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Research Article

A hint on the unknown diversity of eastern Andes: high endemicity and new species of mammals revealed through DNA barcoding

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The eastern Andean slopes harbours a diverse fauna with multiple endemic and endangered species. The region is identified as a biodiversity hotspot with high conservation priority. However, it remains one of the least studied in South America regarding the diversity of mammals. Here we present new data on the diversity of non-volant small mammals (marsupials and rodents) from Parque Nacional del Río Abiseo (PNRA), a poorly known, remote site located in the eastern Andean slopes in central-northern Peru. We sequenced the mitochondrial gene cytochrome b to provide identification of the collected specimens, and to discuss zoogeographic patterns of the species from PNRA and closely related taxa. In 15 days of sampling at PRNA we registered 16 species (12 rodents, 4 marsupials) on montane forests between 2500 and 2800 m above sea level (asl). Combined with results from previous surveys, the diversity of non-volant small mammals at PNRA (23 species) is the highest ever recorded for high Andes. Remarkably, only four of the 16 species recorded in our expedition could be assigned to described species based on molecular identification. The remaining 12 species need urgent taxonomic attention, several of which are potentially new to science. Moreover, 11 of the 16 species (69%) registered are currently unknown from other sites, suggesting a large beta diversity. A combination of exceptional levels of endemism in Andean montane forests and an obvious sampling bias resultant of the lack of comprehensive surveys explain the high number of 'unique' species at PNRA. Our phylogenetic analyses suggest that the non-volant small mammals from PNRA seem to have diverse phylogeographic affinities, with a closer proximity with central Andes. The scarcity of sequenced samples for comparative analyses from multiple Andean sites is, however, a major barrier to the development of accurate historical reconstructions for these endemic faunas.

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Introduction

Mountains are biogeographic features that can play a pivotal role in the diversification of the biota, acting as barriers or bridges, or even as reservoirs of biodiversity (Perrigo et al., 2020). The Andes are the longest continental mountain range on Earth (Boschman, 2021), and the Amazonian slopes of the Andes are home to an unparalleled diversity of species, many of which are endemic (Amori et al., 2013; Myers et al., 2000; Schuler et al., 2011). However, the region is still poorly studied and many aspects of its biodiversity remain largely unknown (Lehr et al., 2013; Lehr & Catenazzi, 2011; Pacheco et al., 1995, 2011; Rodriguez & Catenazzi, 2017). These highly diverse and poorly known regions require targeted efforts in fieldwork exploration and taxonomic revisions in order to allow a better understanding of diversity and endemicity patterns, which are crucial for evaluating research and conservation priorities (e.g., Patton & da Silva, 1998; Voss & Emmons, 1996). Commonly, species surveys and inventories in remote areas are expected to result on the discovery of many unknown species. Therefore, such studies are imperative to help uncover the still hidden biodiversity of the richest areas of the globe, including vast unexplored territories along the Andes.

Vertebrates are commonly the best-known groups of most faunal assemblages globally, but small sized mammals (i.e., rodents and didelphid marsupials) are, still, largely unsampled in vast portions of the Neotropics, including eastern Andean slopes, areas that have been documented as important biodiversity hotspots for these groups (Maestri & Patterson, 2016; Prado et al., 2015; Rengifo et al., 2022). An important factor hindering rapid advances in diversity recognition in these hyperdiverse but poorly studied areas is the difficulty of species identification. For Neotropical small mammals, for example, no revisionary attention has been devoted to many groups, and literature resources for taxonomic identification are often very limited. Even for groups where a taxonomic evaluation is available, the possibility of cryptic and/or endemic species complicates the task of identifying the specimens from a given survey in a short time. The sequencing of molecular markers (DNA barcodes) provides an operational framework for taxonomic identification (Hubert & Hanner, 2015) and the discovery of cryptic species in all vertebrate groups (e.g., Borisenko et al., 2008; Clare et al., 2007; Moraes et al., 2017; Müller et al., 2013; Padial & De La Riva, 2007; Rocha et al., 2011). This technique has been successfully used to accelerate and improve species identification, including Andean inventories (e.g., Pinto et al., 2018).

In an effort to help accelerate biological diversity discovery of the Neotropics, we conducted an exploratory expedition to sample non-volant vertebrates in Parque Nacional del Río Abiseo (PNRA), a remote and poorly sampled area located along the eastern slopes of the Cordillera Oriental of the central Andes (Ramos, 2020), in the departments of San Martín and La Libertad, central-northern Peru. PNRA is a World Heritage Site that protects the watershed of the Río Abiseo, covering an area of 274,520 hectares that range from 350 to 4349 m asl (Ocampo & Calderón, 1997; Ramírez & Vela, 2003–2007). Although PNRA is well known from its numerous archeological sites, its flora and fauna have received comparatively little scientific attention (Leo, 1995). Nonetheless, the few faunal surveys conducted in the area resulted on the discovery of several new species of vertebrates (Lehr et al., 2013; Lehr & Catenazzi, 2011; Leo & Gardner, 1993; Leo & Romo, 1992; Rodriguez & Catenazzi, 2017; Rodríguez & Mamani, 2020), suggesting that much of the local diversity is yet to be revealed.

Herein, we report the diversity of non-volant small mammals (defined as species that are approximately less than 1 kg in weight in groups such as rodents, marsupials, shrews, and tree shrews: Lim & Pacheco, 2016) registered during our expedition to PNRA, which visited montane forests ranging from 2578 to 2780 m asl at the northwestern portion of the park (results from the surveys of amphibians and squamate reptiles will be published elsewhere). We used partial DNA sequences of the mitochondrial gene cytochrome b (CYTB) as an efficient identification method to corroborate or improve the preliminary identifications performed in the field (largely based on external phenotypic characters). For these taxonomically challenging groups, we present the results of molecular phylogenetic analysis using PNRA sequences and other comparative sequences available on GenBank and evaluate, case by case, the possible identity of the specimens collected. Together with phylogenetic results, we consider genetic distances and geographical and ecological information when available to discuss which of the taxa collected might represent distinct lineages that merit further investigation and formal description. We evaluated phylogeographic data of species from PNRA

and closely related taxa to uncover zoogeographic patterns and endemicity along the central Andes.

Materials and methods

Sampling sites

Three main ecological landscapes are present at PNRA: tropical alpine vegetation; humid tropical montane forests; and a humid premontane forest zone (Young et al., 1994). These landscapes are replaced from higher to lower elevations. Montane forests cover 53% of PNRA, and are home to a number of plants and animals found nowhere else on Earth (Lehr et al., 2013; Young et al., 1994). Our expedition sampled only the humid tropical montane forest landscape in the northwestern portion of the PNRA, in the department of San Martín, from August 11 to September 1, 2018. This remote area was accessed after 1.5 days by mule and foot from Los Alisos, Pataz (≈3000 m asl, Department of La Libertad), in the Marañón Valley. Systematic standardized sampling was conducted from 14–29 August at the localities of La Playa and Las Papayas, at the upper Río Montecristo basin (Fig. 1). We sampled sites that range from 2620 to 2780 m asl at La Playa, and from 2660 to 2700 m asl at Las Papayas (Supplemental Table 1). Besides standardized sampling conducted at these sites, we sampled the locality of Macedonio for a single night, August 25, also in the humid tropical montane forest at the upper Río Montecristo area, and accessed after nearly 3 h by foot from La Playa; the sampling sites at Macedonio (Fig. 1) range from 2578 to 2582 m asl (Supplemental Table 1).

Sampling methods

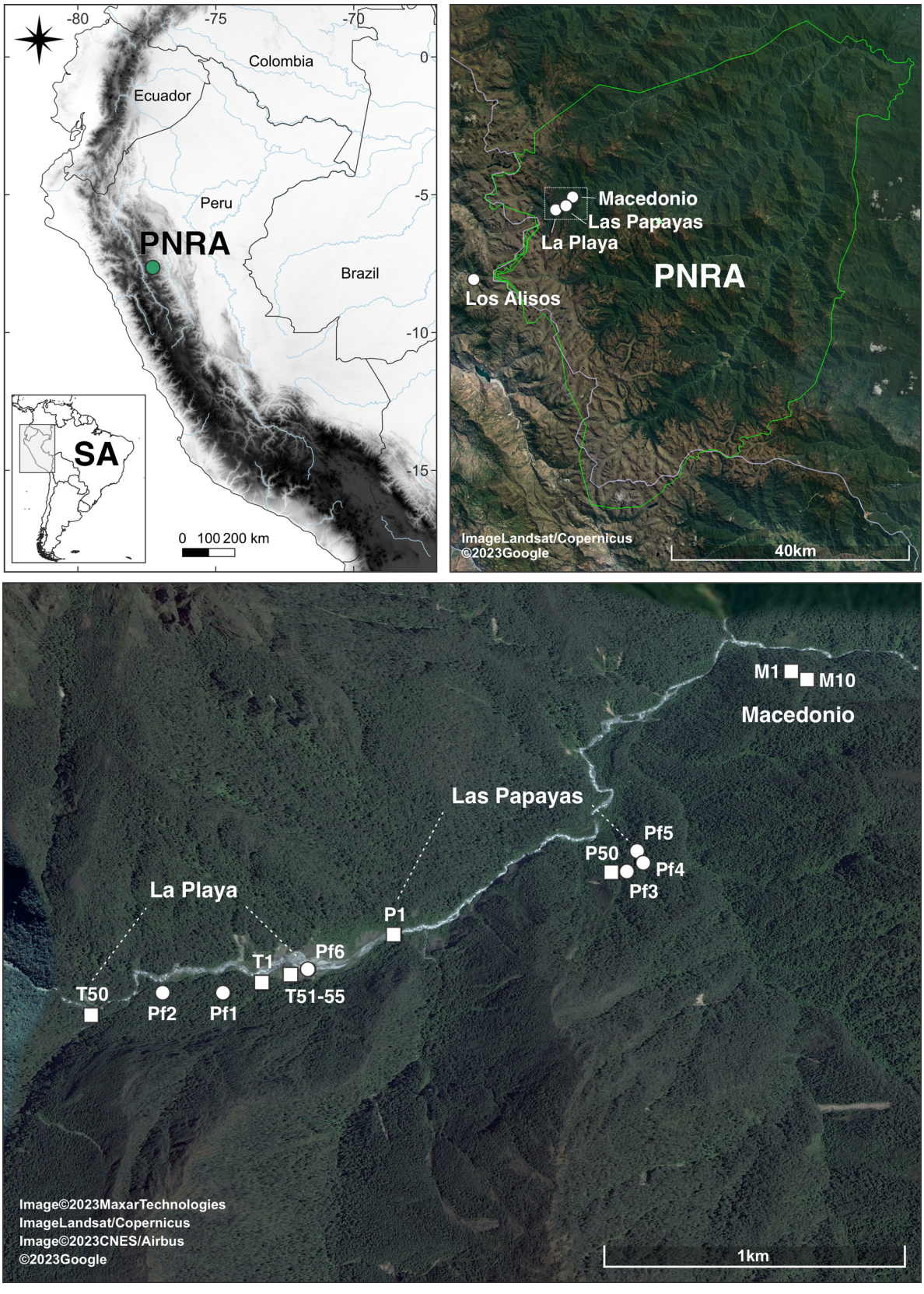
Sherman traps (measuring $25 \times 8 \times 9$ cm and $43 \times 12.5 \times 14$ cm), Victor metal pedal rat traps, Conibears (Duke 110BT Single Spring Body Grip), and pitfall traps with drift fences (with 20 L buckets) were used to survey diversity of non-volant small mammals (Voss & Emmons, 1996). The localities of La Playa and Las Papayas were our main sampling sites, and were sampled using Sherman, Victor and Conibears (hereafter collectively called *standard* traps), and pitfall traps. The standard-trapping for small mammals consisted of two main traplines, one at La Playa and one at Las Papayas, each with 50 stations 10 m apart from each other (T1–T50 at La Playa, and P1–P50 at Las Papayas; Fig. 1; Table 1). Each station contained three traps, two set on the ground (usually next to fallen trunks, inside hollow logs, under large leaved vegetation, or beneath viny tangles and piled branches) and one set on the understory, above the ground at heights up to 2.5 m (tied to lianas, tree trunks, and other woody supports). Most of our stations were mixed, containing either two Shermans + one Victor trap, or two Shermans + one Conibear trap, but some stations were solely composed of Sherman traps. Sherman traps were set both on the ground and above the ground. Victor traps were sometimes set on the ground, but mostly on the understory. Conibears were uniquely set above the ground, tied to tree trunks and other potential paths of small mammals. The traps were baited with a ground-up mixture of rolled oats, peanut butter, birdseed, raisins, and vanilla extract (in 6:3:1:1:1 proportion); the bait was renewed every other day in most situations, or whenever necessary (in cases of baits being consumed by captured individuals, by insects and other animals, or washed away).

The pitfall-trapping effort consisted of 40 20-liters plastic buckets distributed in six lines (Pf1–Pf6, Fig. 1; Table 1). Three lines were installed at La Playa and three lines at Las Papayas. Each pitfall line contained several buckets buried levelled to the soil surface and spaced 5 m apart; a continuous sheet of plastic drift fence supported by wooden stakes ran the whole length of each line. Two of the three pitfall lines set in La Playa contained five buckets (Pf1 and Pf6), while one line contained ten buckets (Pf2). Two of the three pitfall lines set in Las Papayas contained five buckets (Pf3 and Pf5), while one contained 10 buckets (Pf4). Pitfall lines were set nearby our standard trapped trails, which transverse both well-drained and swampy primary vegetation. One pitfall line, however, was set along an open vegetation area with rocky substrate bordering the left margin of the Río Montecristo, close to our camping site in La Playa (Pf6). At this site, we also set ten additional Sherman traps distributed in five stations with two traps each (T51–T55; Fig. 1; Table 1).

The site of Macedonio was sampled for a single night using exclusively standard-trapping. At this site, we set 10 stations 10 apart from each other, each station containing three traps (two Shermans + one Conibear).

Traplines were checked once daily (usually in the early morning). Trapping effort was calculated by multiplying the number of traps or buckets by the nights the traps were open at each site (Table 1). The standard-trap effort at La Playa, Las Papayas, and Macedonio was 2160, 1800, and 30 trap nights, respectively. The pitfall effort at La Playa and Las Papayas was 230 and 240 pitfall nights, respectively. Therefore, the total sampling effort considering the three sites corresponded to 3990 standard-trap nights and 470 pitfall nights.

In addition to traps, we performed active searches along and nearby our trapping trails, targeting diurnal and/or crepuscular mammals (during daylight hours,


-80
-75
-70
0
-5
-10
-15
Colombia
Ecuador
Peru
Brazil
PNRA
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0 100 200 km
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Las Papayas
La Playa
PNRA
Los Alisos
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©2023Google
40km
M1
M10
Macedonio
Las Papayas
Pf5
P50
Pf4
Pf3
La Playa
P1
Pf6
T1
T50
Pf2
Pf1
T51-55
Image©2023MaxarTechnologies
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1km

Fig. 1. Location of Parque Nacional del Río Abiseo (PNRA) in northern Peru (top left), with closer views of the park limits, showing relevant sites mentioned in the text (top right), and the sampling trails and stations at La Playa, Las Papayas, and Macedonio (bottom). In the bottom panel, squares represent traplines in La Playa (T1–T50; T51–T55), Las Papayas (P1–P50), and Macedonio (M1–M10), while circles represent pitfall traps in La Playa (Pf1–Pf2, Pf6) and Las Papayas (Pf3–Pf5). For detailed information on altitude and geographic coordinates, see Supplemental Table 1. For detailed information on sampling effort in each trapline, see Table 1.

Table 1. Sampling effort for each trapline set for non-volant small mammals at Parque Nacional del Río Abiseo.

Locality	Trapline	Survey dates (# of nights)	Sherman	Victor	Conibear	Pitfall	Effort
La Playa	Transect T1–T50	14–28 August (14)	125	15	10		2100
La Playa	Transect T51–T55	23–29 August (6)	10				60
La Playa	Pitfall Pf1	15–28 August (13)				5	65
La Playa	Pitfall Pf2	15–28 August (13)				10	130
La Playa	Pitfall Pf6	22–29 August (7)				5	35
Las Papayas	Transect P1–P50	17–29 August (12)	125	15	10		1800
Las Papayas	Pitfall Pf3	17–29 August (12)				5	60
Las Papayas	Pitfall Pf4	17–29 August (12)				10	120
Las Papayas	Pitfall Pf5	17–29 August (12)				5	60
Macedonio	Transect M1–M10	25–26 August (1)	20		10		30

concentrated on early mornings and late afternoons). Active searches were conducted for 12 days for about 5 h per day, usually in the first (dawn) and last hours (dusk) of the day.

Specimen capture, collection, and preparation

Collections were made under permits issued by the *Servicio Nacional de Áreas Naturales Protegidas por el Estado* (SERNANP 027-2018). Permits to access genetic resources were granted by *Servicio Nacional Forestal y de Fauna Silvestre* (SERFOR 002-2021). Captured specimens of non-volant small mammals were examined and provisionally identified to species with base on morphological characters readily accessible on freshly collected material, and by consulting relevant literature (e.g., Gardner, 2008; Pacheco et al., 1995, 2011; Patton et al., 2015; Voss, 1988, 2003; Voss et al., 2014). Selected live individuals of common species were released, while specimens kept as reference material were collected and preserved following recommendations of the Animal Care and Use Committee of the American Society of Mammalogists (Sikes, 2016).

Collected specimens were prepared as either standard skins with accompanying skulls and carcasses in fluid (preserved in 10% formalin and maintained in 70% ethanol), or as fluids with or without the skulls removed and subsequently cleaned. For all specimens collected, two tissue sample aliquots (liver or muscle tissue) were collected and preserved in 100% ethanol. Voucher specimens were deposited at the Departamento de Mastozoología del Museo de Historia Natural, Universidad Nacional Mayor de San Marcos, Perú (MUSM) and at the Coleção de Mamíferos do Laboratório de Zoologia de Vertebrados da Escola Superior de Agricultura 'Luiz de Queiroz', Universidade de São Paulo, Brasil (LMUSP).

Estimates of species diversity

Based on our records from PNRA, we computed rarefaction and extrapolation (R/E) curves of species diversity based on Hills number (Chao et al., 2014, 2016) using iNEXT Online software, available at https://chao.shinyapps.io/iNEXTOnline/. We computed R/E curves of species diversity based on both abundance and incidence data. These curves provide visualization of the sampled diversity and estimate the expected number of species to be registered if a larger sampling were to be performed.

For both abundance and incidence data curves, we combined data from our two systematically sampled sites (La Playa and Las Papayas) and considered them as a single assemblage as these localities were very close to each other (Fig. 1), and therefore independence could not be assumed. Curves based on abundance data used as information the total number of specimens registered ($N = 278$[1]) and the number of specimens registered for each species. Curves based on incidence data used

[1]Although the total number of specimens registered in La Playa + Las Papayas equals to 309, we excluded 31 records of "*Nephelomys* spp." and computed the R/E abundance curves with the remaining 278 records. The 31 records excluded correspond to the specimens of *Nephelomys* released in the field, that could only be confidently identified to the genus level and therefore could not be included on the R/E abundance curves.

as information the total number of sampling days ($N = 15$), and the number of sampling days in which each species was recorded. As settings, we used a diversity order $q = 0$, number of knots = 100, bootstrap = 1000, and level of confidence = 0.95. The only setting that differed for abundance and incidence data curves was the endpoint, set to 556 for the abundance curves (twice the total number of registers considered), and to 45 for the incidence curves (triple the total of sampling days).

Genetic identification (DNA barcoding)

To provide molecular identification of specimens collected at PNRA, we obtained DNA sequences of the mitochondrial gene cytochrome b (CYTB) from collected specimens and conducted phylogenetic analysis combining these with CYTB sequences available at GenBank. For most specimens, we aimed to obtain partial sequences of ca. 800 bp, but in some cases we attempted to sequence the complete CYTB. This is the molecular marker with the highest number of comparative sequences available for most groups investigated here, and its effectiveness in species identification for small mammals has been repeatedly tested by multiple studies (e.g., Bradley & Baker, 2001; Patton et al., 1996; Rocha et al., 2011; Smith & Patton, 1991).

We extracted DNA of samples using the Wizard Genomic DNA Isolation kit (Promega Corp., Madison, WI) following the manufacturer's protocol. We performed PCR amplifications of the CYTB fragments using either the Illustra puReTaq Ready-To-Go PCR beads (GE Healthcare UK Limited) or PCR Master Mix (Promega Corp., Madison, WI), using the primers MVZ05 and MVZ16 (Smith & Patton, 1993) optimized for mammals. For cases where the complete CYTB was targeted, amplification of the entire gene was done in two overlapping fragments using the primer pairs MVZ05 and MVZ16, and MVZ35 and MVZ 14 (Smith & Patton, 1993). Amplifications with Ready-To-Go PCR beads were done with 0.5–1.0 µL of DNA (for ca. 20–50 ng of total DNA), 0.5 µL of each primer, and sterile water to a final volume of 25 µL. Amplifications with PCR Master Mix were done with 0.5–1.0 µL of DNA, 0.5 µL of each primer, 6.2 µL of PCR Master Mix and sterile water to a final volume of 12.5 µL. CYTB PCRs consisted of initial denaturation at 94 °C for 5 min, followed by 39 cycles with denaturation at 94 °C for 30 s, annealing at 48 °C for 45 s, polymerization at 72 °C for 45 s, and a final extension at 72 °C for 5 min. We cleaned the PCR products using Exonuclease I and Shrimp Alkaline Phosphatase (Hanke & Wink, 1994), and conducted sequencing reactions with the ABI Big Dye chemistry (Applied Biosystems, Inc., Foster City, California, USA), using the same primers used for PCRs. We sequenced the products in both directions on an ABI 3130 DNA Analyzer automatic sequencer (Applied Biosystems, Inc., Foster City, California, USA). Sequencing was performed at the *Laboratório de Biologia Molecular* (Molecular Biology Laboratory) at Museu Paraense Emílio Goeldi, Belém, Brazil. Raw sequence chromatographs were edited using Geneious Pro v8.1.5 (https://www.geneious.com). All sequences generated in this study have been deposited in GenBank (accession numbers in Supplemental Table 2).

We conducted independent phylogenetic analysis for each genus collected at PNRA. We assembled phylogenetic datasets by performing the following steps: (1) After sequence edition, we investigated nucleotide similarity between our sequences from PNRA and other sequences available at the National Center for Biotechnology Information (NCBI) Database (GenBank). This was performed by using the Basic Local Alignment Search Tool (BLAST) of the NCBI; (2) We then retrieved from GenBank the sequences that presented the highest similarity to our newly produced sequences, sequences from other closely related (usually congeneric) samples and species, and sequences from additional taxa to be used as outgroup.

In total, we have produced 10 distinct CYTB datasets, whose alignments were performed using the MUSCLE (Edgar, 2004) plugin in Geneious Pro v8.1.5 – with default parameters. Phylogenetic analyses were conducted using maximum likelihood (ML) in RAxML v8 (Stamatakis, 2014), on the CIPRES Portal (Miller et al., 2010). The substitution model used for each dataset was GTRGAMMA, and the model parameters were estimated from the data. For each dataset, a rapid Bootstrap analysis (of 1000 pseudo replicates) and search for the best-scoring ML tree was conducted in one single program run. Distances for pairwise comparisons (uncorrected *p*-distances) were calculated in MEGA 11.0.11 (Tamura et al., 2021). For some species with comparative samples available on GenBank we produced haplotype networks to visualize the relationships among PNRA haplotypes and haplotypes from other localities, as well as to estimate the number of segregating mutations among them using the Median Joining algorithm (Bandelt et al., 1999) in the program PopART (Leigh & Bryant, 2015).

Results

Sampling success and species diversity

A total of 308 non-volant small mammals were captured (289 rodents, 19 marsupials), of which 195 were

released (192 rodents, 3 marsupials), and 113 were retained as voucher specimens (97 rodents, 16 marsupials; see Supplemental Table 2). Two additional rodent specimens were registered during active searches, but not captured (see details below). Therefore, during our field expedition to PNRA, there were a total of 310 records for non-volant small mammals if we consider the sites of La Playa, Las Papayas, and Macedonio (Table 2). Considering the sampling sites, La Playa contributed with most of the records (249), followed by Las Papayas (60) and Macedonio (1).

Sherman traps were responsible for the highest number of captures, followed by pitfall traps, Victor traps and active search. The average sampling success for all methods was 6.86%, with pitfalls presenting the highest relative success rate, followed by Sherman traps, active searches, and Victor traps. The number of unique species sampled was also higher for pitfalls, followed by Sherman traps and active searches (Table 2).

The total number of non-volant small mammal species registered in the field was 16, with 4 species of marsupials and 12 species of rodents, and the attributed species names are listed in Table 3. From those, we collected samples for 15 species – the species '*Microsciurus*' 'species 2' (*sensu* Abreu et al., 2020) was exclusively recorded through observations and photos during active search at Las Papayas (Fig. 2), but not captured.

Although the number of captures were much higher at La Playa (249, versus 60 at Las Papayas), the number of species registered at each site was not as discrepant, with 12 species (3 marsupials and 9 rodents) registered in La Playa and 10 species (2 marsupials and 8 rodents) registered in Las Papayas. For the site of Macedonio, sampled during a single night with few standard traps, a single specimen (1 rodent) was recorded.

The 15 species sampled during the expedition and provisionally recognized in the field were supported by DNA barcodes. There were, however, misidentification of the collected specimens of two species in the genus *Nephelomys*, indicating that we were unable to consistently identify them in the field. Consequently, the 31 specimens of *Nephelomys* released in the field can only be confidently identified to genus and are treated as '*Nephelomys* spp.' (Table 3).

The rarefaction and extrapolation curves of species diversity based on our records from PNRA are shown in Fig. 3. Both abundance-based and incidence-based curves indicate that the expected number of species recorded would be slightly larger, approximately 17–18 species, if increased sampling were performed. Extrapolations suggest that the local species diversity could be completely sampled with around 500 captures, and about 30 days of sampling.

Molecular identity of small mammals at PNRA

We obtained CYTB sequences for 89 samples of small non-volant mammals collected during our sampling at PNRA (Supplemental Table 2). According to our results, these samples represent 15 species-lineages (4 marsupials and 11 rodents). While 4 of those lineages were assigned to described taxa, we were unable to confidently associate 11 of those to any known valid species for which CYTB data is available on GenBank. Below we provide a detailed description of our results for each group sampled and each species identified by our analyses.

Order Didelphimorphia

Family Didelphidae

Genus *Gracilinanus* Gardner and Creighton, 1989. We captured three specimens of *Gracilinanus* during sampling at PNRA (Fig. 2), all retained as reference material (Supplemental Table 2). Individuals were trapped both at La Playa and Las Papayas, exclusively by pitfall traps (Table 3). CYTB sequences were produced for all three specimens, with a single haplotype observed. BLAST of CYTB sequences indicate that specimens of *Gracilinanus* from PNRA are very

Table 2. Summary of sampling effort and success for non-volant small mammals at Parque Nacional del Río Abiseo.

Trap type	Sampling effort	Total # of records	Record success rate	# of species recorded	Exclusive species[a]
Pitfall	470	56	11.91%	10	6
Sherman	3200	246	7.69%	9	2
Victor	430	4	0.93%	3	0
Conibear	360	0	0%	0	0
Active search	60	4[b]	6.67%	3	2
Total	4520	310	6.86%	16	

[a]Number of species that were exclusively sampled by each sampling method. [b]Active searches registered four specimens of non-volant small mammals, and although two of them were not captured (only photographed; see details on Table 3), they were both included to compute success rate and number of species recorded by this method.

Table 3. Small mammals recorded at Parque Nacional del Río Abiseo by different sampling methods.

	La Playa				Las Papayas				Macedonio
Taxa	**Pt[a]**	**Sh G[b]; Sh T[c]**	**Vt[d]**	**AS[e]**	**Pt**	**Sh G; Sh T**	**Vt**	**AS**	**Sh G; Sh T**
Didelphimorphia/Didelphidae									
Gracilinanus sp.	2 (2)[f]				1 (1)				
Marmosa (*Micoureus*) sp.		1; 1 (2)							
Marmosa (*Stegomarmosa*) sp.	1 (1)								
Marmosops (*Marmosops*) sp.					8 (8)	5; 0 (2)			
Rodentia									
Cricetidae									
Akodon orophilus	7 (6)	38; 0 (7)			3 (2)	3; 0			
'*Chibchanomys*' sp.					1 (1)				
Microryzomys sp.	12 (11)				6 (6)				
Neacomys spinosus					1 (1)				
Nephelomys ricardopalmai		11; 0 (11)	1 (1)						
Nephelomys keaysi		1; 0 (1)				1; 0 (1)			
Nephelomys spp.[g]		26; 0				4; 1			
Thomasomys sp.1 (gr. *cinereus*)	2 (2)								
Thomasomys sp.2 (gr. *aureus*)		1; 0 (1)	1 (1)						
Thomasomys sp.3 (gr. *notatus*)	1 (1)	2; 1 (2)			1 (1)	3; 2 (2)			
Thomasomys sp.4	4 (3)	125; 7 (27)	2 (2)	1[h] (1)	1 (1)	14; 2 (3)			1; 0 (1)
Sciuridae									
'*Microsciurus*' 'species 2'[i]								1[j]	
Echimyidae									
Dactylomys sp.				2[k] (1)					

[a]Pt = Pitfall. [b]Sh G = Sherman set on ground. [c]Sh T = Sherman set on tree. [d]Vt = Victor trap. [e]AS = Active Search. [f]Number of specimens collected are shown within parentheses. [g]Either *Nephelomys keaysi* or *N. ricardopalmai*. These were specimens of *Nephelomys* released in the field, for which taxonomic identity cannot be confidently retrieved for species level. [h]Specimen found dead in the trail. [i]Identification follows Abreu et al. (2020). [j]A single specimen of '*Microsciurus*' 'species 2' was recorded during the expedition, but we were unable to capture it, and only photos were taken (Fig. 2). [k]Two specimens of *Dacylomys* sp. were recorded during the expedition, but only one of them was captured (Fig. 2). The second specimen was photographed in the field, but not captured.

distinctive from any sequence available on GenBank. The highest pairwise identity found was of 88.7%, with a specimen identified as *Gracilinanus aceramarcae* (Tate, 1931) from Cordillera de Vilcabamba, Peru.

We included in the phylogenetic analyses all representatives of *Gracilinanus* available on GenBank and used representatives of closely related genera as outgroups (*Cryptonanus* Voss et al., 2005, *Lestodelphys* Tate, 1934, *Thylamys* Gray, 1843, and *Chacodelphys* [Shamel, 1930], based on the phylogenetic results of Díaz-Nieto et al., 2015). Our phylogenetic reconstruction recovered the PNRA *Gracilinanus* as a sister clade of *Gracilinanus aceramarcae* (Fig. 4), a species known from montane forest localities (above 2000 m asl) in Peru and northern Bolivia (Pacheco et al., 2020; Voss, 2022). Specimens of *Gracilinanus* from PNRA present a *p*-distance at the CYTB locus of 11.31% when compared to the single specimen identified as *Gracilinanus aceramarcae* on GenBank (Fig. 4; Supplemental Table 3). Semedo et al. (2014) found that corrected genetic distances at the CYTB locus among species of *Gracilinanus* average 12.9% (between *G. microtarsus* [Wagner, 1842] and *G. aceramarcae*) to 18.2% (between *G. peruanus* [Tate, 1931] and *G. emiliae* [Thomas, 1909]). Using the same model of correction (Kimura 2-parameter), *Gracilinanus* specimens from PNRA differ from the closest related species, *Gracilinanus aceramarcae*, by 12.6 %. Based on our phylogenetic results and on the high values of divergence between sequencies from PNRA and currently recognized species of *Gracilinanus*, we treat specimens from PNRA as a putative new species, referred to as *Gracilinanus* sp.

Genus *Marmosa* Gray, 1821. Three specimens of *Marmosa* were captured at PNRA, two from the subgenus *Micoureus* Lesson, 1842 (trapped by Sherman traps at La Playa; Fig. 2) and another from the subgenus *Stegomarmosa* Pine, 1972 (trapped by pitfall at La Playa; Fig. 2) (Table 3). All three specimens were retained as vouchers and sequenced for the CYTB (Supplemental Table 2). CYTB sequences of the two specimens of the subgenus *Micoureus* presented a single haplotype, and the highest similarities recovered by BLAST were with specimens of *M.* (*Micoureus) rutteri* Thomas, 1924 (93.4–93.8% of similarity). The PNRA specimen of the subgenus *Stegomarmosa* showed highest similarity in the CYTB with *M.* (*Stegomarmosa)*

Fig. 2. Representatives of non-volant small mammal species registered at Parque Nacional del Río Abiseo. *Gracilinanus* sp. (A), *Marmosa* (*Micoureus*) sp. (B), *Marmosa* (*Stegomarmosa*) sp. (C), *Marmosops* sp. (D), '*Chibchanomys'* sp. (E), *Nephelomys keaysi* (F), *Nephelomys ricardopalmai* (G), *Thomasomys* sp.2 (gr. *aureus*) (H), *Thomasomys* sp.3 (gr. *notatus*) (I), *Thomasomys* sp.4 (J), *Dactylomys* sp. (K), and '*Microsciurus*' 'species 2' (L).

lepida (Thomas, 1888) (91.6–92.9%). We included in the phylogenetic analysis all samples from GenBank assigned to *Marmosa* and used as outgroup representatives of the closest related genera *Monodelphis* Burnett, 1830 and *Tlacuatzin* Voss and Jansa, 2003 (following phylogenetic results in e.g., Beck & Taglioretti, 2020; Silva-Neto et al., 2023; Voss & Jansa, 2009, 2021).

Our phylogenetic analysis recovers the PNRA specimens of the subgenus *Micoureus* as sister of a clade composed by *M.* (*Micoureus) rutteri* and *M.* (*Micoureus*) *parda* Tate, 1931 (Fig. 5). *Marmosa rutteri* is known from lowland rainforest (below about 800 m) in southeastern Colombia, eastern Ecuador, eastern Peru, and western Brazil (Voss et al., 2020), while *M. parda* is known from a few localities on the cloud-forested eastern Andean slopes of central Peru (Voss, 2022). The clade formed by *M. rutteri, M. parda,* and *M. (Micoureus)* from PNRA is recovered as sister to *M. (Micoureus) rapposa* Thomas, 1899. This species is distributed throughout the eastern slopes of the Andes (below about 2500 m asl) from southern Peru to southern Bolivia, and also on the lowlands of eastern Bolivia, Paraguay, and southwestern Brazil (Voss et al., 2020). Although the relationships between *M. rutteri, M. parda,* and *M. (Micoureus)* from PNRA are only weakly supported (<70% bootstrap), the clade formed by these

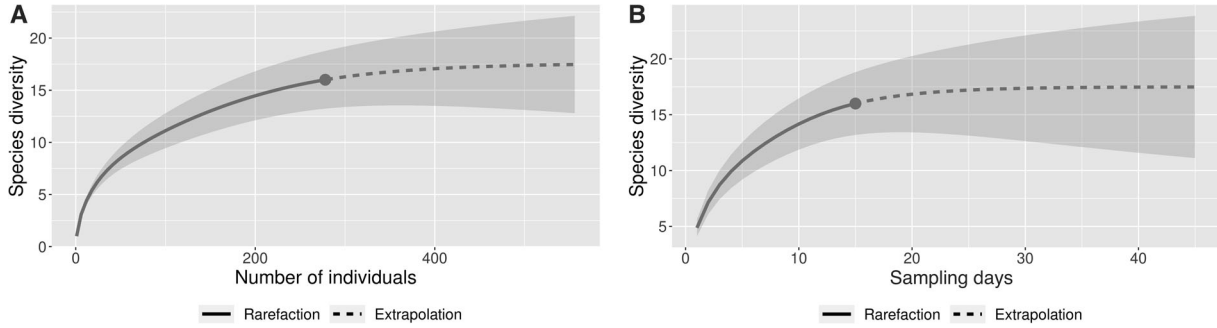

Fig. 3. Sample-size-based rarefaction curves (solid lines) and extrapolation curves (doted lines) of species diversity at Parque Nacional del Río Abiseo, based on combined abundance data and incidence data from our two systematically sampled sites - La Playa and Las Papayas (Fig. 1). Abundance data curves (A) were based on 278 records, and considered the number of records for each of the 16 species registered. Incidence data curves (B) were based on 15 sampling days, and considered the number of days in which each of the 16 species was registered.

three and *M. rapposa* is highly supported, indicating that the *Micoureus* from PNRA can be confidently assigned to the *M. rapposa* species group (sensu Voss et al., 2020). Specimens of *Marmosa* (*Micoureus)* from PNRA present a mean pairwise distance at the CYTB locus of 6.69, 6.72, and 8.11% when compared to *Marmosa rutteri, M. parda,* and *M. rapposa,* respectively. Mean pairwise sequence divergence among recognized species of the *M. rapposa* species group (*M. rutteri, M. parda,* and *M. rapposa*) range from 5 to 7% (Voss et al., 2020). Therefore, we treat specimens of *Marmosa* (*Micoureus)* from PNRA as a putative new species of the rapposa group, referred to as *Marmosa* (*Micoureus*) sp.

The *Stegomarmosa* from PNRA was recovered as closely related to *M. (Stegomarmosa) lepida* (Fig. 5), a species known from Amazonia and contiguous premontane forests along eastern Andes, including localities that range from sea level to about 1.600 m asl in Colombia, Venezuela, Ecuador, Peru, Brazil, Suriname, Guyana, and French Guiana (Guimarães et al., 2018; Voss, 2022). The *Stegomarmosa* from PNRA present a mean pairwise uncorrected distance at the CYTB locus of 7.96% when compared to *Marmosa lepida*. The clade formed by the PNRA specimen and *M.* (*Stegomarmosa) lepida* was highly supported and recovered as sister to the only other species recognized within the subgenus *Stegomarmosa, M. (Stegomarmosa) andersoni* Pine, 1972. This species is exclusively known from rainforest localities between 470 and 1100 m asl along the base of the eastern Andes in Peru (Zeballos et al., 2019), and is seemingly a highly divergent lineage (Voss et al., 2014) with a mean pairwise uncorrected distance at the CYTB locus of 14.74% and 15.13% when compared to *Marmosa (Stegomarmosa) lepida* and to the PNRA *Stegomarmosa*, respectively. Based on our phylogenetic results and on the relatively high values of divergence between the PNRA *Stegomarmosa* and currently recognized species, we treat the specimen from PNRA as a putative new species, referred to as *Marmosa* (*Stegomarmosa*) sp.

Genus *Marmosops* Matschie, 1916. Thirteen specimens of *Marmosops* were captured at PNRA (Fig. 2), all at Las Papayas, eight of which were trapped by pitfalls and five by Sherman traps (Table 3). We retained ten of those specimens as vouchers, and partial CYTB sequence was produced for all (Supplemental Table 2), with a single haplotype observed. Specimens of *Marmosops* from PNRA showed the highest similarity with CYTB sequences of *Marmosops* (*Marmosops*) *noctivagus* (Tschudi, 1845) (90.4–92.1% of similarity) and *M.* (*Marmosops*) *creightoni* Voss et al., 2004 (91.5–91.7%). We included in the phylogenetic analysis all samples from GenBank assigned to the subgenus *Marmosops* Matschie, 1916, and used as outgroup representatives of species in the subgenus *Sciophanes* Díaz-Nieto et al., 2016 (following phylogenetic results in Díaz-Nieto et al., 2016). Our phylogenetic reconstruction recovered the PNRA specimens as a clade sister of *Marmosops noctivagus* (Fig. 6). *Marmosops noctivagus* is a widespread species that occur in the Andes (usually below 2000 m asl) from Ecuador to Bolivia, and in the Amazonian lowlands as far eastward as the left bank of the Rio Tapajós (Gardner & Creighton, 2008; Voss, 2022), and includes at least four deeply divergent CYTB haplogroups (Díaz-Nieto et al., 2016). Although the sister relationship between the PNRA *Marmosops* and *Marmosops noctivagus* was not strongly supported, these two formed a highly supported clade with *Marmosops creightoni*, a species exclusively known from montane forests above 2000 m asl on the eastern slopes of the Andes in La Paz department, Bolivia (Voss, 2022). *Marmosops* from PNRA present a mean

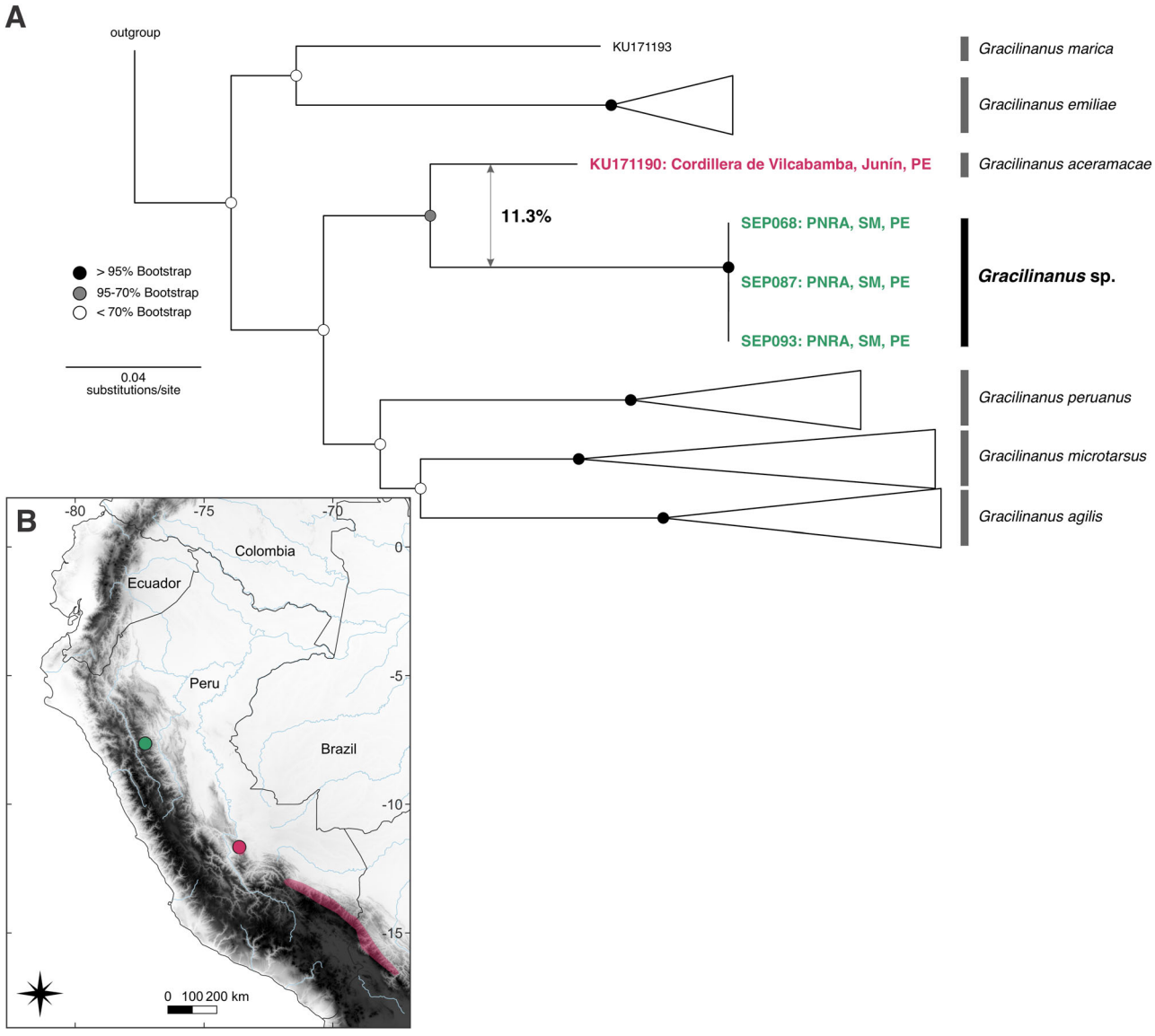

Fig. 4. Cytochrome b (CYTB) gene tree showing the relationships between *Gracilinanus* sp. from Parque Nacional del Río Abiseo (PNRA) (green) and other *Gracilinanus* samples available on GenBank (A), and sampling localities of the PNRA species and its sister taxa, *Gracilinanus aceramarcae* (pink) (B). The percentage value shown in the tree correspond to mean pairwise uncorrected distance at the CYTB locus. The phylogenetic tree was inferred using maximum likelihood in the program RAxML and included data for all species of *Gracilinanus* available on GenBank. Geographic information from the specimens included in the map are provided in the Supplemental Table 3. Species range (pink shadow) was obtained from IUCN (https://www.iucnredlist.org).

pairwise distance in the CYTB of 8.52% and 8.39% when compared to *Marmosops noctivagus* and *Marmosops creightoni* respectively, while *Marmosops noctivagus* and *Marmosops creightoni* differ by 9.32% on average (Fig. 6; Supplemental Table 3). Uncorrected genetic distances at the CYTB locus between recognized species of the subgenus *Marmosops* average 4.2–17.2% (Díaz-Nieto et al., 2016). Based on our phylogenetic results and on the relatively high values of divergence between sequencies from PNRA and currently recognized species of *Marmosops*, we treat specimens from PNRA as a putative new species referred to as *Marmosops* sp.

Order Rodentia

Family Cricetidae

Subfamily Sigmodontinae. Tribe Akodontini. Genus *Akodon* Meyen, 1833. We recorded 51 specimens of *Akodon* at PNRA. Individuals were trapped in both sites (La Playa and Las Papayas; Table 3) with pitfall (10

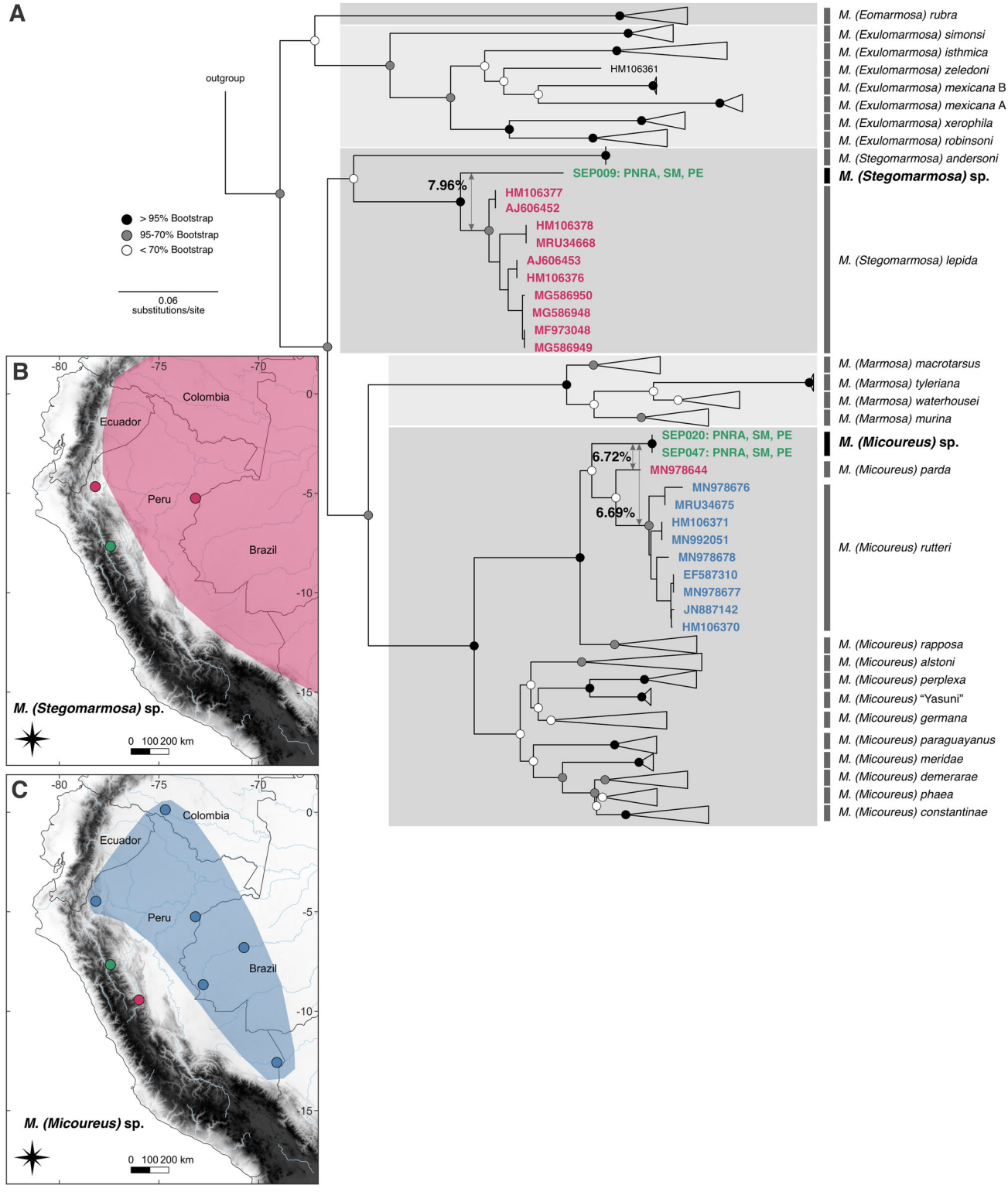

Fig. 5. Cytochrome b (CYTB) gene tree showing the relationships of *Marmosa* haplotypes sequenced from Parque Nacional del Río Abiseo (PNRA) specimens (green) (A), and sampling localities of the PNRA species and closely related taxa, *Marmosa (Stegomarmosa) lepida* (pink) (B), *Marmosa (Micoureus) parda* (pink) and *M. (Micoureus) rutteri* (blue) (**C**). Percentage values shown in the tree correspond to mean pairwise uncorrected distance at the CYTB locus. The phylogenetic tree was inferred using maximum likelihood in the program RAxML and included data for all species of *Marmosa* available on GenBank. Geographic information from the specimens included in the maps are provided in Supplemental Table 3. Species ranges (pink and blue shadows) were obtained from IUCN (https://www.iucnredlist.org).

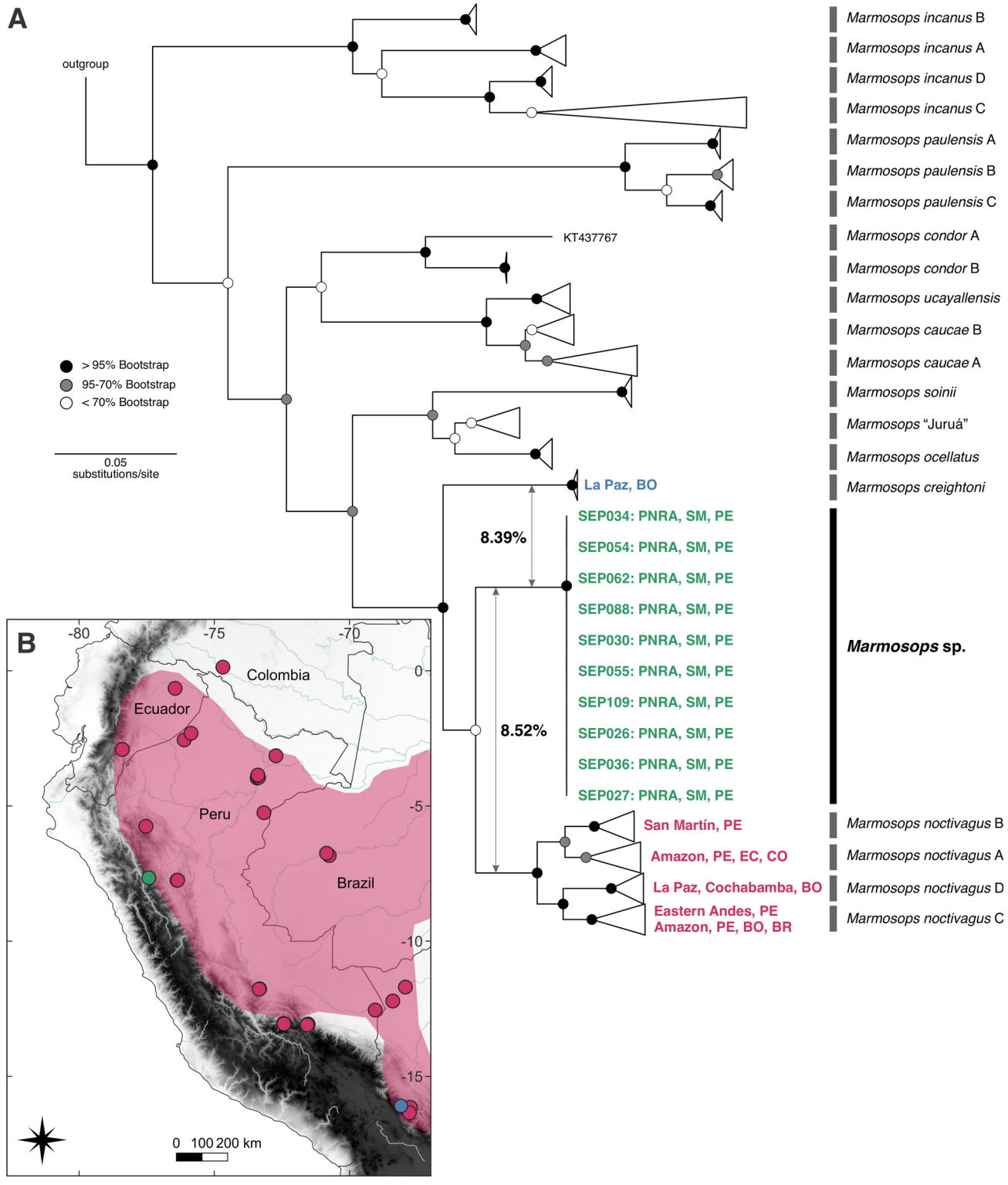

Fig. 6. Cytochrome b (CYTB) gene tree showing the relationships of *Marmosops* haplotypes sequenced from Parque Nacional del Río Abiseo (PNRA) specimens (green) (A), and sampling localities of the PNRA species and closely related taxa, *Marmosops noctivagus* (pink) and *Marmosops creightoni* (blue) (B). Percentage values shown in the tree correspond to mean pairwise uncorrected distance at the CYTB locus. The phylogenetic tree was inferred using maximum likelihood in the program RAxML and included data for all species of *Marmosops* available on GenBank. Geographic information from the specimens included in the map are provided in Supplemental Table 3. Species range (pink shadow) was obtained from IUCN (https://www.iucnredlist.org).

events) and Sherman (41 events) traps. We collected 15 specimens and produced partial CYTB sequences for 10 of those (Supplemental Table 2). Two unique haplotypes were recovered in the samples from PNRA, and the most common haplotype (found in 9 of 10 samples) differs from haplotypes observed in specimens of *A. orophilus* Osgood, 1913 from Chachapoyas, Amazonas, Peru (2804 m asl) and Mariscal Cáceres, San Martín, PE, by a single mutation (Fig. 7; Supplemental Table 3). All specimens of *Akodon* collected at PNRA were, therefore, identified as *A. orophilus*. This species is endemic to northern Peru and occurs only in humid forests on the eastern Andean slopes (between 1900 to 2860 m asl) east of the Río Marañón in the departments of Amazonas and San Martín (Jiménez et al., 2013; Pardiñas et al., 2015).

Tribe Ichthyomyini. Genus '*Chibchanomys*'. A single specimen tentatively assigned to the genus *Chibchanomys* Voss, 1988 was trapped by pitfall at Las Papayas (Table 3; Fig. 2). The partial CYTB sequence produced (Supplemental Table 2) showed the highest similarity with CYTB sequences of an unnamed species, '*Chibchanomys'* n. sp. from Cusco, Peru (90.5% of similarity). Phylogenetic analyses included all GenBank sequences available for the Tribe Ichthyomyini, and sequences of most extant genera in the Sigmodontinae as outgroup (following Salazar-Bravo et al., 2023). Our phylogenetic analysis recovered the PNRA specimen as sister of '*Chibchanomys'* n. sp., suggested as a possible unnamed genus and species from south Peru (Salazar-Bravo et al., 2023). The '*Chibchanomys'* from PNRA present a mean pairwise uncorrected distance at the CYTB locus of 9.48% when compared to '*Chibchanomys'* n. sp. from Cusco (Fig. 8; Supplemental Table 3). Based on our phylogenetic results and on the divergence values between the sequence from the PNRA and currently recognized species of the tribe Ichthyomyini, we treat the specimen from PNRA as a putative new species of the same unnamed genus and species from Cusco, referred to as '*Chibchanomys'* sp.

Tribe Oryzomyini. Genus *Microryzomys* Thomas, 1917. Eighteen specimens of *Microryzomys* were trapped using pitfall traps at PNRA, 12 in La Playa and 6 in Las Papayas (Table 3). We sequenced CYTB for 10 out of 17 collected specimens (Supplemental Table 2), and they are represented by six distinct haplotypes (Fig. 9). Currently, there are only two species of *Microryzomys* recognized in the literature (*M. altissimus* [Osgood, 1933] and *M. minutus* [Tomes, 1860]), and both are widely distributed along the Andean Cordillera, including montane forests at mid elevations (between 2000 and 3500 m; Carleton, 2015). Our phylogenetic reconstruction, including, in addition to PNRA individuals, one sample identified as *M. altissimus* (from Ecuador) and three samples identified as *M. minutus* (from Peru; Supplemental Table 3), recovered the PNRA specimens composing a clade sister of the *M. altissimus* haplotype. Although the clade composed of PNRA *Microryzomys* and the *M. altissimus* specimen from Ecuador is weakly supported, the clade formed by these two and *M. minutus* is highly supported (Fig. 9). Haplotypes of PNRA *Microryzomys* are 40 mutations apart in the CYTB from the other known sequences of *Microryzomys*, and exhibit a mean sequence divergence of 6.39% and 7.31% when compared to *M. altissimus* and *M. minutus*, respectivelly. Mean pairwise distance at the CYTB locus between *M. altissimus* and *M. minutus* is 6.99%. However, it is critical to include sequences from the type locality of *M. altissimus* (from Junin, Peru, currently unavailable), as PNRA samples might be more related to Junin than to Ecuador. Although further investigation is clearly pending, based on the relatively high genetic distances between our samples and the available sequences, currently identified as representatives of the two recognized species of *Microryzomys*, we provisionally treat the individuals sampled at PNRA as *Microryzomys* sp.

Genus *Neacomys* Thomas, 1900. A single specimen of *Neacomys* was trapped by pitfall at Las Papayas (Table 3). The partial CYTB sequence produced (Supplemental Table 2) showed the highest similarity (recovered by BLAST) to CYTB sequences of *Neacomys spinosus* (Thomas, 1882) and *Neacomys amoenus* Thomas, 1903. Phylogenetic analyses included all GenBank sequences available for *Neacomys* and sequences of closely related genera as outgroup (following Percequillo et al., 2021). Our phylogenetic reconstruction recovered the PNRA specimen as nested within *Neacomys spinosus,* more closely related to two specimens from Bongará, Amazonas, PE (Fig. 10; Supplemental Table 3). The single haplotype from PNRA differs from Bongará haplotypes, KX258228 and KY886327, by 9 and 11 mutations, respectively, which correspond to sequence divergence of 2.25–2.27%. The single specimen of *Neacomys* collected at PNRA was, therefore, identified as *N. spinosus*. This species was recently restricted to northern Peru and occurs in mountain cloud forests south and east of the Río Marañón in the departments of Amazonas, San Martín, and Huánuco (Hurtado & Pacheco, 2017).

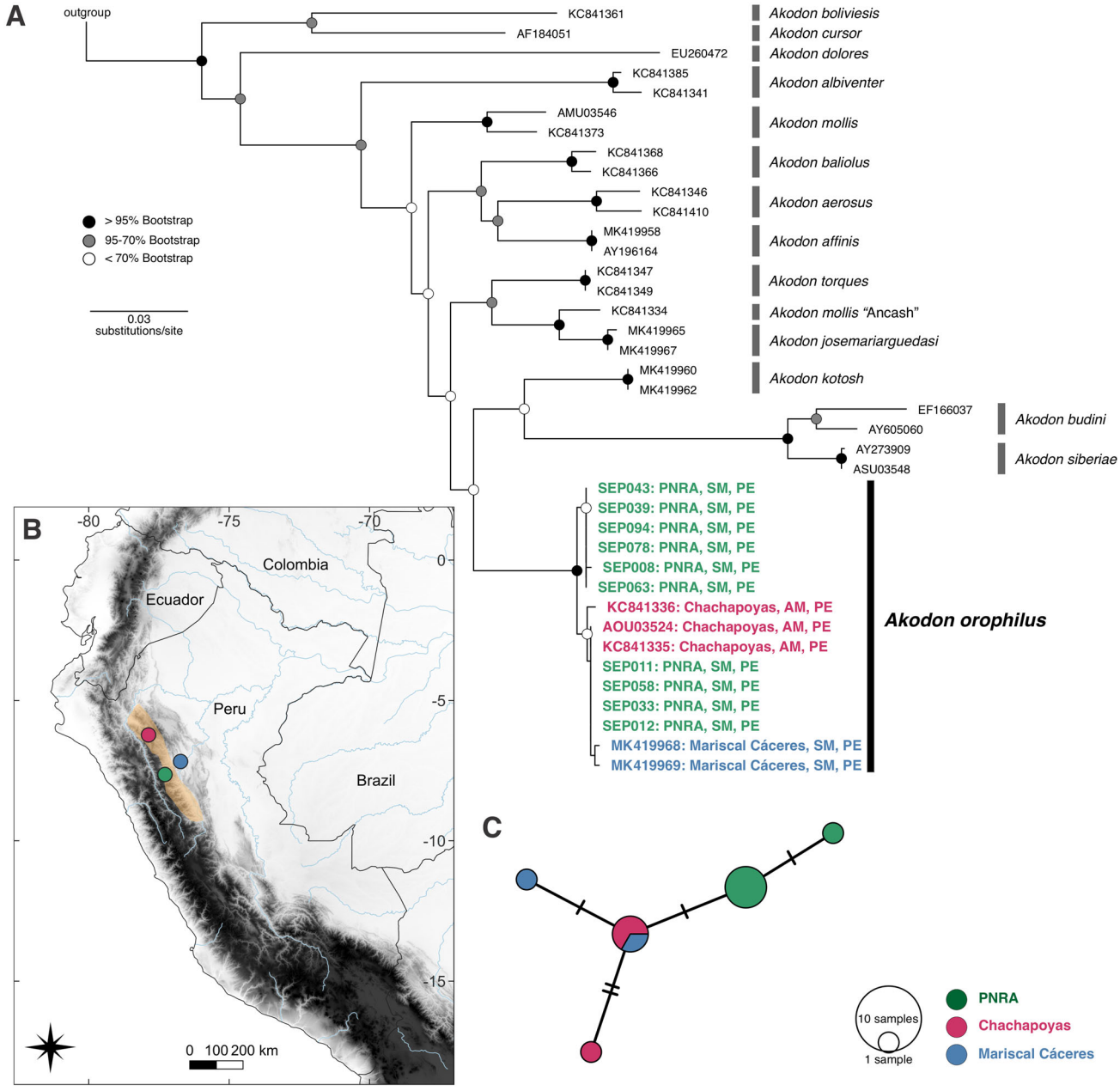

Fig. 7. Cytochrome b (CYTB) gene tree showing the relationships of *Akodon orophilus* haplotypes sequenced from Parque Nacional del Río Abiseo (PNRA) specimens (green) (A), sampling localities of all *A. orophilus* specimens included in the phylogeny (B), and haplotype network showing substitutions in the CYTB (hash marks) separating the PNRA haplotypes from comparative samples (C). The phylogenetic tree was inferred using maximum likelihood in the program RAxML and included data for representatives of all species in the *Akodon aerosus* group, in addition to one representative of all other species-groups (i.e., *A. cursor*, *A. boliviensis*, *A. dolores*). Geographic information from the specimens included in the map are provided in Supplemental Table 3. Species range (yellow shadow) was obtained from IUCN (https://www.iucnredlist.org).

Genus *Nephelomys* Weksler, Percequillo, and Voss, 2006. We trapped 45 *Nephelomys* at PNRA, most of those at La Playa ($n = 39$) and using Sherman traps ($n = 44$) (Table 3). Of the collected specimens, we sequenced CYTB of 14 individuals (Supplemental Table 1) and found two very distinct haplotypes. The first haplotype (represented by two samples) clustered with haplotypes identified as *Nephelomys keaysi* (J. A. Allen, 1900) in our phylogenetic reconstruction, whereas the second one (represented by 12 samples) was nested

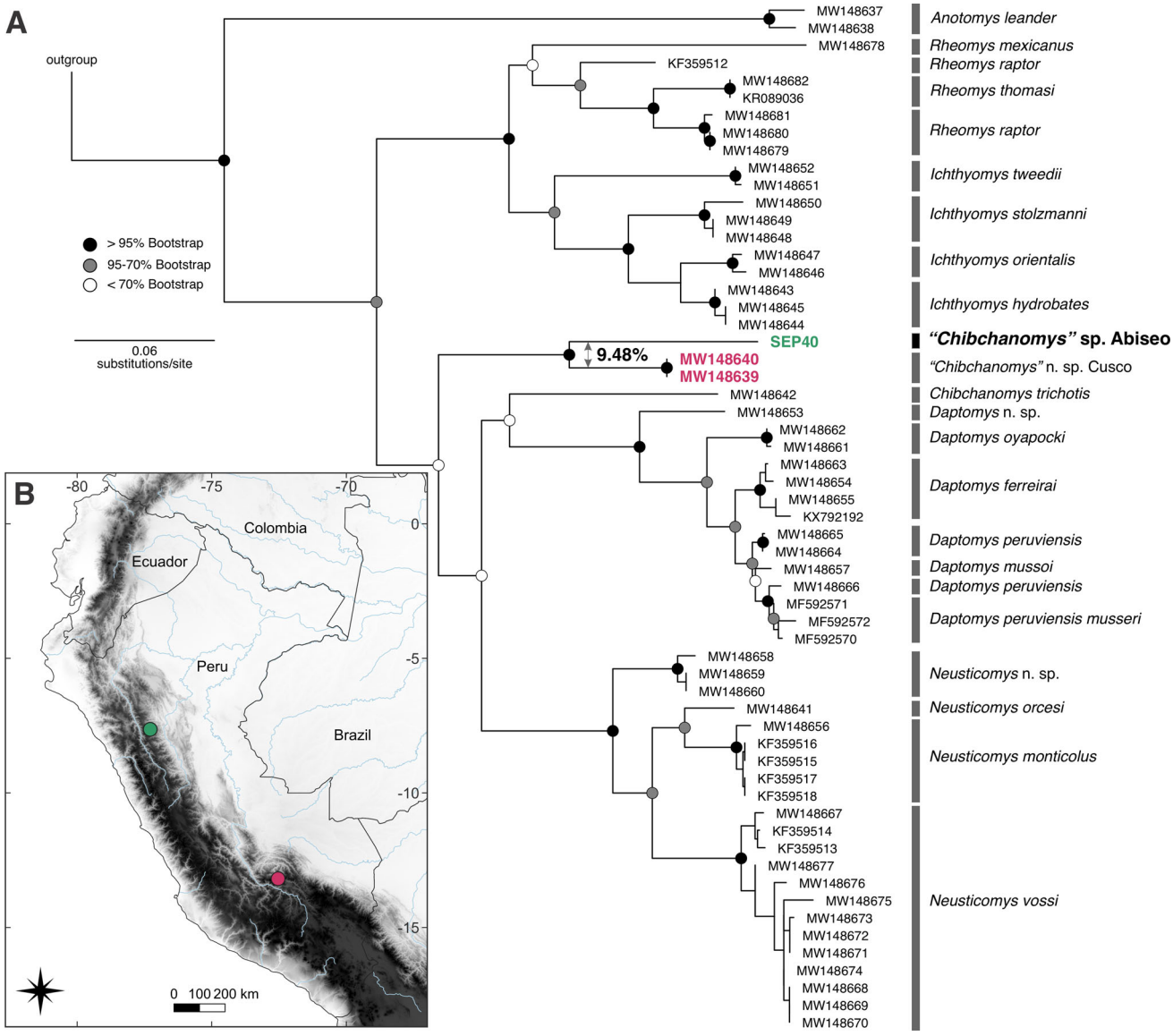

Fig. 8. Cytochrome b (CYTB) gene tree showing the relationships of the '*Chibchanomys*' from Parque Nacional del Río Abiseo (PNRA) (green) (A), and sampling localities of the PNRA species and the closest related species, '*Chibchanomys*' n. sp. Cusco (pink) (B). The percentage value shown in the tree correspond to mean pairwise uncorrected distance at the CYTB locus. The phylogenetic tree was inferred using maximum likelihood in the program RAxML and included data for all species of Ichthyomyini rodents available on GenBank. Geographic information from specimens of '*Chibchanomys*' n. sp. Cusco included in the map are provided in Supplemental Table 3.

within *Nephelomys ricardopalmai* Ruelas, Pacheco, Inche, and Tinoco, 2021 (Figs 2 and 11). Remarkably, the mean sequence divergence among PNRA samples of *N. keaysi* and the other haplogroups of this species ranged from 8.23 to 8.7%. These values are higher, for instance, than the mean sequence divergence between *N. ricardopalmai* and its sister species, *N. albigularis* (Tomes, 1860) (6.43% on average). Comparing our samples of *N. keaysi* with the geographically and genetically closest sample (from Oxapampa, Pasco; Supplemental Table 3) we observed 63 mutations in a fragment of less than 800 pb of the CYTB gene (resulting in a pairwise distance of 8.13%). Additionally, our samples of *N. keaysi* fall outside the species known geographic range, which include forested areas on eastern Andean slopes, from central Peru to central Bolivia (Percequillo, 2015). Although further investigation is clearly required for the *N. keaysi* complex, we treat these samples from

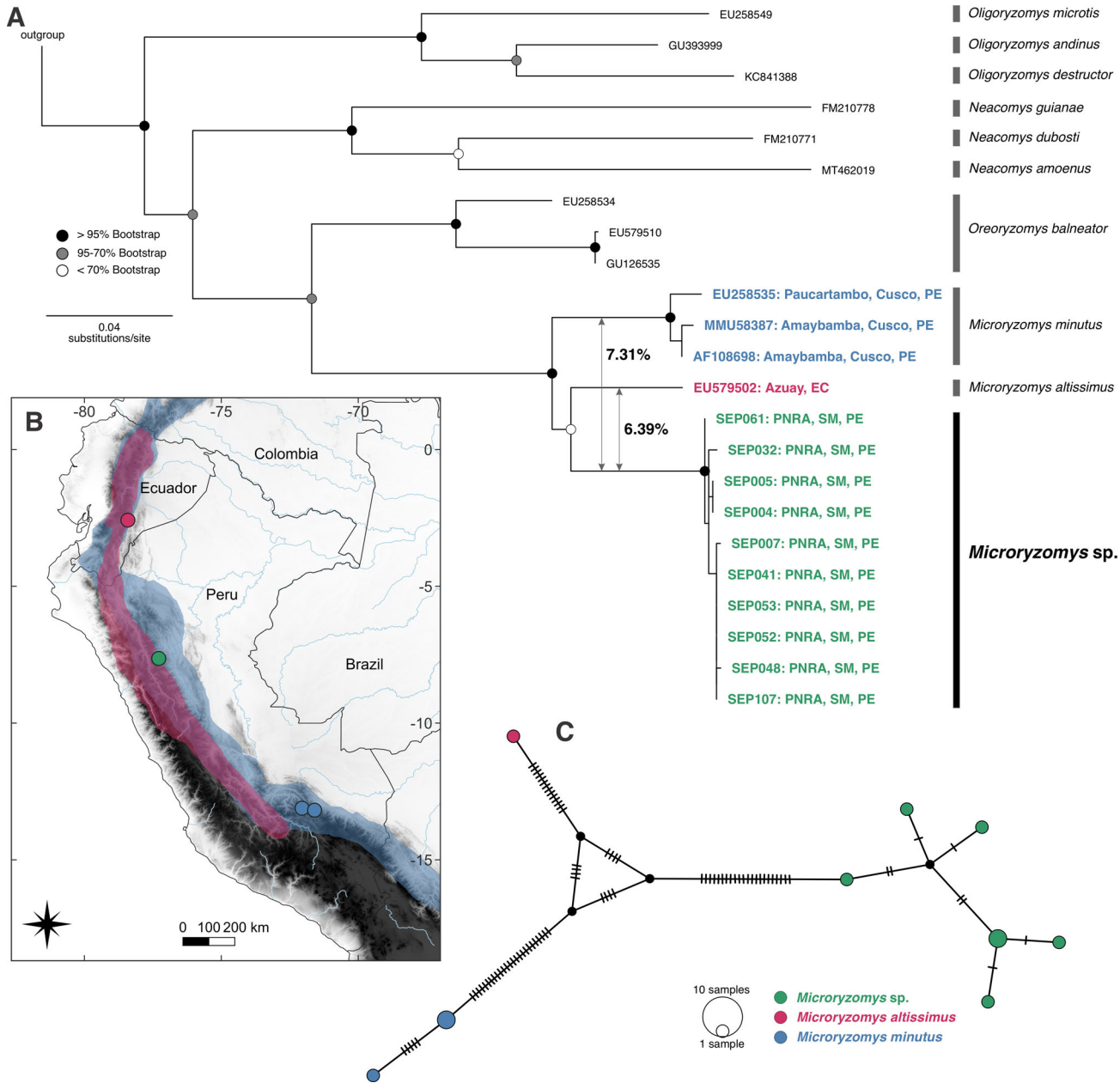

Fig. 9. Cytochrome b (CYTB) gene tree showing the relationships of *Microryzomys* haplotypes sequenced from Parque Nacional del Río Abiseo (PNRA) specimens (green) (A), sampling localities of the PNRA species and its close related taxa (B), and haplotype network showing substitutions in the CYTB (hash marks) separating the PNRA haplotypes from comparative samples (C). Percentage values shown in the tree correspond to mean pairwise uncorrected distance at the CYTB locus. The phylogenetic tree was inferred using maximum likelihood in the program RAxML and included data for all species of *Microryzomys* available on GenBank. Geographic information from the specimens included in the map are provided in Supplemental Table 3. Species ranges (pink and blue shadows) were obtained from IUCN (https://www.iucnredlist.org).

PNRA as *N. keaysi*. Regarding *N. ricardopalmai*, our samples do not diverge substantially from the available samples and are recovered as part of this species in the phylogenetic analyses. PNRA samples diverge from samples from Luya, Peru, by four to six mutations (Fig. 11), resulting in an average pairwise distance of 0.87% when compared to those haplotypes. Therefore, we treat the samples from PNRA as *N. ricardopalmai*. This species is endemic to Peru, and it was recently described based on specimens collected in montane cloud forest in

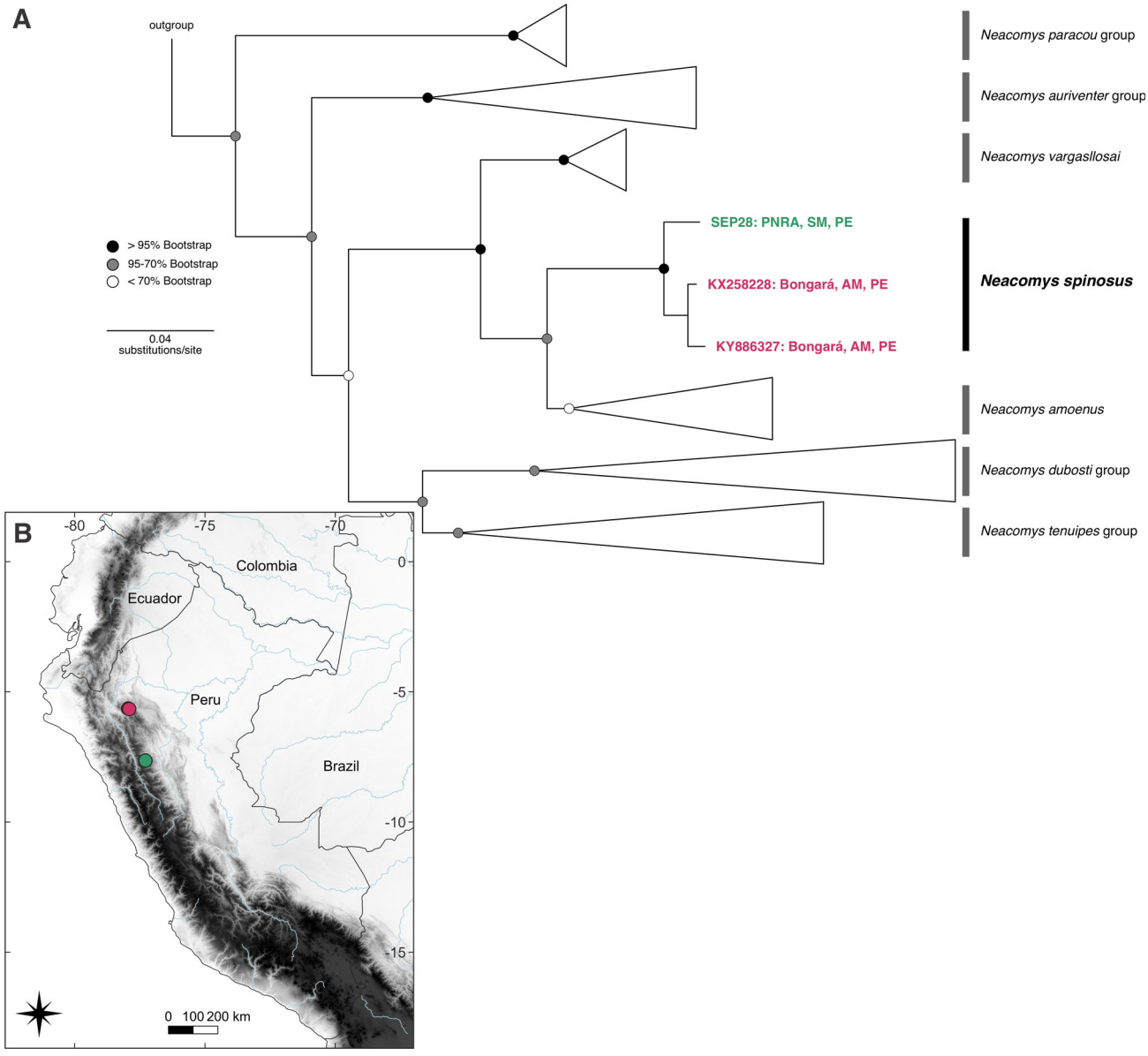

Fig. 10. Cytochrome b (CYTB) gene tree showing the relationships of the *Neacomys spinosus* haplotype sequenced from Parque Nacional del Río Abiseo (PNRA) specimen (green) (A), and sampling localities of all *N. spinosus* specimens included in the phylogeny (B). The phylogenetic tree was inferred using maximum likelihood in the program RAxML and included data for all species of *Neacomys* available on GenBank. Non-target species are collapsed into species groups. Geographic information from the specimens included in the map are provided in Supplemental Table 3.

the departments of Amazonas and San Martín (including specimens from PNRA), east of the Río Marañón (Ruelas et al., 2021).

Tribe *Thomasomyini*. Genus *Thomasomys* Coues, 1884. We recorded 171 captures of *Thomasomys* at La Playa and Las Papayas, and 1 capture at Macedonio, making it by far the most frequent captured genus of small mammals at PNRA (Table 3). Four morphotypes of *Thomasomys* sampled at PNRA were easily differentiated in the field (using external phenotypic characters), although their taxonomic affinities were only inferred using DNA barcodes. This genus is incredibly diverse, with 51 species formally described – including some species very recently named – , in addition to several lineages pending formal description (see Brito et al., 2019, 2021; Lee et al., 2022; Pacheco & Ruelas, 2023; Ruelas & Pacheco, 2021). *Thomasomys* occurs mainly

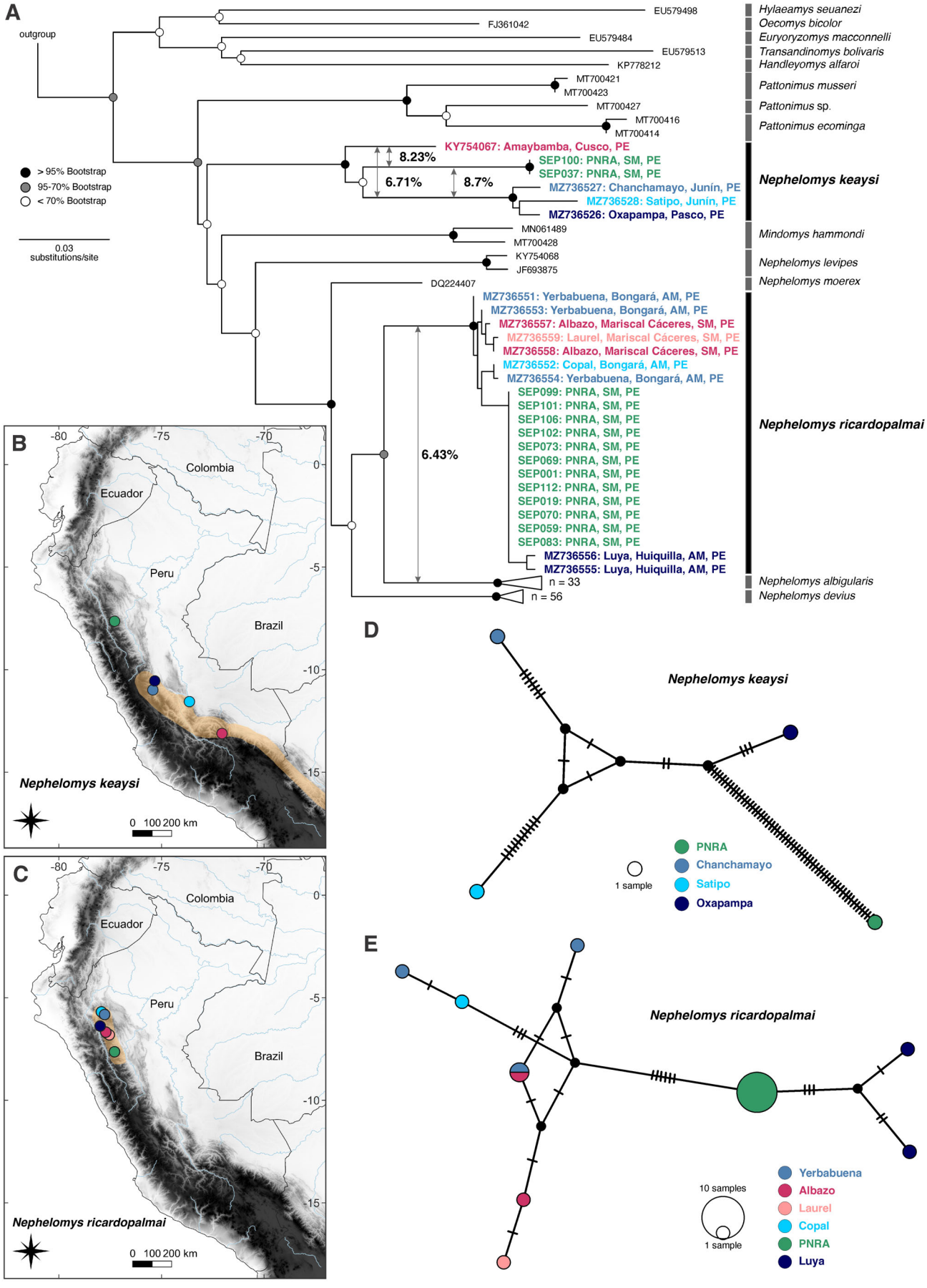
A
outgroup
EU579498
FJ361042
EU579484
EU579513
KP778212
MT700421
MT700423
MT700427
MT700416
MT700414
KY754067: Amaybamba, Cusco, PE
SEP100: PNRA, SM, PE
SEP037: PNRA, SM, PE
MZ736527: Chanchamayo, Junín, PE
MZ736528: Satipo, Junín, PE
MZ736526: Oxapampa, Pasco, PE
MN061489
MT700428
KY754068
JF693875
DQ224407
MZ736551: Yerbabuena, Bongará, AM, PE
MZ736553: Yerbabuena, Bongará, AM, PE
MZ736557: Albazo, Mariscal Cáceres, SM, PE
MZ736559: Laurel, Mariscal Cáceres, SM, PE
MZ736558: Albazo, Mariscal Cáceres, SM, PE
MZ736552: Copal, Bongará, AM, PE
MZ736554: Yerbabuena, Bongará, AM, PE
SEP099: PNRA, SM, PE
SEP101: PNRA, SM, PE
SEP106: PNRA, SM, PE
SEP102: PNRA, SM, PE
SEP073: PNRA, SM, PE
SEP069: PNRA, SM, PE
SEP001: PNRA, SM, PE
SEP112: PNRA, SM, PE
SEP019: PNRA, SM, PE
SEP070: PNRA, SM, PE
SEP059: PNRA, SM, PE
SEP083: PNRA, SM, PE
MZ736556: Luya, Huiquilla, AM, PE
MZ736555: Luya, Huiquilla, AM, PE
n = 33
n = 56
8.23%
6.71%
8.7%
6.43%
> 95% Bootstrap
95-70% Bootstrap
< 70% Bootstrap
0.03 substitutions/site
Hylaeamys seuanezi
Oecomys bicolor
Euryoryzomys macconnelli
Transandinomys bolivaris
Handleyomys alfaroi
Pattonimus musseri
Pattonimus sp.
Pattonimus ecominga
Nephelomys keaysi
Mindomys hammondi
Nephelomys levipes
Nephelomys moerex
Nephelomys ricardopalmai
Nephelomys albigularis
Nephelomys devius
B
Colombia
Ecuador
Peru
Brazil
Nephelomys keaysi
0 100 200 km
C
Colombia
Ecuador
Peru
Brazil
Nephelomys ricardopalmai
0 100 200 km
D
Nephelomys keaysi
1 sample
PNRA
Chanchamayo
Satipo
Oxapampa
E
Nephelomys ricardopalmai
10 samples
1 sample
Yerbabuena
Albazo
Laurel
Copal
PNRA
Luya

Fig. 11. Cytochrome b (CYTB) gene tree showing the relationships of *Nephelomys* haplotypes sequenced from Parque Nacional del Río Abiseo (PNRA) specimens (green) (A), sampling localities of all *N. keaysi* (B) and *N. ricardopalmai* (C) specimens included in the phylogeny, and haplotype networks showing substitutions in the CYTB (hash marks) separating the PNRA haplotypes from comparative samples of *N. keaysi* (D) and *N. ricardopalmai* (E). Percentage values shown in the tree correspond to mean pairwise uncorrected distance at the CYTB locus. The phylogenetic tree was inferred using maximum likelihood in the program RAxML and included data for all species of *Nephelomys* available on GenBank. Geographic information from the specimens included in the maps are provided in Supplemental Table 3. Species ranges (yellow shadows) were obtained from IUCN (https://www.iucnredlist.org) for *N. keaysi* and manually drawn for *N. ricardopalmai* based on Ruelas et al. (2021).

above 1200 m asl in premontane and montane forests, and in the Páramo along the Andes (Pacheco, 2015). We recorded *Thomasomys* in all sampled sites at PNRA, and we produced CYTB sequences for 36 individuals out of 48 individuals retained as voucher material (Supplemental Table 2).

Our phylogenetic inference included all samples of *Thomasomys* available on GenBank, which comprise 32 described species and representatives of seven additional lineages not yet formally named. Four distinct haplogroups were recovered from PNRA sequences. The first group is composed of two identical haplotypes, and it was recovered as part of the *T. cinereus* (Thomas, 1882) species group, sister of *Thomasomys onkiro* Luna and Pacheco, 2002 (Fig. 12), although low support was inferred for this relationship. This haplogroup from PNRA exhibits a mean sequence divergence of 12.5% from *T. onkiro* and is hereafter treated as *Thomasomys* sp.1 (gr. *cinereus*). Mean pairwise sequence divergence at the CYTB locus among recognized species of the *Thomasomys cinereus* group range from 5.06 to 16.39% (Pacheco & Ruelas, 2023). Currently, *Thomasomys onkiro* is considered endemic to the Cordillera Vilcabamba (Fig. 13; Supplemental Table 3) in southern Peru (Pacheco, 2015). The only two specimens of *Thomasomys* sp.1 recorded in the field were tapped using pitfalls in La Playa.

The second haplogroup from PNRA (Fig. 2) is composed of two haplotypes (differentiated by one mutation from each other) and it was supported as sister group to a putative undescribed species from Paucartambo, Cusco, PE (Figs 12 and 13*B*; Supplemental Table 3), which belongs to the *T. aureus* (Tomes, 1860) species complex (referred to as *Thomasomys* 'sp. 1' by Pacheco, 2015 and Ruelas & Pacheco, 2021; and as *T. aureus* 'Paucartambo' by Brito et al., 2021). These two groups exhibit a CYTB mean sequence divergence of 8.58%, and we refer this second lineage from PNRA as *Thomasomys* sp.2 (gr. *aureus*). Mean pairwise sequence divergence at the CYTB locus among recognized species of the *T. aureus* species complex range from 4.49% to 14.44% (Ruelas & Pacheco, 2021). The only two specimens of *Thomasomys* sp.2 registered were captured in La Playa, one using Sherman trap and the other with a Victor trap.

The third haplogroup identified in our samples (Fig. 2) is sister to *Thomasomys notatus* Thomas, 1917, currently the single species of the *T. notatus* group (Pacheco, 2015). Five individuals from PNRA were sequenced, all with the same haplotype. This lineage from PNRA exhibits a mean sequence divergence of 5.48% from *T. notatus* from Paucartambo, Cusco, PE (Figs 12 and 13; Supplemental Table 3). To provide a context, one of the latest species described in the genus, *T. antoniobracki* Ruelas and Pacheco, 2021, diverges from a closely related species in 5.47%, and there are uncorrected generic distances below 5% between sister species of *Thomasomys* (Ruelas & Pacheco, 2021). Thus, we treat this haplogroup as *Thomasomys* sp.3 (gr. *notatus*). We recorded *Thomasomys* sp.3 at both La Playa (four individuals) and Las Papayas (six individuals) using pitfall (two captures events) and Sherman traps (eight capture events).

The fourth haplogroup from PNRA (Fig. 2) includes 27 sequenced specimens represented by four haplotypes. This group is recovered as sister to *T. kalinowskii* (Thomas, 1894) from Palca, Junín, PE (Figs 12 and 13; Supplemental Table 3). The two lineages present a mean sequence divergence of 6.5% in the CYTB gene. We refer to this PNRA haplogroup as *Thomasomys* sp.4 (referred to as *Thomasomys* 'sp. 5′ by Pacheco, 2015). This species was the most frequently captured, with 158 capture events recorded (Table 3). We sampled *Thomasomys* sp.4 at the three sites: 140 in La Playa, 17 in Las Papayas, and one in Macedonio. Sherman traps accounted for the largest number of captures, 150, followed by pitfall (five captures), Victor (two captures), and active search (one capture).

Although the four putative species of *Thomasomys* represented in our samples are here denoted with proxy identifiers (species 1–4), some described species of this genus are not represented on GenBank (e.g., *T. incanus, T. ischyrus*, *T. rosalinda*). Therefore, it is possible that some the PNRA *Thomasomys* might represent described species for which comparative CYTB data is currently unavailable.

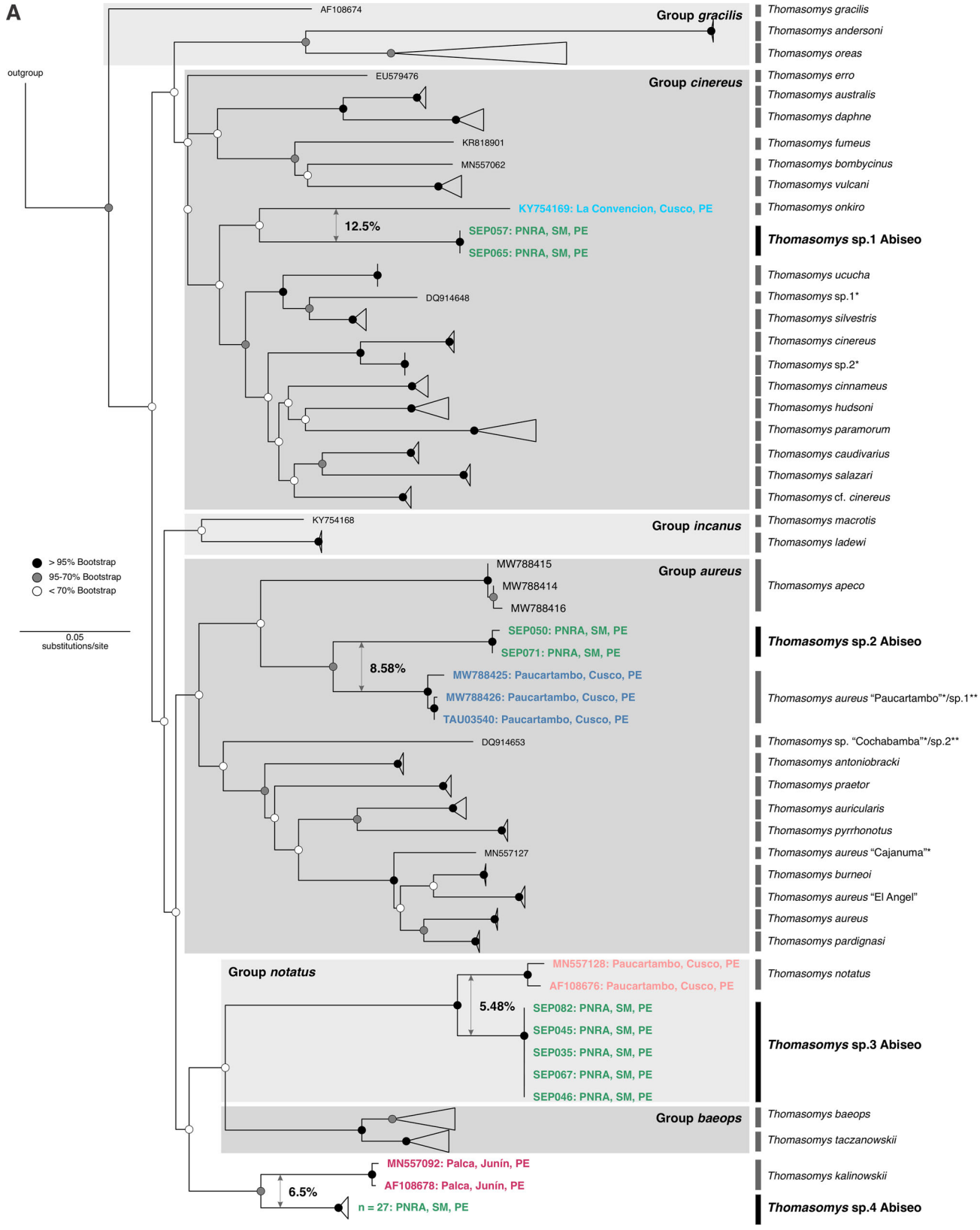

Fig. 12. Cytochrome b (CYTB) gene tree showing the relationships of *Thomasomys* haplotypes from Parque Nacional del Río Abiseo (PNRA) (green) with other *Thomasomys* samples. Species from PNRA are listed followed by the world 'Abiseo', to avoid confusion with other species denoted with proxy identifiers (e.g., 'sp. 1', 'sp. 2') from previous studies. Percentage values shown in the tree correspond to mean pairwise uncorrected distance at the CYTB locus. The phylogenetic tree was inferred using maximum likelihood in the program RAxML and included data for all species of *Thomasomys* available on GenBank. Non-target species are collapsed to facilitate visualization of target groups.

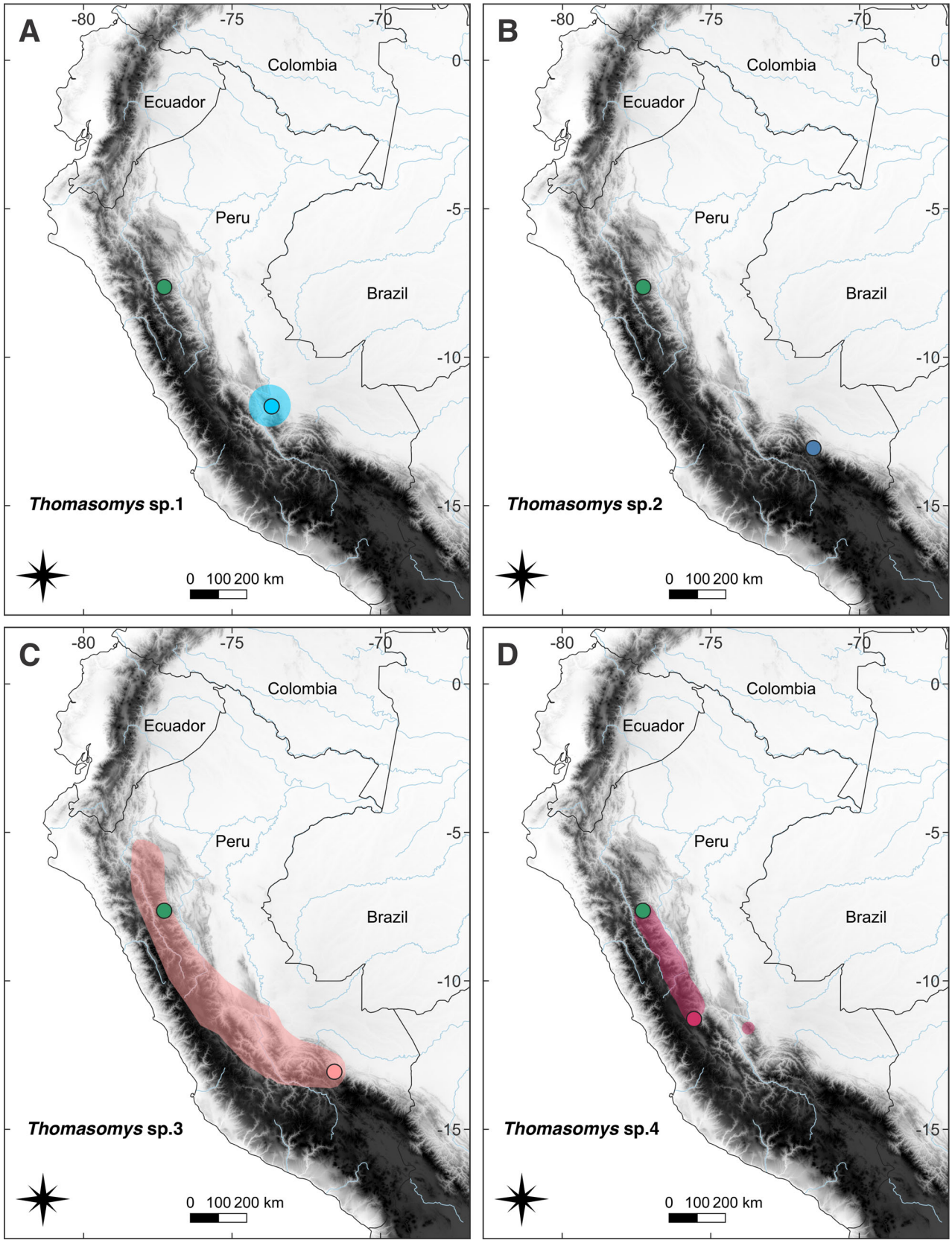

Fig. 13. Sampling localities of the Parque Nacional del Río Abiseo species of *Thomasomys* (green) – *Thomasomys* sp.1 (gr. cinereus) (A), *Thomasomys* sp.2 (gr. aureus) (B), *Thomasomys* sp.3 (gr. notatus) (C), and *Thomasomys* sp.4 (D) – and their closest related species – *Thomasomys onkiro* (blue) (A), *Thomasomys aureus* Paucartambo/sp.1 (blue) (B), *Thomasomys notatus* (rose) (C), and *Thomasomys kalinovskii* (pink) (D). Geographic information from the specimens included in the maps are provided in Supplemental Table 3. Species ranges (light blue, pink, and red shadows) were obtained from IUCN (https://www.iucnredlist.org).

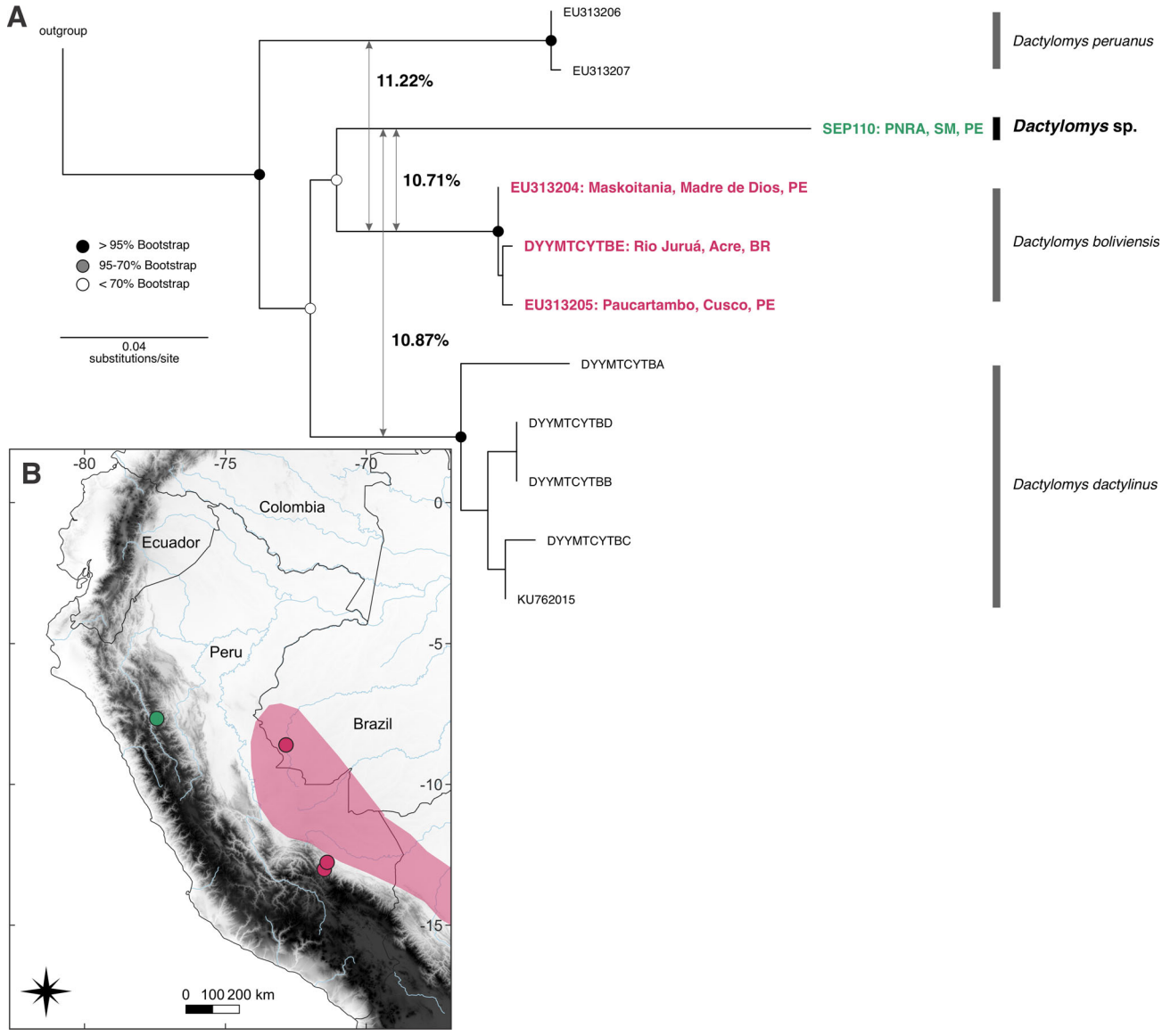

Fig. 14. Cytochrome b (CYTB) gene tree showing the relationships of the *Dactylomys* from Parque Nacional del Río Abiseo (PNRA) (green) with other *Dactylomys* species (A), and sampling localities of the PNRA species and the closely related species *Dactylomys boliviensis* (pink) (B). The percentage value shown in the tree correspond to mean pairwise uncorrected distance at the CYTB locus. The phylogenetic tree was inferred using maximum likelihood in the program RAxML and included data for all specimens of *Dactylomys* available on GenBank. Geographic information from the specimens included in the map are provided in Supplemental Table 3. Species range (pink shadow) was obtained from IUCN (https://www.iucnredlist.org).

Family Echimyidae

Genus *Dactylomys* I. Geoffroy St.-Hilaire, 1838. Two specimens of *Dactylomys* were recorded together during active search at La Playa (Table 3), an adult specimen accompanied by a juvenile specimen, although only the juvenile was captured (Fig. 2). The partial CYTB sequence produced from the single specimen collected (Supplemental Table 2) showed only 88.7–89.4% of similarity with CYTB sequences of *Dactylomys boliviensis* Anthony, 1920, *D. dactylinus* (Desmarest, 1817), and *D. peruanus* Allen, 1900. We included in the phylogenetic analysis all samples from GenBank assigned to *Dactylomys* and used as outgroup representatives of the closest related genera *Olallamys* Emmons, 1988 and *Kannabateomys* Jentink, 1891 (following phylogenetic results of Fabre et al., 2016; Upham et al., 2013, 2019). Our phylogenetic reconstruction recovered PNRA *Dactylomys* as sister to *D. boliviensis* (Fig. 14), a species known from Southwestern margins of the Amazon Basin, from central Peru south to central Bolivia, and

east as far as the central Rio Juruá in western Brazil (Emmons et al., 2015) (Supplemental Table 3). The clade formed by *Dactylomys* from PNRA and *D. boliviensis* was recovered as sister of *D. dactylinus*, and specimens identified on GenBank as *D. peruanus* formed a clade sister of all remaining *Dactylomys*. However, interspecific relationships within *Dactylomys* were not highly supported by our analyses. *Dactylomys* from PNRA present a mean pairwise distance at the CYTB locus that range from 10.71% to 11.22% when compared to other species of *Dactylomys*, and the genetic distances between the remaining three species of *Dactylomys* range from 7.7% to 9.4%. Currently, there are only three recognized species of *Dactylomys* (Emmons et al., 2015), but our phylogenetic results combined with the high level of divergence between the PNRA sequence and remaining sequences available on GenBank indicate that the genus *Dactylomys* apparently includes four distinct species. Therefore, the sample from PNRA is treated as *Dactylomys* sp.

Discussion

Diversity of non-volant small mammals at PNRA and underestimated diversity along high Andes

The results of our survey at PNRA indicate a high diversity of non-volant small mammals, with 16 species (12 rodents and 4 marsupials) registered on tropical montane forest sites ranging from about 2500 to 2800 m asl. The recorded diversity is noticeable when compared to other communities from high Andes. Rengifo et al. (2022) compiled information from 630 mammal surveys along the Andes, including data from sites at 2000 m asl and above in Venezuela, Colombia, Ecuador, Peru, Bolivia, Argentina, and Chile. Andean non-volant small mammal communities were found to harbour a range of 1 to 17 species, with most localities having from 6 to 10 species recorded, and less than 5% of the sites included more than 10 species. Only three of the sites surveyed had 16 or more species recorded (see below). Therefore, the 16 species of small mammals recorded during 15 days of sampling represents a remarkable diversity compared to previously available data.

Although surveys of non-volant small mammals often employ multiple sampling methods, most of the inventories performed along the Andes did not include as many methods as in our sampling. Less than 15% of surveys in the Andes employed pitfall traps (see Figure 9 in Rengifo et al. 2022), which proved to be the most effective method for sampling success, number of species recorded, and unique species sampled in our study. Pitfall traps exclusively sampled six species, versus two species exclusively sampled with Sherman traps (Table 2), the most prevalent method to sample small mammals along the Andes as observed by Rengifo et al. (2022). These comparisons are especially noticeable considering that the sampling effort was much lower for pitfalls than Shermans. Another relevant method that we used was active search, which resulted on the record of two unique species at PNRA (*Dactylomys* sp. and '*Microsciurus*' 'species 2'), that would have otherwise not been sampled in our study. Therefore, we hypothesize that diversity of small mammals along the Andes is still vastly underestimated, even in sites that have been already surveyed, due to limited sampling techniques employed.

Despite employing multiple sampling methods, we only conducted sampling for 15 days, and therefore species diversity at PNRA is probably underestimated. Extrapolation curves of species diversity based on our data suggest that about 17–18 species should be expected if sampling was increased (Fig. 3). This would represent an addition of one–two species from the 16 species we report. These estimates seem modest considering that during our expedition we recorded previously unsampled species on the final two days of sampling. The records of *Dactylomys* sp. and '*Microsciurus*' 'species 2', for example, occurred on our penultimate and final day of sampling, respectively. The fact that we were recording new species during our last days in the field reinforce the hypothesis that we are still undersampling non-volant small mammal diversity at PNRA (Voss & Emmons, 1996). For instance, among didelphids, we did not sample any species of *Monodelphis*, a specious genus that is widespread in South America (Pavan & Voss, 2016), and known from humid tropical montane forest sites of similar altitudes along the Peruvian Andes (Pacheco et al., 2021), although rare in montane forest of northern Peru (Pacheco, personal observation). Among rodents, representatives of the genera *Oligoryzomys* Bangs, 1900 and *Rhipidomys* Tschudi, 1845 would also be expected to occur in the sampling area (Pacheco et al., 2021; Tribe et al., 2015; Weksler & Bonvicino, 2015). Another rodent expected for the area is *Echimys saturnus* O. Thomas, 1928, which has been recorded at PNRA at the site of Los Pinchudos, at 2700 m asl (Juárez-Pérez et al., 2021). Los Pinchudos is also a humid tropical montane forest site located on the northwestern portion of the park, very close to our sampling sites. Therefore, the species likely occur on the sites visited by our expedition, but was not recorded during our sampling. The use of camera traps in future efforts could help to increase the chance of a more

complete inventory for arboreal species, including echimyids (e.g., Mosquera et al., 2016).

Comparing our results with the small mammal assemblage recorded at PNRA by Leo and Romo (1992), it seems that we did sample most of the rodent species previously sampled in montane forest of a similar altitudinal range at PNRA. As part of the Peruvian Association for Conservation of Nature (APECO), these authors conducted the first field expeditions to sample vertebrate species at PNRA (see Leo, 1995). Between 1987 and 1990, four distinct ecosystems were sampled between 2150 and 3850 m asl at the northwestern portion of PNRA, including the sites sampled by us and several other sites. This effort recorded 14 species of rodents of subfamily Sigmodontinae (Leo & Romo, 1992). Eight of the species recorded by Leo and Romo (1992) seem to correspond to species recorded by us (Supplemental Table 4). The remaining six species (unsampled by us) were registered by Leo and Romo in a different altitudinal range than the range we sampled, five at higher and one at lower altitudes. Our expedition, however, registered four species of rodents not listed by Leo and Romo (1992) (*Dactylomys* sp., '*Microsciurus*' 'species 2', '*Chibchanomys*' sp., *Nephelomys keaysi*). Considering the combined results of Leo and Romo (1992) (14 species registered between 1150 and 3850 m), ours (12 species registered between 2578 to 2780 m asl, four of which correspond to species previously unsampled by Leo and Romo, 1992), and Juárez-Pérez et al. (2021) (which additionally registered *Echimys saturnus* at 2700 m asl), we conclude that at least 19 species of rodents occur in the northwestern portion of PNRA. With the addition of the four marsupial species recorded by us, the diversity of non-volant small mammals of PNRA is, minimally, equal to 23 species (Supplemental Table 4). Some of the best-sampled and most diverse sites known along high Andes includes Rocotal in Peru (Medina et al. 2012), Cajas (Barnett, 1999) and Cerca Papallacta in Ecuador (Voss, 2003), where the number of non-volant small mammals registered above 2000 m asl range from 16 to 19 (Pacheco et al., 2007; Voss, 2003). Therefore, the impressive diversity of 23 species registered at PNRA makes it the richest site ever sampled for non-volant small mammals in the high Andes, reinforcing its importance as an area of high biological diversity and high endemism.

Species identification and putative new species

Identification of species of non-volant small mammals from PNRA was challenging, and the use of DNA barcodes proved very helpful to assist with the delimitation of potential independent lineages of collected material, that we are interpretating as species. The analyzes of CYTB data indicate 15 distinct species collected, and while four of those can be assigned to described taxa, we were unable to unequivocally associate 11 of those to any named species. Remarkably, all the four marsupials registered at PNRA exhibit high levels of divergence at the CYTB, and might represent unnamed species (*Gracilinanus* sp., *Marmosa* [*Micoureus*] sp., *Marmosa* [*Stegomarmosa*] sp., and *Marmosops* sp.). Among rodents, four out of the 11 sampled species were assigned to described taxa (*Akodon orophilus, Neacomys spinosus, Nephelomys ricardopalmai, Nephelomys keaysi),* and the remaining seven species merit taxonomic attention (*Microryzomys* sp., *Thomasomys* sp.1–sp.4, *Dactylomys* sp., and '*Chibchanomys*' sp.). Although further systematic investigation is pending, it is likely that several of those represent unnamed species. Samples tentatively assigned to *Nephelomys keaysi* fall outside the known geographic distribution of this species and have a relatively high genetic distinction when compared with available DNA sequences of *Nephelomys keaysi* (8.23–8.70% uncorrected distance at the CYTB locus). Therefore, our record from PNRA could represent either a range extension for *N. keaysi* or an indication that this taxon likely represents a species complex composed of multiple distinct evolutionary lineages.

The identity of some rodents from PNRA merit special note. Besides representing a putative new species, '*Chibchanomys*' sp. was recovered as sister of '*Chibchanomys'* n.sp. Cusco, highlighted as a possible new genus and species from central Peru by Salazar-Bravo et al. (2023). The only squirrel registered by us at PNRA (exclusively through visual observation and photos), also seems to represent a new species from an unnamed genus, referred to as '*Microsciurus*' 'species 2'. Based on mitochondrial and nuclear DNA sequence data (obtained from historical samples collected by Leo et al. in 1989), the species from PNRA clusters with a group of tree squirrels that apparently lacks a genus name (Abreu et al., 2020, 2022). Finally, the identity of the *Dactylomys* from PNRA is still uncertain. The identification of the GenBank sequences currently referred to as *Dactylomys peruanus* is dubious, as there is a chance that these specimens, in fact, correspond to an undescribed species (Louise H. Emmons, personal communication). If GenBank sequences currently labeled as *D. peruanus* are misidentified, there is a chance that the *Dactylomys* from PNRA might represent *D. peruanus*. Indeed, external morphology of the specimens registered at PNRA (such as soft fur and furred tail) suggest some morphological affinities with *D. peruanus*. However, the

record from PNRA would fall out of the known range of the species, presently known only from central-southern Peru and northern Bolivia (Emmons et al., 2015). Further comparative analyses in this group including type specimens are pending before confident identification can be reached.

The Cordillera Oriental of upper Andes has been identified as one of the least known mammalian faunas in South America (Patterson et al., 2012; Voss, 2003), and this still applies today. PNRA is located on the northern range of central Andes and illustrates well that scenario, where over 70% (12 out of 16) of the species of non-volant small mammals recorded by us need taxonomic attention, and several of which are potentially new to science.

Endemicity of small mammals at PNRA and zoogeographic affinities

The montane forests of Peru harbour the highest level of mammal endemicity in the country (Pacheco et al., 2021), and the exceptional endemicity levels of such forests at PNRA has been noted before, not only for mammals, but also for birds and anurans (Leo, 1995). Eleven out of the 16 species of non-volant small mammal registered by us at PNRA are presumably unknown from other sites and could be tentatively listed as endemics to the area (Fig. 15). However, our current knowledge on distribution and taxonomy of these species is still very limited, and it is likely that at least some of those unique species are also distributed in other areas. Proper sampling on extensive areas of High Andes in northern Peru is still pending (Pacheco et al., 2021), and a noticeable gap is observed for sites between 2000 and 3000 m asl (Voss, 2003). Only additional sampling will allow for more advanced discussions on the limits of these putative species, and help to determine which of those species are unique to PNRA, and which are also found elsewhere.

Based on phylogenetic results and distributional data currently available for PNRA species and closely related taxa, the small mammals from PNRA seem to have diverse geographic affinities, including with central Andes, northern Andes (localities north of the Huancabamba Deflection; see Duellman, 1979; Mutke et al., 2014), and Amazonian lowlands (Fig. 15). There are only a few species registered at PNRA for which sequence data from specimens sampled elsewhere are available (five out of 16 species). From those five species, four share closest affinities with populations from montane forests of central Andes (*Akodon orophilus*, *Nephelomys keaysi, Nephelomys ricardopalmai*, and *Neacomys spinonus*), whereas PNRA '*Microsciurus*' 'species 2' closest populations are from lowland Amazonian forests of Peru and western Brazil (specimens from Madre de Dios, Peru, and Acre, Brazil; Abreu et al., 2020).

Regarding phylogenetic affinities, sister taxa of seven PNRA species are also predominantly distributed along central Andes ('*Chibchanomys*' sp., *Thomasomys* sp.1, *Thomasomys* sp.2, *Thomasomys* sp.3, *Thomasomys* sp.4, *Gracilinanus* sp., *Marmosa* [*Micoureus*] sp.). A close affinity with taxa known from the department of Cusco was found for '*Chibchanomys*' sp. (closely related to '*Chibchanomys*' n. sp. Cusco from Salazar-Bravo et al., 2023), and *Thomasomys* sp.2 (sister group to a putative undescribed species from Paucartambo, Cusco, that belongs to *T. aureus* species complex; Brito et al., 2021; Ruelas & Pacheco, 2021). Because Cusco contain some of the few examples of high montane forest localities in Peru for which collected specimens have DNA sequences available on GenBank, we cannot rule out this affinity to Cusco as a bias of existing sampling. For example, *Thomasomys* sp.2 might be more closely related to *T. rosalinda* or to another member of the *T. aureus* group from northern Peru, and *Thomasomys* sp.4 might be more closely related to *T. ischyrus* or another lineage of the *T. incanus* group, also from northern Peru. However, sequence data are still missing for those species.

Additionally, some species recorded at PNRA have sister taxa that are widespread in the Amazon lowlands and extend to variable elevations on the eastern Andean slopes (e.g., *Dactylomys* sp., *Marmosops* sp., *Marmosa* [*Stegomarmosa*] sp., *Marmosa* [*Micoureus*] sp.). The *Marmosa* (*Micoureus*) sp. was recovered as sister to a clade formed by two species, one widespread in the Amazon (*M. rutteri*) and another from high Andes in central Peru (*M. parda*). An Andean-Amazon historical connection is well documented in the diversification of some groups of small mammals, including arboreal spiny rats from the family Echimyidae (Upham et al., 2013) and marsupials of the genus *Marmosops* (Díaz-Nieto et al., 2016).

A few species from PNRA have their sister species distributed in the northern Andes (*Microryzomys* sp., *N. ricardopalmai*). The Huancabamba Deflection, located in northern Peru about 250 Km north of the PNRA, is well-recognized in the literature as one of the major geological features acting as a fauna dispersion barrier for montane species along the Andean Cordillera (e.g., Duellman, 1979; Pacheco, 2002, 2015). The Río Marañón, located eastward through the depression, has been described as the main barrier that limits the distribution of several species of sigmodontine rodents (Jiménez et al., 2013; Pacheco, 2002; Pacheco &

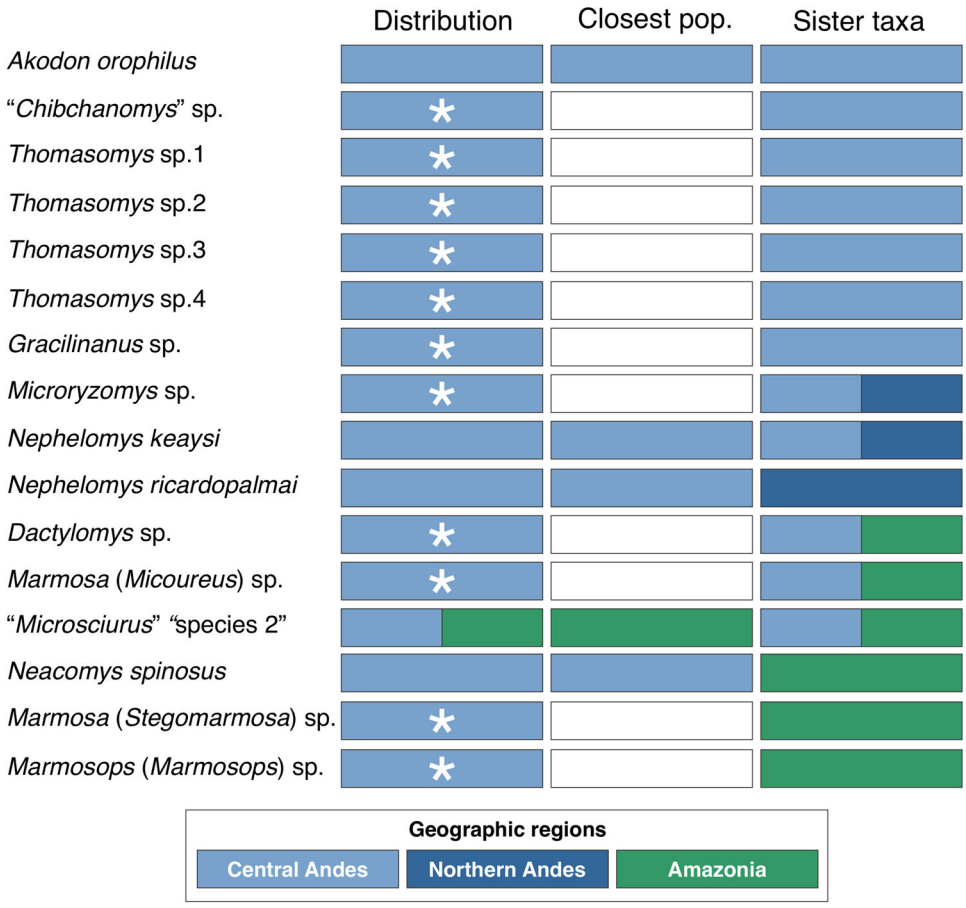

Fig. 15. Zoogeographical affinities of non-volant small mammals from Parque Nacional del Río Abiseo (PNRA) and their closest related populations/species based on molecular comparisons. Species marked with asterisks are currently only know from PNRA. In this schematic representation of geographic zones, Central Andes is represented by light blue, Northern Andes is represented by dark blue, and Amazonia is represented by green. Only species distributed at high Andes (above 2000 m asl) are listed as 'Northern Andes' (north of Huancabamba Deflection) or 'Central Andes' (south of Huancabamba Deflection), while species distributed on Amazonian lowlands that also extend into eastern Andean slopes below 2000 m asl are listed as 'Amazonia'.

Ruelas, 2023; Ruelas et al., 2021) and could contribute to the lack of phylogenetic affinities between small mammals from central Andes with northern Andes.

It is important to mention, however, that in several of these cases our data do not recover high support for phylogenetic hypotheses. Although a valuable marker to identify genetic diversity, CYTB has its limitations (as its matrilineal heritage, and high polymorphism that may leads to saturation), and gene trees are not completely adequate to delimit species. Moreover, the scarcity of localities with sequence data available precludes more comprehensive phylogenetic analyses that will allow the development of accurate historical reconstructions for mammal communities from PNRA and other highly diverse and endemic faunas from middle and high elevation Andean sites. Sampling these habitats should therefore be a high priority for future surveys (Pacheco et al., 2021; Patterson et al., 2012).

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No potential conflict of interest was reported by the author(s).

Supplemental material

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