002), including New World bats (Stevens & Willig, 2002; Willig *et al.*, 2003b; Willig & Bloch, 2006). Since the 19th century, more than thirty hypotheses were proposed to explain this pattern (Hawkins *et al.*, 2003; Willig *et al.* 2003a; Brown, 2014), and in the last few decades, this pattern became clear not only to species of plants and animals, but also to genomes and clades of higher taxa. However, even with recent new approaches and techniques, the LDG explanations have remained equivocal (Brown, 2014; Morinière *et al.*, 2016).

The LDG explanations have been focused mostly on ecological or historical process and are supported by empirical and theoretical evidences (Willig *et al.* 2003a; Brown, 2014). For example, according to the “out of the tropics” model, the tropics are both a “cradle” and a “museum” of biodiversity, because most taxa originate there and expand toward the poles without losing their tropical presence (Jablonski *et al.*, 2006). This is a historical approach that suggests that LDG is a result of past events. On the other hand, according to the tropical niche conservatism hypothesis (NC), species tend to retain niche-related ecological traits over time and, therefore, the species dispersal out of the tropics is limited by these traits retention (Wiens *et al.*, 2010). This is a historical, ecological and evolutionary approach which suggests that LDG is not only caused by past events, this is a pattern caused and maintained by biological responses to abiotic conditions (Brown, 2014).

The NC is a broader approach that account for process that can be acting synergistically and improve our knowledge about LDG process. However, this hypothesis does not explain by itself several issues of LDG (Brown, 2014). And for bats, NC can play a role in the diversity of families with tropical origins that is not found in Vespertilionidae, a family with temperate origin (Pereira & Palmerim, 2013).

Therefore, the relative effects of historical, ecological or climatic processes can be context-dependent and climate and history probably interact, which can difficult the isolation of the NC process (Stevens, 2011).

Some gaps in the hypotheses that try to explain LDG can be related to the majority of latitudinal gradients studies, that uses species richness as a surrogate for biodiversity (Stevens & Willig, 2002). Although species richness is very informative about biogeographic patterns, this is a taxonomic view of biodiversity (Wilsey *et al.*, 2005; Stevens *et al.*, 2006) that offers limited information about the ecological and evolutionary process that module them (Swenson, 2014). Global patterns of biodiversity can result from different ecological and evolutionary processes (Wiens & Donoghue, 2004) that may not be understood by the perspective of a taxonomic view alone. For example, Stevens *et al.* (2006) found that latitudinal gradients in bat phenetic diversity were not solely a consequence of species richness patterns. Therefore, we can better understand the global patterns of biodiversity, if the term “biodiversity” do not be restricted to a taxonomic approach, and be expanded to ecological and evolutionary approaches.

Biodiversity approaches considering evolutionary and ecological components, such as phylogenetic or functional measures of biodiversity, have been used to better understand ecological and evolutionary processes that modulate biodiversity at different scales (e.g. Safi *et al.*, 2011; Cisneros *et al.*, 2014). Phylogenetic diversity (PD) is a measure of evolutionary differences among species based on the time of species divergence (Faith, 1992), so it can be used to better understand evolutionary processes. Peixoto *et al.* (2013), for example, used a phylogenetic beta diversity approach to investigate the processes that lead to bat lineages differentiation. Functional diversity (FD), on the other hand, is a measure of interspecific differences in ecological attributes based on species traits (Schleuter *et al.* 2010), so it can be used to better understand ecological processes. Cisneros *et al.* (2015) used FD to account for effects of human-modified landscapes on bat diversity, and found characteristics that promote bat ecosystem functions.

Spatial patterns of biodiversity are not the result of ecological or evolutionary processes separately, but from a synergetic effect of different ecological and evolutionary processes (Wiens & Donoghue, 2004). A recent approach proposed by Safi

*et al.* (2011) includes both PD and FD measures to better understand the synergetic effects of ecological and evolutionary processes. Since PD represents the accumulated amount of evolutionary history, and is a measure of time, the divergence of functional traits has to be related to PD. Although this relationship is yet not completely known, these authors suggest a nonlinear relationship in which FD is expected to increase with PD until a limit. This limit marks a point from which the time of species divergence can increase, but the functional traits divergence cannot (Fig 1). In other words, the species can always diverge from each other and these species functional traits are expected to diverge at the same rates of phylogenetic divergence. However, these species traits can diverge only up to a limit, since there is a limit of possible traits to species.

The expected relationship between PD and FD can be used to infer ecological and evolutionary processes that can drive biodiversity patterns (Fig 1). Communities or assemblages with FD lower than expected by PD, for example, result from processes that lead the species to diverge functionally slower than phylogenetically. On the other hand, communities with FD above that expected by PD result from processes that lead to the species to diverge functionally faster than phylogenetically. Therefore, FD below or above the expected can be the result of several non-mutually exclusive processes. For example, if a community is in an area of limited resources, the species should occupy wider ecological niches to secure their energy intake; therefore, this community should be more functionally over-dispersed. In addition, if this area is very environmentally heterogeneous, the coexisting species should adapt to different environmental conditions, which can reinforce the functional over-dispersion (Fig 1). On the other hand, if a community is in an area of very harsh climatic conditions and low environmental heterogeneity, the species should specialize to these conditions; therefore, the community should be less functionally distinct than the expected (Fig 1).

This multidimensional approach is a good alternative to the characterization of the spatial patterns of New World bats biodiversity. Bats are the second richest mammal family (Wilson & Reeder, 1993) and have a great variability of ecological functions (Simmons & Conway, 2003; Patterson *et al.*, 2003). Therefore, they are also a good model to the study of phylogenetic and functional diversity patterns and process. Here we investigate PD and FD relationship and FD divergences of the expected by PD to search for the drivers of bat biodiversity spatial patterns. We hypothesized that FD is greater than expected by PD at tropical regions, since the space of these regions are

more environmentally heterogeneous (Ricklefs, 1977); in the same way, we hypothesized that FD is lower than expected at temperate regions, since the space of these regions are more environmentally homogeneous (Ricklefs, 1977) and have harsh climatic conditions that can act as environmental filters (Algar *et al.*, 2011). Also, we hypothesized that FD deviations from the expected by PD are more driven by the environmental characteristics (annual mean temperature, precipitation seasonality and canopy height) than by the spatial structure or the species richness of the areas, and that annual mean temperature is a better predictor of these deviations than precipitation seasonality or canopy height. And, since the bat families have different origins that can be exposed to different processes (e.g. Pereira & Palmerim, 2013), we expect that the processes driven the three major bat family's diversity are different.

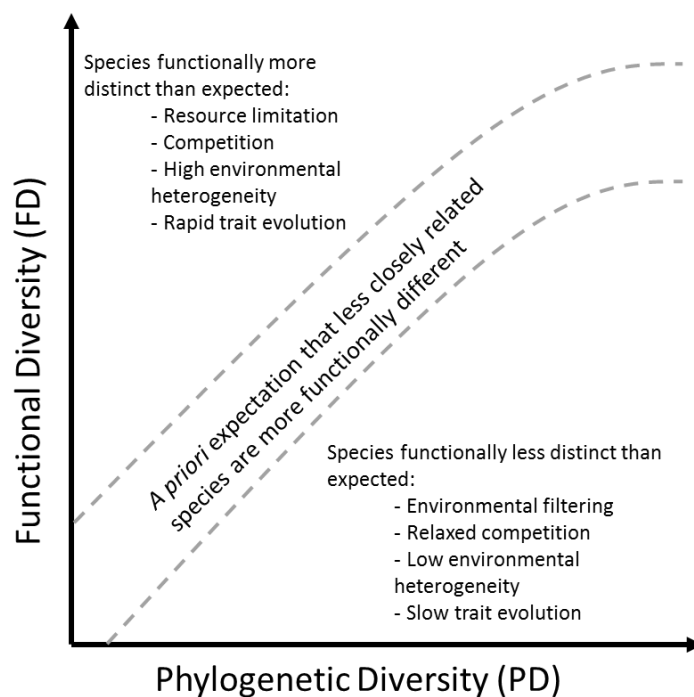


Fig 1: Expected phylogenetic and functional diversity relationship, and possible drivers of this relationship deviations (Adapted from Safi *et al.*, 2011).

## 1.2 METHODS

### 1.2.1 Species distributions and diversity metrics

We used the New World bat species distribution maps of NatureServe version 2 (Patterson *et al.* 2007). The continental New World was divided into 100 x 100 Km grid

cells and bat distributions were overlapped to the grid. We used equal-area Goodes Homolosine projection to allow diversity measures represents similar cells areas independent of their latitudinal position. Each grid cell was considered occupied by those species whose distribution overlapped at least 50% of the cell. Using these species compositions, we estimated taxonomic (TD), phylogenetic (PD) and functional diversity (FD) for each grid cell. Since the evolutionary and ecological processes can act at different taxonomic scales, we also estimated these three measures to the major New World bat families: Phyllostomidae, Vespertilionidae and Molossidae.

There are several taxonomic diversity measures available in the literature, here we consider TD as the number of species occurrences in each grid cell. PD is a measure that uses the sum of branch lengths between taxa in a phylogenetic tree to assess species relatedness in a community. We calculated the commonly used PD metric, the mean pairwise distance method or mpd (Swenson, 2014), using a recent species level mammalian phylogenetic supertree (Fritz *et al.*, 2009). This supertree included divergence times and the phylogenetic relationships of 5020 mammal species. To avoid bias, bat species that aren't present in the phylogenetic supertree were pruned from the database, resulting in a loss of 17 species from the initial 293 (5.8% of the species).

In the same way, we calculated FD by mean pairwise distance (Swenson, 2014) but using a trait dendrogram. Thus, we used the sum of branch lengths between taxa of a trait dendrogram to assess the species trait similarity (low values) or trait distance (high values) in a community. We generated the trait dendrogram with size, diet, foraging strategy and roost type attributes (Table 1). Missing categorical data, when possible, were imputed by values from congeners. We used Gower distance to produce the distance matrix and trait dendrogram.

There are several other metrics to compute TD, PD and FD. We chose species richness to TD because this is the simplest and the most used metric to biodiversity, therefore, it allows more comparisons with other studies. In the same way, we choose the mean pairwise distance to PD and FD because this is a commonly used index and is highly correlated with other metrics, which are redundant among each other (Swenson, 2014).

### 1.2.2 Environmental data

We extracted the environmental variables annual mean temperature and precipitation seasonality at a 10' resolution from WorldClim 1.4 (Hijmans *et al.*, 2005), and canopy height from SDAT (Simard *et al.* 2011). These environmental data resolutions were rescaled to grid cells averaging the values. We tested for multicollinearity among variables using the variance inflation factor (VIF) and model multicollinearity using the Condition Number (CN) approach. All environmental variables had VIF values lesser than 10 and the largest CN was 5.2, which are both indicative of low multicollinearity, so we used all these variables as predictors in statistical analyses.

Table 1: Trait attributes used to estimate functional diversity of New World bats, and its references.

Data type	Functional component and references	Attribute	Trait value
Categorical	Diet (Nowak, 1994; Eisenberg & Redford, 1999; Redford & Eisenberg, 1992; Gardner, 2008; Reid, 2009; Ceballos, 2014, Hurtado <i>et al.</i> 2014)	fruit or plant	0, 1
		nectar or pollen	0, 1
		invertebrates	0, 1
		tetrapods	0, 1
		Fish	0, 1
		blood	0, 1
	Foraging strategy (Nowak, 1994; Gardner, 2008; Reid, 2009; Ceballos, 2014; Mammalian Species, 2016)	aerial	0, 1
		gleaning	0, 1
		hover	0, 1
		pounce	0, 1
	Roost type (Nowak, 1994; Eisenberg & Redford, 1999; Redford & Eisenberg, 1992; Gardner, 2008; Reid, 2009; Ceballos, 2014; Mammalian Species, 2016)	tree cavities	0, 1
		foliage or branches	0, 1
		termite nest	0, 1
		bird nest	0, 1
		buildings	0, 1
Continuous	Size (Smith <i>et al.</i> 2003; Bernardi <i>et al.</i> 2007; Jones <i>et al.</i> 2009; Mammalian Species, 2016; Hurtado <i>et al.</i> 2014)	forearm length	Mean (mm)
		body mass	Mean (g)

### 1.2.3 Analysis

We tested the relationship between PD and FD measures along the New World by linear regressions. Cells with zero value were excluded from these analyses. After

fitting the linear model (Fig 2) we use the residuals ( $FD_{res}$ ) as our response variables for all analyses, since these values represent FD that were distant from expected by PD, and therefore, can be used to infer ecological and evolutionary processes (Fig 1).  $FD_{res}$  were plotted in the New World map. We tested the relative importance of environmental variables in explaining  $FD_{res}$  using the standardized coefficients of the best OLS models selected by Akaike information criterion (AIC) approach. Positive (residuals  $\geq$  zero) and negative (residuals  $\leq$  zero)  $FD_{res}$  were analyzed separately because they represent, respectively, species functionally more or less distinct than expected, which we expected to be derived from different ecological and evolutionary processes (Fig 1).

The majority of statistical approaches used for biodiversity analyses assume the independence of the data (Diniz-Filho & Bini, 2005). However, pairs of data across a geographical space are not independent, there is a spatial autocorrelation (Fortin & Dale, 2005). Therefore, we tested spatial autocorrelations in our models residuals using Moran's I correlogram (Sokal & Oden, 1978). Since the tests pointed to the presence of spatial autocorrelations, we added linear combinations of spatial filters (Spatial EigenVectors Mapping - SEVM) to the models to reduce the spatial autocorrelations of these residuals, the approach suggested by Diniz-Filho & Bini (2005) to eliminate this statistical bias.

We also conducted partial regressions to partition the  $FD_{res}$  variance into purely environmental, spatial (SEVM), and taxonomical (TD) components. This way we could address the specific variations on  $FD_{res}$  due to environment, spatial structure or species richness. The analyses of model selection, spatial autocorrelations and partial regressions were conducted using SAM v. 4.0 (Rangel *et al.*, 2006).

### **1.3 RESULTS**

Spatial gradients of New World bat Phylogenetic Diversity (PD) and Functional Diversity (FD) are according to Taxonomical Diversity (TD) patterns: larger in Equatorial regions and smaller in Temperate Regions (Fig 2a). The linear relationship between FD and PD indicates that 81 per cent of New World bats FD variation is explained by PD (Fig 2a). However, when the analyses were conducted for each bat family, PD is a weaker predictor of FD. To Phyllostomidae PD explains only 30 per

cent of variation in FD (Fig 2b) and less than one per cent to Vespertilionidae (Fig 2c) and Molossidae (Fig 2d).

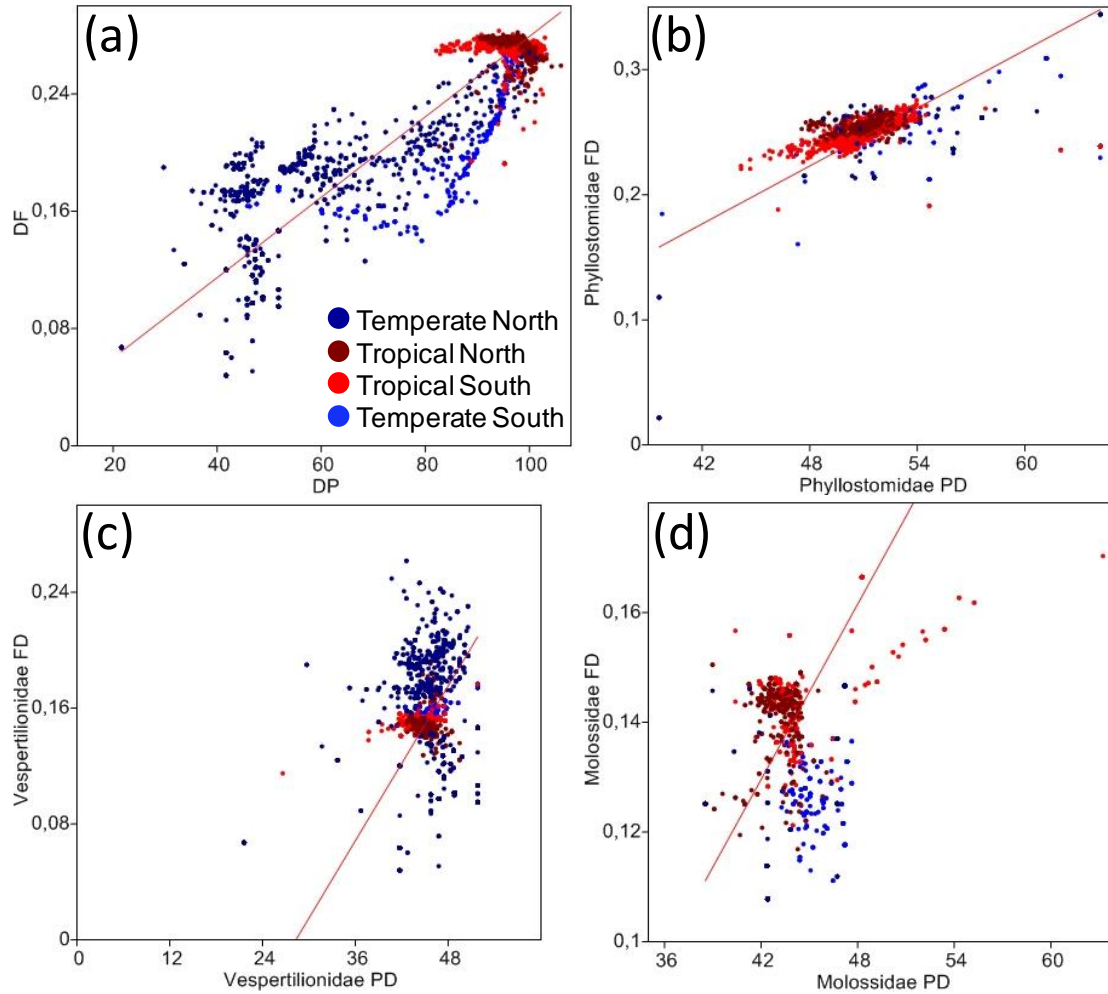


Fig 2: Linear relationship between New World (a) bats Phylogenetic Diversity (PD) and Functional Diversity (FD) ( $r^2 = 0,81$ ,  $p < 0,001$ ), (b) Phyllostomidae PD and FD ( $r^2 = 0,30$ ,  $p < 0,001$ ), (c) Vespertilionidae PD and FD ( $r^2 = 0,008$ ,  $p < 0,001$ ) and (d) Molossidae PD and FD ( $r^2 = 0,003$ ,  $p = 0,02$ ).

Mapping the residuals of observed FD and predicted FD (according to the linear relationship with PD) suggest that tropical areas have FD similar to what would be expected by PD. However, temperate areas have less FD than expected in some areas, and more FD than expected in other areas (Fig 3a). Similarly, Vespertilionidae have values distant from the expected, based on PD, predominantly in temperate North Hemisphere. The FD values of Vespertilionidae are greater than expected, by PD alone,

in most of temperate areas and lower than expected in the coldest temperate areas, the North extremes of its distribution (Fig 3b). Phyllostomidae and Molossidae, on the other hand, have FD values distant from the expected only in the latitudinal extremes of their distribution (Fig 3c and 3d). Most of these values are lower than expected by PD.

Partial regression analyses showed a general pattern where species richness (TD) has a minor role in explaining the species position in functional space, except for Phyllostomidae FD lower than expected by PD, to which TD is the most important predictor (Table 2). The pure effects of environmental variables are the most important predictor of FD higher than expected in New World bats and Molossidae, and to FD lower than expected in Vespertilionidae. However, pure spatial effects have a major role as predictor to species position in functional space to half of all analyses (Table 2).

Table 2: Partial regression analysis of functional (FD) and phylogenetic diversity (PD) positive (+) and negative (-) regression residuals (Res.), showing the variance explained by environment, spatial structure or species richness (TD), and shared explained variance ( $r^2$ ). Major values are detached. Positive residuals indicate FD higher than expected by PD, and negative residuals indicate FD lower than expected by PD.

	Res.	Environmental	Spatial	TD	Shared ( $r^2$ )
New World Bats	+	0.078	0.037	0.008	0.472
	-	0.007	0.090	0.022	0.376
Phyllostomidae	+	0.021	0.418	0.007	0.594
	-	0.031	0.002	0.036	0.336
Vespertilionidae	+	0.066	0.45	0.014	0.651
	-	0.173	0.072	0.016	0.623
Molossidae	+	0.119	0.105	0.020	0.370
	-	0.023	0.123	0.013	0.559

Spatial structure is the most important environmental variable predicting FD for most of the best models selected (Table 3). In only two models selected, annual mean temperature is the most important variable. However, annual mean temperature is more important than precipitation seasonality and canopy height in most of the selected models. Precipitation seasonality is more important than annual mean temperature and canopy height to higher than expected FD (positive residuals) in Phyllostomidae and Molossidae. This variable is inversely related to the most of the group of residuals analyzed (higher and lower than expected FD). Canopy height is more important than

annual mean temperature to Phyllostomidae higher than expected FD and Molossidae lower than expected FD. The same variable is more important than precipitation seasonality to lower than expected FD in all the bat families analyzed, and was inversely related to half of the group of residuals analyzed.

Table 3: Importance of environmental variables (annual mean temperature, precipitation seasonality, canopy height and spatial structure) according to the standardized coefficient of the best OLS model (Akaike Information Criterion) to FD higher than expected and lower than expected by the linear relationship between functional and phylogenetic diversity. Positive (+) regression residuals (Res.) indicates higher than expected FD, and negative (-) regression residuals indicates lower than expected FD. Major values are detached.

	Res.	Annual temp.	Precipit.	Canopy	Spatial	r <sup>2</sup>
New World Bats	+	-0.633	-0.087	0.086	0.185	0.463
	-	0.474	ex	ex	0.550	0.352
Phyllostomidae	+	-0.099	-0.174	-0.166	0.772	0.587
	-	0.275	-0.063	0.118	0.294	0.300
Vespertilionidae	+	0.226	-0.149	-0.104	0.819	0.637
	-	0.847	-0.057	-0.205	0.260	0.606
Molossidae	+	-0.313	0.322	-0.085	0.472	0.350
	-	0.075	0.069	0.184	0.636	0.547

ex = variables excluded from the best model

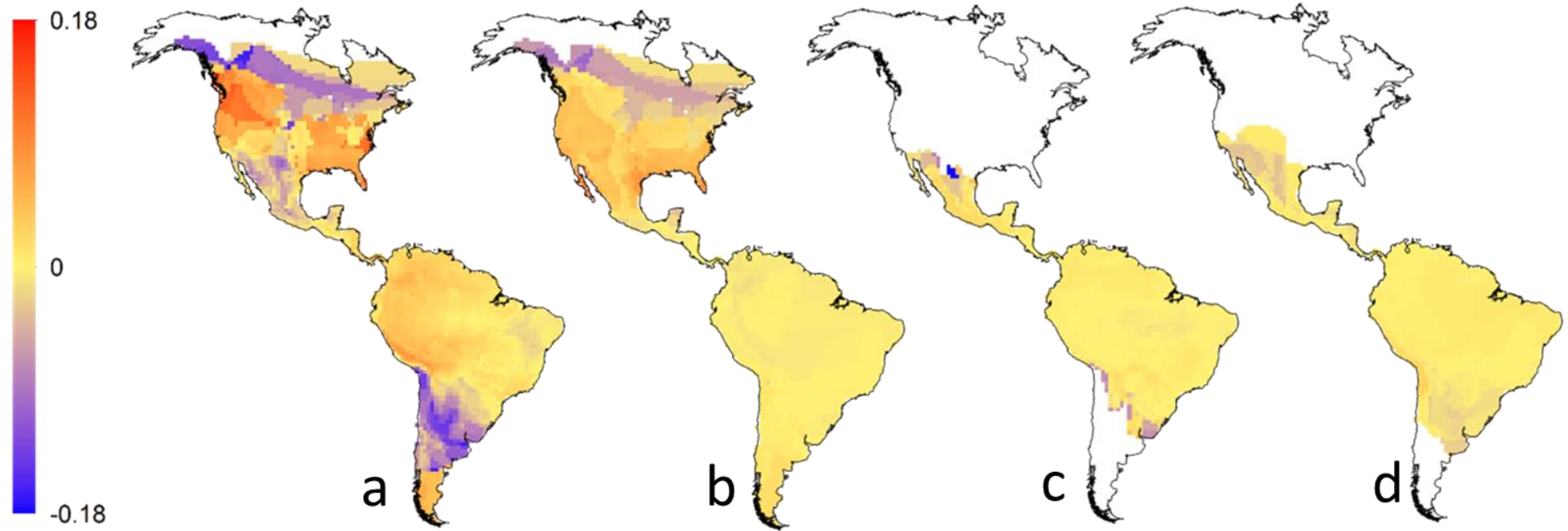


Fig 3: Residuals of observed FD and predicted FD (according to linear regressions with PD) to (a) New World bats, (b) Vespertilionidae, (c) Phyllostomidae and (d) Molossidae. Cold colors depict areas of lower FD than expected and hot colors depict areas with higher FD than expected by the linear regression with PD.

## 1.4 DISCUSSION

Diversity metrics in New World bats follows the global trend of higher diversity in the tropics. However, while New World bat Functional Diversity is well predicted by Phylogenetic Diversity, lowering the level of analysis to bat families reveals different relationships between FD and PD, which suggests that the processes accounting for local functional diversities are scale dependent and so, under control of other process beyond evolutionary history. Although the differences found to the families are indicatives of the differences in their evolutionary history processes, and these are important processes, other processes have to be related to the relationships we found between FD and PD. Our result does not corroborate the hypothesis that FD should be greater than expected by PD at tropical regions and lower than expected at temperate regions. However, at northern coldest latitudes, we found lower than expected FD, which seems to be resulted from environmental filtering, so environmental processes seem to be important processes driven New World bat diversity.

Although bats are true flight animals with good dispersal abilities, geographical barriers are important drivers of these mammals biodiversity patterns. At a global scale, Atlantic and Pacific oceans were the strongest barriers to bat dispersal (Proches, 2006) during their Eocene diversification (Simmons, 2005). In the same way, geographical distances are either drivers of the current global bat phylogenetic diversity patterns (Peixoto *et al.*, 2014). At the New World continental scale, spatial structure was shown as the main cause of FD deviations from expected by PD to all families analyzed (Table 2). Therefore, even in the continental scale we present here, spatial structure is an important process to bat functional and phylogenetic diversity (Table 2 and 3).

Except to spatial structure, annual mean temperature was the first or the second most important environmental FD predictor to most of the best models selected. Furthermore, species functionally less distinct than expected by PD can be an indicative of environmental filtering (Fig 1). Therefore, temperature should act as an environmental filter in the temperate areas where FD was lower than expected (Fig 3). Lower ambient temperatures and the declines in food supply during the winter in temperate areas make thermoregulation increasingly difficult and costly for bats, but, some bats escape from these limitations by migrating seasonally (Speakman & Thomas,

2003). Long-distance migrations in bats require relative narrow, aerodynamically efficient wings with pointed wing tips. These wing characteristics are also determinants of a feeding habit among bats: aerial insectivory (Fleming & Eby, 2003). Therefore, the functional similarity found in the extreme latitudinal distributions of New World bats and its family Phyllostomidae can be associated to the restriction of morphology and consequent feeding habits in these areas imposed by the harsher environment, since this bat family has more dietary diversity than any other Chiroptera family (Simmons & Conway, 2003).

Molossidae and Vespertilionidae are both aerial insectivore bat families. Even though, Molossidae ranges reach only the lower latitudes of temperate zone whereas Vespertilionidae dominate major temperate latitudes. Although both families have morphological traits that allows migration from cold temperate winters, sustained flight during migration has a high energetic cost (Fleming & Eby, 2003). Therefore, the most common strategy to escape from winter stress for temperate-zone species is hibernation (Speakman & Thomas, 2003), and to our knowledge, among New World bats only Vespertilionidae species hibernate (Nowak, 1994; Speakman & Thomas, 2003; Ceballos, 2014; Hamilton, 2016). Thus, temperate winter seems to limit the Molossidae distribution and FD but not Vespertilionidae.

The Vespertilionidae greatest values of FD above of the expected by PD are found at temperate areas (Fig 3). The only piscivorous Vespertilionidae species, *Myotis vivesi*, which is the only to have a pounce foraging strategy is a temperate species. In the same way, the only Vespertilionidae that was considered to eat vertebrates with gleaning foraging strategy, *Anthrozous pallidus*, and the only that was considered to roost in bird nests, *Myotis ciliolabrum*, are temperate species. Thus, our results can be explained by the major Vespertilionidae functional peculiarities, that are located in temperate zones.

Species functionally more distinct than expected by PD (points above the expected relationship) can be an indicative of competition (Fig 1). Temperate mammals are functionally more distinct than expected, and it was suggested that competition related to lower energy availability of high latitudes (Safi *et al.* 2011) is a key mechanism to this pattern. This hypothesis was supported by evidences of high rates of mammal extinction in temperate regions in comparison to the tropics (Weir & Schluter,

2007) and the tendency to some mammal species to have larger range sizes at these regions (Ojeda, 2013), which can be an indicative of high level of resource competition (Safi *et al.*, 2011). In the same way, the higher Vespertilionidae functionality in temperate areas can be a response of competition by lower resource availability, since bat species ranges are also larger at extratropical regions (Willig *et al.*, 2003b). However, other process can be related to this pattern, and in addition or alternatively to the competition hypothesis, past glaciations events with extinctions and recolonization processes have to be considered to occur at temperate areas. These historical climate processes are supported by the temperate phylogenetic nestedness pattern found by Dobrovolski *et al.* (2012). The patterns found by these authors indicate a loss of mammal phylogenetic diversity at high latitudes. Therefore, competition and historical climate changes can be forces that lead Vespertilionidae to be more functionally diverse than expected by PD in temperate regions.

Vespertilionidae seems to be the only bat family with a temperate origin (Morgan & Czaplewski, 2012). Therefore, its high functionality in temperate regions (Fig 3) goes against the niche conservatism hypothesis, which predictions stated that basal taxa tend to occur in their original fundamental niche, while more derived taxa should occur outside these conditions (Pereira & Palmerim, 2013). Our results to Vespertilionidae show the opposite pattern for areas with higher FD than expected by PD: niche evolution or niche shifts, since more derived functions were found at temperate areas. These processes are the expansion of the effective niche or the specialization to new conditions, and were also found to Vespertilionidae in other approaches (Buckley *et al.*, 2010; Pereira & Palmerim, 2013). However, lower FD than expected by PD are also found at temperate regions (Fig 3) which can be an indicative that niche conservatism can also be acting at these regions. A similar result was found by Olalla-Tárraga *et al.* (2011) to mammals at global scales. They found congruent patterns of niche conservatism, with some assemblages formed by species that scape from this conservatism.

Precipitation variables were already known as environmental drivers of New World bat diversity. Annual precipitation is directly related to all New World families' richness (Patten, 2004) and precipitation seasonality is inversely related to Atlantic Forest's Phyllostomidae richness (Stevens, 2013). Therefore, the negative relationship found between precipitation seasonality and FD distant from expected supports that

precipitation seasonality is an environmental filter to New World bats. Canopy height is also known to influence bat activities, for example, even in a single family, some species are more active in higher strata and others, in lower strata (Müller *et al.*, 2013, Marques *et al.*, 2015). In the same way, some species are more active in open habitats, and other in cluttered habitats, like edges or canopies (Pettit & Wilkins, 2012). Although canopy height does not show a great power to predict FD, the diversity of results we found, with direct and inverse relationships with FD deviations of the expected, can be directed by this diversity of behaviors and habitats even for bats phylogenetically close. Besides, canopy height can be related with habitat quality and a possibility of major environment heterogeneity, which can be a driver of high FD than expected by PD (Fig 1).

Our results showed that New World bat diversity patterns seems to be the result of synergistic effects of different process. Since the spatial structure is the most important variable in FD prediction, geographical barriers or distances can affect bat community assembly. Environmental filtering, especially by temperate temperatures, are processes spatially structured, and also are important drivers of bat community assembly. Furthermore, the other processes we consider to be potentially acting on bat assembly, the niche conservatism and niche evolution, are both processes that can be spatially structured and temperature-dependent. Therefore, the New World bat diversity is a result of a synergetic effect of all these processes. Besides, these processes seem to occur at family level, with the relative importance of the environmental variables been different to each family. And these processes are especially different to Vespertilionidae, which seem to be the only family that has been originated at temperate zones.

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## CAPÍTULO 2

### **NESTEDNESS OR TURNOVER: PATTERNS AND PROCESS OF PHYLOGENETIC BETA DIVERSITY IN NEW WORLD BATS**

## 2.1 INTRODUCTION

One of the oldest goals of ecology is to understand the processes that generate biodiversity patterns at broad spatial scales (Hawkins, 2001), and alpha diversity is the component of biodiversity most commonly used in the investigation of these patterns and processes (Magurran, 2004). However, the diversity of any region is a consequence of the richness of the smaller areas (local spatial scales) that compose it and the turnover of species between these smaller areas (regional spatial scale), and alpha diversity is a measure of biodiversity to a determined spatial unity, used to local-scale ecological studies (Stevens & Willig, 2002; Willig *et al.*, 2003a). Although beta diversity (BD) is the amount of variation in species composition among different biotas, which can be different communities, assemblages or sampling sites (Baselga, 2010; Ricotta & Pavoine, 2015) that can be at regional spatial scales or even at temporal scales (Melo *et al.*, 2012). Therefore, to understand broad scale biodiversity patterns, we should understand the mechanisms that act in the beta diversity patterns (Willig *et al.*, 2003a).

The BD approach can better improve the understanding of central biogeographic, ecological and conservation issues (Baselga, 2010). For example, Socolar *et al.* (2016) investigated how beta-diversity is impacted by human activities, and concluded that understanding beta-diversity is essential for protecting regional diversity and can directly assist conservation planning. Melo *et al.* (2009) investigated the environmental drivers of BD patterns in New World birds and mammals, using ecological and biogeography concepts. Likewise, BD is an approach that can be used to better understand of the differentiation of communities along habitat gradients (Whittaker, 1972).

The difference or dissimilarity measured by BD between two biotas is not unidimensional, since these biotas can differ in species compositions, species richness or both (Baselga & Leprieur, 2015). Therefore, this dissimilarity can be resulted of two different and complementary processes that can act simultaneously: (I) turnover, which is the replacement of some species by others between biotas along geographical gradients in a determined space; and (II) nestedness, which is the species losses in which some biotas are subsets of richer biotas (Baselga, 2010). As these BD components represent different processes causing changes in community composition, they can be the outcome of different ecological and/or evolutionary processes (Graham

& Fine, 2008) and, therefore, can uncover the processes and mechanisms generating geographical patterns of biodiversity (Ricotta & Pavoine, 2015).

The comprehension of global patterns of biodiversity depends on a combined framework of ecology and evolution (Wiens & Donoghue, 2004), since the composition of local-scale communities are a result of a regional species pool and the interaction of these species, and this pool, on the other hand, is a result of large-scale historical biogeographical process (Webb *et al.*, 2002). To account for these evolutionary process in community ecology, some approaches with the incorporation of phylogenies in diversity metrics have been developed (Swenson, 2014). In the same way, additional approaches, incorporating phylogenies branch lengths, have been used within the BD framewok: the phylobetadiversity (PBD). While BD is a measure of species composition dissimilarities between sites, PBD is a measure of how evolutionary related these lineages are (Graham & Fine, 2008). This PBD approach can elucidate the mechanisms that generate biodiversity patterns connecting local processes, like biotic interactions and environmental filtering, with more regional processes, including trait evolution, speciation and dispersal (Leprieur *et al.*, 2012).

One of the best-known biogeographical patterns is the temperate to tropical increase of species richness (Whittaker, 1972; Hawkins, 2001; Ricklefs, 2004). In the same way, several evidences pointed to BD to be higher at tropical regions (Whittaker, 1972). The same patterns are found in New World bats, to which both alpha and beta diversity increase towards the tropics (Stevens & Willig, 2002, Willig *et al.*, 2003b). Diverse hypotheses have been made to explain these alpha (Hawkins *et al.*, 2003) and beta diversity gradient patterns (Baselga, 2010; Dobrovolski *et al.*, 2012; Baselga *et al.*, 2012). Baselga (2010), for example, found that beetles' spatial turnover is higher in southern than in northern Europe, whereas nestedness is higher in northern than in southern Europe, and proposed that these latitudinal differences can result from past glaciations. Dobrovolski *et al.* (2012) tested this hypothesis to different New World Tetrapoda groups and found that extinctions and slow recolonization of areas covered by ice in the last glaciations explain the patterns of more nestedness in high latitudes, especially to groups with lower dispersal capability. Therefore, a historical climate change has been an accepted hypothesis to the turnover/nestedness latitudinal pattern. Besides, with the same gradient patterns of biodiversity, Baselga *et al.* (2012) proposed the existence of geographical thresholds that separate two global regions according to

the global climatic history. Castro-Insua *et al.* (2016) results corroborated with this hypothesis, finding that the turnover component of vertebrate biodiversity increased from Equator until a latitudinal breakpoint, after that, the turnover component decreased while nestedness increased. With terrestrial Mammals and a phylogenetic approach, Peixoto *et al.* (2017) expected to find more phylogenetic turnover at Tropical regions and more phylogenetic nestedness at Temperate regions. However, their results don't fit these expectations because there wasn't a latitudinal pattern of phylogenetic beta diversity in any of the components. However, they found that higher latitudes seemed to be associated with lineage losses and, therefore, to phylogenetic nestedness.

Although past climate history can be a process that generates patterns of BD, physiological constraints are suggested as more important than dispersal ability to non-volant mammals and birds (Castro-Insua *et al.*, 2016) and terrestrial mammals (Peixoto *et al.*, 2017) community assembly. Furthermore, measures of energy, water or water-energy balance are known to explain several plant and animal variations in richness (Hawkins *et al.*, 2003; Whittaker *et al.*, 2007). Therefore, besides climate history (Baselga, 2010; Dobrovolski *et al.*, 2012), current climate and others biomes environmental features can be drivers of the current assembly patterns and dissimilarities.

Following the patterns found by Baselga (2010), Dobrovolski *et al.* (2012), Baselga *et al.* (2012) and Castro-Insua *et al.* (2016), here we aim to test the hypothesis of more phylogenetic turnover at Tropical regions and more phylogenetic nestedness at Temperate regions, with a different approach: the comparison between New World biomes. We hypothesize that higher PBD values found between Tropical biomes are resulted from phylogenetic turnover, since the space of these areas are environmentally more heterogeneous. On the other hand, we expected that higher PBD values found between Tropical and Temperate biomes are resulted from phylogenetic nestedness. Furthermore, we expected lower PBD values between Temperate biomes, since the loss of lineages due to environmental constraints should result in the persistence of the same lineages at these biomes.

## 2.2 METHODS

### 2.2.1 Species distribution, biomes and phylogenetic information

We used the New World bat species distribution maps of NatureServe version 2 (Patterson *et al.*, 2007) and the global biomes maps of TEOW (Olson *et al.*, 2001) to produce species lists to each terrestrial biome of the New World. A recent species level mammalian phylogenetic supertree (Fritz *et al.*, 2009) was used to calculate the bat phylobetadiversity (PBD) between all these terrestrial New World biomes. This supertree included divergence times and the phylogenetic relationships of 5020 mammal species. To avoid bias, bat species that aren't present in the phylogenetic supertree were pruned from the database, resulting in a loss of 16 species of the 323 listed (5% of the species). The percentages of pruned species at each biome were between 0 and 5%.

### 2.2.2 Phylobetadiversity (PBD) and betadiversity (BD)

We calculated PBD between biomes using 1 minus the PhyloSor index (Bryant *et al.*, 2008). This index measures whether two communities are phylogenetically more or less similar based on the proportion of shared branch lengths compared to the total branch length of communities. Although there are other metrics that account for PBD, they are very redundant among each other (Swenson, 2014). PhyloSor, as well as other PBD indexes, can be considered as a “broad-sense” metric of phylogenetic turnover, since there's no adjustment for differences in phylogenetic diversity (Leprieur *et al.*, 2012). Therefore, the phylogenetic diversity (associated with nestedness) component ( $PBD_{\text{nest}}$ ) cannot be distinguished from the “true” species turnover ( $PBD_{\text{turn}}$ ). To distinguish these components, we used the additive partitioning framework of Leprieur *et al.* (2012) extended from the Baselga (2010) framework. Thus, we partitioned the PBD into its two components: turnover ( $PBD_{\text{turn}}$ ) and nestedness ( $PBD_{\text{nest}}$ ).

To model the amount of PBD variations between biomes that can be explained by beta diversity (BD) between biomes, we performed a linear regression between PBD and BD. In the same way, we performed a linear regression between  $PBD_{\text{nest}}$  and  $BD_{\text{nest}}$

(the nestedness component of beta diversity), and between  $PBD_{turn}$  and  $BD_{turn}$  (the turnover component of beta diversity). We calculated BD and its components ( $BD_{nest}$  e  $BD_{turn}$ ) using the Sorensen dissimilarity index and the Baselga (2010) approach with the R package betapart (Baselga *et al.*, 2017).

In order to test whether pairs of biomes were more or less phylogenetic dissimilar than expected by chance alone, we compared observed values of PBD and its components ( $PBD_{turn}$  e  $PBD_{nest}$ ) with expected values generated by a null model. In a similar approach to that of Leprieur *et al.* (2012), we generated a null distribution of PBD values by randomizing species across the phylogeny tips 999 times and calculating PBD and its components each run, holding species richness and BD constant. We calculate de standard effect size (SES) for PBD and its components comparing the observed values with the mean and standard deviation of the null distribution following Leprieur *et al.* (2012). If SES values are greater than 1.96 the PBD are higher than expected by BD; if SES values are below -1.96, the PBD are lower than expected by BD.

To represent the pattern of PBD found between biomes, we performed a cluster analysis based on these values using unweighted pair-group method with arithmetic mean (UPGMA). All analyses were performed using R 3.3.1.

## 2.3 RESULTS

Phylogenetic beta diversity among the 91 pairs of New World terrestrial biomes was heterogeneous with values greater than 0.5 to the majority of the pairs of biomes (54 pairs), but also with values below 0.25 to 30 pairs of biomes (Fig 1, Appendix 1). The PBD variation between biomes was more explained by the nestedness component ( $PBD_{nest}$ ) than by the turnover component ( $PBD_{turn}$ ), which can be observed by the ratio overall larger than 0.5 between  $PBD_{nest}$  and PBD (Fig 1). However, the majority of the  $PBD_{nest}$  and  $PBD_{turn}$  values were not different from expected by BD (Fig. 2).

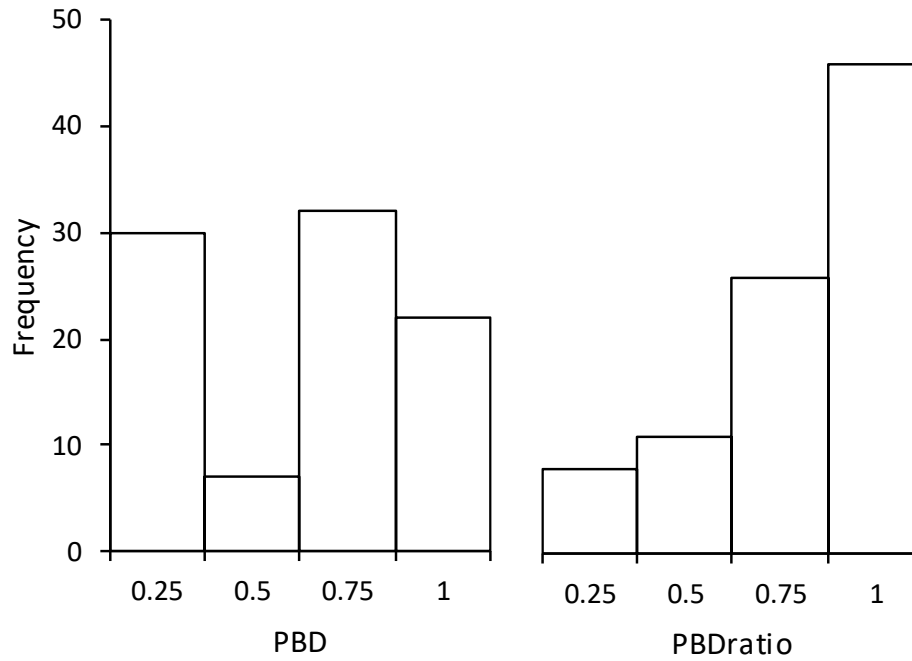


Fig 1: Frequency of different classes of bats phylobetadiversity (PBD) and its ratio ( $PBD_{\text{nest}}/PBD$ ) among New World terrestrial biomes.  $PBD_{\text{ratio}}$  values higher than 0.5 indicate more nestedness than turnover of lineages.

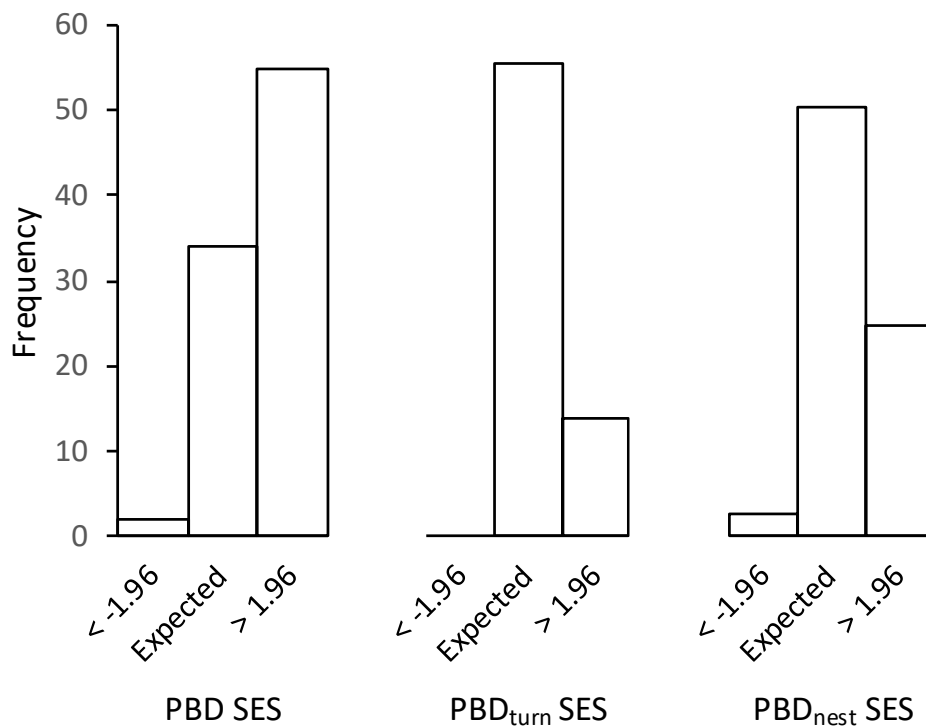


Figure 2: Frequency of Standard Effect Sizes (SES) values of bats Phylobetadiversity (PBD) and its turnover and nestedness components between New World terrestrial biomes.

Ninety-eight percent of the New World bats PDB variation was explained by the BD between biomes (Fig. 3a). In the same way, 87% of the  $PBD_{turn}$  was explained just by the species turnover between biomes (Fig. 3b), and 81% of the  $PBD_{nest}$  was explained just by the species nestedness between biomes (Fig. 3c). However, observing the data for  $BD_{turn}$  and  $PBD_{turn}$  (Fig. 3b) we can see that the species turnover was higher than the phylogenetic turnover between biomes. Which means that even where the turnover of species between biomes is higher, these different species found in each biome are from the same lineages.

Cluster analysis showed tree groups (dissimilarity greater than 50%) of New World terrestrial biomes according to bat phylogenetic dissimilarity (Fig. 4). The larger group (Fig. 4a) was composed by tropical and subtropical biomes. The other groups were composed by temperate coldest biomes (Fig. 4b) and temperate and mediterranean biomes (Fig. 4c). These groups show that PBD is greater between temperate and tropical (or subtropical) biomes and between temperate and temperate coldest biomes. However, between pairs of tropical, temperate or temperate coldest biomes, PBD is very low.

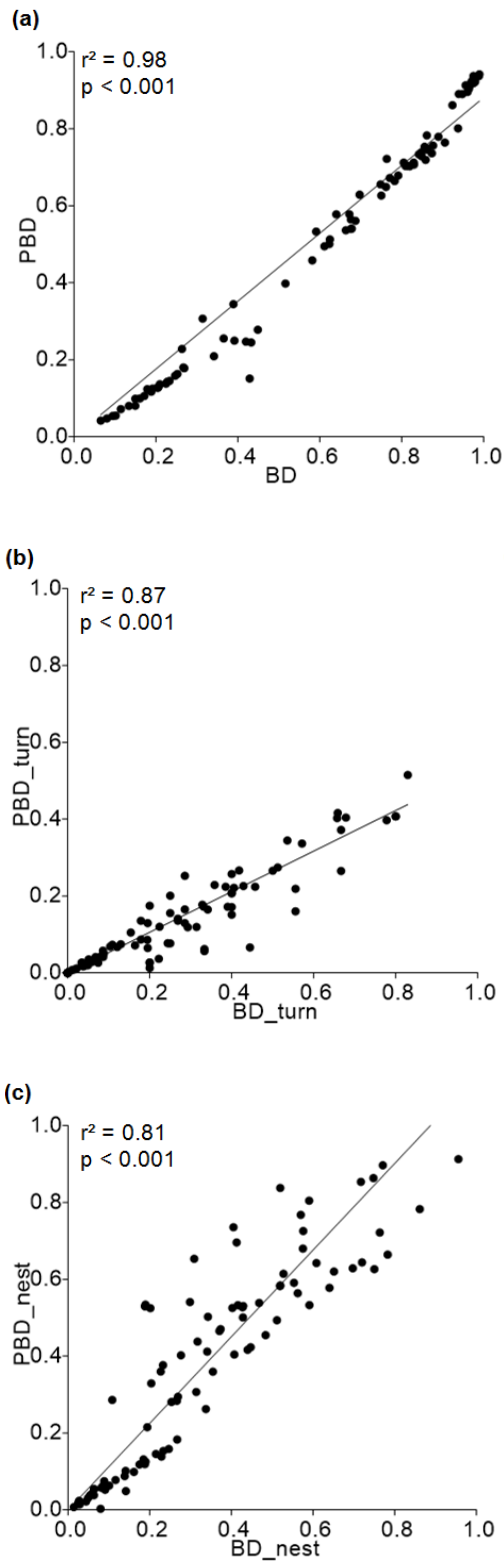


Fig 3: Linear relationship among (a) taxonomic (BD) and phylogenetic beta diversity (PBD), and among its turnover (b) and nestedness (c) components.

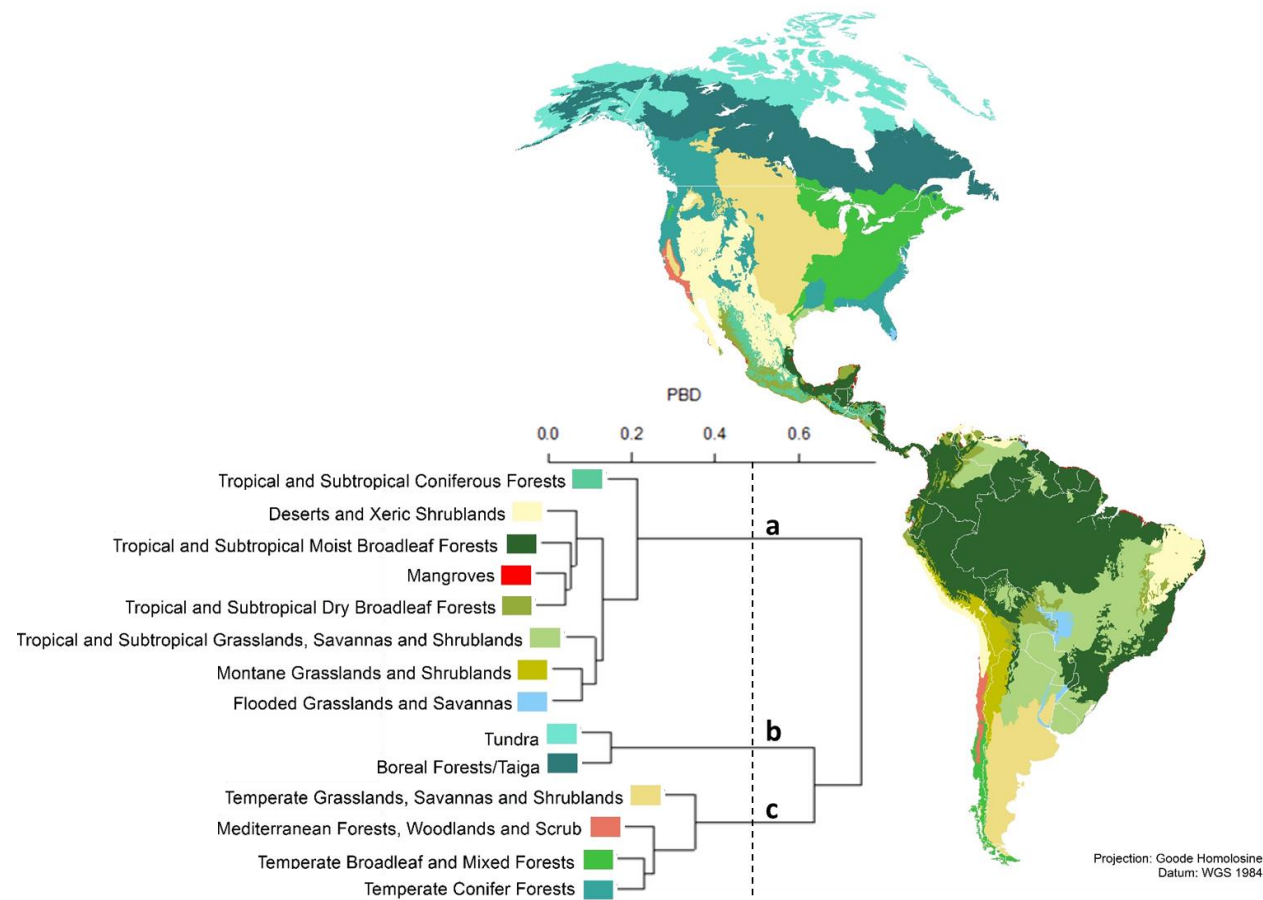


Fig 4: UPGMA (unweighted pair-group method using arithmetic averages) cluster analysis for bats phylogenetic beta diversity (PBD) values among terrestrial New World biomes. Nodes that are to the left of the dashed line have values under 50% of dissimilarity, showing tree groups of New World terrestrial biomes: (a) tropical and subtropical biomes, (b) temperate coldest biomes and (c) temperate and mediterranean biomes.

## 2.4 DISCUSSION

Our results showed that bat phylogenetic dissimilarities between New World biomes result, primarily, from loss of lineages (nestedness) instead of lineages turnover (Fig 1). This result differs from the pattern of PBD at global scales, in which the turnover is a major phenomenon in the promotion of bats phylogenetic dissimilarities between biogeographical regions (Peixoto *et al.*, 2013). Since these global scale results are between biogeographical regions, high speciation rates are expected to occur between these regions, which can generate new lineages and higher lineage turnover. Besides, at larger scales, oceans are known to be the strongest geographical barriers (Proches, 2006) in bat diversification history (Simmons, 2005), and these barriers are responsible for greater phylogenetic turnover. At regional scales however, bats dispersion abilities are more efficient to transpose geographical barriers, and nestedness becomes the dominant process in bat community assembly (Riedinger *et al.*, 2013; Varzinczak *et al.*, 2015). At the continental scale, we found nestedness as the dominant process, and environmental filters, instead of geographical barriers, seem to be the drivers of the phylogenetic nestedness we found.

Closely related species tend to be similar in their ecological niches (Wiens *et al.*, 2010), therefore, at local scales, interspecific competition can result in assemblages whose species are less related than expected by chance (Cavender-Bares *et al.*, 2004). The comparison between these assemblages should result in low phylobetadiversity measures coupled with high beta diversity measures if both assemblages are in a similar habitat (Graham & Fine, 2008). In contrast, if close relatives tend to be similar in their ecological niches, they often are similar on traits that are required for species survival in a particular environment. Thus, at regional scales, habitat filtering can produce assemblages with the coexistence of species that are more closely related than expected by chance (Gómez *et al.*, 2010). Many studies have narrowed the interpretation of assemblages' phylogenetic patterns to these niche-based processes: competition and habitat filtering (Cavender-Bares *et al.*, 2004; Emerson & Gillespie, 2008; Kembel, 2009). However, other evolutionary or biogeographical processes can generate PBD patterns similar to competition or habitat filtering, such as speciation and historical dispersion rates (Emerson & Gillespie, 2008). If speciation occurs across assemblages, then closely related species are unlikely to co-occur, so one would expect a low phylobetadiversity than the expected by BD. In contrast, if limited dispersal of species

is the dominant process structuring some assemblages, then one would expect high beta diversity and phylogenetic beta diversity, because each region would contain distinct clades that have diversified within it (Gómez *et al.*, 2010).

Considering both niche-based (environmental filtering and competition) and evolutionary or biogeographical (speciation and dispersal rates) processes, we found that the majority of SES values do not differ from what would be expected by the null model to the nestedness and turnover components of PBD (Fig 2), which means that these values do not differ from the expected by BD. This way, the phylogenetic structures of assemblages are unlike to be the result of competition or speciation, since both processes would result in PBD lower than expected by BD (see above). Furthermore, we found larger species turnover ( $BD_{\text{turn}}$ ) than phylogenetic turnover ( $PBD_{\text{turn}}$ ) between biomes (Fig 3b), which can indicate the coexistence of species that are more closely related than expected by BD, and the existence of environmental filtering processes.

All New World bat families occur at lower latitudes, however, with the increase of latitude, there is a decrease in family lineages until only Vespertilionidae persist at the larger biomes latitudes (Patterson *et al.*, 2007). This way, the predominant bats at New World greater latitudes, in Tundra, Taiga or temperate biomes, are widespread distribution Vespertilionidae (Arita *et al.*, 2014). The lower temperatures and declines in food supply in winter in temperate areas make the thermoregulation increasingly difficult and highly costly for bats, and the most common strategy to escape from winter stress for temperate-zone species is hibernation (Speakman & Thomas, 2003). To our knowledge, among New World bats only Vespertilionidae species are known to hibernate (Nowak, 1994; Speakman & Thomas, 2003; Ceballos, 2014; Hamilton, 2016). Thus, temperate winter seems to limit other New World bats distribution, but not Vespertilionidae.

Several models suggested that Vespertilionidae was the only New World bat family originated at temperate latitudes in North America (Lim, 2009), which would explain its occurrence at these cold latitudes. Considering the niche conservatism hypothesis (Wiens *et al.*, 2010), all the New World bats could retain niche-related ecological traits over time. This way, only Vespertilionidae could occupy temperate biomes. However, Pereira & Palmeirim (2013) found that even families supposedly to

have a tropical origin (Phyllostomidae and Molossidae), have the most basal clades at the highest latitudes of their range, at temperate lower latitudes. Besides, a substantial proportion of Vespertilionidae genus is present in the Neotropics. Therefore, these authors suggest that the patterns they found are unlikely to be result of niche conservatism.

Physiological constraints are probably more important than dispersal ability to New World bat community assembly, since higher PBD are found between temperate and tropical biomes. Similar conclusions were made by Castro-Issua *et al.* (2016) to New World latitudinal gradients of bats, non-volant mammals and birds; and Peixoto *et al.* (2017) to latitudinal gradients of mammals at global scales.

The greatest PBD values we found are between tropical and temperate biomes (Fig 4). These results represent the decrease in phylogenetic diversity of all families, except Vespertilionidae, as latitude increases. The phylogenetic diversity loss, instead the phylogenetic turnover, we found between New World biomes seems to be a result of habitat filtering. Our results are in line with this hypothesis and highlight that physiological constraints are probably more important than dispersal ability to bat community assembly.

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## APPENDIX 1

Appendix 1: Pairwise phylobetadiversity (PBD) values, turnover component of PBD (PBD\_turn) and nestedness component of PBD (PBD\_nest) among New World biomes, together with their respective standardized effect size (SES) values (SES > |1.96|, in bold, indicates values above or below the expected by null models) and the PBD\_ratio (PBD\_nest/PBD > in bold, indicates values with more nestedness than turnover).

Biome pairs*	PBD	PBD_turn	PBD_nest	SES.PBD	SES.PBD_turn	SES.PBD_nest	PBDratio (PBD_nest/PBD)
1_2	0.053951357	0.023144331	0.030807025	0.164976118	-0.953550891	1.121260609	<b>0.571014837</b>
1_3	0.209132855	0.026164619	0.182968236	-0.926130672	-1.683902712	0.171731665	<b>0.874889964</b>
1_4	0.733751855	0.119427008	0.614324847	<b>3.811609542</b>	-0.179385368	<b>3.324038042</b>	<b>0.83723788</b>
1_5	0.702926876	0.118778281	0.584148595	<b>3.593916231</b>	-0.153668159	<b>3.368296271</b>	<b>0.831023276</b>
1_6	0.903852952	0.066032752	0.837820199	<b>3.523888751</b>	-1.375365767	<b>3.449088368</b>	<b>0.926943036</b>
1_7	0.10587605	0.007208594	0.098667456	0.078633809	0.153612895	0.020281532	<b>0.931914778</b>
1_8	0.540508638	0.085902143	0.454606495	<b>2.769911755</b>	-0.325118333	<b>2.898991739</b>	<b>0.841071655</b>
1_9	0.158436556	0	0.158436556	0.160791383	NA	0.160791383	1
1_10	0.127652743	0.008719445	0.118933298	-0.165059263	-0.468995617	0.035618927	<b>0.931694022</b>
1_11	0.923494258	0.026629292	0.896864966	<b>2.714357351</b>	-0.598371221	<b>2.141953595</b>	<b>0.971164637</b>
1_12	0.719119148	0.076701822	0.642417327	1.877519232	-0.633418509	<b>2.267659886</b>	<b>0.893339203</b>
1_13	0.080405956	0.028247686	0.052158271	-0.947162043	-1.221527017	0.17275168	<b>0.64868665</b>
1_14	0.054775553	0.01666615	0.038109402	0.216704834	-1.237127186	1.348572082	<b>0.695737432</b>
2_3	0.179823322	0.026751646	0.153071676	-0.130758472	0.989484665	-0.627965901	<b>0.851233725</b>
2_4	0.75315676	0.225977789	0.527178972	<b>4.3568947</b>	1.900168729	1.459434344	<b>0.699959158</b>
2_5	0.703337267	0.164734163	0.538603105	<b>3.877493</b>	1.18977717	<b>2.320525239</b>	<b>0.765782121</b>
2_6	0.91461725	0.218700475	0.695916774	<b>4.023883486</b>	1.772759105	0.045802867	<b>0.760883063</b>
2_7	0.136250978	0.073170732	0.063080247	0.133099532	0.794406471	-0.670587657	0.462970963
2_8	0.536368135	0.119887285	0.416480849	<b>2.968984497</b>	0.661353737	<b>2.156736377</b>	<b>0.776483207</b>
2_9	0.144888369	0.019887933	0.125000436	-0.684125946	-0.530484448	-0.371456446	<b>0.862736165</b>
2_10	0.099283589	0.011528639	0.08775495	-0.988334942	-0.611961843	-0.665480657	<b>0.883881724</b>
2_11	0.933875592	0.208128942	0.725746651	<b>3.230916874</b>	<b>3.068565854</b>	-1.882835342	<b>0.777134188</b>
2_12	0.706939424	0.08660914	0.620330284	<b>2.89910784</b>	0.993722099	1.22456768	<b>0.877487183</b>
2_13	0.047424354	0.025821896	0.021602458	-0.819303093	0.101990203	-0.931934969	0.455514013
2_14	0.041948579	0.034974133	0.006974446	0.571610243	0.415797525	0.133631342	0.166261788
3_4	0.672077706	0.206663448	0.465414258	<b>4.084734041</b>	0.641455633	<b>2.727222972</b>	<b>0.692500665</b>
3_5	0.577827367	0.07706448	0.500762887	<b>3.348796668</b>	-1.287171934	<b>4.132150852</b>	<b>0.866630617</b>
3_6	0.861238443	0.056524036	0.804714407	<b>3.646047716</b>	-1.162702829	<b>3.458798035</b>	<b>0.934368889</b>
3_7	0.247052989	0.172418131	0.074634858	-1.788835164	-1.636989308	0.146066767	0.302100608
3_8	0.458098988	0.177269234	0.280829754	<b>2.509923439</b>	-0.172174468	<b>2.720341945</b>	<b>0.613032906</b>
3_9	0.244861865	0.221225209	0.023636656	<b>-2.240657841</b>	-1.777567224	-0.078811344	0.096530574
3_10	0.277902417	0.22399262	0.053909797	-0.638105798	-0.533669818	0.012929426	0.193988226
3_11	0.890093369	0.026629292	0.863464077	<b>2.665182925</b>	-0.710017243	<b>2.265889569</b>	<b>0.970082586</b>
3_12	0.648918856	0.155480984	0.493437872	<b>2.850697149</b>	1.653607244	0.918846399	<b>0.760399959</b>
3_13	0.163051161	0.031783303	0.131267857	-0.856226966	-1.198911362	0.014532632	<b>0.805071591</b>
3_14	0.178050953	0.032747704	0.145303249	-0.655370403	-0.055361041	-0.624772877	<b>0.816076782</b>
4_5	0.228001505	0.174633832	0.053367673	1.926727542	1.341733053	0.463595985	0.234067196
4_6	0.532938564	0	0.532938564	<b>2.407906528</b>	NA	<b>2.407906528</b>	1
4_7	0.703995401	0.171253823	0.532741578	<b>3.670920186</b>	-0.009811178	<b>3.031591882</b>	<b>0.75674014</b>
4_8	0.306739567	0	0.306739567	<b>3.012125506</b>	NA	<b>3.012125506</b>	1
4_9	0.738741879	0.33655239	0.402189489	<b>4.716022437</b>	<b>2.322085374</b>	1.054178717	<b>0.544424921</b>
4_10	0.779258246	0.402704008	0.376554238	<b>5.239755854</b>	<b>3.622085253</b>	-0.166111111	0.483221371

\* Biomes: 1-Tropical and Subtropical Moist Broadleaf Forests; 2-Tropical and Subtropical Dry Broadleaf Forests; 3-Tropical and Subtropical Coniferous Forests; 4-Temperate Broadleaf and Mixed Forests; 5- Temperate Conifer Forests; 6- Boreal Forests/Taiga; 7-Tropical and Subtropical Grasslands, Savannas and Shrublands; 8-Temperate Grasslands, Savannas and Shrublands; 9-Flooded Grasslands and Savannas; 10-Montane Grasslands and Shrublands; 11-Tundra; 12-Mediterranean Forests, Woodlands and Scrub; 13-Deserts and Xeric Shrublands; 14-Mangroves

Appendix 1 (continuation): Pairwise phylobetadiversity (PBD) values, turnover component of PBD (PBD\_turn) and nestedness component of PBD (PBD\_nest) among New World biomes, together with their respective standardized effect size (SES) values (SES > |1.96|, in bold, indicates values above or below the expected by null models) and the PBD\_ratio (PBD\_nest/PBD > in bold, indicates values with more nestedness than turnover).

4_11	0.626439791	0	0.626439791	1.110809907	NA	1.110809907	<b>1</b>
4_12	0.255232139	0.252535007	0.002697131	0.49276393	1.828919704	-1.880864919	0.010567366
4_13	0.711850412	0.129406084	0.582444328	<b>4.0827147</b>	0.434655417	<b>2.90021497</b>	<b>0.818211689</b>
4_14	0.749519406	0.224046354	0.525473051	<b>4.075720197</b>	1.334648849	1.732324061	<b>0.701079982</b>
5_6	0.577691021	0	0.577691021	<b>2.654687936</b>	NA	<b>2.654687936</b>	<b>1</b>
5_7	0.712025583	0.274179864	0.437845719	<b>4.167943338</b>	1.667912638	1.630682141	<b>0.614929757</b>
5_8	0.344407177	0.129383484	0.215023693	<b>2.766383711</b>	0.881787025	1.882483553	<b>0.624329884</b>
5_9	0.745171839	0.416006787	0.329165052	<b>4.737250056</b>	<b>2.858197805</b>	0.421918084	0.441730396
5_10	0.801055623	0.514988688	0.286066935	<b>5.353082478</b>	<b>4.222800768</b>	-1.03866135	0.357112449
5_11	0.664195788	0	0.664195788	1.312183418	NA	1.312183418	<b>1</b>
5_12	0.249512378	0.2007031	0.048809278	-0.13420429	1.23205976	-1.619930684	0.195618664
5_13	0.655486693	0.064621041	0.590865653	<b>3.636980724</b>	-0.524632097	<b>3.710153067</b>	<b>0.901415175</b>
5_14	0.702386095	0.171945701	0.530440394	<b>3.578504892</b>	0.569072341	<b>2.520390814</b>	<b>0.755197743</b>
6_7	0.895635051	0.160063391	0.735571659	<b>3.760289149</b>	0.140272092	1.792464014	<b>0.82128503</b>
6_8	0.7216995	0	0.7216995	<b>3.391210355</b>	NA	<b>3.391210355</b>	<b>1</b>
6_9	0.912685882	0.371896461	0.540789421	<b>4.664701973</b>	<b>3.489539427</b>	-1.618194262	<b>0.59252524</b>
6_10	0.922124015	0.397253038	0.524870977	<b>4.565012179</b>	<b>3.459133798</b>	-1.843355774	<b>0.569197818</b>
6_11	0.151204819	0.012613875	0.138590944	<b>-2.213641633</b>	-1.588650295	-0.674368689	<b>0.916577558</b>
6_12	0.564225248	0.061806656	0.502418592	<b>1.986436963</b>	-1.808081029	<b>3.632243333</b>	<b>0.890457479</b>
6_13	0.890196551	0.036450079	0.853746471	<b>3.778793631</b>	-0.827823133	<b>3.327086102</b>	<b>0.959053897</b>
6_14	0.918593082	0.265187533	0.653405549	<b>4.050312306</b>	<b>2.060254609</b>	-0.391695197	<b>0.711311202</b>
7_8	0.500595711	0.140978567	0.359617144	<b>2.847314597</b>	0.166038126	<b>2.561719155</b>	<b>0.718378396</b>
7_9	0.098722157	0.041196433	0.057525725	0.139726308	-0.019166663	0.154509283	<b>0.582703276</b>
7_10	0.123546538	0.104888727	0.018657811	0.965833584	0.83227931	-0.06301833	0.151018484
7_11	0.91927743	0.151366503	0.767910927	<b>2.989857029</b>	1.356665816	-0.103880742	<b>0.835341869</b>
7_12	0.736184872	0.265739853	0.470445019	<b>2.919701918</b>	<b>2.055462713</b>	0.02243296	<b>0.639031087</b>
7_13	0.116964629	0.074430486	0.042534142	-0.674369675	-0.538506561	-0.045931009	0.363649618
7_14	0.125143777	0.068446653	0.056697124	-0.165204343	0.615922715	-0.812904647	0.453055882
8_9	0.512428143	0.228673896	0.283754247	<b>3.628470986</b>	1.507120161	1.785777525	<b>0.553744463</b>
8_10	0.560849672	0.26650158	0.294348092	<b>4.028130679</b>	<b>2.275026411</b>	1.358228892	<b>0.524825291</b>
8_11	0.782767545	0	0.782767545	<b>2.100117766</b>	NA	<b>2.100117766</b>	<b>1</b>
8_12	0.397851856	0.135506552	0.262345304	1.17210873	1.349919217	-0.089098451	<b>0.6594045</b>
8_13	0.494667875	0.071385877	0.423281998	<b>2.683238688</b>	-0.580428871	<b>2.956748419</b>	<b>0.855689281</b>
8_14	0.53977996	0.135599009	0.404180951	<b>2.690960535</b>	0.30867559	<b>2.195902231</b>	<b>0.748788359</b>
9_10	0.08003488	0.042498619	0.037536261	-0.230451376	-0.38622151	0.191928295	0.468998782
9_11	0.936792559	0.407147863	0.529644696	<b>3.545962919</b>	<b>3.375803939</b>	<b>-2.579588116</b>	<b>0.565380981</b>
9_12	0.763987342	0.404122723	0.359864619	<b>3.723077406</b>	<b>3.28086156</b>	-1.078574708	0.471034792
9_13	0.142610107	0.041314813	0.101295294	-0.702583078	-1.064864132	0.158922842	<b>0.710295335</b>
9_14	0.137774847	0.019730092	0.118044755	-1.128478668	-1.110143219	-0.44573932	<b>0.856794671</b>
10_11	0.941325381	0.407147863	0.534177518	<b>3.619293519</b>	<b>3.690978277</b>	<b>-2.917462738</b>	<b>0.567473829</b>
10_12	0.756326482	0.344519016	0.411807466	<b>3.794326506</b>	<b>3.772817955</b>	-1.272869054	<b>0.544483733</b>
10_13	0.129315628	0.067055819	0.062259809	-0.299094127	-0.236486438	-0.063743867	0.481456186
10_14	0.127205106	0.049653411	0.077551695	-0.478277697	0.303701061	-0.769989948	<b>0.609658664</b>
11_12	0.628627196	0	0.628627196	<b>2.028444371</b>	NA	<b>2.028444371</b>	<b>1</b>
11_13	0.912873584	0	0.912873584	<b>2.880068183</b>	NA	<b>2.880068183</b>	<b>1</b>
11_14	0.937106918	0.257182901	0.679924017	<b>3.477036764</b>	<b>4.18439657</b>	<b>-2.996159334</b>	<b>0.725556501</b>
12_13	0.678514419	0.03451582	0.6439986	<b>2.328359958</b>	0.498055482	1.871785682	<b>0.949130308</b>
12_14	0.728846104	0.165068712	0.563777392	<b>2.783771895</b>	<b>2.349923796</b>	0.072771955	<b>0.773520485</b>
13_14	0.071701435	0.057612512	0.014088923	-0.733562238	0.131230084	-0.981654228	0.1964943

\* Biomes: 1-Tropical and Subtropical Moist Broadleaf Forests; 2-Tropical and Subtropical Dry Broadleaf Forests; 3-Tropical and Subtropical Coniferous Forests; 4-Temperate Broadleaf and Mixed Forests; 5- Temperate Conifer Forests; 6- Boreal Forests/Taiga; 7-Tropical and Subtropical Grasslands, Savannas and Shrublands; 8-Temperate Grasslands, Savannas and Shrublands; 9-Flooded Grasslands and Savannas; 10-Montane Grasslands and Shrublands; 11-Tundra; 12-Mediterranean Forests, Woodlands and Scrub; 13-Deserts and Xeric Shrublands; 14-Mangroves

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