

RESEARCH ARTICLE

Potential mammalian species for investigating the past connections between Amazonia and the Atlantic Forest

Arielli Fabrício Machado^{1,7}*, Camila Duarte Ritter^{2,3}*, Cleuton Lima Miranda^{4,7}‡, Yennie Katarina Bredin⁵‡, Maria João Ramos Pereira⁶‡, Leandro Duarte¹‡

1 Phylogenetic and Functional Ecology Lab (LEFF), Post-Graduation Programme in Ecology, Universidade Federal do Rio Grande do Sul (UFRGS), Porto Alegre, Rio Grande do Sul, Brazil, **2** Eukaryotic Microbiology, University of Duisburg-Essen, Essen, Germany, **3** Grupo Integrado de Aquicultura e Estudos Ambientais, Departamento de Zootecnia, Universidade Federal do Paraná, Curitiba, Paraná, Brazil, **4** Post-Graduation Program in Zoology, Museu Paraense Emílio Goeldi, Universidade Federal do Pará (UFPA), Belém, Pará, Brazil, **5** Faculty of Environmental Sciences and Natural Resource Management, Norwegian University of Life Sciences, Ås, Norway, **6** Bird and Mammal Evolution, Systematics and Ecology Lab (BiMa-Lab), Post-Graduation Programme in Animal Biology and Post-Graduation Programme in Ecology, Universidade Federal do Rio Grande do Sul (UFRGS), Porto Alegre, Rio Grande do Sul, Brazil, **7** Laboratório de Evolução e Genética Animal (LEGAL), Universidade Federal do Amazonas (UFAM), Manaus, Amazonas, Brazil

* These authors contributed equally to this work.

‡ These authors also contributed equally to this work.

* ariellifm@gmail.com (AFM); kmicaduarte@gmail.com (CDR)



OPEN ACCESS

Citation: Machado AF, Ritter CD, Miranda CL, Bredin YK, Ramos Pereira MJ, Duarte L (2021) Potential mammalian species for investigating the past connections between Amazonia and the Atlantic Forest. *PLoS ONE* 16(4): e0250016. <https://doi.org/10.1371/journal.pone.0250016>

Editor: Paulo Corti, Universidad Austral de Chile, CHILE

Received: December 24, 2020

Accepted: March 29, 2021

Published: April 9, 2021

Peer Review History: PLOS recognizes the benefits of transparency in the peer review process; therefore, we enable the publication of all of the content of peer review and author responses alongside final, published articles. The editorial history of this article is available here: <https://doi.org/10.1371/journal.pone.0250016>

Copyright: © 2021 Machado et al. This is an open access article distributed under the terms of the [Creative Commons Attribution License](https://creativecommons.org/licenses/by/4.0/), which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited.

Data Availability Statement: All relevant data are within the manuscript and its [Supporting Information](#) files.

Abstract

Much evidence suggests that Amazonia and the Atlantic Forest were connected through at least three dispersion routes in the past: the Eastern route, the central route, and the Western route. However, few studies have assessed the use of these routes based on multiple species. Here we present a compilation of mammal species that potentially have dispersed between the two forest regions and which may serve to investigate these connections. We evaluate the present-day geographic distributions of mammals occurring in both Amazonia and the Atlantic Forest and the likely connective routes between these forests. We classified the species per habitat occupancy (strict forest specialists, species that prefer forest habitat, or generalists) and compiled the genetic data available for each species. We found 127 mammalian species presently occurring in both Amazonia and the Atlantic Forest for which, substantial genetic data was available. Hence, highlighting their potential for phylogeographic studies investigating the past connections between the two forests. Differently from what was previously proposed, the present-day geographic distribution of mammal species found in both Amazonia and the Atlantic Forest points to more species in the eastern portion of the dry diagonal (and adjoining forested habitats). The Central route was associated with the second most species. Although it remains to be seen how this present-day geography reflects the paleo dispersal routes, our results show the potential of using mammal species to investigate and bring new insights about the past connections between Amazonia and the Atlantic Forest.

Funding: AFM was supported by a doctoral fellowship (grant 141008/2016-4) provided by the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq). LD is a member of the National Institute for Science and Technology (INCT) in Ecology, Evolution and Biodiversity Conservation, supported by MCTIC/CNPq (proc. 465610/2014-5) and FAPESP (proc. 201810267000023). LD and MJRP were supported by CNPq Productivity Fellowships (grants 307527/2018-2 and 311297/2018-8). CDR thanks the financial support from Alexander von Humboldt Foundation.

Competing interests: The authors have declared that no competing interests exist.

Introduction

Amazonia and the Atlantic Forest are among the most diverse tropical rainforests in the world [1, 2]. Biogeographical patterns of these South American megadiverse forests have been investigated since the 19th century [3, 4]. Currently, the forests are separated by the 'dry diagonal' comprising the Caatinga, the Cerrado and the Dry Chaco ecoregions. However, different sources of evidence, including biogeographical [5–10], palynological [11–13], and geological [14] show that these forests have been connected in the past.

The origin of the tropical rainforests in South America is dated to at least 65 million years ago (mya) [15–17]. Since then, these forests have undergone several changes, expanding and retracting. From the Oligocene (~ 23 mya) to the Pliocene (~ 3 mya), successive tectonic events led to the Andean uplift, restricting the entry of rainfall from the Pacific into the interior of the continent resulting in a drier climate with a forest reduction and the expansion of savannas, giving rise to the dry diagonal, and, consequently, the separation of Amazonia and the Atlantic Forest [15, 18–20]. Furthermore, there is evidence of more recent forest expansions and retractions caused by Quaternary climatic fluctuations, such as glacial cycles during the Pleistocene and recurrent periods of extreme rainfall during the Holocene [11–14]. Indeed, the high rates of vegetation cover changes in the dry diagonal and the Atlantic Forest [21, 22] suggest not just ancient but also recent connections and disruptions between Amazonia and the Atlantic Forest [9].

Although the time scale of changes in South American rainforests can be extremely large, making it difficult to accurately punctuate the total possible connective routes between these forests, three routes have been suggested: one through the forests of North-eastern Brazil (the northeast route), another through the gallery forest of the Brazilian Cerrado ecoregion (the central route) and a third through the forests of the Paraná Basin, the Moist Chaco, and the Pantanal (the southeast-northwest route) [5, 6, 23]. To facilitate the nomenclature, we will hereafter refer to these routes as the Eastern, Central, and Western routes.

According to Por [5], the Western route would have been the most ancient connection and would have occurred more often over time, followed by the Eastern route. In a study aimed to test Por's hypothesis [5], Ledo & Coli [10] reviewed the literature for molecular evidence of connections between Amazonia and the Atlantic Forest for ca. 60 vertebrates, including 10 mammals. They found more studies that evidenced connections through the Western route (with most evidence dating from the Miocene) compared to the Eastern route (dated to the Pleistocene) [10]. However, this result could be biased due to the poor sampling in the north-eastern region [24]. Thus, it remains uncertain whether the Western route was indeed the most frequently formed connection and therefore the most used route in the past.

Furthermore, although three routes have been proposed, some authors considered only two major routes. For example, both Batalha-Filho et al. [8] and Ledo & Colli [10], did not consider the Central route as an independent route but included it as part of the Eastern route. However, the Central route has been well documented as a potential separate migratory pathway in the literature for both animals and plants [5, 6, 23, 25, 26]. Moreover, investigating the phylogeography of eight small mammals, Costa [6] found a larger number of related, small mammals occurring in Amazonia and the Atlantic Forest that could have come through the Central route. However, this study was limited to small mammals which have specific traits, such as limited dispersion ability. Considering more species with different traits and divergence times may therefore add further evidence on the past use of the Central connection, as well as for the other routes, and their time scales.

Other molecular studies investigate the role of the historical connections between Amazonia and the Atlantic Forest in terms of dispersion and diversification of several animal species,

such as mammals [6, 27], birds [8], reptiles [28–30], amphibians [31] (for a literature revision of vertebrate evidence see [10]), and insects [32]. Yet, the totality of species that may evidence past connections between Amazonia and the Atlantic Forest has not been mapped and such information is particularly scarce for mammals. In this context, a compilation of available data, including geographic, ecological, and genetic data, for species that could be used to test the past connections between Amazonia and the Atlantic Forest could assist future investigations of the aforementioned hypotheses.

Here we aim to identify mammal species of potential use for investigating the past connections between Amazonia and the Atlantic Forest through geographical distribution patterns, habitat preferences, and genetic data. For this, we created a list of mammal species that occur in both Amazonia and the Atlantic Forest and we identify their possible past use of the three proposed connective routes. We highlight the potential of using these species to further investigate the frequency and time scales of the connective routes. We believe that our results may serve as a basis for future biogeographic studies considering different mammalian taxa to test hypothesis about connection routes between Amazonian and Atlantic forests.

Material and methods

We considered mammal species to be of interest for investigating the past connections between Amazonia and the Atlantic Forest if they fulfilled the following two criteria: they had to 1) occur in both Amazonia and the Atlantic Forest, and 2) use forest habitat. For these species, we quantified the genetic data available in GenBank [33]. We also identified potential past connective routes between Amazonia and the Atlantic Forest by investigating the distribution maps for each species.

Geographical data

Geographical distribution maps of forest mammalian species from Amazonia and the Atlantic Forest were compiled from the IUCN—International Union for Conservation of Nature [34]. We used the IUCN distribution data since these maps are created and verified by specialists based on occurrence records already checked and thus restrict species occurrences to areas with presumably suitable habitat where the species is known, following a precautionary principle to guide conservation efforts [35, 36]. Although these maps were designed for conservation purposes and recent studies suggest new methods for improving the IUCN maps and classifications [37, 38], these maps have proved to be an important source of information for many macroecological studies [39–44] and represent the most complete currently available species distribution maps for different mammal taxon.

To identify the mammalian species that occur in the two regions, Amazonia and the Atlantic Forest, the IUCN maps were overlaid on the Ecoregion maps [45] using the Amazonian and the Atlantic Forest limits, through the *gIntersection* function of the R package ‘rgeos’ v. 0.5.5 [46] in R v. 3.6.3 [47]. Subsequently, only species with occurrences in both Amazonia and the Atlantic Forest were selected. The predefined identifications based on the overlaid IUCN occurrence maps were revised using the annotated list of mammals in Brazil [48] since this reference agrees with current geographical and genetic data available in the databases used in this study.

Habitat classification

We selected solely species that are associated with forests by accessing the IUCN information on species habitat use through the *rl_habitats* function of the R package ‘rredlist’ v. 0.6.0 [49]. We generated a scale of habitat preference for each species from forest specialist to generalist,

as this is key information for studies about the connective routes between Amazonia and the Atlantic Forest. We based this scale of habitat preference on the detailed text about species' habitat and ecology, available in the IUCN database [34] and additional literature reviews [50–56]. The criteria used for classifying the species according to habitat were as follows: 1) Strict forest specialists (SF), encompassing species that only occur in forests; 2) Species that prefer forest habitat (PF), encompassing species that use not only forested habitats but prefer these environments; or 3) Generalists (G) encompassing species that use both forests and open environments. Then, we used a Pearson's Chi-squared test to assess the relationship between the species' habitat preferences and the routes that they used through the *chisq.test* function in the R package 'stats' v. 3.6.3 [47].

Genetic data

We compiled genetic data for each species from the Genbank database [33]. Data compilation was done in January 2020, by registering the amount of molecular data available (nucleotide sequences) for each species. The genetic data was used to assess the taxonomic representativeness (i.e., which taxonomic groups represented the highest availability of published genetic data) and, consequently, their potential usefulness in evaluating the past existence and use of connections between Amazonia and the Atlantic Forest.

Using the quantile function of the R package 'stats' [47] we created categories to denote the availability of genetic data and assess the potential usefulness of the mammalian species. We considered species with one to 22 nucleotide sequences in Genbank to have low availability of genetic data; species with 23 to 74 sequences were considered to have regular genetic data; species with 75 to 225 sequences in Genbank were considered to have intermediate data availability; and species with 226 to over 1000 sequences were considered to have high data availability. Species without genetic data were not included in these categories, but are listed in the supplementary material (S1 Table). To compare the availability of genetic data among the different taxonomic groups, we also calculated the average number of sequences per species within each taxonomic order.

Identification of potential connective routes

To identify the connective routes that mammals potentially have used between Amazonian and Atlantic forests, we first delimited the geographical areas of the connections using Olson's ecoregion polygons overlaid on the ecoregion maps [45]. The area of the Eastern route was initially delimited using the boundaries of the Caatinga ecoregion, the transition areas between the Caatinga, the northern Cerrado and eastern Amazonia, the Babaçu Forest, and adjacent dry forests, which represent transition areas between Amazonia and the Atlantic Forest. The area of the Central route was selected using the limits of the Cerrado ecoregion (excluding the northern part, which was selected for the Eastern route). The area of the Western route was delimited using the boundaries of the Pantanal and the Chaco ecoregions, the transition areas between Amazonia and the Pantanal (such as Chiquitano Dry Forests), the southern Cerrado and the southwestern Atlantic Forest. For the final delimitation of these routes, we included additional potential areas based on the biogeographical [5–10], palynological [11–13], and geological [14] evidence of these past connections.

To explore how many species might have used each connective route, the delimited area for each route (Eastern, Central, and Western) was intersected with the species distribution maps using the function *gIntersection* in the R package 'rgeos' v. 0.5–5 [46]. Thereby, we quantified the total number of species associated with each route and the number of routes associated with each species. To visualize this result in the geographic space, we calculated the sum of rasters using the R package 'raster' v. 3.3 [57].

Results

We compiled geographic distribution maps, information about habitat preferences, and genetic data for 127 mammal species occurring in both Amazonia and Atlantic Forest. The mammals belonged to nine taxonomic orders: Didelphimorphia (7), Pilosa (4), Cingulata (5), Perissodactyla (1), Cetartiodactyla (3), Primates (2), Carnivora (12), Chiroptera (84) and Rodentia (9). For the information per species see [S1 Table](#). According to the IUCN, the geographic distribution of 113 of the species appear to be continuous between Amazonia and the Atlantic Forest, whereas the remaining 14 species present disjunct distributions ([S1 Table](#)).

For four species it was not possible to attribute a potential connective route, as these present extremely disjunct distributions between Amazonia and Atlantic Forest ([S1 Table](#)). From the 123 species with attributed routes, 19 species were associated with the Eastern route only, four species were associated with the Central route only and three species were associated with the Western route only ([Fig 1](#)). The remaining 97 species were associated with more than one connective route. Of these, 50 species were associated with all three connective routes, 30 species were associated with both the Eastern and the Central routes, 13 species were associated with

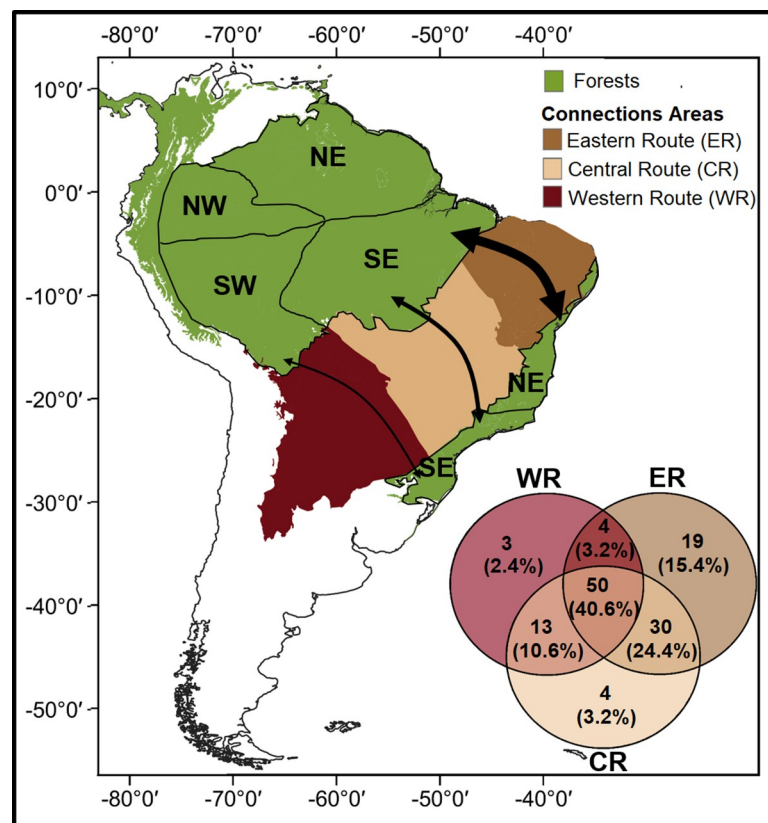


Fig 1. Distribution of tropical moist forests in South America (in green) and potential past dispersal routes (in browns) between Amazonia and the Atlantic Forest. Internal arrows represent connective routes between these forests through the Eastern route (dark brown), the Central route (light brown) and the Western route (reddish-brown). The width of the arrows represents the potential frequency by which the routes have been used in the past and is based on mammal species distributions. The coloured regions in the map were delimited using the Ecoregions shapefile from Dinerstein et al. (2017) licensed under CC-BY 4.0 (<https://creativecommons.org/licenses/by/4.0/>). The map was created in QGIS v.3.6.2 (<https://www.qgis.org/>) licensed under CC-BY-SA 3.0 (<https://creativecommons.org/licenses/by-sa/3.0/>) (<https://creativecommons.org/licenses/by/4.0/>). The Venn diagram shows the number of mammalian species that may have used the past connective routes between Amazonia and the Atlantic Forest, based on the IUCN geographical distribution maps.

<https://doi.org/10.1371/journal.pone.0250016.g001>

the Central and Western routes, and four species were associated with both the Eastern and Western routes (Fig 1). The distribution patterns of the species associated with each route, more than one route, or no attributed routes, can be seen in Fig 2.

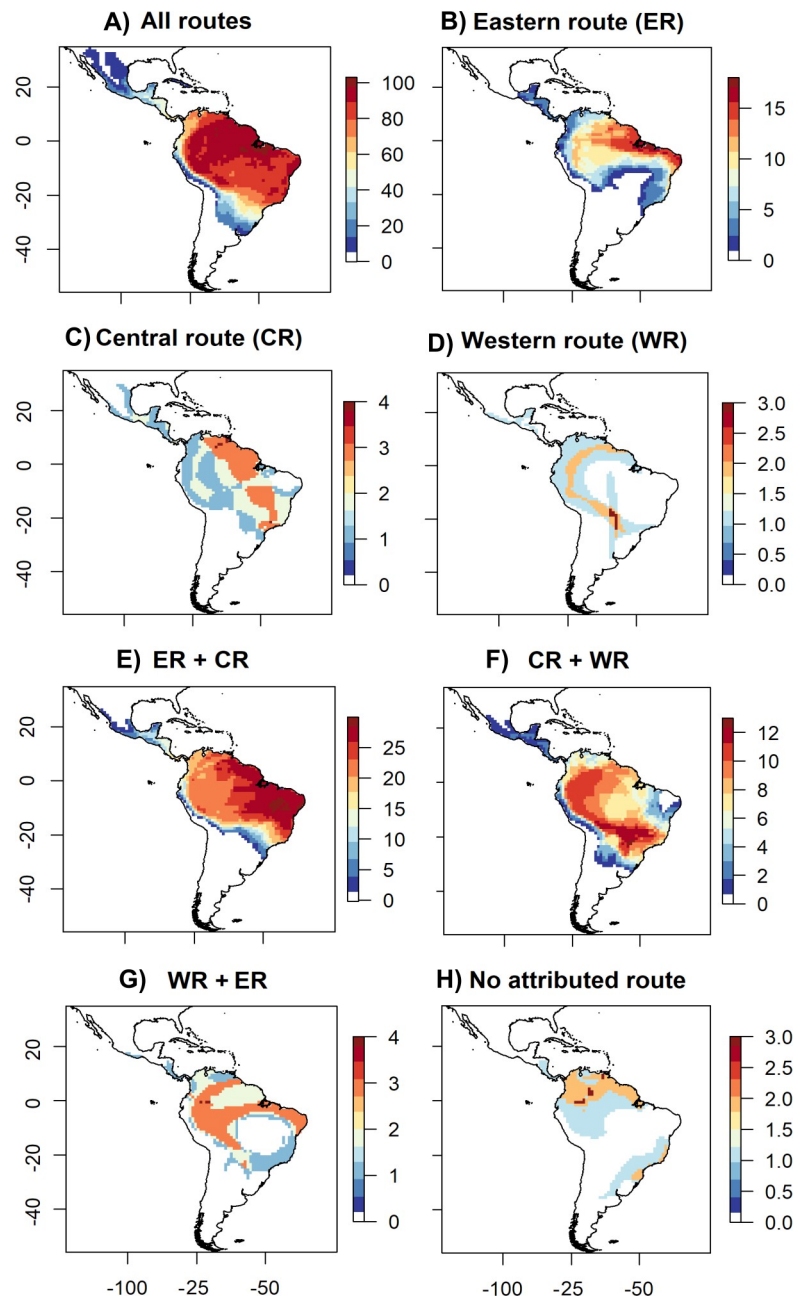


Fig 2. Overlap in mammal species distributions and tropical moist forest connective routes. The colour scale represents the number of species per pixel in the map. A) Overlap in species distributions with tropical moist forest habitat for all mammal species sampled in this study; B) Overlap in species distributions with the Eastern route; C) Overlap in species distributions with the Central route; D) Overlap in species distributions with the Western route; E) Overlap in species distributions with both the Eastern and Central routes; F) Overlap in species distributions with both the Central and Western routes; G) Overlap in species distributions with both the Western and Eastern routes; and H) Overlap in species distributions with no attributed route. Most species were associated with the Eastern route, followed by the Central route and finally the smallest number of species were associated with the Western route.

<https://doi.org/10.1371/journal.pone.0250016.g002>

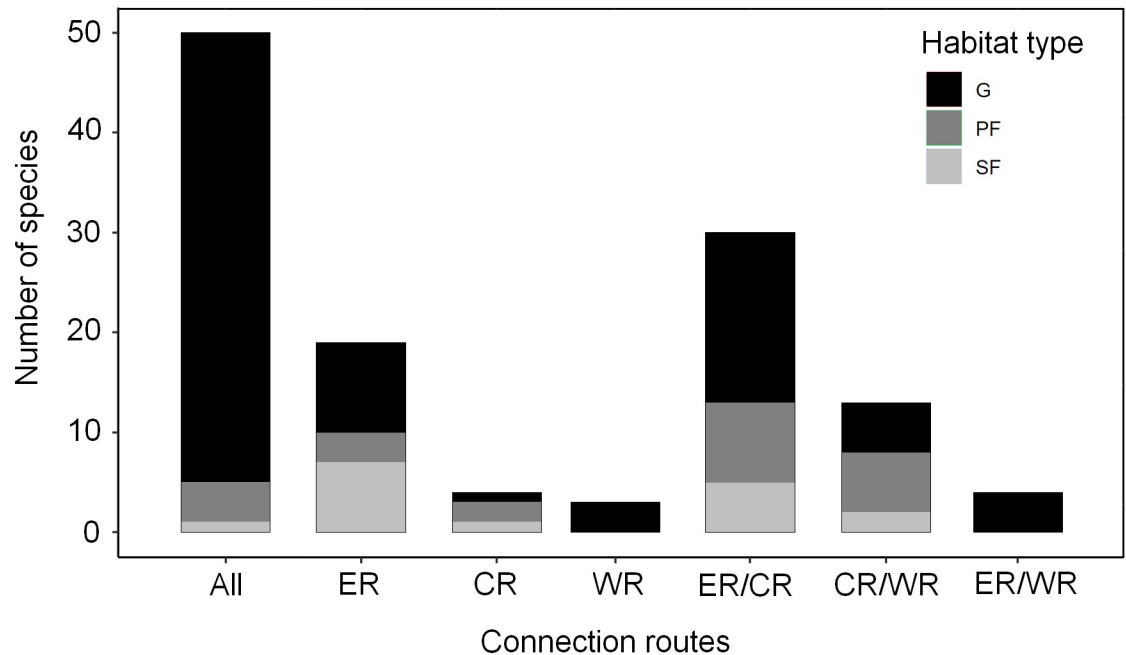


Fig 3. Number of mammalian species assumed to have dispersed by each of the connective routes between Amazonia and the Atlantic Forest. The routes are presented along the x-axis: Eastern route (ER), Central route (CR), and Western route (WR), and combinations of routes (ER + CR, ER + WR, CR + WR, and "All" for ER + CR + WR). The grayscale represents species habitat preferences where SF = Strict forest specialists, PF = Species that prefer forest habitat, and G = Generalists.

<https://doi.org/10.1371/journal.pone.0250016.g003>

In terms of habitat use, 17 species were classified as strict forest specialists (SF), 24 species preferred forest habitat (PF) and 86 species were generalists (G). From the 19 species associated with the Eastern route, seven species were SF, three PF and nine were G (Fig 3). From the four species associated with the Central route, one species was SF, two PF and one was G, whereas the three species associated with the Western route were G (Fig 3). From the 30 species associated with both the Eastern and the Central routes, five were SF, eight PF, and 17 were G (Fig 3). From the 13 species associated with the Central and West routes, two were SF, six PF and five were G, whereas the four species associated with the Eastern and Western routes were G. Finally, from the 50 species associated with all three connective routes; one was SF, four PF and 45 were G (Fig 3 and S1 Table). The result of the chi-square test for the habitat preference was significant ($\chi^2 = 35.255$, $df = 12$, $p\text{-value} = 0.0004$). Thus, we reject the null hypothesis, which stated that habitat preference was independent from choice of connective route.

Most of the species identified in this study as potentially useful for assessing the connections between Amazonia and the Atlantic Forest have large amounts of genetic data available in the investigated database (high or intermediate availability of genetic data) including different molecular markers (Fig 4 and S1 Table for total number of available molecular data and Genbank access link for each species). Twenty-six of the investigated species showed low availability of genetic data in Genbank, 34 species show regular genetic data availability, 33 intermediate and 31 high availability of genetic data (Fig 4 and S1 Table).

Considering the orders, the Cingulata and Chiroptera contained most of the available genetic data (averaging 1,000 and 590 sequences per species, respectively; Fig 5), followed by the Pilosa, Primates, Cetartiodactyla, Perissodactyla (averaging 330, 300, 220, 200 and 190 sequences per species respectively; Fig 5). The Didelphimorphia and Rodentia also showed a

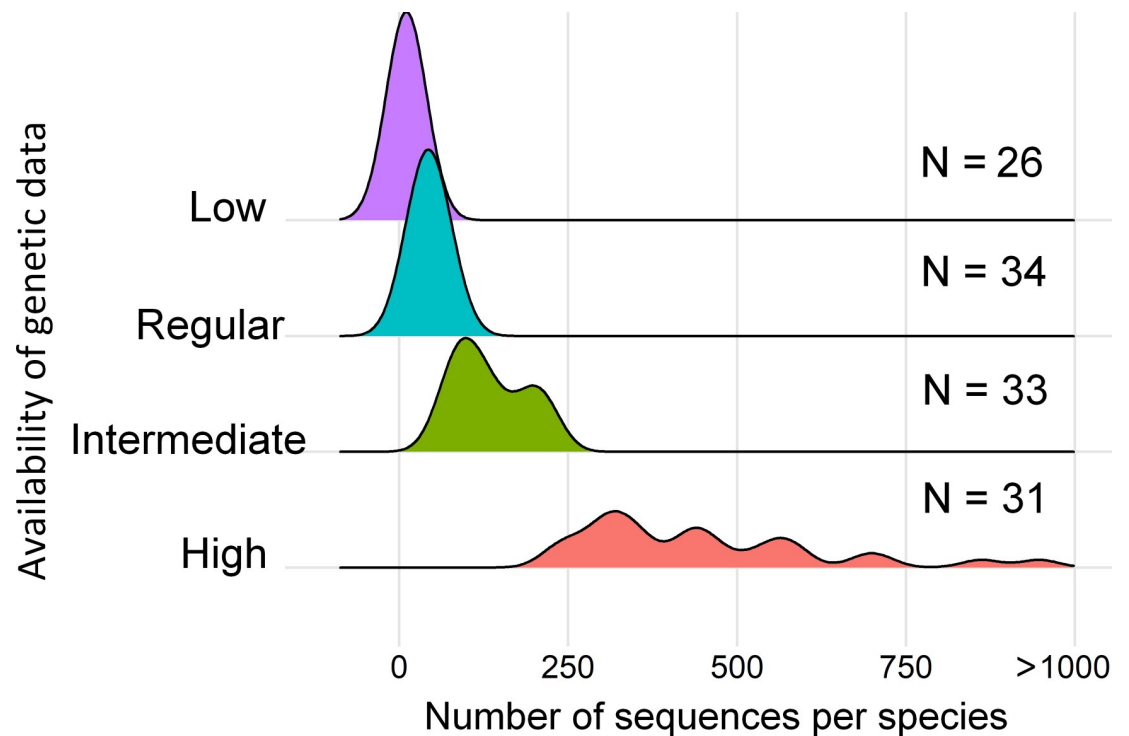


Fig 4. Availability of genetic data for mammalian species that occur in both Amazonia and the Atlantic Forest. Species with “Low” availability of genetic data have one to 22 sequences; Species with “Regular” availability of genetic data have 23 to 74 sequences; Species with “Intermediate” availability of genetic data have 75 to 225 sequences; and Species with “High” availability of genetic data have 226 to over 1000 sequences.

<https://doi.org/10.1371/journal.pone.0250016.g004>

considerable number of available nucleotide sequences (averaging 115 and 93 sequences per species, respectively: Fig 5). The availability of genetic data was high and intermediate for most orders. Some orders had regular data and few orders had low availability of genetic data (Fig 5 and S1 Table).

Discussion

Here we present an unprecedented list of mammalian species with potential for investigating the past connections between Amazonia and the Atlantic Forest. Previous studies, including data compilations, analysed a limited number of mammalian species [10]. We were able to include 127 species of mammals currently occurring in both Amazonia and the Atlantic Forest to add information about the potential past connections between these two ecoregions. We compiled information about the species’ distributions, habitat preferences, and the quantity of genetic data available. We show that mammal habitat use is significantly associated with their respective dispersal routes and that three routes have probably connected the two rainforest regions in the past. The species list compiled herein has the potential to subsidize future mammal phylogenetic and phylogeographic studies and to shed light on the temporal and spatial use of the connections between Amazonia and the Atlantic Forest in relation to the ecology and evolution of South American mammals.

By overlaying the present-day geographic distribution maps of the candidate species over the three proposed historic routes between Amazonia and the Atlantic Forest we show that most of the 127 mammalian species were associated with the Eastern route. These species also evidenced strikingly continuous distributions across the dry diagonal between the forest

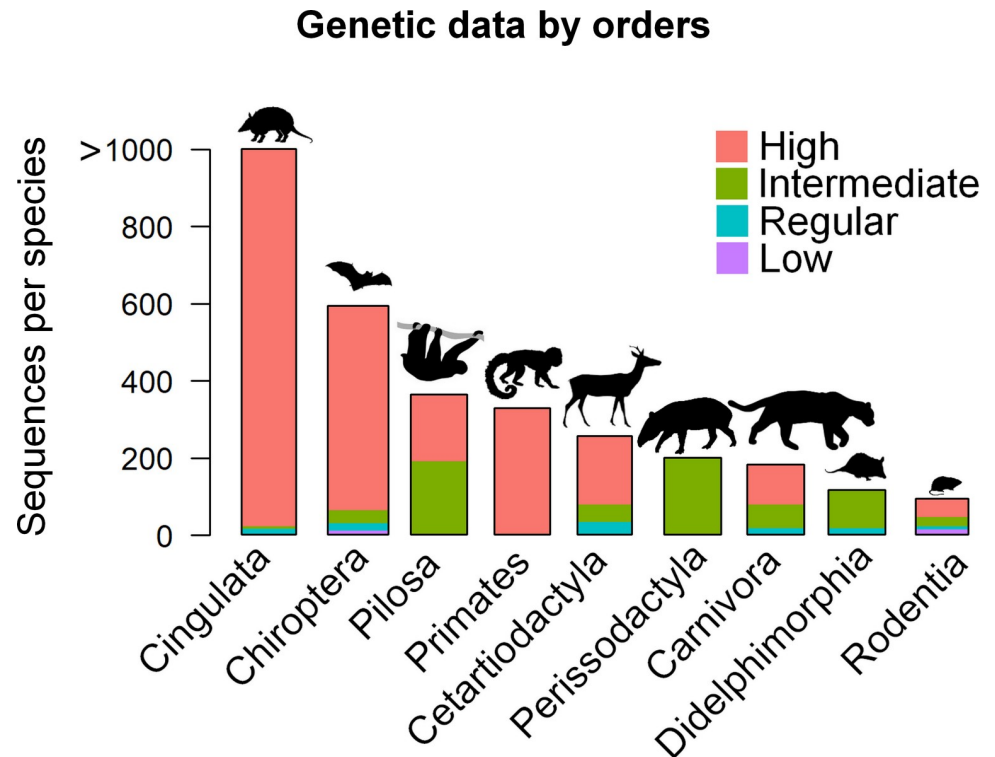


Fig 5. Availability of genetic data by order for species of mammals that occur in both Amazonia and the Atlantic Forest. The x-axis shows the mammalian orders and the y-axis shows the average number of sequences per species. Colours represent availability of genetic data. Animal silhouettes are reprinted from PHYLOPIC (<http://www.phylopic.org/>) under a CC-BY 4.0 license (<https://creativecommons.org/licenses/by/4.0/>), with permission from Michael Keesey, 2019.

<https://doi.org/10.1371/journal.pone.0250016.g005>

habitats—albeit biased toward the coast. Thus, their present-day geography provides a compelling indication that the Eastern route, with its possible access to coastal habitats, may have been preferred over the other routes. The Central route was associated with the second most species, and, contrary to previous suppositions, the Western route was associated with the fewest species. Because most data previously used to test the existence of the connective routes over time came from interspecific molecular evidence from a few species, and because most species split before the Plio-Pleistocene (~5 mya to 12 thousand years ago) [58], such data may have biased results toward older routes, e.g., toward the Western route which would have occurred for the first time at least between ~30 to 20 mya in the Oligo-Miocene [5, 8, 10]. In contrast, studies on paleo vegetation, pollen data and biogeographic approaches indicate that several past connections through the Eastern route could have occurred during the Pleistocene (~2.5 mya) [11–14, 21, 29, 59, 60]. Hence, these insights highlight a need of more intraspecific studies that look at the genetic divergence within multiple taxa since such studies may shed light on the complexity of the evolution and existence of the connections between Amazonia and the Atlantic Forest over time [61–64].

The Eastern and Western routes were associated with species that had a great variety of habitat preferences. Thus, considering that the current distribution patterns of most species reflect past dispersions, their past use of the connective routes seems related to the environmental heterogeneity of these areas. For instance, the present-day geographic distribution of most generalist species aligned with the Eastern route which passed through the Caatinga and the Cerrado/Caatinga transition, a region of high environmental heterogeneity [65, 66]. In

contrast, the Central route was predominantly associated with strict forest specialists or species that prefer forest habitat. As highlighted by Costa [6], the forest environments in the Cerrado ecoregion represent relic forest fragments from historic ecological corridors [67], which allow forest species to be present in the region. Hence, our results highlight the probable importance of the Central route as an independent past connection for several forest specialist species.

Although the Central route had already been considered a potentially independent route in some studies [5, 6, 23, 25], other studies based on regional climatic similarities, considered only two major connections between Amazonia and the Atlantic Forest [8, 10, 18]. Reconciling these views, one may argue that we found two major dispersal patterns with more species distributions through the eastern connections (i.e. through the northern Central route and the Eastern route combined) than through the western connections (i.e. through the southern Central route and the Western route combined). Still, our findings point to three independent connection routes. Hence, we believe that looking past present-day climatic similarities to include past environmental changes [11–13] and analyses of species with a wider range of habitat preferences could bring new insights about the past prevalence and use of the connections between Amazonia and the Atlantic Forest.

Many of the species that show extreme disjunct distributions, such as the four bat species in this study, may represent either sampling deficiencies or even cryptic diversity [68]. Hence, sampling deficiencies in the north-eastern dry diagonal, in addition to the non-inclusion of specimens deposited in museum collections or published records of species in this region [24] may have led to faulty estimates of the number of potential taxa that could have spread along the Eastern route. As new records appear with increased sampling effort through systematic biogeographic studies in this region, future reassessments will thus, almost certainly, find additional species, which evidence past dispersions along the Eastern route [69–73, 76]. For example, several recent studies have presented new records of common forest species, such as for marsupials [74–77] and rodents [78, 79] along the Eastern route. Hence, updating the known distributions of these species, and others, are crucial for correctly assessing the past connective routes between Amazonia and the Atlantic Forest.

According to the IUCN maps, used in our study, many mammalian species show continuous present-day distributions between Amazonia and the Atlantic Forest through deciduous and semi-deciduous forests in the interior of the dry diagonal. However, phylogeographic studies have revealed that some of these species, with seemingly continuous distributions, actually consist of currently isolated populations [e.g., 80]. Moreover, many isolated populations show evolutionary well-structured lineages with significant genetic divergence, suggesting that the taxonomic status of these species needs revision as they could represent species complexes [e.g., 6, 52, 62, 80]. Hence, further phylogeographic studies are necessary if we are to reveal whether these mammalian populations are indeed connected or isolated in function of the current fragmentation patterns of the South American forests. Furthermore, such studies could help identify population isolations of anthropic origin, for example in the highly fragmented Atlantic Forest remnants and the Amazonian arc of deforestation.

Indeed, as we continue to lose forest habitat, the landscape becomes increasingly fragmented. Unfortunately, the environmental protection system has hitherto failed to connect the forest environments between Amazonia and the Atlantic Forest [81]. Due to the stance and actions of the current Brazilian, federal government, which has inspired serious negligence of Brazilian environmental laws [82], actions to increase the connectivity between the two ecoregions are currently unlikely. Given the relationship that we observe between species' habitat preferences and their associations with past connection routes this is unfortunate since continued forest loss and habitat fragmentation could have dire consequences for the populations along these dispersal pathways.

The availability of genetic data for our 127 species, revealed that many of them would serve for assessing the existence and importance of the past connections between Amazonia and the Atlantic Forest. Depending on the geographic distribution of data, species with regular to high availability of genetic data could serve this purpose. Hence, this initial compilation can be extremely useful in facilitating more detailed evaluations and future phylogeographic explorations of the past connections between Amazonia and the Atlantic Forest. For instance, *Marmosa demerarae* and *Marmosa murina* had regular ($n = 47$ sequences) and intermediate ($n = 77$ sequences) genetic availability, but adequate geographic distribution of samples (totaling 31 and 39 localities along their respective ranges) and hence serve for investigating the Eastern and Central routes respectively (Machado et al., in prep.). An example of a species with low genetic availability ($n = 13$ sequences) but good geographic coverage (11 localities) was *Caluromys philander*. Increasing the number of sequences per locality would thus render *C. philander* a good candidate for investigating the Central route. For other species increasing the geographical coverage rather than the number of sequences per locality might be more important. Although most mammalian species had high availability of genetic data, it is noteworthy that the two groups with the highest availability of genetic data are groups of high public health interest [83]. This result therefore showcases the extreme importance of making scientific data available for the development of new studies that go beyond the focus areas of the projects that generated the data.

In conclusion, we present information about the distributions, habitat preferences, and availability of genetic data for 127 mammal species currently occurring in both Amazonia and the Atlantic Forest. These data will certainly help future phylogeographic and phylogenetic studies to unravel the evolutionary history of these mammals and the past connections between Amazonia and the Atlantic Forest. Furthermore, the initial data exploration presented herein shows that more species presently occur along the Eastern route. Thus, unlike previously thought, we hypothesise that the Eastern route may have been used by more taxa and may have occurred more frequently than the other routes in the recent past. However, further data curation is needed to test this hypothesis and it remains to be seen to what extent the present-day geography of the 127 mammals can inform us about the past dynamics of these megadiverse, and highly threatened, forests.

Supporting information

S1 Table. Potential mammal species for investigating the past connections between Amazonia and the Atlantic Forest with geographic, taxonomic, ecological and molecular data (including GenBank accession data).
(XLSX)

Acknowledgments

We thank Renan Maestri, Fabricio Villalobos and Thales R. O. de Freitas for their critical revision of this manuscript. We also thank Henry Hooghiemstra and one anonymous reviewer for their detailed and constructive comments, which thoroughly helped us improve this manuscript.

Author Contributions

Conceptualization: Arielli Fabrício Machado, Maria João Ramos Pereira, Leandro Duarte.

Data curation: Arielli Fabrício Machado, Cleuton Lima Miranda, Maria João Ramos Pereira.

Formal analysis: Arielli Fabrício Machado, Camila Duarte Ritter.

Investigation: Arielli Fabrício Machado.

Methodology: Arielli Fabrício Machado.

Project administration: Arielli Fabrício Machado.

Visualization: Camila Duarte Ritter.

Writing – original draft: Arielli Fabrício Machado.

Writing – review & editing: Arielli Fabrício Machado, Camila Duarte Ritter, Cleuton Lima Miranda, Yennie Katarina Bredin, Maria João Ramos Pereira, Leandro Duarte.

References

1. Mittermeier RA, Myers N, Thomsen JB, Da Fonseca GA, Olivieri S. Biodiversity hotspots and major tropical wilderness areas: approaches to setting conservation priorities. *Conservation Biology*. 1998; 12(3): 516–520.
2. Jenkins CN, Pimm SL, Joppa LN. Global patterns of terrestrial vertebrate diversity and conservation. *Proc. Natl Acad. Sci. USA*. 2013; 110: E2602–E2610. <https://doi.org/10.1073/pnas.1302251110> PMID: 23803854
3. Bates HW. Contributions to an insect fauna of the Amazon Valley: Lepidoptera: Heliconidae. *Transactions of the Linnean Society (London)*. 1981; 23: 495–566.
4. Wallace AR. On the monkeys of the Amazon. *Annals and Magazine of Natural History*. 1854; 14(84): 451–454.
5. Por FD. *Sooretama: the Atlantic rain forest of Brazil*. SPB Academic. The Hague: SPB Academic Publishing; 1992.
6. Costa LP. The historical bridge between the Amazonia and the Atlantic Forest of Brazil: a study of molecular phylogeography with small mammals. *Journal of Biogeography*. 2003; 30: 71–86.
7. Fouquet A, Loebmann D, Castroviejo-Fisher S, Padial JM, Orrico VG, Lyra ML, et al. From Amazonia to the Atlantic forest: Molecular phylogeny of *Phyzelaphryninae* frogs reveals unexpected diversity and a striking biogeographic pattern emphasizing conservation challenges. *Molecular phylogenetics and evolution*. 2012; 65(2): 547–561. <https://doi.org/10.1016/j.ympev.2012.07.012> PMID: 22842094
8. Batalha-Filho H, Fjeldså J, Fabre PH, Miyaki, CY. Connections between the Atlantic and the Amazonian forest avifaunas represent distinct historical events. *Journal of Ornithology*. 2013; 154(1): 41–50.
9. Sobral-Souza T, Lima-Ribeiro MS, Solferini VN. Biogeography of Neotropical Rainforests: past connections between Amazonia and Atlantic Forest detected by ecological niche modeling. *Evolutionary Ecology*. 2015; 29(5): 643–655.
10. Ledo RMD, Colli GR. The historical connections between the Amazonia and the Atlantic Forest revisited. *Journal of biogeography*. 2017; 44(11): 2551–2563. <https://doi.org/10.1111/jbi.13049>
11. de Oliveira PE, Barreto AMF, Suguio K. Late Pleistocene/Holocene climatic and vegetational history of the Brazilian caatinga: the fossil dunes of the middle São Francisco River. *Palaeogeography, palaeoclimatology, palaeoecology*. 1999; 152(3–4): 319–337.
12. Behling H, Arz HW, Pätzold J, Wefer G. Late Quaternary vegetational and climate dynamics in north-eastern Brazil, inferences from marine core GeoB 3104–1. *Quaternary Science Reviews*. 2000; 19(10): 981–994.
13. Auler AS, Wang X, Edwards RL, Cheng H, Cristalli PS, Smart PL, et al. Quaternary ecological and geomorphic changes associated with rainfall events in presently semi-arid northeastern Brazil. *Journal of Quaternary Science*. 2004; 19(7): 693–701.
14. Wang X, Auler AS, Edwards RL, Cheng H, Cristalli PS, Smart PL, et al. Wet periods in northeastern Brazil over the past 210 kyr linked to distant climate anomalies. *Nature*. 2004; 432(7018): 740–743. <https://doi.org/10.1038/nature03067> PMID: 15592409
15. Morley RJ. *Origin and evolution of tropical rain forests*. 1st ed. Chichester: John Wiley & Sons; 2000.
16. Jaramillo C, Hooen C, Silva SA, Leite F, Herrera F, Quiroz L, et al. The origin of the modern Amazonia rainforest: implications of the palynological and palaeobotanical record. In: Hooen C, Wesselingh FP, editors. *Amazonia, landscape and species evolution*. Hoboken: Wiley-Blackwell. 2010; pp. 317–334.
17. Wing SL, Herrera F, Jaramillo CA, Gómez-Navarro C, Wilf P, Labandeira CC. Late Paleocene fossils from the Cerrejón Formation, Colombia, are the earliest record of Neotropical rainforest. *Proceedings of*

- the National Academy of Sciences. 2009; 106(44): 18627–18632. <https://doi.org/10.1073/pnas.0905130106> PMID: 19833876
18. Bigarella JJ, Andrade-Lima D. Paleoenvironmental changes in Brazil. In: Prance GT, editor. *Biological Diversification in the Tropics*. New York: Plenum Press. 1982; pp. 27–40.
 19. Barreda V, Palazzesi L. Patagonian vegetation turnovers during the Paleogene-early Neogene: origin of arid-adapted floras. *The botanical review*. 2007; 73(1): 31–50.
 20. Hoorn C, Wesselingh FP, Ter Steege H, Bermudez MA, Mora A, Sevink J, et al. Amazonia through time: Andean uplift, climate change, landscape evolution, and biodiversity. *Science*. 2010; 330(6006): 927–931. <https://doi.org/10.1126/science.1194585> PMID: 21071659
 21. Werneck FP, Costa GC, Colli GR, Prado DE, Sites JW Jr. Revisiting the historical distribution of Seasonally Dry Tropical Forests: new insights based on palaeodistribution modelling and palynological evidence. *Global Ecology and Biogeography*. 2011; 20(2), 272–288.
 22. Costa GC, Hampe A, Ledru MP, Martinez PA, Mazzochini GG, Shepard DB, et al. Biome stability in South America over the last 30 kyr: Inferences from long-term vegetation dynamics and habitat modelling. *Global Ecology and Biogeography*. 2017; 27(3): 285–297.
 23. Oliveira-Filho AT de Ratter JA. A study of the origin of central Brazilian forests by the analysis of plant species distribution patterns. *Edinburgh Journal of Botany*. 1995; 52(02): 141–194.
 24. Carmignotto AP, Astúa D. Mammals of the Caatinga: Diversity, Ecology, Biogeography, and Conservation. In: da Silva JMC, Leal IR, Tabarelli M, editors. *Biodiversity, ecosystems services and sustainable development in Caatinga: the largest tropical dry forest region in South America*. Berlin: Springer-Verlag; 2017. Pp. 211–254.
 25. Silva JD. Distribution of Amazonian and Atlantic birds in gallery forests of the Cerrado region, South America. *Ornitologia neotropical*. 1996; 7(1): 1–18.
 26. Ledru MP. Late Quaternary history and evolution of the cerrados as revealed by palynological records. In: Oliveira PS, Marquis RJ, editors. *The Cerrados of Brazil: ecology and natural history of a Neotropical savanna*. New York: Columbia University Press. 2002. pp. 33–50.
 27. Machado LF, Loss AC, Paz A, Vieira EM, Rodrigues FP, Marinho-Filho J. Phylogeny and biogeography of *Phyllomys* (Rodentia: Echimyidae) reveal a new species from the Cerrado and suggest Miocene connections of the Amazonia and Atlantic Forest. *Journal of Mammalogy*. 2018; 99(2): 377–396.
 28. Pellegrino KCM, Rodrigues MT, James Harris D, Yonenaga-Yassuda Y, Sites JW Jr. Molecular phylogeny, biogeography and insights into the origin of parthenogenesis in the Neotropical genus *Leposoma* (Squamata: Gymnophthalmidae): Ancient links between the Atlantic Forest and Amazonia. *Molecular Phylogenetics and Evolution*. 2011; 61: 446–459. <https://doi.org/10.1016/j.ympev.2011.07.010> PMID: 21801842
 29. Prates I, Rivera D, Rodrigues MT, Carnaval AC. 2016. A mid-Pleistocene rainforest corridor enabled synchronous invasions of the Atlantic Forest by Amazonian anole lizards. *Molecular Ecology*. 2016; 25(20): 5174–5186. <https://doi.org/10.1111/mec.13821> PMID: 27564209
 30. Prates I, Melo-Sampaio PR, de Oliveira Drummond L, Teixeira M Jr, Rodrigues MT, Carnaval AC. Biogeographic links between southern Atlantic Forest and western South America: rediscovery, re-description, and phylogenetic relationships of two rare montane anole lizards from Brazil. *Molecular Phylogenetics and Evolution*. 2017; 113: 49–58. <https://doi.org/10.1016/j.ympev.2017.05.009> PMID: 28502765
 31. de Sá RO, Tonini JFR, van Huss H, Long A, Cuddy T, Forlani MC, et al. Multiple connections between Amazonia and Atlantic Forest shaped the phylogenetic and morphological diversity of *Chiasmocleis* Mehely, 1904 (Anura: Microhylidae: Gastrophryninae). *Molecular phylogenetics and evolution*. 2019; 130: 198–210. <https://doi.org/10.1016/j.ympev.2018.10.021> PMID: 30347238
 32. Peres EA, Silva MJ, Solferini VN. Phylogeography of the spider *Araneus venatrix* (Araneidae) suggests past connections between Amazonia and Atlantic rainforests. *Biological Journal of the Linnean Society*. 2017; 121(4): 771–785.
 33. Benson DA, Cavanaugh M, Clark K, Karsch-Mizrachi I, Lipman DJ, Ostell J, et al. GenBank. Nucleic acids research. 2012; 41(D1): D36–D42. Available from: <http://www.ncbi.nlm.nih.gov/GenBank/>.
 34. IUCN. The IUCN Red List of Threatened Species. Version 2018–2; 2019. Available from: <http://www.iucnredlist.org/>.
 35. IUCN Red List Technical Working Group. Mapping Standards and Data Quality for IUCN Red List Spatial Data. Prepared by the Standards and Petitions Working Group of the IUCN SSC Red List Committee. Version 1.18; 2019. Available from: <https://www.iucnredlist.org/resources/mappingstandards>.
 36. IUCN Standards and Petitions Committee. Guidelines for Using the IUCN Red List Categories and Criteria. Prepared by the Standards and Petitions Committee. Version 14; 2019. Available from: <http://www.iucnredlist.org/documents/RedListGuidelines.pdf>.

37. Brooks TM, Pimm SL, Akçakaya HR, Buchanan GM, Butchart SH, Foden W, et al. Measuring terrestrial area of habitat (AOH) and its utility for the IUCN Red List. *Trends in ecology & evolution*. 2019; 34(11): 977–986.
38. Jung M, Dahal PR, Butchart SH, Donald PF, De Lamo X, Lesiv M, et al. A global map of terrestrial habitat types. *Scientific data*. 2020; 7(1): 1–8. <https://doi.org/10.1038/s41597-019-0340-y> PMID: 31896794
39. Sandom C, Dalby L, Fløjgaard C, Kissling WD, Lenoir J, Sandel B, et al. Mammal predator and prey species richness are strongly linked at macroscales. *Ecology*, 2013; 94: 1112–1122. <https://doi.org/10.1890/12-1342.1> PMID: 23858651
40. Belmaker J, Jetz W. Relative roles of ecological and energetic constraints, diversification rates and region history on global species richness gradients. *Ecology Letters*. 2015; 18: 563–571. <https://doi.org/10.1111/ele.12438> PMID: 25919478
41. Mouchet M, Levers C, Zupan L, Kuemmerle T, Plutzer C, Erb K, et al. Testing the effectiveness of environmental variables to explain European terrestrial vertebrate species richness across biogeographical scales. *PLOS ONE*. 2015; 10: e0131924. <https://doi.org/10.1371/journal.pone.0131924> PMID: 26161981
42. Vilela B, Villalobos F. letsR: a new R package for data handling and analysis in macroecology. *Methods in Ecology and Evolution*. 2015; 6(10): 1229–1234.
43. Maestri R, Luza AL, de Barros LD, Hartz SM, Ferrari A, de Freitas TRO, et al. Geographical variation of body size in sigmodontine rodents depends on both environment and phylogenetic composition of communities. *Journal of Biogeography*. 2016; 43(6): 1192–1202.
44. Gonçalves-Souza D, Verburg PH, Dobrovolski R. Habitat loss, extinction predictability and conservation efforts in the terrestrial ecoregions. *Biological Conservation*. 2020; 246: 108579. <https://doi.org/10.1016/j.biocon.2020.108579>
45. Dinerstein E, Olson D, Joshi A, Vynne C, Burgess ND, Wikramanayake E, et al. An ecoregion-based approach to protecting half the terrestrial realm. *BioScience*. 2017; 67(6): 534–545. <https://doi.org/10.1093/biosci/bix014> PMID: 28608869
46. Bivand R, Rundel C. rgeos: Interface to Geometry Engine-Open Source ('GEOS'). R package version 0.5–5; 2020. Available from: <https://CRAN.R-project.org/package=rgeos>.
47. R Core Team. R: A language and environment for statistical computing. v. 3.6.3. R Foundation for Statistical Computing, Vienna, Austria; 2020. Available from: <http://www.R-project.org/>.
48. Paglia AP, da Fonseca GAB, Rylands AB, Herrmann G, Aguiar LMS, Chiarello AG, et al. Annotated Checklist of Brazilian Mammals. 2nd ed. Occasional papers in conservation biology, 6. Arlington: Conservation International; 2012.
49. Scott C. rredlist: 'IUCN' Red List Client. R package version 0.6.0; 2020. Available from: <https://CRAN.R-project.org/package=rredlist>.
50. Emmons LH, Feer F. Neotropical rainforest mammals: a field guide. Chicago: University of Chicago Press; 1997.
51. Eisenberg JF, Redford KH. Mammals of the Neotropics: The central Neotropics: Ecuador, Bolivia, Brazil. Chicago: University of Chicago Press; 1999.
52. Gardner AL. Mammals of South America, volume 1: marsupials, xenarthrans, shrews, and bats. Chicago: University of Chicago Press; 2008.
53. Patton JL, Pardiñas UF, D'Elía G. Mammals of South America, volume 2: rodents. Chicago: University of Chicago Press; 2015.
54. Nowak RM. Walker's Mammals of the World, volume 2. Baltimore: Johns Hopkins University Press; 1999.
55. Luza AL, Graham CH, Hartz SM. A global database on non-volant small mammal composition in natural and human-modified habitats. *Data in brief*. 2019; 23: 103842. <https://doi.org/10.1016/j.dib.2019.103842> PMID: 31372469
56. Wilson DE, Mittermeier RA. Handbook of the mammals of the world. Vol. 1. Carnivores. Barcelona: Lynx Edicions; 2009.
57. Hijmans RJ. Package 'raster': Geographic Data Analysis and Modeling. R package version 2.6–7; 2017. Available from: <https://CRAN.R-project.org/package=raster>.
58. Rull V. Speciation timing and neotropical biodiversity: the Tertiary–Quaternary debate in the light of molecular phylogenetic evidence. *Molecular Ecology*. 2008; 17: 2722–2729. <https://doi.org/10.1111/j.1365-294X.2008.03789.x> PMID: 18494610
59. Andrade-Lima DD. Present-day forest refuges in northeastern Brazil. *Biological diversification in the tropics*. 1982; 245: 251.

60. Auler AS, Smart PL. Late Quaternary paleoclimate in semiarid northeastern Brazil from U-series dating of travertine and water-table speleothems. *Quaternary Research*. 2001; 55(2): 159–167.
61. Machado AF, Nunes MS, Silva CR, dos Santos MA, Farias IP, da Silva MNF, et al. Integrating phylogeography and ecological niche modelling to test diversification hypotheses using a Neotropical rodent. *Evolutionary ecology*. 2019; 33(1): 111–148.
62. Voss RS, Fleck DW, Jansa SA. Mammalian diversity and Matses ethnomammalogy in Amazonian Peru. Part 3: Marsupials (Didelphimorphia). *Bulletin of the American Museum of Natural History*. 2019; 432: 1–90.
63. Gutiérrez EE, Jansa SA, Voss RS. Molecular systematics of mouse opossums (Didelphidae: *Marmosa*): assessing species limits using mitochondrial DNA sequences, with comments on phylogenetic relationships and biogeography. *American Museum Novitates*. 2010; 3692: 1–22.
64. Faria MB, Oliveira JAD and Bonvicino CR. Filogeografia de populações brasileiras de *Marmosa (Marmosa) murina* (Didelphimorphia, Didelphidae). *Revista Nordestina de Biologia*. 2013; 21(2): 27–52.
65. Nogueira Ferraz EM, Nogueira Rodal MJ, Sampaio EV. Physiognomy and structure of vegetation along an altitudinal gradient in the semi-arid region of northeastern Brazil. *Phytocoenologia*. 2003; 33(1): 71–92.
66. de Queiroz LP, Cardoso D, Fernandes MF, Moro MF. Diversity and evolution of flowering plants of the Caatinga Domain. In: da Silva JMC, Leal IR, Tabarelli M. Caatinga. The Largest Tropical Dry Forest Region in South America. Cham: Springer. 2017. pp. 23–63.
67. Fonseca GAB, Redford KH, Pereira LA. Notes on *Didelphis albiventris* (Lund, 1841) of central Brazil. *Ciência e Cultura*. 1982; 34(10): 1359–1362.
68. Hintze F, Arias-Aguilar A, Dias-Silva L, Delgado-Jaramillo M, Silva CR, Jucá T, et al. Molossid unlimited: extraordinary extension of range and unusual vocalization patterns of the bat, *Promops centralis*. *Journal of Mammalogy*. 2020; 101(2): 417–432.
69. Coimbra RTF, Miranda FR, Lara CC, Schetino MAA, Santos FRD. Phylogeographic history of South American populations of the silky anteater *Cyclopes didactylus* (Pilosa: Cyclopedidae). *Genetics and molecular biology*. 2017; 40(1): 40–49. <https://doi.org/10.1590/1678-4685-GMB-2016-0040> PMID: 28199442
70. Nascimento FF, Oliveira-Silva M, Veron G, Salazar-Bravo J, Gonçalves PR, Langguth A, et al. The evolutionary history and genetic diversity of Kinkajous, *Potos flavus* (Carnivora, Procyonidae). *Journal of Mammalian Evolution*. 2017; 24(4): 439–451.
71. de Vivo M, Carmignotto AP. Suborder Sciuromorpha Brandt, 1855. Infraorder Sciurida Carus, 1868. In: Patton JL, Pardiñas UF, D'Elía G, editors. *Mammals of South America, Rodents 2*. Chicago: University of Chicago Press; 2015. pp. 1–48.
72. Gregorin R. Taxonomia e variação geográfica das espécies do gênero *Alouatta* Lacépède (Primates, Atelidae) no Brasil. *Revista brasileira de Zoologia*. 2006; 23(1): 64–144.
73. Viana MC, Bonvicino CR, Ferreira JG, Jerusalinsky L, Langguth A, Seuánez H. Understanding the relationship between *Alouatta ululata* and *Alouatta belzebul* (Primates: Atelidae) based on cytogenetics and molecular phylogeny. *Oecologia Australis*. 2015; 19: 173–182.
74. Miranda CL, Rossi RV, Silva Junior JDS, Lima MGM, Santos MPD. Mammalia, Didelphimorphia, Didelphidae, *Metachirus nudicaudatus*, Municipality of José de Freitas, State of Piauí, Northeastern Brazil: distribution extension. *Check List*. 2009; 5(2): 360–363.
75. Miranda CL, Lima MGM, Santos MPD, Silva Júnior JS. Ocorrência de *Micoureus demerarae* (Thomas, 1905) no Estado do Piauí. *Publicações Avulsas em Conservação de Ecossistemas*. 2005; 2: 1–4.
76. Vieira OQ, Oliveira TGD. Non-volant mammalian species richness in the ecotonal Brazilian midnorth: checklist for Maranhão State. *Biota Neotropica*. 2020; 20(2). <https://doi.org/10.1590/1676-0611-bn-2019-0912>
77. Pavan SE, Jansa SA, Voss RS. Molecular phylogeny of short-tailed opossums (Didelphidae: *Monodelphis*): taxonomic implications and tests of evolutionary hypotheses. *Molecular Phylogenetics and Evolution*. 2014; 79: 199–214. <https://doi.org/10.1016/j.ympev.2014.05.029> PMID: 25017146
78. Gurgel-Filho NM, Feijó A, Langguth A. Pequenos mamíferos do Ceará (marsupiais, morcegos e roedores sigmodontíneos) com discussão taxonômica de algumas espécies. *Revista Nordestina de Biologia*. 2015; 23(2): 3–150.
79. Malcher SM, Pieczarka JC, Geise L, Rossi RV, Pereira AL, O'Brien PCM, et al. *Oecomys catherinae* (Sigmodontinae, Cricetidae): Evidence for chromosomal speciation? *PLOS ONE*. 2017; 12(7): e0181434. <https://doi.org/10.1371/journal.pone.0181434> PMID: 28727788
80. Moraes-Barros N, Arteaga MC. Genetic diversity in Xenarthra and its relevance to patterns of neotropical biodiversity. *Journal of Mammalogy*. 2015; 96(4): 690–702.

81. Gonçalves-Souza D, Verburg PH, Dobrovolski, R. Habitat loss, extinction predictability and conservation efforts in the terrestrial ecoregions. *Biological Conservation*. 2020; 246: 108579. <https://doi.org/10.1016/j.biocon.2020.108579>
82. Abessa D, Famá A, Buruaem L. The systematic dismantling of Brazilian environmental laws risks losses on all fronts. *Nature ecology & evolution*. 2019; 3(4): 510–511. <https://doi.org/10.1038/s41559-019-0855-9> PMID: 30886371
83. Loughry WJ, Superina M, McDonough CM, Abba AM. Research on armadillos: a review and prospectus. *Journal of Mammalogy*. 2015; 96(4): 635–644.