

Differences in Alpha and Beta Diversities of Epigeous Arthropod Assemblages in Two Ecoregions of Northwestern Argentina

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Andrea Ximena González Reyes, José Antonio Corronca, and Norma Carolina Arroyo (2012) Differences in alpha and beta diversities of epigeous arthropod assemblages in two ecoregions of northwestern Argentina. *Zoological Studies* 51(8): 1367-1379. Ecoregions are regional-scale biodiversity units. Several of them converge in Salta Province, Argentina, where Puna and Monte are priority conservation areas for different reasons. The aims of our research were to (1) analyze the inventory obtained by determining the alpha and beta diversities of the arthropod communities in the ecoregions; (2) attempt to establish the most likely factors responsible for the distribution patterns of the epigeous communities present in the Monte and Puna take off; and (3) show the main changes in abundance and species richness of the most diverse arthropod groups recorded over space. Pitfall traps were used to collect epigeous arthropods. Several soil variables were measured in the field in addition to climatic variables. The total inventory and data by sites were evaluated using nonparametric estimators. Observed and estimated diversity values were used to compare epigeous arthropod communities between ecoregions. Beta diversity was assessed by different methods. The abundance-based Morisita index was used to investigate the degree of association between ecoregions and sampling sites. We used a non-metric multidimensional scaling analysis to show the ordination of the studied sites following the similarity of arthropod assemblages and possible relationships with environmental variables that could explain it. Species richness differed between ecoregions, and the true diversity showed that Puna was 1.30-times more diverse than Monte de Sierras y Bolsones. The inventory completeness was adequate (78%), and differed between sites. Species turnover was high with a clear ecoregional faunal separation. The most diverse arthropods orders were spiders, coleopterans, and hymenopterans, which exhibited differences in abundance and species richness between ecoregions. Different factors of soil heterogeneity and climate, which are important in arid environments, exerted an influence on the assemblages of epigeous arthropods obtained. <http://zoolstud.sinica.edu.tw/Journals/51.8/1367.pdf>

Key words: Biodiversity, Monte de Sierras y Bolsones, Puna, Local diversity, Species turnover.

Bailey (1998) defined ecoregions as “major ecosystems resulting from large-scale, predictable patterns of solar radiation and moisture, which in turn affect the kinds of local ecosystems and animals and plants found within”. Thus, they are regional-scale biodiversity units (Dinerstein et al. 2000), that contain groups of characteristic natural communities that share a great number of species, ecological dynamics, and environmental conditions

(Dinerstein et al. 1995, Groves et al. 2000). Ecoregions are generally defined as finite spatial areas, smaller than a biome, where environmental conditions and species assemblages are supposedly relatively homogeneous, compared to the heterogeneity occurring in wider spatial areas (Olson et al. 2001).

Five ecoregions converge in Salta Province, Argentina, where the Central Andean Dry Puna

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(PU) with a vulnerable estimated conservation status, according to Global 200, is highly relevant as one of the priority conservation areas (Olson and Dinerstein 2002). On the other hand, Argentina is solely responsible for conservation of the Monte (MO), an ecoregional complex not shared with any other country, and with a high degradation level, partly due to natural desertification processes and degradation of its environments caused by anthropogenic activities. Two ecoregions are recognized within the MO, Monte de Sierras y Bolsones (hills and ravines monte) and Monte de Sierras y Llanuras (hills and plains monte) (Bertonatti and Corcuera 2000), with only the former present in Salta Province.

The PU ecoregion is located in the north-western corner of the country and covers a surface area of 12,457,000 ha; it is a cold desert situated at 3000–4000 m in elevation, surrounded by Andes Mountain ranges to the east and west (Bertonatti and Corcuera 2000). The relief is relatively flat, but occasionally crossed by hills that act as limiting elements of closed basins, characteristic of this environment. It has a high level of endemism, but it is being degraded by erosion, overexploitation of ligneous and cactaceous species, and mining activities. The Monte de Sierras y Bolsones, on the other hand, is a relatively narrow strip, that extends in a latitudinal direction and is characterized by a lack of permanent water. Different landscapes with characteristic soils and vegetation can be distinguished within each ravine, such as *huayquerías*, *barriales* (wetlands), *medanales* (dunes), and *salares* (salt marshes) (Morello 1958). The Monte is currently suffering conservation problems due to overgrazing, desertification, salinization of soils, forestry overexploitation for the production of posts and lumber, and inadequate management of fire, among other issues.

Desertic and semi-desertic environments are characterized by long periods without rain, lack of permanent water courses, great daily thermal ranges, and very high mean temperatures during summer; the associated faunas exhibit significant morphological, physiological, and behavioral adaptations to allow development (Mares et al. 1977). In these arid environments, arthropods play important roles (mainly in and above the ground) as decomposers, herbivores, granivores, and predators, controlling nutrient cycling and energy flows through different levels of the food chain (Polis 1991, Greenslade 1992, Ayal 2007). Given their roles in natural systems, they are

considered a model taxon for habitat-dependent community comparisons (Lassau et al. 2005), and some taxa can be used to monitor changes in the environment because of their high abundance, species richness, and habitat fidelity (Andersen and Majer 2004), which together with their diverse characteristics and ecological requirements (Wettstein and Schmid 1999), make them useful indicators of environmental changes.

The present work assessed differences in the diversity and composition of arthropod assemblages in these 2 ecoregions in northwestern Argentina, since to this date no similar studies have been conducted in this country. The aims of our research were to (1) compare the alpha and beta diversities in the 2 ecoregions, (2) attempt to establish the most likely factors responsible for distribution patterns of epigeous communities present in the MO and PU, and (3) show major changes in abundance and species richness of the most diverse arthropod groups recorded over space. The following hypotheses were tested: (1) different environmental conditions of each ecoregion will lead to different fauna of epigeous arthropods; and (2) there is a high beta diversity in the composition of the epigeous arthropod fauna between ecoregions, higher than that among sites within the same ecoregion.

MATERIALS AND METHODS

Study area

Arthropods were collected at 6 sampling sites, three in each ecoregion (Fig. 1, Table 1). The PU is characterized by cold and dry weather, with little rain during summer that descends from northeast to southwest (100–200 mm/yr) and with minimum temperatures in winter of -15°C , but the extreme dryness of the environment leads to a great daily thermal amplitude, with variations of more than 25°C in summer (Reboratti 2006). Its vegetation is typical of a steppe, constituted mainly by low bushes of *Paraestrepia* spp., *Adesmia horridiscula*, and *Azorella yareta* as at sampling sites PU2 and PU3, while grasses appear occasionally in *vegas* (PU1 site), local depressions where spring water accumulates, creating a different microenvironment. The Monte de Sierras y Bolsones ecoregion (MO) has a subtropical dry climate, with summer precipitation ranging 80–200 mm, being concentrated in the north. Very marked changes in temperature occur, both daily

and seasonally (Bertonatti and Concuera 2000). *Larrea* sp. gives phyto-sociological unity to the MO region, forming 1.5-3.0-m-high thickets, together with *Prosopis* sp. and various species of cacti (Bertonatti and Concuera 2000).

Sampling

Two samplings were carried out, one in spring (Nov. 2005) and the other in summer (Feb. 2006), since those are the seasons when the greatest diversity of arthropods can be found in the region (Arroyo 2009). At each of the 6 geo-reference sites, epigeous arthropods were collected in 10 pitfall traps. Traps dimensions were 7.5 (upper diameter) × 12.2 (depth) × 5.2 cm (lower diameter), and contained a saline solution (1 kg of salt in 8 L of water, plus detergent drops); they were placed along a linear transect in an east-west direction to capture the heterogeneity of the slope, 10 m apart from each other, and were used for

sampling at least 7 d each season. All arthropods collected were placed in polyethylene bags containing 70% ethanol, properly labeled, and considered independent. They were then taken to the lab where they were sorted under a binocular microscope and fixed. Collected specimens were placed in the Instituto para el Estudio de la Biodiversidad de Invertebrados-Museo de Ciencias Naturales, Univ. Nacional de Salta collection (IEBI-MCN). The collected arthropods were recorded on electronic spreadsheets, and sorted by order, family, genus, and species/morphospecies depending on the availability of keys (De Santis 1969, Borror et al. 1989, CSIRO 1991, Dippenaar and Joqué 1997, Ramírez 1999, Ribes Escolá 2007-2010). Species/morphospecies data were used to generate a database with digitalized photographs of the distinctive characters for each of them, using TAXIS 3.5 software (Meyke 1999-2004).

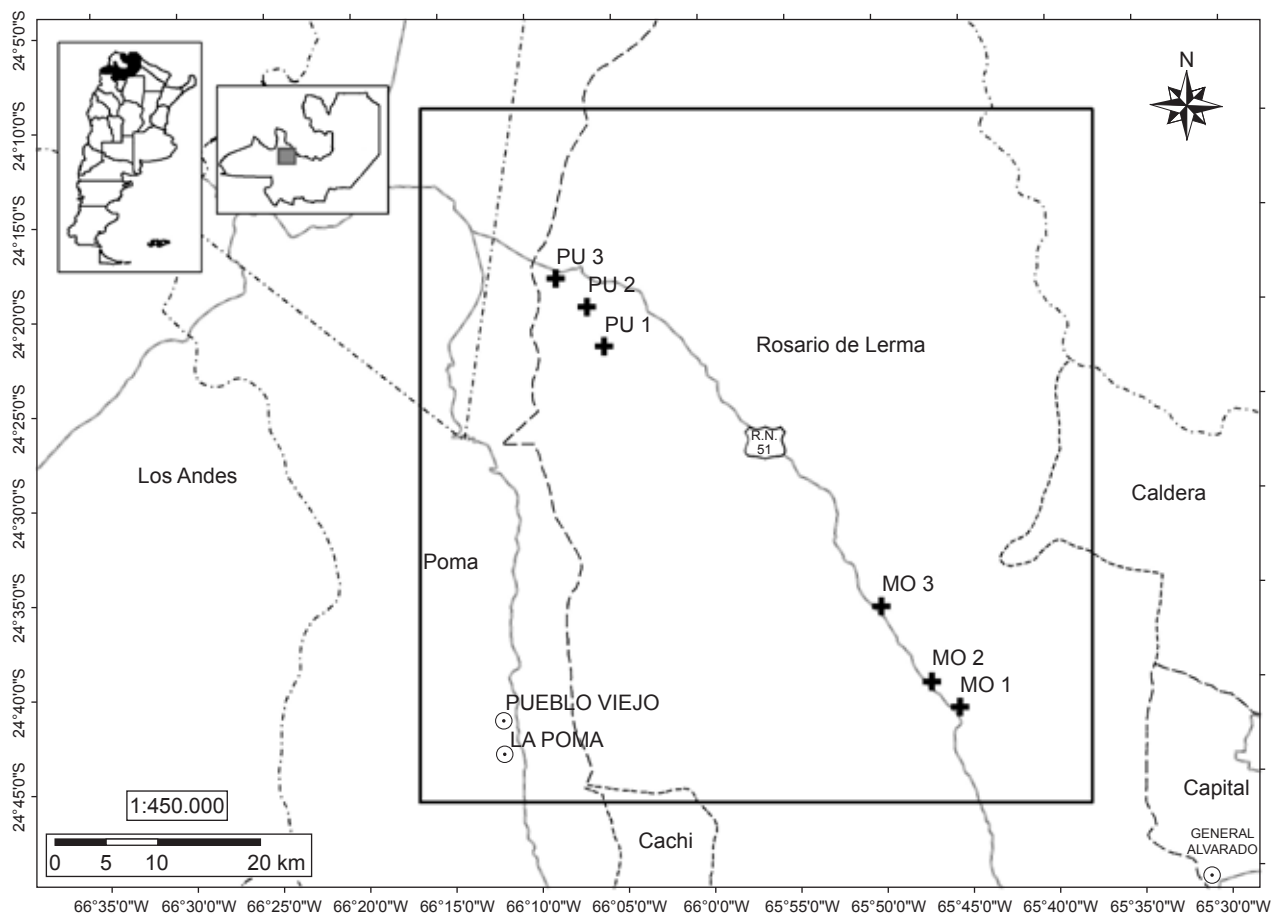


Fig. 1. Geographic location of the study area, showing sample sites in the different ecoregions in Salta Province, Argentina. MO, Monte de Sierras y Bolsones; PU, Puna.

Selection of variables

Twenty-three climatic variables related to temperature, precipitation, and bio-climate, were obtained from Worldclim USGS-WIST (NASA) (www.worldclim.org) with a spatial resolution of about 1 km² (Hijmans et al. 2005), for each sampling site. Soil variables were measured in the field at each sampling site, where 5 separate randomly selected 0.5 × 0.5-m quadrants were plotted and photographed vertically with a Canon Powershot G10 digital camera (Tokyo, Japan), in order to analyze the soil heterogeneity. Quantification of each soil variable at each site was the average of values obtained from each photograph for each variable. Values for each variable were calculated using Adobe Photoshop C4 software (San Jose, California, USA); by assigning different colors to each variable, we obtained the pixel value as a percentage of the total amount of pixels in the photograph (Gilbert and Butt 2009). These variables included %soil-veg.cover which was the percentage of soil with living plant cover; %soil-litter which was the percentage of soil covered by dead leaves; %soil-rocks which was the percentage of soil with rocks; %soil-silt which was the percentage of soil with a silt-clay matrix; %soil-sand which was the percentage of soil with sand; and %soil-gravel which was the percentage of soil with

gravel. Each group of variables (soil and climatic) were subjected to a collineality analysis through the SPSS 16.0 program (SPSS 2007) to select those predictors that were used to generate the final model. After that, the following uncorrelated explanatory variables were used in the analyses: seasonality of precipitation, annual precipitation, %soil-litter, %soil-rocks, %soil-sand, and %soil-veg.cover.

Inventory and alpha diversity

We assessed how complete the obtained inventory was compared to estimated values using different nonparametric estimators of species richness in the EstimateS 7.0 program (Colwell 2004). We compared the species richness of each ecoregion using sample-based rarefaction curves with the same software, and the completeness of the inventories at different scales was calculated as the percentage of species observed with respect to that estimated by nonparametric estimators closer to the observed values. The structure of the arthropod community in each ecoregion was compared using Whittaker curves, because these plots are often the best way to illustrate differences in evenness and species richness (Magurran 2005). A substantial fraction of a community is often represented by many rare species, often singletons, which remain undetected by most

Table 1. Data on sampling sites, location, number of observed species richness and abundance, and soil and climate-related variables

Site	Geographical position	Elevation (m)	Ecoregion	S	N	%soil-veg.cover	%soil-litter
Site1	24°44.28'S, 65°45.28'W	2417	Monte	182	2086	0.38	2.67
Site2	24°41.34'S, 65°45.62'W	2367	Monte	125	1251	6.21	10.13
Site3	24°39.97'S, 65°47.21'W	2554	Monte	87	1061	2.07	1.68
Site4	24°21.88'S, 66°05.76'W	3705	Puna	140	1076	5.83	4.45
Site5	24°19.77'S, 66°06.68'W	3861	Puna	114	978	3.55	3.12
Site6	24°18.24'S, 66°08.44'W	3989	Puna	60	194	4.65	2.63

Site	Geographical position	%soil-sand	%soil-gravel	%soil-rocks	annual-precip.	season-precip.
Site1	24°44.28'S, 65°45.28'W	37.07	20.21	39.68	127.529	111.233
Site2	24°41.34'S, 65°45.62'W	0	8.58	17.8	123.76	111.64
Site3	24°39.97'S, 65°47.21'W	20.35	25.46	44.07	123.607	112.493
Site4	24°21.88'S, 66°05.76'W	0	55.7	13.67	70.552	112.957
Site5	24°19.77'S, 66°06.68'W	0	52.18	14.28	66.42	110.7
Site6	24°18.24'S, 66°08.44'W	27.26	46.6	12.83	65.69	119.033

S, species richness; N, abundance; %soil-veg.cover, percent of soil with live plant cover; %soil-litter, percent of soil covered by dead leaves; %soil-sand, percent of soil with sand; %soil-gravel, percent of soil with gravel; %soil-rocks, percent of soil with rocks; Annual-precip., annual precipitation; season-precip., seasonal precipitation.

biodiversity surveys (Chao et al. 2009). Since rare species usually contain information about incomplete sampling, we used nonparametric estimators to control for undersampling bias (Colwell and Coddington 1994, Beck and Schwanghart 2010). These are based on frequency counts and information on rare species in the collection to estimate the “true diversity” (Jost 2006 2007), through the “effective number of species” using the software SPADE (Chao and Shen 2010): (1) estimates of total species richness (0D , the true diversity of order zero) was estimated by the abundance-based coverage (ACE) estimator for highly heterogeneous communities ($CV_{rare} > 0.8$) (Chao and Shen 2010); (2) the bias-controlled Shannon’s entropy (1D , the true diversity of order 1), and (3) the inverse Simpson index (2D , the true diversity of order 2), calculated using an approximate minimum-variance unbiased estimator (MVUE) (Moreno et al. 2011). The same calculations were performed independently for the most diverse groups of arthropods recorded in the study. In addition, we calculated the percentage of the inventory completion as a proportion of the ACE relationship with the observed species.

Beta diversity

SPADE software was also used to estimate the similarity (or species turnover) of arthropod communities between sites using the mean of the abundance-based Morisita index (Chao et al. 2008), that investigates the degree of association taking into account ecoregions and sites in each ecoregion. The ordination of sites was carried out following procedures suggested by McCune and Grace (2002); first, descriptive statistics were calculated, and then we transformed the main matrix using the Hellinger distance because it is a measure recommended for clustering or ordination of species abundance data (Rao 1995), and is an appropriate alternative that assigns low weights to rare species (Legendre and Gallagher 2001). We carried out a non-metric multidimensional scaling (NMS) analysis on the species abundance data with PC-ORD vers. 6 (McCune and Mefford 2006). Two data matrices were used, the 1st one with arthropod data and a 2nd one of environmental variables corresponding to soil and climate. The relationship between environmental data and species abundance ordination was graphically represented in a joint plot by a series of vectors. The length of the vector represents the strength of the correlation of an environmental factor with

a particular direction or gradient in the ordination obtained from data on species abundances. The NMS analyses examined relationships of site distribution and environmental variables most closely related to this distribution. First, we ran on Autopilot slow and thorough mode, using Sorensen as a measure of distance, 500 iterations, a random start configuration, 250 runs with real data, and 1 run to reduce the dimensionality of each cycle. To evaluate when the NMS extracted more-robust axes than those randomly expected, we used a Monte Carlo test. This analysis was repeatedly carried out to confirm the results described above, with the intention of reducing stress to a minimum. Once an ordination of sites was obtained, values of similarity between the different groups of sites were submitted to a multidimensional permutation procedure [MRPP] to assess whether there were significant differences between values of similarity of the arthropod fauna among them. The complementarity of the inventories between ecoregions and for each pair of sites was analyzed using the index of Vane-Wright et al. (1991). In addition, we used this method to partition the beta diversity proposed by Carvalho et al. (2012) to determine the relative contribution of species turnover and the difference in the species richness patterns of beta diversity recorded. Finally, we compared abundances and observed species richness of epigeal arthropods of the most diverse families registered in each ecoregion using a SIMPER analysis which took into account Bray-Curtis dissimilarity using the PAST software (Hammer et al. 2003) to determine which families of those arthropod groups most contributed to the dissimilarity between ecoregions.

RESULTS

We collected 6646 adults of epigeous arthropods belonging to 400 species/morphospecies, with the MO ecoregion exhibiting greater abundance and species richness ($n = 4398$, $S = 292$) than PU ($n = 2248$ and $S = 213$), as was also evidenced in the curves of observed species accumulation per sample (Fig. 2A). Community structures in the 2 ecoregions differed, with MO exhibiting a greater number of dominant species, few species with intermediate abundances, and many rare species, whereas in the PU only 2 dominant species were recorded, along with several species of intermediate abundances and a smaller number of rare species than in the MO (Fig.

3). In the PU, the dominant species (with > 100 individuals) were a species of *Pogonomyrmex* sp. (Hymenoptera: Formicidae: Myrmicinae) and 1 oribatid mite (Acari: Acariformes), accounting for 22% of the total abundance of arthropods for this ecoregion. In the MO, on the other hand, species with greater abundances were 1 *Camponotus* sp. (Hymenoptera: Formicidae: Formicinae), followed by 2 Entomobryiidae (Collembola), 2 species of dipterans (Tephritidae and Chloropidae), 3 others species of Formicidae and 1 species of Ceraphronidae (Hymenoptera), and 2 oribatid mite species (Acari, Acariformes), which accounted for 62% of the total abundance. Both the species richness and abundance of arthropods declined at sites located at greater elevations within an ecoregion (Table 1).

The inventory obtained in this study was adequate, achieving 78.21% of the richness

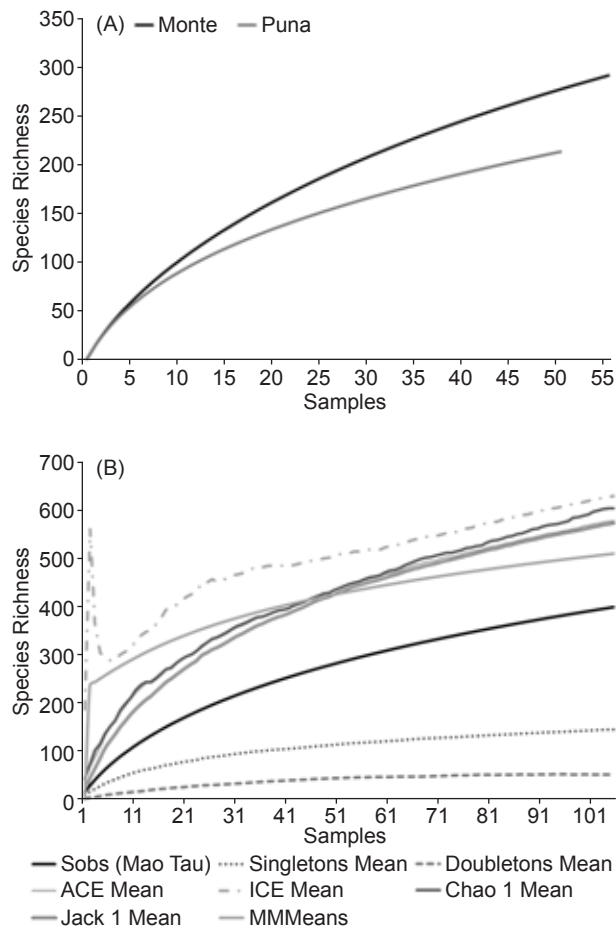


Fig. 2. Total inventory and diversity comparison between ecoregions. (A) Species accumulation curves based on samples from each ecoregion; (B) performance of different non-parametric estimators considering all samples.

expected by the nearest estimator (Michaelis-Menten), with values close to 70% for the Jack1 and ACE estimators (Fig. 2B). In the case of the MO inventory, the Jack1 and Michaelis-Menten estimators estimated 32% and 31% more species than observed, whereas for PU, the Michaelis-Menten estimator recorded 22% more species than observed, followed by the other 2 estimators, Jack1 (31%) and Chao1 (32%). The percentage of singletons in MO was moderate, reaching 40%, whereas doubletons were low (15%); values for PU were similar but lower (37% and 14.8%, respectively).

When comparing the “true diversity” of the communities with the “effective number of species”, the degree of completeness of the inventory obtained was good, achieving values of > 65% of completeness (Table 2). Thus, the arthropod community at the PU was 1.30-times more diverse than that at MO when comparing 1D observed values (the true diversity of order 1). Moreover, when we evaluated the true diversity of the most diverse arthropod groups recorded in the study, the completeness of the inventories was generally good to very good, with between 55% and 95% of species estimated by the 0D value (ACE) being observed, except for coleopterans from PU (27%). Spiders, coleopterans, and ants exhibited greater species richness in the MO than the PU, whereas other hymenopteran and dipteran families were richer in the PU ecoregion (Table 2).

The NMS showed that the sampled sites were ordered in 2 groups that corresponded with the ecoregions, with the ordering on 2 axes explaining 72.8% of the variance (axis 1 of 0.667 and axis 2 of 0.061) with stress of 0.0568 (Fig. 4). The MRPP confirmed the difference between arthropod

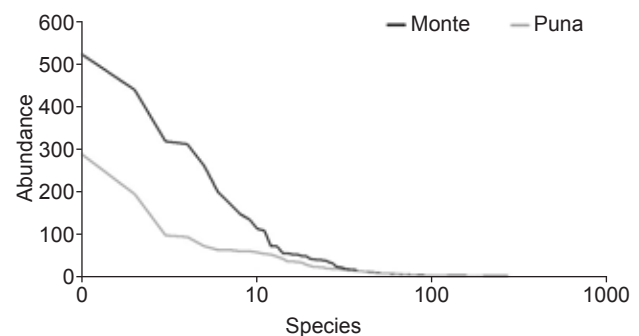


Fig. 3. Comparison of the structures of the epigeous arthropod communities in the Puna and Monte de Sierras y Bolsones by Whittaker curves, showing differences between the dominant and rare species compositions.

communities of these ecoregions ($A = 0.3651$, $p = 0.0227$). Annual precipitation ($r = -0.97$) and %soil-rocks ($r = -0.73$) were strongly negatively correlated with axis 1, while %soil-gravel ($r = 0.93$) and seasonal precipitation ($r = 0.55$) had strong positive correlations with it; %soil-litter ($r = -0.33$), and %soil-veg.cover ($r = 0.37$) also showed an association with the same axis.

The ecoregions had very dissimilar arthropod

communities ($1 - C = 0.699$). According to the Morisita index, sites within each ecoregion exhibited a high dissimilarity in fauna, with values approaching 85% for MO sites ($C33 = 0.153$), whereas among PU sites, this value was 63% ($C33 = 0.372$). Table 3 shows similarity values between pairs of sites within each ecoregion, with a greater similarity in epigeous arthropod fauna being evident at PU sites. The change in composition

Table 2. “True diversity” considering all inventories and by ecoregion, showing values of the observed and estimated diversities, and the percentage of the inventory completion (inv. compl.) taking into account the S_{obs} and the abundance-based coverage estimator (ACE) value

Taxa	Both ecoregions						
	Observed diversity			Estimated diversity			Percent of inv. compl.
	0D	1D	2D	$^0D_{(ACE)}$	$^1D_{(MLE_{bc})}$	$^2D_{(MVUE)}$	
ARTHROPODS	400	73.6	32.78	579.3 ± 31.4	46.9 ± 9.26	32.9 ± 0.13	69.05%
ARANEAE	46	24.09	13.6	66.5 ± 10.10	28.6 ± 5.69	14.6 ± 0.24	69.17%
COLEOPTERA	34	14.1	7.22	68.1 ± 17.50	17.5 ± 5.30	7.5 ± 0.27	49.93%
DIPTERA	101	30.5	15.25	122.0 ± 8.60	31.6 ± 5.84	15.4 ± 0.23	82.79%
HYMENOPTERA	89	14.86	8.11	137.6 ± 17.90	15.3 ± 2.82	8.1 ± 0.23	64.68%
Formicidae	19	6.98	5.22	19.9 ± 1.40	7.0 ± 1.48	5.2 ± 0.28	95.48%
Hymenoptera w/o Formicidae	70	21.51	10.18	124.2 ± 20.60	24.5 ± 5.69	10.4 ± 0.22	56.36%

Taxa	Monte ecoregion						
	Observed diversity			Estimated diversity			Percent of inv. compl.
	0D	1D	2D	$^0D_{(ACE)}$	$^1D_{(MLE_{bc})}$	$^2D_{(MVUE)}$	
ARTHROPODS	292	47.32	21.18	448.1 ± 38.4	49.8 ± 7.35	21.3 ± 0.16	65.16%
ARANEAE	34	16.83	9.09	58.5 ± 12.9	20.9 ± 5.81	9.7 ± 0.29	58.12%
COLEOPTERA	25	10.13	5.26	41.5 ± 12.9	12.0 ± 3.70	5.5 ± 0.26	60.24%
DIPTERA	83	19.81	9.09	108.4 ± 10.3	20.8 ± 5.29	9.2 ± 0.26	76.57%
HYMENOPTERA	69	11.1	5.74	124.3 ± 22.1	11.6 ± 3.15	5.8 ± 0.29	55.51%
Formicidae	15	5.67	3.83	16.0 ± 1.7	5.7 ± 1.37	3.8 ± 0.29	93.75%
Non-Formicidae	54	13.02	5.23	115.8 ± 25.6	15.8 ± 5.86	5.3 ± 0.23	46.63%

Taxa	Puna ecoregion						
	Observed diversity			Estimated diversity			Percent of inv. compl.
	0D	1D	2D	$^0D_{(ACE)}$	$^1D_{(MLE_{bc})}$	$^2D_{(MVUE)}$	
ARTHROPODS	213	61.39	27.14	323.9 ± 26.0	65.9 ± 11.94	27.5 ± 0.24	65.76%
ARANEAE	22	11.89	6.09	35.0 ± 9.00	15.9 ± 5.96	6.7 ± 0.27	62.86%
COLEOPTERA	15	9.78	6.45	56.5 ± 31.40	23.9 ± 18.7	7.9 ± 0.32	26.55%
DIPTERA	53	23.7	14.43	66.6 ± 7.50	25.1 ± 3.65	14.8 ± 0.19	79.58%
HYMENOPTERA	47	11.46	5.89	63.5 ± 8.80	11.9 ± 3.08	5.9 ± 0.28	74.02%
Formicidae	13	5.27	3.63	14.2 ± 1.80	5.3 ± 1.31	3.6 ± 0.29	91.55%
Non-Formicidae	34	14.58	7.63	50.6 ± 9.4	16.7 ± 4.32	7.9 ± 0.26	67.19%

Observed and estimated diversity, 0D , 1D , and 2D (denote diversity measures of orders 0, 1 and 2, respectively). Observed diversity (using PAST software), $^0D = S_{obs}$ (observed species richness); 1D = exponential of Shannon Index; 2D = inverse of Simpson index. Estimated diversity (using SPADE software): $^0D = ACE$; 1D = bias-controlled Shannon index; 2D = minimum variance unbiased estimator.

of epigeous arthropods between ecoregions was high ($\beta_{CC} = 73.75\%$), with 73.22% of this value representing species replacement, whereas 26.78% represented species loss (Table 4). High complementarity was recorded between MO sites as well, with species replacement representing > 70% of the value of the compositional change and 49.73% of species being lost for MO1-MO3. PU sites exhibited an increase in complementarity between the higher-elevation sites of PU2 and PU3, with species loss representing 59.70% of the total change in composition of epigeous arthropods among sites PU1-PU3 (Table 4).

The most diverse arthropod orders in our study were spiders, coleopterans, dipterans,

and hymenopterans, which exhibited changes in richness and abundance between ecoregions (Fig. 5). For spiders, according to the SIMPER analysis, the Lycosidae (4 species) and Anyphaenidae (7 species) were families that contributed the most to the dissimilarity between ecoregions (25.19% and 15.83%, respectively) followed by families that were recorded in only one of the ecoregions, such as the Corinnidae in PU and the Philodromidae and Amaurobiidae in MO. Although families of spiders were shared by both ecoregions, several of them were recorded only in one, with MO showing a greater diversity of spider families. For coleopterans, the families Bostrichidae, Carabidae, and Staphylinidae had

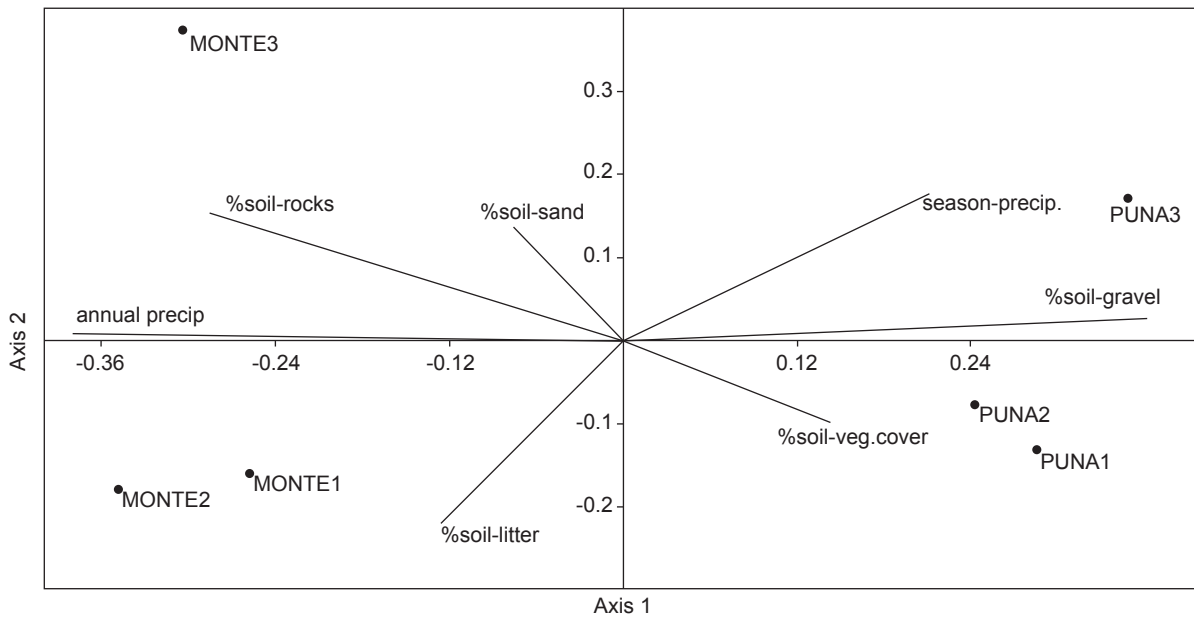


Fig. 4. Ordination by an NMS analysis of the sampled sites showing differences between ecoregional faunas, considering the most important ones. It includes the most important soil- and climate-related variables that explain the ecoregional grouping of the epigeous arthropods.

Table 3. Similarity (Abundance-based Morisita index) between pairs of sites within each ecoregion

C (Morisita)	PU1	PU2	PU3	SITES
MO1		0.432	0.291	PU1
MO2	0.165		0.256	PU2
MO3	0.054	0.241		PU3
SITES	MO1	MO2	MO3	C (Morisita)

MO, Monte de Sierras y Bolsones; PU, Puna.

high contributions to the dissimilarity between ecoregions (of 36.78%, 18.13%, and 17.56%, respectively), and although the diversity of families was greater in the MO, the Histeridae was only recorded in the PU. The Otitidae, Tachinidae, and Syrphidae were recorded only in the PU, whereas the Tephritidae, Chloropidae, and Sciaridae were dipterans responsible for the dissimilarity between ecoregions caused by this order (19.71%, 13.34%, and 12.29%, respectively). Finally, the hymenopteran families Formicidae (68.20%) and Ceraphronidae (16.46%) had very different relative abundances between ecoregions, with a replacement of dominant species of ants between them. The Mutillidae and Chalcididae were recorded only at PU sites, although the MO exhibited a higher species richness of hymenopterans ($S_{Monte} = 95$ vs. $S_{Puna} = 76$).

DISCUSSION

This is the 1st study that compares the diversity of epigeous arthropods in these ecoregions of Argentina, and we collected a high number of species and achieved a rather-complete inventory, with values of > 70% of species predicted by the nonparametric estimators closest to the observed richness, which took into account estimators of the incidence and abundance. The results obtained here show that the community of epigeous arthropods of the PU differs from that of the Monte de Sierras y Bolsones, supporting

the idea that each ecoregion exhibits a particular composition of arthropods.

The PU ecoregion was catalogued by Mihoc et al. (2006) as a complex zone due to relationships of different biotic elements. This is consistent with our results because values of the true diversity of epigeous arthropods indicated that the PU possesses a more-diverse community of them than the Monte de Sierras y Bolsones. The more-diverse plant communities found in the PU could create particular microhabitats that can explain the high diversity of arthropods recorded there. The areas sampled above 3500 m in elevation represented environments characterized by the presence of grasses and bushes, which play a key role in the PU since they increase plant diversity (López and Ortuño 2008). There was greater vegetation cover on the soil, which was a determining factor of the diversity and assemblage of epigeous arthropods recorded in this ecoregion, as shown by the ordering produced by the NMS (Fig. 4). Our results agree with those by De Szalay and Resh (2000), who stated that plant cover can affect the composition and abundance of certain taxa, and influence their distribution, which may have occurred with families in the hyper-diverse orders reported here. Since much is still unknown regarding the diversity of arthropods and the dynamics of these communities in the Argentine PU, this is an important research line to pursue in the future.

The lower diversity reported for the Monte de Sierras y Bolsones supports previous conclusions

Table 4. Complementarity between ecoregions and pairs of sites. The table shows values of the compositional differences between them, for the overall beta diversity (β_{cc}), and its 2 components: species replacement (β_{-3}) and species richness differences (β_{rich})

	MO1-MO2	MO2-MO3	MO3-PU1	PU1-PU2
β_{cc}	0.7865	0.8541	0.8238	0.6907
β_{rich}	0.2253	0.2054	0.2746	0.134
β_{-3}	0.5612	0.6487	0.5492	0.5567
Percent species replacement	71.35%	75.95%	66.67%	79.87%
Species loss	28.65%	24.05%	33.33%	20.13%
	PU2-PU3	MO-PU	MO1-MO3	PU1-PU3
β_{cc}	0.7482	0.7375	0.8304	0.8024
β_{rich}	0.3885	0.1975	0.413	0.479
β_{-3}	0.3597	0.54	0.4174	0.3233
Percent species replacement	48.08%	73.22%	50.26%	40.30%
Species loss	51.92%	26.78%	49.73%	59.70%

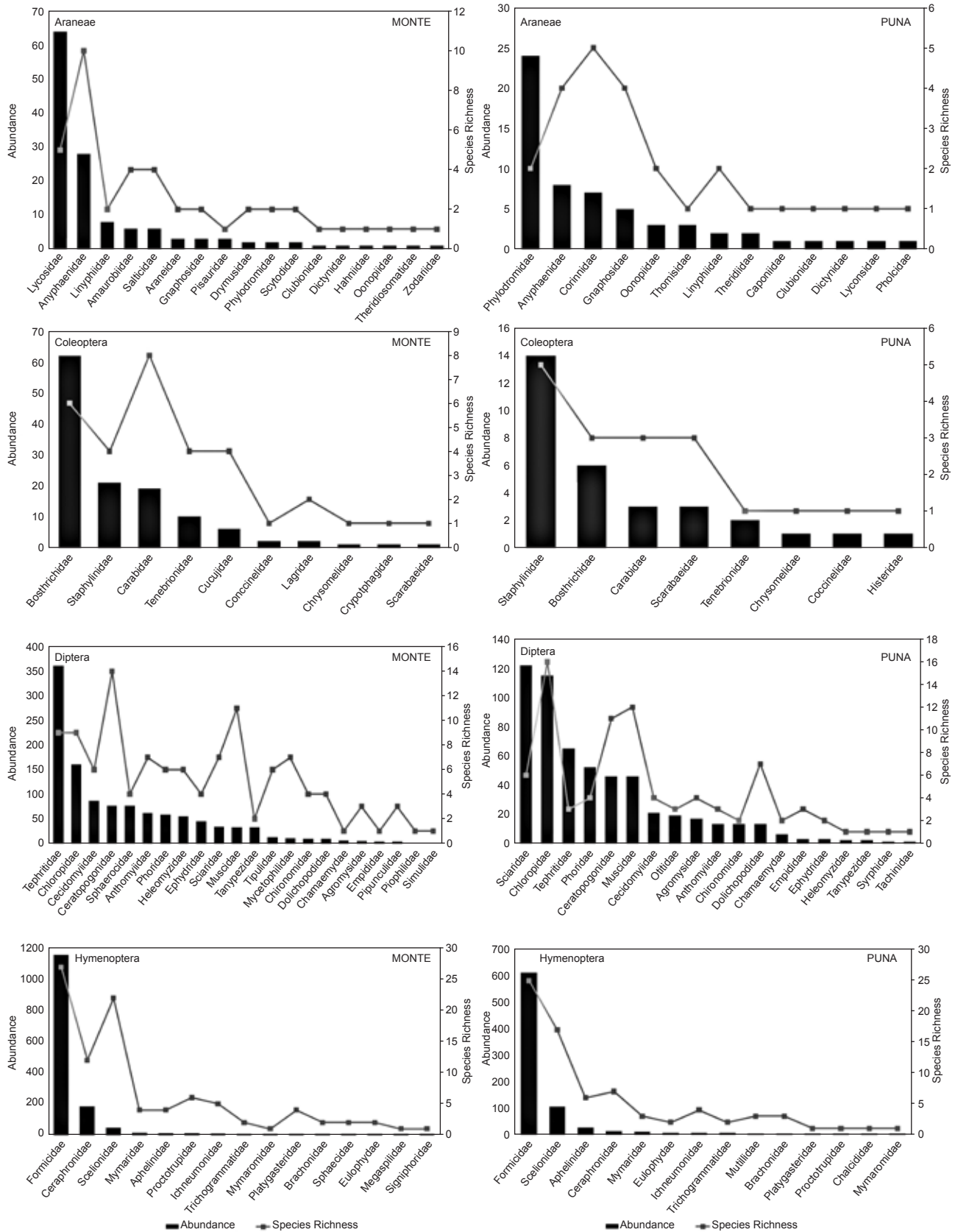


Fig. 5. Abundance and species richness of the most represented epigeous arthropods recorded in this study.

stating that the MO is an impoverished Chaco (Stange et al. 1976), with a decreased diversity compared to the Chaco ecoregion. This was proven for the Monte de Sierras y Llanuras by Roig Juárez et al. (2001) who analyzed the arthropod diversity and compared it to that of the Chaco, although those authors remarked that the percentage of endemism was high, and the evolutionary history of this ecoregion differed from that of the Chaco. Ours is the 1st evaluation of the diversity of arthropods for the Monte de Sierras y Bolsones ecoregion, and it supports the hypothesis by those authors that the alpha diversity of the MO is low.

Shmida et al. (1985) discussed how the structure and functioning of arid ecosystems rest on the complementarity between the oscillatory arid and humid phases that the systems experience. The arid stage is the characteristic, dominant, predictable phase of the system, while the humid stage is a brief, occasional, and unpredictable moment, which most likely exerts a certain effect on the arthropod assemblages in these ecoregions. This was recorded by the NMS, which indicated that annual precipitation was a key climatic factor in communities of epigeous arthropods in the MO, whereas the seasonality of the precipitation was key for PU arthropods, where periods of rainfall briefly occur in summer. Moreover, different soil characteristics also played important roles in assemblages of epigeous arthropods in these ecoregions. In the MO, the presence of leaf litter, rocks, and a higher percentage of sand in the soil was important, while in the PU, the proportion of gravel and the vegetation cover contributed to creating different microenvironments.

Our results showed a decrease in species richness and arthropod abundance in each ecoregion with an increase in elevation. Elevation is an environmental gradient along which organisms shift their life-history strategies (Lu 2011). This supports the idea that significant changes in the physical environment lead to deep alterations in the biological communities along elevational gradients (Dillon et al. 2006), since these and other quantitative and qualitative variables relative to the edaphic component and plant resources (Sánchez and Amat-García 2005) can also determine the variability found in different groups of epigeous arthropods in these ecoregions.

Assemblages at sites within the same ecoregion did not exhibit very high similarity values. Although there was a pool of regional

species shared between the sites sampled in each ecoregion, species replacement between sites was very high. This was likely due to the response of epigeous arthropods to local habitat conditions, since they are not mitigated by their ability to fly. Therefore, those groups with little dispersal ability are more sensitive to local changes than are highly vagile species (Ewers and Didham 2006).

The most important orders in terms of abundance and species richness in this study were the Hymenoptera, Coleoptera, Araneae, and Diptera. Although the latter was not common in pitfall traps and was not part of the epigeous fauna, the water in the traps might have acted as an attractant since this is a limiting resource in desert environments. This same community pattern was reported for other arid environments in Argentina (Gardner et al. 1995, Molina et al. 1999, Lagos 2004, Cheli et al. 2010), and for other regions in the world (Bromham et al. 1999, Seymour and Dean 1999), where the 1st arthropod orders mentioned above were dominant. The richness and abundance of the hyper-diverse groups were markedly lower at PU sites, probably because the species richness of many taxa was generally higher at lower elevations, as shown for trees (Kricher 1997), birds (Terborgh 1977), and insects (Hanski and Niemelä 1990, McCoy 1990, Escobar et al. 2005, Maveety et al. 2011) in tropical environments. This same pattern might be observed in subtropical and temperate environments, which have been studied to a lesser extent.

The high complementarity value obtained between ecoregions led us to believe that both regions are important when planning biodiversity conservation activities. This was supported by the hypothesis that ecoregions function effectively as conservation units at regional scales because they contain similar biological communities and their boundaries roughly coincide with the area over which key ecological processes most strongly interact (Orlans 1993). The high complementarity values recorded among sites within an ecoregion might have been due to differences in elevation, thus representing different habitats within the same ecoregion. These differences may indicate that they are also unique and may need to be considered different conservation units.

In conclusion, we were able to show that each ecoregion possesses a unique epigeous arthropod fauna, and even with a pool of regional species shared between them, there are high beta diversity levels between and within these

ecoregions. Furthermore, different factors related to the heterogeneity of the soil and climate, which are important in arid environments, exerted an effect on the assemblages of epigeous arthropods in these ecoregions.

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