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Dynamics of species composition of small non-volant mammals from the northern Cordillera Central of Colombia

Abstract: On the basis of our recent fieldwork and historical records, we document the diversity of small non-volant mammals in the northern end of Cordillera Central of Colombia, an important region in the context of vertebrate biodiversity. From February 2004 to February 2006, we completed mammal surveys in three localities at the department of Antioquia, with elevations ranging from 1650 to 2000 m. We recorded a total of 14 species: three marsupials, one shrew, one heteromyid, and nine sigmodontinae rodents, including three species endemic in Cordillera Central. The rodents *Heteromys australis*, *Nephelomys pectoralis*, and *Rhipidomys latimanus* were recorded in all localities. *Nephelomys pectoralis* was captured in all surveys and was the most abundant species. Nearby historical records exist for 16 species, seven of which were not captured during our surveys. The community of small mammals in the northern Cordillera Central has species richness similar or higher than that in other Andean localities with a broader elevational range. We show that small mammal communities from middle elevations are a mixture of middle elevation endemics and highland species, but with little contribution from the lowlands. Finally, the occurrence of endemic and threatened species in this region suggests its importance from a conservational and biogeographical standpoint for small terrestrial mammals.

Keywords: Andean small mammals; diversity; elevational range profile; mammal inventories; Northern Andes.

DOI 10.1515/mammalia-2014-0018
Received February 16, 2014; accepted August 22, 2014

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Introduction

The Andes is considered as one of the world's most important biodiversity hotspots, containing 16% of all terrestrial vertebrates of which 60% are endemics (Ceballos and Ehrlich 2006, Loyola et al. 2009). Although Andean diversification is a complex topic (Santos et al. 2009, Patterson et al. 2012), topography heterogeneity is one of the most important features explaining Andean biotic richness (Ribas et al. 2007, Patterson et al. 2012). The Andes probably achieves its greatest geomorphological complexity in Colombia (Cediel et al. 2003), where the main range of the Andes coming from Ecuador branches off into three ranges (i.e., Cordillera Occidental, Cordillera Central, and Cordillera Oriental) that are separated by deep inter-Andean valleys (i.e., Cauca and Magdalena) (Kattan et al. 2004). Among these three main ranges, the north of Cordillera Central is of particular biogeographic interest, not only because of its high levels of species richness and endemism in vertebrates (Cuervo et al. 2008a) and plants (Callejas et al. 2005), but also because elements from several other biogeographic areas (e.g., Chocó, Central America, and inter-Andean valleys) converge in this region (Cuervo et al. 2008b). Although the northern Andes have long been recognized as an important biogeographic area (Chapman 1917), such interesting biogeographic patterns have been recently refined by intense fieldwork conducted in this region for groups such as birds, frogs, and reptiles, which have resulted in the description of nine new endemic vertebrates in merely a decade: two species of birds (Cuervo et al. 2001, Cuervo et al. 2005), three snakes (Passos et al. 2009), one lizard (Velasco et al. 2010), and three frogs (Bravo-Valencia and Rivera-Correa 2011, Rivera-Correa and Gutiérrez-Cárdenas 2012, Rivera-Correa and Faivovich 2013). Despite such relevant findings for several vertebrate groups, a detailed understanding of the patterns of diversity and processes of mammal diversification in the northern Andes has been hampered by lack of detailed knowledge on the composition of Andean mammalian communities (Mena et al. 2011).

The history of mammalian fieldwork in the northern parts of the Central Andes is hardly extensive. Between 1910 and 1915, a large expedition – primarily ornithological (Chapman 1917) – was conducted in Colombia but it included only a few mammalogists. Nonetheless, the extreme north of the Cordillera Central was not a priority, and only a few localities north of 5°N latitude in this cordillera were included in their fieldwork (Allen 1916). Between November 1914 and March 1915, Leo E. Miller and Howarth S. Boyle visited a few localities in the north of Cordillera Central, collecting 175 specimens (Allen 1916, AMNH 2014). From 1948 to 1952, Philip Hershkovitz collected extensively in Colombia, including localities at the extreme north of Cordillera Central (Patterson 1987). His collections have been the basis for numerous taxonomic studies (Hershkovitz 1947, 1948a,b, 1949a,b, 1950, 1954, 1960, Pine 1981, Tribe 1996, Pacheco 2003, Percequillo 2003, Díaz-N et al. 2011), and have also served as the foundation for basic knowledge on the distribution and composition of mammalian communities in the region (Alberico et al. 2000, Cuartas-Calle and Muñoz-Arango 2003, Solari et al. 2013). After Hershkovitz made his collections, no other intensive fieldwork in the northern Cordillera Central has been made, and only a handful of scattered collections have been sampled. In addition, the results of such works are only available as unpublished literature (Delgado-V and Palacio-V 2002). As a contribution for a better understanding on the community composition of the small non-flying mammals in the Northern Andes, we present the results of recent fieldwork conducted in the Cordillera Central, comment our results with historical surveys in the area with special reference to Hershkovitz collections, and briefly discuss trapping methods for small mammal inventories in Andean forests.

Materials and methods

Study area

Fieldwork was conducted at four localities in the northern Cordillera Central, with elevations ranging from 1760 and 1950 m (Figure 1). Field sites are all located in Antioquia Department in the municipalities of Amalfi (Vereda Costa Rica: 6°52′25″N, 75°05′56.7″W; 1840 m); Anorí (Vereda El

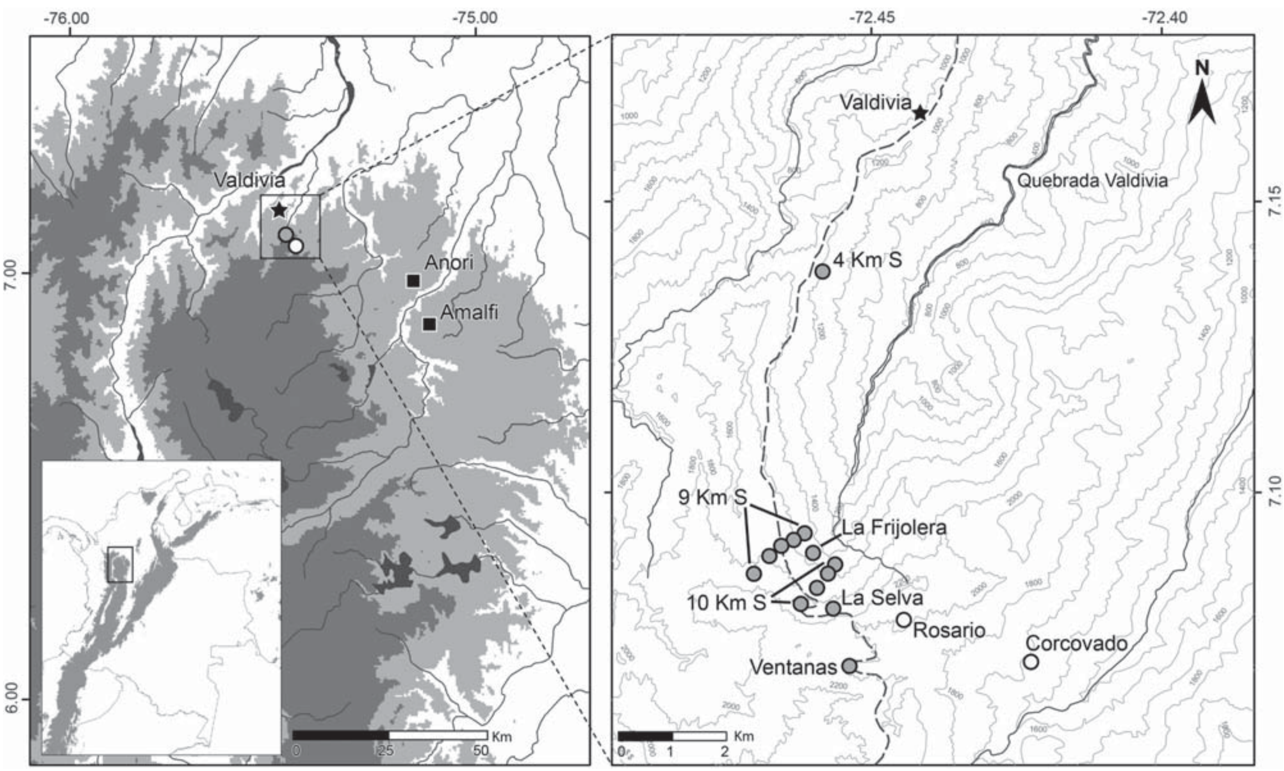

Figure 1 Collection localities of P. Hershkovitz (gray circles) and of this study (open circles and black squares) in the northern Cordillera Central (left) and a close-up near Valdivia (right). Light-gray shaded regions correspond to localities between 1000–2000 m and dark-gray shaded regions are localities above 2000 m. The dashed line corresponds to the highway between the town of Yarumal (not shown) and Vadivia (star).

Roble: 6°58′59.9″N, 75°08′01″ W; 1800 m); and two localities in the municipality of Yarumal, in the region known as "Alto de Ventanas" (Vereda El Rosario: 7°05′0.9″N, 75°26′41.2″W; 1950 m; and Vereda Corcovado: 7°04′21.7″N, 75°25′16.5″ W; 1760 m) (Figure 1). The study sites in Amalfi and Anorí correspond to the transition between a wet forest and a premontane wet forest (bmh/bp-PM), and in Yarumal to low montane wet forest (bp-MB) (Holdridge 1967). In general, these areas are characterized by high relative humidity (between 77% and 95%), annual rainfall between 3500 and 4000 mm, annual average temperature ranging from 12 to 24°C, and a bimodal rainfall regime with the driest season extending from December to February, and the wettest season from September to November (Espinal 1992, Cuervo et al. 2001, Patiño 2004).

The landscape in these areas is a mosaic of secondary forest fragments of different sizes (mainly on steep slopes with difficult access) surrounded by cattle pastures and agricultural fields (Díaz-N et al. 2011). In the margins of forest fragments, the canopy ranges from 7 to 15 m in height, but taller trees (up to 30 m) occur in the forest interior and along stream banks (Cuervo et al. 2001). These forests, which are drained by many small streams, are dominated by plant species of the families Annonaceae, Clusiaceae, Ericaceae, Lauraceae, Melastomatacea, Moraceae, Rubiaceae, and Sapindaceae, and also support abundant epiphytes and dense understory vegetation (Araceae and Piperaceae). Likewise, there is a high density of palms such as *Dictyocaryum lamarckianum* (Mart.) H. Wendl., *Wettinia* spp. Poepp. and *Geonoma undata* Klotzsch, as well as several species of large ferns (Cuervo et al. 2001, Zapata 2004, Sánchez-Giraldo and Díaz-N 2010).

Fieldwork

Small non-volant mammals were captured in a series of surveys from February 2004 to February 2006 in the northern part of Cordillera Central (Delgado-V 2004, Sánchez-Giraldo and Díaz-N 2010, Díaz-N et al. 2011). A total of nine surveys, ranging from 5 to 10 days each, were completed in Amalfi (5 surveys), Anorí (1), and Yarumal (3). We sampled for 56 nights, and a total effort of 4752 traps-night (Table 1).

Small non-volant mammals were captured using Sherman (H.B. Sherman Traps, Tallahassee, USA) folding live traps [extra-large (ca. 10×11×38 cm), large (ca. 8×9×23 cm), and small (ca. 5×5×23 cm)], snap traps, and for Yarumal only, pitfall traps (10-liter plastic buckets sunk flush with the soil surface without a drift fence) (Table 1). We placed the traps both in the forest interior and along the forest edge, and arranged in lines ca. 10 m away from each another. Inside the forest, the traps were set along streams, in the understory, and 2–12 m above the ground on tree branches connected to higher canopy levels. We used strips of Velcro® to hold arboreal Sherman traps and snap traps to tree branches (Díaz-N et al. 2011). The traps were baited every morning with a mixture of rolled oats, banana, and vanilla essence, or sometimes only with a slice of banana. We recorded standard measurements and reproductive conditions from every captured individual (Hall 1962). Ectoparasites and liver tissue samples associated with each specimen were collected and preserved in 96% ethanol. The material collected was preserved as fluid and dry specimens, and was subsequently deposited in the Colección Teriológica Universidad de Antioquia, Medellín (CTUA), and the Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Bogotá (ICN) (Supplementary material – Appendix 1).

Table 1 Capture effort measured as the number of traps-night per sampling method (columns) in each of the surveyed localities (rows).

Surveys	Nights	Trapping methods[a]			
		Sh	Sn	Pf	Total
Amalfi					
Feb. 2004	7	405	144	–	549
Jun. 2004	10	660	–	–	660
Oct. 2004	6	263	218	–	481
Jan. 2005	5	330	165	–	495
Jul. 2005	5	209	168	–	377
Subtotal	33	1867	695	–	2562
Anorí					
Jun. 2004	7	489	246	–	735
Yarumal					
Sep. 2005	5	283	114	24	421
Jan. 2006	6	288	216	27	531
Feb. 2006	5	253	203	41	497
Subtotal	16	824	533	92	1449
Total	56	3180	1474	92	4746

[a]Trapping methods: Sherman (Sh), snap (Sn), and pit-fall (Pf) traps.

Data analysis

We used a composite measure of abundance and activity to estimate the relative abundance (RA) of species. We estimated the RA of each species on each survey as the number of captured individuals (including released individuals) per 100 traps-night (total individuals of species i/total trapping effort in survey ×100 traps-night), and calculated the mean RA for each locality (e.g., Jayat and Ortíz 2010, Pacheco et al. 2011). We chose 100 traps-night as a parameter to standardize the RA because the number of traps-night differed among localities.

To assess the adequacy of the survey, we used rarefaction curves and species richness estimators. We generated accumulation and individual-based rarefaction curves from the number of captured individuals for each species using the Mao Tao (S_{obs}) estimator. The rarefaction curve of each locality was fitted to the asymptotic accumulation function of Clench to estimate the asymptotic number of species (Fagan and Kareiva 1997, Jiménez-Valverde and Hortal 2003):

$$S_{(e)} = ae/(1+be),$$

where $S_{(e)}$ is the number of species found per sampling-effort unit (e), and a and b are the parameters of the function. Parameters were adjusted using the Simplex and quasi-Newton method. Additionally, we calculated the non-parametric abundance-based estimators of Chao 1 and abundance-based coverage (ACE), and the incidence-based estimators of Chao 2, first Jackknife (Jack 1), second Jackknife (Jack 2), and incidence-based coverage to estimate the expected species richness on each locality (e.g., Sánchez et al. 2008, Rocha et al. 2011). The calculation of the Mao Tao estimator, species richness estimators, and standard deviation were made in EstimateS 8.2 (http://viceroy.eeb.uconn.edu/estimates) (Colwell 2006), with the sample randomized 100 times. The adjustment of rarefaction curve was developed in Statistica 7.0 (StatSoft, Inc., Tulsa, USA) (StatSoft 2004).

Historical records

To obtain historical records of small non-volant mammal species (SNVM) in the northern Cordillera Central, we queried online mammalian databases from museums holding the most important collections of the region: American Museum of Natural History (AMNH), Field Museum of Natural History (FMNH), and National Museum of Natural History, Washington DC (USNM). Given that we were interested in comparing historical and contemporary records, we restricted our search to the ecogeographic areas broadly encompassed by our surveys (wet forest, low montane wet forest, premontane wet forest) above 1200 m from the extreme north of Cordillera Central (i.e., municipalities of Anorí, Amalfi, Yarumal, and Valdivia). For our queries, we defined as SNVM those species that can be typically collected with the trapping methods implemented in our fieldwork. Squirrels (family Sciuridae) and weasels (genus *Mustela*) are seldom collected using the traps and baits we implemented (Voss and Emmons 1996) and were consequently excluded from our database search. Whenever possible, we inspected collector's field notes in search of relevant information such as trapping effort and trapping success. With the information retrieved from the databases, we compared the alpha diversity between historical records and those obtained by our fieldwork.

Results

Species richness and composition

We captured a total of 224 individuals (159 in Amalfi, 19 in Anorí, and 46 in Yarumal) corresponding to 14 species: three didelphid marsupials, one shrew, one heteromyid rodent, and nine sigmodontine rodents (Table 2). Amalfi and Yarumal had a species richness of 11 and 12 species, respectively, whereas only four species were recorded in Anorí. Three species of rodents, namely, *Heteromys australis* Thomas, 1901, *Nephelomys pectoralis* Allen, 1912, and *Rhipidomys latimanus* Tomes, 1860, were present at all three localities, and seven species (three marsupials and four rodents) were present at two localities: six species in Amalfi and Yarumal, and one rodent species (an unidentified Oryzomyini) in Anorí and Yarumal (Table 2). Four species were present at a single locality and captured only once: the rodents *Chilomys instans* Thomas, 1895 and *Oligoryzomys fulvescens* Saussure, 1860 were recorded only for Amalfi, whereas the rodent *Microryzomys minutus* Tomes, 1860 and the shrew *Cryptotis medellinius* Thomas, 1921 were exclusively captured in Yarumal (Table 2).

Yarumal was the only locality where we used pitfall traps, from which 45 individuals were captured using standard methods (i.e., Sherman, snap, and pitfall traps), and only five individuals belonging to five different species were captured with pitfall traps (Table 2). Three species were exclusively captured using pitfall traps (*Cryptotis medellinius*, *Microryzomys minutus*, and *Neacomys tenuipes*), six species were captured using only snap or Sherman traps, and two species were caught using all the trapping methods (Table 2). The species *Marmosa* (*Micoureus*) *regina* O. Thomas, 1898 was captured by hand. Thus, although it is listed as a species occurring in Yarumal, it was not included in the analyses of species richness.

When considering only those species captured with standard methods, the community was composed of 11

Table 2 Small non-volant mammal species and number of individuals captured at three localities in northern Cordillera Central.

Species	Amalfi	Anorí	Yarumal	Trap[f]	Valdivia
Didelphidae					
Marmosa cf. *waterhousei*[a]					FMNH 69824, 69850
Marmosa regina	3		1		
Marmosops caucae[b]	7		2	Ct	
Marmosops handleyi[d]	3		4	Pf/Ct	FMNH 69823, 69838
Marmosops cf. *bishopi*[c]					FMNH 69822
Monodelphis adusta					FMNH 70539
Cricetidae					
Akodon affinis					FMNH 70537
Chilomys instans	1				
Handleyomys alfaroi					AMNH 37737; FMNH 70507–70510, 70527, 70528
Handleyomys intectus[d]	11		5	Ct	FMNH 70332–70338
Melanomys caliginosus	2		3	Ct	AMNH 37723–37730; FMNH 70357–70384, 70387, 70395
Microryzomys minutus			1	Pf	FMNH 70541
Neacomys tenuipes	3		1	Pf	FMNH 70124, 70125, 70137–70140, 70555
Nephelomys pectoralis[e]	71	9	21	Ct	AMNH 37717–37722; FMNH 70396–70430
Oligoryzomys fulvescens	1				
Reithrodontomys mexicanus					FMNH 70167–70169
Rhipidomys latimanus	20	6	2	Ct	FMNH 70250–70254, 70257, 70259
Thomasomys aureus					FMNH 70321–70324
Unidentified Oryzomyini		2	2	Pf/Ct	
Heteromyidae					
Heteromys australis	37	2	3	Ct	AMNH 37745; FMNH 70459–70467, 70469, 70474–70482
Soricidae					
Cryptotis medellinius[d]			1	Pf	FMNH 69812, 69813
Total (# species)	11	4	12		16

[a]Following Rossi (2005).
[b]Following Díaz-N et al. (2011).
[c]Following Díaz-Nieto, Voss, and Jansa (in prep.), previously identified as *Marmosops parvidens* (Pine, 1981).
[d]Endemic species from the Cordillera Central.
[e]Following Percequillo (2003).
[f]Trapping methods used in Yarumal: conventional traps, including Sherman and snap traps (Ct), and pit-fall traps (Pf).
Valdivia column includes specimens retrieved from our database search (see text).

species in both Amalfi and Yarumal (Table 2). In both localities, the rarefaction curves showed that the rate of species accumulation decreased with increased numbers of captured individuals, but without evidence of having reached a complete asymptotic value (Figure 2), and the expected species richness showed variable values among estimators (Table 3). Owing to the paucity of data, we did not calculate species richness estimators for Anorí.

In Amalfi, the rarefaction curve presented confidence intervals closer to the observed species richness and a tendency toward stabilization, reaching an asymptotic number of species of 12.6 (Clench function, R^2=0.994, parameters a=2.332 and b=0.185) and a slope on the end of the adjusted curve <0.1. The species richness estimators were closer to the observed richness, where the 11 species recorded represented between 79% (Jack 2) and 95% (Chao 2) of the estimated richness (Table 3). The behavior of the rarefaction curve (slope <0.1) and the richness estimators indicates a highly reliable survey in Amalfi (see Jiménez-Valverde and Hortal 2003).

In Yarumal, the rarefaction curve had no signs of stabilization and the expected number of species was higher than the observed value in most richness estimators, suggesting an incomplete survey (Table 3). The asymptotic number of species was 17.92, with the slope at the end of the curve of 0.25 (R^2=0.999, a=1.756 and b=0.098). Abundance-based estimators, Chao 1 (11.75 species), and ACE (12.55) predicted values near the observed richness, whereas the incidence-base estimators predicted a higher number of species, between 14.13 (Chao 2) and 18.43 species (Jack 2) (Table 3). Based on the results of the estimators, our survey included between 60% and 93% of the expected species richness in this locality (Table 3).

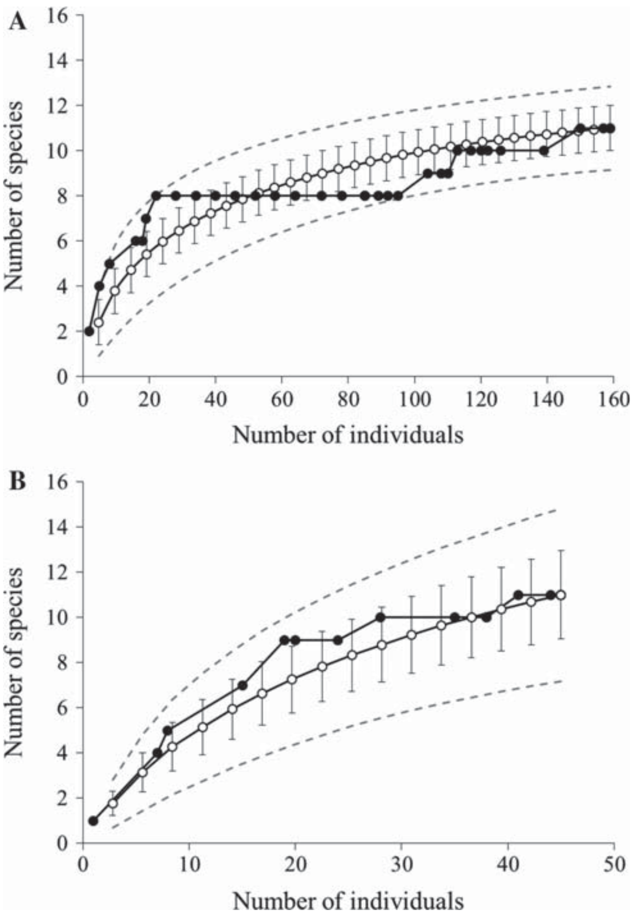

Figure 2 Species accumulation and rarefaction curves (scaled by number of individuals) for Amalfi (A) and Yarumal (B). Solid line: expected species richness (S_{obs} estimator); dashed lines: 95% confidence intervals; bars: standard deviation.

Table 3 Species richness, abundance and incidence-based richness estimators (±standard deviation) in Amalfi and Yarumal localities.

Estimators		Amalfi	Yarumal
Species richness	S_{obs}	11±1.28	11±1.96
Richness estimators			
Clench Function		12.6	17.92
Abundance	Chao 1	12.00±1.30	11.75±1.42
	ACE	12.38±0.72	12.55±1.20
Incidence	Chao 2	11.48±1.27	14.13±0.90
	ICE	12.30±0.71	17.67±2.06
	Jack 1	12.94±1.35	15.69±2.26
	Jack 2	13.91±1.40	18.43±1.98

Relative abundance (RA)

The rodent *Nephelomys pectoralis* was the most frequently captured species in all localities and the only species captured continuously in all surveys at Amalfi and Yarumal (Table 2). Overall, *N. pectoralis* was largely dominant with respect to the other species, representing between 45% and 47% of all captured individuals in Amalfi and Yarumal, respectively. In Amalfi, *N. pectoralis* and *Heteromys australis* presented mean RAs greater than one individual (2.47 and 1.65 individuals, respectively), and maximum values of 7.73 and 3.71, respectively (Table 4). Other species at this locality with high RA included the rodents *Handleyomys intectus* Thomas, 1921 and *Rhipidomys latimanus*, which had mean RAs above 0.6 and maximum values greater than one individual (Table 4). Among the species captured in Anorí, *N. pectoralis* and *R. latimanus* reached the highest RA values with 1.22 and 0.82, respectively. In Yarumal, *N. pectoralis* was the only species with a mean RA and maximum value above one individual (1.44 and 2.05, respectively) (Table 4). The marsupial *Marmosops caucae* Thomas, 1900 and the rodents *H. intectus* and the unidentified Oryzomyini had intermediate mean RA of 0.48 and maximum values below one individual.

Historical records

We recovered a total of 12 localities all from the municipality of Valdivia from material deposited at the AMNH and FMNH mammal collections. Nonetheless, only seven localities (encompassing nine altitudes) followed our ecogeographic search criteria and these were therefore used for comparison purposes (Table 5). The material deposited at AMNH was collected by L.E. Miller and H.S. Boyle from December 1914 to January 1915 at a single locality known as “Valdivia, La Frijolera” (Table 5), whereas the material deposited at FMNH was collected entirely by Philip Hershkovitz during his fieldwork in Valdivia from June to July 1950 (Hershkovitz field notes) (Table 5). From the seven localities selected, we recovered a total of 139 specimens (AMNH=16, FMNH=123) representing 16 species that include four didelphid marsupials, 10 sigmodontine rodents, one heteromyid rodent, and one shrew (Table 2). All the species collected by Miller and Boyle (*Handleyomys alfaroi* J.A. Allen, 1891, *Melanomys caliginosus*, and *Nephelomys pectoralis*) were also included in the collections made by Hershkovitz (Table 2).

We restricted the inspection of field notes to those of P. Hershkovitz because he collected most of the specimens and species uncovered in our database search (Table 2). Nonetheless, although Hershkovitz’s field notes included fascinating and detailed information about his daily life and impressions, these notes did not provide information to evaluate trapping effort or

Table 4 Mean relative abundance (individual per 100 traps-night) of non-volant small mammals in Amalfi, Anorí, and Yarumal.

Species	Amalfi		Anorí	Yarumal	
	Mean	N[a]		Mean	N[a]
M. caucae	0.37 (0.18–0.62)	4		0.48	1
M. handleyi	0.23 (0.20–0.27)	3		0.43 (0.38–0.48)	2
M. regina	0.30 (0.18–0.42)	2			
C. medellinius				0.24	1
H. australis	1.65 (0.15–3.71)	5	0.27	0.33 (0.19–0.48)	2
C. instans	0.27	1			
H. intectus	0.63 (0.15–1.59)	4		0.48 (0.40–0.56)	2
M. caliginosus	0.17 (0.15–0.18)	2		0.31 (0.24–0.38)	2
M. minutus				0.2	1
N. tenuipes	0.37 (0.20–0.53)	2		0.24	1
N. pectoralis	2.47 (0.40–7.73)	5	1.22	1.45 (0.60–2.07)	3
O. fulvescens	0.18	1			
R. latimanus	0.72 (0.20–1.36)	5	0.82	0.22 (0.20–0.24)	2
Unidentified Oryzomyini			0.27	0.48	1

[a]Number of surveys in which the species was recorded.

Table 5 Localities retrieved from AMNH and FMNH databases that matched our search criteria.

Museum	Locality	Altitude (m)	Source
FMNH	**4 km S**	1200	This study
FMNH	5 km S	1100	This study
FMNH	**9 km S**	1200	Anderson (2000)
FMNH	**9 km S**	Including localities at 1400, 1500, 1650, 1700, 1950	Díaz-N et al. (2011)
FMNH	**10 km S**	Including localities at 1200, 1500, 1600, 1700, 1950	This study
FMNH	La Cabaña	ca. 900	This study
AMNH	**La Frijolera**	1500	This study
FMNH	**La Selva**	1900	This study
FMNH	Quebrada Oro, 4 km S Valdivia	Including localities at 900, 950	This study
FMNH	Quebrada Valdivia	Including localities at 850, 900	Anderson (2000)
FMNH	Rio Negrito, near[a] Valdivia*	1650	This study
FMNH	**Ventanas**	2000	This study

[a]This locality is not part of Valdivia collections. The “Rio Negrito” is located in the Municipality of Sonsón, a locality approximately 150 km south of Valdivia. Collection dates of material from “Rio Negrito” do not coincide with the dates Heshkovitz spent in Valdivia, instead those dates correspond to his fieldwork at Sonsón. Moreover, in his field notes, Hershkovitz makes reference to a “Rio Negrito” while he was in Sonsón and no such locality was ever mentioned during his fieldwork in Valdivia.
All localities correspond to municipality of Valdivia (Antioquia Department) but only those shown in bold conform to our ecogeographic criterion (see text). Voucher material collected at these localities shown in bold is shown in Table 2. All geographic coordinates from “This study” (see Source column) were obtained after the inspection of Hershkovitz field notes.

capture success. As a result, we could not implement richness estimators using Hershkovitz data, and comparisons between our collections and historical records were thus limited to species richness and supplemented by anecdotal information.

Among the sampled localities, those in Yarumal are as close as 2 km from the localities visited by AMNH and FMNH expeditions (Figure 1). Within the 16 species already in the collections from Valdivia, nine were also collected by us in Yarumal. Seven species were exclusively represented by historical records: *Akodon affinis* J.A. Allen, 1912, *Handleyomys alfaroi*, *Marmosa* cf. *waterhousei* Tomes, 1860, *Marmosops* cf. *bishopi* Pine, 1981, *Monodelphis adusta* Thomas, 1897, *Reithrodontomys mexicanus* Saussure, 1860, and *Thomasomys aureus* Tomes, 1860. Three species collected by us at Yarumal, namely, *Marmosa (Micoureus) regina*, *Marmosops caucae* and an unidentified Oryzomyini, had not been previously recorded in any of the Valdivia localities (Table 2).

Discussion

Species richness

Comparisons of species richness and species composition among inventories are usually a challenging task because of the different methods and effort employed by each particular study. Nonetheless, at least four other localities in Cordilleras Central and Oriental were sampled by methods and effort similar to that used in our fieldwork and therefore can be useful for comparisons. In Cordillera Central, studies in montane forests recorded 13 species [Reserva Forestal Protectora Bellavista, 1628–2469 m, 5537 traps-night (Rojas Briñez 2008)], 12 species [PRN Ucumarí, 1900–2580 m, 2367 traps-night (Gómez-Laverde 1994)], 13 species [Reserva Rio Blanco, 2500–3500 m, 6642 traps-night (Gómez Valencia 2004)]. In a single locality in Cordillera Oriental, a study recorded 13 species [Reserva Carpanta, 3100 m; 7000 traps-night (López-Arévalo and Montenegro-Díaz 1993)]. The species richness found in those localities show values comparable to those found by us in Amalfi (11 species, 2562 traps-night) and Yarumal (12 species, 1449 traps-night). Conversely, the low number of species captured in Anorí (four species, 735 traps-night) falls within the richness found in other studies conducted north of the Cordillera Central (5–7 species) with similar low sampling effort (288–460 traps-night) (Delgado-V and Palacio-V 2002, Sánchez-Giraldo 2006). Anorí, Amalfi, and Yarumal are localities that resemble each other in terms of vegetation and abiotic conditions. Therefore, the low species richness recovered in Anorí is most likely a consequence of the small trapping effort rather than the evidence of a species-impoverished area.

According to the maximum value of the richness estimators (ca. 14 species) obtained in Amalfi, the community of SNVM could include three or four additional species. Given that habitats in the north of Cordillera Central along the same altitude can be similar, it is possible that the species absent in Amalfi could be represented by those found in Yarumal. Amalfi is located in the northeastern extreme of the Cordillera Central, an area where the Andes does not rise above 1800 m. Consequently, we expect that the missing species in our survey would be those from lower elevations (e.g., *Handleyomys alfaroi*, *Marmosa* cf. *waterhousei* Goldman, 1912, *Marmosops* cf. *bishopi*, *Monodelphis adusta*, and *Reithrodontomys mexicanus*) rather than those from higher elevations (e.g., *Akodon affinis*, *Cryptotis medellinius*, *Microryzomys minutus*, and *Thomasomys aureus*).

In Yarumal, incidence-based estimators suggest that up to 18 species can compose the SNVM community. Interestingly, when the species collected by Hershkovitz were added to our Yarumal records, the resulting 17 species were close to the expected value obtained for this locality (Table 3). Moreover, it is likely that other rare or less abundant species (e.g., *Chilomys instans* and *Oligoryzomys fulvescens*) can occur in the area but are still absent from collections. Based on the species recorded in the area, including Hershkovitz collections and our own data, incidence-based estimators seem to provide more accurate results for predicting species richness.

Species composition

Species composition was very similar among the SNVM communities of Amalfi, Anorí, and Yarumal. Nine species were common to both Amalfi and Yarumal, and the species recorded in Anorí were also found in our other two localities (Table 2). These nine species, but particularly those found by other studies (*Handleyomys intectus*, *Melanomys caliginosus*, *Nephelomys pectoralis*, *Rhipidomys latimanus*, and *Heteromys australis*) (Gómez-Laverde 1994, Delgado-V and Palacio-V 2002, Gómez Valencia 2004, Sánchez-Giraldo 2006, Rojas Briñez 2008), can be considered a common component of SNVM communities in montane habitats of the Cordillera Central. Conversely, *Chilomys instans*, *Microryzomys minutus*, and *Neacomys tenuipes*, which were recorded only once or on a single survey, are species infrequently encountered in other montane localities in the northern Andes. *Microryzomys minutus* appears to be more abundant in localities above 2500 m (Gómez-Laverde 1994, Delgado-V and Palacio-V 2002, Gómez Valencia 2004, Rojas Briñez 2008).

Records of *Oligoryzomys fulvecens* and an unidentified Oryzomyini are noteworthy for the northern Andes. *Oligoryzomys fulvecens* had not been previously recorded in the northern Cordillera Central (Gómez-Laverde 1994, Delgado-V and Palacio-V 2002, Gómez Valencia 2004, Sánchez-Giraldo 2006, Rojas Briñez 2008) and, although its known distribution includes habitats ranging from lowlands up to 2000 m, the species is rarely found above 1500 m (Weksler et al. 2008). Similarly, four sigmodontine individuals were positively identified as members of the Oryzomyini tribe, but they could not be associated to any of the currently described genera of the tribe (Weksler et al. 2006, Percequillo et al. 2011, Pine et al. 2012). Understanding the taxonomic identity of these specimens is a matter that merits its own research and is a topic on which we are currently working. Six species of didelphid marsupials found in our study area (including Hershkovitz records) belong to genera frequently distributed in the northern Andes (Alberico et al. 2000, Solari et al. 2013). However, although species of these genera are found in other localities of the Cordillera Central, the number of didelphids seldom exceeds one or two species per community (Gómez-Laverde 1994, Delgado-V and Palacio-V 2002, Gómez Valencia 2004, Sánchez-Giraldo 2006, Rojas Briñez 2008), making Yarumal and Amalfi atypically rich in marsupials.

To evaluate the species of SNVM in our three sampled localities in a vertical gradient, we assembled an elevational range profile of SNVM in the north of Cordillera Central (north of 5° N) and surrounding lowlands (Figure 3, supplementary material – Appendix 2). It is evident from these results that most of the species recorded in Amalfi, Anorí, and Yarumal exclusively inhabit middle elevations (1000–2000 m) with little contribution from the lowlands. Other studies in the Andes have shown similar patterns where a turnover of rodent species occurs between lowlands and areas above 1000 m (Patterson et al. 1998, Presley et al. 2012). Moreover, species considered typical of middle elevations (i.e., *Heteromys australis*, *Melanomys caliginosus*, and *Neacomys tenuipes*) have broader altitudinal ranges and therefore extend their distributions into the lowlands (<1000 m). A larger number of species at middle elevations have more affinities with highlands than with lowlands, especially species such as *Akodon affinis*, *Cryptotis medellinius*, *Marmosops caucae*, *Nephelomys pectoralis*, *Reithrodontomys mexicanus*, and members of the Thomasomyini tribe (Figure 3). Finally, the extremely narrow elevational distribution of some species (e.g., *Oligoryzomys fulvescens* and the unidentified Oryzomyini) seems to reflect the lack of sampling in the northern Andes, where additional fieldwork is still required to further understand the community composition and distributional patterns of mammal species.

Abundance

The ubiquity across surveys and overall high capture frequency of *Nephelomys pectoralis* in Amalfi, Anorí, and Yarumal is one of the main patterns emerging from our results and is one that seems common to other localities in the Cordillera Central. Other studies in the Cordillera

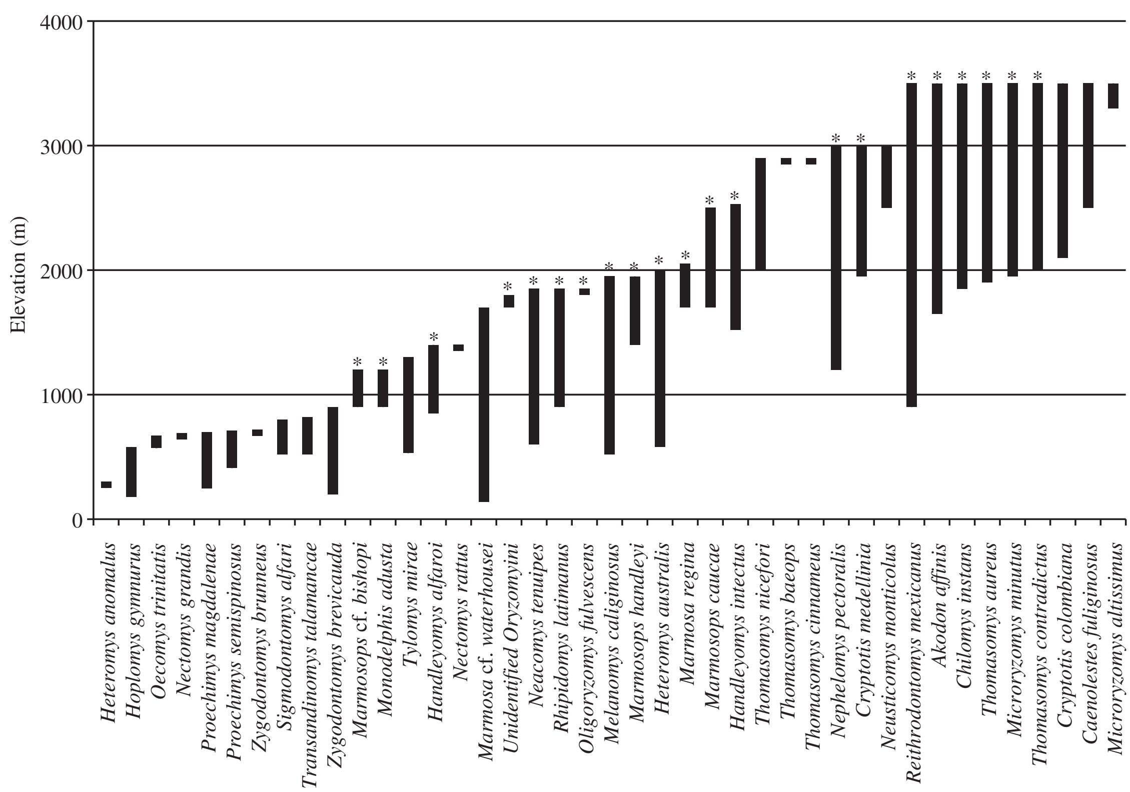

Figure 3 Elevational range profile of SNVM in the northern Cordillera Central using records from supplementary material – Appendix 2. Stars show the species collected by Hershkovitz and by us in Amalfi, Anorí, and the Valdivia/Yarumal area.

Central (8 out of 12 localities) show a similar pattern where species of the genus *Nephelomys* (*N. childi* and *N. pectoralis*) are either the dominant species (56%–41% of captured individuals), or show intermediate abundances (41%–29% of captured individuals) (Gómez-Laverde 1994, Delgado-V and Palacio-V 2002, Sánchez-Giraldo 2006, Rojas Briñez 2008). In only a few other localities in Cordillera Central (4 out of 12 localities), the species was either not recorded (Delgado-V and Palacio-V 2002, Rojas Briñez 2008) or present only in low abundances [10%–17% (Gómez Valencia 2004, Rojas Briñez 2008)]. However, at elevations above 2500 m (two localities), *N. pectoralis* is present in very low abundance (2%), and it seems to be replaced as the dominant species by members of the Thomasomyini tribe (Gómez Valencia 2004).

The capture of *Heteromys australis* in Amalfi, Anorí, and Yarumal during most of the surveys and its high abundance in Amalfi (Table 4) is another noteworthy result. The high relative abundance of this species contrasts with the findings in other studies in Cordillera Central (12 localities between 1690 and 2500 m), where the species is absent from most surveys (Delgado-V and Palacio-V 2002, Sánchez-Giraldo 2006, Rojas Briñez 2008) or present only at very low abundances [2% of captured individuals (Gómez-Laverde 1994)]. Ecological niche models for this species show that most of the Cordillera Central between 0 and 2500 m in elevation has suitable habitat for the potential distribution of the species (Anderson et al. 2002). Our results suggest that *H. australis* is apparently more common, and perhaps more frequently encountered, in the northern portion of Cordillera Central.

Interestingly, historical records (Hershkovitz's fieldwork) also document the rodents *Nephelomys pectoralis* and *H. australis* as two of the most common and abundant species in the community. Philip Hershkovitz, while working in the area, highlighted in his field notes (June 22, 1950, page 584) the following: "Within the altitudinal limits worked [900–2000 m], there are found three common species of [rodents]. The commonest is [*Melanomys*] *caliginosus*. It is very abundant in rastrojos and cultivated fields. It is more abundant at lower [a]ltitudes. Next is [*Nephelomys*] *albigularis*, most abundant in the middle and higher altitudes (1400–2000 m). *Heteromys* [*australis*] is third in line". As clarified by Hershkovitz, *M. caliginosus* seems to be the most abundant species at lower elevations, whereas *N. pectoralis* and *H. australis* were the most abundant at higher elevations, which correspond to the altitudes covered by our fieldwork.

Trapping methods and effort

Using a variety of trapping methods in mammalian inventories has proved to be necessary because different methods can target particular species (Pizzimenti 1979, Patterson et al. 1989, Voss and Emmons 1996, Voss 2003). Nonetheless, most mammalian inventories in the northern Andes have neglected the use of different methods such as pitfall traps (e.g., López-Arévalo and Montenegro-Díaz 1993, Gómez-Laverde 1994). Our work reinforces the idea that using multiple methods is important for inventorying more effectively SNVM communities in the northern Andes. For instance, in Yarumal, the species *Cryptotis medellinius*, *Microryzomys minutus*, and *Neacomys tenuipes* were exclusively captured using pitfalls and the single record of *Marmosa* (*Micoureus*) *regina* in Yarumal was caught by hand through active search.

Although our work does not have an experimental design to statistically test the relative effectiveness of different capture methods, our results suggest that short inventories can be rewarded with captures of new species to the inventory and more individuals of rare or less abundant species by including pitfall traps and active search. We strongly encourage researchers to use a combination of trapping methods when inventorying SNVM communities in the northern Andes that includes, at least but not exclusively), live traps, snap traps, pitfall traps, and active search.

How many traps and how many nights are needed to adequately inventory the SNVM community of a particular locality? This is probably a question that many mammalogists have faced from students and professionals of different fields of biology, and nonetheless it remains as a very challenging one. Although our work does not provide a definitive answer to this question, our results and analyses provide estimates of what could be considered a poor sampling effort, which consequently could partially answer the other end of the initial question: what is a low sampling effort for inventories of Andean SNVM? Our results and those of other studies (Delgado-V and Palacio-V 2002, Sánchez-Giraldo 2006) suggest that efforts near 1500 traps-night are insufficient for adequately inventorying the SNVM community in montane forests at the north of Cordillera Central. A trapping effort of 1449 traps-night in Yarumal and 2562 traps-night in Amalfi resulted in 40% (including Hershkovitz's records) and 21%, respectively, of missing species based on richness estimators. We do not suggest that the values here provided for trapping effort (and their associated percentages of capture success) can be directly extrapolated to other localities of the Andes. Rather, we present these results in the hope that they can be used as a starting point to make educated decisions when designing SNVM inventories with emphasis on montane forests of the northern Andes.

Implications for conservation

Andean small mammal communities in middle elevations have revealed important patterns of high richness and substantial degrees of endemism in localities from Ecuador and Peru. Such findings have been essential for starting to understand Andean biogeographic patterns (Voss 2003, Patterson et al. 2012). However, middle elevations remain poorly studied and very little is still known on the overall richness and endemism patterns for small mammals in the northern Andes (Voss 2003). Although the northern Cordillera Central does not reach the high levels of species richness reported for other Andean localities (Voss 2003) – some of which have been sampled with even less effort than our own work (e.g., Solari et al. 2006) – our results suggest that the region contains areas (i.e., Amalfi and Yarumal) with high species richness in a regional context as they reached values similar or higher than those in other northern Colombian Andean localities. Likewise, the presence of three endemic species for Cordillera Central (*Cryptotis medellinius*, *Handleyomys intectus*, and *Marmosops handleyi* Pine, 1981), the recent finding of new populations of the threatened marsupial *M. handleyi* (Díaz-N et al. 2011), and the occurrence of complex taxonomic entities (e.g., unidentified Oryzomyini) are relevant results that suggest the importance of the region from a conservational and biogeographical standpoint, and its high priority for future surveys.

Acknowledgments: We sincerely thank the campesinos of finca Costa Rica in Amalfi, finca La Linda and finca Villanueva in Yarumal, and finca Chaquiral in Anorí for letting us live in their homes and providing us the necessary field support for our work. We thank colleagues and friends who selflessly helped us in fieldwork: Juliana Cardona-Duque, Jorge Gonzalez, David Marín, Juan D. Sanchez, Ursula Herrera, and Lina M. Arcila. We acknowledge our friend Carlos A. Delgado-V for providing us unpublished data of his Amalfi fieldwork in June 2004 and Bibiana Gómez Valencia for giving us access to her unpublished undergraduate research project. Sergio Solari provided comments to an early version of the original manuscript. We are grateful to two reviewers, and especially to Bruce D. Patterson who carefully read the original manuscript and gave insightful comments for its improvement. Fieldwork of this research was funded through "Iniciativa para las Especies Amenazadas" of Fundación Omacha and Conservation International-Colombia, The Youth Activity Fund Grant of the Explorers Club-NY, partial grant of the Organization for Tropical Studies (OTS), and the local environmental authority Corporación Autónoma Regional del Centro de Antioquia-CORANTIOQUIA. J.F.D. is currently supported by a Francisco José de Caldas Fellowship from the Colombian department of science, technology, and innovation (COLCIENCIAS).

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Supplemental Material: The online version of this article (DOI 10.1515/mammalia-2014-0018) offers supplementary material, available to authorized users.