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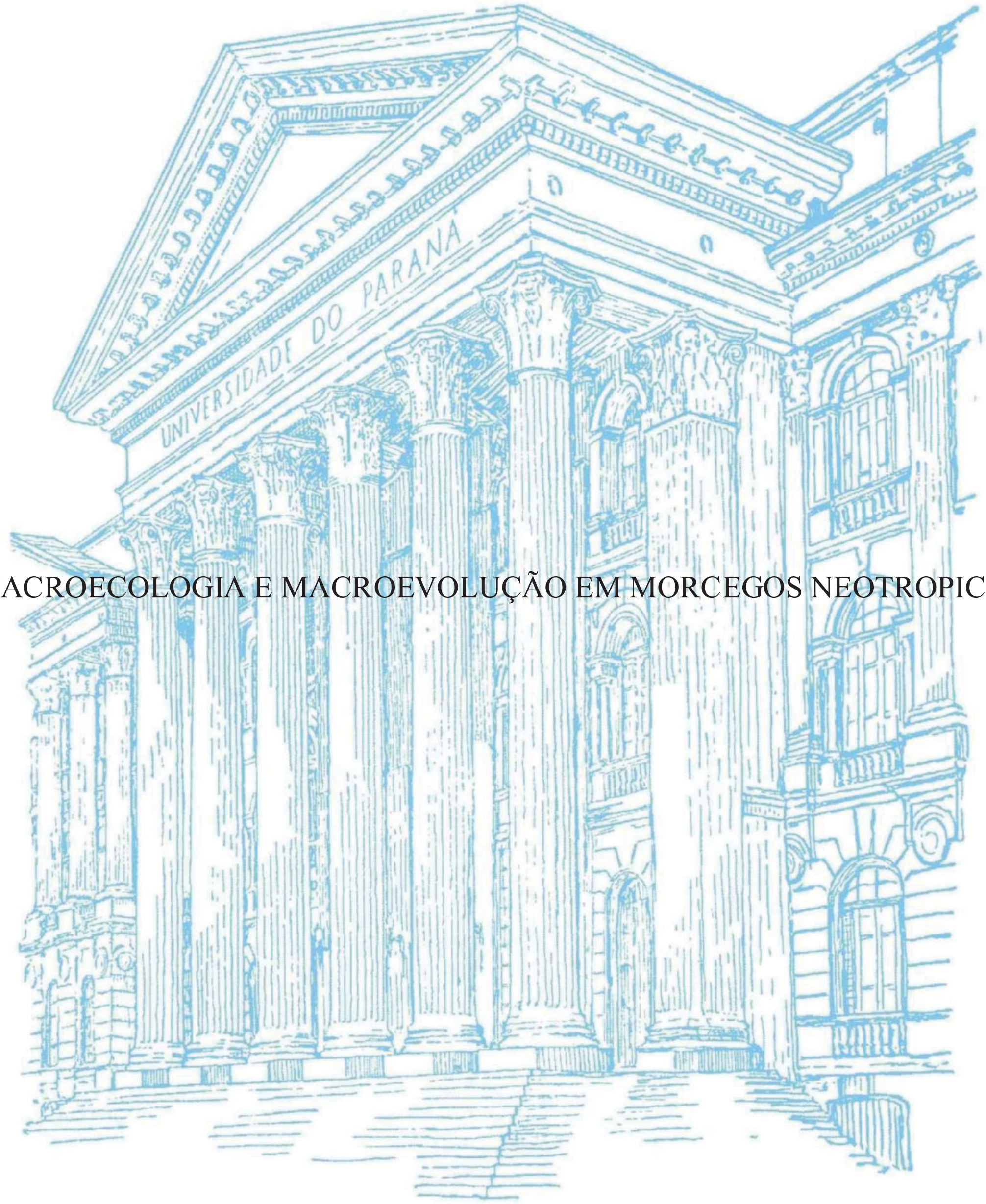

# MACROECOLOGIA E MACROEVOLUÇÃO EM MORCEGOS NEOTROPICAIS

CURITIBA

2021

LUIZ HENRIQUE VARZINCZAK

# MACROECOLOGIA E MACROEVOLUÇÃO EM MORCEGOS NEOTROPICAIS

Tese apresentada como requisito parcial à obtenção do título de Doutor em Ecologia e Conservação, no Curso de Pós-Graduação em Ecologia e Conservação do Setor de Ciências Biológicas da Universidade Federal do Paraná.

Orientador: Dr. Fernando C. Passos

Coorientador: Dr. Mauricio O. Moura

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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 tese de Doutorado de **LUIZ HENRIQUE VARZINCZAK** intitulada: **Macroecologia e Macroevolução em morcegos Neotropicais**, sob orientação do Prof. Dr. FERNANDO DE CAMARGO PASSOS, que após terem inquirido o aluno e realizada a avaliação do trabalho, são de parecer pela sua APROVAÇÃO no rito de defesa.

A outorga do título de doutor está sujeita à homologação pelo colegiado, ao atendimento de todas as indicações e correções solicitadas pela banca e ao pleno atendimento das demandas regimentais do Programa de Pós-Graduação.

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*...Certas luas,*

*Dias incertos...*

(Blindagem)

# RESUMO

Processos ecológicos e evolutivos atuam em conjunto determinando a distribuição das espécies e os padrões de diversidade. Nesta tese dividida em três capítulos, avaliamos aspectos macroecológicos e macroevolutivos associados à distribuição de morcegos Neotropicais. Esta tese está estruturada em três capítulos que abordam, respectivamente, 1) a evolução do nicho climático nesses morcegos; 2) os determinantes do tamanho de distribuição geográfica; e 3) gradientes de extinção e colonização local e sua relação com padrões de biodiversidade. Nossos resultados principais indicam que a maioria das espécies ocupa regiões tropicais do espaço de nicho climático, embora apresentem múltiplas e recentes mudanças em direção à diferentes ótimos climáticos, o que pode estar intimamente relacionado com a conservação tropical de nicho nesses morcegos. Em relação ao tamanho de distribuição geográfica, encontramos que a amplitude de nicho climático afeta positivamente a distribuição das espécies. No entanto, observamos uma tendência negativa relacionada à capacidade de dispersão: embora todas as espécies sejam positivamente influenciadas pela amplitude de nicho climático, a maioria não demonstra efeito da dispersão sobre sua área de distribuição geográfica. Estes resultados desafiam a tradicional visão de que uma maior habilidade de dispersão se traduz automaticamente em maiores distribuições geográficas, destacando que particularidades durante a evolução de cada grupo podem ter desempenhado papel crucial na determinação da importância de diferentes processos relacionados à sua distribuição. Por fim, observamos que maiores taxas de colonização e extinção são encontradas fora dos trópicos, na periferia da distribuição destes morcegos. Além disso, as taxas de colonização e extinção local apresentam forte estruturação espacial, variando no grau de correlação com a riqueza de espécies e na resposta às influências de dinâmicas contemporâneas e históricas. Ambos os processos atuam sinergisticamente na origem e manutenção dos gradientes de diversidade observados para esse grupo.

**Palavras-chave:** Biogeografia, dispersão, distribuição geográfica, gradiente latitudinal de diversidade, nicho climático, Phyllostomidae

# ABSTRACT

Ecological and evolutionary dynamics act together to determine species distributions and patterns of diversity. This dissertation has been divided into three chapters in which we address macroecological and macroevolutionary dynamics related to the distribution of Neotropical bats. We focused, respectively, on 1) the evolution of climatic niches; 2) geographical range-size determinants; and 3) gradients in local extinction and colonization and their relationships with broad-scale patterns of species diversity. Our main results indicate that most species are found in tropical regions of the climatic niche space. Yet, we observed multiple and evolutionarily recent changes towards several climatic optima, which is likely linked to the tropical niche conservatism hypothesis in these bats. Considering range-size dynamics, we found that climatic niche breadth positively affects the size of species geographical ranges. However, we found an opposite trend when considering the effects of dispersal abilities, for which range sizes of most species are not affected. These results challenge the traditional and historical view that increased dispersal abilities automatically translate into increased geographical ranges. We highlight that idiosyncrasies during bat evolution might have played a key role in determining the role and complementarity of different processes affecting species distributions. Finally, we found that increased extinction and colonization rates are observed outside the tropics, in the periphery of the Neotropical bats distributions. Both rates show also strong spatial structuring, with the degree of correlation depending on species richness and the mechanism underlying their geographical patterning. Overall, local extinction and colonization act synergistically in the origins and maintenance of complex biodiversity gradients in phyllotomids.

**Keywords:** Biogeography, dispersal, geographical distribution, climatic niches, latitudinal gradient of species diversity, Phyllostomidae

# SUMÁRIO

# INTRODUÇÃO

## *Sobre a Ecologia e Evolução*

Não é possível separar Ecologia e Evolução quando o objetivo é entender os famosos *drivers*, isto é, os fatores por trás da distribuição das espécies no espaço e no tempo. Dinâmicas ecológicas e evolutivas atuam em conjunto influenciando a ampla diversidade que observamos hoje. Se em 1973 Dobzhanski afirmou que *nada na biologia faz sentido exceto sob à luz da evolução*, hoje sabemos que a ecologia leva à evolução e a evolução leva à ecologia. Isso representa um fluxo contínuo, totalmente interligado. Uma via de mão dupla. Os efeitos da ação conjunta entre ecologia e evolução são observados em diferentes escalas temporais e espaciais intrínsecas da biodiversidade, da distribuição individual das espécies e dos indivíduos que a compõe, passando pela organização e estruturação das comunidades e das interações ecológicas, até chegar à complexidade da formação e função dos ecossistemas (Ricklefs 1987; Cavender-Bares et al. 2009; Mittelbach & Schemske 2015). Abandonar essa premissa é ignorar parte crucial de como os sistemas biológicos são estruturados. Mais ainda: é ignorar a essência sob a qual a distribuição e diversidade de formas de vida na Terra são fundamentadas.

## *Sobre a distribuição das espécies e da diversidade*

Há muitos fatores determinantes da distribuição das espécies e esse é de fato um tema central da pesquisa ecológica-evolutiva, evidenciado pela enorme quantidade de teorias, abordagens e revisões no tema (e.g. Wiens & Donoghue 2004; Jablonski et al. 2013; Stein et al. 2014; Fine 2015). Há dois fatores, no entanto, que são encarados como entre os principais, seja por seus efeitos diretos ou indiretos e que são diretamente abordados nesta tese: clima e dispersão.

O clima pode ser encarado de diferentes formas. Por exemplo, o clima pode representar uma das dimensões do clássico conceito de nicho como hipervolume n-dimensional nas ideias de Hutchinson (1957) e como abordaremos nos Capítulos 1 e 2 desta tese. Nesse caso, o clima é uma unidade operacional representando um atributo da espécie, seja ele a posição de uma determinada espécie no espaço de nicho climático (hipervolume climático), ou a amplitude de nicho de cada espécie, refletindo em adequabilidade à maior gama de condições climáticas e em seus padrões de distribuição geográfica (Soberón 2007; Holt 2009). Por outro lado, o clima pode atuar em um contexto espacial, seja de maneira direta ou indireta, determinando os gradientes geográficos de diversidade, que refletem o papel da variação climática no acúmulo de espécies ou, ainda na variação nas taxas de colonização e extinção ao longo de gradientes geográficos (Wiens & Donoghue 2004; Svenning et al. 2015, Harrison et al. 2020), como consideraremos no Capítulo 3 a seguir.

Complementar ao clima, a habilidade de dispersão das espécies também é um fator determinante da diversidade. Afinal, uma espécie pode ter uma grande amplitude de nicho, mas não ser capaz de chegar nas áreas adequadas para sua ocorrência (Soberón 2007; Holt 2009). Isso tende a influenciar os padrões de ocorrência das espécies no espaço de nicho climático, nas comunidades, bem como no tamanho de distribuição geográfica (Lester et al. 2007; Capítulos 1 e 2). Além disso, a capacidade de dispersão está intimamente ligada à capacidade de colonização de novas áreas quando as espécies enfrentam barreiras espaciais que podem representar resistência à sua ampliação de distribuição, ou à manutenção de populações viáveis em paisagens heterogêneas, evitando extinções de populações locais (a seguir no Capítulo 3).

## *Sobre esta tese*

É muito difícil escolher um tema de pesquisa. A ampla diversidade de espécies e grupos, bem como diversidade de formas de vida, leva também à diversidade de temas e teorias que poderiam ser abordadas. Esta tese foi desenvolvida a partir da escolha de alguns dos muitos questionamentos e interesses que surgiram nos últimos anos sobre morcegos, especialmente os da família Phyllostomidae. Morcegos, no geral, por si só são um grupo que atrai atenção entre todos os mamíferos. Isso ocorre principalmente pela capacidade de voo verdadeiro, característica única no grupo (Norberg & Rayner 1987). Mas dentre as cerca de 1400 espécies de morcegos do Mundo, as aproximadamente de 200 espécies da família Phyllostomidae (Solari et al. 2019) que ocorrem exclusivamente no Novo Mundo chamam ainda mais atenção. Seria como afirmar que os Phyllostomidae são ainda mais únicos, como se isso fosse possível uma vez que toda forma de vida é evolutivamente única.

Amplamente diversos, tanto ecologicamente quanto morfologicamente, esses morcegos diferem enormemente quando comparados com outras famílias Neotropicais (Stevens 2004, Arita et al. 2014). Além disso, padrões biogeográficos e de evolução que emergem da distribuição dessa família são complexos e revelam muito sobre diferentes aspectos da diversificação Neotropical (Rojas et al. 2016; Tavares et al. 2018). Os picos de riqueza dessa família ocorrem em regiões tropicais e de baixa latitude próximas ao Equador (Willig & Selcer

1989; Stevens 2004; Stevens 2011; Arita et al. 2014). Por muitos anos, foi considerado que esses padrões de diversidade surgiram principalmente pela Conservação Tropical de Nicho devido às origens tropicais da família e à exacerbada influência climática nestes morcegos. Porém, a maior parte das evidências sempre foram indiretas e a partir de dados de comunidades e padrões de diversidade, sem levar em conta o contexto evolutivo de maneira explícita (Stevens 2011, Ramos Pereira & Palmeirim 2013; Villalobos et al. 2013). Apenas recentemente é que aspectos evolutivos mais gerais começaram a ser testados (Peixoto et al. 2017). Além disso, não há evidência sobre se os gradientes de diversidade se dariam por maior colonização destas áreas, ou se por menores taxas de extinção nesses locais, deixando de fora da explicação mecanismos evolutivos que, em última análise, são os responsáveis pela geração dos padrões de diversidade. Entender esses mecanismos é essencial, pois padrões de diversidade de morcegos influenciam os padrões de diversidade quando consideramos os mamíferos como um todo. Além disso, a história diferenciada da família Phyllostomidae tem potencial para lançar luz sobre novas perspectivas relacionadas à distribuição geográfica das espécies e dos padrões de diversidade em ampla escala.

Esta tese está estruturada em uma interface Macroecológica e Macroevolutiva em três capítulos. No capítulo 1, abordamos as dinâmicas relacionadas à evolução do nicho climático nessa família. No capítulo 2, focamos em como a amplitude de nicho climático e habilidade de dispersão determinam o tamanho de distribuição geográfica das espécies. Por fim, no capítulo 3 testamos a presença e importância de gradientes latitudinais em taxas de extinção e colonização na geração dos padrões de diversidade para a família no Novo Mundo.

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# CAPÍTULO 1

## *Shifts to multiple optima underlie climatic niche evolution in New World phyllostomid bats* *

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# Shifts to multiple optima underlie climatic niche evolution in New World phyllostomid bats

## ABSTRACT

Climate underlies species distribution patterns, especially in species where climate limits distributions, such as the phyllostomid bats that are mostly restricted to the New World tropics. Evolutionary dynamics that shaped phyllostomid climatic niches remain unclear and a broad phylogenetic perspective is required to uncover their patterns. We used geographical distributions and evolutionary relationships of 130 species, climate data, and phylogenetic comparative methods to uncover dynamics of phyllostomid climatic niche evolution. Diversification of climatic niches began early in phyllostomid evolution (~34 million years ago, Ma), with most changes taking place around 20 Ma. While most of these bats were found in tropical regions, shifts towards different evolutionary optima were common. Shifts were mostly towards temperate climates, reflecting complexities in phyllostomid evolution highlighted by the probable role of species-specific adaptations to cope with these climates, the influence of paleoclimatic events, as well as biogeographical effects related to the evolution and dispersal of clades in the New World. Our results broaden the understanding of the relationships between phyllostomid bats and climate, filling an important gap in knowledge and suggesting a complex evolution in their occupation of the climatic niche space.

**Keywords:** Chiroptera, climate, Grinnellian niche, leaf-nosed bats, New World, Phyllostomidae

# INTRODUCTION

A noteworthy interplay between ecology and evolution comprises the different ways by which climate shapes patterns of species distributions and biological diversity in space and time (Mittelbach *et al*., 2007; Rolland *et al*., 2018). Climatic conditions (temperature and rainfall) are linked to species fitness and habitats, as species-specific thermal tolerances and metabolic constraints influence where they are likely to occur and thrive (Calosi *et al*., 2010; Bozinovic *et al*., 2011; Buckley *et al*., 2012). For example, ectotherms are excluded from colder regions because they depend on external energy sources to regulate body temperature and metabolism (Bozinovic *et al*., 2011; Buckley *et al*., 2012; Rolland *et al*., 2018). Conversely, endotherms can cope with colder and dryer regions, though their geographic distributions may still be constrained by extreme climatic conditions of drought and high or low temperatures (Bozinovic *et al*., 2011; Buckley *et al*., 2012). Climate, therefore, must be included as an important dimension within the classical *n*-dimensional niche hypervolume concept (Hutchinson, 1957), within the abiotic and coarser components in complement to biotic and finer components of the niche, such as interspecific interactions (Soberón, 2007).

Evolutionarily, climatic niches are variable with respect to phylogenetic conservatism, i.e. the degree to which species and their ancestors have similar climatic niches (Wiens *et al*., 2010; Peterson, 2011). Indeed, this is why closely related species are expected, and tend, to have more similar climatic niches than distantly related species (Wiens *et al*., 2010; Peterson, 2011). Although climatic niches can be evolutionarily conserved across different phylogenetic scales (Buckley *et al*., 2010; Peterson 2011; Peixoto *et al*., 2017; Rodrigues *et al*., 2019), evolutionary constraints may also be lost over evolutionary time, indicating niche divergence (Jezkova & Wiens, 2018). This occurs because species face different selective pressures along their geographical ranges causing their climatic niches to change appropriately (Pearman *et al*., 2008; Cadena *et al*., 2011; Lawson & Weir, 2014; Rolland *et al*., 2018). Also, climatic niches may evolve asymmetrically and at variable rates in different parts of the phylogeny (Araújo *et al*., 2013; Pie *et al*., 2017). This may be the due to shifts and adaptations of species and entire clades in coping with different climates, or changes in their geographic ranges following major biogeographical events (Broenniman *et al*., 2007; Pearman *et al*., 2008; Araújo *et al*., 2013; Pie *et al*., 2017).

Among the factors influencing climatic niche evolution the process of clade adaptation to different climates is often important (Lawson & Weir, 2014; Rolland *et al*., 2018). Thus, the evolution of climatic niches requires that species evolved physiological or behavioral responses that enable them to cope with different climatic conditions in areas with contrasting climates (Bozinovic *et al*., 2011; Buckley *et al*., 2012; Lawson & Weir, 2014; Rolland *et al*., 2018). These responses are especially likely early in the evolutionary history of clades, such as in the evolution of endothermy by birds and mammals (Buckley *et al*., 2012; Rolland *et al*., 2018), or later, when selection pressures cause climatic niche divergence at the levels of genus and species (Broennimann *et al*., 2007; Cadena *et al*., 2011; Lawson & Weir, 2014). However, climatic niche evolution can also be constrained by limitations in species dispersal (Cooper *et al*., 2011), which explains why the observed patterns cannot always be distinguished from those expected under purely neutral biogeographical dynamic models of species distribution (Boucher *et al*., 2014). Inferences drawn from dynamics of climatic niche evolution are fundamental to uncover the role of biogeographical dynamics of clade dispersal and the formation of regional assemblages on broad spatial scales (Cooper *et al*., 2011; Olalla-Tárraga *et al*., 2011; Rolland *et al*., 2018), the impact of climatic niche evolution on correlated evolution of other traits (Lawson & Weir, 2014), as well as the influence of forecasted climatic changes on species distributions (Araújo *et al*., 2013). Thus, studying climatic niches from a broad phylogenetic perspective is clearly important to better understand those factors that underlie species distributions over spatial, temporal, and phylogenetic scales (Buckley *et al*., 2010; Cadena *et al*., 2011; Pie *et al*., 2017; Rolland *et al*., 2018; Rodrigues *et al*., 2019).

In this study, we examined evolutionary dynamics of climatic niches for the leaf-nosed bats, family Phyllostomidae. Bats have flight and complex echolocation adaptations that make them unique among mammals (Teeling *et al*., 2018). Phyllostomids are endemic to the Americas, where they are the most species-rich bat family, and have undergone remarkable ecological radiation resulting in their having the greatest family-level ecological diversity of all mammalian families (Monteiro & Nogueira, 2011; Dumont *et al*., 2012). Although flight abilities allowed bats to colonize most regions of the world (Teeling *et al*., 2018), climate has repeatedly been an important factor regulating phyllostomid geographical distribution and patterns of diversity at different scales (Stevens, 2004; Stevens, 2011; Villalobos *et al*., 2013; Alroy, 2019). The influence of broad scale climate on phyllostomid distribution is probably the result of physiological and thermal tolerances linked to dietary adaptations to a plant-based diet for most species (Stevens, 2004; Stevens, 2011; Alroy, 2019). Furthermore, the influence of climate has been traced back to their tropical origin and tropical niche conservatism in these bats (Stevens, 2004; Stevens, 2011; Villalobos *et al*., 2013). Together, these factors prevented phyllostomid species from occupying temperate climates at high latitudes (Stevens, 2004; Stevens, 2006; Stevens, 2011; Villalobos *et al*. 2013; Alroy, 2019). Howevewr, several phyllostomid species are found outside the tropics, which suggests adaptations to cope with these climates (Ortega-García *et al*., 2017), as well as shifts in different climatic niches during phyllostomid radiation.

Despite the influence of climate on phyllostomid distributions, the evolutionary dynamics underpinning climatic niches in this family have only recently begun to be thoroughly studied. For example, Peixoto *et al*. (2017) did not find the expected support for phylogenetic conservatism of climatic niches in phyllostomids (e.g. Stevens, 2011; Villalobos *et al*., 2013). In addition, Ortega-García *et al*. (2017) identified phylogenetic variation in thermal niche limits for nectar-feeding phyllostomids, thereby demonstrating important variability at the lower limits of their thermal niches. Nevertheless, although both studies elucidated important features of the phyllostomid climatic niche, the evolution of their climatic niche remains unclear. Unresolved aspects include, for example, when and how climatic niches diversified during phyllostomid evolution. Accordingly, addressing the tempo and mode of phyllostomid climatic niche evolution, together with biogeographical (e.g. Tavares et al. 2018) and morphological (e.g. Monteiro & Nogueira 2011; Dumont *et al*., 2012) advances, will broaden our understanding of the dynamics that now determine phyllostomid distributions in the New World.

Here we integrate phyllostomid geographical distributions and evolutionary relationships among species and couple them with climatic data in a phylogenetic comparative framework to address the dynamics of phyllostomid climatic niche evolution. Our main goals are twofold. First, to understand when and how climatic niches diversified for the phyllostomids we focus on the tempo and mode of phyllostomid climatic niche evolution. Second, to identify timing and shift in position of the niches towards distinct climatic optima as they accompanied the phyllostomid radiation. Considering the importance of the tropics in phyllostomid macroecological and biogeographical patterns (Stevens 2011; Tavares et al. 2018), we predicted that we would find a tropical imprint in phyllostomid climatic niches as well. Therefore, we expect to find most phyllostomid species, as well as optimum values of climatic niches, related mainly to tropical climates.

## MATERIALS AND METHODS

### Evolutionary relationship among phyllostomids

We obtained phylogenetic information (evolutionary relationships and divergence times) for the phyllostomids in a time-calibrated phylogeny from Shi & Rabosky (2015). This phylogenetic hypothesis was built from a combined set of mitochondrial and nuclear nucleotide sequences with strong node support (Shi & Rabosky, 2015). Besides being strongly correlated with previous hypotheses of evolutionary relationships among bats, it is also strongly correlated with a more recent hypothesis on the evolutionary relationships and divergence times for Neotropical bat species ($r = 0.992$, $p < 0.001$, Rojas *et al*., 2016). Thus, we used both the tree and taxonomy from Shi & Rabosky (2015).

### Phyllostomid geographical distributions

We gathered information on phyllostomid geographical distributions from the IUCN database version 5.2 (IUCN, 2017). This database contained data for 160 continental phyllostomid species in the New World. Of these 130 species (81%) had phylogenetic information available and were used in our analysis. All geographical data handling was performed with the *raster* package (Hijmans, 2017). All analyses were performed with R version 3.5.0 software (R Core Team, 2018).

### Climatic niche characterization for phyllostomids

Considering the lack of complete information on species climatic tolerances from physiological experiments, to characterize phyllostomid climatic niches we relied on widely-used approaches to approximate realized climatic niches (i.e. the Grinnellian niches, hereafter called climatic niches for sake of simplicity; Soberón, 2007) of species on broad geographical scales (e.g. Araújo *et al*., 2013; Lawson & Weir, 2014; Duran & Pie, 2015; Peixoto *et al*., 2017; Pie *et al*., 2017; Rodrigues *et al*., 2019). Therefore, we characterized phyllostomid realized climatic niches based on climate within the geographic range of each species. For each species, we overlaid a grid with cells of 0.5º resolution (approximately 55 x 55 km) on their polygons of geographical distribution using an equal-area projection. Phyllostomid geographical range sizes varied from $12 \times 10^3$ to $19 \times 10^6$ km$^2$. Thus, setting the grid to a resolution of 0.5º captured geographic information for small ranged species. We then used information of 19 bioclimatic variables from the WorldClim database (Hijmans *et al*., 2005), that reflected temperature and precipitation gradients (Table 1). To characterize phyllostomid climatic niches, we extracted the mean of each bioclimatic variable (the position in the climatic niche space) for each species, including all cells that overlapped the geographical distribution of each species. Climatic variables were extracted with the *letsR* package in R (Vilela & Villalobos, 2015).

Bioclimatic variables are typically multicollinear. |So, we summarized the climatic information for phyllostomid bats with a phylogenetic principal component analysis (pPCA) to reduce the dimensionality, thereby eliminating collinearity while maintaining the evolutionary relationship among species in the ordination process (Revell, 2009). We used species scores of the phylogenetic principal components (pPCs) as their climatic niches (Lawson & Weir, 2014; Duran & Pie, 2015; Pie *et al*., 2017). We then retained the first 3 axes (pPC1, pPC2 and pPC3) and which explained ~90% of the variance (Table 1) for analysis of climatic niche evolution. We carried out pPCA with the *phytools* package (Revell, 2012). Climatic data for all species is available in Appendix 1.

### Test of phylogenetic signal in phyllostomid climatic niches

To determine whether similarities in phyllostomid climatic niches are a consequence of the evolutionary distances among species, we tested for a phylogenetic signal for each of the pPCs using Blomberg's *K* (Blomberg *et al*., 2003). Large and positive *K* values indicate a strong phylogenetic signal for any given trait. We estimated probabilities for the observed *K* values using 10000 randomizations of the original dataset. We conducted tests of phylogenetic signal with the *phytools* package.

### Tempo and mode of climatic niche evolution in phyllostomids

We used two graphical approaches to explore the tempo of evolution of phyllostomid climatic niches. First, we examined the evolution of the observed trait values in time by projecting the phylogeny into a space defined by the phenotype (i.e. the climatic trait values) on the *y*-axis and the time since the root on the *x*-axis, with the position of nodes and branches estimated via ancestral character reconstruction (Revell, 2013). This analysis used the *phytools* package. Second, we used a disparity through time approach in which we calculated the variance in climatic trait values using pairwise comparisons between species with averaged Euclidean distances in the climatic niche space and for time slices of speciation events along phyllostomid evolution (Harmon *et al*., 2003), using the *geiger* package (Pennel *et al*., 2014).

To address the mode of evolution of phyllostomids climatic niches, we fitted four (of potentially many) macroevolutionary models. These models provide a broad and general picture, and are useful to determine the mode of evolution of climatic niches (Munkenmuller *et al*., 2015; Harmon, 2018). We fitted all models with the *geiger* package, including:

*Brownian Motion* (*BM*): this simplest model describes the case of variance in trait values accumulating over time by a random-walk process (Munkenmuller *et al*., 2015; Harmon, 2018).

*Ornstein–Uhlenbeck* (*OU*): this model incorporates the random-walk from *BM* and models the evolution under selection strength on traits towards one or multiple optimal values, and which may indicate stabilizing selection (Munkenmuller *et al*., 2015; Khabbazian *et al*., 2016; Harmon, 2018).

*Early Burst* (*EB*): this model predicts a slowdown in the evolutionary rates of a trait over time in the phylogeny, often being linked to the evolution of traits under scenarios of adaptive radiation (Munkenmuller *et al*., 2015; Harmon, 2018).

*Speciational* (*SP*): this model detects changes in trait values following punctuated events of evolution. For example, if allopatric speciation were predominant, species might have shifted their geographic range after speciation events took place (Cardillo, 2015), which in turn could influence their distribution in the climatic niche space.

We compared model fit in two ways. First, we used an information theoretical approach to estimate parameters and likelihood of each evolutionary model. We chose the best model based on the lowest corrected Akaike's information criterion (AICc) in relation to alternative models (Burnham & Anderson, 2002). To account for model uncertainty, we calculated Akaike weights for each model (Burnham & Anderson, 2002). However, this method's ability to choose among evolutionary models has been questioned due to the influence of some data properties, including low sample size or small errors in the original datasets (Boettiger *et al*., 2012; Cooper *et al*., 2016). Thus, we also used an alternative approach of paired comparisons based on candidate model fit in a parametric bootstrap (Boettiger *et al*., 2012). For this approach, we first estimated the maximum likelihood from the original data and for each competing macroevolutionary model. We then performed a Monte Carlo simulation of trait evolution with 1,000 simulations using the parameters of each model. We estimated maximum likelihoods and calculated the likelihood-ratios between models. Finally, we compared the observed likelihood ratio to the simulated distribution, which allowed us to determine which model best described the mode of trait evolution (Boettiger *et al*., 2012). These analyses used the *pmc* package (Boettiger *et al*., 2012).

To test selected model adequacy, we used a parametric bootstrap (Pennell *et al*., 2015). We computed a set of test statistics describing the observed data using estimated parameters of the best model and a tree with branch lengths rescaled to unit value (Pennell *et al*., 2015). These statistics cover different properties that could potentially influence the fit of a given model of trait evolution. For each index, we compared its observed value with those from 10,000 simulated datasets. The rationale behind this approach is to estimate the probability of generating a model that generates the observed data and adequate models are those with $p \geq 0.05$ for the test statistics (Pennell *et al*., 2015). All model adequacy tests used the *arbutus* package (Pennell *et al*., 2015) with the following six standard indexes:1) the squared contrast means ($M_{\mathrm{SIG}}$), and 2) the coefficient of variation of the contrast absolute value ($C_{\mathrm{VAR}}$), both of which are associated with the rate of trait evolution. While $M_{\mathrm{SIG}}$ accounts for over or underestimation of trait evolution rate, $C_{\mathrm{VAR}}$ provides an estimate for the heterogeneity of evolution rate along the phylogeny; 3), the slope of a linear model fitted to the absolute value of the contrast against their expected variances ($S_{\mathrm{VAR}}$), which indicates branch length errors; 4) the slope of the linear model fitted to the absolute value of the contrast against the inferred ancestral state at the corresponding node ($S_{\mathrm{ASR}}$), which allows inference of variation in the rates of trait evolution; 5) the slope of linear model fit to the absolute value of the contrast against node depth ($S_{\mathrm{HGT}}$), useful to inform about trait evolution over time; and 6) an index that compares the distribution of the contrast to a normal distribution with mean 0 and standard deviation equal to the expected contrast distribution under BM ($D_{\mathrm{CDF}}$). A detailed description of these indexes and their extensions can be found in Pennel *et al*. (2015).

### Identifying macroevolutionary shifts in phyllostomid climatic niches

To detect shifts and convergences towards different climatic optima during phyllostomid climatic niche evolution, we used the *l*1ou method (Khabbazian *et al*., 2016). The *l*1ou method is robust and has advantages over other approaches. For example, *l*1ou does not require *a priori* hypotheses about the nodes in the phylogeny of potential shifts and convergences towards optimum trait values. In addition, it uses a phylogenetic Bayesian information criterion (pBIC) to compare multiple models of trait shifts and convergences (Khabbazian *et al.*, 2016). By recognizing that phylogenetic data are not independent, pBIC was more accurate compared to previous information criteria approaches used to compare evolutionary shifts and convergences for multiple traits at once (Ho & Ané, 2014; Khabbazian *et al*., 2016). The *l*1ou method refines the search for trait shifts towards different optimum values through evolution in two main steps. First, trait shifts were defined as the change in the configuration that minimizes pBIC, in which climatic niche space includes the first three pPCs together. In this step, we also estimated the support for shift positions using 300 bootstrapped replicates as the proportion of times a given shift occurred in the same node as that observed (Khabbazian *et al*., 2016). Second, we determined trait shift convergence into the same optimal values at different parts of the phyllostomid phylogeny using a backward procedure in which shifts were dropped until the best solution as the number of regimes that minimized the pBIC. We conducted the *l*1ou analysis as implemented in the *l1ou* package (Khabbazian *et al*., 2016).

## RESULTS

### Patterns in the occupation of climatic niches by phyllostomids

The first 3 pPCA axes accounted for 90% of variation in the phyllostomid climatic niches. pPC1 explained 65% of the variation and which ordered species from cold and dry regions of strong seasonality to warm and wet regions of low seasonality (Table 1; Figure 1). pPC2 explained 16% of the climatic data and ordered species by wet and hot regions to dry and cold regions (Table 1; Figure 1). Finally, pPC3 (9%) that ordered regions by precipitation in the driest months and quarters (Table 1; Figure 1).

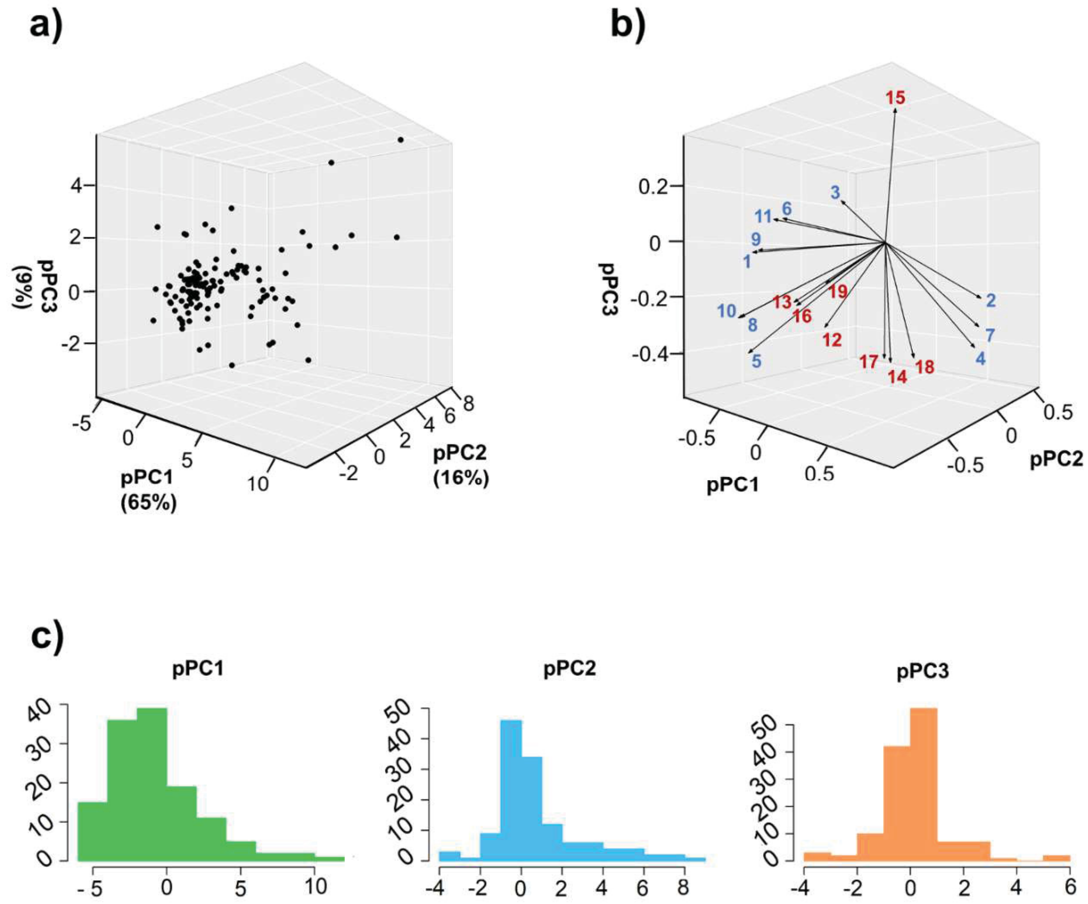

**Figure 1.**

(a) Phyllostomid bat species distributions in climatic niche space in the first three phylogenetic principal components (pPC), baed on climate found within the geographical range of each species (usingbioclimatic variables from the WorldClim database). (b) Loadings of the 19 bioclimatic variables (Table 1) indicating how each variable influenced the pPCs (blue numbers indicate temperature variables, red numbers indicate precipitation variables) (c) Species frequency distributions along the range of values the first three pPCs (climatic niche space).

**Table 1.** Bioclimate variables used to characterize the climatic niche of phyllostomid bats and their relationships with the first three phylogenetic principal components (pPC)* that explained 91% of the variance.

| **Bioclimatic variables** | **Loadings** | | |
|---|---|---|---|
| | **pPC1** | **pPC2** | **pPC3** |
| Bio 1: Annual mean temperature | -0.856 | -0.490 | -0.037 |
| Bio 2: Mean diurnal range | 0.895 | -0.132 | -0.190 |
| Bio 3: Isothermality | -0.870 | 0.329 | 0.222 |
| Bio 4: Temperature seasonality | 0.893 | -0.196 | -0.340 |

| | | | |
|---|---|---|---|
| Bio 5: Warmest month maximum temperature | -0.183 | -0.899 | -0.356 |
| Bio 6: Coldest month minimum temperature | -0.972 | -0.171 | 0.116 |
| Bio 7: Temperature annual range | 0.929 | -0.208 | -0.274 |
| Bio 8: Mean temperature of wettest quarter | -0.542 | -0.748 | -0.267 |
| Bio 9: Mean temperature of driest quarter | -0.894 | -0.423 | -0.027 |
| Bio 10: Mean temperature of warmest quarter | -0.531 | -0.769 | -0.269 |
| Bio 11: Mean temperature of coldest quarter | -0.948 | -0.266 | 0.107 |
| Bio 12: Annual precipitation | -0.877 | 0.159 | -0.375 |
| Bio 13: Precipitation of wettest month | -0.789 | -0.196 | -0.243 |
| Bio 14: Precipitation of driest month | -0.519 | 0.586 | -0.557 |
| Bio 15: Precipitation seasonality | 0.558 | -0.487 | 0.381 |
| Bio 16: Precipitation of wettest quarter | -0.820 | -0.150 | -0.259 |
| Bio 17: Precipitation of driest quarter | -0.578 | 0.567 | -0.539 |
| Bio 18: Precipitation of warmest quarter | -0.088 | 0.407 | -0.490 |
| Bio 19: Precipitation of coldest quarter | -0.867 | 0.162 | -0.170 |
| **Eigenvalue** | 1.76 | 0.42 | 0.23 |
| **Percentage of variance explained** | 65 | 16 | 9 |

* Phylogenetic principal component analysis conducted on standardized variables (mean = 0, standard deviation, s.d. = 1).

Most bat species have climatic niches in warmer and wetter regions (the negative side of pPC1), mainly with warmer and wet summers, with less seasonality in temperature but more seasonality in precipitation (Figures 1, 2A). By contrast, few phyllostomid species occupied regions of the climatic niche space related to colder and dryer environments, as indicated by greater and more positive values of pPC1, pPC2 and pPC3 (Figure 1A-C).

Phyllostomid climatic niches were variable in their degree of phylogenetic signal, and closely-related species sometimes had similar climatic niches but which depended on the niche axis. We observed a strong and positive phylogenetic signal for pPC2 ($K = 0.42$, $p < 0.001$). Conversely, a phylogenetic signal was absent in pPC1 ($K = 0.20$, $p = 0.63$) and pPC3 ($K=0.24$, $p = 0.37$).

### Tempo and mode of phyllostomid climatic niche evolution

Early in phyllostomid evolution their climatic niches began to diversify, around 34 Ma for pPC1 and pPC2 (Figure 2A-B). An accentuated divergence in climatic niches of pPC3 began around 25.5 Ma (Figure 2c).

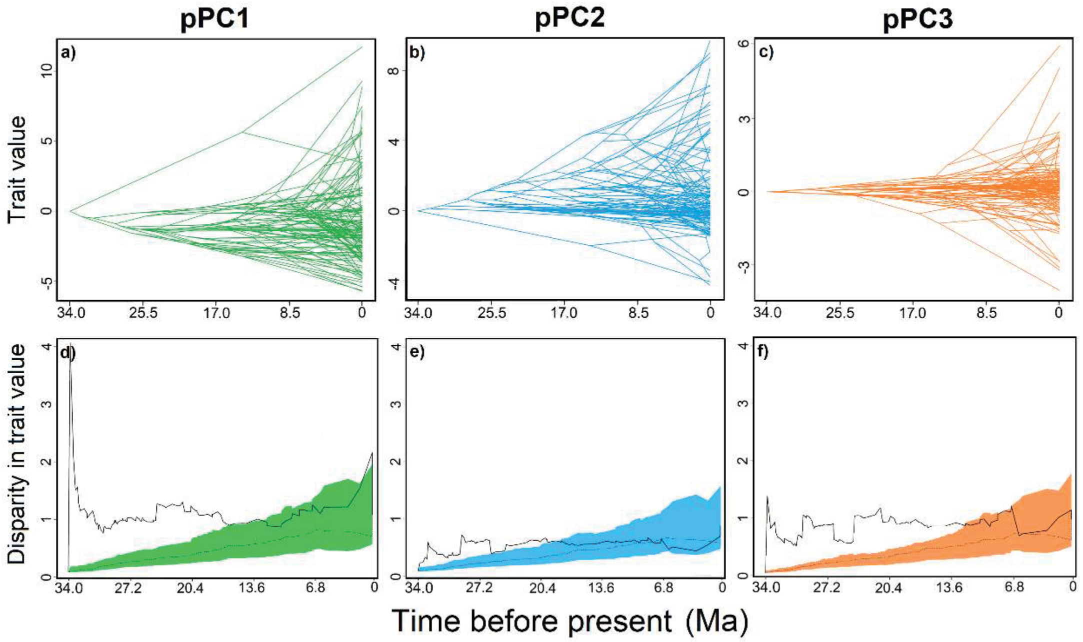

**Figure 2.** Diversification of climatic niches in the phyllostomid bat species over time based on scores of the three pPCs. Panels a), b) and c) indicate changes in trait values over time during speciation for the first three pPCs. Panels d), e) and f) indicate disparity in trait values of climatic niches over time. Solid lines are observed disparity, dashed lines and the colored regions are the mean and 95% confidence intervals based on 1,000 pseudo-replicates of the original dataset.

While the climatic niches of most species tend to diversify towards hotter and wetter values (towards the left in pPC1), most species also tend to concentrate around intermediate values with respect to pPC2 (wet and hot regions to dry and cold regions), and pPC3 (from low to high precipitation in the driest months and quarters, Figure 2A-C). Considering the wide variance in climatic trait values during phyllostomid evolution, pPC1 had two conspicuous peaks followed by decreasing disparity. The first peak occurred in the early diversification of this family and the second very recently (Figure 2d). By comparison, pPC2 and pPC3 were less variable over time, with greater variance early in phyllostomid evolution followed by increasing and decreasing variance in climatic traits (Figure 2E-F).

Among the four macroevolutionary models of trait evolution, the Ornstein–Uhlenbeck (OU) was the best descriptor for phyllostomid climatic niche evolution, which suggests that phyllostomid climatic niches evolved under the influence of strong attraction towards climatic optima. The OU model was largely supported for all pPC (Table 2), regardless of the method used to compare competing models of trait evolution, i.e. whether using information theoretical approach (Table 2) or parametric bootstrap (Appendix 2). Additionally, model adequacy indicated that OU fit the evolution of climatic niches reasonably well for most statistics. For pPC1, the $M_{\mathrm{SIG}}$, $S_{\mathrm{HGT}}$ and $D_{\mathrm{CDF}}$ statistics demonstrated a good fit to the data under an OU model (Table 3). For pPC2, the data was well accommodated by the $M_{\mathrm{SIG}}$ and $S_{\mathrm{HGT}}$ statistics (Table 3). Finally, for PC3, all statistics but $C_{\mathrm{VAR}}$ showed good adequacy with OU as the model of climatic niche evolution (Table 3).

### Macroevolutionary shifts in phyllostomid climatic niches

By refining the OU model to allow for the detection of multiple optima of climatic traits, we found 20 shifts towards different climatic regimes during phyllostomid evolution (pBIC = 1574.3). Most shifts were well supported by bootstrap (> 70%) and are widespread throughout the phyllostomid phylogeny (Figure 3). In addition, shifts are located mainly at terminal, species-level, branches, indicating recent evolutionary changes in climatic niches (Figure 3). Most shifts (coloured bars in Figure 3) occurred towards temperate regimes, changing phyllostomid climatic niches to new optimum trait values in the positive quadrant of both pPC1 and pPC2 (Figure 3). After accounting for convergences, climatic niches of phyllostomids consolidated into 16 climatic regimes with shifts also at the tips of the phylogenetic tree, and which reached the minimum value for pBIC (pBIC = 1568.4; Figure 3).

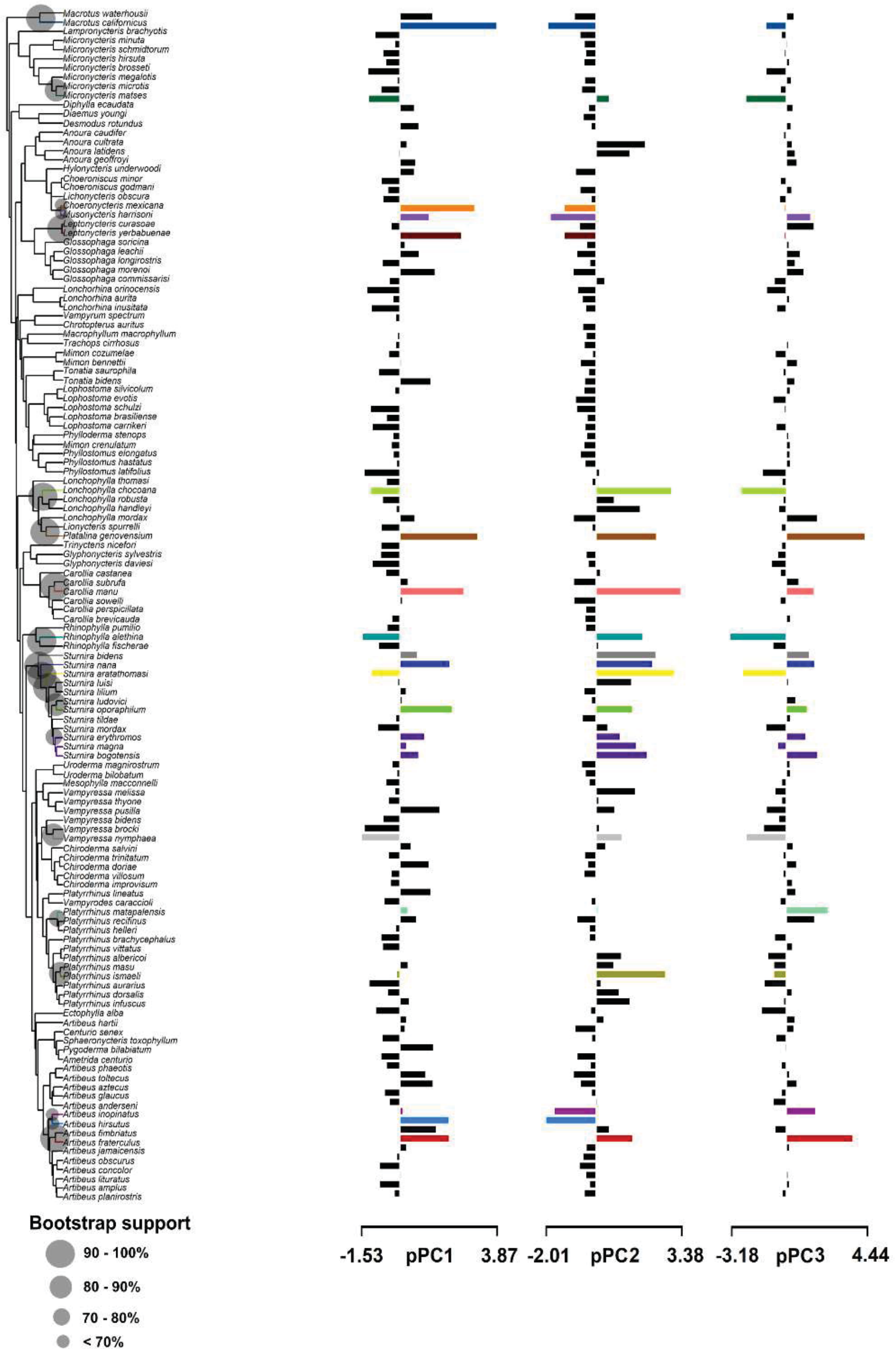

**Figure 3.** Position and bootstrap support for the 20 shifts towards different climatic optima in the evolution of climatic niches of phyllostomid bats, based on the first three phylogenetic principal components (pPC1, pPC2, pPC3). New, distinct climatic regimes (colored bars, colors arbitrarily vary by species to facilitate separating new from ancestral regimes) are indicated in comparison to the ancestral climate (black bars).

**Table 2.** Fit of 4 evolutionary models of the mode of evolution of climatic niches for phyllostomid bats, including log-likelihood, corrected Akaike's information criterion (AICc), and weight for each pPC. Ornstein Uhlenbeck (OU), that includes selection strength in trait values.Speciational (SP), that detects changes in trait values following punctuated evolutionary events. Brownian motion (BM), that describes variance in trait values accumulating over time.Early burst (EB), that describes decreasing rate of trait evolution over time. Bold type indicates models with strong support, which was the OU model.

| | **Model** | **logL** | **AICc** | **ΔAICc** | **Weight** |
|---|---|---|---|---|---|
| pPC1 | | | | | |
| | **OU** | **-336.5** | **679.2** | **0** | **1.00** |
| | SP | -353.7 | 713.6 | 34.3 | 0.00 |
| | BM | -385.9 | 775.9 | 96.7 | 0.00 |
| | EB | -385.9 | 778.0 | 98.8 | 0.00 |
| pPC2 | | | | | |
| | **OU** | **-277.4** | **561.0** | **0** | **0.99** |
| | SP | -283.8 | 573.8 | 12.7 | 0.01 |
| | BM | -293.3 | 590.8 | 29.8 | 0.00 |
| | EB | -293.3 | 592.9 | 31.9 | 0.00 |
| pPC3 | | | | | |
| | **OU** | **-217.5** | **441.0** | **0** | **1.00** |
| | SP | -239.9 | 486.1 | 45.1 | 0.00 |
| | BM | -253.9 | 512.0 | 71.0 | 0.00 |
| | EB | -253.9 | 513.9 | 72.9 | 0.00 |

**Table 3.** Tests of the Ornstein Uhlenbeck model of trait evolution with the observed (Obs) and *p*-values (*p*) based on 10,000 replicates of parametric bootstrap (Pennel *et al.*, 2015). $M_{\mathrm{SIG}}$: the squared contrast means; $C_{\mathrm{VAR}}$: the coefficient of variation of the contrast absolute values; $S_{\mathrm{VAR}}$: the slope of a linear model fitted to the absolute value of the contrast against their expected variances; $S_{\mathrm{ASR}}$: the slope of the linear model fitted to the absolute value of the contrast against the inferred ancestral state at the corresponding node; $S_{\mathrm{HGT}}$: the slope of linear model fit to the absolute value of the contrast against node depth; $D_{\mathrm{CDF}}$: comparison of the distribution of the contrast to a normal distribution with mean 0 and standard deviation equal to the expected contrast distribution under BM.

| **Statistic** | | **pPC1** | **pPC2** | **pPC3** |
|---|---|---|---|---|
| $M_{\mathrm{SIG}}$ | | | | |
| | **Obs** | 1.007 | 1.007 | 1.007 |
| | **p** | 0.92 | 0.91 | 0.91 |
| $C_{\mathrm{VAR}}$ | | | | |
| | **Obs** | 0.86 | 0.953 | 0.96 |
| | **p** | **0.03** | **<0.001** | **<0.001** |
| $S_{\mathrm{VAR}}$ | | | | |
| | **Obs** | -0.104 | -0.291 | -0.171 |
| | **p** | **0.03** | **0.003** | 0.16 |
| $S_{\mathrm{ASR}}$ | | | | |
| | **Obs** | 0.13 | 0.227 | 0.127 |
| | **p** | **<0.001** | **<0.001** | 0.1 |
| $S_{\mathrm{HGT}}$ | | | | |
| | **Obs** | -1.248 | -0.063 | -3.178 |
| | **p** | 0.12 | 0.19 | 0.42 |
| $D_{\mathrm{CDF}}$ | | | | |
| | **Obs** | 0.085 | 0.124 | 0.077 |
| | **P** | 0.42 | **0.02** | 0.62 |

## DISCUSSION

### Patterns of phyllostomid climatic niches

Climate is a crucial dimension of species niches (Soberón *et al*. 2007), has widely been considered an important factor influencing phyllostomid distributions in the New World (Stevens, 2004; Stevens, 2006; Stevens, 2011; Alroy, 2019) and we found strong support of the importance of climate here. Previously, few studies employed an integrative approach to understand the dynamics underpinning phyllostomid climatic niche evolution (e.g. Ortega-Garcia *et al*. 2017; Peixoto *et al*. 2017). We explicitly examined phyllostomid climatic niches from a phylogenetic framework and thus found that most species occupy tropical regions of the climatic niche space. This supports our initial predictions of the importance of the tropics for phyllostomid ecological and evolutionary dynamics. For example, phyllostomid origins and radiations in the New World tropics (e.g. Tavares *et al*. 2018) contributed to the high diversity levels of phyllostomid throughout the tropics (Stevens, 2004; Stevens, 2006; Stevens, 2011; Villalobos *et al*., 2013; Alroy, 2019). This pattern is the result of the combined effects of metabolic constraints, resource abundance and complex habitat structure that productive tropical sites provide to these bats, and which may have prevented most species from expanding their geographical distribution to the temperate New World (McNab, 1982; Stevens, 2004; Villalobos *et al*., 2013; Alroy, 2019). Indeed, the few phyllostomids that reached non-tropical climate regimes (high latitudes altitudes) tend to have specific traits that include a generalist diet and increased capacity to cope with these conditions (McNab, 1969; McNab, 1982; Carvalho *et al*., 2019). In these cases, phyllostomid climatic niches became related mostly to colder and dryer environments in extra-tropical locations. This is best exemplified by *Sturnira spp*., which concentrated most evolutionary shifts towards these climates, as we will discuss below (Figure 3). Despite the tendency to stay in the tropics, we still found multiple and conspicuous shifts in climatic niches to multiple optima in phyllostomid evolution. Overall, our results suggest that the relationships between phyllostomids and climate were not static and constant during evolution, but rather were instead complex patterns underlying the climatic niche evolution in these bats.

### Tempo, mode and shifts in phyllostomid climatic niches evolution

We found multiple and punctuated events of recent evolutionary shifts across phyllostomid phylogeny with strong bootstrap support (Figure 3). Shifts from tropical towards temperate regimes in phyllostomids may be a consequence of tropical niche conservatism (Stevens, 2006; Stevens, 2011) because most species shift from tropical to non-tropical climates were recent evolutionary events. In addition to contributing to weakening the climatic niche phylogenetic signals (as observed here, Peixoto *et al*. 2017), recent shifts help explain the recent evolutionary increase in variability of climatic trait values, especially for pPC1 (Figure 2d). The presence of multiple shifts towards several climatic optima at terminal branches of phyllostomid phylogeny, reflected by a refinement of the OU model, emphasizes the effect of species-specific adaptations in coping with temperate climates. While mainly a tropical family, some species (e.g. *Carollia* ssp. and *Sturnira* ssp.) have evolved adaptations that allowed them to occupy colder and dryer environments. These adaptations include optimizing energetic costs by altering oxygen consumption, metabolic rates, body temperature and torpor when facing extreme and harsh climates (McNab, 1969; Soriano *et al*., 2002; Kelm & Von Helversen, 2007; Geiser & Stawski, 2011). The evolution of these strategies highlights the importance of behavior and physiology to cope with distinct climates, influencing phyllostomid distribution and the patterns of climatic niche evolution for this family.

We found a predominance of shifts and different climatic optima in the yellow-shouldered bats of the genus *Sturnira* (all with strong bootstrap support, ~ 25%). Many *Sturnira* species are recent evolutionarily (< 5 Ma) and their geographical distributions are restricted to the highlands of the Andean region in South America (Velazco & Patterson, 2013). In addition to *Sturnira* ssp., most changes in phyllostomid climatic niches occupation occurred in species restricted to the Andean region, such as *Lonchophylla chocoana*, *Platyrrhinus ismaeli*, and *Carollia manu* (Figure 3). Mountains tend to form geographical barriers for bats (McCain, 2006; Varzinczak *et al*., 2018; Carvalho *et al*., 2019), influencing allopatric speciation and playing a crucial role in phyllostomid diversification and distribution (López-Aguirre *et al*., 2018; Carvalho *et al*., 2019). Moreover, while evolutionary conservatism of climatic niches provides a reasonable explanation for diversity patterns in mountainous regions (Cadena *et al*., 2011), climatic niche divergence among sister species also may exert an important influence during allopatric speciation (Jezkova & Wiens, 2018). Although this remains to be explicitly tested for Neotropical bats, our results suggest that it influenced *Sturnira* and other species which had climatic niches shifts towards colder and dryer environments, typical of the Andean region. High altitudes have harsh climates, posing increased selective pressures and selection strengths on bat distributions (McCain, 2006; Carvalho *et al*., 2019). This favors an OU model with multiple optima associated with non-tropical climates in comparison with other models of trait evolution. These results specifically indicate that idiosyncrasies during phyllostomid radiations and their distributions in the New World played important roles in their climatic niche evolution.

Phyllostomids began diversifying during a period of global climatic instability (Zachos *et al.*, 2001). Paleoclimatic reconstructions demonstrated that at the beginning of phyllostomid evolution (Rojas *et al*., 2016; Figure 2), between the Oligocene (around 34 Ma) through the mid-Miocene (approximately 15 Ma), globally, climates underwent drastic fluctuations (Zachos *et al.*, 2001). This climatic instability included glaciation events that led to a cooling of the planet (Zachos *et al.*, 2001). This time-interval matches with both the much greater variation in climatic trait values and the main diversification of phyllostomid climatic niches (Figure 2). Paleoclimatic events have been emphasized as important for the climatic niche evolution during the radiation of different taxonomic groups, including primates (Duran & Pie, 2015) and squamate reptiles (Pie *et al*., 2017). For phyllostomids, this likely effect of paleoclimate on climatic niche evolution is even more strongly exemplified in nectar-feeding species. These bats radiated when global cooling of the Miocene seems to have selected for adaptations to the changing climatic regimes and ultimately adjusting their thermal niche limits (Ortega-García *et al*., 2017). This implies that the global climate history was influential in phyllostomid climatic niche evolution that was a response to oscillating climate during the phyllostomid radiation in the New World.

## CONCLUSIONS AND PROSPECTS

Our results provide a better understanding of bat climatic niche evolution in the very diverse Phyllostomidae. Moreover, they raise additional questions about the evolutionary dynamics underpinning phyllostomid climatic niches. For example, climatic niche evolution can be correlated with the evolution of additional traits that influence the ability of a species to occupy an area with a different climate regime (Lawson & Weir, 2014). For phyllostomids, feeding habits have clearly influenced the diversification of species and their phenotypes (Monteiro & Nogueira, 2011; Rojas *et al*., 2012; Dumont *et al*., 2012). Although diversification of their climatic niches began early in phyllostomid evolution, we found most adaptation to different climatic zones occurred 14 million years later (around 20 Ma), and following the main changes in phyllostomid dietary habits (Figure 2A-C; Rojas *et al*., 2011). This timing coincides with the radiation of the subfamily Stenodermatinae, comprising mostly frugivores and a remarkable evolutionary pattern among bats (Shi & Rabosky, 2015; Rojas *et al*., 2016; Tavares *et al*., 2018). Thus, in the future, elucidating the relationship between phyllostomids and climate will be to examine how diet influenced climatic niche evolution. Perhaps reduced competition due to evolutionary changes in feeding habits allowed phyllostomids to colonize extra-tropical areas in the New World, thereby occupying empty ecological niche space, as well as allowing species with different feeding habits to remain or become sympatric. Clearly diet can influence the ability of species to optimize or at least mitigate energetic costs when facing harsh climates (McNab, 1982). We recommend that diet and climate be examined further, because on broad geographical scales their synergistic interactions were probably crucial in determining the current distribution and relationship with climate of the extremely diverse and widespread bat family Phyllostomidae.

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# APPENDIX.

**Table S1.** Phyllostomid bat species and their bioclimatic data used in our analyses. Data correspond to the mean of each variable within species' geographical ranges.

| **Species** | **Bio 1** | **Bio 2** | **Bio 3** | **Bio 4** | **Bio 5** | **Bio 6** | **Bio 7** | **Bio 8** | **Bio 9** | **Bio 10** | **Bio 11** | **Bio 12** | **Bio 13** | **Bio 14** | **Bio 15** | **Bio 16** | **Bio 17** | **Bio 18** | **Bio 19** |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Ametrida centurio* | 25.8 | 10.4 | 7.8 | 55.4 | 32.6 | 19.3 | 13.3 | 25.5 | 25.8 | 26.4 | 25.0 | 2167.1 | 334.5 | 48.8 | 57.3 | 920.7 | 180.2 | 347.4 | 617.6 |
| *Anoura caudifer* | 23.7 | 10.8 | 7.5 | 108.8 | 30.9 | 16.2 | 14.7 | 24.2 | 22.9 | 24.9 | 22.2 | 1887.3 | 279.4 | 57.8 | 53.1 | 763.5 | 204.7 | 433.0 | 429.0 |
| *Anoura cultrata* | 20.0 | 10.9 | 8.1 | 61.2 | 26.7 | 13.1 | 13.5 | 20.1 | 19.6 | 20.7 | 19.1 | 2092.4 | 288.9 | 68.9 | 45.9 | 781.5 | 246.4 | 501.0 | 495.7 |
| *Anoura geoffroyi* | 22.6 | 11.4 | 7.2 | 128.6 | 30.3 | 14.3 | 15.9 | 23.3 | 21.6 | 24.0 | 20.7 | 1586.1 | 260.0 | 37.6 | 65.1 | 698.6 | 137.4 | 399.1 | 298.9 |
| *Anoura latidens* | 21.4 | 10.7 | 8.3 | 52.8 | 27.9 | 15.0 | 13.0 | 21.3 | 21.2 | 22.0 | 20.7 | 2082.4 | 301.2 | 62.7 | 50.7 | 817.8 | 229.8 | 434.6 | 598.9 |
| *Artibeus amplus* | 25.2 | 9.9 | 8.1 | 54.2 | 31.6 | 19.4 | 12.2 | 24.8 | 25.3 | 25.8 | 24.5 | 2119.5 | 325.8 | 56.5 | 55.2 | 881.1 | 209.3 | 368.6 | 652.9 |
| *Artibeus anderseni* | 24.7 | 10.8 | 7.7 | 66.9 | 31.5 | 17.4 | 14.2 | 24.8 | 24.1 | 25.3 | 23.7 | 2191.0 | 300.4 | 73.0 | 46.6 | 838.7 | 252.9 | 487.0 | 445.7 |
| *Artibeus aztecus* | 21.8 | 13.0 | 6.8 | 175.2 | 31.3 | 12.0 | 19.3 | 22.9 | 20.7 | 23.8 | 19.4 | 1417.8 | 280.7 | 16.7 | 87.2 | 730.8 | 64.4 | 401.0 | 175.8 |
| *Artibeus concolor* | 26.0 | 10.1 | 7.9 | 58.6 | 32.6 | 19.8 | 12.8 | 25.7 | 26.0 | 26.6 | 25.2 | 2117.8 | 317.6 | 57.4 | 55.5 | 875.7 | 206.7 | 343.1 | 614.7 |
| *Artibeus fimbriatus* | 20.9 | 10.9 | 6.0 | 247.3 | 29.7 | 11.5 | 18.2 | 22.6 | 18.5 | 23.8 | 17.6 | 1392.7 | 197.8 | 54.4 | 43.4 | 536.3 | 190.6 | 454.0 | 229.5 |
| *Artibeus fraterculus* | 17.7 | 11.6 | 7.5 | 114.0 | 25.3 | 9.9 | 15.3 | 18.8 | 16.9 | 19.2 | 16.3 | 713.3 | 133.2 | 16.6 | 88.4 | 345.1 | 56.9 | 302.3 | 67.6 |
| *Artibeus hirsutus* | 23.0 | 14.6 | 6.3 | 285.2 | 34.0 | 10.8 | 23.3 | 25.7 | 22.4 | 26.4 | 19.2 | 924.8 | 236.1 | 3.8 | 107.5 | 616.4 | 19.2 | 419.7 | 62.6 |

| | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Artibeus inopinatus* | 25.1 | 11.4 | 7.4 | 85.0 | 33.0 | 17.8 | 15.2 | 24.9 | 24.7 | 26.2 | 24.0 | 1626.1 | 343.3 | 3.3 | 92.2 | 846.8 | 15.8 | 274.9 | 210.4 |
| *Artibeus jamaicensis* | 23.7 | 10.7 | 7.2 | 131.6 | 31.2 | 16.0 | 15.1 | 24.4 | 22.9 | 25.2 | 21.8 | 1760.3 | 290.9 | 41.7 | 68.7 | 760.0 | 150.3 | 456.2 | 316.9 |
| *Artibeus lituratus* | 24.2 | 11.0 | 7.4 | 107.0 | 31.6 | 16.5 | 15.1 | 24.6 | 23.5 | 25.4 | 22.7 | 1832.5 | 285.3 | 45.5 | 59.8 | 777.8 | 164.3 | 398.3 | 397.7 |
| *Artibeus obscurus* | 24.8 | 10.9 | 7.5 | 93.9 | 32.0 | 17.2 | 14.7 | 25.0 | 24.1 | 25.8 | 23.4 | 1891.2 | 290.5 | 47.5 | 57.7 | 799.3 | 171.3 | 393.8 | 419.5 |
| *Artibeus planirostris* | 24.9 | 10.5 | 7.5 | 110.5 | 32.0 | 17.7 | 14.3 | 25.4 | 24.1 | 26.1 | 23.4 | 1903.7 | 285.3 | 55.4 | 53.7 | 782.8 | 198.4 | 395.9 | 471.6 |
| *Artibeus toltecus* | 22.8 | 12.4 | 6.7 | 187.6 | 31.9 | 13.2 | 18.7 | 24.0 | 21.7 | 24.9 | 20.2 | 1537.5 | 297.1 | 20.7 | 84.2 | 770.0 | 78.1 | 415.0 | 213.5 |
| *Carollia brevicauda* | 24.8 | 10.6 | 7.7 | 72.5 | 31.8 | 17.9 | 13.9 | 24.8 | 24.5 | 25.6 | 23.8 | 1943.7 | 296.3 | 49.3 | 58.2 | 813.5 | 178.1 | 375.5 | 472.3 |
| *Carollia castanea* | 24.4 | 10.1 | 7.9 | 66.3 | 30.9 | 18.1 | 12.8 | 24.3 | 24.2 | 25.1 | 23.5 | 2184.8 | 313.0 | 68.3 | 49.9 | 853.5 | 245.3 | 457.1 | 551.0 |
| *Carollia manu* | 13.6 | 14.0 | 7.3 | 121.6 | 22.2 | 3.1 | 19.1 | 14.3 | 11.8 | 14.7 | 11.7 | 1514.0 | 246.2 | 39.7 | 65.3 | 676.5 | 139.2 | 483.9 | 142.0 |
| *Carollia perspicillata* | 24.4 | 10.8 | 7.4 | 103.8 | 31.7 | 16.8 | 14.9 | 24.7 | 23.6 | 25.5 | 22.9 | 1866.6 | 286.6 | 47.3 | 57.5 | 782.9 | 170.6 | 398.8 | 411.6 |
| *Carollia sowelli* | 24.5 | 10.4 | 6.7 | 148.3 | 32.1 | 16.8 | 15.4 | 25.2 | 23.9 | 26.1 | 22.4 | 1942.7 | 332.9 | 36.9 | 66.3 | 865.2 | 133.8 | 457.6 | 299.9 |
| *Carollia subrufa* | 23.7 | 11.4 | 7.2 | 109.4 | 31.7 | 15.9 | 15.8 | 23.9 | 23.2 | 25.0 | 22.2 | 1841.2 | 346.4 | 19.2 | 80.7 | 890.7 | 71.2 | 386.8 | 216.0 |
| *Centurio senex* | 24.3 | 10.9 | 7.2 | 128.7 | 32.0 | 16.6 | 15.4 | 24.9 | 23.8 | 25.8 | 22.5 | 1699.8 | 293.0 | 30.1 | 71.0 | 769.0 | 113.4 | 396.9 | 347.3 |
| *Chiroderma doriae* | 22.6 | 11.5 | 6.6 | 181.7 | 30.7 | 13.2 | 17.4 | 23.9 | 20.5 | 24.5 | 20.0 | 1276.7 | 214.6 | 27.0 | 62.7 | 577.6 | 98.9 | 408.8 | 134.3 |
| *Chiroderma improvisum* | 25.5 | 7.4 | 7.0 | 109.2 | 30.4 | 19.8 | 10.5 | 26.3 | 24.0 | 26.6 | 23.9 | 1592.2 | 200.9 | 61.2 | 34.7 | 564.3 | 215.8 | 494.0 | 223.0 |
| *Chiroderma salvini* | 22.2 | 11.4 | 7.5 | 105.7 | 29.7 | 14.3 | 15.4 | 22.6 | 21.5 | 23.3 | 20.7 | 1786.8 | 277.1 | 46.4 | 62.9 | 748.2 | 168.1 | 448.2 | 371.7 |

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|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Chiroderma trinitatum* | 25.1 | 10.7 | 7.7 | 70.1 | 32.1 | 18.1 | 14.0 | 25.1 | 24.7 | 25.9 | 24.1 | 2097.7 | 314.2 | 53.0 | 55.0 | 866.6 | 192.0 | 406.7 | 504.1 |
| *Chiroderma villosum* | 25.0 | 10.7 | 7.6 | 80.7 | 32.0 | 17.8 | 14.3 | 25.1 | 24.5 | 25.8 | 23.8 | 2055.0 | 311.9 | 51.1 | 56.3 | 855.3 | 185.1 | 415.0 | 473.5 |
| *Choeroniscus godmani* | 25.0 | 10.1 | 7.7 | 80.7 | 31.9 | 18.6 | 13.3 | 24.9 | 25.0 | 25.9 | 23.9 | 2026.8 | 329.5 | 41.5 | 63.1 | 880.6 | 161.2 | 363.9 | 535.7 |
| *Choeroniscus minor* | 24.9 | 10.1 | 8.0 | 57.5 | 31.4 | 18.7 | 12.7 | 24.7 | 24.8 | 25.5 | 24.1 | 2231.1 | 321.2 | 68.9 | 49.8 | 888.0 | 244.9 | 411.0 | 620.4 |
| *Choeronycteris mexicana* | 20.2 | 15.2 | 5.9 | 389.2 | 33.2 | 6.7 | 26.4 | 23.3 | 19.0 | 24.9 | 15.0 | 700.2 | 156.3 | 7.0 | 87.7 | 399.2 | 29.0 | 253.9 | 64.4 |
| *Chrotopterus auritus* | 24.5 | 10.8 | 7.3 | 110.6 | 32.0 | 16.9 | 15.1 | 24.9 | 23.7 | 25.7 | 23.0 | 1838.1 | 283.8 | 45.6 | 57.9 | 776.0 | 164.6 | 388.8 | 403.3 |
| *Artibeus glaucus* | 25.1 | 10.3 | 7.9 | 69.7 | 31.7 | 18.7 | 13.0 | 24.9 | 24.9 | 25.8 | 24.1 | 2115.3 | 308.1 | 62.5 | 49.9 | 848.6 | 228.5 | 416.3 | 568.9 |
| *Artibeus phaeotis* | 24.8 | 10.1 | 7.7 | 83.5 | 31.5 | 18.4 | 13.2 | 24.8 | 24.7 | 25.7 | 23.6 | 2139.5 | 325.5 | 60.5 | 57.8 | 880.1 | 220.1 | 431.2 | 563.4 |
| *Desmodus rotundus* | 22.7 | 11.5 | 7.0 | 160.0 | 31.0 | 14.0 | 17.0 | 23.5 | 21.5 | 24.5 | 20.5 | 1582.7 | 247.5 | 39.7 | 62.3 | 673.4 | 143.2 | 363.9 | 332.9 |
| *Diaemus youngi* | 24.5 | 10.9 | 7.4 | 106.5 | 31.9 | 16.8 | 15.0 | 24.9 | 23.7 | 25.7 | 23.0 | 1845.8 | 284.5 | 45.3 | 58.3 | 778.5 | 164.6 | 390.1 | 412.9 |
| *Diphylla ecaudata* | 23.2 | 11.5 | 7.1 | 128.9 | 31.1 | 14.7 | 16.4 | 23.9 | 22.0 | 24.6 | 21.4 | 1650.2 | 262.3 | 34.4 | 62.3 | 711.4 | 126.8 | 414.1 | 262.2 |
| *Ectophylla alba* | 25.1 | 8.4 | 7.1 | 92.8 | 31.2 | 19.4 | 11.8 | 25.4 | 25.2 | 26.1 | 23.8 | 2718.5 | 405.2 | 63.5 | 51.1 | 1086.6 | 235.6 | 602.5 | 533.0 |
| *Artibeus hartii* | 22.5 | 11.1 | 7.6 | 93.0 | 29.8 | 15.1 | 14.7 | 22.8 | 21.9 | 23.6 | 21.2 | 1835.1 | 288.6 | 45.7 | 62.9 | 777.0 | 165.5 | 442.3 | 403.2 |
| *Glossophaga commissarisi* | 24.0 | 10.6 | 7.9 | 77.9 | 30.8 | 17.2 | 13.6 | 24.0 | 23.7 | 24.8 | 22.9 | 2214.1 | 312.9 | 75.4 | 49.6 | 853.1 | 265.1 | 486.1 | 534.3 |
| *Glossophaga leachii* | 22.9 | 12.2 | 7.0 | 129.7 | 31.5 | 14.2 | 17.3 | 23.4 | 22.1 | 24.4 | 21.0 | 1633.9 | 313.7 | 18.6 | 83.7 | 820.9 | 68.3 | 377.4 | 158.4 |

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|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Glossophaga longirostris* | 25.0 | 9.8 | 8.1 | 54.0 | 31.3 | 19.3 | 12.1 | 24.7 | 25.1 | 25.7 | 24.3 | 1988.0 | 310.3 | 51.7 | 55.8 | 840.7 | 192.8 | 359.5 | 608.5 |
| *Glossophaga morenoi* | 22.1 | 13.7 | 6.9 | 155.5 | 31.8 | 12.0 | 19.8 | 22.9 | 21.1 | 23.9 | 19.9 | 1307.0 | 278.9 | 12.1 | 95.4 | 740.7 | 44.5 | 349.9 | 70.0 |
| *Glossophaga soricina* | 23.9 | 11.1 | 7.3 | 117.2 | 31.5 | 16.0 | 15.5 | 24.3 | 23.1 | 25.2 | 22.2 | 1770.6 | 276.7 | 44.1 | 60.9 | 753.7 | 159.2 | 391.6 | 381.1 |
| *Glyphonycteris daviesi* | 26.1 | 9.8 | 8.0 | 53.3 | 32.4 | 20.2 | 12.2 | 25.8 | 26.2 | 26.7 | 25.4 | 2383.4 | 334.8 | 77.6 | 45.7 | 927.3 | 273.8 | 416.0 | 668.9 |
| *Glyphonycteris sylvestris* | 25.5 | 10.0 | 7.8 | 72.4 | 32.1 | 19.1 | 13.0 | 25.4 | 25.3 | 26.3 | 24.5 | 2229.9 | 331.9 | 63.5 | 53.0 | 912.7 | 227.6 | 414.1 | 603.2 |
| *Hylonycteris underwoodi* | 23.3 | 12.0 | 6.9 | 145.5 | 31.9 | 14.6 | 17.3 | 24.1 | 22.7 | 25.0 | 21.3 | 1799.8 | 339.0 | 29.9 | 83.0 | 887.6 | 108.8 | 459.7 | 237.1 |
| *Lampronycteris brachyotis* | 26.0 | 9.8 | 7.9 | 62.3 | 32.5 | 20.1 | 12.4 | 25.7 | 26.2 | 26.7 | 25.2 | 2244.0 | 348.0 | 60.5 | 54.6 | 948.4 | 215.7 | 340.2 | 732.0 |
| *Leptonycteris curasoae* | 25.1 | 9.8 | 7.8 | 60.1 | 31.5 | 19.1 | 12.4 | 24.7 | 25.0 | 25.8 | 24.3 | 1635.3 | 261.0 | 25.3 | 61.7 | 698.8 | 107.2 | 296.9 | 506.3 |
| *Leptonycteris yerbabuenae* | 20.9 | 14.5 | 6.0 | 338.1 | 32.9 | 8.4 | 24.5 | 24.1 | 20.1 | 25.0 | 16.4 | 906.1 | 197.6 | 10.2 | 88.8 | 505.5 | 40.2 | 317.8 | 80.1 |
| *Lichonycteris obscura* | 25.1 | 10.1 | 7.8 | 63.5 | 31.7 | 18.7 | 13.0 | 25.1 | 24.9 | 25.8 | 24.3 | 2200.4 | 320.5 | 64.2 | 50.3 | 880.4 | 227.9 | 428.6 | 555.4 |
| *Lionycteris spurrelli* | 25.1 | 10.2 | 8.0 | 53.6 | 31.7 | 18.8 | 12.9 | 24.9 | 25.0 | 25.7 | 24.4 | 2230.0 | 322.9 | 64.8 | 50.6 | 891.2 | 232.3 | 396.9 | 619.4 |
| *Lonchophylla chocoana* | 21.5 | 8.6 | 8.9 | 26.0 | 26.5 | 16.8 | 9.7 | 21.7 | 21.3 | 21.9 | 21.2 | 3015.3 | 369.7 | 144.2 | 31.4 | 1013.3 | 510.9 | 939.0 | 672.9 |
| *Lonchophylla handleyi* | 22.3 | 10.8 | 8.3 | 47.2 | 28.8 | 16.0 | 12.9 | 22.3 | 21.9 | 22.9 | 21.7 | 1913.4 | 213.7 | 109.6 | 22.9 | 588.5 | 356.9 | 489.4 | 403.7 |
| *Lonchophylla mordax* | 23.9 | 10.9 | 7.1 | 122.9 | 31.3 | 16.0 | 15.3 | 24.4 | 22.9 | 25.3 | 22.2 | 1212.1 | 233.3 | 15.9 | 76.9 | 622.1 | 58.9 | 277.7 | 237.4 |
| *Lonchophylla robusta* | 23.5 | 9.5 | 8.1 | 52.9 | 29.5 | 17.9 | 11.6 | 23.4 | 23.5 | 24.2 | 22.8 | 2330.3 | 327.2 | 71.5 | 50.1 | 874.9 | 260.4 | 492.0 | 646.4 |

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| *Lonchophylla thomasi* | 24.8 | 10.6 | 7.9 | 61.5 | 31.6 | 18.0 | 13.5 | 24.7 | 24.5 | 25.4 | 23.9 | 2171.9 | 318.6 | 60.2 | 52.3 | 879.8 | 216.7 | 416.1 | 556.2 |
| *Lonchorhina aurita* | 24.9 | 10.6 | 7.6 | 81.8 | 31.9 | 17.8 | 14.1 | 25.0 | 24.5 | 25.8 | 23.8 | 1935.1 | 299.3 | 46.8 | 59.4 | 819.2 | 169.4 | 387.8 | 448.7 |
| *Lonchorhina inusitata* | 26.1 | 9.7 | 8.0 | 46.9 | 32.4 | 20.3 | 12.1 | 25.7 | 26.3 | 26.6 | 25.5 | 2347.9 | 347.0 | 72.0 | 48.9 | 953.7 | 252.9 | 368.0 | 703.9 |
| *Lonchorhina orinocensis* | 26.3 | 10.0 | 7.8 | 70.8 | 33.4 | 20.6 | 12.8 | 25.4 | 26.8 | 27.2 | 25.3 | 2674.5 | 392.9 | 60.7 | 51.8 | 1095.2 | 247.1 | 318.7 | 1059.9 |
| *Lophostoma brasiliense* | 25.1 | 10.2 | 7.8 | 69.6 | 31.7 | 18.6 | 13.2 | 25.0 | 24.9 | 25.8 | 24.1 | 2053.4 | 308.6 | 56.8 | 55.1 | 844.7 | 203.7 | 376.6 | 541.2 |
| *Lophostoma carrikeri* | 26.1 | 9.8 | 8.0 | 51.8 | 32.4 | 20.2 | 12.2 | 25.8 | 26.2 | 26.7 | 25.4 | 2351.1 | 342.6 | 71.2 | 49.6 | 947.2 | 253.3 | 381.9 | 671.8 |
| *Lophostoma evotis* | 24.8 | 10.1 | 6.6 | 151.7 | 32.2 | 17.2 | 15.0 | 25.6 | 24.5 | 26.4 | 22.6 | 2004.1 | 326.4 | 45.5 | 58.9 | 858.3 | 161.0 | 501.4 | 288.1 |
| *Lophostoma schulzi* | 26.1 | 9.1 | 7.8 | 59.7 | 32.7 | 21.1 | 11.6 | 25.7 | 26.9 | 26.9 | 25.4 | 2302.4 | 376.3 | 62.2 | 51.9 | 981.9 | 225.9 | 239.3 | 681.8 |
| *Lophostoma silvicolum* | 24.7 | 10.7 | 7.6 | 82.3 | 31.8 | 17.5 | 14.3 | 24.8 | 24.2 | 25.6 | 23.6 | 1909.2 | 294.3 | 46.3 | 59.1 | 806.2 | 167.9 | 388.8 | 438.1 |
| *Macrophyllum macrophyllum* | 24.4 | 10.8 | 7.5 | 94.9 | 31.7 | 17.0 | 14.6 | 24.7 | 23.8 | 25.5 | 23.1 | 1902.9 | 291.5 | 47.9 | 57.4 | 797.3 | 172.9 | 398.8 | 427.7 |
| *Macrotus californicus* | 19.5 | 16.0 | 5.1 | 569.8 | 35.6 | 4.2 | 31.4 | 23.3 | 20.9 | 26.9 | 12.4 | 325.3 | 74.0 | 3.5 | 75.4 | 177.7 | 17.6 | 147.8 | 71.4 |
| *Macrotus waterhousii* | 22.7 | 12.6 | 6.6 | 196.1 | 31.9 | 12.8 | 19.1 | 24.1 | 21.4 | 24.9 | 19.9 | 1246.1 | 242.8 | 21.9 | 81.6 | 633.3 | 80.1 | 405.7 | 113.3 |
| *Mesophylla macconnelli* | 25.0 | 10.5 | 7.8 | 63.2 | 31.8 | 18.2 | 13.6 | 24.9 | 24.7 | 25.7 | 24.1 | 2166.6 | 319.7 | 58.1 | 53.3 | 881.9 | 209.4 | 421.6 | 538.5 |
| *Micronycteris brosseti* | 26.1 | 9.6 | 8.2 | 48.6 | 32.2 | 20.5 | 11.7 | 25.7 | 26.2 | 26.6 | 25.4 | 2482.3 | 340.4 | 91.1 | 41.4 | 939.9 | 318.1 | 431.4 | 713.6 |
| *Micronycteris hirsuta* | 25.3 | 10.2 | 7.8 | 66.6 | 32.0 | 18.8 | 13.1 | 25.1 | 25.1 | 26.0 | 24.3 | 2016.6 | 304.8 | 53.7 | 57.2 | 834.2 | 193.1 | 366.1 | 541.2 |

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| *Micronycteris matses* | 26.5 | 10.0 | 8.3 | 42.0 | 32.4 | 20.4 | 12.0 | 26.5 | 25.9 | 26.9 | 25.8 | 2534.8 | 279.5 | 126.6 | 23.7 | 788.4 | 426.5 | 645.8 | 444.4 |
| *Micronycteris megalotis* | 24.6 | 10.9 | 7.6 | 86.6 | 31.7 | 17.2 | 14.5 | 24.7 | 24.0 | 25.5 | 23.3 | 1866.0 | 288.6 | 45.3 | 60.3 | 792.2 | 163.8 | 384.7 | 424.4 |
| *Micronycteris microtis* | 25.6 | 10.1 | 7.7 | 69.7 | 32.3 | 19.1 | 13.2 | 25.5 | 25.5 | 26.4 | 24.6 | 2222.4 | 341.1 | 57.0 | 56.2 | 930.2 | 203.5 | 394.4 | 616.5 |
| *Micronycteris minuta* | 24.7 | 10.7 | 7.5 | 85.8 | 31.8 | 17.5 | 14.4 | 24.9 | 24.2 | 25.7 | 23.5 | 1937.8 | 297.3 | 47.8 | 58.0 | 814.9 | 173.2 | 396.6 | 444.7 |
| *Micronycteris schmidtorum* | 25.4 | 9.9 | 7.8 | 73.9 | 31.9 | 19.1 | 12.8 | 25.3 | 25.3 | 26.2 | 24.3 | 2104.2 | 315.0 | 59.0 | 54.2 | 858.7 | 211.4 | 383.0 | 588.9 |
| *Mimon bennettii* | 24.3 | 10.4 | 7.3 | 117.0 | 31.4 | 17.0 | 14.5 | 24.7 | 23.5 | 25.6 | 22.7 | 1682.8 | 282.6 | 34.9 | 63.7 | 765.9 | 129.9 | 338.8 | 432.7 |
| *Mimon cozumelae* | 24.4 | 9.7 | 7.4 | 106.3 | 31.1 | 17.8 | 13.4 | 24.7 | 24.2 | 25.5 | 22.9 | 2265.9 | 339.7 | 57.3 | 54.6 | 897.8 | 212.1 | 482.4 | 543.2 |
| *Gardenycteys crenulatum* | 24.9 | 10.6 | 7.7 | 72.6 | 31.9 | 18.0 | 13.9 | 24.9 | 24.6 | 25.7 | 23.9 | 1965.3 | 301.1 | 48.4 | 58.7 | 825.6 | 174.9 | 381.2 | 464.8 |
| *Musonycteris harrisoni* | 24.0 | 13.6 | 7.0 | 142.7 | 33.6 | 14.0 | 19.6 | 24.6 | 23.5 | 25.8 | 22.1 | 1089.3 | 261.4 | 2.9 | 107.3 | 700.3 | 13.6 | 338.8 | 34.2 |
| *Phylloderma stenops* | 24.7 | 10.5 | 7.6 | 80.1 | 31.7 | 17.7 | 14.0 | 24.7 | 24.2 | 25.6 | 23.6 | 1952.9 | 296.9 | 50.9 | 57.3 | 813.8 | 183.1 | 387.6 | 469.4 |
| *Phyllostomus elongatus* | 25.1 | 10.8 | 7.6 | 78.8 | 32.1 | 17.8 | 14.3 | 25.1 | 24.6 | 25.9 | 23.9 | 1917.2 | 297.2 | 45.5 | 59.6 | 818.0 | 164.9 | 376.0 | 442.8 |
| *Phyllostomus hastatus* | 24.6 | 10.8 | 7.6 | 85.9 | 31.7 | 17.3 | 14.4 | 24.7 | 24.0 | 25.5 | 23.3 | 1891.3 | 292.4 | 45.6 | 59.4 | 800.6 | 165.6 | 394.0 | 427.8 |
| *Phyllostomus latifolius* | 25.8 | 9.6 | 8.4 | 48.6 | 31.9 | 20.5 | 11.4 | 25.3 | 26.2 | 26.3 | 25.1 | 2593.5 | 370.6 | 100.4 | 43.6 | 1008.5 | 345.6 | 415.5 | 854.1 |
| *Platalina genovensium* | 14.0 | 13.3 | 7.3 | 145.8 | 22.6 | 4.5 | 18.1 | 15.4 | 13.1 | 15.8 | 12.1 | 457.2 | 93.5 | 6.2 | 92.5 | 242.9 | 23.2 | 216.3 | 25.2 |
| *Platyrrhinus albericoi* | 22.7 | 11.2 | 7.8 | 88.6 | 29.7 | 15.1 | 14.6 | 23.1 | 21.7 | 23.6 | 21.4 | 2135.0 | 286.1 | 85.5 | 41.6 | 793.5 | 287.8 | 598.4 | 381.3 |

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| *Platyrrhinus aurarius* | 25.1 | 10.3 | 8.4 | 47.2 | 31.5 | 19.3 | 12.2 | 24.6 | 25.3 | 25.6 | 24.4 | 2627.5 | 392.0 | 84.5 | 46.9 | 1085.3 | 301.6 | 447.6 | 842.6 |
| *Platyrrhinus brachycephalus* | 25.4 | 10.3 | 7.8 | 60.5 | 32.2 | 18.9 | 13.3 | 25.3 | 25.3 | 26.1 | 24.6 | 2279.7 | 326.4 | 68.4 | 48.6 | 904.0 | 244.2 | 429.1 | 574.9 |
| *Platyrrhinus dorsalis* | 23.1 | 9.6 | 8.3 | 46.3 | 29.0 | 17.4 | 11.6 | 23.0 | 22.9 | 23.6 | 22.5 | 2113.8 | 294.9 | 68.5 | 50.2 | 788.9 | 246.3 | 496.0 | 543.5 |
| *Platyrrhinus helleri* | 24.3 | 10.9 | 7.6 | 84.0 | 31.4 | 16.9 | 14.5 | 24.5 | 23.8 | 25.2 | 23.1 | 2005.0 | 306.3 | 49.5 | 57.7 | 839.9 | 179.3 | 419.2 | 454.8 |
| *Platyrrhinus infuscus* | 21.4 | 11.5 | 7.8 | 84.0 | 28.4 | 13.6 | 14.8 | 21.7 | 20.5 | 22.2 | 20.1 | 1942.9 | 260.2 | 72.1 | 44.0 | 718.4 | 250.7 | 525.4 | 370.9 |
| *Platyrrhinus ismaeli* | 20.3 | 10.5 | 8.5 | 45.8 | 26.6 | 14.3 | 12.3 | 20.2 | 20.2 | 20.8 | 19.6 | 2227.5 | 254.4 | 124.9 | 25.2 | 709.4 | 408.3 | 526.5 | 571.0 |
| *Platyrrhinus lineatus* | 21.9 | 11.8 | 6.7 | 178.5 | 30.4 | 12.6 | 17.8 | 23.0 | 20.2 | 23.9 | 19.4 | 1327.7 | 213.4 | 32.1 | 60.5 | 577.2 | 115.8 | 390.6 | 168.1 |
| *Platyrrhinus masu* | 22.4 | 12.0 | 7.6 | 90.0 | 29.8 | 14.1 | 15.7 | 22.9 | 21.1 | 23.3 | 21.1 | 2053.4 | 298.5 | 62.7 | 50.1 | 836.6 | 215.2 | 628.2 | 224.9 |
| *Platyrrhinus matapalensis* | 22.7 | 9.1 | 7.9 | 75.2 | 28.6 | 17.1 | 11.6 | 23.5 | 21.9 | 23.7 | 21.8 | 1227.9 | 246.0 | 19.9 | 93.8 | 663.9 | 77.0 | 602.6 | 114.4 |
| *Platyrrhinus recifinus* | 23.7 | 10.8 | 7.1 | 137.7 | 31.1 | 15.8 | 15.3 | 24.4 | 22.5 | 25.2 | 21.7 | 1189.6 | 224.5 | 19.4 | 73.9 | 598.4 | 71.4 | 299.9 | 243.0 |
| *Platyrrhinus vittatus* | 24.9 | 9.6 | 8.1 | 51.5 | 30.9 | 19.0 | 11.8 | 24.6 | 24.7 | 25.4 | 24.2 | 2094.9 | 304.8 | 56.4 | 55.5 | 809.6 | 206.4 | 433.6 | 560.7 |
| *Pygoderma bilabiatum* | 21.9 | 11.7 | 6.4 | 213.8 | 30.5 | 12.2 | 18.3 | 23.5 | 19.6 | 24.3 | 18.9 | 1330.4 | 210.1 | 36.9 | 56.0 | 568.3 | 131.5 | 452.3 | 164.4 |
| *Rhinophylla alethina* | 23.4 | 8.7 | 8.5 | 43.6 | 28.7 | 18.4 | 10.2 | 23.6 | 23.1 | 23.9 | 22.9 | 3275.6 | 433.9 | 141.7 | 54.0 | 1196.4 | 485.0 | 932.9 | 802.9 |
| *Rhinophylla fischerae* | 25.0 | 10.3 | 8.1 | 49.3 | 31.5 | 18.6 | 12.9 | 24.7 | 24.9 | 25.5 | 24.3 | 2377.5 | 326.7 | 76.6 | 45.6 | 913.8 | 271.6 | 441.1 | 677.2 |
| *Rhinophylla pumilio* | 25.2 | 10.4 | 7.8 | 66.2 | 32.0 | 18.5 | 13.5 | 25.0 | 25.0 | 25.9 | 24.2 | 2027.1 | 302.4 | 56.4 | 54.9 | 834.0 | 201.5 | 370.5 | 526.7 |

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|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Sphaeronycteris toxophyllum* | 25.4 | 10.3 | 7.9 | 60.0 | 32.0 | 18.8 | 13.2 | 25.3 | 25.0 | 26.0 | 24.5 | 2209.3 | 310.7 | 70.3 | 48.4 | 865.4 | 247.2 | 457.1 | 526.9 |
| *Sturnira aratathomasi* | 20.8 | 9.4 | 8.8 | 29.6 | 26.3 | 15.7 | 10.6 | 20.6 | 20.9 | 21.1 | 20.4 | 3194.8 | 387.6 | 150.8 | 31.1 | 1060.8 | 515.2 | 707.8 | 968.8 |
| *Sturnira bidens* | 18.6 | 11.1 | 8.2 | 61.1 | 25.3 | 11.8 | 13.5 | 18.7 | 18.2 | 19.3 | 17.7 | 1774.0 | 244.8 | 63.7 | 51.1 | 660.0 | 226.6 | 437.7 | 459.1 |
| *Sturnira bogotensis* | 18.9 | 10.5 | 8.1 | 76.2 | 25.6 | 12.5 | 13.1 | 19.3 | 18.6 | 19.8 | 17.9 | 1611.6 | 229.8 | 56.2 | 62.2 | 609.5 | 204.0 | 408.9 | 430.6 |
| *Sturnira erythromos* | 20.5 | 11.8 | 7.5 | 114.2 | 28.1 | 12.1 | 15.9 | 21.1 | 19.3 | 21.7 | 18.8 | 1526.9 | 233.4 | 42.0 | 64.2 | 632.4 | 150.4 | 410.0 | 324.2 |
| *Sturnira lilium* | 24.0 | 11.1 | 7.2 | 132.4 | 31.8 | 15.9 | 15.9 | 24.6 | 23.1 | 25.5 | 22.2 | 1762.2 | 273.5 | 44.6 | 59.1 | 745.3 | 160.7 | 393.5 | 377.4 |
| *Sturnira ludovici* | 23.5 | 10.7 | 7.6 | 101.9 | 30.8 | 16.3 | 14.5 | 23.8 | 23.0 | 24.7 | 22.1 | 1791.4 | 294.2 | 41.7 | 66.5 | 783.6 | 153.1 | 404.7 | 406.0 |
| *Sturnira luisi* | 21.5 | 9.8 | 8.0 | 71.0 | 27.8 | 15.5 | 12.3 | 22.0 | 21.1 | 22.4 | 20.6 | 2129.6 | 291.8 | 80.8 | 61.2 | 781.9 | 279.5 | 542.2 | 523.8 |
| *Sturnira magna* | 21.2 | 11.4 | 7.9 | 82.0 | 28.2 | 13.5 | 14.7 | 21.4 | 20.4 | 22.0 | 19.9 | 2098.2 | 268.3 | 86.0 | 43.2 | 748.9 | 298.6 | 511.6 | 457.8 |
| *Sturnira mordax* | 23.2 | 9.6 | 7.7 | 62.3 | 29.8 | 17.3 | 12.4 | 22.9 | 23.3 | 24.1 | 22.4 | 2968.6 | 463.9 | 59.1 | 55.7 | 1201.1 | 221.3 | 560.0 | 766.7 |
| *Sturnira nana* | 16.7 | 14.4 | 7.7 | 89.9 | 25.3 | 6.7 | 18.6 | 17.1 | 15.4 | 17.5 | 15.3 | 1424.4 | 218.7 | 34.7 | 63.0 | 622.1 | 122.6 | 453.4 | 129.7 |
| *Sturnira oporaphilum* | 18.0 | 13.3 | 7.1 | 170.0 | 26.7 | 7.5 | 19.2 | 19.4 | 15.7 | 19.7 | 15.5 | 1242.7 | 198.9 | 33.4 | 68.9 | 542.8 | 115.8 | 432.9 | 127.7 |
| *Sturnira tildae* | 24.8 | 10.9 | 7.6 | 82.9 | 31.9 | 17.4 | 14.5 | 24.9 | 24.2 | 25.6 | 23.6 | 1879.3 | 292.6 | 45.3 | 59.9 | 805.3 | 162.0 | 381.9 | 418.6 |
| *Tonatia bidens* | 22.7 | 11.8 | 6.6 | 193.8 | 31.1 | 13.1 | 18.0 | 24.3 | 20.6 | 24.8 | 19.9 | 1220.9 | 204.2 | 26.6 | 63.6 | 551.2 | 98.3 | 409.3 | 135.4 |
| *Tonatia saurophila* | 25.5 | 9.8 | 8.0 | 61.5 | 31.9 | 19.6 | 12.3 | 25.2 | 25.6 | 26.2 | 24.7 | 2168.7 | 321.6 | 67.2 | 52.3 | 873.5 | 237.9 | 365.8 | 644.3 |
| *Trachops cirrhosus* | 24.6 | 10.7 | 7.5 | 88.7 | 31.8 | 17.3 | 14.4 | 24.8 | 24.1 | 25.6 | 23.4 | 1912.9 | 295.6 | 46.8 | 58.8 | 808.5 | 169.2 | 397.6 | 430.1 |
| *Trinycteris nicefori* | 24.8 | 10.0 | 8.0 | 59.5 | 31.3 | 18.8 | 12.5 | 24.6 | 24.8 | 25.5 | 24.0 | 2242.0 | 326.7 | 65.8 | 50.2 | 893.0 | 238.1 | 400.5 | 639.1 |

| | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Uroderma bilobatum* | 24.5 | 10.8 | 7.5 | 86.7 | 31.6 | 17.2 | 14.4 | 24.7 | 23.9 | 25.4 | 23.3 | 1889.7 | 293.9 | 45.2 | 60.2 | 803.3 | 163.6 | 392.9 | 422.5 |
| *Uroderma magnirostrum* | 25.0 | 10.7 | 7.6 | 75.3 | 32.1 | 18.0 | 14.1 | 25.0 | 24.6 | 25.9 | 24.0 | 1940.6 | 298.4 | 47.3 | 59.0 | 818.8 | 171.4 | 373.4 | 461.2 |
| *Vampyressa bidens* | 24.8 | 10.4 | 7.9 | 58.1 | 31.5 | 18.3 | 13.2 | 24.6 | 24.6 | 25.4 | 24.0 | 2244.5 | 324.1 | 67.0 | 49.7 | 898.3 | 238.7 | 417.8 | 601.0 |
| *Vampyressa brocki* | 26.2 | 9.3 | 8.4 | 47.4 | 32.0 | 21.0 | 11.0 | 25.9 | 26.6 | 26.8 | 25.6 | 2429.3 | 333.7 | 108.4 | 39.3 | 908.8 | 364.7 | 427.4 | 705.3 |
| *Vampyressa melissa* | 22.0 | 11.0 | 8.2 | 53.6 | 28.6 | 15.3 | 13.3 | 22.0 | 21.7 | 22.6 | 21.3 | 2233.1 | 281.7 | 92.4 | 35.9 | 779.4 | 317.4 | 532.9 | 512.6 |
| *Vampyressa nymphaea* | 24.1 | 8.7 | 8.2 | 46.3 | 29.7 | 19.0 | 10.6 | 23.9 | 24.2 | 24.7 | 23.5 | 3248.9 | 448.2 | 104.7 | 46.1 | 1191.1 | 372.6 | 664.3 | 920.9 |
| *Vampyressa pusilla* | 20.3 | 11.5 | 6.0 | 258.6 | 29.3 | 10.2 | 19.1 | 22.3 | 17.7 | 23.3 | 16.8 | 1494.8 | 212.8 | 57.7 | 43.3 | 578.4 | 202.3 | 525.3 | 222.4 |
| *Vampyressa thyone* | 24.3 | 10.3 | 7.8 | 68.5 | 31.0 | 17.8 | 13.2 | 24.3 | 24.1 | 25.1 | 23.4 | 2164.4 | 309.4 | 63.1 | 51.1 | 847.4 | 229.0 | 466.1 | 500.0 |
| *Vampyrodes caraccioli* | 24.9 | 10.4 | 7.8 | 62.7 | 31.7 | 18.3 | 13.3 | 24.8 | 24.7 | 25.6 | 24.1 | 2220.5 | 325.6 | 61.7 | 51.8 | 895.6 | 221.7 | 420.9 | 570.1 |
| *Vampyrum spectrum* | 23.9 | 10.6 | 7.7 | 85.3 | 30.8 | 16.9 | 14.0 | 24.1 | 23.4 | 24.8 | 22.7 | 1993.6 | 297.9 | 54.4 | 54.7 | 808.8 | 198.9 | 441.4 | 467.5 |

Table S2. Comparison between the support of an OU over additional evolutionary models (BM, EB, SP) for the evolution of climatic niches for phyllostomid bats for each pPC. Analyses were based on a parametric bootstrap with 1,000 replicates for which data were simulated considering each model's parameters. P-values are the probabilities of the simulated data from each model in producing a higher likelihood ratio when compared to data simulated under an OU model of trait evolution. OU: Ornstein Uhlenbeck model, which includes a selection strength in trait values; SP: speciational model, which detects changes in trait values following punctuated events of evolution; BM: Brownian motion model, which describes variance in trait values accumulating over time; EB: early burst model which describes a deceleration in trait evolution over time

| | **pPC1** | | **pPC2** | | **pPC3** | |
|---|---|---|---|---|---|---|
| | **Observed likelihood ratio** | **P-value** | **Observed likelihood ratio** | **P-value** | **Observed likelihood ratio** | **P-value** |
| BM x OU | 98.83 | <0.001 | 31.9 | <0.001 | 72.89 | <0.001 |
| EB x OU | 98.83 | <0.001 | 31.9 | <0.001 | 72.9 | <0.001 |
| SP x OU | 34.39 | 0.18 | 12.7 | 0.4 | 44.9 | 0.003 |

# CAPÍTULO 2

## *Strong but opposing effects of climatic niche breadth and dispersal ability shape bat geographical range sizes across phylogenetic scales**

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# Strong but opposing effects of climatic niche breadth and dispersal ability shape bat geographical range sizes across phylogenetic scales

## ABSTRACT

**Aim:** Climatic niche breadth and dispersal ability influence species distributions and are hypothesized as traits determining variations in species range sizes. Here we test the hypothesis on the complementarity of their influences on species ranges in a phylogenetic framework and across phylogenetic scales.

**Location:** New World

**Time period:** Cenozoic

**Major taxa:** leaf-nosed bats, Phyllostomidae

**Methods:** We estimated phyllostomid range sizes from maps of species distributions. We used information on climate found within each species' range and a trait linked to flight performances to determine species climatic niche breadth and dispersal abilities, respectively. We used phylogenetic generalized least squares to test for the influence of climatic niche breadth and dispersal for the whole family, and phylogenetically weighted regressions to determine the influence of each variable at a different phylogenetic scale, at the species-level.

**Results:** Although both variables influence species ranges with a positive climatic niche breadth effect, we found an opposite and counterintuitive pattern for the effect of dispersal, as species with increased dispersal showed smaller ranges. By testing their effects for each species separately, our results showed an overall positive influence of climatic niche breadth, while for most species we did not observe the influence of dispersal, depicting a phylogenetic non-stationarity in such patterns.

**Main conclusions:** We provide new insights on the determinants of species ranges, especially by challenging the traditional view that increased dispersal abilities translate into larger ranges. We highlight that idiosyncrasies during the evolution of major clades can play important roles in determining the influence of different processes in shaping species distributions, reflecting a phylogenetic non-stationarity in such patterns. Further studies addressing these issues across phylogenetic scales will be essential in clarifying processes that underlie species ranges. As range size is correlated to extinction risks, such advances may provide crucial information on factors related to species' vulnerabilities.

**Keywords:** Chiroptera, leaf-nosed bats, New World, niche width, non-stationarity, relative wing loading, species distributions

## INTRODUCTION

Why are some species widely distributed while others have narrow ranges? This question lies at the core of ecological and evolutionary research. Larger ranges generally imply being adapted to a wide array of environments and to having overcome barriers to dispersal, and thus range sizes represent one aspect of species' success (Faurby & Antonelli, 2018). Accordingly, addressing range determinants has become essential to understand which processes underlie species distributions at broad geographical scales and how they impact their vulnerabilities to extinction (Böhm et al., 2017; Brown, Stevens, & Kaufmnan, 1996; Faurby & Antonelli, 2018; Newsome et al., 2020). Several hypotheses have been invoked to explain interspecific variations in species ranges. These can be broadly classified into extrinsic ones related to historical and biogeographical variables such as species ancestral ranges and time available for range expansion after speciation (Linder, Antonelli, Humphreys, Pirie, & Wüest, 2013; Paul, Morton, Taylor, & Tonsor, 2009), or intrinsic factors linked to species traits, such as diet, environmental tolerances, and their ability to colonize new regions (Slatyer, Hirst, & Sexton, 2013; Slove & Janz, 2011). Despite the joint action and mixed evidence with regards to increased ranges due to different processes, two intrinsic traits have been considered of particular importance in explaining interspecific variations in range sizes: species' climatic niche breadth and dispersal abilities (Faurby & Antonelli, 2018; Gaston, 2003; Lester, Ruttenberg, Gaines, & Kinlan, 2007; Slatyer et al., 2013; Stevens, 1989).

The expected influences of climatic niche breadth and dispersal on range sizes are straightforward. On the one hand, climate constitutes a crucial dimension of the ecological niches (Soberón, 2007), and species with increased climatic niche breadth are expected to be physiologically better adapted to different climates (Bozinovic, Calosi, & Spicer, 2011; Calosi, Bilton, Spicer, Votier, & Atfield, 2010; Faurby & Antonelli, 2018; Li et al., 2016; Sheth & Angert, 2014). This plasticity enables them to cope with the strong variations in climatic conditions observed at broad geographical scales and allows species occurrences in different regions and the opportunity of exploring new habitats (Bozinovic et al., 2011; Calosi et al., 2010; Stevens, 1989). These factors positively correlate with their range sizes (Sheth & Angert, 2014; Slatyer et al., 2013). Alternatively, species with high dispersal abilities are more prone to disperse over long distances to colonize and maintain viable populations in new regions (Böhning-Gaese, Caprano, van Ewijk, & Veith, 2006; Gaston, 2003; Lester et al., 2007). Furthermore, these species are more prone to overcome biogeographical barriers, a factor that tends to positively influence the size of their geographical ranges (Faurby & Antonelli, 2018; Lester et al., 2007; Luo et al., 2019; McCulloch, Wallis, & Waters, 2017).

Despite their importance, the effects of climatic niche breadth and dispersal on species geographical ranges have seldom been studied in concert (for exceptions, see Faurby & Antonelli, 2018; Li et al., 2016). This oversight can be particularly misleading because they represent non-mutually exclusive hypotheses related to complementary processes. For example, range sizes of species with increased climatic niche breadths can be reduced if these species are unable to overcome barriers to disperse towards climatically suitable environments (Cardillo, Dinnage, & McAlister, 2019; Slatyer et al., 2013; Soberón, 2007). The opposite is also observed: Species might lack adaptations that allow for their presence in regions with contrasting climates regardless of how good dispersers they are (Lester et al., 2007; Soberón, 2007). This deficit can thus influence their distributions and range size patterns (Lester et al., 2007). Therefore, as both traits are related with the ability of species to colonize and persist in different regions, testing the different ways by which climatic niche breadth and dispersal jointly influence species geographical ranges has the potential to broaden our understanding on how these variables act in shaping species distributions (Brown et al., 1996; Cardillo et al., 2019; Lester et al., 2007; Slatyer et al., 2013). Furthermore, the few studies that have addressed the joint effects of climatic niche breadth and dispersal on range size dynamics covered a much larger taxonomic breadth, such as entire classes or orders (Faurby & Antonelli, 2018; Li et al., 2016). Such a taxonomic scale can make specific trends within these major groups imperceptible (Graham, Machac, and Storch, 2018), masking some signals on the importance of these variables in shaping geographical range sizes.

Here, we used the New World leaf-nosed bats of the Phyllostomidae family as a model system to address the combined influence of the climatic niche breadth and dispersal on species geographical range sizes. Phyllostomids are endemic to the New World and represent the most species-rich and ecologically diverse bat family in this region. Climate is an important abiotic factor that regulates phyllostomid distribution, as they have a tropical origin and are mainly adapted to the climatic conditions found at low latitudes, in accordance with the expectations of the tropical niche conservatism hypothesis (Stevens, 2006, 2011; Varzinczak, Moura, & Passos, 2019; Villalobos, Rangel, & Diniz-Filho, 2013; but also see Ramos Pereira & Palmeirim, 2013). In fact, few phyllostomids present climatic niches related to extra-tropical areas due to metabolic and dietary constraints that limit them to expand their distributions towards temperate, cooler and dryer environments (Stevens, 2004; Varzinczak et al., 2019). Moreover, although flight distinguishes bats from other mammals by reducing limitations to their dispersal (Luo et al., 2019), phyllostomids present smaller and highly variable range sizes compared to other New World bat families (Willig, Patterson & Stevens, 2003). Furthermore, there is a strong spatial signature on phyllostomid distribution that is likely related to the landscape configuration, which limits species dispersal in the New World, regardless of dispersal abilities that flight suggests (Varzinczak, Lima, Moura, & Passos, 2018). Overall, these factors highlight the likely importance of the joint effects of climate and dispersal to influence phyllostomid distributions, making them an interesting group to contrast the influences of these two variables on species geographical range sizes.

Our main goal was to test the hypothesis that climatic niche breadth and dispersal ability jointly influence phyllostomid geographical range sizes. Based on the theoretical background that relates species geographical range sizes to the effects of these two variables, our starting point is the general prediction of a 1) positive effect of climatic niche breadth on phyllostomid range sizes, as species with increased climatic niche breadth present adaptations to a wide range of climatic conditions across the New World in comparison to climatically specialized species, and 2) a positive effect of dispersal abilities on phyllostomid range sizes, as species with increased dispersal abilities tend to have reduced limitations to dispersal, favoring them to be widespread in comparison to poor-disperser species. We tested these effects by integrating data and the phyllostomid evolutionary history using a framework that allowed us to address the effects and implications of climatic niche breadth and dispersal across different phylogenetic scales, i.e., from the whole family to the species level.

## MATERIALS AND METHODS

Our study focused on 74 (Supporting Information Table S1) out of approximately 180 phyllostomid species that make up the family. The number of taxa included in our study was limited by the availability of ecomorphological variables related to species dispersal abilities. Although the number of species included here represents a subset of the overall phyllostomid diversity, we employed sensitivity analyses (described in detail below) to estimate uncertainties related to our taxonomic sampling. We performed all analyses described below in R software (R Core Team, 2018).

### Phyllostomid geographical range sizes

We obtained information on phyllostomid geographical distributions from the IUCN database version 5.2 (IUCN, 2018). For each species, we calculated their geographical ranges considering the area (in km²) spanned by their polygons of geographical distribution across the terrestrial New World. We performed all geographical data handling with the *letsR* package (Vilela & Villalobos, 2015).

### Phyllostomid climatic niche breadth

We characterized phyllostomid climatic niche breadth using bioclimatic data related to temperature and precipitation gradients from the WorldClim database version 1.4 at the resolution of approximately 1km² (30 arc-sec) (Hijmans, Cameron, Parra, Jones, & Jarvis, 2005). Due to the lack of data on species climatic tolerances from physiological experiments, this method represents an approximation for the realized climatic niche (Castro-insua, Gómez-rodríguez, Wiens, & Baselga, 2018; Gómez-Rodríguez, Baselga, & Wiens, 2015; Rolland & Salamin, 2016). On the polygons, which represent the limits of species distributions, we overlaid a grid with cells of 0.5º resolution (approximately 55 x 55 km) using an equal-area projection. Then, we extracted four bioclimatic variables that represent the lower and upper limits of temperature and precipitation for each cell across species ranges. For temperature, we used the 1) Maximum Temperature of Warmest Month (BIO5) and the 2) Minimum Temperature of Coldest Month (BIO6). For precipitation, we used the 3) Precipitation of Wettest Quarter (BIO16) and the 4) Precipitation of Driest Quarter (BIO17). We chose these four variables because they represent the range of climatic conditions in which bat species are distributed (e.g. Castro-Insua et al., 2018; Gómez-Rodriguez et al., 2015). Estimating niche breadth based on such temperature and precipitation gradients let our index represent climatic extremes for each species. We performed the extraction of climatic variables using the *letsR* package.

For calculating phyllostomid climatic niche breadth, we used the approach of Gómez-Rodríguez et al. (2015) and Castro-Insua et al. (2018). First, we standardized each bioclimatic variable considering their ranges (Rg; maximum – minimum values) for each single species and compared to all species present in our dataset:

$$Rgi = [Rg_i - \min(Rg_i:Rg_j)] / [\max(Rg_i:Rg_j) - \min(Rg_i:Rg_j)],$$

in which $i$ represents the value for each species in the total set of $j$ species and $\max(Rg_i:Rg_j)$ and $\min(Rg_i:Rg_j)$ are the maximum and minimum values of the ranges of each variable in the set of $j$ species, respectively. Subsequently, we calculated climatic niche breadth for each species as the product of the standardized values among all four variables. This climatic niche breadth index ranges from 0 to 1, with higher and lower values indicating higher and lower climatic niche breadth, respectively. The main advantage of this approach is that it allows the combination of variables measured in different units into a unique and standardized variable that simultaneously includes measures of temperature and precipitation niche breadths (Castro-insua et al., 2018; Gómez-Rodríguez et al., 2015).

We compared climatic niche breadth measures obtained from the combination of BIO5, BIO6, BIO16 and BIO17 with an alternative approach in which we used the lower and upper limits of mean annual temperature (BIO1) and mean annual precipitation (BIO12) across species ranges. Both climatic niche breadth estimates were strongly correlated ($r = 0.91$, $p < 0.001$) and, therefore, we opted for using the original combination of the four variables representing climatic extremes in further analyses.

In a first glance our climatic niche breadth calculation can suggest that species with increased ranges would have larger climatic niche breadth. However, this is not always the case, since species can have large ranges encompassing similar environmental conditions, which can be defined as the environmental prevalence within their geographical distributions (Meyer & Pie, 2018). These species would present larger ranges, but low variability in geographical climatic conditions. Therefore, there is no reason to assume *a priori* that larger ranges would automatically translate into increased climatic niche breadth. Nevertheless, to improve the reliability of our climatic niche breadth estimates we compared our results using a spatial null model in which we randomized the spatial distribution of the climatic variables while retaining their spatial autocorrelation (Moore, Bagchi, Aiello-Lammens, & Schlichting, 2018). We created 999 simulated climatic layers with the four variables used to calculate climatic niche breadth. For each simulation, we calculated for each species a null climatic niche breadth and tested the relationships between them and the phyllostomid range sizes. Then, we compared if the observed relationship is stronger than expected according to this spatial null model. We implemented this null model following the R script available in Moore et al. (2018).

### Phyllostomid dispersal abilities

To test the influence of dispersal abilities on phyllostomid geographical range sizes, we assembled from the literature data on a morphological variable widely related to flight performance in bats and other flying animals: relative wing loading (RWL) (Luo et al., 2019; Marinello & Bernard, 2014; Norberg & Rayner, 1987; Supporting Information). For each species, RWL is calculated as its wing loading (weight divided by wing area)/mass$^{1/3}$. Species with higher RWL have aerodynamically better flight performance, with reduced costs and increased speed, and directly and positively influences bat dispersal abilities (Luo et al., 2019; Marinello & Bernard, 2014; Norberg & Rayner, 1987). Therefore, we expected to find a positive influence of RWL on phyllostomid ranges.

We compared RWL with another commonly used measure of flight ability in bats, the Aspect Ratio (AR), measured as the square of the wingspan by its area. As both indexes were correlated (Supporting Information Figure S1), we opted to use only the RWL as a measure of dispersal ability in further analysis, given that it has the advantage of being an allometrically corrected measure of flight performance and because results using data on AR would fundamentally resemble those anticipated in our study.

## Phylogenetic framework and statistical analysis

In all analyses, we considered the non-independence of residuals from analyses due to the shared evolutionary history among species (Revell, 2010). Accordingly, our analytical framework was conceived by explicitly considering phylogenetic information on phyllostomid evolutionary relationships and divergence times from a time-calibrated phylogeny (Shi & Rabosky, 2015). This phylogenetic hypothesis was built from a combined set of several mitochondrial and nuclear nucleotide sequences, which present strong node support and a high correlation with previous hypotheses of evolutionary relationships among bats (Shi & Rabosky, 2015; Varzinczak et al., 2019). We pruned this phylogeny to match the 74 phyllostomid species present in our database.

To determine whether similarities in phyllostomid geographical range sizes, climatic niche breadth and dispersal ability are related to the evolutionary distances among species, we tested for the presence of phylogenetic signal for each trait using Blomberg's *K* (Blomberg, Garland, & Ives, 2003). High and positive *K* values support a scenario of a strong phylogenetic signal for a given trait. We estimated the probabilities for the observed *K* values using 10,000 randomizations of the original dataset. We performed tests of phylogenetic signal with the *phytools* package (Revell 2012).

To test our initial hypothesis that climatic niche breadth and dispersal ability positively influence phyllostomid geographical range sizes, we used phylogenetic generalized least squares (PGLS) coupled with an information theoretic approach (Grafen, 1989; Garamszegi &Mundry, 2014; Symonds & Blomberg, 2014). We did not find a correlation between climatic niche breadth and dispersal ability ($r = -0.11$, $p = 0.32$) and, therefore, we created six candidate PGLS models that covered the unique, additive and interaction effects of climatic niche breadth and dispersal ability on phyllostomid range sizes. We also included a seventh model without the effect of these variables and considering only the intercept (Table 1). For all models, we calculated their corrected Akaike's information criterion (AICc), as well as the evidence weights (ω), to account for model uncertainty (Burnham & Anderson, 2002; Garamszegi &Mundry 2014). Then, we conducted a multi-model comparison and chose as the best model the one with the lowest AICc value, with ΔAICc value > 2 and with the highest weight in relation to alternative candidate models (Burnham & Anderson, 2002). We created PGLS models and conducted multi-model comparisons using the *caper* (Orme et al., 2018) and *MuMIn* packages (Barton, 2017), respectively.

We assessed the overall influence of sampling size on parameters estimates using phylogenetic sensitivity analyses (Paterno, Penone, and Werner 2018). We did this by randomly removing a proportion of species (10%, 20%, 30%, 40% and 50%) 999 times from our dataset and detecting the effects of varying sample size on parameter estimates from PGLS's best model. We conducted sensitivity analyses using the sensiPhy package (Paterno et al., 2018).

PGLS is a useful tool for determining the global influence of one or more predictors on the response variable. As a global method, however, it assumes a constant influence of the explanatory variables throughout the whole set of species. It fails to detect variations of such influences across the phylogeny, i.e., at different phylogenetic scales *sensu* Graham et al. (2018). Interspecific variations that consider the importance of each predictor can be observed, for example, when species and clades are influenced to different degrees by the variables included in statistical models. This phenomenon reflects idiosyncrasies along evolution due to latent variables that are not included in original models (i.e., phylogenetic non-stationarity; Davies, Regetz, Wolkovich, & McGill, 2019). Phylogenetically weighted regressions (PWR) were recently proposed as an exploratory tool to be used in complement to PGLS. It allows researchers to deal with phylogenetic non-stationarity that underlies ecological data within such an evolutionary framework (Davies et al., 2019). Thus, to explore the relative effects of climatic niche breadth and dispersal ability on phyllostomid geographical range sizes at the species-level, we applied PWR to our dataset. We performed a PWR using a computer optimization to obtain the optimum bandwidth (bandwidth = 0.032) to be used in this analysis. Also, we used a weighting function related to an Ornstein–Uhlenbeck (OU) model of trait evolution, which was favored in comparison to a Brownian motion model (Supporting Information Table S2). Then, for each species, we obtained slope estimates for the influence of both climatic niche breadth and dispersal ability and built a 95% confidence interval around them. For this case, higher absolute slopes indicate a higher influence of these variables on species range sizes. Further details on this method and the R code for running PWR are available in Davies et al. (2019).

## RESULTS

### Patterns of range size, climatic niche breadth and dispersal ability in phyllostomid bats

Phyllostomids are characterized by highly variable range sizes, with species that present narrow and wide geographical distributions (Fig. 1). Phyllostomid range sizes varied from 0.03 x $10^7$ km² to 1.8 x $10^7$ km² (Fig. 1). However, most species had intermediate ranges, with few species characterized by an extremely small or large geographical range (Fig. 1). A similar pattern was also observed for the dispersal abilities, for which most species were concentrated around intermediate values of dispersal ability (Fig. 1). On the other hand, most species had a low climatic niche breadth (Fig. 1).

We did not find evidence of phylogenetic signal in phyllostomid range sizes ($K$ = 0.35, $p$ = 0.29) or in their climatic niche breadth ($K$ = 0.32, $p$ = 0.40). Conversely, we observed phylogenetic signal for the dispersal abilities ($K$ = 0.46, $p$ = 0.02).

### Influence of CNB and dispersal on phyllostomid range sizes

The best PGLS model selected in our analysis implied that variations in phyllostomid geographical range sizes are largely explained by climatic niche breadth and dispersal abilities acting additively (Table 1). This model presented the lowest AICc, as well as the highest weight, in comparison to additional models (Table 1). Furthermore, it explained more than half of the total variation in the geographical range sizes for these bats ($R^2$ = 0.514). The second-best model added an interaction term with parameter estimates very similar and in the same direction, but with model weight approximately a third of the simpler model including only the additive effects between climatic niche breadth and dispersal abilities (Table 1).

Supporting our initial hypothesis, we observed a positive influence of CNB on phyllostomid range sizes (Fig. 2a; Table 1). However, we surprisingly observed a negative influence of dispersal ability (represented by RWL) on these bats' range sizes, which departed from our initial prediction that bats with higher dispersal abilities have larger ranges (Fig. 2b; Table 1). Results from our sensitivity analyses indicate that parameter estimates were not influenced by sampling size (Supporting Information Figure S2). Also, results from the spatial null model indicate that the observed relationship between range size and climatic niche breadth was higher than that from randomized datasets, highlighting that the climatic niche breadth estimate was unbiased by the method we employed ($p < 0.001$; Supporting Information Figure S3), i.e. calculating species climatic niche breadth from their distributional maps.

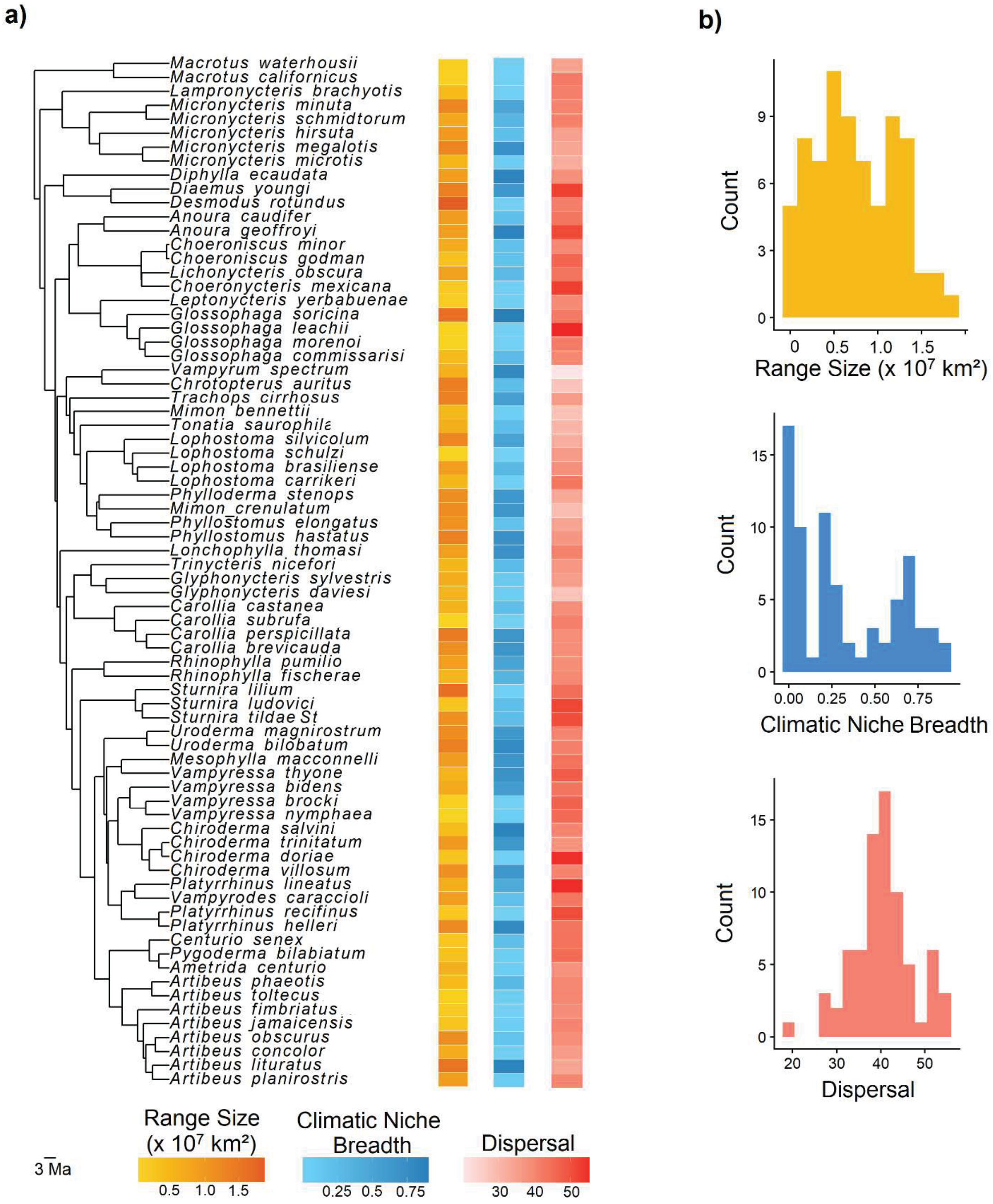

**Fig. 1.** (a) Phylogenetic relationships and the range size, climatic niche breadth and dispersal ability measured as the relative wing loading for phyllostomid species used in this study. (b) Histograms depicting the distribution of each variable. Of the three variables, only dispersal ability showed phylogenetic signal.

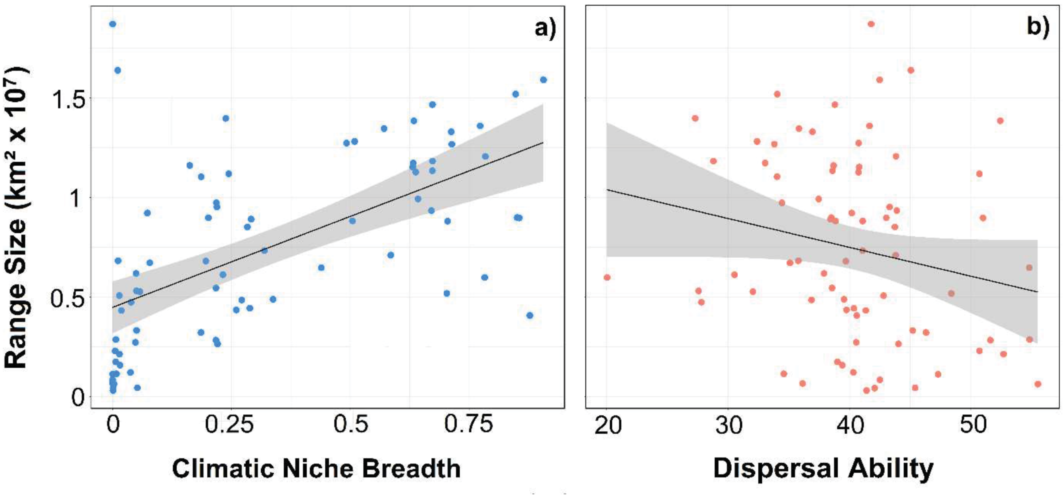

**Fig. 2.** Relationships between a) climatic niche breadth and b) dispersal ability (measured as the relative wing loading) with phyllostomid geographical range sizes. Shaded areas represent 95% confidence intervals from the estimated parameters in the model selected in Table 1.

**Table 1.** Hypotheses on the influence of the climatic niche breadth (CNB) and dispersal abilities (DIS) measured as the relative wing loading on the geographical range sizes of phyllostomid bats. R²: relative explained variation in range sizes; AICc: corrected Akaike's information criterion; ω: model weight. The model selected is in bold.

| | **Intercept** | **CNB** | **DIS** | **CNB:DIS** | **R²** | **AICc** | **ΔAICc** | **ω** |
|---|---|---|---|---|---|---|---|---|
| **DIS+CNB** | **-0.006** | **0.557** | **-0.286** | | **0.514** | **191.3** | **0** | **0.691** |
| **DIS*CNB** | -0.005 | 0.554 | -0.273 | 0.030 | 0.507 | 193.5 | 2.11 | 0.240 |
| **CNB** | 0.055 | 0.660 | | | 0.466 | 197.1 | 5.71 | 0.039 |
| **CNB+CNB*DIS** | 0.048 | 0.635 | | 0.104 | 0.470 | 197.7 | 6.35 | 0.028 |
| **DIS** | -0.094 | | -0.562 | | 0.238 | 223.4 | 32.05 | 0.001 |
| **DIS+DIS*CNB** | -0.091 | | -0.526 | 0.079 | 0.233 | 225.0 | 33.68 | 0.001 |
| **~ 1 (intercept only)** | 0.012 | | | | | 242.5 | 51.14 | 0.000 |

Our results from the PWR indicated that the influences of climatic niche breadth and dispersal abilities on phyllostomid geographical range sizes at the species-level is relatively variable. This finding contrasted with the results observed for the family as a whole. For example, although the ranges for all species are positively influenced by climatic niche breadth, slopes for this variable ranged from 0.33 to 0.69, compared to a slope of 0.55 from the best PGLS model (Figure 3). On the other hand, we found that, although dispersal ability negatively influences phyllostomid range sizes, at the species-level its effects ranged from -0.23 to 0.002 compared to the slope of -0.28 from the best PGLS model (Fig. 3). For this case, however, 45 species (60%) had a 95% confidence interval of their slope estimates that overlapped with 0. These data indicate the absence of effects of dispersal abilities on their geographical ranges (Fig. 3).

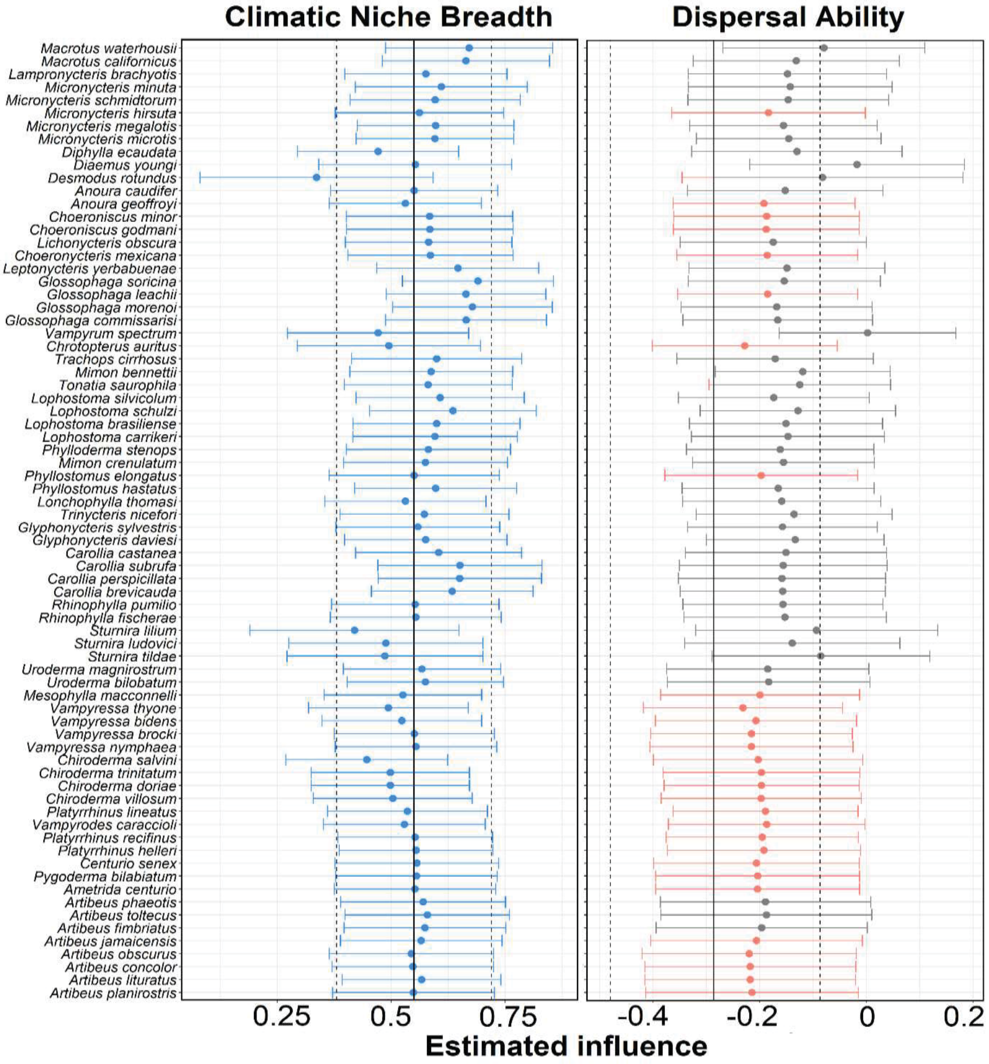

**Fig. 3.** Results from phylogenetically weighted regressions considering the effects of climatic niche breadth and dispersal ability measured as the relative wing loading for each phyllostomid species. For the sake of comparison, vertical solid and dashed lines represent the slopes and 95% confidence intervals, respectively, from the global selected PGLS model considering all species. Horizontal bars represent slope estimates and their 95% confidence intervals considering the influence of each variable for each species. Grey bars indicate confidence intervals that overlapped with zero and, therefore, the absence of an effect of the variable. Species are ordered as in Fig. 1 following their phylogenetic relationships.

## DISCUSSION

Based on the hypothesis that interspecific differences in climatic niche breadth and dispersal play a central role in shaping variations in species ranges, we expected that the geographical range size of the tropical and New World endemic phyllostomid bats would be positively influenced by these two variables. In fact, we found that phyllostomid ranges are best predicted by the additive effect of these two variables, which explained more than half (~51.4 %) of variation in their ranges (Table 1). This result was also supported by the second-best model that added an interaction term between these two variables, but which had much lower weight. This level of variation assigned to climatic niche breadth and dispersal is very expressive given the complexity of the complementary ecological and evolutionary processes thought to influence species distributions in such a macroecological context and that could ultimately influence their ranges (Faurby & Antonelli, 2018; Gaston 2003). However, we found support only for the positive influence of climatic niche breadth. Surprisingly, dispersal negatively influenced phyllostomid ranges. Furthermore, despite the positive effects of climatic niche breadth at different phylogenetic scales (i.e., from the whole family to the species level), for most species dispersal abilities did not influence phyllostomid range dynamics (Fig. 3). Overall, our results indicate important features of the processes that shape phyllostomid ranges and provide new insights, considering the influence of climatic niche breadth and dispersal abilities as determinants of the species geographical range sizes.

### Influences of climatic niche breadth and dispersal on species ranges

Phyllostomids radiated mainly in the tropics (Tavares, Dávalos, Warsi, Balseiro, & Mancina, 2018); their climatic niches are tightly related to tropical climates (Stevens, 2006; Varzinczak et al., 2010). Therefore, as many other tropical clades, phyllostomids are adapted to a narrow range of climatic conditions (Stevens, 2004; Stevens, 2006; Wiens & Donoghue, 2004). Furthermore, metabolic and energetic constraints, a plant-based diet for most species, and a high dependence of the vegetation structure and resources found in the tropics, prevented phyllostomids from expanding their geographical distributions towards the temperate climates at high latitudes outside the tropics (Alroy, 2019; Stevens, 2004; Varzinczak et al., 2019). The New World spans a broad latitudinal extent, and variations in climatic conditions at broad geographical scales impose filters on phyllostomid distributions (Stevens, 2004; Varzinczak et al., 2019; Villalobos et al., 2013). Tropical species should cope with a huge climatic variation to expand their distribution towards high latitudes. Such strong climatic gradients have the potential to exert an accentuated influence on species' ranges, especially for tropical species (Pintor, Schwarzkopf, & Krockenberger, 2015; Stevens, 1989). In fact, phyllostomids present low climatic niche breadth, as observed in our results (Supporting Information), and on average they occur in a reduced latitudinal range compared to other New World's bat families that are better adapted for occurring outside the tropics, such as Molossidae and Vespertilionidae (Arita, Vargas-Barón, & Villalobos, 2014; Willig et al. 2003). Consistent with this general influence of climate on phyllostomid distributions, we further found that climatic niche breadth plays an increased role in shaping their range sizes (Figs. 2 and 3, Table 1). Species with higher climatic niche breadth values are more widely distributed and have larger ranges compared to species with reduced climatic niche breadth because they are likely better adapted to different climatic conditions. This phenomenon increases the probability of finding suitable areas as well as the availability of regions in which they can occur and thrive, a factor that positively influences their geographical distributions and range size patterns (Bozinovic et al., 2011; Calosi et al., 2010; Faurby & Antonelli, 2018; Li et al., 2016; Pintor et al., 2015; Slatyer et al., 2013). Considering the biology of phyllostomid bats, our results suggest that the influence of climatic niche breadth on their ranges likely emerged by similar mechanisms. Phyllostomid distributions are strongly associated with climate, and thus the influence of climatic niche breadth on their ranges tends to be accentuated, a finding that supports our initial predictions.

In a broad sense, flight reduces barriers to dispersal by allowing species to move across longer distances (Luo et al., 2019; McCulloch et al., 2017). For bats, RWL is tightly related to flight performance and the ability to disperse, since it is a wing ecomorphological variable related to the optimization of flight costs from local to broad geographical scales (Luo et al., 2019; Norberg & Rayner, 1987). Thus, we initially expected a positive relationship between phyllostomid flight abilities and their range sizes, as increased RWL translate into energetically efficient flight and long-distance dispersal (Luo et al. 2019; Marinello & Bernard 2014; Norberg & Raynier 1987) However, we observed the opposite pattern: Species with higher relative wing loading and, therefore, increased dispersal abilities, presented reduced ranges (Fig. 2, Table 1).

This result prominently contrasts with that observed for vespertilionid bats, for which dispersal positively influences their geographical ranges (Luo et al., 2019). However, vespertilionids are better adapted for occurring in a wider climate range, including those outside the tropics at high latitudes and sub-tropical climates (Ramos Pereira & Palmeirim, 2013; Stevens, 2004). Therefore, vespertilionid distributions and their ranges are constrained by interspecific interactions and their abilities to disperse towards new regions rather than by climatic filters (Luo et al., 2019; Ramos Pereira & Palmeirim, 2013). This phenomenon explains why patterns of vespertilionid diversity and distribution greatly contrast to those observed for phyllostomids (Arita et al., 2014); they reflect different patterns compared to those revealed in our study as well. In fact, the predicted effects for each species highlights that climatic filters are much more important compared to dispersal in determining phyllostomid ranges (Fig. 3). This result challenges the widespread and traditional view that increased dispersal abilities translate into larger ranges and, in the case of phyllostomids, this finding indicates that results departing from our initial expectations are likely related to the complex evolution experienced by these bats, as we discuss in detail below.

## Phylogenetic non-stationarity and the role of phylogenetic scale on range size determinants

Besides addressing the influence of climatic niche breadth and dispersal for all phyllostomids, we also tested how both variables are related to the geographical range of each species separately (Fig. 3). Different studies have suggested and found changes in ecological and evolutionary patterns when addressing questions across phylogenetic scales (e.g. Davies et al., 2019; Graham et al., 2018). Our results contribute to this knowledge, but from the perspective of the processes that shape species geographical ranges. We found a constant and stationary influence of climate on phyllostomid ranges, as represented by the positive influence of climatic niche breadth for all species. Alternatively, although being globally negatively related to range sizes, the ranges for most phyllostomid species were not influenced by dispersal abilities. These findings highlight that the scale used to conduct our analysis had important implications for detecting the influence of dispersal on species ranges. Specifically, our results clearly indicate that species whose range sizes are negatively influenced by dispersal are mainly the ones evolutionarily closely related to the Stenodermatinae subfamily (Fig. 3). These bats present distinguished biogeographical, ecological and evolutionary patterns among phyllostomids (Dumont et al., 2012; Rossoni, Assis, Giannini, & Marroig, 2017; Shi & Rabosky, 2015; Tavares et al., 2018; Villalobos et al., 2013). For example, during their adaptive radiation, they have evolved adaptations for a very specialized frugivorous diet, which offered them an opportunity to explore and fill unexplored ecological niche spaces. (Monteiro & Nogueira, 2011; Rossoni et al., 2017). Specialized diets are often correlated with smaller geographic ranges (Slatyer et al., 2013; Slove & Janz, 2011) and, therefore, the ability of Stenodermatinae bats to expand their ranges might have been constrained by their high dependence on the spatial availability of these vegetal resources they rely upon, regardless of how good they are at dispersion (Stevens, 2004). These features make these bats very contrasting when compared to other phyllostomids and influence the observed patterns with those in the whole family and challenging the general positive dispersal-range size relationship. In fact, an important feature of PWR is to detect latent variables that may generate a non-stationary ecological pattern within a phylogenetic framework (Davies et al., 2019), which is likely to be the case considering the distinguished patterns of range size in Stenodermatinae bats. The use of PWR thus allowed us to identify divergent trends within the main patterns that characterize phyllostomid range-size dynamics. Accordingly, our results show that evolutionary and biogeographical idiosyncrasies within major groups can potentially play important roles on the influence assigned to different processes thought to influence species geographical range sizes. Our research highlights the importance of addressing range determinants across phylogenetic scales. Moreover, our findings indicate that these characteristics should be explicitly and carefully considered to better understand how different processes shape species distribution and their range size patterns.

## CONCLUSIONS

Ecologists have long asked which factors shape the patterns of geographical range sizes and by what means. Due to their direct effect in species distributions, climatic niche breadth and dispersal have both been hypothesized to be as of central importance in answering this question. By using phyllostomid bats as a model system, we provided new answers and insights for an old ecological and evolutionary question. We demonstrated the joint but opposing effects of these variables in shaping phyllostomid ranges. Species might respond differently to distinct processes as a result of their unique evolutionary history shaped by different selective pressures along their distributions, and thus addressing range determinants in a phylogenetic perspective across scales is essential to broaden the view on the mechanisms that influence range size dynamics. To our knowledge, this study is the first to date that used phylogenetic weighted regressions to uncover factors influencing range sizes. Our results highlight important features that would not be disclosed without a thorough examination of the effects of climatic niche breadth and dispersal at different scale, namely the divergent trends within the general patterns found for the whole family. Considering that this tool is relatively recent, studies that aim to address the factors that underlie species' ranges have much to gain by incorporating additional variables in a similar framework. This endeavor will be crucial to determine the factors that shape patterns of species distributions, to better understand the relative contribution of different processes in determining range sizes, and to reveal specific factors related to species vulnerabilities to extinction.

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## APPENDIX

Table S1. Data of Relative Wing Loading for phyllostomid bats with their respective sources.

| Species | Relative Wing Loading | Source |
|---|---|---|
| *Ametrida centurio* | 37.9 | 1 |
| *Anoura caudifer* | 43.3 | 2 |
| *Anoura geoffroyi* | 51 | 2 |
| *Artibeus concolor* | 35.78 | 3 |
| *Artibeus fimbriatus* | 39 | 2 |
| *Artibeus jamaicensis* | 40.56 | 4 |
| *Artibeus lituratus* | 34.05 | 3, 4 |
| *Artibeus obscurus* | 38.69 | 3 |
| *Artibeus phaeotis* | 40.36 | 4 |
| *Artibeus planirostris* | 40.18 | 3 |
| *Artibeus toltecus* | 40.31 | 5 |
| *Carollia brevicauda* | 38.6 | 3 |
| *Carollia castanea* | 38.56 | 4 |
| *Carollia perspicillata* | 38.8 | 2, 3, 4 |
| *Carollia subrufa* | 41.4 | 6 |
| *Centurio senex* | 44.04 | 6 |
| *Chiroderma doriae* | 54.82 | 7 |
| *Chiroderma salvini* | 40.59 | 5 |
| *Chiroderma trinitatum* | 37.45 | 3 |
| *Chiroderma villosum* | 40.73 | 3, 4 |
| *Choeroniscus godmani* | 46.3 | 8 |
| *Choeroniscus minor* | 39.7 | 3 |
| *Choeronycteris mexicana* | 52.69 | 8 |
| *Chrotopterus auritus* | 27.3 | 3 |
| *Desmodus rotundus* | 41.78 | 2, 3 |
| *Diaemus youngi* | 52.42 | 8 |
| *Diphylla ecaudata* | 38.5 | 2 |
| *Glossophaga commissarisi* | 39.75 | 5 |
| *Glossophaga leachii* | 55.51 | 5 |
| *Glossophaga morenoi* | 42.08 | 6 |
| *Glossophaga soricina* | 42.49 | 3 |
| *Glyphonycteris daviesi* | 27.57 | 3 |
| *Glyphonycteris sylvestris* | 35.1 | 1 |
| *Lampronycteris brachyotis* | 41.34 | 3, 4 |
| *Leptonycteris yerbabuenae* | 39.4 | 8 |
| *Lichonycteris obscura* | 43.73 | 3 |
| *Lonchophylla thomasi* | 41.08 | 3 |
| *Lophostoma brasiliense* | 38.44 | 3 |
| *Lophostoma carrikeri* | 42.8 | 3 |
| *Lophostoma schulzi* | 36.13 | 1 |
| *Lophostoma silvicolum* | 32.39 | 3, 4 |
| *Macrotus californicus* | 42.5 | 8 |
| *Macrotus waterhousii* | 34.59 | 8 |

| | | |
|---|---|---|
| *Mesophylla macconnelli* | 43.9 | 3 |
| *Micronycteris hirsuta* | 34.44 | 3, 4 |
| *Micronycteris megalotis* | 33.81 | 3 |
| *Micronycteris microtis* | 32.04 | 4 |
| *Micronycteris minuta* | 40.76 | 3 |
| *Micronycteris schmidtorum* | 41.09 | 3 |
| *Mimon bennettii* | 27.8 | 2 |
| *Mimon crenulatum* | 28.79 | 3, 4 |
| *Phylloderma stenops* | 33.05 | 3, 4 |
| *Phyllostomus elongatus* | 34.03 | 3 |
| *Phyllostomus hastatus* | 36.94 | 3, 4 |
| *Platyrrhinus helleri* | 43.83 | 3, 4 |
| *Platyrrhinus lineatus* | 54.8 | 2 |
| *Platyrrhinus recifinus* | 50.7 | 2 |
| *Pygoderma bilabiatum* | 45.2 | 2 |
| *Rhinophylla fischerae* | 39.56 | 3 |
| *Rhinophylla pumilio* | 38.85 | 3 |
| *Sturnira lilium* | 45.05 | 3 |
| *Sturnira ludovici* | 51.6 | 8 |
| *Sturnira tildae* | 50.7 | 2 |
| *Tonatia saurophila* | 30.52 | 3, 4 |
| *Trachops cirrhosus* | 35.84 | 3, 4 |
| *Trinycteris nicefori* | 36.87 | 3 |
| *Uroderma bilobatum* | 41.65 | 3, 4 |
| *Uroderma magnirostrum* | 40.79 | 3 |
| *Vampyressa bidens* | 43.8 | 3 |
| *Vampyressa brocki* | 47.29 | 1 |
| *Vampyressa nymphaea* | 45.4 | 4 |
| *Vampyressa thyone* | 48.38 | 5 |
| *Vampyrodes caraccioli* | 43.02 | 8 |
| *Vampyrum spectrum* | 20.04 | 3 |

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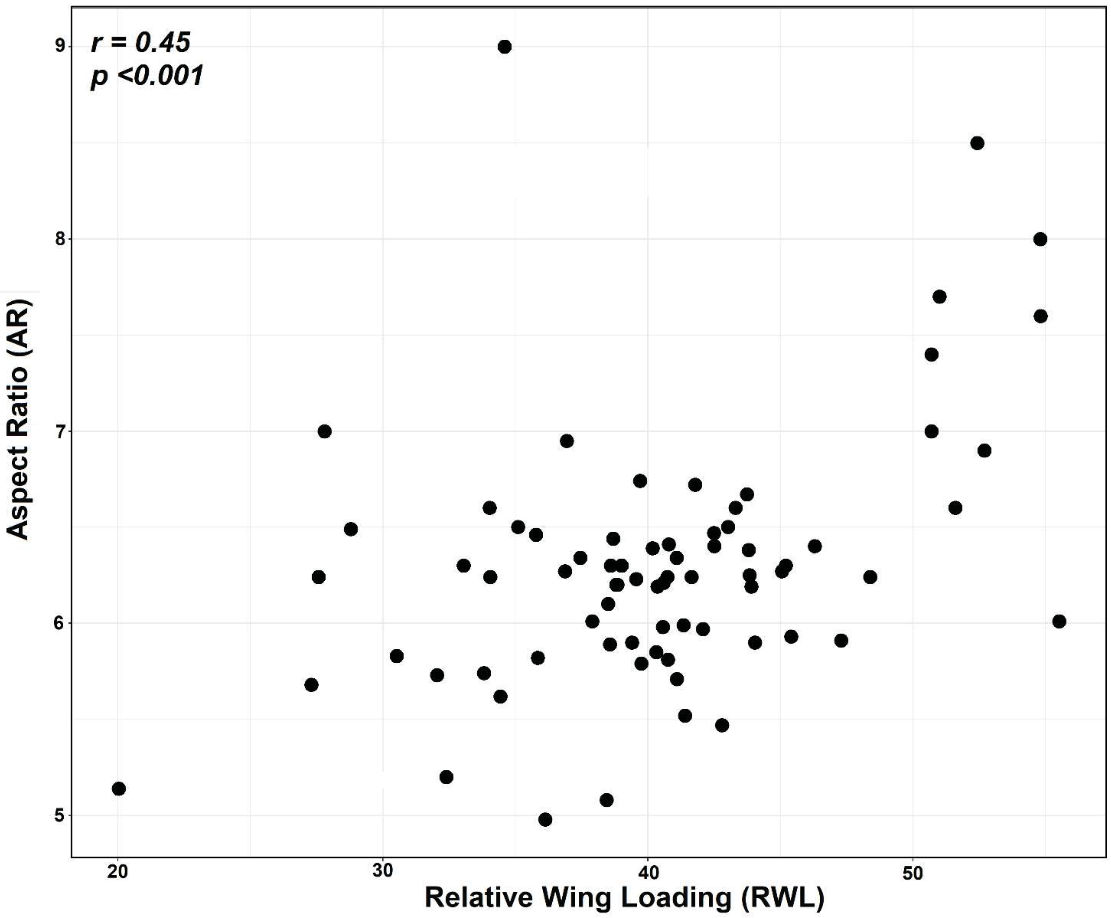

**Figure S1.** Correlation between phyllostomids relative wing loading and wing aspect ratio.

Table S2. **Test of Brownian (BM) and Ornstein-Uhlenbeck (OU) models of trait evolution for each variable included in our analyses. AICc: corrected Akaike's Information criterion. The selected model in bold was used to set the parameters in the phylogenetically weighted regressions.**

| Variable | **Evolutionary Model** | **Log likelihood** | **AICc** | **ΔAICc** |
|---|---|---|---|---|
| Range Size | | | | |
| | **OU** | **-1240.8** | **2488.1** | **0** |
| | BM | -1256.6 | 2517.4 | 29.3 |
| Dispersal (Relative Wing Loading) | | | | |
| | **OU** | **-245.2** | **496.7** | **0** |
| | BM | -253.3 | 510.8 | 14.1 |
| Climatic Niche Breadth | | | | |
| | **OU** | **-15.1** | **36.5** | **0** |
| | BM | -34 | 72.1 | 35.6 |

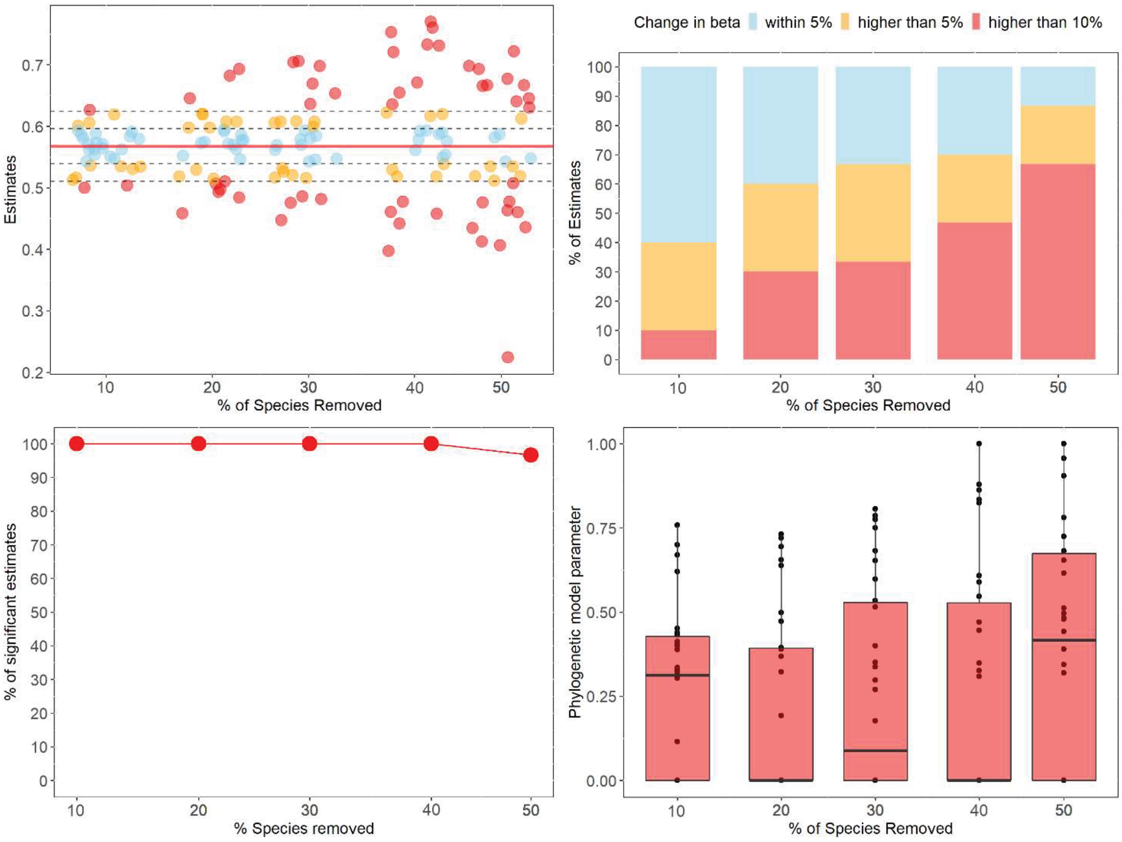

**Figure S2.** Results of sensitivity analyses testing the overall influence of sampling size on parameters estimates. This analysis was performed by randomly removing proportion of species (10%, 20%, 30%, 40% and 50%) 999 times from our dataset and detecting the effects of varying sample size on parameter estimates from PGLS's best model. Parameter estimates held relatively constant across all cases, regardless of the number of species included in each dataset.

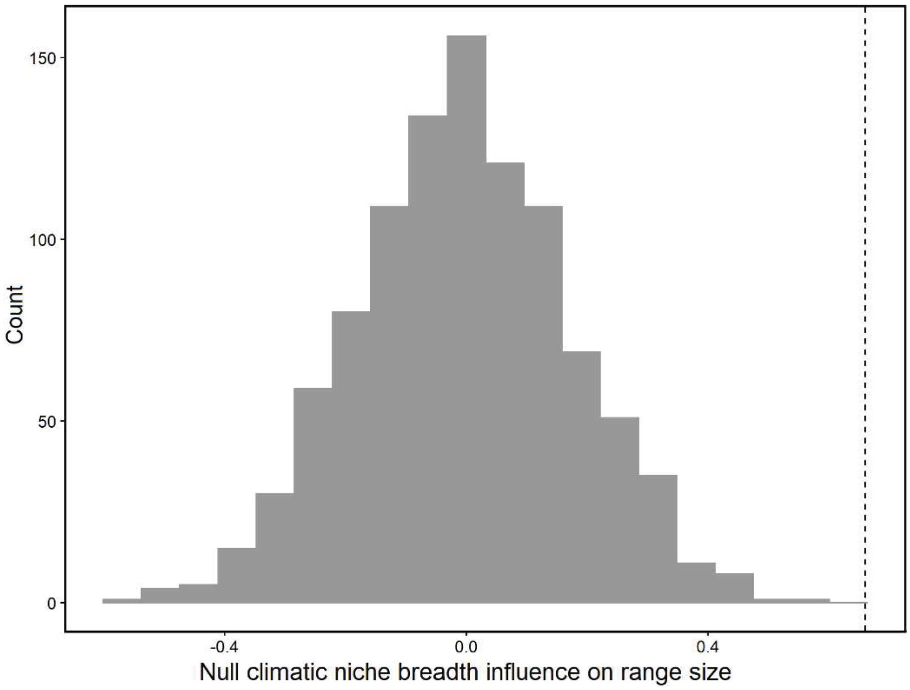

**Figure S3.** Result from the spatial null model that randomize the spatial distribution of the climatic variables while retaining their spatial autocorrelation. The histogram shows the distribution of the parameters representing the influence of the null climatic niche breadth estimates on species ranges from PGLS models. For sake of comparison, the dashed line represents the observed estimate for the relationship between climatic niche breadth – range size from the PGLS best model.

# CAPÍTULO 3

## *Latitudinal gradients in rates of local extinction and colonization: the emergence of biodiversity gradients and the role of contemporary dynamics versus historical legacies **

* Capítulo formatado de acordo com as normas do periódico *Journal of Biogeography*

# Latitudinal gradients in rates of local extinction and colonization: the emergence of biodiversity gradients and the role of contemporary dynamics versus historical legacies

## ABSTRACT

**Aim:** Biodiversity gradients and the processes underlying their structure are ubiquitous across the contemporary biota. Modern approaches acknowledge that global gradients of species diversity ultimately emerge from a balance between extinction and colonization, processes that originate in local assemblages. We addressed predictions of rates of local extinction and colonization along an extensive geographical gradient for phyllostomid bats, a radiation of species that exhibits biodiversity gradients structured in terms of latitude and species responses to contemporary gradients of climate.

**Location:** New World.

**Time period:** Cenozoic.

**Major taxa:** leaf-nosed bats, Phyllostomidae.

**Methods:** Using community data derived from species geographic distribution maps covering the whole New World, we estimated local extinction and colonization rates for each assemblage and examined their geographical patterning related to local species richness and latitude. By means of variation partitioning we determined effects of contemporary climate, spatial dynamics, and historical climate on local extinction and colonization gradients.

**Results:** Local extinction and colonization peaked toward the edge of phyllostomid distributions at high latitudes outside the tropics, being higher in the northern hemisphere and reflecting the role of landscape configurations in concert with biogeographical dynamics of bat distribution in the region. Local extinction and colonization rates were correlated to varying degrees and in opposing directions with species richness and both exhibited strong spatial structuring. The rate of colonization exhibited the strongest climatic gradients being significantly related to contemporary climatic characteristics.

**Main conclusions:** Our results highlight complementarity between rates of local extinction and colonization and how these processes synergistically impact contemporary biodiversity gradients and ultimately determine limits to the distribution of diversity at global scales. Overall, examples from phyllostomid bats reinforce the importance of examining how local assemblages are assembled in terms of biogeographical processes and how these translate into broad-scale patterns of species diversity.

*Keywords:* Biogeography, latitudinal gradient of diversity, leaf-nosed bats, New World, Phyllostomidae, variation partitioning

## INTRODUCTION

Global biodiversity gradients distributed through space and time are some of the most conspicuous patterns in nature and have been widely recognized for more than two centuries (Brown and Sax 2004). For much of this history, investigators have assumed that these gradients resulted from responses to contemporary processes such as climate, productivity, area, heterogeneity or biotic interactions (Field et al. 2009; Brown 2014; Stein et al. 2014). More recently the importance of biogeography, evolution, and their interactions with contemporary processes in generation and maintenance of these gradients has come to the forefront (Wiens & Donoghue 2004; Mittelbach et al. 2007; McGill et al. 2020; Meseguer & Condamine 2020). More than just bridging important gaps and leading to a better understanding of present-day species diversity patterns, the interaction amongst these disciplines has revealed complex processes that go far beyond simplistic and traditional models based on one or a few contemporary environmental processes (Jablonski et al. 2013; Brown 2014; Pulido-SantaCruz & Weir 2016; Rangel et al. 2018).

Macroecological gradients in biodiversity ultimately emerge from patterns of species distributions at finer, local scales (Gaston & Blackburn 2000). Locally, evolutionary and biogeographical dynamics related to the extinction (i.e., extirpation) and colonization of local populations determine assemblage composition defined by species absences or presences in particular local assemblages and which represents a subset of the entire pool of species (Ricklefs 1987; Leibold et al. 2004; Vellend 2010; Pigot & Etienne, 2015; Jønsson et al. 2016). On one hand species occurrence results from their ability to colonize and thrive in a given assemblage and to avoid local extinction, while on the other their absence reflect inability to colonize new regions or local extirpations of their populations, regardless of whether local extinction and colonization occurred by deterministic or stochastic processes (MacArthur & Wilson 1967; Leibold et al. 2004; Vellend 2010; Rosindel et al. 2011). Observed local diversity and species composition therefore represent a balance between rates of local extinctions and colonizations, though they need not counterbalance (i.e., opposite and equal rates) each other. Similarly, biodiversity gradients are determined by the interplay between these very same processes that occur simultaneously across different clades, and reinforce evolutionary and biogeographical signatures of how diversity was assembled through space and time

(Ricklefs 1987; Roy & Goldberg 2007; Pulido-SantaCruz & Weir 2016; McGill et al. 2020).

As primary processes influencing origin and maintenance of biodiversity along geographical gradients, local extinction and colonization are ubiquitous biogeographical forces acting in the background of many ecological patterns (MacArthur & Wilson 1967; Rolland et al. 2014; Meseguer & Condamine, 2020). As such, they are central to several hypotheses attempting to link patterns to specific processes. Take, for example, MacArthur and Wilson's Equilibrium Theory of Island Biogeography (MacArthur & Wilson 1967), in which island diversity is determined by equal and opposing forces of local colonization and extinction that is directly related to the size and isolation from the mainland of islands (MacArthur & Wilson 1967). Another example comes from the increase in species diversity towards low latitudes. One explanation for this pattern is tropical niche conservatism (Wiens & Donoghue 2004; Meseguer & Condamine 2020), in which latitudinal gradients of species diversity arise and are maintained because species of tropical origin have failed to colonize (low rate of colonization) or have gone extinct (high rate of extinction) from regions outside the tropics due to a lack of adaptations to the relatively harsh climates found there. Regardless of whether this particular hypothesis has been supported (e.g. Stevens 2011; Romdal et al. 2012; Kerkhoff et al. 2014) or not (e.g. Ramos Pereira & Palmeirim 2013; Boucher-Lalonde et al. 2015), reduced colonization and increased extinction outside the tropics potentially translated into decreased diversity of temperate regions compared to tropical environments (Wiens & Donoghue 2004; Rolland et al. 2014; Pulido-SantaCruz & Weir 2016; Meseguer & Condamine 2020). Diversity-environment relationships are, therefore, ultimately a by-product of the effect of environmental or other gradients on colonization and extinction dynamics. Thus, achieving comprehensive understanding of the underlying structure of biodiversity gradients requires explicitly considering these complementary biogeographical processes. Overall, it requires understanding of geographic distributions and the kinds of environmental variables that shape them. Here we aim to do so by focusing on the taxonomically and ecologically diverse New World endemic leaf-nosed bats of the family Phyllostomidae as a study system.

Gradients in bat diversity have been extensively studied from numerous perspectives, across several spatial scales, and with complementary approaches (Willig & Selcer 1989; Lyons & Willig 1999; Lyons & Willig 2002, Stevens et al. 2003; Stevens et al. 2020; Alroy 2019). Insights from bat biogeography have provided generalizations on the mechanisms shaping diversity gradients since processes regulating bat diversity greatly contribute to, and appear to converge with mechanisms determining the distribution of other tropical taxa (Lyons & Willig 1997; Buckley et al. 2010). The Phyllostomidae is a tropical clade that exhibits strong latitudinal gradients across multiple dimensions of biodiversity (Stevens et al. 2003; Stevens 2004; Arita et al. 2014; Alroy 2019). Implications to comprehending patterns and processes related to phyllostomid diversity go beyond a simple determination of the importance of complementary processes for just these bats in particular. Considering that phyllostomids represent almost half (~200 species) of New World bat diversity, patterns for this family largely influences what is observed at broad-scales when considering all New World bat families as a group (Arita et al. 2014).

Drivers of phyllostomid biodiversity gradients are complex and no consensus as to their mechanistic bases has emerged. Therefore, much is yet to be learned, especially because only recently have biogeography and evolution been considered potentially important determinants of bat diversity gradients. As a result of having radiated mostly in tropical areas (Arita et al. 2014), as well as their low tolerances to temperate environments (McNab, 1969) and high dependence on forests (Stevens 2004), higher phyllostomid diversity is found near the equator in the tropics (Willig & Selcer 1989, Stevens et al. 2003; Stevens 2004; Stevens 2011; Arita et al. 2014). Moreover, contemporary climate explains much variation in phyllostomid diversity (Stevens 2011; Stevens et al. 2020). Overall, gradients in phyllostomid biodiversity and the role of contemporary climate have primarily been interpreted as responses of these bats to tropical niche conservatism (Stevens 2011; Villalobos et al. 2013). In spite of the importance of extinction and colonization in driving local assemblage structure and giving rise to broad-scale patterns of diversity (Pigot & Etienne 2015; Meseguer & Condamine 2020), as well as importance in determining patterns observed when tropical niche conservatism is at play, the mechanistic effects of colonization and extinction on contemporary diversity gradients or the relative role that different environmental variables play in influencing local extinction and colonization rates are unknown. Determining the importance of local extinction and colonization to biodiversity gradients is of particular importance because geographic characteristics of the New World likely have posed challenges to species distributions due to their broad latitudinal extent, associated strong climatic gradients and topographically heterogeneous landscapes (Rull 2011). These characteristics have possibly left strong imprints on the composition of local assemblages by directly triggering diversification dynamics, local species extinctions and dispersal-mediated colonization of new areas and assemblages (Arita et al. 2014; Varzinczak et al. 2018). Altogether, these factors highlight why phyllostomids represent an interesting model system to address the generality of biogeographical dynamics across extensive geographical gradients, especially considering clades of tropical origins.

Herein we address four predictions: 1) the geographic distribution of phyllostomid extinction and colonization rates are not randomly distributed across the New World, 2) there is a latitudinal gradient in these dynamics, 3) local extinction and colonization are correlated with phyllostomid species richness and 4) due to phyllostomid characteristics such as the importance of tropical origin and niche conservatism to their pattern of diversification, climate is an important determinant of extinction and colonization dynamics.

## MATERIAL AND METHODS

### Phyllostomid geographical distributions and local assemblage composition

We considered data on the geographical distribution of phyllostomid species contained in the International Union for the Conservation of Nature (IUCN) polygons of species distributions version 5.2 (IUCN 2018). These distributional maps were recently revised and updated by Rojas et al. (2018). We overlaid polygons representing species distributions onto a grid with cells of 1º x 1º (~ 110km x 110km in area) in a Mollweide equal-area projection. We considered each cell as an operational unit representing a phyllostomid local assemblage. For each cell, we estimated species composition (presence or absence of all species) and species richness as the overlap of phyllostomid geographic distributions. Our final dataset contained 1871 cells with 157 (~80%) out of approximately 200 species that make up the family Phyllostomidae (Solari et al. 2019). This is the number of species for which phylogenetic information is available for estimating extinction and colonization parameters (as described in detail below). We conducted all geographical data handling with *raster* (Hijmans et al., 2018) and *letsR* (Vilela & Villalobos, 2015) packages in R (R Core Team, 2020).

## Estimating extinction and colonization parameters

For each local assemblage we estimated phyllostomid extinction (μ) and colonization (γ) rates (measured as events per million years) based on a Dynamic Assembly Model Of Colonization, Local Extinction and Speciation (DAMOCLES; Pigot & Etienne 2015). The model assumes that species are added to communities via a balance between addition by local colonization and removal through local extinction. Local colonization and local extinction rates per lineage are assumed to be equal. It is important to highlight that in this model extinction is a process occurring at the population scale (i.e., local extinction) and, therefore, is not necessarily global: it reflects species removal from a particular local assemblage in the geographic space represented by an extirpation of that species population. This way, DAMOCLES allows linkage of population level processes to species occurrences at a macroecological scale. In contrast, composition of the species pool from which communities are assembled is dynamic and resulting from geographic patterns of global speciation and extinction. For each species in a local assemblage, the order of events in terms of speciation, extinction and colonization can be tracked across the entire phylogeny to determine if each species at that site is present or absent because of local extinction or colonization. As a result, DAMOCLES determines the likelihood that each species from the species pool is present in the community given the phylogeny. Often DAMOCLES is used as a null model for examining community structure that is more process-based than traditional ones that simply randomly shuffle tips of a phylogeny or shuffle a species by site presence-absence matrix (e.g. Pinto-Ledezma et al. 2019). An advantage of DAMOCLES is not just that it provides a more process-based null model from which to compare the structure of empirical communities, but it provides maximum likelihood estimates of rates of colonization and extinction that gave rise to those species present in the community. It is these estimates of colonization and extinction that we use to explore gradients in historical processes here. We estimated these rates for each grid cell using the DAMOCLES package in R (Pigot & Etienne 2015).

To estimate extinction and colonization rates for each phyllostomid assemblage we considered a phylogenetic hypothesis of phyllostomid evolutionary relationships provided by Shi & Rabosky (2015), which is characterized by having strong node support and high correlations with other hypotheses of evolutionary relationships among these bats (Shi & Rabosky, 2015), the latter indicating that our analyses would not be biased by the choice of a particular phylogenetic hypothesis over another.

### Determinants of extinction and colonization: contemporary and historical variables

To address determinants of phyllostomid extinction and colonization gradients across the New World, we compared relative and complementary effects of variables related to distinct processes that could potentially influence biogeographical dynamics at broad, macroecological scales. These included contemporary climate, historical climate, and spatial dynamics.

For current climate, we assembled information on bioclimatic variables representing temperature and precipitation gradients from WorldClim version 2.0 (Hijmans et al. 2017). To reduce the dimensionality and multicollinearity of bioclimatic variables, we ran a principal component analysis (PCA) on their standardized (mean = 0, variance = 1) values. The first three PCA axes accounted for 84.3% of variation in contemporary climate and therefore we selected them to represent contemporary climate based on the broken-stick criterion (Peres-Neto et al. 2005). PC1 and PC2 are mainly related to precipitation gradients: PC1 strongly loaded in terms of mean annual precipitation (BIO12), while PC2 is related to precipitation in the coldest quarter (BIO19). PC3, in contrast, is related to seasonality in temperature (BIO4) and precipitation of wettest quarter (BIO16; Supplementary Table S1).

To estimate historical climate, we relied on paleoclimatic reconstructions to estimate temperature and precipitation anomalies, i.e. the magnitude of differences between contemporary and historical climate. Climate changes during Earth's history left signatures on current species distributions, and changes likely influenced local extinctions and species ability to colonize new areas (Svenning et al. 2015; Nogués-Bravo et al. 2018). Regions in which climatic anomalies were greater generally had stronger historical dynamics that may have more strongly influenced current diversity compared to regions in which climate was more stable throughout geological time (Svenning et al. 2015; Nogués-Bravo et al. 2018). We estimated climatic anomalies considering two slices of time using data from the PaleoClim database (Brown et al. 2018). First, we estimated temperature and precipitation anomalies from a deeper geological time, following the changes in these variables from the Pliocene (approximately 3.2 Ma; Hill 2015) to the present. Second, we estimated a shorter geological time period, considering the temperature and precipitation anomalies from the Pleistocene at the Last Glacial Maximum (approximately 21 ka; Karger et al. 2017). By including deeper and shorter periods of time ranging from millions to thousands of years we were able to address more than one geological time frame that could have influenced biogeographical dynamics and phyllostomid distributions. We included climatic anomalies for both periods of time in one matrix representing historical climate used in further analyses described below.

Spatial processes can have different implications at broad macroecological scales, reflecting for example how spatially structured environmental variables affect biological dynamics, or how endogenous processes such as dispersal of individuals among assemblages influence species distributions, colonization and extinction rates (Dray et al. 2006). Also, space can represent effects of spatially autocorrelated but unmeasured environmental variables along a given geographical gradient (Peres-Neto & Legendre 2010). We included a matrix representing spatial processes as a covariate in our analysis by modelling the spatial structure among grid cells using distance-based Moran eigenvector maps (Borcard & Legendre, 2002) in the *vegan* package in R (Oksanen et al. 2017). We created orthogonal and uncorrelated ordination axes representing multiple scales and spatial structures from a matrix comprising the geographical distances between sites (Dray et al. 2006).

### Statistical analyses

We tested for presence and estimated strength of spatial autocorrelation in both extinction and colonization rates using Moran's correlograms (Legendre & Legendre 2012). We computed Moran's I for different distance classes in the *letsR* package.

We tested for correlation between extinction and colonization using Pearson's product-moment correlation coefficients ($r$, Sokal & Rohlf 1995). Also, we tested the correlation between extinction and colonization with latitude considering the geographic coordinates of the centroid of each cell. We tested for correlation between extinction and colonization with phyllostomid richness using Spearman's rank correlation coefficient ($\rho$, Sokal & Rohlf 1995). To test for differences between the average estimates of extinction and colonization rates, we employed a paired $t$-test (Sokal & Rohlf 1995). To determine regions where local extinctions are higher than local colonization and vice-versa we calculated extinction minus colonization: positive values indicate increased local extinction compared to colonization, whereas negative values indicate increased colonization.

To test for effects of contemporary climate, historical climate, and spatial dynamics on phyllostomid extinction and colonization gradients across the New World, we used variation partitioning based on redundancy analysis (Borcard et al. 1992). Variation partitioning allows for the unique effect of each set of predictors to be accounted for while controlling for the effects of additional covariates, as well as for the joint and shared effects between two or more sets of predictors. We treated each response variable (i.e., extinction and colonization) as dependent matrices and determined the total amount of variation explained by the three independent matrices of contemporary climate, historical climate and spatial processes. We estimated the amount of variation explained by our model and the total for each unique and shared fraction amongst matrices based on adjusted coefficients of determination ($R^2_{adj}$; Peres-Neto et al. 2006). We conducted variation partitioning with the *vegan* package (Oksanen et al., 2017). To test the significance of each fraction from the variation partitioning, we used permutation. We broke any possible relationships between the response matrix (i.e., extinction and colonization) with the explanatory matrices by permutating the rows in our original dataset 9999 times. At each iteration, we conducted a new variation partitioning for extinction and colonization estimates, creating a null $R^2$ distribution for all fractions of variation. Then we compared the observed $R^2_{adj}$ for each fraction to estimate the probability of obtaining by chance a value higher or equal in the null $R^2_{adj}$ distribution. We adopted an alpha of 0.05 as the significance level.

## RESULTS

### Geographical gradients of phyllostomid extinction and colonization across the New World

Extinction and colonization rates were variable across the New World, ranging from as high as 3.98 and 2.59 events per million years to close to zero ($2.83 \times 10^{-6}$ and $2.49 \times 10^{-6}$) respectively. Extinction and colonization rates showed a distinct pattern when compared to phyllostomid richness (Figure 1). While a higher number of phyllostomid species have accumulated in tropical assemblages in areas at low latitudes

(Figure 1a), extinction and colonization peaks are found in subtropical environments, very close to the limits of the geographic distributions of many phyllostomids in the New World. In the northern hemisphere, we found increased extinction and colonization rates in assemblages located at the transitional zones between the Neotropics and Nearctic, especially in Mexico (Figure 1b and 1c). In the southern hemisphere, we found that extinction and colonization rates are higher near the Tropic of Capricorn in the southern Neotropics (Figure 1b and 1c), a region that comprises Paraguay, southern Brazil and northern Argentina (Figures 1b and 1c). Comparatively, local extinction is higher than local colonization at high latitudes in both hemispheres, while local colonization is higher especially in the tropics at low latitudes (Figures 1d and 1e).

Although the Caribbean Islands are characterized by having low phyllostomid species richness (Figure 1a), we found that these islands concentrate extinction and colonization rates, which range from intermediate to high values in this region. Comparatively, the Lesser Antilles, have higher extinction and colonization rates compared to the Greater Antilles (Figures 1b and 1c). Local extinctions in the Lesser Antilles are higher than local colonization, while local colonization surpass local extinctions in the Greater Antilles.

## Latitudinal trends and correlations with species richness

Extinction and colonization rates are positively and strongly correlated ($r = 0.8$, $p < 0.001$; Figure 2). Also, extinction rates (mean = 0.38, s.d. = 0.44) are on average higher than colonization rates (0.33; $t = 8.60$, d.f = 1870, $p < 0.001$). Although the relationship between extinction and latitude was not significant ($r = 0.03$, $p = 0.15$; Figure 3a), we found a moderate and significant negative relationship between colonization and latitude (r = -0.38, $p < 0.001$; Figure 3b).

When comparing extinction and colonization with phyllostomid species richness, we observed a weak, yet significant, correlation for extinction ($\rho = -0.14$, $p < 0.001$; Figure 4a). The highest phyllostomid richness was found in assemblages characterized by low extinction rates (Figure 4a). For colonization, we observed a stronger relationship with species richness ($\rho=0.71$, $p < 0.001$; Figure 4b). However, similar to the extinction gradient, increased species richness is found in places with low colonization rates (Figure 4b).

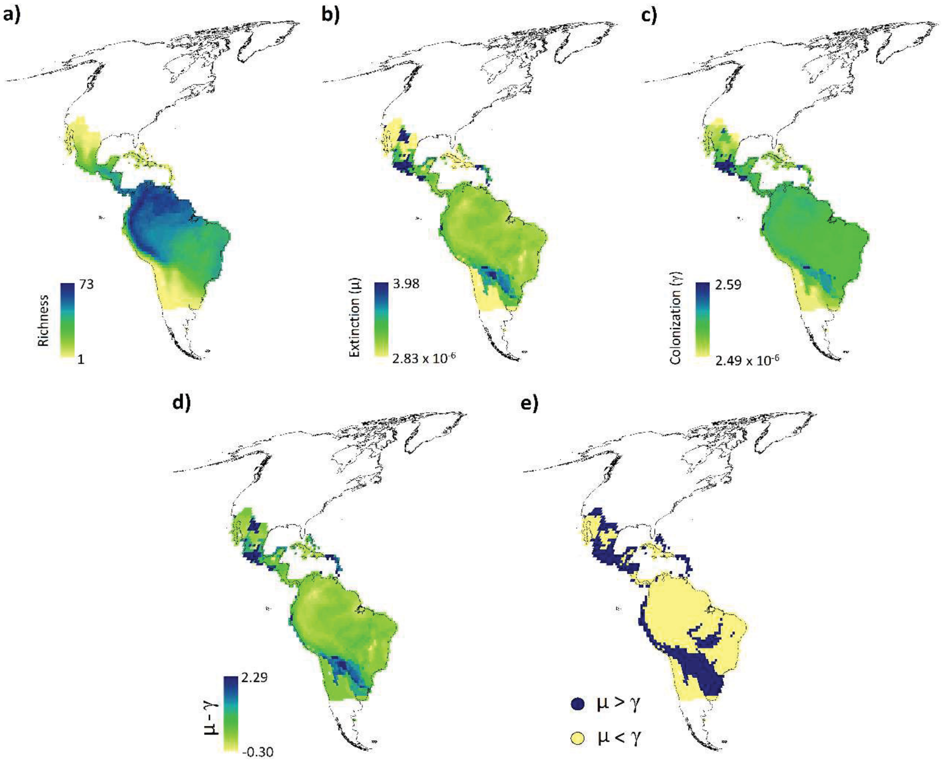

**Figure 1**. Geographical patterns for phyllostomid species richness (a), local extinction (b) and colonization (c) rates (as events per million years), the differences (d) and where extinction and colonization are higher (or lower) and vice-versa compared to the other (e) across the New World.

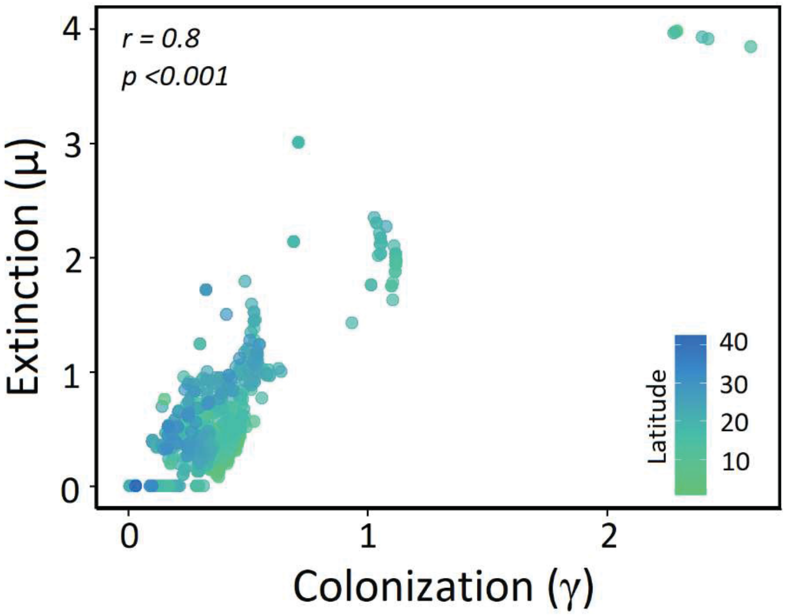

**Figure 2**. Relationship between extinction and colonization in local phyllostomid assemblages across the New World, with its associated Pearson's r and p-value.

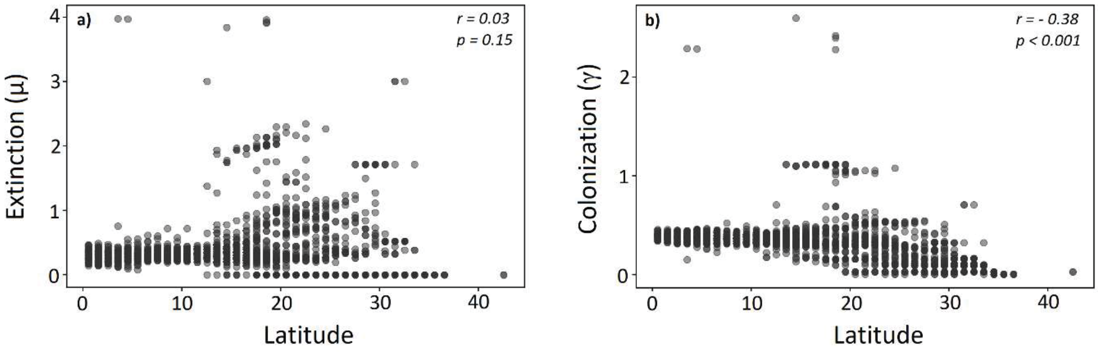

**Figure 3.** Relationship between extinction and colonization with latitude for phyllostomid bat assemblages across the New World and their associated Pearson's r and p-value.

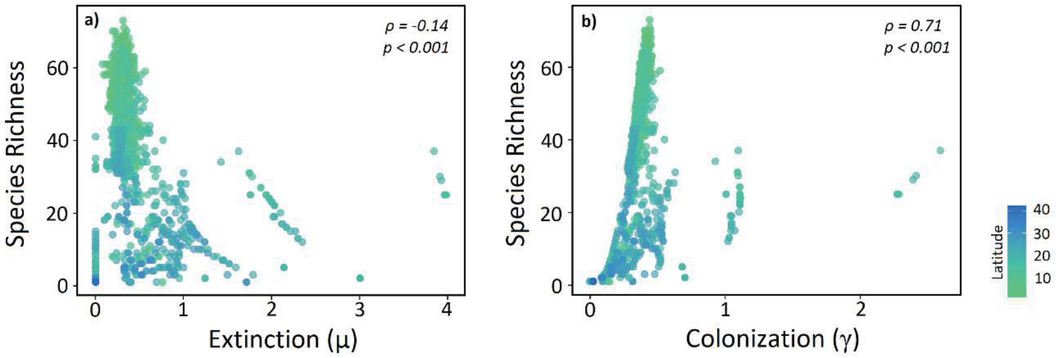

**Figure 4.** Relationship between extinction and colonization with phyllostomid richness in bat assemblages across the New World and their associated Spearman's correlation coefficient ($\rho$) and p-value.

## Spatial structure of extinction and colonization gradients

Extinction and colonization rates exhibited similar spatial structure. Geographically close assemblages are more similar compared to distant sites with regards to these two biogeographical parameters (Figure 5). However, as the inter-site distance increased to values higher than 1000 km, we observed that the spatial structure of extinction rates decreased drastically, represented by very low Moran's I values, which varied around zero (Figure 5). Spatial structure was similar for colonization rates except for high similarity at the largest distances, reflecting similarly reduced rates of colonization at higher latitudes (and the greatest distances) in both hemispheres (Figure 5).

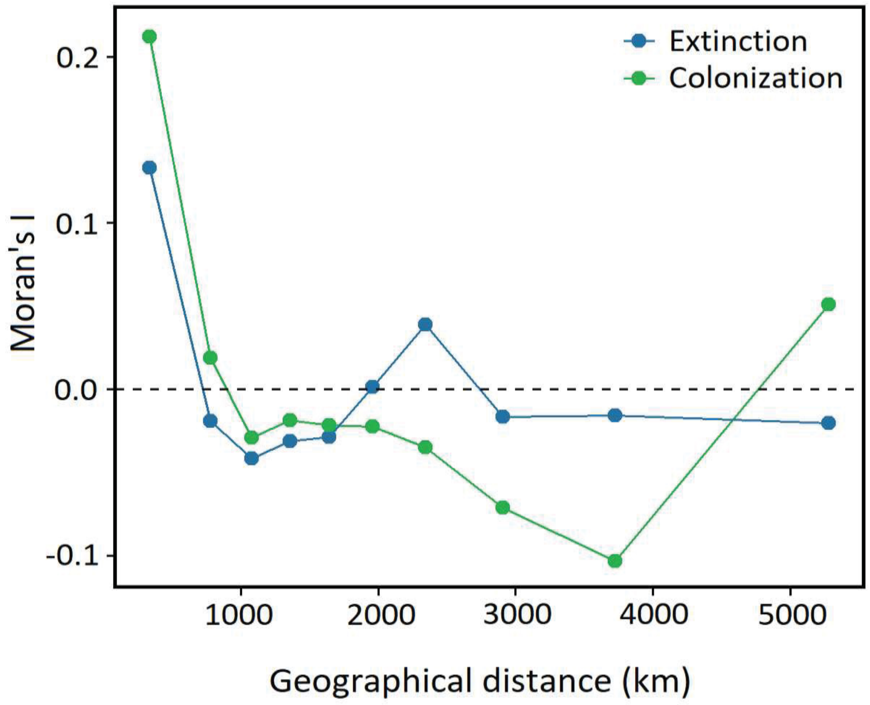

**Figure 5**. Moran's correlograms depicting the strength of the spatial structure for extinction and colonization rates in phyllostomid assemblages.

## Relative contributions of multiple determinants to extinction and colonization gradients in phyllostomids

Contemporary climate, historical climate, and spatial dynamics explained a relatively high amount of variation in phyllostomid extinction and colonization rates (Figure 6). Variation partitioning significantly explained 33% of the variation in extinction rates, for which space contributed the largest explained fraction, with 30%. Contemporary climate (1%) and the joint effect between historical climate and space (2%) completed the total variation explained by the variables included in our model (Figure 6a). For colonization rates, the proportion of variation explained was higher: we found that almost half (49%) of the variation in colonization was explained by the three matrices included in our analyses (Figure 6b). Similar to the results we found for extinction, space held the highest fraction of explanation for colonization, with 27%. However, contemporary climate added an important amount of explanation, whether jointly with space (with 11% Figure 6b), together with space and historical climate (5%), or alone (3%). The influences of historical climate, although significant, was low compared to those of contemporary climate or space.

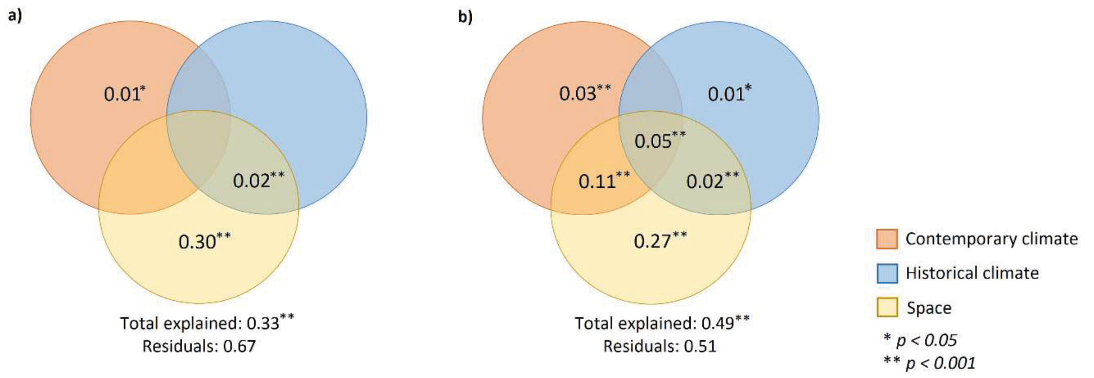

**Figure 6**. Venn's diagram depicting the results from variation partitioning considering the influences of contemporary climate, historical climate, and spatial dynamics on extinction (a) and colonization (b) rates for phyllostomid assemblages.

## DISCUSSION

Global biodiversity gradients are complex and the result of responses of organisms to contemporary factors such as climate, edaphic characteristics, environmental heterogeneity, or biotic interactions (Field et al. 2009; Brown 2014). More recently, it has been increasingly better appreciated that spatial patterns of contemporary biodiversity also result from historical events occurring long ago or evolutionary processes in operation since the inception of particular clades (Ricklefs 1987; Rolland et al. 2014; Meseguer & Condamine 2020). Indeed, important forms of spatial variability characterizing phyllostomid bats are conspicuous gradients in species extinctions and colonization rates at local scales (Figure 1). Extinction rates are greater than colonization rates and both are highly correlated, peaking toward the periphery of the geographic distribution of this family (Figure 1; Figure 2), regions where local extinction is higher than local colonization. Variation in extinction rates was not related to either the underlying gradient of species richness or strongly related to gradients of contemporary or historical climate (Figures 4a and 5a). The extinction rate did have a strong spatial component, but not one strongly related to contemporary or past climate (Figure 5a). In contrast the colonization rate was strongly related to the underlying gradient of species richness and more strongly related to both historical and contemporary climate (Figures 4b and 5b). Biodiversity gradient of Phyllostomidae in the Neotropics appear to be more related to the historical pattern of colonization than historical patterns of extinction.

## Differences between Northern and Southern hemispheres

Extinction rates were higher than colonization rates, exhibited significant spatial structure, peaked toward the periphery of the geographic range of Phyllostomidae but did not follow climatic gradients. Extinction rates were strongly spatially autocorrelated and most similar at the closest spatial distances. Such a pattern suggests relatively high background rates of extinction that likely are important contributors to variation in species composition of phyllostomids at the local level. In addition, the peak in extinction rates is at higher latitudes than the peak in colonization rates and this is more prominent in the Northern Hemisphere. While both rates peak in the subtropics, such a pattern suggests that extension of the geographic extent of Phyllostomidae is strongly facilitated by elevated rates of colonization but geographic extent is ultimately determined by elevated local extinction rates.

In the northern hemisphere, there is an abrupt transition zone between the Nearctic and Neotropics characterized by substantial topographic relief causing discontinuity in the extension of tropical forests (Ortega & Arita 1998, Lopez-Gonzalez et al. 2015). Phyllostomids occurring in or nearby the transition zone between the Nearctic and Neotropics in North America are mostly endemics able to thrive in these environments, such as species belonging to the genera *Macrotus*, *Musonycteris* and *Choeronycteris* (Ortega & Arita 1998; Arita 2014). In this region, tropical primarily deciduous forest as well as distribution of many species of Phyllostomidae are restricted to lower elevations and topographic relief serves to fragment these forests. Topographic relief and associated fragmentation of lowland tropical forest probably imposed filters on bat species occurrences in this region (Ortega & Arita 1998; Arita 2014). Moreover, this may also contribute to increased rates of extinction caused by lack of adaptations of most phyllostomids that allow persistence at high elevation sites, thereby restricting them to lower elevations. Overall, higher local extinctions in the subtropics and the failure of many species to establish there appear to be clearly linked to tropical niche conservatism and its implications to the structure of temperate assemblages of different organisms (e.g. Meseguer & Condamine 2020). Fragmentation of lowland tropical forest may also decrease population sizes and increase extinction rates of local populations. Increased colonization rates are also observed in this region, probably reflecting relictual distributions of the few phyllostomid species capable of colonizing and occurring therein. Indeed, subtropical regions in Mexico exhibit substantial and elevated beta-diversity

(Rodriguez & Arita 2004, Lopez-Gonzalez et al. 2015). Future and more direct analyses addressing how beta-diversity is related to colonization and extinction rates is warranted.

Spatial patterns of colonization rates in the northern Neotropics are stronger compared to those at the southern limits of distribution of phyllostomids and likely reflects historical contingency of the phyllostomid radiation in the New World. A South American origin of most Phyllostomidae subfamilies followed by dispersal towards North America is a highly supported hypothesis (Arita et al. 2014; Rojas et al. 2016. Davalos et al. 2020). These colonization patterns potentially indicate a role of the 'out of the tropics' hypothesis, where latitudinal gradients in species diversity result from species originating in tropical environments and colonizing new regions at high latitudes. Indeed, species occurring in the Nearctic-Neotropics interface belong to different evolutionary lineages making the bat fauna in this region phylogenetically overdispersed, a pattern that can be tracked back to multiple dispersal events (Villalobos et al. 2013). Moreover, the Isthmus of Panama formed only recently (~ 3million years ago, O'dea et al. 2016) and its absence likely slowed colonization into the North America. One reason for elevated rates of colonization at high latitudes in North America may be the recent nature of this process. Moreover, elevated rates of local colonization and extinction in the subtropics of North America might reflect that these two processes have yet to reach equilibrium in this region.

Comparatively weaker gradients in colonization and extinction are observed towards the southern limits of phyllostomid distributions in South America. Environmental heterogeneity, in particular topographic relief, is less pronounced at high latitudes in the southern hemisphere and this region still retains tropical characteristics exemplified by the extension of Atlantic Forest that reaches to even 30º S latitude. This may facilitate the occurrence of tropical species in these regions outside the tropics, reducing variability in gradients of colonization and extinction.

## Insights from the Caribbean

One important characteristic of the New World bat fauna is the impact that resulted from species exchange between the mainland and insular environments, especially from Caribbean islands (Davalos 2007, Rojas et al. 2016; Tavares et al. 2018). As such, more than relevant to understanding biogeographical and evolutionary effects underlying latitudinal gradients in phyllostomid biodiversity, are patterns of extinction and colonization in insular environments, particularly the assembly of the bat fauna of the Caribbean islands. Phyllostomid diversity in these islands is primarily structured in terms of extinction gradients and to a lesser extent by colonization (Figure 1). Local extinctions are much more pronounced in the Lesser Antilles than in the Greater Antilles (Figure 1). Islands of the Lesser Antilles generally are smaller in size than those of the Greater Antilles (Willig et al. 2009) and this combined with patterns of extinction rates for the Caribbean suggest an important role of island size on local extinction dynamics if interpreted through the lens of the Equilibrium Theory of Island Biogeography (MacArthur &Wilson 1967). Moreover, increased extinctions in Caribbean assemblages likely are a result of anthropogenic impacts driving local extinctions that have disrupted the bat faunas of these islands, driving them away from the expected equilibrium based on models considering the effects of time and its relationships with speciation, extinction and colonization dynamics in insular environments (Valente et al. 2017). Colonization rates, however, are similar and relatively low across islands. Inter-island dispersal occurs frequently in the Caribbean and is facilitated by bat flight capabilities (e.g. Carstens et al. 2004; Meyer et al. 2009, Fleming et al. 2010). Thus, because of dispersal, extinction rates may be more important than colonization rates to determining bat species composition on islands in the Caribbean.

The Antilles have been important to phyllostomid diversification and have provided the continental New World with distinct phyllostomid lineages in a process of reverse colonization (Davalos 2007, Rojas et al. 2016; Tavares et al. 2018). Nonetheless, the low colonization rates adjacent to the Caribbean in North and South America suggest that Lesser and Greater Antilles and surrounding islands have exerted little influence in the form of colonization on the assembly of local mainland assemblages where the influence of colonization by Antillean bats would be expected to be higher simply due to spatial proximity between these systems.

### Endogenous versus exogenous spatial processes

Over large geographical extents, barriers to dispersal limit pervasiveness of movement of individuals across the landscape. Also, ecological drift characterized by stochastic fluctuations in population demographics at local scales may ultimately trigger extinctions, increasing the importance of this process in determining the composition of local communities (Vellend 2010). Nonetheless, bats are mobile organisms and increased mobility can increase rescue effects affecting local abundance and persistence of species (Brown & Kodric-Brown 1977) thereby reducing local extinction rates. Similarly, bat species differ in dispersal abilities due to their wing properties (Norberg & Rayner 1987, Varzinczak 2020), and this may dictate their ability to move across the landscape and, therefore, their importance to colonization rates. Indeed, effects of mobility are deeply intertwined with both colonization and extinction rates and comparisons of these rates among more and less mobile organisms are necessary to better understand their impacts on biodiversity gradients.

Based on characteristics of the biology of phyllostomids such as a tropical origin and radiation (Arita et al. 2014; Tavares et al. 2018), and effects of tropical niche conservatism on their distribution (Stevens 2011; Villalobos et al. 2013), a prediction of a key role of contemporary climate as a primary driver of extinction and colonization dynamics seemed valid. However, while climate is related to colonization rates, it was not related to local extinction rates. Moreover, the largest fraction of variation of both colonization and extinction rates was the unique spatial fraction. Therefore, an important question that remains is: what processes are actually accounting for the largest and most significant fraction of variation in colonization and extinction rates, namely the unique spatial effect? Spatial effects on bat distributions have emerged to variable, yet strong, degrees across spatial and ecological scales of biological organization (Stevens et al. 2007; Varzinczak et al. 2018; Stevens et al. 2020). The process of extinction is often characterized as a contagion (Channell & Lomolino 2000) that can manifest as an endogenous spatial process. Endogenous spatial processes are those that result from internal dynamics of populations or communities such as conspecific attraction, dispersal limitation, Allee effects, or mass effects (Chapman et al. 2009). In contrast, exogenous spatial processes are those that are spatially structured and exert an effect on populations or communities. Examples of exogenous spatial processes are numerous types of responses of species and ultimately assemblages to spatially structured environmental gradients (Legendre 1993). If colonization and extinction rates estimated here were endogenous spatial processes then variation underlying much of the spatial fraction and likely all of the unique spatial fraction would be due to these spatial contagia. Indeed, spatial autocorrelation is positive and stronger at finer spatial scales (Figure 4).

Nevertheless, distinguishing whether spatial structure results from endogenous or exogenous spatial processes can be difficult. For example, important exogenous spatial structure from unmeasured environmental variables can disguise as endogenous spatial structure. Such a case would result in a large unique spatial component because it would not be related to an environmental characteristic because that environmental characteristic went unmeasured. Thus, it is difficult to distinguish whether rates of colonization and extinction measured here result from endogenous or unmeasured exogenous spatial processes. We were comprehensive in our measurement of climate, however. Both present and past climates were estimated. Moreover, present climate was estimated from numerous perspectives involving magnitude and variability, both intra- and interannually. It is unlikely that an influential climate variable went unmeasured. We did not measure productivity or topography, environmental characteristics that can be important determinants of biodiversity gradients (Field et al. 2009; Badgley et al. 2017). Nonetheless, because topography and productivity are often strongly correlated with aspects of temperature and precipitation, especially at large spatial extents (Currie 1991, Hawkins et al. 2003, Field et al. 2009), effects of elevation and productivity would be integrated into the spatially and non-spatially structured environmental variation fractions. It is unlikely that topography or productivity would define the unique spatially structured component. Indeed, much more attention should be given to understanding the nature of variation in local colonization and extinction rates, how they contribute to variation in local species composition and whether they represent endogenous spatial processes of important consequence to contemporary gradients of biodiversity.

## CONCLUSIONS

Extinction and colonization act as primary biogeographical forces that generate and maintain diversity gradients. Indeed, their balance determines how species from a particular regional pool are assembled into local communities. By addressing their joint dynamics, we were able to determine how they have likely influenced present-day biodiversity gradients in a clade of tropical origin. Rates of local phyllostomid extinction and colonization are latitudinally structured, with increased importance in the subtropics where extinction is higher. This may have been an important determinant of extent of the geographic distribution of this family in the New World, and appears to support the hypothesis of tropical niche conservatism and reflect the complex biogeographical history observed during phyllostomid radiation and distribution. As with much of the related research aiming to uncover determinants of biodiversity gradients, our results still leave room for additional questions about how biogeography, through extinction and colonization, has affected how local diversity is structured. What mechanisms are we missing to explain the residual variations not captured by the variables included in our variation partitioning? What kind of processes (endogenous or exogenous) are contained within the pure spatial fractions and how are they related to the internal structure of species distributions and local incidences? Answering these questions is of increased importance to understand extinction and colonization dynamics at local scales and the emergence of broad-scale biodiversity gradients.

The evolutionarily and biogeographically unique history of Phyllostomidae facilitates tests of biologically meaningful predictions on how the diversification process contributes to gradients of biodiversity. Historical processes have important impacts on biogeographic patterns and their impacts on local assemblages need to be better understood to be able to interpret major forces underlying biodiversity gradients and processes determining local limits to species distributions. Nevertheless, the endeavor of identifying how these processes are structured and give rise to biodiversity gradients for groups with distinct biogeographical histories remains. We highlight that any general understanding of biodiversity gradients will require an explicit consideration of primary biogeographical processes, both historical and contemporary, that are responsible for generating spatial variations in biodiversity in this case represented by local extinction and colonization dynamics. Considering that at broad geographical extents multiple processes appear to act in concert, understanding them and their interactions is of utmost importance to understand patterns and processes shaping global gradients of biodiversity.

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# APPENDIX

Table S1. **Loadings from Principal Component Analysis on bioclimatic variables.**

| | PC1 | PC2 | PC3 |
|---|---|---|---|
| Bio1 | 0.0029 | 0.0005 | 0.0076 |
| Bio2 | -0.0017 | 0.0010 | -0.0012 |
| Bio3 | 0.0085 | -0.0029 | 0.0255 |
| Bio4 | -0.1289 | -0.0410 | -0.5615 |
| Bio5 | 0.0006 | -0.0008 | 0.0008 |
| Bio6 | 0.0055 | -0.0016 | 0.0134 |
| Bio7 | -0.0048 | 0.0007 | -0.0126 |
| Bio8 | 0.0017 | 0.0020 | 0.0032 |
| Bio9 | 0.0036 | -0.0028 | 0.0097 |
| Bio10 | 0.0014 | -0.0005 | 0.0007 |
| Bio11 | 0.0045 | 0.0006 | 0.0144 |
| Bio12 | 0.8752 | 0.1603 | -0.1418 |
| Bio13 | 0.1098 | 0.0113 | 0.1980 |
| Bio14 | 0.0328 | 0.0101 | -0.1538 |
| Bio15 | -0.0131 | -0.0034 | 0.0945 |
| Bio16 | 0.3101 | 0.0369 | 0.5239 |
| Bio17 | 0.1140 | 0.0246 | -0.4907 |
| Bio18 | 0.1254 | 0.5485 | -0.2337 |
| Bio19 | 0.2813 | -0.8183 | -0.1471 |

# CONCLUSÕES

## *Uma síntese geral*

Nesta tese, abordamos diferentes perguntas e testamos diferentes hipóteses relacionadas à Macroecologia e Macroevolução em morcegos Neotropicais da família Phyllostomidae. De maneira geral encontramos que, embora a maior parte das espécies possuam nichos climáticos tropicais, suportando origem tropical e conservação tropical de nicho, verificamos no Capítulo 1 múltiplas mudanças para diferentes climas, principalmente em espécies evolutivamente recentes comparadas com as mais antigas da família. Além disso, no capítulo 2 observamos ausência de influência ou até mesmo influência negativa da dispersão no tamanho de distribuição geográfica das espécies, refletindo claramente os efeitos da escala filogenética em que conduzimos os testes. Por fim, no capítulo 3 observamos que há gradientes de extinção e colonização e que eles contribuíram para os padrões macroecológicos de diversidade neste grupo.

## *Perspectivas*

Uma das características mais conspícuas em ecologia e evolução é a necessidade de escolha de uma escala operacional para o trabalho, seja ela espacial, temporal, ou ainda filogenética (e.g. Graham et al. 2018). Aqui utilizarmos morcegos da região Neotropical como objeto de estudo e os resultados trazidos nessa tese certamente ampliam o horizonte e trazem novas contribuições sobre a importância de diferentes mecanismos ecológicos e evolutivos e suas implicações nos padrões de distribuição das espécies e da diversidade biológica. De fato, alguns dos resultados aqui apresentados foram surpreendentes por serem contraintuitivos em relação às teorias abordadas ou, especificamente, contrários ao que seria esperado dado a biologia do grupo.

Assim como destacado no Prefácio sobre a dificuldade em escolher temas para pesquisa, há também a infelicidade de uma tese de doutorado atualmente durar apenas 4 anos. Os capítulos apresentados nesta tese representam uma pequena fração de conhecimento e, ao mesmo tempo, levantam novas perguntas e áreas ainda por serem exploradas e que, infelizmente, não foram possíveis de serem aprofundadas ou abordadas no presente estudo. Seria impossível concluir esse trabalho sem ressaltar questões adicionais e possibilidades complementares que permanecem. Pensando nos morcegos

Phyllostomidae, talvez o que chama mais atenção é a grande diversidade ecológica no grupo. Seria essa ampla diversidade um catalizador das discrepâncias encontradas em relação aos padrões esperados? Por exemplo, a evolução da dieta nesta família parece ter afetado o grupo de diferentes formas (e.g. Rojas et al. 2011, 2012; Monteiro & Nogueira 2011), conforme abordamos nas discussões dos três capítulos. De fato, apenas espécies de morcegos desta família na região Neotropical são frugívoras e, além disso, esta família é a que apresenta maior diversificação de hábitos alimentares. Qual terá sido então o papel direto da diversificação da dieta na evolução do nicho climático, no tamanho de distribuição geográfica, e nos padrões de colonização e extinção em amplas escalas? Apesar da classificação da dieta das espécies ainda ser uma questão permanente e de difícil resolução, essa é uma questão que merece atenção dadas implicâncias nas dinâmicas relacionadas ao grupo. Além disso, qual seria o papel da latitude nos padrões de diversificação do nicho climático (e.g. Lawson & Weir 2014)? Considerando a origem tropical da família, bem como a dependência do clima para as espécies, uma hipótese que surge seria a de observar maiores taxas de evolução de nicho climático em espécies ocorrendo fora dos trópicos, em maiores latitudes, o que possibilitaria expansão da distribuição geográfica da família para essas regiões.

Quase metade das espécies de morcegos do Novo Mundo pertencem à família Phyllostomidae. Ou seja, uma ampla diversidade. Assim, outra pergunta que surge leva em conta o papel de outras variáveis na diversificação e evolução do grupo. Seria possível que a diversificação dos nichos climáticos tenha afetado a diversificação em número de espécies da família? Há evidências de que os nichos climáticos podem acelerar a diversificação no número de espécies (Cooney et al. 2016; Reis et al. 2018), e o clima tem sido apontado como fator crucial para estes morcegos (Stevens 2004, Villalobos et al. 2013).

Por fim, por que as regiões diferem no número e em quais espécies as compõe? Variações nas dinâmicas de extinção e colonização local indicam que abordar aspectos biogeográficos é promissor para responder à essa pergunta, conforme levantamos no capítulo 3. No entanto, quais outras variáveis estão sendo omitidas das análises para que ainda haja uma ampla proporção residual ou ampla proporção contida nas dinâmicas consideradas espaciais? Ou de fato estamos observando dinâmicas relacionadas à neutralidade nos sistemas biológicos, principalmente quando levamos em conta dinâmicas acontecendo em um contexto espacial e envolvendo extinção e colonização na escala das comunidades? É totalmente plausível que a influência conjunta de mecanismos determinísticos e neutros esteja por trás das dinâmicas em diferentes escalas. Se há uma coisa que os resultados desta tese ressaltam é a multiplicidade dos processos que podem estar relacionados aos padrões de diversidade e distribuição das espécies no espaço e no tempo. Quantificar a proporção e importância de cada um torna-se então o grande desafio.

Dada a relevância dos temas abordados aqui, esperamos que os resultados dessa tese, bem como a discussão levantada em diferentes tópicos, inspirem novas abordagens e ideias para que os resultados aqui tragam novas perguntas e questões para diferentes grupos. Considerando a urgência em entender o que gera a biodiversidade para podermos maximizar sua preservação, essas questões são de extrema urgência e importância.

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