

UNIVERSIDADE FEDERAL DO PARANÁ

LUIZ HENRIQUE VARZINCZAK

**DIVERSIDADE BETA TAXONÔMICA E FILOGENÉTICA EM COMUNIDADES DE
MORCEGOS NEOTROPICAIS**

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Dissertação apresentada ao Programa de Pós-Graduação em Ecologia e Conservação como requisito parcial para obtenção do grau de Mestre em Ecologia e Conservação, Setor de Ciências Biológicas, Universidade Federal do Paraná.

Orientador: Dr. Fernando de Camargo Passos

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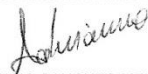
TERMO DE APROVAÇÃO

Os membros da Banca Examinadora designada pelo Colegiado do Programa de Pós-Graduação em ECOLOGIA E CONSERVAÇÃO da Universidade Federal do Paraná foram convocados para realizar a arguição da Dissertação de Mestrado de **LUIZ HENRIQUE VARZINCZAK** intitulada: **Diversidade beta taxonômica e filogenética em comunidades de morcegos Neotropicais.**, após terem inquirido o aluno e realizado a avaliação do trabalho, são de parecer pela sua

APROVAÇÃO

Curitiba, 03 de Fevereiro de 2017.


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Put passion ahead of training. Feel out in any way you can what you most want to do in science, or technology, or some other science-related profession. Obey that passion as long as it lasts. Feed it with the knowledge the mind needs to grow. [...] Decision and hard work based on enduring passion will never fail you.

Edward O. Wilson

RESUMO

A estrutura das comunidades é influenciada por fatores contemporâneos e históricos que atuam sobre a distribuição das espécies. As condições ambientais, o espaço, e a estabilidade climática histórica desde o último máximo glacial estão entre os principais fatores associados à formação das comunidades ao longo de gradientes geográficos. Separar os efeitos destes mecanismos em diferentes dimensões da biodiversidade é essencial para entender seus papéis relativos na formação e composição das comunidades. Aqui nós testamos os efeitos destes três diferentes processos na diversidade beta filogenética e taxonômica entre 108 comunidades de morcegos da família Phyllostomidae na região Neotropical. Considerando a capacidade de dispersão destes morcegos, seus requerimentos de nicho, bem como sua origem tropical, nós esperamos que as condições ambientais contemporâneas exerçam maior influência tanto na variação taxonômica quanto filogenética entre essas comunidades. Utilizando análises espaciais, partições de variância com análises de redundância parciais, e abordagens por modelos nulos, nós encontramos que a maior parte da variação na composição taxonômica e filogenética entre as comunidades foi explicada pelo espaço, seja pelo seu efeito puro ou por sua fração compartilhada com as condições ambientais atuais. Além disso, observamos uma forte e não aleatória estrutura espacial subjacente à diversidade beta taxonômica e filogenética. Comparações pareadas entre as comunidades revelaram que a maior parte das comunidades possui variação aleatória em relação à filogenia, padrão consistente ao longo de diferentes classes de distância entre as comunidades. Nossos resultados mostram que o espaço exerce maior influência do que o ambiente atual e a estabilidade climática histórica na explicação dos padrões de diversidade entre essas comunidades, um padrão que hipotetizamos estar relacionado com a complexidade geológica desta região, a qual tende a limitar a dispersão de espécies independentemente de sua capacidade de dispersão. Em comparação com estudos prévios focando na diversidade destes morcegos em escala local e regional, os quais indicaram maior influência das condições ambientais sobre estas comunidades, nossos resultados ainda sugerem que a estrutura das comunidades de morcegos é relacionada à complementaridade de processos ecológicos e evolutivos em diferentes níveis de diversidade e de escalas geográficas ao longo da região Neotropical.

Palavras-chave: Chiroptera, montagem de comunidades, estrutura filogenética de comunidades, dispersão, processos históricos, último máximo glacial, região Neotropical, teoria de nicho, dinâmicas neutras, Phyllostomidae.

ABSTRACT

Community structure is the result of contemporary and historical processes that exert influence on species distribution. The current environment, space and the climatic stability from the last glacial maximum are widely recognized as fundamental factors underlying community assembly along geographical gradients. Disentangling the effects of these mechanisms at different dimensions of biodiversity is essential to understand their roles on the structure of biological communities. Here we addressed the relative roles of these three processes on the taxonomic and phylogenetic beta diversity among 108 Neotropical Phyllostomid bat assemblages. Considering these bats' dispersal ability, niche requirements, and tropical origin, we predicted that the current environment would explain most of the taxonomic and phylogenetic variation among communities. By utilizing a set of spatial analyses, variance partitioning with partial redundancy analyses, and null model approaches, we found that most of the variation in taxonomic and phylogenetic beta diversities was accounted by space, whether by the pure spatial effect or its shared fraction with the current environment. Additionally, we observed a strong and non-random spatial structure underlying the taxonomic and phylogenetic community composition. A pairwise comparison revealed that most of communities have a random variation with respect to phylogeny, a pattern consistent through all geographic distances between sites. Taken together, our results shows that the space has a stronger importance than the current environment and the historical climatic stability in explaining the diversity patterns among these assemblages, a result that we hypothesize to arise due to the complexity of the geological processes limiting species dispersal along this region, regardless their flight capabilities. In comparison with previous studies focusing on patterns of bat diversity at local and regional scales that indicated a strong influence of environment on these communities, such contrasting results further suggests that the structure of bat assemblages are related to complementary ecological and evolutionary processes at different levels of diversity and geographical scales throughout the Neotropics.

Keywords: Chiroptera, community assembly, community phylogenetics, dispersal, historical processes, last glacial maximum, Neotropical region, niche theory, neutral dynamics, Phyllostomidae

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1 INTRODUCTION

Understanding the main drivers of community assembly and composition has been historically a major task in ecology. Over the past few decades, with the recognition that communities are influenced by regional and historical dynamics (Ricklefs 1987), the concept of beta diversity (i.e. the variation in community composition between sites) has increased in importance, emerging as a key component of biodiversity when one's aims are to understand how communities are assembled through ecological and spatial gradients (Anderson et al. 2011). By linking the effects from different sources to variation in community composition, beta diversity has provided to ecologists insights into the mechanisms underlying community structure, allowing to test several hypotheses regarding community assembly, as well as to link patterns and processes at different scales (Buckley and Jetz 2008, Barton et al. 2013, Arellano et al. 2016, Castro-Insua et al. 2016).

Among the processes that have been widely proposed to explain the geographical distribution of diversity and the variation in species composition between sites, three of them are at the core of ecological research. First, niche theory states that species distribution and their incidence in biological communities are influenced by deterministic processes, mainly reflecting the degree to which each species is adapted to environmental conditions (Chase and Leibold 2003, Leibold et al. 2004). On the other hand, spatial processes tend to limit species occurrence in communities owing to their differences in dispersal ability, stochastic events, and ecological drift (Hubbell 2001, Leibold et al. 2004). Although most of studies considered community assembly within the lens of these two processes (Cottenie 2005, Vellend et al. 2014), the historical dynamics of climatic changes following the late Pleistocene, especially during the Last Glacial Maximum (LGM, 21,000 years before present), are as important as niche and space driving species distribution worldwide (Svenning et al. 2015). Considering that climatic regimes from the LGM to present are spatially heterogeneous, with some areas historically more climatically unstable than others (Dynesius and Jansson 2000), such climatic variation may have caused shifts in species distribution through extinctions in

areas where these events were stronger, by reduction of suitable areas to which they had potential to occur, or even by inducing species to track their environmental optimum (Sandel et al. 2011, Svenning et al. 2015). The effects of post-glacial climatic changes have aroused in the current distribution of several taxa, ranging from trees to terrestrial vertebrates in different realms of the Earth (Jansson 2003, Svenning and Skov 2007, Araújo et al. 2008, Sandel et al. 2011, Svenning et al. 2011).

The degree to which the current environment, space and historical legacy interact to influence community composition is ultimately related to species traits, namely their range of environmental tolerances and dispersal abilities (Hawkins and Porter 2003, Cottenie 2005, Buckley and Jetz 2008, Davies et al. 2009, Dobrovolski et al. 2012). Thus, some predictions emerge on how the environment, space and historical climatic stability interact in shaping community assembly and composition. Species with broad environmental tolerances, for example, should be capable of occurring in a wide range of environments (Chase and Leibold 2003). In addition, these species are more likely to adapt to new environmental regimes, which makes them less influenced by historical climatic changes (Dobrovolski et al. 2012, Svenning et al. 2015). On the other hand, highly vagile species (i.e. good dispersers) tend to be influenced in a lesser degree by spatial dynamics and in a higher degree by environmental conditions, especially when such environmental variation encompasses broad geographical gradients (Arita and Rodríguez 2004). Also, these species are thought to be more likely to migrate and track their climatic optimum and to recolonize areas previously affected by climatic changes, which in turn have diminished the effects of the historical climatic instability on their distribution (Sandel et al. 2011, Dobrovolski et al. 2012, Svenning et al. 2015).

From an evolutionary perspective, however, species are not independent from each other, and their traits are often the outcome of evolutionary and biogeographic dynamics operating at different spatial and temporal scales (Wiens and Donoghue 2004, Cavender-Bares et al. 2009). Such dynamics led to variation in the rates of speciation and extinction, shaping not only the current patterns of species distribution and the gradients of phylogenetic diversity, but also the shared dependence among species in relation to their responses to environmental, spatial and historical processes

(Wiens and Donoghue 2004, Mittelbach and Schemske 2015). In this sense, including information on the degree of evolutionary relatedness among species into community ecology has advanced our understanding on the interplay of ecological and evolutionary dynamics driving community assembly (Cavender-Bares et al. 2009). For example, if traits are conserved over an evolutionary lineage, regardless the effects of other mechanisms (e.g. ecological interactions) affecting community composition, one could expect that closely related species would respond similarly throughout environmental, spatial and historical gradients (Cavender-Bares et al. 2009, Graham et al. 2009, Wiens et al. 2010). Considering that the evolutionary relationship among species varies through geographical gradients, this could lead to changes in the evolutionary composition among communities, giving rise to patterns of phylogenetic beta diversity (Graham and Fine 2008). The importance in including the phylogenetic component of community structure into beta diversity studies relies on the fact that even communities totally different from each other in terms of their taxonomic composition can share some degree of evolutionary history when there is a replacement of species belonging to the same evolutionary lineage (Graham and Fine 2008, Qian et al. 2013).

Several features make the New World leaf-nosed bats of the Phyllostomidae family a good model system to test broad macroecological patterns of assembly and composition of their communities. This family is endemic and the most species-rich among New World bats (Simmons 2005). This is exemplified by their high levels of diversity in foraging habits, diet and morphology (Monteiro and Nogueira 2011). Although the flight capability had allowed bats an almost worldwide distribution, it is likely that the metabolic constraints of the phyllostomid bats, coupled with their dependence of vegetation structure and the strict fruit-based diet for some species, had prevented this family to expand their geographical distribution towards temperate areas, influencing their incidence in communities (Stevens 2004). Furthermore, there is a large amount of evidence suggesting that such dependence of the current environmental conditions is linked to their evolutionary history and tropical origin, which have exerted influence on the speciation rates, as well as on the occurrence both for species and phylogenetic lineages throughout the Neotropics (i.e. following the tropical niche conservatism hypotheses; Stevens 2006, 2011, Villalobos et al. 2013, but also

see Villalobos et al. 2014). The patterns of species diversity for this family in the Neotropics have been the focus of many studies along the past decades, yielding a solid base to compare the results from new findings and approaches. Nonetheless, despite its potential to offer insights into the mechanisms underlying community assembly, the variation of species composition among sites is still overlooked and restricted to small geographic regions (e.g. Stevens et al. 2007, López-González et al. 2015), or even not tested, as it is the case of the phylogenetic component of beta diversity. Accordingly, these studies may have not reflected the broad geographical, environmental and evolutionary factors influencing bat species distribution and their occurrence in biological communities.

Herein, our aims are to explore the patterns underlying the taxonomic and phylogenetic beta diversity of Neotropical phyllostomid bat assemblages. We addressed the relative roles of the current environment (mainly reflecting niche-based processes), space (dispersal-based processes), and the climatic stability (historical processes) from the LGM in driving the taxonomic and phylogenetic variation among these communities. According to the ecological theory, as well as considering these bats' biological features, we expect that, if niche-based processes are indeed important in shaping their community assembly, then the current environmental conditions will exert the stronger influence on the variation of taxonomic composition among these communities. We expect that their flight capabilities not only had reduced the effects of space and the restrictions to their dispersal, but also diminished the effects of the past climatic changes by making these bats more prone to follow their optimum environmental conditions or by allowing them to recolonize previous areas of their occurrence. Likewise, considering their evolutionary history, as well as the previous relationships found between the phylogenetic components of diversity for these bats and the contemporary environmental conditions (Stevens 2006, Stevens 2011), we also expect that the current environment will play a major role on the variation of the shared evolutionary history among these communities.

2 MATERIAL AND METHODS

2.1 Data on Neotropical phyllostomid bat assemblages

We gathered from published literature information on species composition for Phyllostomid bat assemblages throughout the continental Neotropics. Then, we created a binary matrix representing the species occurrence on each community. To reduce biases related to differences in sampling effort and methodology from different sources, we selected only studies that matched the following pre-established criteria: 1) the study should have considered the seasonal variation in community composition, as well as species seasonal migrations, by sampling at different seasons along the year (e.g. winter and summer, dry and wet seasons). The seasonal variation in community composition is a widely known pattern of Neotropical bat assemblages, and it emerges, for example, as a response to seasonal resource-availability (Mello 2009, Bobrowiec et al. 2014); 2) utilized predominantly the same sampling method. For this criterion, we considered studies that have employed mist-nets as the main capture method, since for the phyllostomid bats this is the most effective one (Kalko et al. 1996). Considering taxonomic changes, new species description, as well as recent reviews of species distributional maps, we have established two additional criteria to reduce biases and to make easier corrections whenever we judged necessary. Thus, in addition to the criteria 1 and 2, the study should have been: 3) published in a peer-reviewed journal or specialized book; 4) published between 1991 and 2016, encompassing a 25 years interval.

By applying these filters, we assembled a comprehensive database with 108 communities and 130 species (Figure 1; Appendix 1). The number of species included in our study corresponds to nearly 72% of all species for this family (see below). Overall, all communities are located within a relatively well established geographical and spatial unit, such as forests, natural reserves, national parks or conservation units. We did not include communities located at urban matrices (e.g. urban parks), regions with high levels of fragmentation and with low original vegetal cover due to anthropogenic impacts, and islands, since different ecological processes other than we

are interested might have influenced their species composition. We checked all geographical coordinates and performed taxonomical corrections considering changes in species taxonomy, as well as new information regarding their distribution. For these changes, we followed specialized literature (e.g. Simmons 2005, Gardner 2008, Velazco and Patterson 2008).

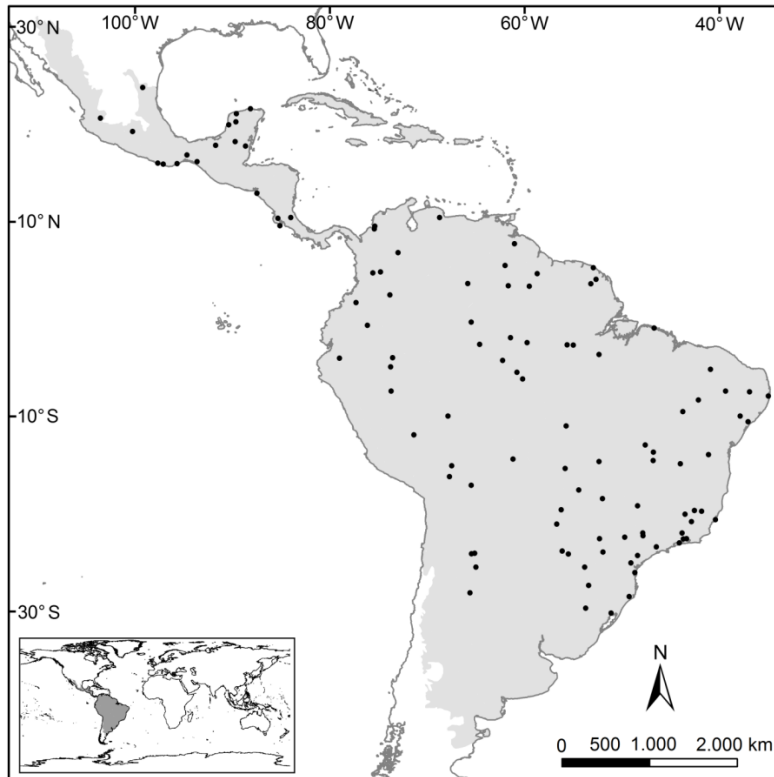


Figure 1. Location of the 108 phyllostomid bat assemblages throughout the Neotropics (shaded area). Overall, 117 species with phylogenetic information available were recorded in these communities and utilized in our analyses. References for all communities and their sources are presented in Appendix 1.

2.2 Measuring the taxonomic and phylogenetic beta diversity

We calculated, in a pairwise comparison between communities, the variation in species composition (taxonomic beta diversity, hereafter TBD) and the variation in terms of shared evolutionary history (phylogenetic beta diversity, hereafter PBD) with the widely used Sørensen (β_{sor} ; Sørensen 1948) and PhyloSor (Bryant et al. 2008) similarity indexes, respectively:

$$\beta_{\text{Sor}} = \frac{2a}{2a+b+c}$$

and

$$\text{PhyloSor} = \frac{2BL_{ij}}{BL_i + BL_j}$$

For β_{Sor} , a is the number of shared species between two communities, and b and c are the number of exclusive species in each community. For the PhyloSor index, BL_{ij} is the total branch length from a phylogenetic tree shared between the communities i and j , and BL_i e BL_j are the total branch length exclusive for each community, respectively. These indexes express the relative similarity between two communities in terms of their taxonomic and evolutionary composition, respectively. Thus, the complement of β_{Sor} and PhyloSor is a measure of compositional differences between communities (i.e. beta diversity). In this case, $\text{TBD} = 1 - \beta_{\text{Sor}}$ and $\text{PBD} = 1 - \text{PhyloSor}$. Both indexes range from zero, when two communities have the same set of species and evolutionary lineages (maximum similarity), to 1, when two communities are totally different with regards to their taxonomic and phylogenetic composition (maximum dissimilarity). We based the calculations of the PBD considering a dated phylogenetic tree for Chiroptera from Shi and Rabosky (2015). This tree is highly correlated with previous phylogenies proposed for bats and it presents a lower number of unsolved nodes considering the species present in our database. Of the 130 species at the 108 communities, 90% (117) had phylogenetic information available. Accordingly, for the calculation of both TBD and PBD we utilized only species present in this phylogeny. However, preliminary analyses did not indicate differences in results between this approach and when we utilized a tree with the missing species randomly inserted within their genus.

The variation in the evolutionary history shared between communities is likely to arise as a consequence of the variation in species composition. Thus, we utilized a null model approach to test whether the PBD is random with respect to the phylogeny by controlling the effects of the species variation (i.e. TBD) on the PBD (Graham et al. 2009, Leprieur et al. 2012). We randomized 9999 times the evolutionary relationship among bat species by shuffling the species identity in the phylogeny. For each iteration,

we calculated a new value of PBD and then estimated, in a pairwise comparison between communities, the Standardized Effect Size (SES; Leprieur et al. 2012):

$$SES = \frac{(X_{obs} - \overline{X_{null}})}{s.d.(X_{null})},$$

from which X_{obs} is the observed value for the PBD index, and $\overline{X_{null}}$ e $s.d.(X_{null})$ are the mean and standard deviation of the null distribution, respectively. Community pairs with SES values higher than 1.96 and lower than -1.96 have higher and lower PBD, respectively, than the expected by the TBD between communities.

2.3 Environmental, spatial and historical climatic stability variables

To test the influence of the current environment, which is thought to mainly reflect niche-based processes, we have adopted a heuristic approach by choosing *a priori* variables that represent different ways by which species distribution are influenced by contemporaneous environmental conditions. These variables have been broadly utilized as proxys for energy, water availability, and habitat complexity and structure (Currie et al. 1991, Field et al. 2009). In addition, it is likely that such variables exert influence on bat distribution as well as on their patterns of diversity at the community-level (Tello and Stevens 2010, López-González et al. 2015). We characterized the climatic gradients related to temperature and precipitation with the 19 bioclimatic variables from WorldClim database (Hijmans et al. 2005). To reduce the multicollinearity among these variables, we first conducted a Principal Component Analysis (PCA), retaining the first two principal components with the broken-stick criterion (Legendre and Legendre 2012). These two PCA axes accounted for nearly 70% of the variation in climatic data and they were aggregated to the following measures: canopy height (Simard et al. 2011), altitude (USGS 2010), potential evapotranspiration (Trabucco and Zomer 2009), actual evapotranspiration (Trabucco and Zomer 2010) and net primary productivity (Justice et al. 1998). We also included the mean annual cloud cover (Wilson and Jetz 2016), which measures the cloud covering along a landscape and may also exert influence on the ecosystem dynamics. These variables have shown low levels of multicollinearity, which

we verified with the Variance Inflation Factors (Appendix 2) (Legendre and Legendre 2012).

We generated spatial variables by modelling the spatial structure among communities with distance-based Moran Eigenvector Maps (dbMEM, formerly called Principal Coordinates of Neighbour Matrices – PCNM; Borcard and Legendre 2002). This approach allows one to create variables representing multiple scales and spatial structures from a matrix containing the geographic distance between sites (Dray et al. 2006, Griffith and Peres-Neto 2006). One of its main advantages is the generation of orthogonal and uncorrelated ordination axes that represent spatial functions among sites (Dray et al. 2006). Axes with positive eigenvalues can be utilized either as predictors or covariates representing the spatial structure among communities (Borcard and Legendre 2002, Peres-Neto and Legendre 2010). Overall, we generated 62 spatial variables to test the relative influence of space on the TBD and PBD.

We tested the influence of the historical climatic stability by utilizing the climatic anomalies (i.e. the magnitude of variation) of temperature and precipitation from the LGM to present (Araújo et al. 2008, Davies et al. 2009). We obtained estimates of temperature and precipitation for the LGM from simulations of the Community Climate System Model Version 4 (CCSM4) based on the Coupled Model Intercomparison Project Phase 5 (CMIP5; Gent et al. 2011) and available at the WorldClim database (Hijmans et al. 2005). We also utilized a measure of the velocity of climatic changes from the LGM to present (climate velocity *sensu* Sandel et al. 2011). The climate velocity is the ratio between the rate of change in temperature through time and the rate of change in temperature along space. All these measures of climatic stability can be complementary to each other. For example, areas with lower climatic anomalies and lower climate velocity are considered climatically more stable than regions where such variation was higher. These three variables have also showed low levels of correlation (Appendix 2).

2.4 Statistical analyses

We utilized central tendency (mean) and dispersion measures (standard deviation and skewness) to describe the general patterns of the TBD and PBD among

Neotropical phyllostomid bat assemblages. Further, we utilized Mantel multivariate correlograms to visualize and test for the presence of spatial autocorrelation in TBD and PBD. Likewise, we used Mantel test to assess the spatial structure in the current environment and historical climatic stability, both calculated as Euclidean distance between sites. At each distance class, we tested the significance of the Mantel statistics with 9999 permutations (Legendre and Legendre 2012). In addition, we assessed the correlation between the TBD and PBD using a Mantel correlation test with the Pearson correlation coefficient, testing the significance of this correlation with 9999 permutations.

To evaluate the relative importance of the current environment, space and historical climatic stability on the TBD and PBD, we conducted analyses of variance partitioning (Borcard et al. 1992) with a distance-based Redundancy (Legendre and Anderson 1999). We entered each matrix of explanatory variables in a forward selection procedure as described by Blanchet et al. (2008). This is a parsimonious way that allows one to eliminate unnecessary variables, which provide little increment in the final model. We then decomposed the TBD and PBD into 12 sources of variation (Figure 2). Each fraction accounts for the pure effect of each predictor when controlling for the effects of covariates, as well as the joint effect between two or more predictors, and the total effect of each predictor. By estimating the pure effect for each source of variation, we controlled for the confounding effects of covariates, which are thought to lead to biased parameters estimation and inflated Type 1 error-rates (Peres-Neto and Legendre 2010). To avoid discrepancy owing to different units and scales among environmental and historical variables, they were all standardized (mean = 0, standard deviation = 1) prior to the variance partitioning.

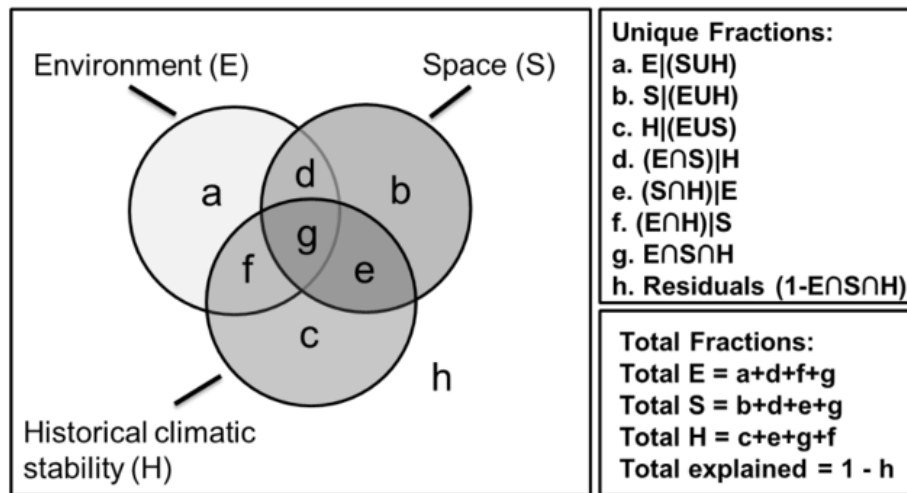


Figure 2. Conceptual Venn's diagram depicting our variance partitioning approach utilized to disentangle the effects of the current environment (niche-based processes; E), space (dispersal-based processes; S) and historical climatic stability (historical processes; H) on the taxonomic and phylogenetic beta diversity among Neotropical phyllostomid bat assemblages. The explained variation of TBD and PBD were decomposed into 12 fractions. Fractions a, b and c represent the pure effect of each predictor while controlling for the effects of the other two covariates. a. $E|(SUH)$: pure environmental effect; b. $S|(EUH)$: pure spatial effect; c. $H|(EUS)$: pure effect of historical climatic stability. Fractions d to f correspond to the joint effects of two predictors when controlling for a third matrix of explanatory variables. d. $E \cap S|H$: joint effect of current environment and space when controlling for the historical climatic stability; e. $S \cap H|E$: joint effect of the space and historical climatic stability when controlling for the current environment; f. $E \cap H|S$: joint effect of the current environment and historical climatic stability when controlling for the space. Fraction g. $E \cap S \cap H$ corresponds to the amount of explanation shared by the three matrices of predictors. Fraction h. $1 - E \cap S \cap H$ corresponds to unexplained variation (residuals). Total E, Total S and Total H correspond, respectively, to the overall variation attributed to the current environment, space and historical climatic stability, respectively. Total explained is the total amount of variation explained by our model ($a+b+c+d+e+f+g$). U: union, \cap : intersection, | after controlling for.

We obtained the total amount of variation explained by our model, as well as the total for each source and unique fractions, through the adjusted coefficient of determination (R^2) (Peres-Neto et al. 2006). By relativizing the variation explained from each source by the amount of variables present in each matrix, the R^2 adjusted provides an unbiased estimative of the variation in TBD and PBD. To test the significance of each fraction we utilized a null model approach similar to Tello and Stevens (2010) and Arellano et al. (2016). We permuted 9999 times the rows in our original community matrix. For each iteration, we repeated the variation partitioning both for TBD and PBD,

acquiring a new value of R^2 adjusted for each fraction presented in Figure 2. By permutating the rows in the original matrix, the relationship between communities and explanatory matrices is broken, yielding a null distribution of R^2 adjusted values (Tello and Stevens 2010, Arellano et al. 2016). We then estimated for each fraction the probability of obtaining by chance in the null R^2 distribution a value higher or equal than the observed R^2 adjusted, adopting 0.05 as the level of significance.

We conducted all analyses in R (R Development Core Team) with the following packages: *betapart* (Baselga and Orme 2012) for the calculation of the TBD and PBD; *fossil* (Vavrek 2012) for the calculation of the geographic distance between communities; *vegan* (Oksanen et al. 2013) for the modelling of spatial functions, Mantel correlograms, PCA and variance partitioning; *ape* (Paradis et al. 2014) for the manipulations of phylogenetic trees; *picante* (Kembel et al. 2015) for the null models related to the phylogenetic composition of communities; and *packfor* (Blanchet et al. 2008) for the forward selection of explanatory variables.

3 RESULTS

3.1 Overall patterns of taxonomic and phylogenetic beta diversity among Neotropical phyllostomid bat assemblages

Most of the phyllostomid bat species occurred in few communities (Appendix 3), and their communities along the Neotropics are characterized by relatively high levels of TBD. The overall mean for the TBD was 0.641 ± 0.16 , ranging from 0.077 to 1.0, the latter representing communities totally different from each other (i.e. communities without shared species). The frequency-distribution of TBD values is left-skewed (skewness = -0.584), indicating that most of the pairwise comparisons between communities were higher than the mean (Appendix 4). On the other hand, the overall PBD values were smaller than the TBD (mean = 0.501 ± 0.142), ranging from 0.065 to 0.942, presenting a slightly left-skewed distribution (skewness = 0.013; Appendix 4).

There was a high and positive correlation between PBD and TBD and they are positively correlated with each other ($r = 0.921$, $p < 0.001$; Figure 3), although for some pairwise comparisons it is possible to observe that even totally different communities (i.e. without shared species) still have evolutionary lineages in common, sharing evolutionary history through the replacement of species within the same lineage. This pattern becomes evident by the conspicuous column of dots in Figure 3 when the TBD reaches 1.0. On the other hand, none of the pairwise comparisons considering the PBD reached its maximum. In addition, only 5.7% ($n = 330$) of all pairwise comparisons showed PBD higher ($SES > 1.96$, 186 pairs) or lower ($SES < -1.96$, 144 pairs) than what would be expected considering only the variation in TBD (Figure 3), indicating that most of PBD can be explained by the TBD.

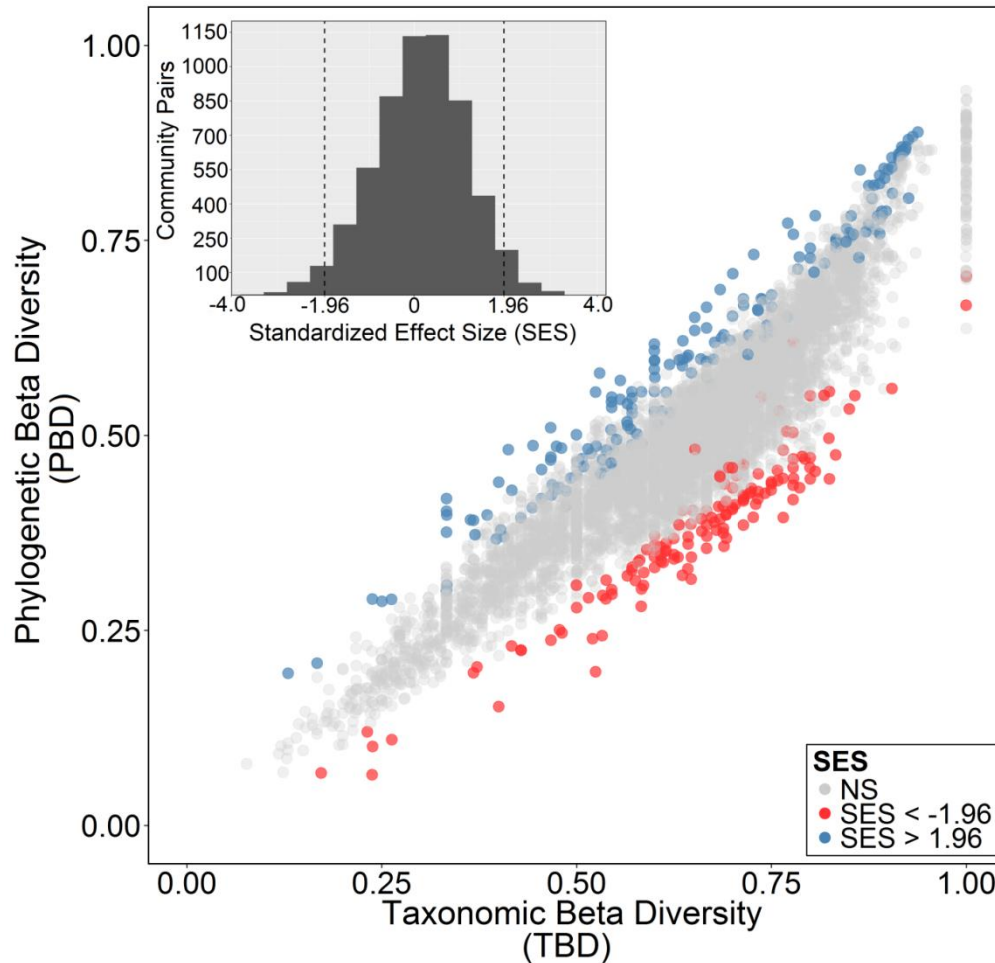


Figure 3. Relationship between the taxonomic (TBD) and phylogenetic beta diversity (PBD) among 108 Neotropical phyllostomid bat assemblages. Blue and red dots represent pairwise comparisons between sites from which the PBD is higher ($SES > 1.96$) or lower ($SES < -1.96$), respectively, than the expected by the variation in species composition (i.e. TBD). These results were based in a null model in which the phylogenetic relationships among species were broken by randomizing the tips of the phylogenetic tree (species identity) while keeping the TBD constant. Grey dots did not show a significant difference ($-1.96 < SES < 1.96$; NS: non-significant). The upper-left panel shows the frequency-distribution of SES values for all pairwise comparisons (Leprieur et al. 2012).

Overall, the TBD and PBD increased with geographic distance. Although both relationships are non-linear, the TBD has a steeper increase and stabilized asymptotically around 2000 km, whereas the PBD increased smoothly and stabilized around 3000 km. The maximum values of TBD started roughly at 1000 km and they are distributed through different pairwise geographic distances (Figure 4a). The pairwise comparison of SES values against the geographic distance showed that most of

communities with PBD higher than the expected by chance (i.e. $SES > 1.96$) are condensed around short to intermediate distances (Figure 4c). Further, communities with PBD lower than the expected by the TBD ($SES < 1.96$) are relatively evenly distributed through all distance classes (Figure 4c).

By utilizing Mantel correlograms, we also found a non-random spatial structure for the TBD and PBD components (Figure 5), indicating that geographically close sites are more similar in taxonomic and phylogenetic composition. Similarly, the current environment and the historical climatic stability are spatially structured, although in a lesser degree than the TBD and PBD at short distances (Figure 5). In this case, the spatial structure of the TBD and PBD are approximately twice as large than that observed for the current environment and historical climatic stability.

3.2 Variance partitioning

Our model explained 38.1% of the variation in TBD. The shared component between the current environment and space explained most of variation in TBD (fraction d, 15.5%; Table 1), which likely reflects the spatial structure of the environmental variables (i.e. spatial gradients of environmental conditions throughout the continental Neotropics). However, when controlling for the effects of the covariates and obtaining the unique and pure fractions for each source of variation, most of the variation in TBD was explained by the pure spatial effect, with nearly 13.9% (fraction b, $p < 0.001$; Table 1). The current environmental conditions explained little but significantly 2.6% of the total variation in TBD. Of the total amount of variation explained, the vast majority has included space as a predictor or covariate (Total S, 34.8%), and all the fractions encompassing the space as a covariate were significant (fractions d, e, g, and the total for each source). The pure effects of the historical climatic stability, as well as its joint effect with the current environment, were not significant.

The results of our variance partitioning considering the phylogenetic variation among Neotropical phyllostomid bat communities were consistent to those observed for the taxonomic composition (Table 1). Overall, 35.4% of the PBD was explained by our model. Of this amount, the shared effect between the current environment and space was predominant, with 15.9% explained variance, followed by the pure spatial effect,

which explained 11.5%. Of the total amount explained, 31.4% involved space as a predictor or covariate, and all fractions involving the space were significant.

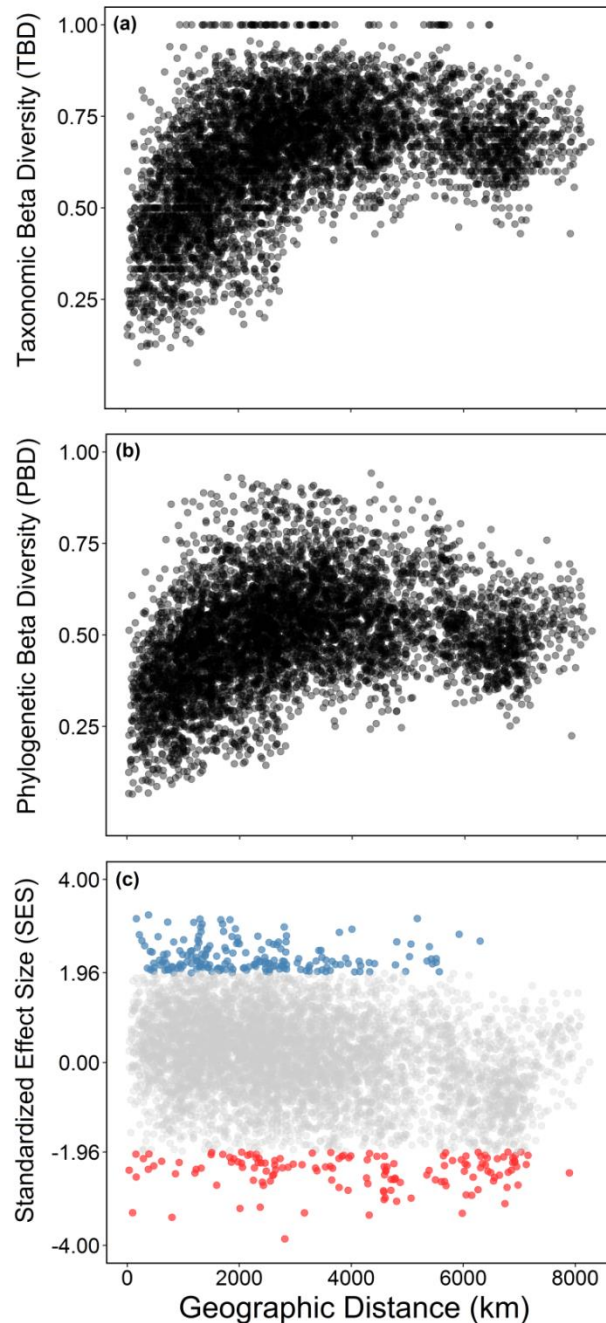


Figure 4. Relationship between (a) Taxonomic Beta Diversity (TBD), (b) Phylogenetic Beta Diversity (PBD), and (c) Standardized Effect Size (SES) with the geographic distance, respectively. In (c) the colors represent the same schema presented in Fig 3, with blue dots representing SES > 1.96, red dots SES < -1.96, and grey dots for PBD random with respect to TBD.

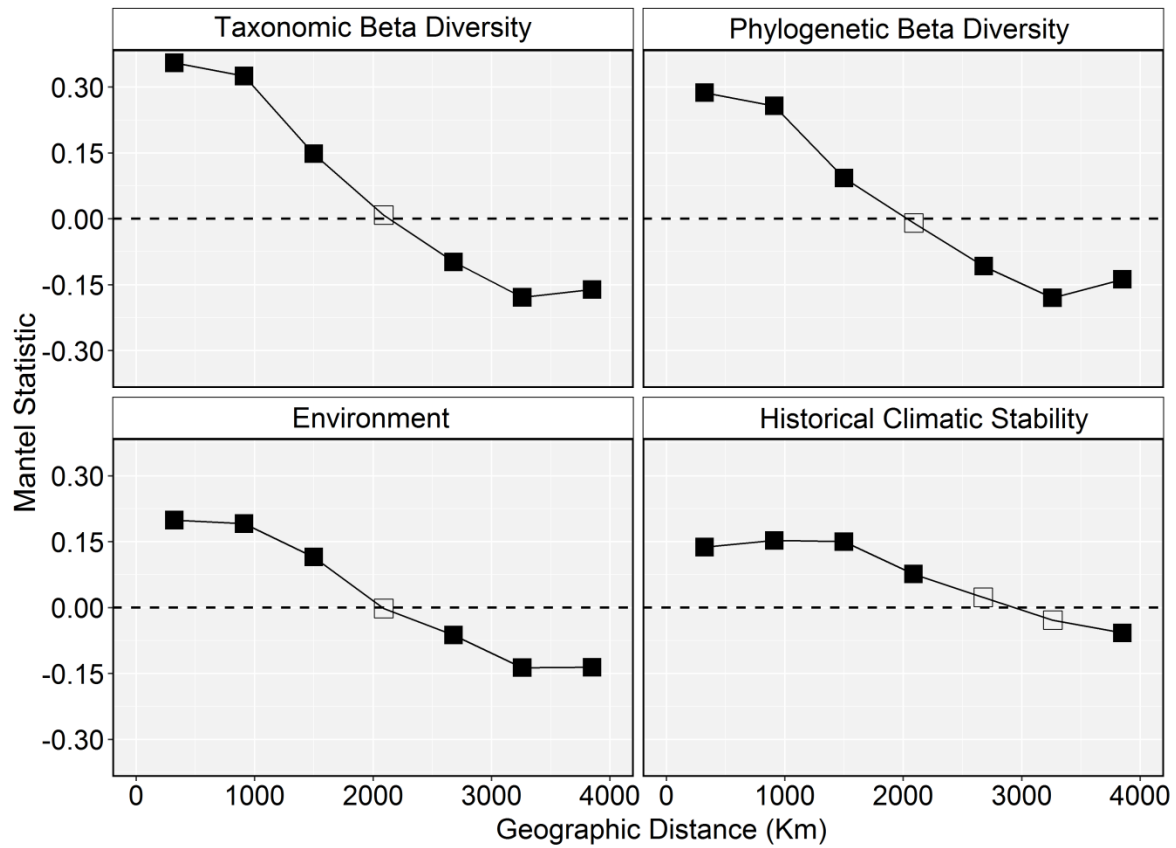


Figure 5. Mantel correlograms depicting the spatial autocorrelation for the Taxonomic and Phylogenetic Beta Diversity, and the spatial structure for the current environment and historical climatic stability. Filled and open squares are distances in which the spatial structure, measured as the Mantel statistic, is significant or non-significant, respectively, at a 0.05 significance level.

Table 1. Results from our variance partitioning considering the effects of the current environment (niche-based processes), space (dispersal-based processes) and historical climatic stability (historical processes) on the taxonomic and phylogenetic beta diversity of Neotropical phyllostomid assemblages. Fractions correspond to those depicted in Figure 2. Bolded values of R^2 adjusted observed are significant at the 0.05 level. The P -value for each fraction was estimated by permuting 9999 times the rows of the original community matrix. U: union, \cap : intersection, | after controlling for.

Fractions	Taxonomic Beta Diversity		Phylogenetic Beta Diversity	
	R^2 adjusted observed	P -value	R^2 adjusted observed	P -value
Unique				
a. E (SUH)	0.026	0.008	0.030	0.005
b. S (EUH)	0.139	<0.001	0.115	< 0.001
c. H (EUS)	0.004	0.173	0.005	0.155
d. E \cap S H	0.155	<0.001	0.159	<0.001
e. S \cap H E	0.034	0.002	0.023	<0.001
f. E \cap H S	0.002	0.259	0.003	0.152
g. E \cap S \cap H	0.018	<0.001	0.015	<0.001
h. Residuals (1- E \cap S \cap H)	0.618	0.99	0.645	0.999
Total				
Total E	0.202	<0.001	0.209	<0.001
Total S	0.348	<0.001	0.314	<0.001
Total H	0.060	<0.001	0.047	0.012
Total explained (1-h)	0.381	<0.001	0.354	<0.001

4 DISCUSSION

Disentangling the effects of multiple processes influencing the taxonomic and phylogenetic composition of communities is essential to understand their redundancy and complementarity underlying the current patterns of species distribution and incidence in communities (Tello and Stevens 2010). Here, contrary to our initial expectations and regardless their high vagility and dispersal abilities, the taxonomic and phylogenetic beta diversities among Neotropical phyllostomid bat communities have markedly signs of spatial structure. This became particularly clear when we partialled out the effects of the current environment, space and historical climatic stability into unique and shared fractions of variation. The total effect assigned to space, as well as the shared effects of space with additional predictors, were higher than for the other variables that we have considered in our model. More importantly, when we controlled the effects of covariates, the space was the best predictor for both TBD and PBD.

The richness and phylogenetic diversity for the phyllostomid bat assemblages have been widely related to current environmental conditions, reflecting the importance of niche-based processes underlying their geographical distribution and patterns of diversity at local scales (i.e. alpha diversity) (Stevens 2004, 2006, 2011). The origin and diversification of phyllostomid bats in tropical areas, coupled with their physiological constraints, may have played a crucial role in shaping their dependence in relation to the environment, thereby hindering these species to expand their geographical distribution towards temperate regions and giving rise to strong latitudinal and geographical richness gradients correlated with climate and habitat structure (Willig and Selcer 1989, Stevens 2004, 2006, 2011). In accordance with these patterns, but from a beta diversity perspective, studies at smaller and regional extents have found a stronger relationship between the variation in bat community composition and current environmental conditions in Neotropical assemblages (e.g. Stevens et al. 2007, López-González et al. 2015). However, considering that because the patterns of diversity are scale-dependent, at large geographical scales the species geographical distribution and the community assembly tend also to be under influence of broad geographical, historical and biogeographical dynamics affecting the rates of speciation, extinction, and dispersal, processes that in turn are responsible for the taxonomic and phylogenetic

variation in community composition (McKnight et al. 2007, Cavender-Bares et al. 2009, Barton et al. 2013, Mittelbach and Schemske 2015). Accordingly, considering such continental extent encompassed by our study, this might be one of the reasons of why we have observed a different pattern underlying the variation of community composition among these communities.

Here, the relative importance of the current environmental conditions is reflected by the pure fraction corresponding to the current environment (niche-based processes), which has shown little power in explaining the variation in community composition for these bats. On the other hand, the shared fraction between the current environment and space has explained most of the variation in TBD and PBD. However, it is hard to elucidate, for this fraction, which processes (i.e. whether the current environment or space) are generating such variation (Peres-Neto and Legendre 2010, Diniz-Filho et al. 2012). This shared effect may arise due to a latent spatial structure underlying the environmental variables or even when both species and environment are responding to a common spatial gradient (Peres-Neto and Legendre 2010). For example, Tello and Stevens (2012) have shown that spurious correlations between environment and diversity may arise even when considering pure spatial and stochastic models of species diversification and distribution. Indeed, we visualized through Mantel correlograms that a spatial structure underlies both the current environment and the historical climatic stability (Figure 5). Accordingly, this is the reason why it is important to estimate the pure effect for each source of variation considered in the analyses. Overall, by doing this, we found that the space is the best predictor in terms of variation in composition, as well as when considering the evolutionary history shared among communities. In comparison with previous studies (e.g. Stevens 2011, López-Gonzalez et al. 2015, and references therein) such contrasting results have emerged as a result of distinct processes structuring the Phyllostomid bat assemblages at different levels of diversity (i.e. alpha and beta diversities) and at different geographical scales (i.e. from regional to continental extents).

The complexity of its geological history has led to high levels of alpha and beta diversity along the Neotropics (McKnight et al. 2007, Hoorn et al. 2010, Rull 2011). Within such scenario, topographical barriers throughout this region have limited species

dispersal and their occurrence in communities, especially if these species have metabolic and physiological constraints preventing them to persist and overcome complex altitudinal gradients (Graham et al. 2009, Presley et al. 2012). This has been verified for bats and such pattern tends to be stronger for the Phyllostomidae family, especially owing to their metabolic requirements coupled with low-temperatures and low-levels of resources available for these bats (for example, fruits and nectar) at higher elevations (Graham 1990, McCain 2006, Presley et al. 2012). In addition, the diversification and distribution of the Phyllostomid bats have been shaped by complex and recurrent cycles of connection and isolation among Neotropical landscapes. This is exemplified by the fact that the main evolutionary radiations for these bats occurred separately at two different centers of diversification along the Neotropics, but the faunal exchange only took place after the full establishment of the Isthmus of Panamá (Arita et al. 2014, Rojas et al. 2016). It is likely that our results considering such strong spatial influence on the TBD and PBD have encompassed these idiosyncratic events related to historical dispersal processes and current topographical isolation, both thought to influence the distribution of species and lineages throughout the Neotropics. Such barriers would prevent species dispersal, resulting in faunal isolation that leads to high levels of variation in species composition among communities at broad geographical gradients (McKnight et al. 2007, Melo et al. 2009, Barton et al. 2013, Castro-Insua et al. 2016).

Operationally, the correct interpretation for the unique fraction assigned to the spatial influence in community dynamics requires that all environmental variables with potential to influence species distribution have been included as predictors. Otherwise, missing spatially-structured variables not included in the model would overestimate the pure spatial effect, especially when taking into account that a latent spatial structure may arise as a consequence of induced spatial-dependence with regards to exogenous and spatially-structured factors (Peres-Neto and Legendre 2010). We have considered, however, a robust set of environmental variables representing different mechanisms by which species distribution are influenced by the current environment and historical climatic stability, which had included also those variables previously thought to influence

bat assemblages at different scales (Stevens 2004, Tello and Stevens 2010, López-González et al. 2015).

Phyllostomid bats tend to occur with phylogenetically closely-related species, a pattern that might be indicative of shared environmental preferences along their evolutionary history (Villalobos et al. 2013). However, even considering the complex geographical extent of the Neotropics, and the conspicuous evolutionary history for this family, we found that the overall PBD tended to be random for the vast majority of our pairwise comparisons. A high and non-random variation of PBD in relation to TBD is expected, for example, when entire phylogenetic lineages are replaced as a response to stronger environmental gradients (Graham et al. 2009). Complementarily, a lower variation in PBD in comparison with the TBD is ascribed to the variation in evolutionary closely related species between communities, especially when these species are recent and have small geographical distribution (Graham and Fine 2008, Qian et al. 2013). Some pairwise comparisons have shown non-random phylogenetic structure, likely reflecting singular features at different distance classes, as can be observed when plotting the SES values against geographic distance. Nonetheless, the overall pattern that we have observed is random with respect to the phylogeny. According to Villalobos et al. (2013), the high variation in geographical range-size, and the lack of phylogenetic signal for this trait, may cause random patterns of association both for species and lineages of the phyllostomid bats. Moreover, we did find that most species in our study have occurred in few communities, which in turn causes a higher TBD. Nonetheless, our results suggests that in general such high variation in species composition is not followed by the replacement of complete phylogenetic lineages, reflecting a lower and random PBD in comparison with the TBD (Graham and Fine 2008).

Lastly, in addition to the traditional hypotheses linking beta diversity to current environment and space (Cottenie 2005, Vellend et al. 2014), we have tested the influence of historical mechanisms, namely the climatic stability from the LGM, on the TBD and PBD. Such historical mechanism was not important in explaining the variation in community composition of the Neotropical phyllostomid bat assemblages, supporting our initial expectation. These bats have filled most of their potential and suitable geographical range in terms of climatic conditions (Weber et al. 2014). From a

perspective of the climatic changes from the LGM, this means that if there was an influence of such dynamics on their distribution, then it was overcome or not detected by our study. Species dispersal ability is intrinsically related to a reduction of the effects of past climatic changes on their distribution (Hawkins and Porter 2003, Sandel et al. 2011, Dobrovolski et al. 2012). Hence, it is feasible that these bats have followed their climatic optimum throughout the last glaciation, or even recolonized areas previously affected by strong climatic changes. In addition, the climatic stability in Neotropics was relatively higher in comparison with regions at high latitudes where such variation was pronounced and with stronger effects on the species distribution (Dynesius and Jansson 2000). Thus, at least for the phyllostomid bats, the climatic variations occurred in Neotropics may have not been enough to cause dramatic shifts on their geographical distribution.

5 CONCLUSIONS

By considering species identity into community ecology, beta diversity has emerged as a useful concept to understand how different mechanisms influence community composition along geographic gradients.. Here we investigated the broad patterns and the main drivers of the beta diversity for the high-diverse Neotropical phyllostomid bat assemblages, both in terms of their taxonomic and phylogenetic composition. In spite of the large amount of evidence suggesting a stronger influence of the current environmental conditions on their distribution, our results have outlined that the space is more important than the current environment in explaining the patterns of diversity among these bat assemblages throughout the Neotropics, whereas the climatic stability from the last glacial maximum was not a good predictor of the taxonomic and phylogenetic variation among these communities. Taken together, these results advance our understanding and gives different insights into the mechanisms and processes influencing these communities. A comparison of our results with previous studies suggests that the structure of Neotropical phyllostomid bat assemblages is likely related to complementary ecological and evolutionary processes at different levels of diversity and geographical scales throughout this region. Yet, further studies

considering how species' ecological and evolutionary traits (for example, functional traits, species' age) exert influence on the different levels of diversity, as well as on the spatial patterns of diversity, could enhance our knowledge of community assembly of phyllostomid bat species. Only a broad of view encompassing such different processes should lead to a better understanding of the main factors driving the assembly and composition of ecological communities.

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7 APPENDIX

Appendix 1. Phyllostomid bat assemblages throughout the Neotropics utilized in our analyses. They were ordinated in order of decreasing richness.

Site	Richness	Latitude	Longitude	Reference
Parque Nacional Canaima, Venezuela	60	5.5	-62	Ochoa et al. (1993)
Iwokrama, French Guiana	54	4.6701	-58.69	Lim and Engstrom (2001)
Projeto Dinâmica de Fragmentos, Brazil	48	-2.417	-59.75	Sampaio et al. (2010)
Imataca, Venezuela	47	7.7433	-61.03	Ochoa (1995)
Alter do Chão, Brazil	46	-2.665	-54.99	Bernard and Fenton (2002)
Arataye, French Guiana	45	4.0833	-52.67	Voss and Emmons (1996)
Reserva Amaná, Brazil	45	-2.591	-64.61	Pereira et al. (2010)
Allpahuayo-Mishana, Peru	45	-3.969	-73.56	Hice et al. (2004)
Paracou, French Guiana	44	5.2842	-52.93	Simmons and Voss (1998)
Tiputini, Equador	44	-0.631	-76.13	Rex et al. (2008)
Cosha Cashu, Peru	43	-11.9	-71.37	Voss and Emmons (1996)
Jenaro Herrera, Peru	42	-4.918	-73.75	Ascorra et al. (1993)
Kanuku Mountain, French Guiana	42	3.3592	-59.51	Emmons (1993)
Serra do Divisor, Brazil	41	-7.394	-73.7	Nogueira et al. (1999)
Yurubi Park, Venezuela	40	10.438	-68.74	Delgado-Jaramillo et al. (2011)
Saul, French Guiana	38	3.6169	-53.2	Simmons et al. (2000)
Guamá-Belém, Brazil	37	-2.65	-55.63	Kalko and Handley (2001)
Uauaçu, Brazil	35	-4.237	-62.27	Bobrowiec et al. (2014)
Rio Xingu-Altamira Brazil	34	-3.65	-52.37	Voss and Emmons (1996)
Parque Carrasco, Bolivia	32	-17.06	-65.47	Espinoza et al. (2008)
Serrania Macarena, Colombia	32	2.4759	-73.82	Sánchez-Palomino et al. (1993)
Pilon Lajas, Bolivia	31	-15.06	-67.47	Flores-Saldaña (2008)

Palo Verde, Costa Rica	31	10.362	-85.34	Stoner and Timm (2004)
Cunucuma, Venezuela	30	3.6557	-65.83	Voss and Emmons (1996)
Ilha de Maracá, Brazil	29	3.4167	-61.67	Robinson (1998)
La Selva, Costa Rica	29	10.431	-84.01	Rex et al. (2008)
Los Chimalapas, Mexico	28	16.859	-94.68	García-García and Santos-Moreno (2014)
Parque Nacional Jaú, Brazil	25	-1.901	-61.45	Barnett et al. (2006)
La Sepultura, Mexico	25	16.175	-93.62	Medinilla et al. (2004)
Rio Teles Pires, Brazil	23	-10.96	-55.74	Miranda et al. (2015)
Parque Rio Doce, Brazil	22	-19.67	-42.55	Tavares et al. (2007)
Rio das Pedras, Brazil	22	-22.99	-44.11	Luz et al. (2011)
Tunquini, Bolivia	20	-16.17	-67.72	Moya et al. (2008)
Podocarpus, Ecuador	20	-4.017	-79.02	Rex et al. (2008)
Lamanai, Belize	20	17.765	-88.65	Fenton et al. (2001)
Rio Aripuanã, Brazil	20	-6.143	-60.2	Bobrowiec (2011)
Parque Noel Kempff, Bolivia	20	-14.38	-61.18	Emmons et al. (2006)
Cabo Blanco, Costa Rica	20	9.5809	-85.12	Timm and McClearn (2007)
Barcelos-Santa Isabel, Brazil	19	-0.265	-65.47	Moratelli et al. (2010)
Rio Madeira, Brazil	19	-5.461	-60.79	Bobrowiec (2011)
Pousada das Araras, Brazil	18	-18.44	-52.01	Zortéa and Alho (2008)
Peninsula Braganca, Brazil	18	-0.934	-46.7	Andrade et al. (2008)
Parque Intervales, Brazil	17	-24.26	-48.4	Passos et al. (2003)
Reserva Tinguá, Brazil	17	-22.55	-43.37	Dias and Peracchi (2008)
Nova Xavantina, Brazil	17	-14.64	-52.36	Sousa et al. (2013)
Fazenda Rio Negro, Brazil	17	-19.58	-56.23	Munin et al. (2012)
Estacion Primates, Colombia	17	9.5275	-75.38	Durán and Pérez (2015)
Pedras Grandes, Brazil	16	-28.48	-49.25	Carvalho et al. (2013)

Serra Confusões, Brazil	16	-9.492	-43.76	Gregorin et al. (2008)
Parque Curió Brazil,	16	-22.58	-43.7	Gomes et al. (2015)
São Carlos, Brazil	16	-21.97	-47.87	Muylaert et al. (2014)
Otun Quimbaya, Colombia	16	4.7309	-75.58	Estrada-Villegas et al. (2010)
Vereda Chorrillo, Colombia	16	4.8286	-74.8	García-Herrera et al. (2015)
La Florera, Colombia	16	9.2486	-75.43	Durán and Pérez (2015)
Reserva Feliciano Miguel Abdala, Brazil	14	-19.73	-41.82	Aguiar and Marinho-Filho (2007)
Estacao Ecologica Caetetus	14	-22.41	-49.7	Pedro et al. (2001)
Parque Mata Seca, Brazil	14	-14.86	-44	Falcão et al. (2014)
Chapada Guimarães, Brazil	14	-15.33	-55.83	Lima et al. (2016)
Chaschoc-Seja, Mexico	14	17.833	-91.73	Gordillo-Chávez et al. (2015)
Guarulhos, Brazil	13	-23.38	-46.47	Chavez et al. (2012)
Bosque Mbaracayu, Paraguay	13	-24.12	-55.5	Stevens et al. (2004)
Estação Ecologica Itirapina, Brazil	13	-22.24	-47.83	Sato et al. (2015)
Serra das Almas, Brazil	13	-5.165	-40.92	Silva et al. (2015)
Calakmul, Mexico	13	18.211	-89.73	Vargas-Contreras et al. (2008)
La Primavera, Mexico	13	20.644	-103.6	Zalapa et al. (2014)
Reserva Hampolol, Mexico	13	19.945	-90.39	Vargas-Contreras et al. (2008)
Cosigüina, Nicaragua	12	12.916	-87.5	Genoways and Timm (2005)
Sonora, Brazil	12	-17.54	-54.43	Cunha et al. (2011)
Paulo Cesar Vinha, Brazil	12	-20.6	-40.41	Oprea et al. (2009)
Parque Iguaçu, Brazil	12	-25.47	-53.83	Sekiama et al. (2001)
Serra Negra, Brazil	12	-21.95	-43.82	Nobre et al. (2009)
Chapada Araripe, Brazil	12	-7.392	-39.36	Novaes and Laurindo (2014)
Alvorada do Norte, Brazil	12	-14.54	-46.8	Bezerra and Marinho-Filho (2010)
Panga Reserve, Brazil	12	-19.17	-48.4	Pedro and Taddei

				(1997)
Patia, Colombia	12	1.7035	-77.31	Sánchez et al. (2007)
Rio Lagartos, Mexico	11	21.587	-88.16	Salas et al. (2012)
Rio Branco, Brazil	11	-9.951	-67.87	Calouro et al. (2010)
Estacao Caetés, Brazil	11	-7.907	-34.95	Silva and Farias (2004)
Chicamocha, Colombia	11	6.8172	-73	Sánchez et al. (2007)
Parque Kabah Mexico	11	20.255	-89.66	Estrella et al. (2014)
Parque Lagunas-Chacahua, Mexico	11	15.999	-97.66	Buenrostro-Silva et al. (2012)
Mata Paraíso-Viçosa, Brazil	10	-20.8	-42.86	Nascimento et al. (2013)
Dzibilchaltun, Mexico	10	21.092	-89.6	Pech-Canche et al. (2011)
Fênix, Brazil	10	-23.91	-51.95	Bianconi et al. (2004)
Parque Campinhos, Brazil	10	-25.03	-49.08	Arnone and Passos (2007)
Puerto Escondido, Mexico	10	15.897	-97.11	García-Grajales et al. (2013)
Mata do Junco, Brazil	10	-10.54	-37.06	Brito and Bocchiglieri (2012)
Morro do Diabo, Brazil	10	-22.54	-52.3	Reis et al. (1996)
Ixtapan Oro, Mexico	10	19.25	-100.3	Alvarez-Castañeda (1996)
Fazenda das Almas, Brazil	10	-7.472	-36.9	Beltrão et al. (2015)
Yaguareté Forest, Paraguay	9	-23.81	-56.13	Stevens et al. (2004)
Serra do Caraça, Brazil	9	-20.05	-43.52	Falcão et al. (2003)
Serra da Bodoquena, Brazil	9	-21.06	-56.71	Camargo et al. (2009)
La Pelegrina, Mexico	9	23.778	-99.21	Arriaga-Flores et al. (2012)
Salina Cruz, Mexico	9	15.96	-95.69	Cervantes and Mulia (1995)
Serra da Guia, Brazil	8	-9.969	-37.87	Rocha et al. (2015)
Volta Velha, Brazil	8	-26.04	-48.68	Sipinski and Reis (2005)
Laja Morada, Argentina	8	-24.04	-65.12	Sánchez (2015)
Frederico Westphalen, Brazil	7	-27.36	-53.42	Bernardi and Passos (2012)

Serra Jitirana, Brazil	7	-8.299	-42.16	Novaes et al. (2015)
Sao Domingos, Brazil	6	-13.67	-46.76	Bezerra and Marinho-Filho (2010)
Paraná-Tocantins, Brazil	5	-12.93	-47.6	Bezerra and Marinho-Filho (2010)
Morro São Pedro, Brazil	5	-30.19	-51.11	Pires and Fabián (2013)
Morro do Elefante, Brazil	5	-29.67	-53.72	Weber et al. (2011)
Las Conchas, Argentina	4	-25.46	-65	Sánchez (2015)
Contenda dos Sincorás, Brazil	4	-13.93	-41.11	Rios et al. (2008)
El Durazno, Argentina	3	-28.1	-65.6	Sánchez (2015)
Potrero Yala, Argentina	2	-24.1	-65.47	Bracamonte (2010)

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Appendix 2.

Table 1. Variance Inflation Factor (VIF) for each variable included in the matrix of current environmental conditions and for the variables included in the matrix of historical climatic stability. Despite the lack of a general rule, variables with VIF values under 10 can be considered suitable for the model. Bioclim PC1 and Bioclim PC2 represent climatic gradients from two Principal Components extracted from the 19 bioclimatic variables. Delta Temperature and Delta Precipitation are the climatic anomalies from the Last Glacial Maximum (21,000 years before present) in relation to current Temperature and Precipitation, respectively.

Predictor Matrix	VIF
Current Environment	
Canopy Height	2.27
Altitude	2.93
PET	3.31
AET	5.56
NPP	2.17
Cloud Cover	2.18
Bioclim PC1	4.94
Bioclim PC2	7.50
Historical Climatic Stability	
Delta Temperature	1.04
Delta Precipitation	1.03
Climate Velocity	1

Appendix 3. Phyllostomid bat species recorded in 108 communities along the Neotropics.

Table 1. Leaf-nosed bats of Phyllostomidae family recorded in 108 communities in the Neotropical region and utilized in our analysis. Species are shown in decreasing order of occurrence in communities.

Species	Occurrences
<i>Desmodus rotundus</i>	95
<i>Artibeus lituratus</i>	94
<i>Glossophaga soricina</i>	92
<i>Carollia perspicillata</i>	89
<i>Sturnira lilium</i>	89
<i>Artibeus planirostris</i>	59
<i>Chrotopterus auritus</i>	52
<i>Phyllostomus hastatus</i>	47
<i>Chiroderma villosum</i>	44
<i>Uroderma bilobatum</i>	44
<i>Artibeus obscurus</i>	43
<i>Phyllostomus discolor</i>	42
<i>Trachops cirrhosus</i>	39
<i>Anoura caudifer</i>	38
<i>Micronycteris megalotis</i>	37
<i>Lophostoma silvicolum</i>	35
<i>Carollia brevicauda</i>	35
<i>Platyrrhinus lineatus</i>	33
<i>Mimon crenulatum</i>	32
<i>Anoura geoffroyi</i>	30
<i>Platyrrhinus helleri</i>	30
<i>Tonatia saurophila</i>	29
<i>Rhinophylla pumilio</i>	28
<i>Sturnira tildae</i>	28
<i>Mesophylla macconnelli</i>	28
<i>Phylloderma stenops</i>	27
<i>Micronycteris minuta</i>	26
<i>Lonchophylla thomasi</i>	25
<i>Lophostoma brasiliense</i>	25

<i>Phyllostomus elongatus</i>	25
<i>Pygoderma bilabiatum</i>	24
<i>Artibeus jamaicensis</i>	24
<i>Chiroderma trinitatum</i>	24
<i>Diphylla ecaudata</i>	22
<i>Uroderma magnirostrum</i>	22
<i>Choeroniscus minor</i>	21
<i>Trinycteris nicefori</i>	21
<i>Vampyrum spectrum</i>	21
<i>Artibeus fimbriatus</i>	21
<i>Vampyressa bidens</i>	21
<i>Vampyressa pusilla</i>	21
<i>Micronycteris microtis</i>	19
<i>Artibeus phaeotis</i>	19
<i>Glyphonycteris sylvestris</i>	18
<i>Vampyressa thyone</i>	18
<i>Artibeus concolor</i>	17
<i>Ametrida centurio</i>	16
<i>Macrophyllum macrophyllum</i>	15
<i>Micronycteris schmidtorum</i>	15
<i>Lampronycteris brachyotis</i>	14
<i>Carollia castanea</i>	14
<i>Vampyrodes caraccioli</i>	14
<i>Lionycteris spurrelli</i>	13
<i>Lophostoma carrikeri</i>	13
<i>Mimon bennettii</i>	13
<i>Sturnira erythromos</i>	13
<i>Platyrrhinus brachycephalus</i>	13
<i>Diaemus youngi</i>	12
<i>Artibeus anderseni</i>	12
<i>Chiroderma doriae</i>	12
<i>Glyphonycteris daviesi</i>	11
<i>Micronycteris hirsuta</i>	11
<i>Tonatia bidens</i>	11
<i>Sturnira ludovici</i>	10

<i>Artibeus glaucus</i>	10
<i>Vampyressa brocki</i>	10
<i>Centurio senex</i>	10
<i>Lichonycteris obscura</i>	9
<i>Artibeus hartii</i>	9
<i>Glossophaga commissarisi</i>	8
<i>Lonchorhina aurita</i>	8
<i>Carollia sowelli</i>	8
<i>Chiroderma salvini</i>	8
<i>Platyrrhinus infuscus</i>	8
<i>Carollia subrufa</i>	7
<i>Rhinophylla fischeræ</i>	7
<i>Platyrrhinus recifinus</i>	7
<i>Choeroniscus godmani</i>	6
<i>Lonchophylla mordax</i>	6
<i>Phyllostomus latifolius</i>	6
<i>Glossophaga longirostris</i>	5
<i>Lophostoma schulzi</i>	5
<i>Sturnira oporaphilum</i>	5
<i>Sturnira magna</i>	5
<i>Artibeus toltecus</i>	5
<i>Leptonycteris yerbabuenae</i>	4
<i>Hylonycteris underwoodi</i>	4
<i>Lonchophylla robusta</i>	4
<i>Sphaeronycteris toxophyllum</i>	4
<i>Anoura latidens</i>	3
<i>Glossophaga leachii</i>	3
<i>Micronycteris brosseti</i>	3
<i>Micronycteris homezi</i>	3
<i>Carollia benkeithi</i>	3
<i>Sturnira parvidens</i>	3
<i>Artibeus amplus</i>	3
<i>Choeronycteris mexicana</i>	2
<i>Glossophaga morenoi</i>	2
<i>Sturnira bidens</i>	2

<i>Artibeus aztecus</i>	2
<i>Artibeus hirsutus</i>	2
<i>Vampyressa nymphaea</i>	2
<i>Vampyressa melissa</i>	2
<i>Anoura cultrata</i>	1
<i>Leptonycteris curasoae</i>	1
<i>Lonchorhina inusitata</i>	1
<i>Lophostoma evotis</i>	1
<i>Macrotus waterhousii</i>	1
<i>Sturnira bogotensis</i>	1
<i>Sturnira luisi</i>	1
<i>Sturnira aratathomasi</i>	1
<i>Sturnira hondurensis</i>	1
<i>Artibeus bogotensis</i>	1
<i>Ectophylla alba</i>	1
<i>Platyrrhinus aurarius</i>	1
<i>Platyrrhinus masu</i>	1
<i>Platyrrhinus vittatus</i>	1

Appendix 4. Frequency-distribution of the taxonomic and phylogenetic beta diversity among the 108 communities utilized in our study.

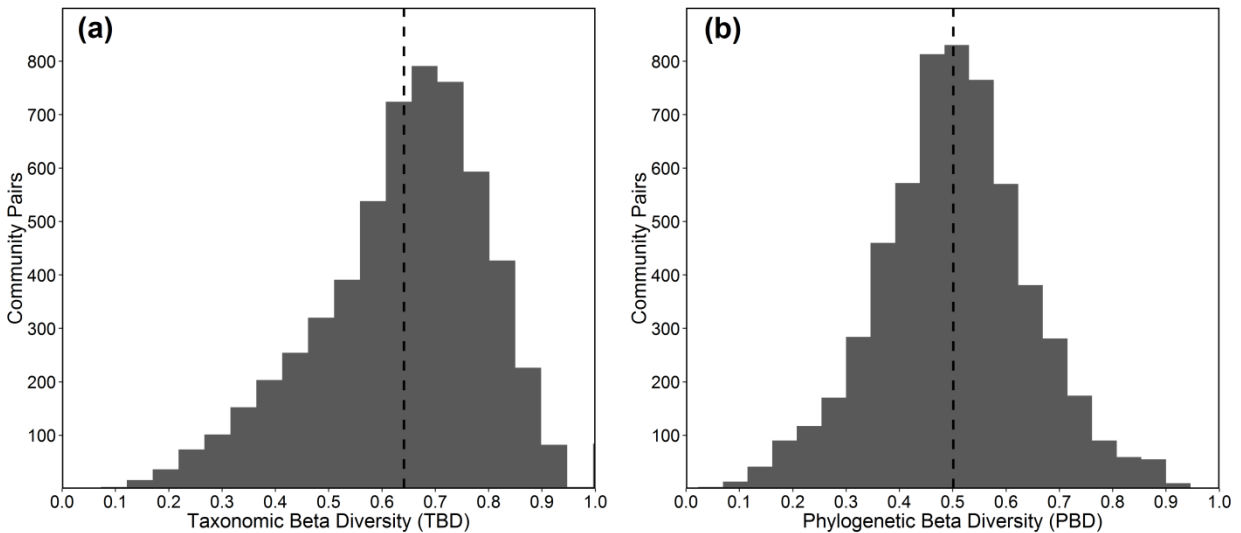


Figure 1. Frequency-distribution of a pairwise comparison between communities and considering the (a) Taxonomic Beta Diversity (TBD) and the (b) Phylogenetic Beta Diversity (PBD) between phyllostomid bat communities throughout Neotropics. Dashed lines indicate the overall mean for TBD and PBD.