

Diversity of rodents in three altitudinal zones in Cloudbridge Nature Reserve, Costa Rica

REBECA JIMÉNEZ-GÓMEZ^{1,4*}, BERNAL RODRÍGUEZ-HERRERA², LILLIANA PIEDRA-CASTRO³, AND JOSÉ D. RAMÍREZ-FERNÁNDEZ⁴

¹Universidad Nacional, Heredia, Costa Rica.

²Centro de Investigación en Biodiversidad y Ecología Tropical (CIBET), Universidad de Costa Rica. San Pedro, Montes de Oca, CP. 2060. San José, Costa Rica. E-mail: bernal.rodriguez@ucr.ac.cr (BR-H)

³Laboratorio de Recursos Naturales y Vida Silvestre (LARNAVISI), Escuela de Ciencias Biológicas, Universidad Nacional, 36-3000, Heredia, Costa Rica. E-mail: lilliana.piedra.castro@una.cr (LP-C)

⁴OneHealth Costa Rica Alliance (OHCRA), San José, Costa Rica. E-mail: josed-rf@hotmail.com (JDR-F)

*Corresponding author: rebecajimgom@gmail.com

Elevation is a natural gradient that shapes wildlife and vegetation communities. Therefore, spatial, climatic and ecological hypotheses have been proposed to describe the diversity of rodents in the altitudinal gradient. Our objective was to describe the biological diversity of rodents at three elevations in relation to microhabitat characteristics and seasonality. We captured rodents using Sherman traps in three altitudinal zones (1600, 1800, 2000 m.a.s.l.) during the dry and rainy season. We measured five microhabitat characteristics at each elevation. We compared the species diversity using coverage-based rarefaction and extrapolation curves and the composition of the rodent's community using the similarity indices of Jaccard and Bray – Curtis. In addition, we identify the species that contributed most to the differences in the community. Through Generalized Linear Models (GLM) we evaluate 1) the rodent occurrence by elevation, seasonality and microhabitat characteristics and 2) the variation of microhabitat characteristics by elevation and seasonality. In 2100 night-trap effort we captured 200 individuals of nine species. The most abundant species was *Peromyscus nudipes*. We found that the species diversity decreases with elevation and in the dry season. In terms of species composition, the low elevation between seasons and the high elevation between seasons were more similar. However, when we analyze the abundance, the 2000 m elevation were more similar between seasons. Rodent occurrence depends on the elevation. Finally, the microhabitat characteristics vary by elevation and seasonality. In conclusion, at Cloudbridge Nature Reserve the elevation influences the diversity and the presence of rodents by changing the microhabitat characteristics. Therefore, sites with microhabitat characteristics that could provide protection against predators and potential food sources harbor more rodent diversity.

Keywords: Central America, microhabitat, mountains, rodents, seasonality, species richness

La elevación es un gradiente natural que moldea las comunidades faunísticas y florísticas. Por lo tanto, se han propuesto hipótesis espaciales, climáticas y ecológicas para describir la diversidad de ratones en el gradiente altitudinal. Nuestro objetivo fue describir la diversidad biológica de las especies de ratones en tres elevaciones en relación con las características del microhábitat y la época. Se capturaron ratones, utilizando trampas Sherman, en un gradiente altitudinal (1600, 1800, 2000 m.s.n.m.) durante la época seca y la lluviosa. Se midieron cinco características de microhábitat en cada elevación. La diversidad de especies se comparó por medio de curvas de rarefacción y extrapolación basadas en la cobertura de muestra y la composición de la comunidad mediante los índices de similitud de Jaccard y Bray – Curits. Además, se identificaron las especies que más contribuían a las diferencias en la comunidad. Por medio de modelos lineales generalizados se evaluó 1) la presencia de ratones por elevación, época y características del microhábitat y 2) la variación de las características de microhábitat por elevación y época. Con un esfuerzo de muestreo de 2100 noches trampa se capturaron 200 individuos de nueve especies. La especie más abundante fue *Peromyscus nudipes*. Se encontró que la diversidad de especies disminuyó con la elevación y en la época seca. En términos de composición de especies, la elevación baja entre épocas y la elevación alta entre épocas fueron más similares. Sin embargo, cuando se analizó la abundancia, la elevación de 2000 m fue más similar entre épocas. La presencia de ratones dependió de la elevación. Finalmente, las características del microhábitat varían según la elevación y la época. En conclusión, en la Reserva Natural Cloudbridge la elevación influye en la diversidad y la presencia de roedores al cambiar las características del microhábitat. Por lo tanto, los sitios con características de microhábitat que podrían brindar protección contra depredadores y posibles fuentes de alimento albergan una mayor diversidad de roedores.

Palabras clave: Centroamérica, microhábitat, montañas, ratones, riqueza de especies, temporalidad

© 2026 Asociación Mexicana de Mastozoología, www.mastozoologiamexicana.org

Elevation constitutes a powerful ecological gradient that influences the structure and composition of wildlife and plant communities across restricted spatial scales. It shapes patterns of species dispersal, colonization, speciation, and extinction, often giving rise to biodiversity hotspots and endemic-rich zones (Brown 2001; Lomolino 2001; Rahbek et al. 2019a, 2019b). To explain these distributional dynamics, a range of spatial, climatic, and ecological hypotheses have been proposed in the context of elevational gradients (McCain and Grytnes 2010).

From the climatic point of view, precipitation affects positively and indirectly the richness and abundance of non-volant rodents because it influences productivity, habitat heterogeneity, plant biomass, and food availability (Nor 2001; McCain and Grytnes 2010). Regarding the habitat heterogeneity, the microhabitat characteristics that might influence the presence of rodents are those that help them search for food or shelter, such as canopy coverage, presence of rocks, logs, live trees, leaf litter depth, density of shrubs, proximity of

water bodies and food resources (e.g., [Ramírez-Bautista and Williams 2019](#); [Sakane et al. 2019](#); [Karasov-Olson and Kelt 2020](#); [Benedek et al. 2021](#)).

Costa Rica is a mountainous country, although there are few studies related to altitudinal gradient, microhabitat characteristics and rodents. Regarding the altitudinal gradient, [McCain \(2004, 2006\)](#) concluded that the diversity of rodents in Monteverde Cloud Forest Biological Reserve and Children's Eternal Rainforest was higher at mid-elevations, apparently due to productivity gradients and climatic conditions such as precipitation, temperature, and cloud distance that were higher at mid-elevation.

In terms of microhabitat characteristics at Cerro de la Muerte Biological Station (CMBS) and the paramo, [Ramírez-Fernández \(2023a\)](#) found that *Peromyscus nudipes* was more abundant in the montane forest that had more bushes and less luminosity because this habitat provides greater structural diversity, food resources, and protection against predators.

As a result of climate change and habitat loss, the mountain ecosystem and the species that inhabit it are being affected ([Yanahan and Moore 2019](#); [Barras et al. 2021](#)). In Costa Rica climate projections indicate a significant reduction in mountain life zones ([Birkel et al. 2022](#)), and modeled scenarios suggest changes in the spatial distribution of birds, lizards, and anurans in the mountains ([Pounds et al. 1999](#); [Liu et al. 2023](#)). Because not all organisms can adapt to climatic and habitat variations, it is necessary to know the species that live in the mountains and establish actions that allow the permanence of individuals. In Costa Rica, there are 17 endemic species of mice, most restricted to mountainous ecosystems at elevations greater than 1500 m.a.s.l. ([McPherson 1985](#); [Rodríguez-Herrera et al. 2014](#); [Ramírez-Fernández et al. 2023b](#)). However, there are gaps in information about ecology and natural history; therefore, we aim to describe the biological diversity of rodents at three elevations in relation to microhabitat characteristics and seasonality.

Materials and methods

Study area. The study was conducted in the Cloudbridge Nature Reserve (CNR), located in the montane oak forest within Talamanca Mountain range, in San Gerardo de Rivas, San José, Costa Rica (9°28'20" N, 83°34'39" W). The CNR presents an area of 255 ha, including 28 ha of primary forest and secondary forest at different levels of regeneration. The CNR connects with the Chirripó National Park at the highest elevations and has an altitudinal gradient of 1500 to 2600 m.a.s.l. (Figure 1). The average daily temperature oscillates between 16 and 19°C. The mean precipitation changes drastically between the dry season and the rainy season (113 to 2470 mm) ([Powell et al. 2022](#)). The life zones are humid to rainy forests in the Premontane and Lower Montane altitudinal belts ([Holdridge 1967](#)).

Rodents trapping. We selected three trapping stations along the Jilguero trail, at 1600, 1800 and 2000 m.a.s.l. We captured rodents using Sherman live traps (5 × 6 ×

16 cm; H. B. Sherman Traps, Inc., Florida) baited with a homogeneous mix of oatmeal, banana, peanut butter, and vanilla extract. We placed the traps in a paired linear transect with a distance of ca. 10 m between traps, and each trap was georeferenced using a GPSMAP Garmin 64sx. Each station was sampled for five consecutive nights per elevation. During the dry season (February – March) we set 30 traps at each elevation (15 paired stations) for a total of 900 night-traps, while in the rainy season (June – July) we set 40 traps at each elevation (20 paired stations) for a total of 1200 night-traps. The number of traps was increased during the rainy season because no rodents were captured at 1800 m during the dry season. Despite the difference in sampling effort between seasons, sample coverage analyses indicated that the sampling effort was sufficient to characterize the rodent diversity in both seasons. Finally, we identified captured individuals to the species level using the key published by [Villalobos-Chaves et al. \(2016\)](#). Voucher specimens of taxonomically debatable species were collected as a reference (Supplementary Data SD1).

Microhabitat characteristics. We measured five vegetative variables at 15 random well-spaced trapping points within each station. We quantified (1) the number of fallen logs > 50 cm long and ≥ 10 cm diameter, and (2) the number of trees with ≥ 10 cm diameter at breast height, in a perimeter of 3 and 5 m around the trap. We measured (3) understory density/cover using a densimeter placed just above the trap and (4) leaf litter depth at the four sides of the trap using a ruler. Finally, (5) ground cover was measured using a 50 x 50 cm grid divided into 100 cells placed on the ground next to the trapping point. We estimated the percentage of ground cover occupied by leaf litter, rocks, herbaceous vegetation, woody material, and bare ground by quantifying the number of cells occupied by each material.

Data analysis. To compare samples of different sizes, we assessed rodents' diversity across elevations and seasonality by generating coverage-based rarefaction and extrapolation sampling curves using Hill numbers. Following the recommendation of [Chao and Jost \(2012\)](#), we determined the base coverage as the minimum coverage among compared groups. For comparisons across elevations, we used a minimum coverage of 0.76 and for seasonal comparisons we used 0.98. Specifically, the diversity indices q_0 (species richness), q_1 (Shannon diversity) and q_2 (dominant species abundance, derived from the Simpson index) were calculated following [Chao and Jost \(2012\)](#) implemented via the *vegan* ([Oksanen et al. 2022](#)) and *iNEXT* ([Hsieh et al. 2016](#)) R packages.

To evaluate compositional differences between elevation and seasonality, we applied an Analysis of Similarity (ANOSIM) and constructed two dendrograms based on Jaccard (presence/absence) and Bray–Curtis (abundance) dissimilarity indices, employing average linkage clustering. To further dissect the patterns of community dissimilarity, we conducted a Similarity Percentage (SIMPER) analysis to identify the species

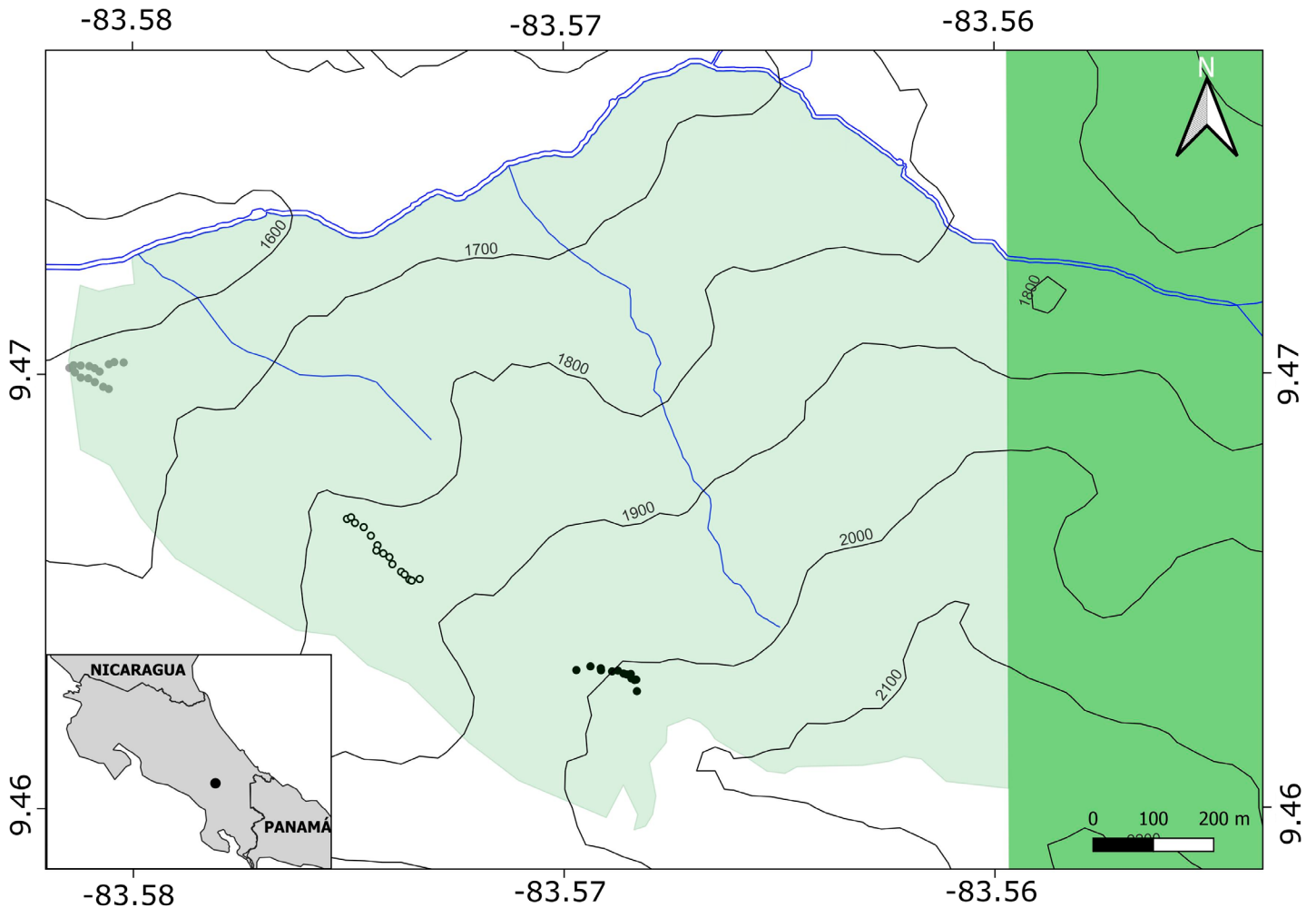


Figure 1. Geographical distribution of sampling sites along an elevational gradient in Cloudbridge Nature Reserve, Talamanca Mountain Range, Costa Rica (2023). Gray, white and black dots represent sampling stations at 1600, 1800, 2000 m.a.s.l., respectively. The light green area indicates the Cloudbridge Nature Reserve; dark green corresponds to Chirripó National Park.

contributing most to differences among sites. To explain if the probability of rodent occurrence was determined by the elevation and microhabitat characteristics, we analyzed the data separately for each season and fitted Generalized Linear Models (GLMs) (family = binomial, link = logit). The most parsimonious model was selected using stepwise model selection based on the lowest Akaike Information Criterion (AIC), for the selected models we report parameter estimate (β) and 95 % confidence intervals (CI).

Also, microhabitat characteristics were analyzed using Generalized Linear Models (GLMs) (family = gaussian, link = identity and family = poisson, link = log), with elevation and seasonality as fixed effects. The best-fitting models were selected based on the Akaike Information Criterion (AIC) (Supplementary Data SD2), and post-hoc comparisons were performed using Tukey's tests to determine pairwise differences.

All statistical analyses were executed in R version 4.4.2 (R Core Team 2024). A significance level of 0.05 was applied to all tests, except for the ANOSIM procedure, where a threshold of 0.1 was used to account for limitations in sample size. This analytical framework allowed for robust evaluation of biodiversity and environmental gradients within the study region.

Ethical statement. Research and handling with live animals followed ASM guidelines (Sikes et al. 2016). This study is framed under MINAE and CONAGEBIO research permits (resolutions SINAC-ACC-PI-R-044-2020, R-SINAC-PNI-ACLAP-028-2020, and R-001-2021-OT-CONAGEBIO).

Results

A total of 200 captures of nine species distributed in three families were captured in 2100 night-trap effort. Of the nine species captured, three are endemic to the Talamanca Mountain range in Costa Rica and Panamá. Two captures corresponded to the mouse opossum *Marmosa zedoni*, and those were excluded from all the analyses (Table 1). Only *Scotinomys teguina* was present at the three elevations. One species, *Nyctomys sumichrasti*, was only captured at 1800 m. While at 2000 m two unique species, *Nephelomys devius* and *Tylomys watsoni* were captured. The most abundant species was *P. nudipes* with 111 captures, and the least abundant were *N. sumichrasti* and *T. watsoni* with only one individual captured. In terms of seasonality, we captured fewer rodents during the dry season compared to the rainy season (Table 1).

Table 1. Abundance of small mammals captured along three elevations in Cloudbridge Nature Reserve, Talamanca Mountain range, Costa Rica (2023), during the dry and rainy season. Endemic species to the Talamanca Mountain range are marked with asterisk (*).

Family	Species	Elevation m.a.s.l.			Total abundance	Season	
		1600	1800	2000		Dry	Rainy
Didelphidae	<i>Marmosa zeledoni</i> E. A. Goldman, 1911	1	1	0	2	0	2
Cricetidae	<i>Scotinomys teguina</i> (Alston, 1877)	9	2	18	29	2	27
	* <i>Peromyscus nudipes</i> (J. A. Allen, 1891)	6	0	105	111	44	67
	<i>Reithrodontomys "mexicanus"</i> ^a Saussure, 1880	19	0	4	23	3	20
	* <i>Nephelomys devius</i> (Bangs, 1902)	0	0	5	5	3	2
	<i>Oligoryzomys costaricensis</i> (J. A. Allen, 1893)	24	1	0	25	4	21
	<i>Nyctomys sumichrasti</i> (Saussure, 1860)	0	1	0	1	0	1
	* <i>Tylomys watsoni</i> O. Thomas, 1899	0	0	1	1	1	0
Heteromyidae	<i>Heteromys desmarestianus</i> Gray, 1868	0	2	1	3	0	3
	Total abundance	59	7	134	200	57	143

^a This species is denoted in quotation marks because it represents a species cryptic complex (Martínez-Borrego et al. 2023); while the species ID is likely to be *Reithrodontomys garichensis* or *Reithrodontomys brevirostris*, we did not perform any molecular analysis to confirm its taxonomy. Two specimens were collected and preserved in a scientific collection for further analysis and proper identification (Supplementary Data SD1).

Sample coverage varied with elevation. At 2000 m elevation it was 0.98, at 1800 m was 0.76, and at 1600 m was 1. For all diversity orders, at both high and low elevations, the sample coverage suggests adequate sampling, as our sample captured most of the diversity. However, at 1800 m elevation, the sample coverage value suggests that a larger sample is required. We found no significant differences when comparing all Hill numbers (q0, q1, q2), between 1800 m and the other two elevations (Figure 2). Also, we did not find a dominant species and the abundances of the captured species were very similar (Table 1), which may explain the greater variability in the standard errors. When comparing low and high elevations, the 1600 m elevation showed greater species richness (q0), greater diversity of common (q1) and abundant species (q2). In contrast, at 2000 m the community was strongly dominated by *P. nudipes*. At low elevation, the community showed a more balanced structure, with the dominance of *Reithrodontomys "mexicanus"* and *Oligoryzomys costaricensis*.

On the other hand, the sample coverage was very similar for seasonality 0.98 in the dry season and 0.99 in the rainy season. We found a low diversity (q1, q2) during the dry season, however, in species richness (q0) there were no differences between seasons (Figure 3). Also, in the dry season the community was dominated by *P. nudipes*. While during the rainy season yielded a broader spectrum of rare species, including *N. sumichrasti* and *Heteromys desmarestianus*. These temporal shifts underscore the role of climatic variability in shaping rodent assemblages along tropical elevational gradients.

The species composition at the CNR showed a weak tendency to vary by elevation (Figure 4, ANOSIM: $R^2 = 0.44$, $P < 0.1$), while no differences were detected between seasons (Figure 4, ANOSIM: $R^2 = -0.11$, $P = 0.8$). According to the Jaccard index, rodent species composition at 1600 m was nearly identical between seasons and at 2000 m also show high seasonal similarity. On the other hand, both elevations were highly dissimilar from the 1800 m elevation. When we compared the abundance of rodents using the Bray – Curtis index the highest similarity between seasons was observed at 2000 m, whereas overall dissimilarity among elevations remained high. In both indices, the rodent community from the 1800 m elevation dry season form a distinct group because there were no captures (Figure 4).

When we compared the species that contribute most to dissimilarity, we found that between low and mid elevations *P. nudipes* contributes most significantly to the dissimilarity, with a contribution of 81 %, followed by *R. "mexicanus"* with 65 %. This high contribution is due to the absence of both species at 1800 m elevation. On the other hand, *O. costaricensis*, which is present at both low and mid elevations, contributes 36 % to the similarity between these two elevations. In contrast, between 1800 and 2000 m elevations only *P. nudipes* contributes to dissimilarity, by 80 %.

In addition, the probability of rodent occurrence during the dry season was positively related with the elevation ($\beta = 0.007$, CI 95 % = 0.004 – 0.011). To better understand this variable, we describe the microhabitat characteristics that varied by elevation and seasonality. Rodent occurrence decreased with increasing the number of trees ($\beta = -0.163$,

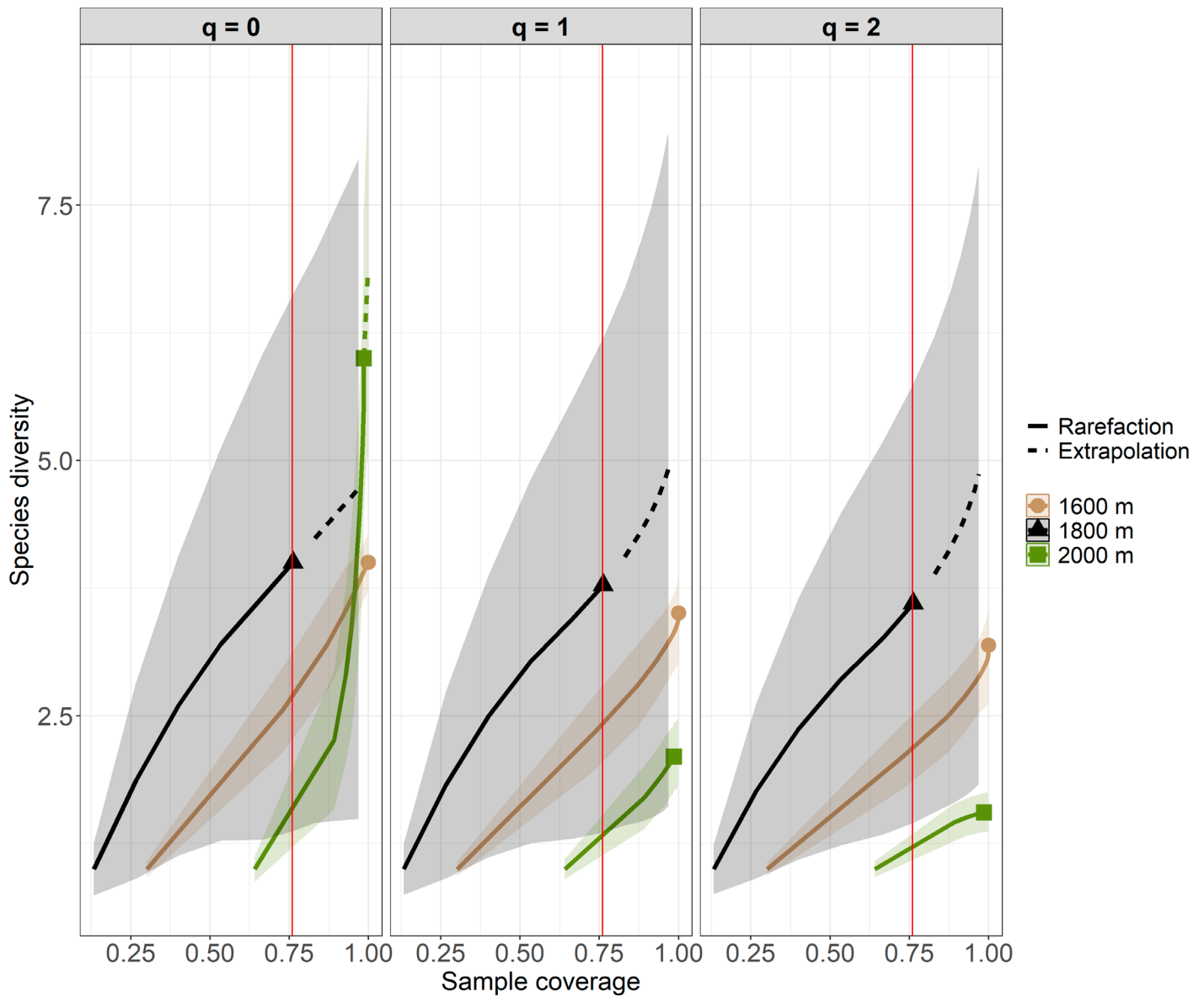


Figure 2. Coverage-based rarefaction and extrapolation sampling curves for q0 (species richness), q1 (Shannon diversity) and q2 (dominant species abundance, derived from the Simpson index) across three elevations at Cloudbridge Nature Reserve, Talamanca Mountain range, Costa Rica (2023). Shaded areas represent standard error, dotted lines indicate extrapolation, red line indicate the minimum coverage.

CI 95 % = - 0.329 – -0.030). During the rainy season, rodent presence decreased with increasing bare ground ($\beta = -0.109$, CI 95 % = -0.228 – -0.013) and leaf litter ($\beta = -0.026$, CI 95 % = -0.053 – -0.001, Table 2).

Specifically, we found more logs at mid elevation ($\beta = 1.61$, SE = 0.34, $z = 4.67$, $P < 0.001$) and high ($\beta = 1.55$, SE = 0.34, $z = 4.56$, $P < 0.001$) elevations during the dry season. There were more trees at mid elevation ($\beta = 0.842$, SE = 0.72, $z = 11.64$, $P < 0.001$; post-hoc Tukey’s tests $P < 0.001$) and during the dry season ($\beta = 2.50$, SE = 0.57, $t = 4.36$, $P < 0.001$). Leaf litter depth was higher in the dry season ($\beta = 0.56$, SE = 0.12, $t = 4.67$, $P < 0.001$), and at both 1800 m and 2000 m elevations, but there was no significant difference between mid and high elevations (post-hoc Tukey’s tests $P = 0.6$, Table 3). Finally, we found that the understory density/cover was higher at 2000 m elevation ($\beta = 4.02$, SE = 0.84, $t = 4.81$, $P < 0.001$; post-hoc Tukey’s tests $P = 0.010$) and during the rainy season (Table 3).

Regarding the ground cover, we found more herbaceous coverage at 1600 m elevation ($\beta = 66.10$, SE = 5.78, $t = 11.43$, $P < 0.001$). Additionally, herbaceous coverage was higher

Table 2. Parameters of Generalized Linear Models (GLMs) assessing the probability of rodent occurrence by the elevation and microhabitat characteristics separated by seasonality at Cloudbridge Nature Reserve, Talamanca Mountain Range, Costa Rica (2023). We represent the confidence intervals (CI) at 95%.

Seasonality	Coefficient	Estimate	Standard error	CI 95 %
Dry	Intercept	-11.806	3.203	-18.602 – -5.895
	Elevation	0.007	0.002	0.004 – 0.011
	Trees number	-0.163	0.076	-0.329 – -0.030
	Woody material	-0.053	0.028	-0.112 – 0.0005
Rainy	Intercept	-3.393	2.817	-9.066 – 2.068
	Elevation	0.002	0.002	-0.0006 – 0.006
	Trees number	0.154	0.091	-0.020 – 0.340
	Bare ground	-0.109	0.054	-0.228 – -0.013
	Leaf litter	-0.026	0.013	-0.053 – -0.001

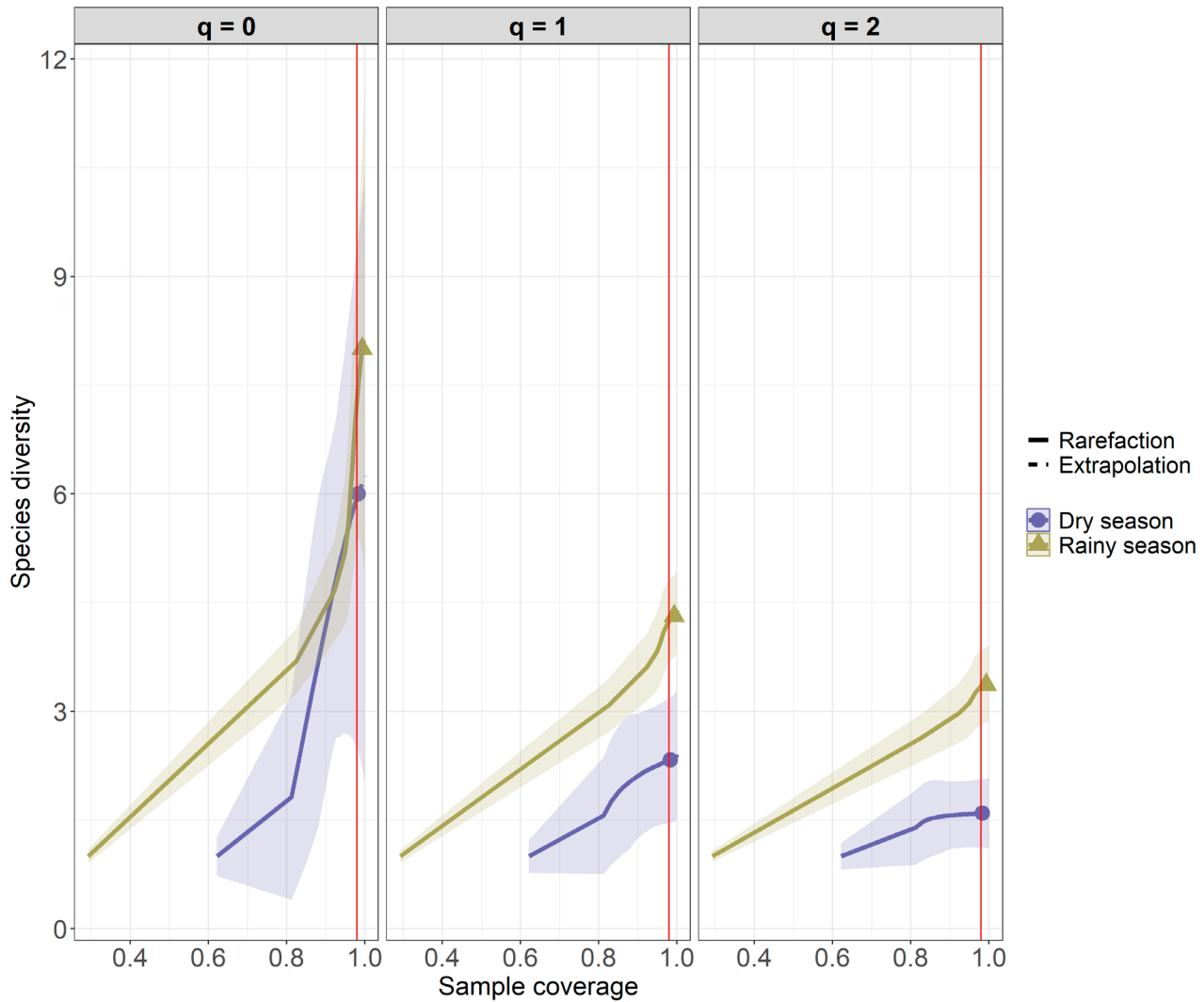


Figure 3. Coverage-based rarefaction and extrapolation sampling curves for q0 (species richness), q1 (Shannon diversity), and q2 (dominant species abundance, derived from the Simpson index) during the dry and rainy seasons at Cloudbridge Nature Reserve, Talamanca Mountain range, Costa Rica (2023). Shaded areas represent standard error, dotted lines indicate extrapolation, red line indicate the minimum coverage.

Table 3. Parameters of Generalized Linear Models (GLMs) assessing the effects of elevation and seasonality on structural microhabitat characteristics at Cloudbridge Nature Reserve, Talamanca Mountain Range, Costa Rica (2023). Int: Intercept.

Variable	Coefficient	Estimate	Standard error	Test statistic	P value
Logs number	1 600 m, Rainy season (Int)	0.693	0.129	z = 5.369	<0.001
	1 800 m elevation	0.569	0.162	z = 3.523	<0.001
	2 000 m elevation	0.847	0.154	z = 5.491	<0.001
	Dry season	-1.609	0.316	z = -5.089	<0.001
	1 800 m elevation x Dry season	1.6094	0.345	z = 4.668	<0.001
	2 000 m elevation x Dry season	1.551	0.339	z = 4.578	<0.001
Trees number	1 600 m, Rainy season (Int)	1.318	0.064	z = 25.870	<0.001
	1 800 m elevation	0.842	0.072	z = 11.639	<0.001
	2 000 m elevation	0.243	0.080	z = 3.002	0.003
	Dry season	0.362	0.057	z = 6.317	<0.001
Leaf litter depth	1 600 m, Rainy season (Int)	1.599	0.119	t = 13.403	<0.001
	1 800 m elevation	0.305	0.146	t = 2.083	0.039
	2 000 m elevation	0.440	0.146	t = 3.011	0.003
	Dry season	0.557	0.119	t = 4.669	<0.001
Understory density/cover	1 600 m, Rainy season (Int)	93.765	0.682	t = 137.524	<0.001
	1 800 m elevation	1.539	0.835	t = 1.843	0.067
	2 000 m elevation	4.018	0.835	t = 4.812	<0.001
	Dry season	-2.342	0.682	t = -3.435	<0.001

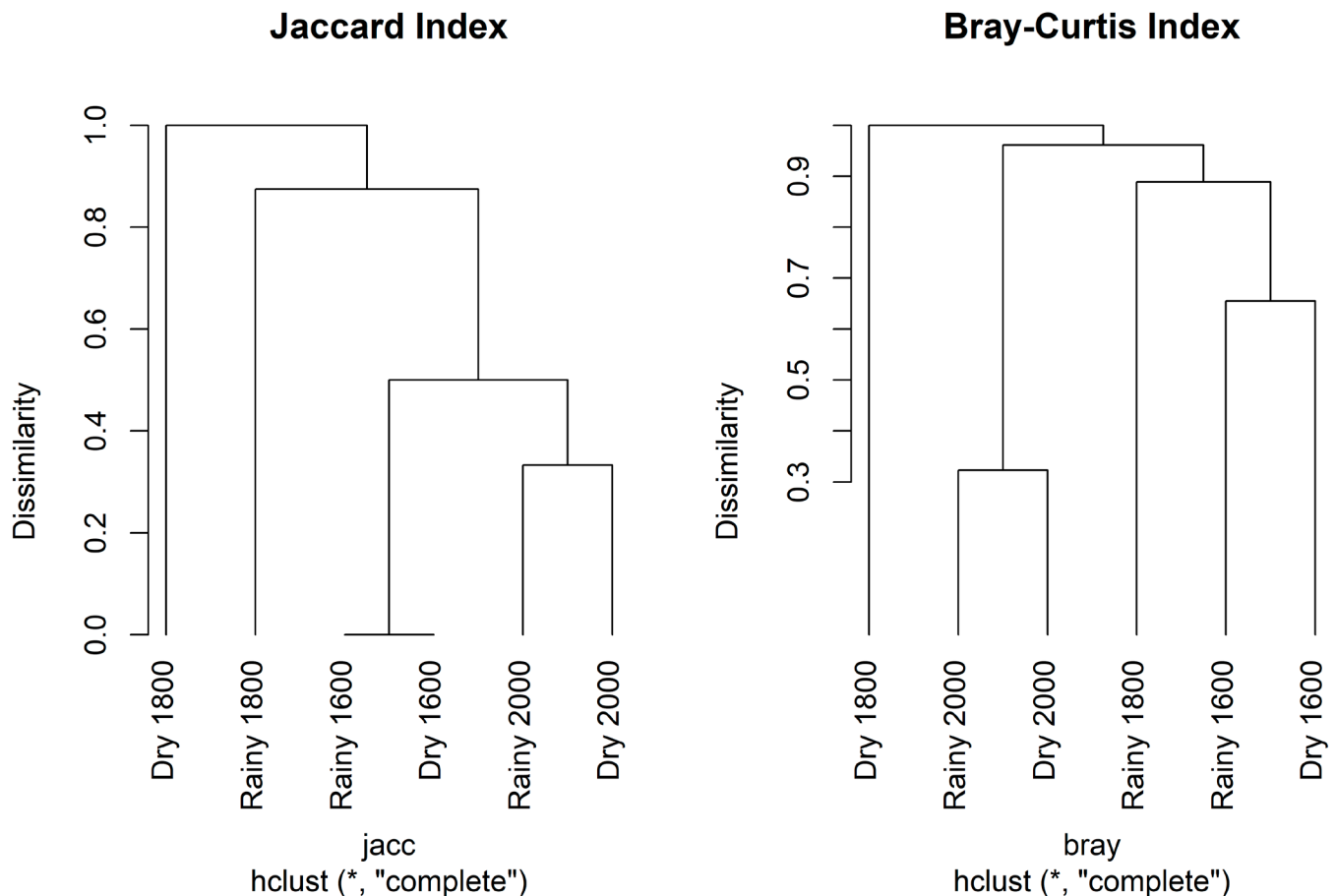


Figure 4. Dissimilarity in rodent assemblages at Cloudbridge Nature Reserve, Talamanca Mountain range, Costa Rica (2023). Based on Presence/Absence (Jaccard index) and Species Abundance (Bray – Curtis index).

at mid elevation during the dry season compared to the other elevations during the same season ($\beta = 30.60$, $SE = 11.57$, $t = 2.65$, $P < 0.009$). The presence of rocks was higher at the 2000 m elevation compared to the other elevations ($\beta = 14.78$, $SE = 2.73$, $t = 5.42$, $P < 0.001$; post-hoc Tukey's tests $P = 0.0001$). The presence of leaf litter was higher at mid elevation and during the rainy season (Table 4), with no difference between mid and high elevations (post-hoc Tukey's tests $P = 0.09$). However, we found more leaf litter at high elevation during the dry season compared to the other elevations during the same season ($\beta = 56.00$, $SE = 12.64$, $t = 4.42$, $P < 0.001$). The average amount of woody material ($\beta = 11.83$, $SE = 2.96$, $t = 4.02$, $P < 0.001$) and bare ground ($\beta = 54.26$, $SE = 4.75$, $t = 11.42$, $P < 0.001$) was higher during the dry season, with bare ground being more abundant at low elevation during the dry season (Table 4).

Discussion

Precipitation has been associated with increased rodents' diversity due to greater habitat heterogeneity (Sánchez-Cordero 2001; Ramírez-Bautista and Williams 2019). Our results support this pattern by documenting higher understory density; this is a habitat feature frequently selected by rodents to feed, shelter, or avoid predation (Brown 2001; Williams et al. 2002; Fardell et al. 2021). Furthermore, it has been reported that rodents are more

active under the rain since it could reduce the risk of predation for two reasons: (1) the rain dissipates the smell of the rodents (Vickery and Bider 1981), and (2) it hides the sounds of movement when walking on leaf litter or branches (Barnum et al. 1992). However, we found that the rodent presence decreased as leaf litter increased, suggesting that further studies are needed to better understand this pattern.

On the other hand, the low diversity and presence of rodent during the dry season, could be due to the high density of trees, which can reduce light availability, thus limiting the development of understory density cover (Klinka et al. 1996). Therefore, bare ground may reduce rodent occurrence, because they are more exposed to predators and could be easily detected and predated (Schulte-Hostedde and Brooks 1997; Roche et al. 1999).

Rodent's presence was associated with elevation, suggesting that changes in microhabitat characteristics along the three elevations might influence rodent distribution and composition at CNR. The 1600 m elevation has open areas within the forest because it has microhabitat characteristics such as herbaceous cover and bare ground. These explain the most abundant species, *O. costaricensis* and *R. "mexicanus"*, because they prefer secondary forest, but also forest glades (Pardiñas et al. 2017).

Table 4. Parameters of Generalized Linear Models (GLMs) evaluating the effects of elevation and seasonality on ground cover microhabitat characteristics at Cloudbridge Nature Reserve, Talamanca Mountain Range, Costa Rica (2023). Int: Intercept.

Variable	Coefficient	Estimate	Standard error	T value	P value
Herbaceous	1600 m, Rainy season (Int)	66.100	5.783	11.430	<0.001
	1 800 m elevation	-47.800	8.178	-5.845	<0.001
	2 000 m elevation	-27.733	8.178	-3.391	0.001
	Dry season	-8.967	8.178	-1.096	0.274
	1 800 m elevation x Dry season	30.600	11.566	2.646	0.009
	2000 m elevation x Dry season	-0.800	11.566	-0.069	0.945
Rocks	1600 m, Rainy season (Int)	-0.589	2.228	-0.264	0.792
	1 800 m elevation	2.917	2.729	1.069	0.287
	2 000 m elevation	14.783	2.729	5.417	<0.001
	Dry season	1.178	2.228	0.529	0.598
Woody material	1600 m, Rainy season (Int)	25.611	2.958	8.658	<0.001
	1 800 m elevation	6.167	3.623	1.702	0.091
	2 000 m elevation	0.233	3.623	0.064	0.949
	Dry season	11.878	2.958	4.015	<0.001
Leaf litter	1600 m, Rainy season (Int)	105.200	6.325	16.633	<0.001
	1 800 m elevation	31.867	8.945	3.563	<0.001
	2 000 m elevation	1.933	8.945	0.216	0.829
	Dry season	-61.533	8.945	-6.879	<0.001
	1 800 m elevation x Dry season	23.800	12.649	1.881	0.062
	2 000 m elevation x Dry season	56.000	12.649	4.427	<0.001
Bare ground	1600 m, Rainy season (Int)	4.267	3.360	1.270	0.206
	1 800 m elevation	3.333	4.752	0.702	0.484
	2 000 m elevation	8.800	4.752	1.852	0.0657
	Dry season	54.267	4.752	11.421	<0.001
	1 800 m elevation x Dry season	-49.700	6.720	-7.396	<0.001
	2 000 m elevation x Dry season	-56.967	6.720	-8.477	<0.001

At 2000 m elevation, the greater density of understory vegetation and increased rock cover likely create favorable microhabitats for forest-dwelling rodents such as *N. devius*, *P. nudipes*, and *T. watsoni*. The structural complexity of the terrain enhances concealment opportunities, with rock formations offering reliable shelter from predators, a behavior well documented in *Peromyscus* spp. (Dooley and Dueser 1990; Millus and Stapp 2008). These microhabitat features may play a key role in shaping community composition at higher elevations.

The notable abundance of *P. nudipes* at this elevation is plausibly linked to trophic specialization, particularly its association with oak (*Quercus* spp.) seed consumption (Rojas and Barboza 2007; Ramirez-Fernández 2019), a food resource encountered exclusively at 2000 m elevation in this study. This dietary preference underscores the influence of vegetation composition on species distribution and highlights the importance of integrating habitat and resource availability when interpreting elevational patterns in rodent assemblages.

The low rodent capture at 1800 m elevation could be due to rodents reducing their activity. This is because logs and leaf litter cover/depth were found at this elevation. Additionally, there was herbaceous coverage at mid elevation during the dry season. These microhabitat

characteristics could be used by rodents to hide from predators, and semi-arboreal species could move more easily through trees. However, our results suggest that more sampling effort is needed to better understand which variables affect the rodent presence at mid-elevation.

The singing mouse *S. teguina* was the only one found in the three elevations in both seasons. This could be due to its flexibility on habitat selection since it occurs within the forest, as well as in disturbed sites with grass or herbs (Hooper and Carleton 1976; Ribble and Rathbun 2018). Changes in food availability could also play a role, as it is a primarily insectivorous species (Hooper 1972; Hooper and Carleton 1976). The three elevations had leaf litter and logs, which are suitable microhabitats for larval development and the presence of various beetles in both seasons (Gossner et al. 2013; Cole et al. 2016), which are preferred by *Scotinomys* spp. (Hooper and Carleton 1976). However, this factor was not directly evaluated in the present study.

Mountain ecosystems are characterized by a high level of endemism. At CNR, we captured three endemic species; this reinforces the importance of highlands conservation and protection (Sakane et al. 2019). Our results suggest that elevation indirectly influences species diversity and occurrence through changes in microhabitat characteristics. Therefore, maintaining forested areas with understory

density/cover, rocks, and leaf litter favors the diversity of rodents and the permanence of endemic species, possibly because it provides diverse food resources and protection against predators. However, this relationship should be explicitly evaluated in future studies.

Acknowledgements

Querida Livia, desde Costa Rica te agradezco todo tu aporte al conocimiento de la mastofauna de la región. También admiro tu impacto como formadora de excelentes profesionales. Muchas gracias por tanta dedicación y cariño en tu trabajo. Bernal Rodríguez-Herrera. We thank the staff and volunteers of Cloudbridge Nature Reserve for logistical support, the Oncilla Conservation project of the Costa Rica Wildlife Foundation for financial support. The Laboratorio de Recursos Naturales y Vida Silvestre (LARNAVISI) of the UNA for loan of equipment. Eduardo Chacón for the help in the statistical analysis. David Vela as a field assistant. This work is part of Rebeca undergraduate research project (Licenciatura) at Universidad Nacional de Costa Rica.

Declaration of Artificial Intelligence use

Authors used ChatGPT for grammar checking.

Author contributions

Rebeca Jiménez-Gómez: conceptualization, study design and fieldwork planning, data collection, analysis and interpretation of the results, and preparation of the first draft of the manuscript. Bernal Rodríguez-Herrera: conceptualization, study design, and fieldwork planning; reviewed and provided critical revisions to the manuscript. Lilliana Piedra-Castro: conceptualization, reviewed, and provided critical revisions to the manuscript. José D. Ramírez-Fernández: conceptualization, study design and fieldwork planning, funding acquisition, reviewed and provided critical revisions to the manuscript.

Supplementary data

SD1. Catalog of voucher specimens of some of the species captured at the Cloudbridge Nature Reserve deposited in the Zoology Museum University of Costa Rica.

SD2. Generalized Linear Models (GLM) evaluating the effects of the elevation and the season on microhabitat characteristics at three elevations of the Cloudbridge Nature Reserve, Talamanca Mountain Range, Costa Rica (2023). The model with the best fit, based on the Akaike Information Criterion (AIC), is indicated in bold.

Literature cited

Barnum SA, Manville CJ, Tester JR, and Carmen WJ. 1992. Path selection by *Peromyscus leucopus* in the presence and absence of vegetative cover. *Journal of Mammalogy* 73:797–801. <https://doi.org/10.2307/1382198>

Barras AG, Braunisch V, and Arlettaz R. 2021. Predictive models of distribution and abundance of a threatened mountain species show that impacts of climate change overrule

those of land use change. *Diversity and Distributions* 27:989–1004. <https://doi.org/10.1111/ddi.13247>

- Benedek AM, Sîrbu I, and Lazăr A. 2021. Responses of small mammals to habitat characteristics in Southern Carpathian forests. *Scientific Reports* 11:1–13. <https://doi.org/10.1038/s41598-021-91488-6>
- Birkel C, Dehaspe J, Chavarría-Palma A, Venegas-Cordero N, Capell R, and Durán-Quesada AM. 2022. Projected climate change impacts on tropical life zones in Costa Rica. *Progress in Physical Geography: Earth and Environment* 46:180–200. <https://doi.org/10.1177/03091333211047046>
- Brown JH. 2001. Mammals on mountainsides: elevational patterns of diversity. *Global Ecology and Biogeography* 10:101–109. <https://doi.org/10.1046/j.1466-822x.2001.00228.x>
- Chao A, and Jost L. 2012. Coverage-based rarefaction and extrapolation: standardizing samples by completeness rather than size. *Ecology* 93:2533–2547. <https://doi.org/10.1890/11-1952.1>
- Cole RJ, Holl KD, Zahawi RA, Wickey P, and Townsend AR. 2016. Leaf litter arthropod responses to tropical forest restoration. *Ecology and Evolution* 6:5158–5168. <https://doi.org/10.1002/ece3.2220>
- Dooley J L and Dueser R D. 1990. An experimental examination of nest-site segregation by two *Peromyscus* species. *Ecology* 71:788–796. <https://doi.org/10.2307/1940330>
- Fardell LL, Nano CE, Pavey CR, and Dickman CR. 2021. Small prey animal habitat use in landscapes of fear: effects of predator presence and human activity along an urban disturbance gradient. *Frontiers in Ecology and Evolution* 9:1–17. <https://doi.org/10.3389/fevo.2021.750094>
- Gossner MM, Floren A, Weisser WW, and Linsenmair KE. 2013. Effect of dead wood enrichment in the canopy and on the forest floor on beetle guild composition. *Forest Ecology and Management* 302:404–413. <http://dx.doi.org/10.1016/j.foreco.2013.03.039>
- Holdridge LR. 1967. Life Zone Ecology. San José (CR): Tropical Science Center. Available at: <https://app.ingemmet.gob.pe/biblioteca/pdf/Amb-56.pdf>
- Hooper ET. 1972. A synopsis of the rodent genus *Scotinomys*. *Occasional Papers of the Museum of Zoology, University of Michigan* 665:1–32.
- Hooper ET, and Carleton MD. 1976. Reproduction, growth and development in two contiguously allopatric rodent species, genus *Scotinomys*. *Miscellaneous Publications Museum of Zoology, University of Michigan* 151:1–60.
- Hsieh TC, Ma KH, and Chao A. 2016. iNEXT: An R package for rarefaction and extrapolation of species diversity (Hill numbers). *Methods in Ecology and Evolution* 7:1451–1456. <https://doi.org/10.1111/2041-210X.12613>
- Karasov-Olson A, and Kelt DA. 2020. Small mammal assemblage composition and habitat associations across an elevational gradient in southern California. *Journal of Mammalogy* 101:92–106. <https://doi.org/10.1093/jmammal/gyz178>

- Klinka K, Chen HY, Wang Q, and de Montigny L. 1996. Forest canopies and their influence on understory vegetation in early-seral stands on West Vancouver Island. *Northwest Science* 70:193–200.
- Liu Z, Sandoval L, Sherman LB, and Wilson AM. 2023. Vulnerability of elevation-restricted endemic birds of the Cordillera de Talamanca (Costa Rica and Panama) to climate change. *Neotropical Biodiversity* 9:115–127. <https://doi.org/10.1080/23766808.2023.2261196>
- Lomolino MV. 2001. Elevation gradients of species-density: historical and prospective views. *Global Ecology and Biogeography* 10:3–13. <https://doi.org/10.1046/j.1466-822x.2001.00229.x>
- Martínez-Borrego D, Arellano E, González-Cózatl FX, Ospina-Gárce S, and Rogers DS. 2023. Species delimitation and integrative taxonomy of the *Reithrodontomys mexicanus* (Rodentia: Cricetidae) cryptic complex. *Ecology and Evolution* 13:1–18. <https://doi.org/10.1002/ece3.10355>
- McCain CM. 2004. The mid-domain effect applied to elevational gradients: species richness of small mammals in Costa Rica. *Journal of Biogeography* 31:19–31. <https://doi.org/10.1046/j.0305-0270.2003.00992.x>
- McCain CM. 2006. Do elevational range size, abundance, body size patterns mirror those documented for geographic ranges? A case study using Costa Rican rodents. *Evolutionary Ecology Research* 8:435–454.
- McCain CM, and Grytnes JA. 2010. Elevational gradients in species richness. *Encyclopedia of Life Sciences* 1–10. <https://doi.org/10.1002/9780470015902.a0022548>
- McPherson AB. 1985. A biogeographical analysis of factors influencing the distribution of Costa Rican rodents. *Brenesia* 23:97–273.
- Millus SA, and Stapp P. 2008. Interactions between seabirds and endemic deer mouse populations on Santa Barbara Island, California. *Canadian Journal of Zoology* 86:1031–1041. <https://doi.org/10.1139/Z08-081>
- Nor SM. 2001. Elevational diversity patterns of small mammals on Mount Kinabalu, Sabah, Malaysia. *Global Ecology and Biogeography* 10:41–62. <https://doi.org/10.1046/j.1466-822x.2001.00231.x>
- Oksanen J, Simpson G, Blanchet F, Kindt R, Legendre P, Minchin P, et al. 2022. *Vegan: Community Ecology Package*. R package version 2.6-4.
- Pardiñas U, Myers P, León-Paniagua L, Ordóñez-Garza N, Cook J, Kryštufek B, et al. 2017 Family Cricetidae (true hamsters, voles, lemmings and New World rats and mice). In: Wilson DE, Lacher TE, Mittermeier, RA, editors. *Handbook of the mammals of the world*. Vol. 7, *Rodents II*. Barcelona (SPA): Lynx Edicions; p. 204–535.
- Pounds JA, Fogden MPL, and Campbell JH. 1999. Biological response to climate change on a tropical mountain. *Nature* 398:161–167. <https://doi.org/10.1038/19297>
- Powell JR, Slifkin JP, Spooner FT, Roth J, Allnatt L, Andrews R, et al. 2022. Bird species inventory in secondary tropical montane cloud forest at Cloudbridge Nature Reserve, Talamanca Mountains, Costa Rica. *Check List* 18:17–65. <https://doi.org/10.15560/18.1.17>
- R Core Team. 2024. *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. R Foundation for Statistical Computing. V. 4.4.2. Vienna (Austria). <https://www.R-project.org/>
- Rahbek C, Borregaard MK, Antonelli A, Colwell RK, Holt BG, Nogues-Bravo D, et al. 2019a. Building mountain biodiversity: geological and evolutionary processes. *Science* 365:1114–1119. <https://doi.org/10.1126/science.aax0151>
- Rahbek C, Borregaard MK, Colwell RK, Dalsgaard BO, Holt BG, Morueta-Holme N, et al. 2019b. Humboldt's enigma: what causes global patterns of mountain biodiversity? *Science* 365:1108–1113. <https://doi.org/10.1126/science.aax0149>
- Ramírez-Bautista A, and Williams JN. 2019. The importance of productivity and seasonality for structuring small rodent diversity across a tropical elevation gradient. *Oecologia* 190:275–286. <https://doi.org/10.1007/s00442-018-4287-z>
- Ramírez-Fernández JD. 2019. *Uso del hábitat y estructura poblacional de Peromyscus nudipes (Rodentia: Cricetidae) en las zonas altas de la Cordillera de Talamanca, Costa Rica*. [Undergraduate thesis]. [San Pedro (CR)]: University of Costa Rica.
- Ramírez-Fernández JD, Barrantes G, Sánchez-Quirós C, and Rodríguez-Herrera B. 2023a. Habitat use, richness, and abundance of native mice in the highlands of the Talamanca Mountain range, Costa Rica. *Therya* 14:49–54. <https://doi.org/10.12933/therya-23-2227>
- Ramírez-Fernández JD, Sánchez R, May-Collado LJ, González-Maya FJ, and Rodríguez-Herrera R. 2023b. Revised checklist and conservation status of the mammals of Costa Rica. *Therya* 14:1–12. <https://doi.org/10.12933/therya-23-2142>
- Ribble DO, and Rathbun GB. 2018. Preliminary observations on home ranges and natural history of *Scotinomys teguina* in Costa Rica. *Mammalia* 82:490–493. <https://doi.org/10.1515/mammalia-2017-0065>
- Roche BE, Schulte-Hostedde AI, and Brooks RJ. 1999. Route choice by deer mice (*Peromyscus maniculatus*): reducing the risk of auditory detection by predators. *The American Midland Naturalist* 142:194–197. [https://doi.org/10.1674/0003-0031\(1999\)142\[0194:RCBDMP\]2.0.CO;2](https://doi.org/10.1674/0003-0031(1999)142[0194:RCBDMP]2.0.CO;2)
- Rodríguez-Herrera B, Ramírez-Fernández JD, Villalobos-Chaves D, and Sánchez R. 2014. Actualización de la lista de especies de mamíferos vivientes de Costa Rica. *Mastozoología Neotropical* 21:275–289.
- Rojas RL, and Barboza RM. 2007. Ecología poblacional del ratón *Peromyscus mexicanus* (Rodentia: Muridae) en el Parque Nacional Volcán Poás, Costa Rica. *Revista de Biología Tropical* 55:1037–1050.
- Sakane KK, Percequillo AR, and Setz EZF. 2019. Community of small mammals along an elevational gradient in Biological Reserve of Serra do Japi, municipality of

- Jundiaí-SP, Brazil. *Austral Ecology* 44:1236–1244. <https://doi.org/10.1111/aec.12801>
- Sánchez-Cordero V. 2001. Elevation gradients of diversity for rodents and bats in Oaxaca, Mexico. *Global Ecology and Biogeography* 10:63–76. <https://doi.org/10.1046/j.1466-822x.2001.00235.x>
- Schulte-Hostedde AI, and Brooks RJ. 1997. An experimental test of habitat selection by rodents of Algonquin Park. *Canadian Journal of Zoology* 75:1989–1993. <https://doi.org/10.1139/z97-831>
- Sikes RS, Bryan II JA, Byman D, Danielson BJ, Eggleston J, Gannon MR, et al. 2016. Guidelines of the American Society of Mammalogists for the use of wild mammals in research. *Journal of Mammalogy* 97:663–688. <https://doi.org/10.1093/jmammal/gyw078>
- Vickery WL, and Bider JR. 1981. The influence of weather on rodent activity. *Journal of Mammalogy* 62:140–145. <https://doi.org/10.2307/1380484>
- Villalobos-Chaves D, Ramírez-Fernández JD, Chacón-Madrigal E, Pineda-Lizano W, and Rodríguez-Herrera B. 2016. Clave para la identificación de los roedores de Costa Rica. Escuela de Biología, Universidad de Costa Rica. San José, Costa Rica.
- Williams SE, Marsh H, and Winter J. 2002. Spatial scale, species diversity, and habitat structure: small mammals in Australian tropical rain forest. *Ecology* 83:1317–1329. [https://doi.org/10.1890/0012-9658\(2002\)083\[1317:SSS DAH\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2002)083[1317:SSS DAH]2.0.CO;2)
- Yanahan AD, and Moore W. 2019. Impacts of 21st-century climate change on montane habitat in the Madrean Sky Island Archipelago. *Diversity and Distributions* 25:1625–1638. <https://doi.org/10.1111/ddi.12965>

Associated editors: *Giovani Hernández Canchola and Pablo Colunga Salas*

Submitted: *Noviembre 1, 2025; Reviewed: December 16, 2025*

Accepted: *April 11, 2026; Published online: May 29, 2026*

