



Response of beetle communities to the heterogeneity of vegetation in high altitude habitats in north-western Argentina

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ABSTRACT. The dynamics and complexity of plant communities influence the diversity and distribution of animals in various environments. Coleoptera are the most diverse group of insects and are valued as monitoring and environmental assessment tools. However, their diversity and dynamics in these high-altitude environments are poorly known. Using pitfall traps and suction sampling, we collected beetles to study their community responses to changes in different vegetation heterogeneities (low, intermediate, and high). The heterogeneity gradient was determined by considering the dominant plant species in each habitat, the percentage of vegetation coverage, and the percentage of vertical strata. Guild's responses to vegetation heterogeneity were analysed in conjunction with the patterns of alpha and beta diversity in beetles. Representatives of 41 species/morphospecies of beetles, 16 families, and four guilds were reported. Significant variations were observed in guild composition and alpha and beta diversity, especially between high and low vegetation heterogeneity habitats. The significant species turnover between sites is the main factor responsible for the high beta diversity, supporting considerable habitat heterogeneity within these environments. Phytophagous, detritivorous, necrophagous, and predatory beetles exhibited distinct responses to the vegetation's heterogeneity. This suggests that every habitat under investigation possesses a distinct structure of beetle communities. Predators were important in habitats with more diverse vegetation, while phytophagous were important in the most homogeneous ones. Beetle communities in the Puna and Altos Andes of Salta province respond positively to vegetation heterogeneity, which plays a crucial role in determining the composition of small-scale beetle communities in arid high-altitude environments.

Key words: Arid area, beta diversity, Coleoptera, guild composition, mountain ecoregions

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INTRODUCTION

Vegetation provides the primary structure of the environment in the majority of habitats (Rutten et al., 2015). The complexity has the potential to increase biodiversity (Gardner et al., 2009), and support ecosystem services. Plant community dynamics can influence the biodiversity of animals (Franklin et al., 2016). Vegetation heterogeneity expands niche space, allowing more coexistence of animal species (Tews et al., 2004). The phenomenon implies that environments with more structurally complex vegetation have more micro-habitats, food resources, shelters, and sites for hibernation, reproduction, and oviposition as well as opportunities for specialisation (Stein et al., 2014, Lawton, 1983).

Coleoptera is the most diverse insect order (Betancourt et al., 2009) and they play important roles in the ecosystem because they occupy all trophic levels from decomposers to predators and phytophages (Crowson, 1981; Alonso-Zarazaga, 2015), so they are a useful tool for environmental monitoring and assessment (Abdel-Dayem et al., 2007; Aldhafer et al., 2016). Beetle communities react to environmental changes such as the degree of vegetation cover, vertical stratification, vegetation density, soil type, and all of which influence the micro-spatial distribution of their species (Escobar & Chacón, 2000). The bioecological characteristics of beetles lead to group them into guilds, which are non-phylogenetic groups of species that share one or more vital resources (Blondel, 2003). The use of guilds is a useful method for determining how biotic communities respond to habitat changes (Cardoso et al., 2011).

The Puna and Altos Andes ecoregions are critical for biodiversity preservation because they are classified as "vulnerable" in the Global 200 (Olson & Dinerstein, 2002) and have been designated as global priority areas. In the past few years, mining and ecotourism have grown a lot, which has put a great deal of stress on the desert environments (Morello et al., 2012), as well as mountain species are sensitive to climate change and especially susceptible to global warming (Wilson et al., 2007; Dieker et al., 2013). The species that live in these regions would be more vulnerable to extinction if these events occurred environmental hazards because they would be unable to explore higher altitudes in search of the conditions required for survival (Lovejoy, 2010). The mentioned ecoregions are distinguished by strong winds, high diurnal temperatures and scant precipitation, which prevent the formation of dense vegetation covers. Furthermore, the landscape contains "vegas," or areas where water accumulates in the spring, resulting in the formation of distinct micro-environments (Morello et al., 2012). As a result, the type of soil and the accumulation and/or persistence of water in it have an impact on the vegetation in these high-altitude ecoregions. The environmental condition causes the dominant plants to be small (usually less than 1.5 m in height), to have little canopy coverage, and to be irregularly dispersed throughout the area (Morello et al., 2012). As a consequence, they form patches where the plants are close together, reducing the impact of strong winds.

Until now, the diversity and dynamics of beetles in the Puna and Altos Andes environments of the Argentine province of Salta have been poorly known. The study of the group of insects in the high-altitude environments is thus thought to be worthwhile because beetles that live in these regions must adapt to changing climatic conditions (with large daily and seasonal amplitudes) and fluctuations in resource availability. Therefore, the objective of this study is to determine the effect of vegetation heterogeneity on beetle communities of Salta's Puna and the Altos Andes.

MATERIAL AND METHODS

Study area. The study comprises the Cachi, La Poma, and Los Andes departments of the province of Salta (Argentina), which are included in the Puna and Altos Andes ecoregions according to Morello et al. (2012) (Fig. 1 a–b). Beetles were collected in protected natural environments of the Reserva Natural de Fauna Silvestre Los Andes, one of the country's largest reserves, as well as in unprotected natural environments of the Los Cardones-La Poma Longitudinal Corridor. Arid mountain ranges above 2500 m a.s.l. in the country's far northwest serve as a representation of these ecoregions' overall landscape. The climate is dry, windy, and cold, with significant daily temperature fluctuations (approximately 30 °C) and annual rainfall ranging from 100 to 800 mm during the summer (Morello et al., 2012). The

shrubby steppe of the Puna consists basically of low, woody, perennial, and aromatic shrubs of *Aloysia salsoloides* (Griseb.) Lu-Irving & N. O'Leary, 2014 (rica-rica) (Fig. 1g), a plant of spinescent branches, sessile leaves, small, and lobed revolute margin; *Parastrephia* sp. Nutt., 1841 (tola) (Fig. 1i), with branches without thorns, sessile leaves, small, scamiforms, and inflorescence in a chapter; *Adesmia horrida* Gillies ex Hook. & Arn., 1832 (añagua) (Fig. 1h) with spinescent branches and small, compound leaves; and, finally, *Senecio friesii* Cabrera, 1935 (Senecio) (Fig. 1f) with branched stems from the base, sessile leaves, small, and inflorescence in a chapter (Morello et al., 2012). The environments of the Altos Andes are characterised by "iros grasslands" (*Festuca orthophylla* Pilg., 1898), a perennial herb, caespitose, with rhizomes and erect and needle-like leaf lamina (Szumik et al., 2016); shrubby formations of *A. salsoloides* can also be found at lower altitudes.

Sampling. Beetles were collected on the first days of December 2014, June 2015, and February 2018, in nine geo-referenced sites (Fig. 1b) that were at least 4 km apart. At each site, samples were taken from an area that was about one hectare in magnitude, taking into account that the vegetation in the area around it (about 600m) was the same. Different degrees of vegetation heterogeneity determined by dominant species and soil cover were taken into account when selecting sampled sites, classifying them as low (LH), intermediate (IH), or high (HH). The three low vegetation heterogeneity (LH) sites (LH1: S24° 31.99' W67° 21.13', LH2: S24° 29.60' W67° 21.53', and LH3: S24° 21.31' W66° 59.01') all had a single dominant plant species (*A. salsoloides*), a vertical stratification of less than 50 cm, and a soil cover percentage of less than 10% (Fig. 1e). Sites with intermediate vegetation heterogeneity (IH) (IH1: S25° 01.65' W66° 05.49'; IH2: S24° 17.50' W66° 13.12'; and IH3: S24° 34.72' W67° 10.01') possessed two dominant plant species (*A. salsoloides* and *Parastrephia* sp./*S. friesii*), vertical stratification up to 100 cm, and a percentage of soil coverage between 10–25% (Fig. 1d). Finally, three dominant plant species (*A. salsoloides*, *Parastrephia* sp., and *A. horrida*) were found at the three high vegetation heterogeneity (HH) sites (HH1: S24° 53.98' W66° 08.74', HH2: S24° 51.74' W66° 08.79', and HH3: S24° 15.57' W66° 23.20') (Fig. 1c), with a vertical stratification of 0–100 cm and a coverage percentage between 25–40%.

A total of 270 samples were taken using two different material collection techniques. Thus, at each of the nine sites sampled at three different times, five pitfall traps were placed to record the soil-dwelling beetles, and five suction samples were taken to collect the vegetation-dwelling beetles. Pitfall traps were placed along a 20 m-long linear transect and were active for 10 days at each sampling. As pitfall traps, cylindrical plastic containers measuring 7.5×12.2×5.2 cm (upper diameter × depth × lower diameter) were buried at ground level and preserved with supersaturated saline (salt [Kg] water [l], 1:8 ratio with detergent drops). Simultaneously, at each site, suction samples were collected at random over vegetation, covering a 50 m strip on either side of the linear transect. For this, a Stihl vacuum cleaner with a 1.10 m-long, 12 cm diameter tube with a thin mesh that collects arthropods was used. Each sample was defined as a one-minute suction of vegetation in a one-square-metre area.

The collected materials were placed in polyethene bags with 70% ethanol, labelled, and transported to the laboratory for cleaning, sorting, and identification. The collected specimens were recorded on electronic sheets and classified into trophic guilds, families, and species/morphospecies using a database of digitised photos of the species/morphospecies with distinguishing characteristics, which was compared with the Instituto para el Estudio de la Biodiversidad de Invertebrados (IEBI) database. The samples were collected with permission from the Ministerio de Ambiente y Desarrollo Sustentable, Government of the Province of Salta, Argentina (Resolution No. 826).

Coleopteran families were identified using the key developed by Betancourt et al. (2009) and classified into trophic guilds according to Susilo et al. (2009) and Norfolk et al. (2012). To identify the Tenebrionidae species, various taxonomic keys and comparisons were used with material from the collection of the Instituto Argentino de Investigaciones de las Zonas Áridas (IADIZA). For Curculionidae, the taxonomic keys and descriptions from the Catalogue of Naupactini Species from Argentina and Uruguay (Lanteri & del Río, 2021) were used. Analía Lanteri, Guadalupe del Río, and Sergio Roig-Juñent were consulted and confirmed the identifications of the families Curculionidae and Carabidae.



Figure 1. Location of the sampling sites, type of environments sampled and dominant plant species. **a.** Map of the sampling area located in Northwestern Argentina. **b.** Satellite image showing the location of the sites considering the vegetation heterogeneity: low (LH), intermediate (IH) and high (HH). **c.** The environment with high vegetation heterogeneity. **d.** Environment with intermediate vegetation heterogeneity. **e.** Environment with low vegetation heterogeneity. **f.** *Parastrephia* sp. (tola); **g.** *Aloysia salsoloides* (rica-rica); **h.** *Adesmia horrida* (añagua); **i.** *Senecio friesii* (senecio).

Vegetation heterogeneity variables. As a first step, we used linear and polynomial regressions to rule out the idea that temperature and altitude could change the beetle communities at the sampled sites. This prompted us to select vegetation heterogeneity variables for evaluation. Thus, at each site and by sampling date, the richness of plant species (SP), the percentage of vegetation coverage (%COV), and the percentage of vertical strata (%VS) were measured. This allowed for the definition of high (HH), intermediate (IH) and low (LH) vegetation heterogeneity habitats in advance. The percentage of vegetation coverage per site was determined by randomly selecting five 5×5m quadrants. The percentage of vertical stratum was calculated using the VESTA photographic method (Vertical Vegetational Structure Analysis) (Zehm et al., 2003) and measured at each site by selecting three points at random and photographing each of them four times (one for each cardinal point up to a metre of height), with a white panel of 1×1 m (with marks every 50cm) for vegetation contrast. Using the Adobe Photoshop CS6 software, the variable's value was calculated as a percentage of each stratum.

Data analysis

Inventory, Alpha Diversity, and Trophic Guilds. To determine whether the sample obtained was representative of beetle diversity, sample completeness profiles by habitats and rarefaction extrapolation curves based on individuals with the same level of sample coverage were calculated. Chao et al. (2020) proposed a methodology based on Hill numbers, where q^0 represents species richness, q^1 the Shannon exponential index, and q^2 the Simpson inverse index (Hill, 1973). Using 95% confidence intervals and 100 permutations, calculations were done using the bootstrap method and the free online app iNEXT-4steps (Hsieh et al., 2016). Also, the estimated completeness values of the sample were evaluated using the criteria of Cardoso (2009), which sets up three categories: "reasonable" (50–70% completeness), "complete" (70–80%), and "exhaustive" (90–100%). The beetles collected for the study were divided into four guilds based on their food source (Blondel, 2003): necrophagous (consume dead animals), detritivorous (consume decomposing organic matter), phytophagous (consume plant substances), and predators (consume live animals). The abundance range curves were used to analyse the guild structure by habitat (Magurran, 2004).

Beta Diversity

Vegetation heterogeneity and beetle diversity. To determine whether there are differences in the composition of species associated with the degree of vegetation heterogeneity of the sampled sites, a Canonical-Correlation Analysis (CCA) was performed with Bray-Curtis as a distance measure, using PC-ORD software version 7.04 (McCune & Mefford, 2016) and the protocol proposed by Peck (2010). Following sorting, the similarity values of the various groups formed were subjected to a multidimensional permutation procedure (MRPP) to determine their statistical significance, with Bray-Curtis as a distance measure.

Beetle community composition. Using the Bray-Curtis similarity index as a distance measure and the PC-ORD version 7.04 software (McCune & Mefford, 2016), a conglomerate analysis was used to compare the taxonomic composition of beetle communities between sites. Lastly, the method proposed by Baselga (2010) was used to evaluate beta diversity between habitats by measuring total beta diversity with the Sorensen dissimilarity index (β_{SOR}). Beta diversity (β_{SOR}) can reflect two underlying phenomena (Baselga, 2010): spatial species turnover (β_{SIM}) and nestedness (β_{SNE}), both of which are caused by different processes (species replacement and species loss, respectively). So, the relative importance of these two parts was measured, and their values were given as percentages. The Betapart package in R was used for this analysis (Baselga et al., 2013).

RESULTS

Inventory, Alpha Diversity, and Trophic Guilds. A total of 178 beetles were collected from 16 families, four guilds, and 41 species/morphospecies (Table 1). Habitats with intermediate heterogeneity (IH)

had higher species richness and abundance ($S = 21$; $N = 93$), followed by HH habitats ($S = 17$; $N = 30$), while LH habitats had low species richness but intermediate abundance ($S = 10$; $N = 55$) (Table 1). Ptinidae ($N = 46$) and Bruchidae ($N = 33$) were the most abundant families, while Tenebrionidae ($S = 9$) and Curculionidae ($S = 7$) were the most diverse (Table 1), with the latter family present in all habitats. The completeness values of the samples for $q=0$ (species richness) indicate that the beetle inventory obtained in LH habitats was "complete" (87%) and in IH "reasonable" (63%).

In habitats with HH, the inventory was not complete (<50%), but almost all of the abundant and highly abundant species were recorded, based on the estimated undetected diversity of $q = 1$ and $q = 2$ (Table 2). As a result, the sample size used provides data that is representative of the beetle diversity present in the habitats studied and is sufficient to infer the true diversity of the communities. Extrapolation/interpolation analysis of rarefaction for the same level of sample coverage revealed that HH and IH habitats had significantly higher species diversity ($q=0$) than LH habitats (Table 2). Meanwhile, HH had significantly higher $q=1$ and $q=2$ values (Table 2). This study identified four guilds (Figs 2-3), with phytophagous ($S = 17$) and predators ($S = 15$) having the most species diversity, followed by necrophagous ($S = 9$) and detritivorous ($S = 8$). The structure and composition of the coleopteran guilds varied across the habitats studied (Fig. 3), indicating that phytophagous had a greater diversity of families (seven), whereas the remaining guilds had only four. In HH habitats, there were more predators than in LH habitats, but phytophagous were more common in LH habitats than in IH habitats. Detritivorous beetles were abundant in LH, whereas their abundance was lowest in IH habitats, which were dominated by necrophagous species (Fig. 3).

Among detritivorous, *Physogaster andinus* Peña, 1995 (Tenebrionidae) dominated in the LH habitats, while the same species of Ptinidae (Ptinidae sp.2) dominated in the IH and HH habitats. In the case of phytophagous and necrophagous beetles, there were changes in species dominance across the habitats studied, as well as a tendency to increase species richness from LH to HH habitats (Fig. 2). A few phytophagous species (one or two) were shared between habitats with different vegetation heterogeneity, with one species of curculionid (Curculionidae sp.1) dominating the IH and HH habitats and a bruchid (Bruchidae sp.1) dominating the LH habitats (Fig. 2). Although the necrophagous guild exhibited a different species composition in HH and IH habitats (Fig. 2), *Adistemia watsoni* Wollaston, 1871 (Lathridiidae) was the only species reported in LH habitats, and was found in association with other species in HH habitats (Fig. 2). Finally, predators showed a high species richness in IH habitats (Fig. 2); despite an intermediate abundance (Fig. 3), few species are shared between habitats with different heterogeneities. The relationship between predators and vegetation heterogeneity was directly proportional, but not for the other guilds (Fig. 3).

Beta Diversity

Vegetation heterogeneity and beetle diversity. The beetle assemblages from the three habitats studied were arranged in a gradient pattern of heterogeneity, with the X-axis being the most prominent (Fig. 4). To assess the effect of the variables on these communities, a CCA analysis was performed, yielding an ordering that explained 65.20% of the total variance (axis 1=61.10% and axis 2=4.10%; $p=0.01$), with the first eigenvalue of 0.56 and the second of 0.42. The MRPP analysis revealed that there are statistically significant differences between the communities of the LH and HH habitats ($A=0.04909514$; $p=0.02$), but no significant differences were detected between these and the IH sites. Among the variables measured in the field, it is shown that %COV ($r=0.80$) correlated positively with the first axis, as well as VS ($r=0.82$), influencing the communities of the HH and IH habitats because there is a higher percentage of vegetation coverage and a greater vertical stratification (VS) compared to the communities of the LH habitats. Predators and phytophagous, on the other hand, were positively and negatively correlated with the first axis ($r=0.55$ and 0.76 , respectively). The detritivorous guild was weakly and positively ($r=0.22$) correlated with the second axis, whereas the necrophagous guild was negatively ($r=0.27$) correlated with the same axis.

Table 1. Abundance of beetle species by families recorded in the Puna and Altos Andes ecoregions, Salta province (Argentina). LH (low), IH (intermediate) and HH (high) vegetation heterogeneity.

Family	Species/Morphospecies	Abundance		
		HH	IH	LH
Anthicidae	Anthicidae sp.1	4	7	0
Bruchidae	Bruchidae sp.1	0	0	33
Carabidae	<i>Selenophorus</i> sp.	1	2	0
	<i>Bembidion</i> sp.	0	1	0
Coccinellidae	<i>Hippodamia convergens</i> Guérin-Ménéville	0	1	0
	Coccinellidae sp.1	4	0	0
	Coccinellidae sp.2	0	2	0
	Coccinellidae sp.3	0	2	0
	Coccinellidae sp.4	0	1	0
Cryptophagidae	Cryptophagidae sp.1	0	0	1
Cucujidae	Cucujidae sp.1	1	0	0
Curculionidae	<i>Cylindrorhinus</i> sp.	2	4	3
	<i>Sibina</i> sp.2	0	0	2
	<i>Sibina</i> sp.1	0	6	0
	Curculionidae sp.1	3	7	0
	Curculionidae sp.2	1	0	0
	Curculionidae sp.3	0	0	1
	Curculionidae sp.4	1	0	0
Dermestidae	Dermestidae sp.1	1	0	0
Elateridae	Elateridae sp.1	0	1	0
Lathridiidae	<i>Adistemia watsoni</i> Wollaston	1	0	2
Leiodidae	<i>Nargomorphus</i> sp.	0	1	0
Melyridae	Melyridae sp.1	1	0	0
Ptinidae	Ptinidae sp.1	1	0	0
	Ptinidae sp.2	4	40	0
	<i>Ptinus</i> sp.	1	0	0
Scarabaeidae	<i>Melolonthinae</i> sp.1	1	0	0
Staphylinidae	Staphylinidae sp.1	0	0	2
	Staphylinidae sp.2	2	0	0
	Staphylinidae sp.3	0	1	0
	Staphylinidae sp.4	0	1	0
	<i>Euconnus</i> sp.	1	0	0
Tenebrionidae	<i>Praocis magnoi</i> Molinari	0	7	0
	<i>Praocis pentachorda</i> Burmeister	0	1	0
	<i>Psectrascelis cariosicollis</i> Fairmaire	0	0	4
	<i>Physogaster andinus</i> Peña	0	0	6
	<i>Epipedonota interandina</i> Vidal y Flores	0	1	0
	<i>Scotobius planatus</i> Erichson	0	1	0
	<i>Praocis ecostata</i> Kulzer	0	4	0
	<i>Entomochilus varius</i> (Kulzer)	0	0	1
<i>Omophres</i> sp.	0	2	0	
Total		30	93	55

Table 2. Completeness of the inventory of beetles obtained in the Puna and Altos Andes ecoregions of the province of Salta (Argentina). The observed, estimated (extrapolation/ interpolation analysis of rarefaction for the same level of sample coverage) and unseen diversity values for each of the parameters are shown for q^0 (species richness), q^1 (the Shannon exponential index), and q^2 (the Simpson inverse index). Values in parentheses mean the percentage of inventory completeness. (* = the significant differences with a confidence level of 95%).

Habitat	Diversity	Observed (%)	Estimated	Unseen (%)
HH	q0	17.00 (37)	46.24	29 (63)
	q1	14.07 (64)	28.36*	10 (36)
	q2	11.84 (92)	18.91*	2 (8)
IH	q0	21.00 (63)	33.37	12 (37)
	q1	9.13 (89)	11.07*	2 (11)
	q2	4.70 (100)	4.89	0 (0)
LH	q0	10.00 (87)	11.47*	1 (13)
	q1	4.38 (95)	4.89*	0 (5)
	q2	2.60 (99)	2.68	0 (1)

Abbreviations — **HH:** Environment with high vegetation heterogeneity; **IH:** Environment with intermediate vegetation heterogeneity; **LH:** Environment with low vegetation heterogeneity.

Composition of beetle communities. conglomerate analysis revealed that the LH3 site (*A. salsoloides*) has a distinct beetle species composition in comparison to the other sites under study (Fig. 5); in contrast, the other sites of the same habitat shared approximately 91.2% of their species. In contrast, habitats with three dominant plant species (HH2 and HH3) shared more than 80% of their species, and IH1 (*A. salsoloides* and *Parastrephia* sp./*Senecio friesii*) shared nearly 70% of its species with HH1 (Fig. 5). Finally, the recorded values of total beta diversity between sites of the same habitat (on a local scale) were high, with IH having the highest value (Table 3). Spatial turnover of species was primarily responsible for beta diversity in all habitats ($\beta_{SOR} > 86\%$), but not nestedness ($\beta_{SNE} < 13.1\%$). This pattern was maintained when beta diversity between habitats was taken into account, with high β_{SOR} values and a significant role in species turnover (Table 3). With increased species loss between HH and LH habitats, nestedness between those communities accounted for only 3% and 6% of the total (Table 3).

Table 3. Values of beta diversity (β_{SOR}) and their components of turnover (β_{SIM}) and nestedness (β_{SNE}) for Coleoptera comparing between sites of the same habitat and by habitats. LH (low), IH (intermediate) and HH (high) vegetation heterogeneity.

Habitat	β_{SOR}	β_{SIM} (%)	β_{SNE} (%)
LH	0.77	0.70 (91)	0.07 (9)
IH	1.00	1.00 (100)	0.00 (0)
HH	0.84	0.73 (87)	0.11 (13)
HH-IH	0.73	0.70 (96)	0.03 (4)
HH-LH	0.85	0.80 (94)	0.05 (6)
IH-LH	0.93	0.90 (97)	0.03 (3)

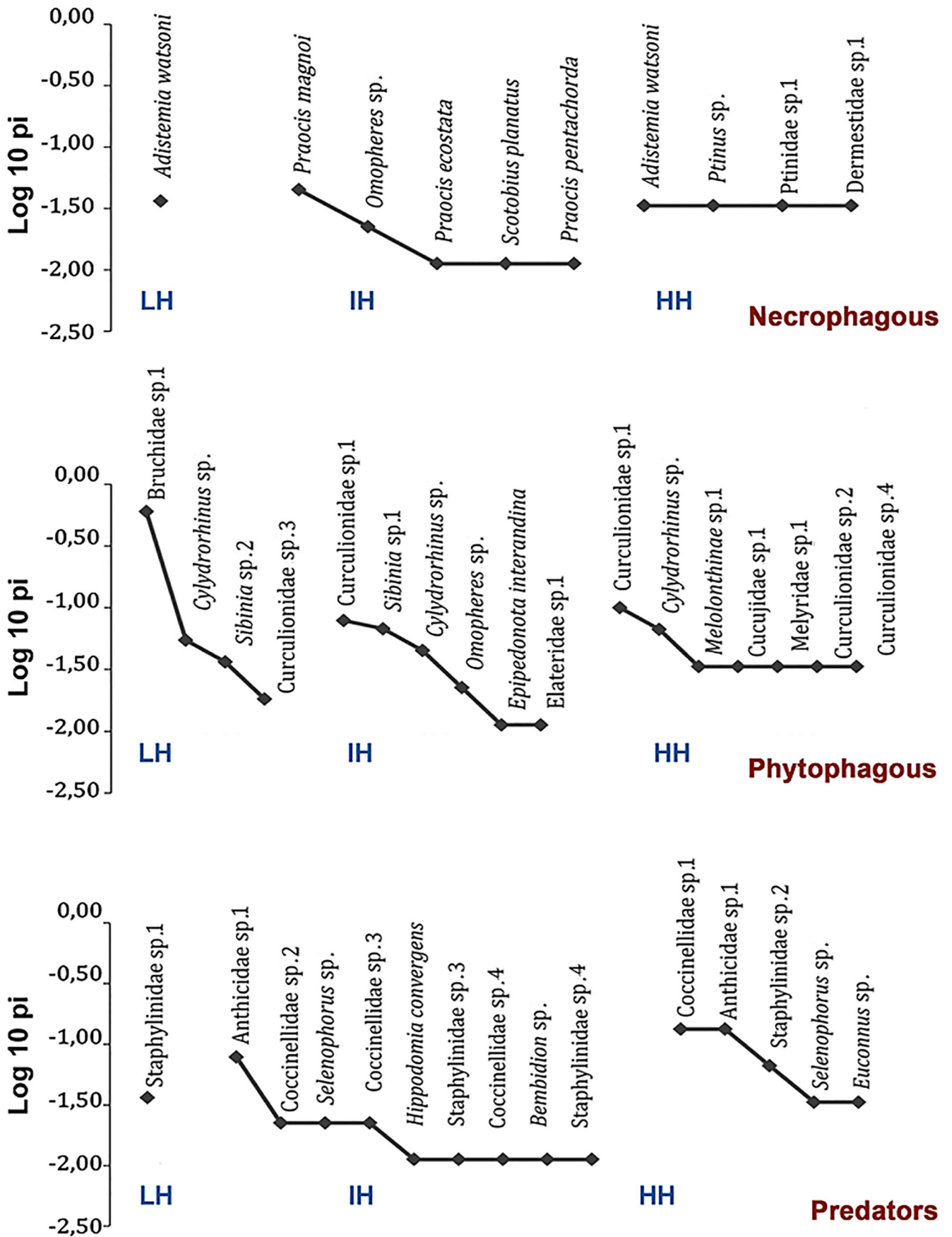


Figure 2. Range/abundance curves by guilds of beetle species collected in high-altitude habitats in north-western Argentina. **LH:** low heterogeneity; **IH:** intermediate heterogeneity; **HH:** high heterogeneity.

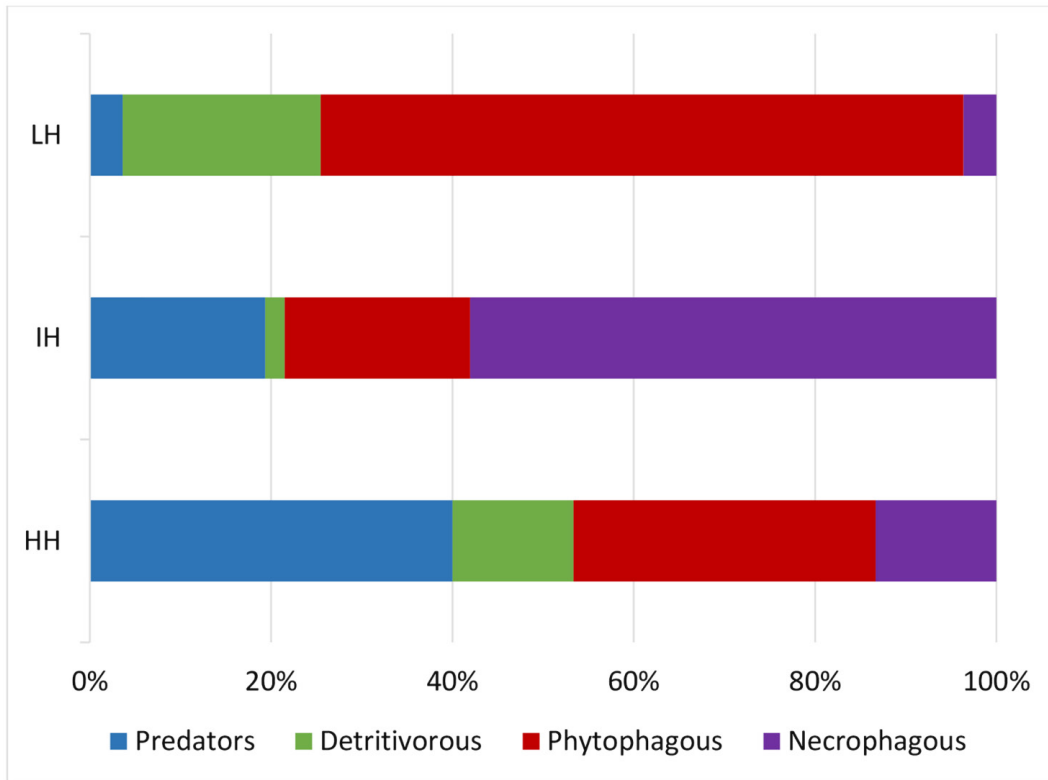


Figure 3. Composition of beetle guilds collected in high-altitude habitats in north-western Argentina (LH: low heterogeneity; IH: intermediate heterogeneity; HH: high heterogeneity).

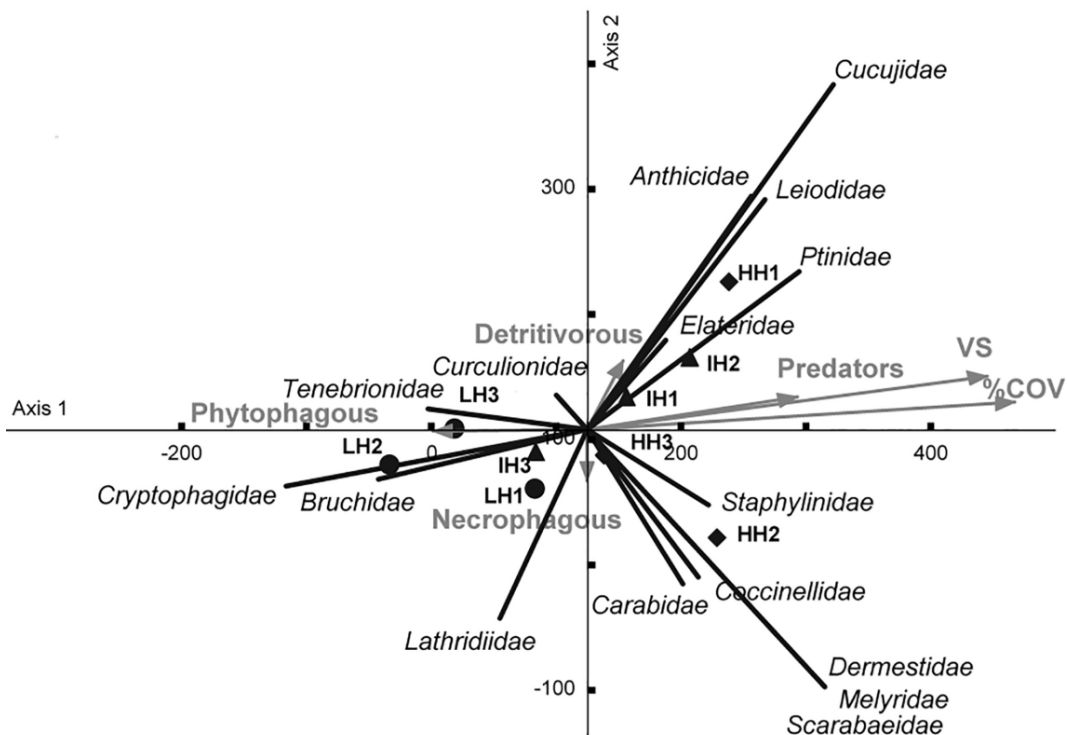


Figure 4. Ordination obtained by CCA of the assemblages of families of Coleoptera in relation to the vegetation heterogeneity variables (%COV: the percentage of vegetation coverage; VS: the percentage of vertical strata), and beetle guilds.

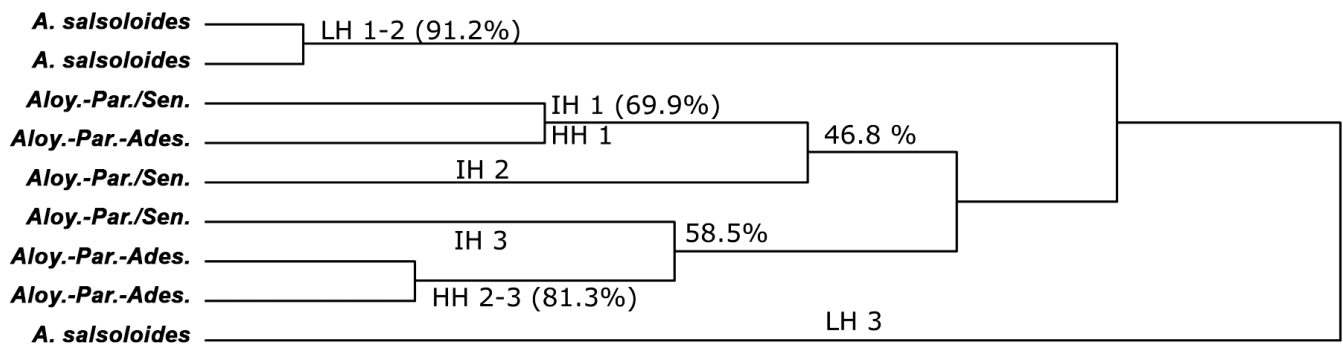


Figure 5. Cluster resulted from a conglomerate analysis to compare the similarity of the taxonomic composition of beetle communities between studied sites (**LH**: low heterogeneity; **IH**: intermediate heterogeneity, and **HH**: high heterogeneity). Abbreviations: *Aloy.*=*Aloysia salsoloides*; *Ades.*=*Adesmia horrida*; *Par.*= *Parastrephia* sp.; *Sen.*=*Senecio friesii*.

DISCUSSION

There is little knowledge in Argentina about the diversity of beetles in these high-altitude ecoregions, such as the Puna and the Altos Andes, where high altitude, extreme aridity, and marked seasonal and daily climatic fluctuations are the common denominators. It is important to note that a single species of beetle from the genus *Cyhdrorhinus* Guérin-Méneville, 1838 (Curculionidae) was found in all of the environments studied. According to Elgueta (1988) and Jerez (2000), species of this genus are dominant and endemic to the Chilean Andes. It is also worth noting that Tenebrionidae has a high species richness in these ecoregions, which corresponds to the findings of Cruz (2017) and Macagno et al. (2023). As evidenced by its diverse dietary preferences and morphological, physiological, and ethological adaptations, this family is one of the most diverse in our country's arid regions (Cheli et al., 2021); they also play an important role in the fragmentation of vegetal and animal matters and food webs (Aballay et al., 2016; Cheli et al., 2022). According to this study, the LH (55 individuals) and HI (93 individuals) habitats had a greater abundance of insects. Nevertheless, it is critical to highlight that within HI, 43% of the documented specimens belonged to a sole necrophagous beetle species, Ptinidae sp.2. An analogous trend was noted in LH, where 60% of the specimens gathered belonged to the Bruchidae sp.1.

Because beetles are megadiverse, the inventory obtained is representative, according to Chao et al. (2009). Due to the difficulty of recording all of their species, this order of insects typically has incomplete inventories. Consequently, it is frequently required to supplement the information with additional methods (Chao et al., 2020). Taking into account the sample's estimated completeness values ($q=1$ and $q=2$), we can say that almost all abundant and highly abundant species were recorded in each habitat. This leads us to believe that, while no statistically significant differences in species richness ($q=0$) were found between the IH and HH habitats, the latter could be the most diverse habitat because it would contain the greatest number of undiscovered beetle species (Table 2). This supports the notion that a more diverse beetle community correlates with more heterogeneous vegetation.

The guilds analysed in this study respond differently to vegetation heterogeneity, indicating that each of the considered habitats has a distinct beetle community structure. According to Megías et al. (2011) in arid and semi-arid environments, phytophagous and detritivorous beetles are typically more abundant than predators. Our research does not fully support this claim because phytophagous and detritivorous beetles were abundant in extremely arid habitats with a single dominant plant species (LH). However, this was not the case for other arid habitat types, with necrophagous organisms being numerically significant in IH habitats and predators being prevalent in HH. Some authors (Doblas-Miranda et al., 2007; Sagi & Hawlena, 2021) have also proposed that detritivores are the predominant

primary consumers in desert environments due to the brief presence of living plant matter and the predominance of dried plant remains or leaf litter as the primary resource. In our study, the percentage of detritus feeders was higher in the LH habitats with less vegetation coverage, which are the aridest. However, the phytophagous guild dominated these environments with low vegetation coverage and plant diversity. As a result, only a few families of beetles with specialised adaptations are dominant in environments with a single dominant plant species, little ground cover, and the lowest layer of vegetation. In our study, this was predominantly observed in bruchid species, which dominated in these arid, high-altitude environments with limited plant resources. In general, adult bruchids feed on nectar and pollen and can be abundant during the fruiting season to lay eggs in those that have formed (Kingsolver, 2004; Betancourt et al., 2009); however, other species seek out ripe seeds. The highest abundance of the dominant bruchid species (*Bruchidae* sp.1) was observed during flowering, spring, and summer, indicating a strong association between the species and the dominant plant in the environment. In the future, this type of relationship should be studied in depth. The same four guilds are recorded in the different habitat types, but the abundance and species composition of these guilds vary depending on the habitat type. Except for detritivorous, whose species diversity is high in LH habitats, the remaining guilds tend to increase their species diversity in both the IH and the HH. Although there are more species of predators in IH habitats, their abundance is greatest in environments with more dominant plant species (HH). On the other hand, the guilds of phytophagous and predatory organisms are more diverse in species in habitats with intermediate and high heterogeneity, even though the abundance of these guilds is nearly identical in these latter habitats. Vegetation may play an important role in predator-prey interactions in this case (Li et al., 2018), and our findings would support the enemies' hypothesis. According to this hypothesis, plant species diversity is positively related to the abundance of predatory arthropods (Root, 1973; Russell, 1989). Our study demonstrates that the abundance of the predator guild increased positively as plant diversity/vegetation heterogeneity increased. This could be because phytophagous animals find more food and shelter from predators in these habitats (Lassau et al., 2005) and predators may have access to more prey (Li et al., 2018).

The CCA supports the idea that vegetation heterogeneity (vegetation coverage and vertical structure) is important for predator abundance, but it also shows a weak relationship with detritivorous. In the case of necrophagous beetles, their abundance is greater in IH, which may be explained by the greater presence of wild and domestic vertebrates in these high-altitude environments, increasing the likelihood that these beetles will have access to a food source. The latter is mentioned by Aballay et al. (2016) for the tenebrionids collected with carrion-baited traps and on vertebrate carcasses in arid and semiarid areas of Buenos Aires, Catamarca, Mendoza, and San Juan provinces of Argentina. A greater vegetation heterogeneity (more vegetation coverage and the higher vegetation layer) provided by a greater number of dominant plant species has a positive impact on the assemblages of altitude beetles, not only on the richness of species but also on their abundance, demonstrating that LH habitats are characterised by specific assemblages. Thus, the beetle assembly in IH habitats is more similar to that in habitats with more dominant plant species (HH), indicating that the vertical structure of the vegetation and its coverage above ground are driving forces of beetle diversity in environments above 2500 m a.s.l. These latter habitats share a gradient of change in the vertical structure of the vegetation, primarily in the lower stratum (less than one metre), due to the landscape being dominated by low shrubby species and grasses (1.5 m) that are dispersed irregularly (Morello et al., 2012).

According to Mazía et al. (2006), vegetation coverage is an important predictor of species richness and abundance when working at small scales, because plants can modify the surrounding micro-environment. As shown by our study, the vegetation coverage in these environments was different in each habitat. The vegetation in these mountain environments is distributed discontinuously, resulting in patches with a high concentration of nutrients in a scarce matrix. These changes in vegetation heterogeneity in high-altitude landscapes have a direct impact on arthropod assemblages. Thus, the

low vegetation coverage in our habitat with a dominant plant species (LH) gives its soils little humidity and greater exposure to high temperatures and erosion. This poses a problem for scarabaeids, carabids, staphylinids, and tenebrionids (Chung et al., 2000; Medina-Reyes et al., 2021) whose life cycles occur in the soil (Lescano et al., 2017). As a result, habitats dominated by *Aloysia salsoloides* support a different community of beetles, with a highly dominant species of Bruchidae, a constituent of the phytophagous guild, which is undoubtedly highly specialised to exploit a specific plant resource of those extreme environments.

Species turnover is the main factor responsible for the high beta diversity observed in the habitats studied here, indicating a large number of exclusive species in each of them. According to Si et al. (2016), this component of beta diversity reflects species habitat selection. Following this idea, Barton et al. (2013) established that the smaller the sampled area, the greater the difference in the composition of species between sites, because they respond differently to the characteristics of each habitat. In our case, beetles respond to the number of plant species present, the vertical structure of the plants, and the percentage of soil cover in each of the habitats studied. So, each habitat type has its own group of beetle species, which may be a response to the micro-climates (Pérez-Hernández & Zaragoza-Caballero, 2015) caused by the different percentages of vegetation coverage. In this way, vegetation is an important factor in determining the composition of small-scale beetle communities (micro-habitats) in the Puna and Altos Andes environments, where they respond by changing their assemblages and abundances in response to a vegetation gradient. However, not only vegetation is a determining factor for beetles because a wide range of factors interacts simultaneously (temperature, rainfall, soil, salinity, among others) (Kistler, 1995; Bubenias et al., 2013; Cheli et al., 2021), generating a network of interactions that define the characteristics of the habitat and, consequently, that of the communities of beetles responding to them differently, by their food and reproductive requirements (Barton et al., 2013).

We conclude that beetle communities in the Puna and Altos Andes of Salta province respond positively to a gradient of vegetation heterogeneity. At each end of the gradient, from low to high heterogeneity, there are very different communities, and species replacement is the key to explaining the high beta diversity we saw. Thus, Coleoptera communities are more diverse and complex in terms of guild composition, as the plant communities of the Puna and the Altos Andes are more diverse and structurally more heterogeneous. Except for detritivorous species, the composition of species within trophic guilds varies between habitat types, with a tendency for species richness to increase in proportion to the diversity of dominant plants. In the high-altitude environments studied here, the abundance of predators increases positively with plant heterogeneity, supporting the enemies' hypothesis. The diversity of plant communities and vegetation cover on the ground are some of the major forces that contribute to the diversity of beetles in the arid, high-altitude environments of Puna and Altos Andes in Salta province. We must not lose sight of the fact that the biota and its distribution in these arid mountain systems are the results of a variety of current environmental factors, both local and regional, as well as historical events that resulted in the formation of diverse and heterogeneous environments. As a result, we must continue to investigate additional potential factors that may be influencing beetle and other habitat-dependent arthropod communities.

AUTHOR'S CONTRIBUTION

The authors confirm their contribution in the paper as follows: J.A.C.: Conceptualization, sampling design and provided funding; H.B.M., I.G.C., J.A.C. and A.X.G.R.: Fieldwork; H.B.M., I.G.C., and M.B.: Sample processing; G.E.F. and H.B.M.: Identification of beetles; A.X.G.R., H.B.M., M.B., and J.A.C.: Data analysis; M.B., H.B.M. and A.X.G.R.: Writing-original draft preparation; J.A.C. and G.E.F.: Writing-review and editing. The authors read and approved the final version of the manuscript.

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AVAILABILITY OF DATA AND MATERIAL

The specimens listed in this study are deposited in IEBI Collection-MCNS-UNSa (Museo de Ciencias Naturales Salta; Universidad Nacional de Salta, Argentina) and are available from the curator, upon request.

ETHICS APPROVAL AND CONSENT TO PARTICIPATE

This research followed the guidelines specified by the Secretaría de Medio Ambiente y Desarrollo Sustentable, Salta province (Argentina), for the collection of entomological material approved by Resolution No. 826.

CONSENT FOR PUBLICATION

Not applicable.

CONFLICT OF INTERESTS

The authors declare that there is no conflict of interest regarding the publication of this paper.

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بررسی واکنش جمعیتی سخت‌بال‌پوشان به ناهمگنی پوشش گیاهی در مناطق مرتفع شمال غربی آرژانتین

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چکیده: پویایی و پیچیدگی اجتماعات گیاهی بر تنوع و توزیع گونه‌های جانوری در محیط‌های مختلف تأثیر دارد. سخت‌بال‌پوشان، پرتعدادترین گروه حشرات هستند و شاخص‌های ارزشمندی برای ارزیابی و تحت‌نظر داشتن محیط محسوب می‌شوند. با این حال، تنوع و پویایی آنها در مناطق مرتفع به خوبی شناخته نشده است. با استفاده از تله‌های گودالی و مکنده، نمونه‌های سخت‌بال‌پوشان را جمع‌آوری کرده و واکنش جمعیتی آنها به تغییرات تراکم پوشش گیاهی (کم، متوسط و بالا) بررسی شد. گرادیان ناهمگنی با در نظر گرفتن گونه‌های گیاهی غالب در هر زیستگاه، درصد پوشش گیاهی و طبقاتی تعیین شد. واکنش جمعیت به ناهمگنی گیاهی به همراه الگوهای تنوع آلفا و بتا در سوسک‌ها مورد تجزیه و تحلیل قرار گرفت. ۴۱ گونه / گونه ریختی سخت‌بال‌پوشان، متعلق به ۱۶ خانواده و چهار گروه هم‌زیستگاهی گزارش شدند. تغییرات قابل توجهی در ترکیب گروه‌های هم‌زیستگاهی و تنوع آلفا و بتا، خصوصاً بین محیط‌های با ناهمگنی گیاهی بالا و کم مشاهده شد. تغییرات قابل توجه گونه‌ها بین مناطق مورد مطالعه، عامل اصلی و مسئول ایجاد بیشترین تنوع بتا است که اهمیت ناهمگنی زیستگاهی در این محیط‌ها را نشان می‌دهد. سوسک‌های گیاه‌خوار، پوسیده‌خوار و جسدخوار و شکارگر به ناهمگنی گیاهی پاسخ‌های متمایزی را نشان دادند. این نشان می‌دهد جوامع سخت‌بال‌پوشان در هر یک از این زیستگاه‌ها، ساختار متمایزی دارد. گونه‌های شکارگر در محیط‌های با گیاهان متنوع تأثیرگذار بودند در حالی که گیاهخواران در محیط‌های بیشتر همگن تأثیرگذار بودند. جمعیت‌های سخت‌بال‌پوشان در Puna و Altos Andes منطقه Salta به ناهمگنی گیاهی به طور مثبت پاسخ می‌دهند و این پدیده نقش حیاتی در تعیین ترکیب جمعیتی آنها در مناطق مرتفع خشک دارد.

واژگان کلیدی: مناطق خشک، تنوع بتا، سخت‌بال‌پوشان، ترکیب هم‌زیستگاهی، مناطق اکولوژیک کوهستانی