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Pleistocene distribution of MacConnell's Bat (Phyllostomidae) suggests intermittent connections between Amazonia and Atlantic Forest

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The historical biogeography of the major South American forested biomes has long intrigued scientists. Paleoclimatic events during the last 130 thousand years promoted connections between forested biomes in the Neotropical region, leading to disjunct distributions of some of the biota. In this context, MacConnell's Bat, *Mesophylla macconnelli*, appears to represent a forest-restricted species with its current distribution bisected by dry areas. In this study, we infer past connections between the Amazonia and Atlantic Forest using MacConnell's Bat and ecological niche models. We obtained 681 records of the species, and estimated its potential distribution during the Last Interglacial (LIG), Last Glacial Maximum (LGM), and current periods. Our generated models, based on 260 filtered occurrence records, had very good predictive power, with AUC and TSS adherence values above 0.9. Temperature seasonality and annual precipitation had the highest relative contribution. The potential distribution for the LIG suggested a suitable area connection between the southwestern Atlantic Forest and southern Cerrado and Amazonia. The potential distribution in the LGM suggests range expansion toward northern and eastern Amazonia. The current and inferred past distributions of *Mesophylla macconnelli* suggest at least two periods of past connection between Amazon and Atlantic Forest. This pattern is found in other forest-associated vertebrates in South America, suggesting that Pleistocene climatic cycles were central to the generation of disjunct distributions in the region.

La biogeografía histórica de los principales biomas de selvas de América del Sur ha intrigado a los científicos durante mucho tiempo. Los eventos paleoclimáticos durante los últimos 130 mil años promovieron conexiones entre biomas de selvas en la región neotropical, lo que llevó a distribuciones disjuntas de parte de la biota. En este contexto, el murciélago de MacConnell, *Mesophylla macconnelli*, parece ser un ejemplo de especie restringida al bosque con su distribución actual atravesada por las áreas secas de América del Sur. En este estudio, inferimos las conexiones pasadas entre la Amazonía y el Bosque Atlántico utilizando modelos de nicho ecológico y el murciélago de MacConnell. Obtuvimos 681 registros de la especie, y estimamos su distribución potencial durante el Último Interglacial (LIG), Último Máximo Glacial (LGM) y períodos actuales. Nuestros modelos generados, basados en 260 registros de ocurrencia filtrados, tuvieron muy buen poder predictivo, con valores de adherencia AUC y TSS superiores a 0.9. La estacionalidad de la temperatura y la precipitación anual tuvieron la mayor contribución relativa. La distribución potencial en el LIG sugiere una conexión de área adecuada entre el suroeste del Bosque Atlántico y el sur del Cerrado y la Amazonía. La distribución potencial en el LGM sugiere una expansión del rango hacia el norte y el este de la Amazonía. Las distribuciones actuales y pasadas inferidas de *Mesophylla macconnelli* sugieren al menos dos períodos de conexión pasada entre la Amazonía y el Bosque Atlántico. Este patrón se encuentra en otros vertebrados asociados a los bosques en América del Sur, lo que sugiere que los ciclos climáticos del Pleistoceno fueron fundamentales para la generación de distribuciones disjuntas en la región.

Keywords: Fruit-eating bat; *Mesophylla macconnelli*; Last Glacial Maximum; Last Interglacial; Stenodermatinae.

Introduction

The Amazonia and Atlantic Forest are the two major tropical rainforests of South America (Hueck 1972). These two large forests are currently separated by the dry forests of the Caatinga, the Chaco shrublands and the savanic Cerrado (Ab'Saber 1977; Solari *et al.* 2012). Paleoclimatic, biogeographic, and niche modeling studies have suggested intermittent past connections between Amazonia and Atlantic Forest, during the last interglacial period (Wang *et al.* 2004; Sobral-Souza *et al.* 2015; Ledo and Colli 2017).

Traditionally, the disjunct distribution pattern of rainforest-adapted mammals has been considered as evidence that the Amazonia and Atlantic Forest were connected (Coimbra-Filho and Câmara 1996; de Vivo 1997). Notable examples include medium and large arboreal species such as the red-handed howler (*Alouatta belzebul*), the kinkajou (*Potos flavus*), and the silky anteater (*Cyclopes didactylus*). The existence of similar patterns for small mammals, such as bats, has been little investigated (but see Costa 2003 and Rocha *et al.* 2015). To explain these biogeographic patterns, hypotheses often invoke the fragmentation of forests that occurred during the Pleistocene (Vanzolini and Williams 1970; Martins 1971; Haffer 1997). One way to test this hypothesis is to obtain paleoclimatic data from this epoch (Vanzolini and Williams 1970), and to examine the divergence times and amount of genetic divergence among the involved species (Moritz 2000).

MacConnell's Bat, *Mesophylla macconnelli* Thomas, 1901, is one of the smallest species of frugivorous bat in the world, weighing 6 to 8 g (Solari *et al.* 2019). This tent-roosting bat has been recorded from the rainforests of Nicaragua, to the Amazon basin in South America, reaching northern Bolivia and western Brazil (Arroyo-Cabrales 2008). However, recent studies extended its range to the Atlantic Forest and to the Cerrado of, respectively, eastern and central Brazil (Zortéa and Tomaz 2006; Gregorin *et al.* 2014). With the new records, the disjunct distribution pattern of *M. macconnelli* is strikingly similar to what has been observed for other forest-dependent mammals that occur in both the Amazonia and Atlantic Forest. A recent study identified 127 species of mammals that occur in both ecosystems, suggesting them as good candidates for phylogeographic studies that investigate this putative vicariant pattern, but *M. macconnelli* was not mentioned by the authors (Machado *et al.* 2021).

Using paleoclimatic data and ecological niche models, we estimate the past potential distribution of *M. macconnelli* during the last 130,000 years. Our objective is to assess the potential for past connections between the Amazonia and Atlantic Forest that may explain the apparently disjunct distribution pattern of the species.

Materials and methods

Mesophylla macconnelli *occurrence data.* Occurrence records for *M. macconnelli* were obtained from museum specimens held in the Instituto de Desenvolvimento Sustentável Mamirauá (IDSM), Natural History Museum, London (BMNH), Universidade Federal de Lavras (CMUFLA), Museu de Zoologia da Universidade de São Paulo (MZUSP), Universidade Federal de Mato Grosso (UFMT), Universidade Federal de Minas Gerais (UFMG), and National Museum of Natural History, Smithsonian Institution (USNM).

We also incorporated secondary records in online databases such as Global Biodiversity Information Facility – GBIF (www.gbif.org), SpeciesLink (http://splink.cria.org.br/) and Instituto Chico Mendes de Conservação da Biodiversidade – ICMBio (https://biodiversidade.icmbio.gov.br/). Additionally, existing records in the scientific literature were included (see Supplementary material 1).

Our database went through a process of cleaning and removing records with missing or repeated geographic coordinates and records outside the known geographic distribution of the species. After this procedure, a single occurrence record was randomly selected within an area equivalent to two cells of resolution of the environmental layers (each cell = 9.24 x 9.24 km; Velazco *et al.* 2019). This was to prevent sampling bias from propagating biased ecological niche models.

Environmental Data. The Neotropical region was determined as our study area to calibrate our model (Olson *et al.* 2001), considering the wide distribution range of *M. macconnelli* in Central and South America, and potential dispersion ability. Ecological niche models (ENM) for current conditions were adjusted based on 19 bioclimatic variables related to temperature and precipitation (Hijmans *et al.* 2005). Detailed information about each variable is available in Supplementary material 2, Table S1. Paleoclimatic conditions for the Last Interglacial (LIG; 120,000 to 140,000 years ago) and Last Glacial Maximum (LGM; ~21,000 years ago) were obtained from the PaleoClim.org database (Brown *et al.* 2018). All variables were obtained at the resolution of 5 arc-minutes and were cropped to the same extent of our study area. To avoid overfitting and to assess correlation among biotic variables a Pearson's correlation test was applied to the bioclimatic variables. This test was performed using the "raster.cor.matrix" function of the ENMTools package in R (Warren *et al.* 2021). From each pair of strongly correlated variables, *i. e.*, $r \geq |0.7|$, we kept the one with the highest biological meaning for the species (Da Silva *et al.* 2020). After this procedure, five variables remained: Mean Diurnal Range (bio2), Temperature Seasonality (bio4), Max Temperature of Warmest Month (bio5), Annual Precipitation (bio12), and Precipitation Seasonality (bio15).

Modelling procedures. We used four algorithms to construct ENM: Bayesian Gaussian – GAU (Golding 2014), Maximum Entropy - MXD (Phillips *et al.* 2017), Random Forest – RDF (Liaw and Wiener 2001), Support Vector Machine – SVM (Karatzoglou *et al.* 2004). The same number of pseudoabsences were generated to fit the models (Barbet-Massin *et al.* 2012). An environmental restriction method was used to allocate the pseudoabsences in climatically different regions of the environmental space in which the species occurs (Engler *et al.* 2004). We used the checkboard method to calibrate and evaluate models. This method consists of dividing the geographic space into blocks, splitting the occurrences into two groups, one for model adjustment and another for model evaluation (Roberts *et al.* 2017).

Model performance was evaluated using two metrics: Area Under Curve (AUC) Receiver Operating Characteristic (ROC; Phillips *et al.* 2006), and True Skill Statistic (TSS = sum of sensibility and specificity – 1; (Allouche *et al.* 2006). AUC ranges from 0 to 1, where values closer to 1 indicate a good distinction between presence and pseudoabsence records. Whereas, values below 0.5 indicate that the model did not perform better than expected by chance (Fielding and Bell 1997). TSS ranges from -1 to +1, values above 0.7 indicate models with statistically reliable performance (Allouche *et al.* 2006; Zhang *et al.* 2015). To reduce the uncertainty in the prediction generated by the use of distinct algorithms, we build ensemble models (Araújo and New 2007). The ensemble model was calculated selecting models with TSS value greater than the average TSS value of all algorithms and then calculated the mean suitability model between all algorithms that met this condition. Finally, we projected the current climatic suitability conditions for *M. macconnelli* under past climatic conditions (LIG, ~ 120,000 years ago; LGM, ~21,000 years ago) for each algorithm and then created an ensemble model for each period. For LGM we also used different climatic conditions estimated by 3 distinct Atmosphere-Ocean General Circulation Models (AOGCMs): CCSM4, MIROC-ESM e MPI-ESM-P (Hijmans *et al.* 2005). Specifically, for LGM models a final model was created by calculating the average suitability values obtained through the three AOGCM's ensemble models. Finally, we use the threshold that maximizes the sum of sensitivity and specificity (Liu *et al.* 2005), to turn continuous suitability values into binary presence-absence models.

To test the hypothesis of connection between the distribution of *M. macconnelli* through Amazon and Atlantic Forest, we overlapped the ensemble models of the three time periods. In this way we could identify areas of climate stability, or areas of connection and reconnection that may have been lost in the species current distribution.

Results

Current records. We found 681 records of *Mesophylla macconnelli* in Central and South America and after the filtering process, 260 unique records were used in modelling procedures. Most of the records (565, 83.21 %) are located east of the Andes, but some (114, 16.79 %) occur west of the Cordillera (Figure 1). The majority of the records (627, or 92.7 %) are in Tropical & Subtropical Moist Broadleaf Forests, of which 625 are in the Amazon rainforest and

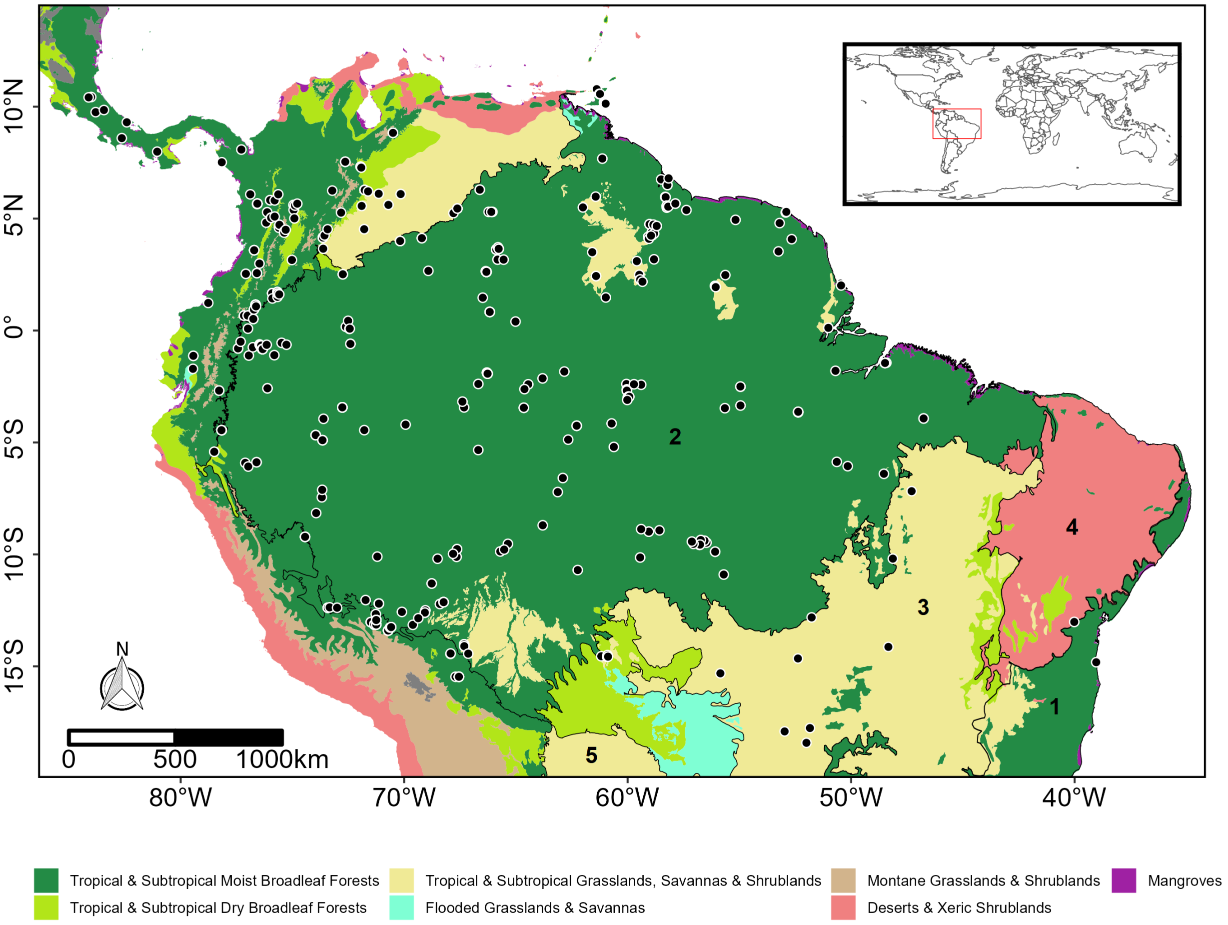

Figure 1. Occurrence records of MacConnell's Bat (*Mesophylla macconnelli*) in the American continent. Colors on map indicate the biomes classified according to Olson (2001). Numbers show the ecoregions of the Neotropical Realm following Olson (2001) (1 – Atlantic Forest, 2 – Amazon Forest, 3- Cerrado, 4 - Caatinga, 5 - Chaco).

two from the Atlantic Forest. Some records are from the savanna formations of the Cerrado (33, or 4.85 %) and Tropical and Subtropical Dry Broadleaf Forests (21, or 3.08 %). Of all the occurrence points, 85.5 %, or 590, are from altitudes below 900 m above sea level. The remaining 91 localities are from above 900 m, with a maximum altitude of 2,355 m from the cloud forests of Cuzco, Perú.

Geographic distribution models. The evaluation values for the ensemble models, AUC = 0.998 SD=0.028 and TSS = 0.980 SD = 0.027, indicated good performance of the models – for more information about other evaluation metrics and evaluation for each algorithm see Supplementary Material 3. The temperature seasonality (45.3 %) and annual precipitation (36.4 %) provided the highest relative contributions to model *M. macconnelli* distribution. The current distribution model shows a wide area with high suitability values in the Amazon and in the central and northern areas of the Atlantic Forest, with suitable areas also in the Cerrado biome (Figure 2).

During all three projected periods (*i. e.,* LIG, LGM, and Current), the Chocó region, Panama, western Amazonia, and central/northern Atlantic Forest were estimated as highly suitable areas for *M. macconnelli* (Figure 2). The projected distribution for the LIG shows that areas in the southern part of the Amazon, in the Cerrado, and in the Atlantic Forest had suitable climatic conditions, showing a possible connection between the southwestern Atlantic Forest and southern Cerrado (Figure 2). During the LGM we infer a great expansion of appropriate areas towards northern and eastern Amazonia (Figure 3). This occurs concomitantly with a retraction of the southern distribution of the species. This pattern suggests the loss of the connection between the appropriate areas of the Cerrado and Atlantic Forest.

Discussion

The current distribution of *M. macconnelli* seems to be associated with humid forested areas. Even in localities within the Cerrado biome, such as Serra do Roncador (Mato Grosso state, Brazil), and Serranópolis (Goiás state), it has been captured in forest enclaves and riparian areas (Pine *et al.* 1970; Handley 1976; Zortéa and Tomaz 2006). In fact, these transitional areas and forest enclaves in the Cerrado are known to harbor some typical Amazonian mammalian taxa such as *Ateles marginatus, Callicebus vieirai*, *Chiroderma trinitatum, Didelphis marsupialis, Gracilinanus peruanus, Marmosops noctivagus,* and *Saguinus niger* (Lacher and Alho 2001; Antunes *et al.* 2021; Garbino *et al.* 2015, 2020; Lima-Silva *et al.* 2022; Semedo *et al.* 2022). Besides forests, temperature seasonality, calculated as the standard deviation of monthly temperature averages, seems to be a limiting factor for the species. This is evident, as *M. macconnelli* occurs in tropical areas between 10° N and -18° S, where there are no abrupt temperature oscillations (Figure 1).

The species is absent in the cooler areas of the Atlantic Forest of southern and southeastern Brazil, which have more seasonal climates than the central Atlantic Forest, where the species occurs. This hypothesis seems more plausible than assuming that the drier formations of the Cerrado acted as a barrier, especially because the Amazon and Atlantic Forest were recently connected by riparian corridors in the region of Goiás, Brazil, where *M. macconnelli* has been recorded (Ab'Saber and Costa-Junior 1950). The dependence on leaves modified into tents to use as daytime roosts (Rodriguez-Herrera *et al.* 2007; Garbino and Tavares 2018) may help explain why the distribution of *M. macconnelli* is intimately associated with forests.

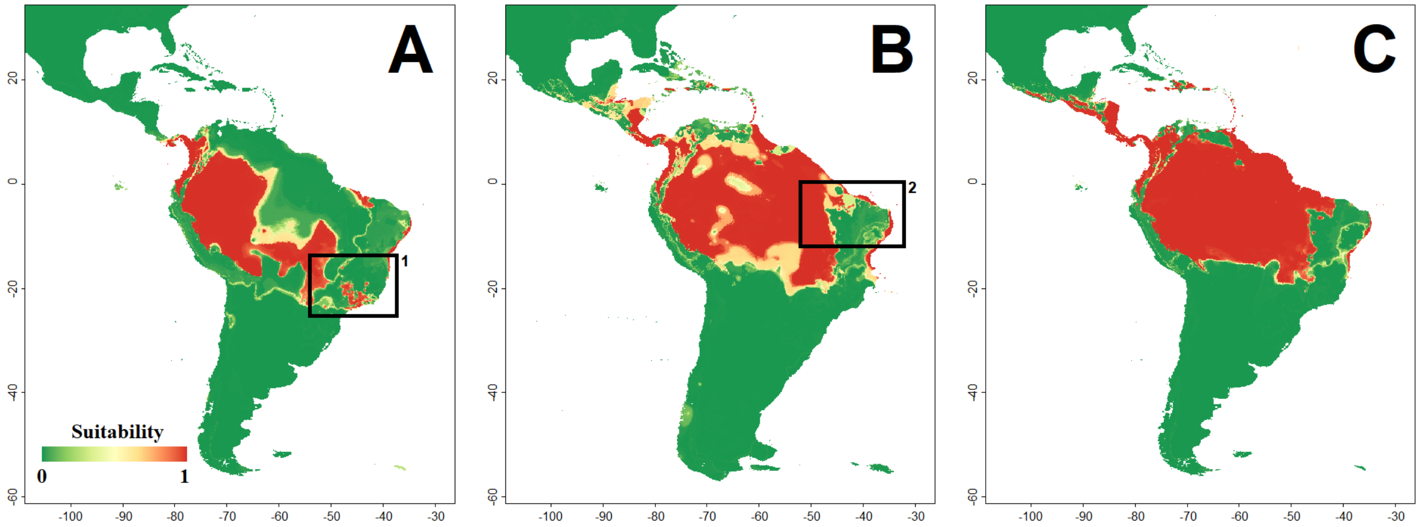

Figure 2. Ecological niche models (ENM) projections of MacConnell's Bat (*Mesophylla macconnelli*) during the (A) Last Interglacial (LIG) – ~120 000 years ago, (B) Last Glacial Maximum (LGM) - ~21 000 years ago, and (C) current distribution. Ensemble models were adjusted based on four algorithms (Bayesian Gaussian – GAU (Golding 2014), Maximum Entropy - MXD (Phillips *et al.* 2017), Random Forest – RDF (Liaw and Wiener 2001), Support Vector Machine – SVM (Karatzoglou *et al.* 2004). Black empty squares indicate possible connections between Atlantic Forest and Amazonia on LIG (1) and LGM (2). The color scale indicates suitability values for *M. macconnelli* occurrence.

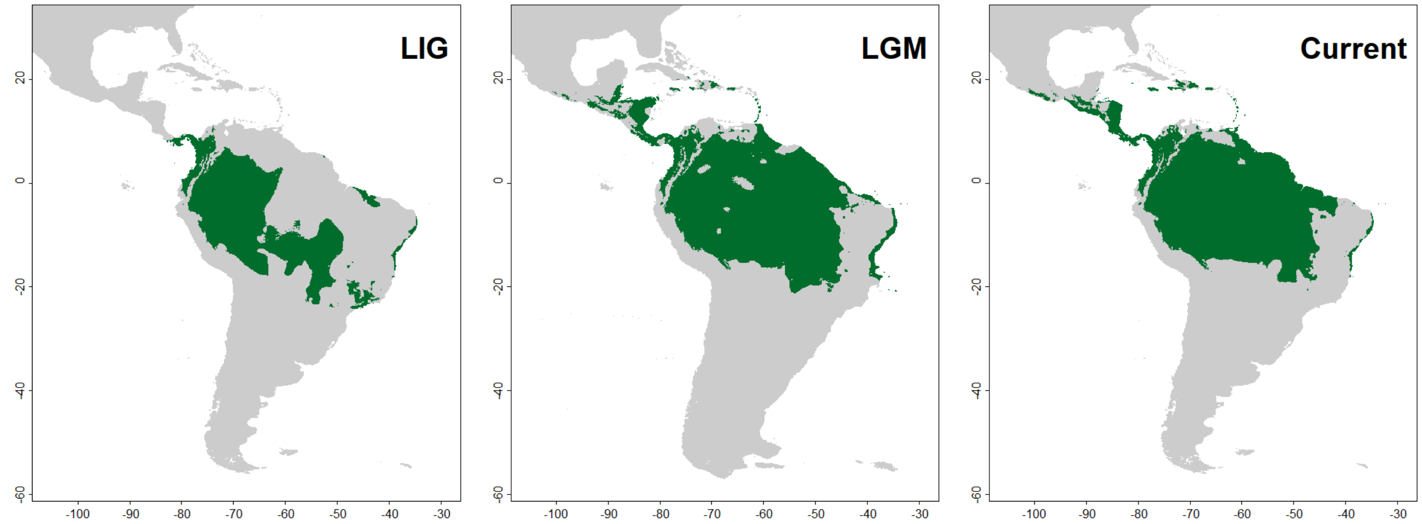

Figure 3. Distributional binary maps of MacConnell's Bat (*Mesophylla macconnelli*) during the transition from the Last Interglacial period to the Last Glacial Maximum (LIG - LGM) and from the Last Glacial Maximum to the current period (LGM - Current). Ensemble models were adjusted based on four algorithms (Bayesian Gaussian – GAU (Golding 2014), Maximum Entropy - MXD (Phillips *et al.* 2017), Random Forest – RDF (Liaw and Wiener 2001), Support Vector Machine – SVM (Karatzoglou *et al.* 2004). Green areas indicate predicted species occurrence. Species absence throughout the study area is represented in gray.

According to our model, in the last interglacial period the Andes cordillera acted as a barrier for the species, with suitable areas on the east and west slopes but not in the Andean highlands and plateaus (Figure 2). However, the model suggests that the current period allows for more permeability between the transandean and cisandean populations, which may explain the low genetic structure found in the species (Tavares *et al.* 2022). The model considering the current distribution also indicates that the populations from the Atlantic Forest (eastern Brazil) are disconnected from the Amazonia/Cerrado populations (Figures 2 and 3). Future surveys in poorly sampled areas where the presence of *M. macconnelli* is not known, may show if the absence of the species in these areas is due to sampling deficiencies.

Some historical biogeographic patterns observed in other vertebrates are suggested in our projected distribution of *M. macconnelli*. The western Amazonia, an area considered an important center of diversity for vertebrates (Hoorn *et al.* 2010; Oliveira *et al.* 2017), is recovered as suitable in all three periods (Figure 3). The area where the species occurs in the Atlantic Forest, with climatic stability during all three periods (Figures 2, 3), is known as "Bahia Refuge" and has been identified as a stable climatic area based on other species of vertebrates (Carnaval and Moritz 2008).

The modelled distribution of *M. macconnelli* suggests at least two historical periods of connection between the Atlantic Forest and the Amazonia (Figure 2). In the Last Interglacial, where the climate was more humid, our models recovered suitable areas to the southwest (Figure 2). In the Last Glacial Maximum, when the climate was cooler and drier, our model recovered a northeastern connection of *M. macconnelli*'s range (Figure 2A, B). These two connections may have formed repeatedly over the Pleistocene climatic oscillations, with the southwest connection between Amazon and Atlantic forests the more ancient and frequent, and the northeast the more recent one (Ledo and Colli 2017). This scenario may have led to the apparent disjunct distribution of *M. macconnelli*. In another forest-dwelling frugivore bat, *Carollia perspicillata*, there is genetic evidence of geographically restricted intraspecific lineages that reflect Pleistocene glacial cycles (Pavan *et al.* 2011).

Future phylogeographic studies, including genetic samples from the Cerrado of central Brazil, the Atlantic Forest of eastern Brazil, and from eastern and southern Amazonia, will allow verification of the pattern suggested here. We also suggest that niche modelling based on past climates may open new venues of investigation on the biogeographic patterns of the Neotropical fauna.

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