




# Small mammal diversity of a poorly known and threatened Amazon region, the Tapajós Area of Endemism

Joyce Rodrigues do Prado<sup>1,2</sup>  · Rita G. Rocha<sup>3,4,5</sup> · Heitor Bissoli-Silva<sup>1,2</sup> · Ana Cristina Mendes-Oliveira<sup>6</sup> · Regeane C. L. Pontes<sup>6</sup> · Paula Cristina R. de A Maués<sup>6</sup> · Leonora Pires Costa<sup>1,5</sup>

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## Abstract

The Amazon region is a mosaic of distinct areas of endemism (AoE), each with its evolutionary relationships and biotic assemblages. Among them, the Tapajós AoE is one of the least sampled, and it has been identified as one of the regions with the lowest conservation value. Here we provide a checklist of small mammals based on field and molecular-based identification. We report small mammal taxa from the Tapajós River region identified at the species level and three only identified at the genus level (including lineages of the genera *Oecomys*, *Mesomys*, and *Monodelphis*). An intense sampling effort using complementary methods was undertaken during which specimens were sampled at twelve sampling units, six on each riverbank, then combined with molecular identification to help species identification. Most of the taxa occurring in the Tapajós region are widely found in the eastern part of the Amazon Forest, and three species are endemic. Here, we highlight the unique and important mammal assembly of the Tapajós region and its significance with conservation priorities, which had been neglected until now due to a deficit of sampling efforts. We also point out that increasing research efforts to sample small mammals in the Amazon is crucial to understanding this biome's biodiversity patterns and biogeography.

**Keywords** Neotropics · Rodentia · Didelphimorphia · Species richness · Biogeography

## Introduction

Although the Amazon region harbors some of the highest diversity of fauna in the world, including approximately one-third of all South American mammal species (Bonvicino and Weksler 2012), vast areas remain that have never been visited by scientists (Mendes-Oliveira et al. 2015). Presenting a high level of endemic mammals with around 60% of its diversity being endemic, mainly bats, rodents, and primates (Fonseca et al. 1999; Abreu-Júnior et

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al. 2020), the Amazon Biome is not homogeneous in its biodiversity communities. In fact, it is a mosaic of distinct areas of endemism (AoE) separated by major rivers, each with its own evolutionary relationships and biotic assemblages (Silva et al. 2005). This pattern has been corroborated by several studies (Wallace 1852; Haffer 1969; Cracraft 1985; Silva and Oren 1996; Patton et al. 2000; Pinto-da-Rocha et al. 2005; Silva et al. 2005; Avila-Pires et al. 2009, among others), although the geographic distribution of these areas of endemism varies depending on the studied group.

Different AoEs have been recognized for terrestrial vertebrates (birds, lizards, frogs, and mammals) in lowland Amazonia. Cracraft (1985) identified seven areas of endemism (i.e., Imeri, Napo, Inambari, Rondônia, Guiana, Belém, and Pará), which have generally been corroborated with only a few modifications. For example, the Pará AoE has been divided into two areas, the Tapajós AoE and the Xingu AoE, separated by the Xingu River (Silva et al. 2002). Other modifications include the limits (and sometimes the presence) of the Imeri, Napo, Inambari AoEs (Silva et al. 2002; Naka 2011; Borges and Silva 2012).

These endemic areas are important as they serve as biogeographic units to study the structuring processes of Amazonian diversity, and, ultimately, they can serve as a basis for the development of conservation plans. However, we note that concerning mammals, these AoEs are largely delimited by data on the distribution of primates (Wallace, 1852; Silva and Oren, 1996); thus, no other group of mammals has been used to evaluate these areas. This issue likely is a function of the scarce sampling of other mammals across the Amazon Biome. There are reliable and complete inventories of Amazonian mammals from only a few study sites, which often do not include abundance data (Mendes-Oliveira et al. 2015; Oliveira et al. 2016). A comprehensive review of the literature (i.e., scientific papers, book chapters) reveals only about 15 reports including small mammal surveys (inventories) in the Amazon (including 29 different localities). These field inventories are unevenly distributed throughout the Amazon, with the greatest effort in the Guiana (Avila-Pires 1964; Barnett and Cunha 1994; Voss and Emmons 1996; Rossi et al. 2017; Abreu-Júnior et al. 2017), Inambari (Carvalho 1957; Patton et al. 2000; da Silva et al. 2007; Abreu-Júnior et al. 2016), and the Rondônia AoEs (George et al. 1988; da Silva et al. 2007; Percequillo et al. 2011; Semedo et al. 2011). The Xingu (Voss and Emmons 1996; Gettinger et al. 2011), Napo (Hice and Velazco 2013), and Belém AoEs (Pine 1973) account for a smaller number of studies. We are not aware of any small mammal surveys within the Tapajós region, supporting Leite and Rogers' (2013) conclusion that this AoE is among the least surveyed regions in the Amazon Basin. Likely reflecting this lack of data, the Tapajós AoE is considered one of the regions with the lowest conservation value (López-Osorio and Miranda-Esquivel 2010). Increasing the number of field inventories, ensuring that they encompass all the AoEs, is essential to assess the power of these units in gathering endemic species and clarifying patterns of distribution and endemism of Amazonian biodiversity.

Like other areas of the Amazon Forest, the Tapajós region suffers from habitat loss, degradation, and fragmentation caused by deforestation (Gascon et al. 2001). Although the Tapajós AoE has until recently been considered the least deforested AoE in the Amazon Biome (Silva et al. 2005), the state of Pará, where this area of endemism is located, has led the deforestation ranking in the Brazilian Amazon in the last 15 years (INPE 2019), and this has been particularly true in the last two years (Fonseca et al. 2021). This region has long suffered from illegal logging, road construction, illegal mining, implementation of hydroelectric plants (Zemp et al. 2017), and more recently from intensive cattle ranching and soy

farming (Rajão et al.2020). Estimates show about 74% of Primary Forest cover remains, against 26% of areas with variable anthropogenic land use (INPE 2018).

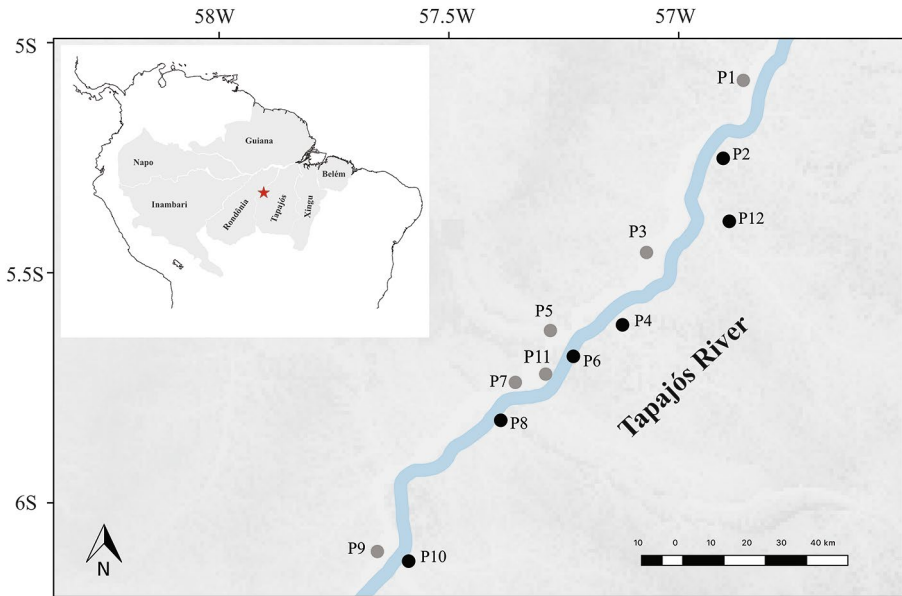
The Tapajós AoE is located between the Tapajós and Xingu rivers, two important tributaries of the Amazon River. It is the fourth-smallest AoE (648,862 km<sup>2</sup>); only the Imeri, Xingu, and Belém AoEs are smaller (Silva et al.2005). It also has 28.26% of its territory protected by Brazilian legislation (Silva et al.2005). Historically, the Tapajós River basin has received little attention since the beginning of the great naturalist expeditions in South America. Naturalists of the earlier centuries, who sailed the Amazon rivers, traced their main routes through the Amazon River, leaving the Tapajós River unsurveyed for a long time (Cunha 1991). Notwithstanding this region is of great biogeographic importance, as it is located in a climatic, geomorphological, and vegetational transition zone, which have been associated with the diversification patterns of its biota (Moraes et al. 2016, 2020).

Here, we contribute to understanding the nonvolant small mammal's biodiversity in the Amazon Biome, providing a list of species of the Tapajós AoE based on extensive fieldwork and molecular analysis. The small mammal species that we sampled include the nonvolant mammals of the families Cricetidae and Echimyidae of the order Rodentia and representatives of the family Didelphidae from the order Didelphimorphia. Around the world, small mammals provide important ecosystem services such as seed dispersal, pollination, and insect control. They also aerate the soil, which allows for increased plant diversity, support for forest regeneration, maintenance of forest health, and they are a source of food for carnivorous species (Wilson and Mittermeier2015; Wilson et al.2017). Further, this group has been widely used in biogeographic studies due to their rapid responses to environmental changes (Rowe and Terry2014). We also discuss whether the Tapajós AoE represents a region of least concern for conservation purposes in terms of species richness and composition. Finally, we highlight how the increasing sampling efforts on remote areas of the Amazon Biome are crucial for understanding biogeographical processes and conservation concerns.

## Materials and methods

### Study area

We conducted surveys along the mid-portion of the Tapajós River, one of the main tributaries of the Amazon River, in the Brazilian state of Pará. This river results from the confluence of the Teles Pires and the Juruena rivers, flowing from the Brazilian Shield. Among other rivers in the Brazilian Shield, the Tapajós River is one of the largest clear water rivers in the main sub-basin of the Amazon drainage basin (Latrubesse 2008). The climate is Tropical monsoon, Am of the Köppen-Geiger classification, with a short dry season and rainfall below 60 mm (Kottek et al. 2006). The mean annual rainfall ranges from 1600 to 2700 mm, and the mean annual temperature is around 25 °C. The vegetation is mostly composed of Dense Submontane Ombrophylous Forest, Open Submontane Ombrophilous Forest, and areas of secondary vegetation (Olson et al. 2001). Intensive mining and livestock activities are present near highway BR-230 (Transamazônica; INPE, 2018). The study area is located between 4°42'42.2" S to 6°7'36.78" S and 56°37'46.7" W to 57°41'25.27" W (Fig. 1).



**Fig. 1** Study area. Location of the Tapajós River in eastern Amazon Biome, and the distribution of the twelve-sampling units, six in each river bank. In the detail the distribution of seven areas of endemism (AoE) within the Amazon region (modified version based on Cracraft (1985), Silva et al. (2002), Silva et al. (2005))

## Small mammal sampling

We established twelve sampling units in the study area, six on each river bank (Fig. 1). Each sampling unit included five sampling points, established at 1-km intervals away from the river (i.e., 50, 1050, 2050, 3050, and 4050 m from each river bank) (Supplementary Material, Appendix S1). Sampling units were at least 4 km apart to ensure spatial independence. At each sampling point, the sampling design consisted of: (i) one line of 20 Tomahawk traps (15×15×32 cm) and 20 Sherman traps (25×8×9 cm) placed both on the ground and in the understory (~1.5 m above the ground), totaling 200 live traps per sampling unit, and (ii) three parallel lines of five 60 L pitfalls with black plastic fences, 1 m height and 10 m long between buckets (40 m per pitfall), totaling 15 groups (75 buckets) of pitfalls per sampling point. Small holes were opened at the bottom of each bucket to allow water drainage and avoid accidental mortality. Traps were baited with a mixture of fruit, oil, peanut butter, and canned sardines, and baits were replaced whenever needed. Sampling was conducted during four expeditions of 30 days each in 2012 and 2013, totaling a sampling effort of 48,000 live traps-nights and 18,040 pitfall traps-nights. All traps were checked daily in the early morning for five consecutive days in the four expeditions carried out, thus totaling 20 days of sampling in each of the 60 sampling points spread across the twelve sampling units (Supplementary Material, Appendix S1).

Four field teams were working simultaneously over the sampling units for such an intense sampling effort. Each team consisted of at least two researchers and three field assistants to

help place and remove the traps. Each team was responsible for collecting data from two or three sampling units per expedition. The pitfall traps were installed in the first campaign and remained until the end of sampling, requiring only maintenance in each expedition. The Sherman and Tomahawk traps were installed on each expedition, with each set of 200 traps being used in two or three sampling units. This work was a part of a major survey of fauna and flora, in addition to a socioeconomic diagnosis of the region, for assessing the possibility of installing a hydroelectric dam.

Initial (field) identification of specimens was based on morphological and morphometric analysis. This step was important in order to select candidate specimens and samples that would be subsequently submitted to the molecular analysis. Voucher specimens of each species were collected and deposited at the Museu de Zoologia da Universidade Federal do Pará (MZUFPA) Belém, Brazil. The authorization for voucher collection was issued by the Brazilian Institute for the Environment and Renewable Natural Resources (SISBIO n° 158/2012). All other individuals were measured, weighed, and released at their capture location. Animals collected during this study were handled following procedures recommended by the American Society of Mammalogists (Sikes and the Animal Care and Use Committee of the American Society of Mammalogists 2016).

## Molecular identification

We applied molecular methods to identify 139 specimens of the total sample collected during the field expeditions. DNA was extracted from liver, muscle, or skin of each individual using the salt extraction protocol (Bruford et al. 1992). Two mitochondrial markers (cytochrome oxidase subunit 1 - COI; and cytochrome b - CYTB) were selected, due to their wide use in molecular identification of Neotropical species of small mammals (e.g. Patton et al. 2000; Rocha et al. 2011, 2015; Agrizzi 2012).

The fragments were amplified through a polymerase chain reaction (PCR), using specific primers for CYTB (MVZ05 and MVZ16, (Smith and Patton 1993) and COI (coquetel B, Ivanova et al. 2007). PCR reactions were performed in 25 µl total volume, containing 1 µl of extracted DNA, 2.5 µl of 10 x PCR buffer, 1.0 µl of MgCl<sub>2</sub> (50 mM), 0.5 µl of deoxyribonucleotide triphosphate (dNTP) mixture (10 mM), 0.25 µl of Platinum® Taq DNA polymerase (Invitrogen Life Technologies), and 0.3 µl of each primer (10 mM). Amplifications were performed using the following PCR profiles: (1) CYTB, initial denaturation at 94 °C for 2 min (min), followed by 39 cycles at 94 °C for 30 s (s), annealing temperature at 47–48 °C for 45 s and 72 °C for 45 s, with a final extension at 72 °C for 5 min; and (2) COI, initial denaturation at 94 °C for 5 min, followed by 39 cycles at 94 °C for 30 s, annealing temperature at 57–62 °C for 45 s and 72 °C for 1 min, with a final extension at 72 °C for 5 min. All PCR reactions included a negative control to monitor possible cross-contamination. PCR products were visualized by electrophoresis on 2% agarose gels. The amplified products were purified with the ExoSAP enzyme (GE Healthcare Life Sciences) and the sequencing reaction was performed with a Big Dye v3.1 kit (Applied Biosystems Inc.), following the manufacturer's protocol. Sequencing was performed in an automated sequencer ABI 3500 (Thermo Fisher Scientific, Applied Biosystems) with the above-listed primers.

Electropherograms were checked by eye to ensure sequence quality. High-quality sequences were BLAST searched in the online database GenBank (<https://www.ncbi.nlm>

[nih.gov/genbank/](http://nih.gov/genbank/)) in order to determine genetic proximity with sequences from other studies. Phylogenetic relationships among sequences were inferred using the Maximum Likelihood (ML) in RAxML v. 8.2.10 (Stamatakis 2014), using a GTR-GAMMA model, and nodal support estimated by bootstrap with 1,000 replicates. Species identification was based on matches among our collected sequences (barcodes) and sequences from reference databases (GenBank; BOLD, <http://www.boldsystems.org>; Supplementary Material, Appendix S2, Fig. S4–S26). Sequences were aligned by ClustalW in MEGA7 (Kumar et al. 2016).

## Results

### Small mammal species in the Tapajós region

Based on molecular data, we identified 26 different putative taxa of small mammals occurring in the Tapajós region (Table 1; Supplementary Material, Appendix S3–S26). The order Rodentia is the richest ( $n=14$ ), with eight species of cricetid rodents (plus one unidentified *Oecomys*) and four species of echimyid rodents (plus one unidentified *Mesomys*). The order Didelphimorphia is represented by 12 lineages from the family Didelphidae. Six species were recorded only once in our sampling: *Philander opossum*, *Marmosa lepida*, *Marmosa macrotarsus*, *Marmosa murina*, *Oecomys bicolor*, *Lonchothrix emilae*.

Phylogenetic analyses, using both CYTB and COI sequences, allowed the identification of 23 putative taxa at the species level. Still, three were only identified at the genus level, including lineages of the genera *Oecomys*, *Mesomys*, and *Monodelphis* (see Supplementary Material, Appendix S12–13, S20–21, S23–24 for phylogenetic trees used for molecular identifications).

The samples UFPA M 1379, 1457, 1178, 1180, and 1179 form a distinct clade of *Oecomys* in both CYTB and COI phylogenetic analysis (Supplementary Material, Appendix S20 and S21), which could not be clustered with any other species (available here and in the online databases) with support greater than 60%, and thus are referred here as *Oecomys* sp. Six other samples (UFPA M1160, 1161, 1157, 1158, 1159, 1551) grouped with sequences previously identified as *Mesomys hispidus* and/or *M. stimulax*. No phylogenetic relationship was recovered in these analyses (Supplementary Material, Appendix S23 and S24). Therefore, we refer to these samples as *Mesomys* sp.

For one sample (UFPA M1482) of the genus *Monodelphis*, we obtained the COI sequence only. This sequence showed a sister relationship to a cluster encompassing specimens of *Monodelphis glirina*, *M. brevicaudata*, and *M. americana* (Supplementary Material, Appendix S12). Because few COI sequences are available for the genus *Monodelphis*, and we lacked the CYTB sequence for this sample, we could not identify this specimen with precision.

The number of specimens and taxa recorded during sampling was similar in both river banks (75 specimens and 17 taxa on the right (east) bank, and 64 specimens and 19 taxa on the left (west) bank, Table 1). However, the number of exclusive species in each bank is conspicuously different. *Marmosa lepida*, *Monodelphis glirina*, *Monodelphis* sp., *Neacomys vossi*, *Oecomys paricola*, *O. tapajinus* and *Philander opossum* were collected only in the right bank of the river. In contrast, *Lonchothrix emilae*, *Marmosa macrotarsus*, *M. murina*,

**Table 1** List of small mammals recorded at the mid-Tapajós River, including number of specimens (N) recorded at each river bank (left river bank=west; right river bank=east). For the individuals respective catalog number, field number, locality and sample site, as well as the molecular marker each specimen was sequenced see Supplementary Material, Appendix S3

Taxon	Left river bank (N)	Right river bank (N)
Didelphimorphia		
<i>Didelphis marsupialis</i>	3	2
<i>Philander opossum</i>	0	1
<i>Marmosa demerarae</i>	15	14
<i>Marmosa lepida</i>	0	1
<i>Marmosa macrotarsus</i>	1	0
<i>Marmosa murina</i>	1	0
<i>Monodelphis emiliae</i>	2	4
<i>Monodelphis glirina</i>	0	2
<i>Monodelphis</i> sp.	0	1
<i>Metachirus nudicaudatus</i>	2	3
<i>Marmosops noctivagus</i>	2	9
<i>Marmosops marina</i>	4	2
Rodentia		
Cricetidae		
<i>Neusticomys ferreirai</i>	1	3
<i>Hylaeamys megacephalus</i>	9	13
<i>Neacomys vossi</i>	0	13
<i>Neacomys elieceri</i> <sup>1</sup>	2	1
<i>Oecomys bicolor</i>	1	0
<i>Oecomys cleberi</i>	5	0
<i>Oecomys paricola</i>	0	5
<i>Oecomys tapajinus</i>	0	2
<i>Oecomys</i> sp.	5	0
Echimyidae		
<i>Lonchothrix emilae</i>	1	0
<i>Mesomys</i> sp.	3	3
<i>Proechimys goeldii</i>	1	3
<i>Proechimys roberti</i>	1	3
<i>Proechimys longicaudatus</i>	4	0

*Marmosops noctivagus*, *Neacomys elieceri*, *Oecomys bicolor*, *O. cleberi*, *Oecomys* sp., and *Proechimys longicaudatus* were collected only in the left bank of the Tapajós River.

Regarding sampling methods, eleven lineages were exclusively recorded using pit-fall traps (*Hylaeamys megacephalus*, *Lonchothrix emilae*, *Marmosa lepida*, *Marmosops marina*, *Monodelphis emiliae*, *M. glirina*, *Monodelphis* sp., *Neacomys elieceri*, *N. vossi*, *Neusticomys ferreirai*, and *Oecomys tapajinus*). This method allowed the sampling of a total of 85 specimens. Three species were recorded using only Sherman traps (*Marmosa macrotarsus*, *M. murina*, and *Marmosops noctivagus*), and this method allowed the sampling of 27 specimens. Finally, two species were sampled only by the Tomahawk traps (*Philander opossum* and *Proechimys roberti*), which allowed the sampling of a total of 19 individuals.

## Discussion

Our results bolster our understanding of the mammal biodiversity of the Amazon region, which is essential for understanding the biogeographic relationships among the recognized Areas of Endemism (AoEs). Through intensive fieldwork and molecular-based study of small mammal species from a poorly sampled region, we also highlight the relevance of the Tapajós region's unique diversity for generating public policies for the conservation of the Amazon.

### Mammal diversity in the Tapajós region

Although the Tapajós region has been neglected by previous researchers, we showed that it has a diverse small mammal fauna. We were able to identify 23 putative taxa of rodents and marsupials at the species level. Three lineages were identified only to the genus level, including representatives of *Oecomys*, *Mesomys*, and *Monodelphis*. Lack of molecular data and/or systematic revisions and detailed species descriptions prevented us from identifying these lineages with greater accuracy. However, these taxa may represent previously unrecognized taxa within each genus and deserve future attention. Combined analysis of CYTB (for which we included samples of all species of *Oecomys* distributed throughout the region) and COI strongly suggests that *Oecomys* sp. represents a novel entity within the genus. Suárez-Villota et al. (2018) recently revised the systematics of *Oecomys*, revealing a large number of putative new taxa. However, as we did not recover any relationship with other species within this genus, we could not assign this cluster to the putative new taxa identified by Suárez-Villota et al. (2018). The genus *Mesomys* lacks proper systematic revision (Patton and Emmons 2015), but both *M. hispidus* and *M. stimulax* occur near the Tapajós region. Phylogenetic analysis with available sequences of these two species did not recover monophyletic clades, precluding the identification of the specimens from the Tapajós. Finally, *Monodelphis* has few sequences of the COI gene available in public repositories, precluding more precise identification of this specimen.

Noteworthy are the single records of five species, *Philander opossum*, *Marmosa lepida*, *M. macrotarsus*, *Oecomys bicolor*, and *Lonchothrix emilae*, despite the high sampling effort employed in this study. These records highlight the need for further fieldwork to document regional diversity as well as to furnish scientific collections with voucher specimens, particularly in poorly known and surveyed areas such as the Tapajós region.

We note that the use of pitfall traps significantly increased the number of recorded species in the Tapajós region, with eleven lineages exclusively recorded using these traps. This corroborates the highly recommended guideline of using complementary methods for surveying small mammals (Voss and Emmons 1996, Lyra-Jorge and Pivello 2001, Umetsu et al. 2006, Ribeiro-Júnior et al. 2011, Rocha et al. 2015).

### Diversity patterns in the Amazon region

Several studies show that species richness is not evenly distributed across the Amazon Basin (e.g., Sigrist and Carvalho 2009; Juen and Marco Jr. 2012; Ribas et al. 2012; Alvez-Valles



et al. 2018), and some indicate a major partition between the western and eastern parts of the Amazon (e.g., Juen and Marco Jr. 2012; Alvez-Valles et al. 2018). Diversity patterns reported here agree with this east-west partition of the Amazon forest. We found that 78% of the species (18 species) recovered in the Tapajós region are distributed in the eastern portion of the Amazon forest. The remaining species, including the rodent *Proechimys longicaudatus*, and the marsupials *Marmosa lepida*, *Marmosa macrotarsus*, *Marmosops noctivagus*, and *Monodelphis emiliae* occur, mainly across the western part of the Amazon Forest. Only two species recorded in the Tapajós region are not restricted to the Amazon forest – the rodent *Oecomys cleberi* and the marsupial *Marmosa murina*. This is the northwesternmost record of *O. cleberi*, also reported by Saldanha et al. (2019), and *murina* also occurs in other biomes in central and eastern Brazil (Wilson and Mittermeier 2015).

The east-west break in the diversity patterns of Amazonian communities may be related to several characteristics of the geography and history of the Amazonian landscape. For example, the formation of the Amazon River basin, especially the Madeira and Negro rivers, which are among the major tributaries of the Amazon River and are each over 2,250 km long. The importance of these rivers in the diversity of Amazonian mammals has been highlighted since Wallace (1852) reported that they formed the limits beyond which certain species never passed. These observations were precursors of the modern interpretations of the river-barrier hypothesis, which has been used to delimit the areas of endemism for different taxa. The Madeira River, in particular, has been postulated as a barrier to dispersal for species of various taxa, including birds (Aleixo 2004; Ribas et al. 2012; Fernandes et al. 2014), frogs (Simões et al. 2008; Kaefer et al. 2013; Dias-terceiro et al. 2015), and mammals (Wallace 1852; Van Roosmalen et al. 2002). However, this hypothesis is not always accepted, depending on the species and river investigated, and the role of rivers as the limits to endemism areas has been questioned for several groups (Santorelli et al. 2018). In fact, alternative hypotheses can be proposed to explain the diversity patterns of the Amazon communities. For example, this west-east separation coincides with the Purus structural arch, located between the Solimões, Negro, and Madeira rivers (Patton et al. 2000; Leite and Rogers 2013). Structural arches are geomorphological features that demarcate geological units associated with the origin of the rivers in the Amazon (Albert et al. 2018). During the Pliocene, these arches may have blocked the transport of Andean-derived sediments from the west part of the Amazon (van Soelen et al. 2017).

Regardless of the mechanism underlying the division between western and eastern small mammal biota, they result from the historical process of changes in the Amazonian landscape. Diversity patterns in western Amazonia are highly correlated with the geological formation of the Amazon landscape, which was shaped by the uplift of the Andes and its effect on regional climate (Hoorn et al. 2010). During the Miocene, geotectonic changes in the Amazon Basin, caused by the uplift of the Andes, gradually submerged western Amazonia, creating a continental water body known as Lake Pebas (Wesselingh et al. 2002). Subsequently, this landscape of mega-wetlands changed to a system with reduced and seasonal flooded areas (Wesselingh et al. 2002). At the same time that the water flow was gradually draining out of the Pebas mega-wetland, there was a change in the direction of drainage, from north-trending in the Western Amazon to east-trending and transcontinental (Hoorn et al. 2017; Albert et al. 2018).

On the other hand, biodiversity patterns in the eastern part of the Amazon seem to respond more to the climatic oscillations during Pliocene and Pleistocene (Cheng et al.

2013), than to geologic events (Rossetti et al. 2005; Aleixo and Rossetti 2007). The alternation of drier and colder climates during the glacial cycles influenced the retraction and expansion of the forests, especially in the eastern Amazon (Haffer 1969; Van Der Hammen and Hooghiemstra 2000).

Although the vast majority of species are widely distributed in the eastern part of the Amazon Forest, important examples of endemism highlight the importance of this region as a cradle of diversity. The Tapajós region houses two endemic lineages recently described within the genus *Marmosops* (Guimarães et al. 2021), one from the left bank of the Tapajós River (suggested by the authors as putative new undescribed species), and another extending from the right bank of the river to the left bank of the Xingu River (*Marmosops marina*). The same pattern was found for the genus *Neacomys* (Semedo et al. 2020, 2021); the endemic *N. vossi* is found exclusively on the right bank of the Tapajós River, while *N. elieceri* (also endemic) is found on both banks of this river.

The species richness and endemism of the Tapajós region highlight that this region presents a unique and vital mammal assembly that deserves attention concerning conservation priorities, which had been neglected until now due to a deficit of sampling efforts. The variation in the number of small mammal surveys published across the Amazon Biome is remarkable (Mendes-Oliveira 2015). Furthermore, the approach used in each survey is also variable, including fully field-based studies (e.g., Abreu-Júnior et al. 2017) and integrated field and molecular-based studies (e.g., Patton et al. 2000, the present study), with differing resolution in species identification and therefore in the completeness of the species lists. All these facts prevent us from quantitatively comparing the diversity patterns of small mammals across the Amazon. At the same time, these biases also highlight our poor knowledge of the Amazon Forest biodiversity. Indeed, sampling bias is often referred to as a drawback in biodiversity studies in the Amazon (Kress et al. 1998; López-Osorio and Miranda-Esquivel 2010). Increasing research efforts to remote areas of the Amazon, filling basic knowledge gaps about biological diversity, and investigating the processes that led to currently observed biodiversity patterns are crucial. This data can be used as a source of information for future studies on conservation, resource management, biodiversity, and biogeography.

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**Authors' contributions:** Joyce R. Prado: Conceptualization, Formal analysis, Methodology, Validation, Visualization, Writing – original draft. Rita G. Rocha: Conceptualization, Funding acquisition, Methodology, Validation, Visualization, Writing – original draft. Heitor B. Silva: Formal analysis, Methodology, Validation, Visualization, Writing – original draft. Ana Cristina Mendes-Oliveira: Conceptualization, Funding acquisition, Investigation, Methodology, Validation, Visualization, Writing – original draft. Regeane C. L. Pontes: Investigation, Methodology, Validation, Visualization, Writing – original draft. Paula Cristina R. de A. Maués: Investigation, Methodology, Validation, Visualization, Writing – original draft. Leonora P. Costa: Conceptualization, Funding acquisition, Investigation, Methodology, Validation, Visualization, Writing – original draft.

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**Data Availability** Sequences will be deposited at the Genbank after acceptance of the manuscript.

**Data Availability** All data generated or analyzed during this study are included in this article and its supplementary information files. All generated sequences will available in the GenBank Nucleotide Database after manuscript acceptance.

**Code Availability** Not applicable.

## Declarations

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## Authors and Affiliations

Joyce Rodrigues do Prado<sup>1,2</sup> · Rita G. Rocha<sup>3,4,5</sup> · Heitor Bissoli-Silva<sup>1,2</sup> · Ana Cristina Mendes-Oliveira<sup>6</sup> · Regeane C. L. Pontes<sup>6</sup> · Paula Cristina R. de A Maués<sup>6</sup> · Leonora Pires Costa<sup>1,5</sup>

✉ Joyce Rodrigues do Prado  
[joycepra@gmail.com](mailto:joycepra@gmail.com)

<sup>1</sup> LaMaB, Laboratório de Mastozoologia e Biogeografia - Departamento de Ciências Biológicas, Centro de Ciências Humanas e Naturais, Universidade Federal do Espírito Santo, Av. Fernando Ferrari 514, 29075-910 Goiabeiras, Espírito Santo, Brasil

<sup>2</sup> Departamento de Ciências Biológicas, Escola Superior de Agricultura “Luiz de Queiroz”, Universidade de São Paulo, Piracicaba, SP, Brasil

<sup>3</sup> Centro de Investigação em Biodiversidade e Recursos Genéticos, CIBIO, InBIO Laboratório Associado, Universidade do Porto, Campus de Vairão, 4485-661 Vairão, Portugal

<sup>4</sup> BIOPOLIS Program in Genomics, Biodiversity and Land Planning, CIBIO, Campus de Vairão, 4485-661 Vairão, Portugal

<sup>5</sup> Programa de Pós-Graduação em Ciências Biológicas, Centro de Ciências Humanas e Naturais, Universidade Federal do Espírito Santo, Av. Fernando Ferrari 514, 29075-910 Goiabeiras, Espírito Santo, Brasil

<sup>6</sup> Laboratório de Ecologia e Zoologia de Vertebrados, Instituto de Ciências Biológicas, LABEV, Universidade Federal do Pará, Belém, Brasil