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Habitat use, richness, and abundance of native mice in the highlands of the Talamanca mountain range, Costa Rica

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The Costa Rican highlands are considered hotspots of diversity and endemism, but studies on rodents are scarce. We compared the richness and abundance of mice between the montane forest and the paramo at the summit of the Talamanca mountain range. We selected two study sites within the Talamanca mountain range: the Cerro de la Muerte Biological Station and the paramo. The former is a montane forest dominated by oaks, and the latter is dominated by an herbaceous layer, and some scattered bushy patches. We captured mice in two different microhabitats within each montane forest and paramo, so we had four different sampling microhabitats: (1) paramo–bush, (2) paramo–*Chusquea*, (3) montane forest–bush, and (4) montane forest–*Chusquea*. Mice were marked to identify recaptures. We captured four mouse species and their abundance varied largely between habitats and among microhabitats (Table 1). The most abundant species, representing 85 % of all mouse captures, was *Peromyscus nudipes*. Mice were more abundant in the montane forest than in the paramo. Within the montane forest, mice were more abundant in the microhabitat containing bushes. The montane forest has a more complex vegetation structure with more diversity of food resources and shelters than the paramo. As well as at the habitat level, we argue that differences in abundance among microhabitats are directly related with the structure of vegetation. A more complex habitat structure may provide rodents with better conditions.

Las tierras altas de Costa Rica son consideradas un punto caliente de diversidad y endemismo, pero los estudios sobre roedores son escasos. Comparamos la riqueza y abundancia de ratones entre el bosque de robledal y el páramo en la cima de la Cordillera de Talamanca. Seleccionamos dos sitios de estudio en la Cordillera de Talamanca: la Estación Biológica Cerro de la Muerte y el páramo. El primero es un bosque montano dominado por robles, y el segundo está dominado por una vegetación herbácea y algunos parches dispersos de arbustos. Capturamos ratones en dos microhábitats diferentes en el robledal y el páramo. Por lo que tuvimos cuatro microhábitats de muestreo: (1) páramo–arbustos, (2) páramo–*Chusquea*, (3) bosque montano–arbustos, y (4) bosque montano–*Chusquea*. Los ratones fueron marcados para identificar recapturas. Capturamos cuatro especies de ratones y sus abundancias variaron considerablemente entre hábitats y microhábitats (Tabla 1). La especie más abundante, con 85 % del total de capturas, fue *Peromyscus nudipes*. Los ratones fueron más abundantes en el robledal que en el páramo. Dentro del robledal, los ratones fueron más abundantes en el microhábitat compuesto por arbustos. El bosque montano posee una estructura vegetal más compleja, con mayor diversidad de recursos alimenticios y refugios que el páramo. Al igual que a nivel de hábitat, discutimos que las diferencias en abundancia entre microhábitats están directamente relacionadas con la estructura de la vegetación. Un hábitat con una estructura más compleja es de esperar que provea a los roedores de mejores condiciones.

Keywords: Cerro de la Muerte; *Chusquea*; Cricetidae; endemic mice; montane forest; paramo; *Peromyscus*; species richness.

Introduction

Climate change has been identified as one of the main threats to highland ecosystems in the tropics (Epstein 2000; Hughes 2000; Hilbert *et al.* 2004; Rull and Vegas-Vilarrúbia 2006; Laurance *et al.* 2011). In Costa Rica, the negative effects of this global phenomenon have been modeled for highland amphibians, reptiles, and birds (Pounds *et al.* 1999, 2006; Karmalkar *et al.* 2008). As a consequence of climate change, the temperature, dry season length, and number of dry days have increased in tropical highlands (Pounds *et al.* 1999).

These climatic changes have affected the distribution and interaction of species along tropical altitudinal gradients. Many middle elevation species have recently expanded the upper limit of their altitudinal distribution, moving into the habitat of those species that occur at highest elevations (Morales-Betancourt and Estévez-Varón 2006; Dirnböck *et al.* 2010; Bellard *et al.* 2012; Ripple *et al.* 2014). However, species that inhabit the summit of tropical mountains are trapped in sky islands as their habitat contracts and competition with lowland invading species increases. The synergistic effect of these factors imposes a serious extinction threat on endemic and highland-restricted species (Thomas *et al.* 2004; Malcom *et al.* 2006; Urban 2015; Pyšek *et al.* 2017).

In Costa Rica, the highlands have relatively low diversity but a high percentage of endemic species from different taxonomic groups (Barrantes 2005; Vargas and Sánchez

2005; Barrantes *et al.* 2019). For instance, 22 (73 %) mammal species are endemic at middle and high elevations (Ramírez-Fernández *et al.* in press), and in the highlands many of these species accomplish an important ecological role, such as the dispersal of seed and fungal spores (Lacher *et al.* 2016).

Most Costa Rican mammal research has centered on lowland habitats. Thus, information on the highlands is scarce and fragmented (Carrillo *et al.* 2005). Considering that rodents are an abundant component of the highland fauna (González-Maya *et al.* 2015), and that their role as seed and arthropod predators, fungal spore and seed dispersers, and prey for birds and larger mammals is important, we sought to quantify the richness and abundance of the mice community in the high montane forest and the paramo in the Talamanca mountain range. This is the largest and highest Costa Rican mountain range, and it is recognized as the terrestrial region with the highest endemism in Central America (Holz and Gradstein 2005; Powell *et al.* 2022).

Materials and methods

Study site. To conduct this research, we selected two study sites in the highlands of the Costa Rican Talamanca mountain range: the Cerro de la Muerte Biological Station (CMBS) and the paramo (Figure 1). The CMBS is located in the high montane oak forest at an elevation of 3,100 m (9° 33´N, -83° 44´ W) and the paramo at 3,400 m elevation (9º 33´ 20″ N, -83º 45´ 41″ W). The two sites are separated by a distance of 2.5 km. The mean annual precipitation is 2,500 mm, with a relatively dry period between December and April, with a mean annual temperature 11° C for the CMBS and 7.6° C for the paramo (Herrera 2005). The temperature oscillates drastically during the day, particularly in the paramo (–5° to 35°). Forests dominated by oaks (*Quercus costaricensis*) with abundant epiphytes, bushes (*e. g.*, ferns, Ericaceae, Asteraceae, Onagraceae), and large patches of bamboo (*Chusquea talamancensis*) cover most of the CMBS study site (Calderón-Sanou *et al.* 2019). On the contrary, the paramo is dominated by an herbaceous layer with a large diversity of Asteraceae and Poaceae (mainly *Chusquea subtesellata*), and some scattered bushy patches in which Ericaceae, Asteraceae, and Hypericaceae are abundant (Vargas and Sánchez 2005).

We selected two microhabitats in each habitat, the montane forest and the paramo, to assess rodent habitat use, species richness, and abundance. In the montane forest, we sampled mice in (1) patches dominated by bamboo (*Chusquea talamancensis*), and in (2) patches dominated by bushes. In the paramo, we sampled in (1) patches dominated by bushes and an herbaceous layer (*e. g.*, Asteraceae, Cyperaceae) and short bushes (*e. g.*, *Pernettya*, *Vaccinium*, and *Hypericum*); and (2) in homogeneous patches dominated by *Chusquea subtessellata*. In each microhabitat we established a circular 10 m–diameter plot, so that we had the following combination of microhabitats in each ecosystem: paramo–bush, paramo–*Chusquea*, montane forest–bush, and montane forest–*Chusquea* (Figure 2).

Figure 1. Sample sites at the Talamanca mountain range, Costa Rica. A) High montane oak forest at Cerro de la Muerte Biological Station; B) paramo habitat.

Capture, recapture, and tattooing mice. We used baited Sherman live traps (5 × 6 × 16 cm; H. B. Sherman Traps, Inc., Florida) to capture mice. The bait was made of barley, oatmeal, banana, peanut butter, and vanilla extract. In each habitat, we placed 50 traps (25 in each microhabitat) for two consecutive nights, each 3 to 4 weeks from May 2015 through April 2016. We placed each trap at 5 to 10 m from a transect we established within each plot and at 5 to 10 m from any other trap. The distance from the transect and from other traps varied depending on the topographic characteristics of the terrain. We registered the geographic position of each trap in each sampling using a GPS Garmin 60Csx (Garmin Corp., Olathe, Kansas) and changed the location of the traps in each sampling to maximize the capture in each microhabitat. In addition, we placed 4 to 8 traps on branches at 1.5 to 3 m above the ground to capture arboreal or climbing mice.

We identified each individual captured to species level using the key published by Villalobos-Chaves *et al.* (2016). For each individual captured, we recorded species, date, habitat, microhabitat, and trap coordinates. Given that taxonomy within the group is in debate, voucher specimens were collected prior and after the sampling period as a reference (Appendix 1).

We tattooed large adult *Peromyscus* using a Spaulding Revolution I (Spaulding and Rogers, Inc., New York) machine for animal tattooing. Individuals were tattooed at the base of the tail. For juvenile *P. nudipes* and small species, we cut a patch (or patches) of hair from the lumbar region to identify each individual; the tattooing machine is not recommended for small animals. In addition, we recorded any distinctive mark of an individual that facilitated their identification (*e. g.*, tip tail coloration, scars, ear cuts), in case they were recaptured. For the recaptured individuals, we recorded the individual mark or tattoo, trap coordinates, habitat, and microhabitat. After each individual was marked and its information recorded, we released it at the site where it was captured. We then waited until each individual had found a retreat or a protected site before leaving the release site to avoid predation.

Data analyses. We captured four mouse species and compared their abundance among the four microhabitats with a chi-squared contingency analysis and a Fisher paired test. We did not analyze richness since we only captured four species. We used the statistical language R, version 3.4.0 (R Core Team 2017) for the analyses.

Results

Species richness and abundance. We captured 108 mice of four species in the family Cricetidae, from a 2,100 night-trap effort distributed equally between habitats. We captured three species at each habitat, two of which were present in both habitats (Table 1). *Scotinomys xerampelinus* was captured only in montane forest, *Reithrodontomys creper* only in the paramo, *R. sumichrasti* was found in the Montane forest-*Chusquea* and Paramo-bush microhabitats, and *P. nudipes* was the only species captured in all four microhabitats (Table 1).

Peromyscus nudipes was the most abundant species captured with 85% of all captures (Table 1). The number of mice captured (all species combined) differed between habitats ($X^2 = 43.75$, d. f. = 1, $P < 0.001$) and among microhabitats ($X^2 = 36.83$, d. f. = 9, $P < 0.001$). We captured more mice in the montane forest than in the paramo and more in the montane forest/bush microhabitat ($n = 58$) than in any other microhabitat (Table 1). On the contrary, the microhabitat with the fewest mice captured was paramo–*Chusquea* with only 6 individuals (Table 1).

Discussion

We found four mouse species in the montane forest and the paramo, the two dominant ecosystems at the Costa Rican highland. At this elevation, richness and abundance of mice vary according to the characteristics of the habitat and microhabitat. For instance, the vegetation structure directly influences density (*e. g.*, Pardini *et al.* 2005; Blaum *et al.* 2006), diversity (*e. g.*, Johnson and Vaughan 1993; Muñoz *et al.* 2009), and richness of small rodents (*e. g.*, Brehme *et al.* 2011; Thompson and Gese 2013) in Costa Rica and other ecosystems.

Our results showed that some species are present only in a particular habitat and some microhabitats, but not in others. Specifically, we captured *S. xerampelinus* only in the montane forest and *R. creper* only in the paramo; although both species have sporadically previously been recorded in

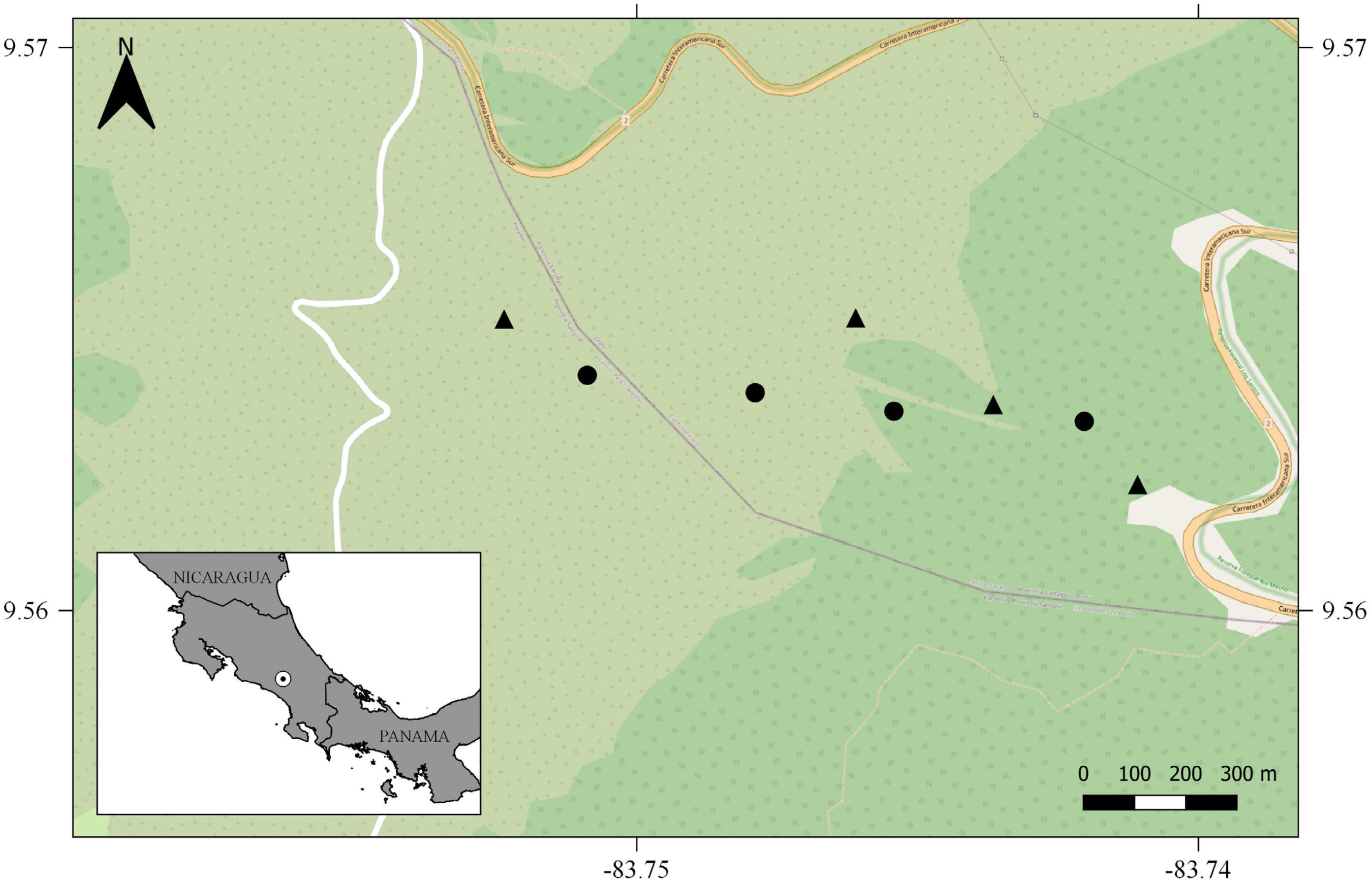

Figure 2. Location of the sample sites in the Talamanca Mountain range. Light green background represents paramo; dark green represents montane forest. Black dots show bush microhabitat; black triangles, *Chusquea* microhabitat.

Table 1. Percentage and number (in parentheses) of mice captured in each microhabitat.

Species	Montane forest-bush	Montane forest-Chusquea	Paramo-bush	Paramo-Chusquea
Peromyscus nudipes	93 (54)	91 (31)	66.6 (12)	67 (4)
Scotinomys xerampelinus	7 (4)	6 (2)	-	-
Reithrodontomys creper	-	-	16.7 (3)	33 (2)
Reithrodontomys sumichrasti	-	3 (1)	16.7 (3)	-

both habitats (Reid 2009; JDRF unpublished data). Therefore, our findings suggests that even when both species are present in both habitats, each of them preferred one particular habitat over the other, likely related to the structural differences in the vegetation (McCloskey 1976; Johnson and Vaughan 1993).

The abundance of mice varied largely between habitats and among microhabitats, as reported in other studies (Mohammadi 2010). In the montane forest, a more complex vegetation structure and greater diversity of food resources and hiding places likely permit the coexistence of more individuals than in the paramo. The abundance of mice among microhabitats showed a similar pattern. Structurally complex microhabitats, such as the montane forest / bush microhabitat, allow more species to coexist (Torres-Pulliza *et al.* 2020). On the contrary, the microhabitat dominated by *Chusquea subtessellata* in the paramo, which is structurally simple with large exposed open areas, had the lowest mice abundance.

Differences in abundance among microhabitats of *P. nudipes*, further support that habitat structure influences in the abundance of mice in Costa Rican highlands. This species is present in all microhabitats and its abundance increased with the microhabitat complexity. More complex structure in the vegetation elicits a series of synergetic effects that affect the abundance of different species. For example, a structurally complex vegetation provides a larger number of microhabitats, food resources, and hiding places that can be used for more rodents than those provided by more simple microhabitats (Tews *et al.* 2004).

The paramo–*Chusquea* is the simplest microhabitat, composed by homogeneous patches of *Chusquea subtessellata* with open spaces in between. The vegetation composition and the simple structure likely provide fewer food resources and retreats than any other microhabitat (Johnson and Vaughan 1993; Mohammadi 2010; García *et al.* 2011). In addition, rodents tend to avoid foraging in areas deprived of vegetation, since they are more likely detected by predators (Kotler *et al.* 1988; Morris and Davidson 2000).

Summarizing, the species richness of mice at the highest vegetation ecosystems, the montane forest and paramo, in the Talamanca mountain range is low. However, the abundance of some species is very high, and this abundance varies greatly among microhabitats. The variation in mice abundance is presumably determined by the characteristics of the habitat, primarily related to the structure of vegetation. A more complex structure is expected to provide rodents with more diverse and abundant food resources (Johnson and Vaughan 1993; García *et al.* 2011), more retreats, and better protection from predators (Kotler *et al.* 1988; Morris and Davidson 2000).

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Appendix 1

List of voucher specimens of all four species trapped at the study site in the collection of the University of Costa Rica's Zoology Museum.

Taxa	Museum specimen number
Scotinomys xerampelinus	MZUCR–1929, 4905
Reithrodontomys creper	MZUCR–4372, 4548, 4981, 5097
Peromyscus nudipes	MZUCR–4373
Reithrodontomys sumichrasti	MZUCR–5135