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Structure of ground-dwelling arthropod assemblages in vegetation units of Área Natural Protegida Península Valdés, Patagonia, Argentina

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Abstract
Knowing the spatial variation of insect and arachnid assemblages and their relationship with habitat variables is critical to understand the structure and dynamics of these communities in arid environments. The aim of this paper was to analyze the variation in ground-dwelling arthropod assemblages across three representative vegetation units of the Área Natural Protegida Península Valdés (Patagonia, Argentina). We asked whether environmental differences among representative vegetation units were associated to distinct arthropod assemblages. We selected three plant communities: grass, dwarf-shrub, and shrub steppes, and established three sampling sites within each of them. We measured variables of vegetation structure and soil characteristics and collected the arthropods using 10 pitfall traps per site. We analyzed the structure of arthropod assemblages at both family and ant species taxonomic levels. Each plant community displayed a distinctive assemblage, with differences in diversity, taxa abundance, trophic structure and functional groups of ants. Vegetation variables explained a higher proportion of the variation in the structure of the ground-dwelling arthropod assemblages than the soil variables. This work highlights the importance of the different vegetation units for the conservation of ground-dwelling arthropod biodiversity in Península Valdés.

Introduction

The spatial dynamics of the assemblages and their relationship with environmental variables is a fundamental topic that contributes to a better understanding of the regional importance of different habitat types for animal communities (Battisti et al. 2016). The environmental characteristics of each habitat can lead to a differentiation of the assemblages at local scale, contributing in this way to a higher

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regional diversity (González-Reyes et al. 2017; Cheli 2009). Therefore, knowing this information is a valuable tool for the development of management plans and conservation strategies (Samways 1994; Gessé et al. 2014; Staubus et al. 2015).

Arthropods are abundant and diverse in drylands because they are more tolerant to low water availability and extreme thermal conditions than other animal groups (Andersen et al. 2004; Cheli et al. 2010; Baldi et al. 2017). At the same time, insects and arachnids are essential for several ecological processes including nutrient cycling, pollination, and seed dispersal, and contribute to maintain soil structure and fertility (Prather et al. 2013). They constitute both biological controls of other organisms and sources of food for other taxa (Scudder 2009). Thus, arthropods control the flow of critical resources and modify the structure and function of desert ecosystems (Whitford 2000).

Both vegetation and soil characteristics are important determinants of arthropod assemblages (Schowalter 2016). Vegetation provides shelter, buffering climatic variations, and is a source of food for phytophages and detritivores (Li et al. 2013; González-Reyes et al. 2017). Moreover, edaphic features like coarse soil texture and low compaction are also

important for ground-dwelling arthropods, facilitating the construction of nests and affecting microclimatic conditions (Boulton et al. 2005; Farji-Brener et al. 2008; Ríos-Casanova et al. 2015).

These habitat variables, in turn, differ among vegetation types typical of arid and semiarid ecosystems. For instance, in shrub steppes vegetation is typically distributed in patches of high plant cover immersed in a matrix of bare soil and sparse grass bunches (Bisigato and Bertiller 1997; Pazos et al. 2010). Conversely, grass steppes are dominated by perennial-grass species distributed in a spatial pattern of finer grain than shrub steppes, resulting in a more homogeneous distribution of the plant cover at the stand scale (Gibson 2009). Other vegetation types may characterize regional floras, such as dwarf-shrub steppes dominated by clonal species colonizing extensive fields of sand dunes (Bertiller et al. 2017). In this sense, the heterogeneity of vegetation units may affect regional ground-dwelling arthropod assemblages via variability in vegetation and soil habitat variables. Thus, it is expected that distinctive arthropod assemblages could be identified across habitat types, providing critical information for the conservation of regional biodiversity (Staubus et al. 2015). However, the knowledge about the effect of environmental variables on the structure of arthropod assemblages is relatively scarce in arid and semiarid ecosystems (Bestelmeyer and Wiens 2001; Tews et al. 2004; Mazía et al. 2006; Feng et al. 2015).

The Area Natural Protegida Península Valdés (henceforth Península Valdés), a UNESCO Natural World Heritage Site (1999) and Biosphere Reserve (2014), is located in north-eastern Patagonia, Argentina. It is one of the biggest arid protected areas of this country and possess a series of singular environmental characteristics. Particularly, the terrestrial environments of Peninsula Valdés are characterized by the occurrence of a heterogeneous mosaic of landforms and associated vegetation types (Bertiller et al. 2017; Bouza et al. 2017a). The vegetation units of Península Valdés were defined by Bertiller et al. (2017) based on vegetation, landform and soil characteristics. Shrub, dwarf-shrub and grass steppes are the main units and they establish on a mosaic of either Plio-Pleistocene soils rich in clay/silt content or Holocene stabilized aeolian deposits (Bouza et al. 2017b). These features make Península Valdés an excellent area to study the relationship between arthropod assemblages and natural habitat variation in arid lands. Our working hypotheses were: (1) the structure of the community of ground-dwelling arthropods in Península Valdés changes across vegetation units, and (2) this variation is mostly explained by soil and vegetation habitat variables. Therefore, it was expected to find distinctive assemblages of insects and arachnids for each vegetation unit, and that this variability would be highly correlated to soil and vegetation variables differing among the vegetation units.

Materials and methods

Study area

Península Valdés is located in northeastern Patagonia, Argentina, between 42°05′–42°53′S and 63°35′–65°04′W (Fig. 1a). It is a 3600 km^2 protected area with sustainable resource management, where extensive sheep farming is the main economic activity in the ranches of the region (Cheli et al. 2016). Its climate is characterized by a precipitation gradient that increases in the west-east direction, with an annual average of 218 mm at the isthmus and 260 mm on the east coast. The inter-annual variation ranges mostly within 100–300 mm (Coronato et al. 2017).

This study was carried out in the Reserva de Vida Silvestre San Pablo de Valdés (henceforth San Pablo), located in the southwest portion of Península Valdés (Fig. 1a), a 73.6 km^2 strict wildlife reserve excluded from livestock grazing since 2005 (Arias et al. 2017). San Pablo is particularly appropriate for this study because their limits enclose a complex mosaic of different vegetation units representative of Península Valdés vegetation (Bertiller et al. 2017; Pazos et al. 2017).

We studied arthropod assemblages in the three most representative plant communities of San Pablo, which in turn are representative of three vegetation units of Peninsula Valdés displaying contrasting vegetation and soil characteristics (Bertiller et al. 2017; Pazos et al. 2017): (1) shrub steppes (SS), which are mainly composed of shrubs of *Chuquiraga avellanedae* Lorentz, *Lycium chilense* Miers ex Bert, *Schinus johnstonii* Barkley, *Menodora robusta* (Benth.) A. Gray, and *Acantholippia seriphioides* (A. Gray) Mold, associated with perennial grasses such as *Nassella tenuis* (Phil.) Barkworth, *Piptochaetium napostaense* (Speg.) Hack, *Poa ligularis* Nees ex Steud, and *Pappostipa speciosa* (Trin. & Rupr.) Romasch. This community establishes on flat reliefs with predominance of a xeric Natrargids–Haplocalcids soil complex, characterized by a clayey–loamy upper horizon (Rostagno et al. 2017), and corresponds to the vegetation unit 5 defined in Bertiller et al. (2017). (2) Dwarf-shrub steppes (DS), predominantly composed by *Hyalis argentea* D. Don ex Hook. & Arn. var. *latisquama* Cabrera accompanied by grasses such as *N. tenuis* and *Poa lanuginosa* Poir. This plant community dominates on sand deposits from the coastal sector (Alvarez et al. 2010) and corresponds to vegetation unit 6 in Bertiller et al. (2017). (3) Grass steppes (GS), which are dominated by the perennial grasses *Sporobolus rigens* (Trin.) Desv. and *N. tenuis*, and develop on xeric Torripsamments characterized by sandy mantles with varying thickness and a uniform landscape of slight undulations (Rostagno et al. 2017). This plant community corresponds to vegetation unit 1 in Bertiller et al. (2017).
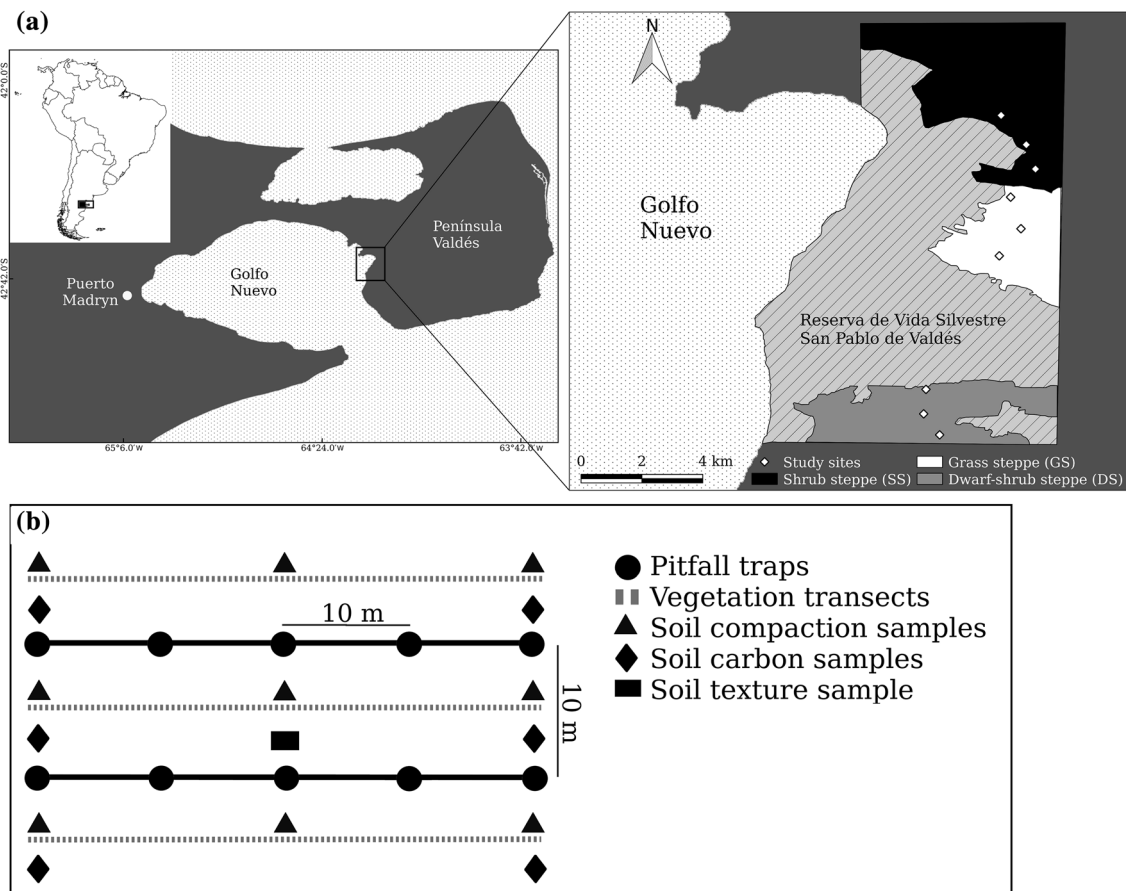
Fig. 1 a Location of the study area, plant communities and sampling sites; **b** schematic diagram of a sampling site detailing the number of vegetation transects, pitfall traps, and samples of the measured soil variables

Within each plant community, we randomly selected three sampling sites (n = 9) separated from each other by a minimum distance of 800 m (Fig. 1a). The three plant communities were released from livestock grazing at the same time in 2005, and since then no other disturbances were introduced in the area. This was essential for our study as we were aimed at assessing the regional variability in arthropod assemblages associated only with environmental heterogeneity (vegetation units). The effects of grazing disturbance on vegetation and arthropod assemblages were evaluated in previous studies (Cheli 2009; Cheli et al. 2016).

Arthropod sampling

We used pitfall traps to collect ground-dwelling insects and arachnids according to Cheli and Corley (2010), who optimized this arthropod sampling technique to this study area. We established 10 traps (12 cm diameter and 12 cm depth) placed within each site along two transects of 50 m with 10 m distance between traps (10 traps × 3 sites × 3 plant communities = 90 traps) and oriented in east–west direction (Fig. 1b). Each pitfall trap was filled with 300 ml

of 30% ethylene glycol and remained active for 15 days during the summer (February 2010), which coincides with the period of highest activity of arthropods in the region (Sola et al. 2016).

We determined the specimens at the family level using binocular stereomicroscopes (ZEISS Stemi SV6 and Nikon SMZ-745), taxonomic keys (Triplehorn et al. 2005; Roig-Juñent et al. 2014) and reference material deposited in the Entomological Collection of the IPEEC (CCT CONICET-CENPAT). We classified all identified families of arthropods (except the ants) into predators, herbivores, and detritivores according to Triplehorn et al. (2005). The ants were determined to species/morpho-species levels based on Fernández (2003) and by consulting specialists. We analyzed these insects separately from the rest of arthropods due to their large dominance and importance in the arthropod assemblages of the region (Cheli et al. 2010; Baldi et al. 2017). Finally, we assigned the ants to functional groups based on Bestelmeyer and Wiens (1996), Hoffmann and Andersen (2003), Andersen and Majer (2004) and Cheli 2009. The assignment of families and ant species to trophic guilds and functional groups are shown in the second section of results.

Analyses were conducted using the pooled data from the 10 traps per site.

Environmental characterization of plant communities

In relation to hypothesis 2, we measured vegetation and soil habitat variables in the three plant communities. We used the modified Point Quadrat method (Passera et al. 1986) to assess floristic composition and vertical complexity of vegetation, at sampling intervals of 1 m. Within each site, we delimited three linear transects 50 m long with the same orientation as arthropod sampling transects (Fig. 1b). At each sampling point along transects, we recorded the intercepted species by a vertically disposed pin. We also registered the total number of plant interceptions, at intervals of 25 cm in height, along the pin. We calculated the number of intercepts in three height intervals: 0–25, 25–50 and 50–75 cm to evaluate vertical complexity. At ground level, we registered the presence of biological soil crusts (association of bryophytes, lichens, cyanobacteria, fungus, algae and soil particles), bare soil, desert pavement, and litter.

To assess soil organic carbon content, we extracted six soil samples at each site using a core sampler of 7 cm diameter and 3 cm depth. Then, we determined the organic carbon content by the Walkley and Black method (1934). In order to evaluate the texture of the surface soil, we took a sample in the center of each site using a core sampler of 10 cm diameter and 10 cm depth. Subsequently, the percentage of sand, silt, and clay fractions was determined using the hydrometer method (Bouyoucos 1965). Finally, we obtained nine soil compaction records on each site using a cone penetrometer (Davidson 1965). Each soil compaction estimation was expressed in kPa through the specific calibration curve (see Cheli et al. 2016). All habitat variables were averaged per site, except soil texture data (one measurement per site). The vegetation variables was expressed as cover (percentage), except for species richness (number of plant species) and vertical complexity (number of interceptions per hight interval).

Statistical analysis

To test hypothesis 1, we assessed the variation of arthropod assemblages among plant communities at two main taxonomic levels: arthropod families and ant species. Firstly, we inspected the variation in the structure of arthropod assemblages among plant communities by using a nonmetric multidimensional scaling (NMDS) (Legendre and Legendre 2012) based on the Bray–Curtis similarity matrix calculated from the squared-root of abundances. Differences in the structure of the assemblages detected by NMDS were tested by a non-parametric one-way analysis of similarity

(ANOSIM). The ANOSIM's R statistic is a tool to detect differences between groups (Clarke and Warwick 2001). A value of R statistic close to 1 suggests dissimilarity among groups, whereas an R value near 0 implies no difference among groups (Legendre and Legendre 2012). Due to the iterative process to build the pair-wise tests in ANOSIM, when there are only three replicates within groups (plant communities in our case), their associated p values will be always over 0.1 (Clarke and Warwick 2001; Jung et al. 2008). In this case, the R statistic is more important than the significance level since it gives an absolute measure (Clarke and Warwick 2001), so that we only have considered the R value to identify differences in pair-wise tests.

To test for differences in the abundance of dominant families and ant species with abundances higher than 1% (see second section of results), we used generalized linear models (GLM) with Poisson (link function: Log) error distribution (Crawley 2013) and plant community as fixed effect. We check the dispersion of the models (*dispersiontest* function) and, following Zuur et al. (2009), we used the negative binomial distribution (link function: logit) for that models with high overdispersion. We used the same structure of GLM models to analyze the variation in the abundance of trophic guilds and functional groups of ants. To assess differences in habitat variables among plant communities, we performed GLM with Gaussian distribution (link function: identity) and plant community as fixed effect. We evaluated the statistical significance of each model by comparing them against a null model lacking fixed effects through the *anova* function in R (Crawley 2013). Finally, we performed pairwise differences among plant communities using the Tukey HSD test (Hothorn et al. 2008).

To compare the richness and diversity of the assemblages among plant communities, we used Hill numbers and rarefaction-extrapolation curves (Chao et al. 2014). The significance of the differences is evaluated by means of the overlapping of the confidence intervals. This approach is advantageous since the bias due to the dependence between the diversity estimates and sample size is lower (Colwell et al. 2012; Chao et al. 2014). For these analyses, we added the abundance of families or ants species of the three sites per plant community. We derived two indexes from Hill numbers: q = 0 (richness) and q = 1 (the exponential of Shannon entropy) (Jost 2006). We extrapolated each curve to the double of the overall abundance (sample size) and estimated the 95% confidence intervals through the bootstrap method (100 replicates) (Hsieh et al. 2016).

To test hypothesis 2, changes in the structure of arthropod assemblages among plant communities were related to habitat variables using distance-based redundancy analysis (db-RDA), an alternative to the classical RDA that can be used with distance measures more appropriate for community data (e.g. Bray–Curtis) (Legendre and Legendre

2012). We performed the db-RDA on the basis of the same data used for the NMDS (Bray–Curtis similarity matrix of square-root of abundances). We selected habitat variables of recognized biological importance for ground-dwelling arthropods (Bestelmeyer and Wiens 2001; Hoffmann and Andersen 2003; Boulton et al. 2005; Mazía et al. 2006; Li et al. 2013; Magoba et al. 2015; Ríos-Casanova et al. 2015). At the same time, highly collinear variables were removed computing the variance inflation factors (VIF > 10; Legendre and Legendre 2012). We standardized the habitat variables before analyses (Legendre and Legendre 2012). Finally, we performed a variation partitioning analysis (VARPART; Borcard et al. 2011; Legendre and Legendre 2012) via db-RDA to assess the relative importance of soil and vegetation variables on the changes in the structure of assemblages at both family and ant species levels. We used Monte Carlo permutations to evaluate the statistical significance for the overall test and each testable fraction of the variation (Borcard et al. 2011; Oksanen 2015).

Most of the graphical and statistical analyses were conducted using 'stats', 'AER', 'MASS', 'vegan', 'iNEXT' and 'ggplot2' packages for R (Venables and Ripley 2002; Hothorn et al. 2008; Wickham 2009; R Core Team 2015; Hsieh et al. 2016; Oksanen et al. 2017). ANOSIM and post hoc tests were performed with PAST software (Hammer et al. 2001).

Results

General characterization of the ground-dwelling arthropod assemblage

From a total of 18,189 collected arthropod specimens, ants (Hymenoptera: Formicidae) were the most abundant family with 16,973 individuals. The remaining 1216 specimens belonged to one out of 41 taxa, being Machilidae (20.72%), Mummucidae (16.69%), Mutillidae (10.94%) and Tenebrionidae (10.36%) the dominant families (Table 1). A total of 18 ant species/morphoespecies were collected, with *Forelius* sp1 (25,41%), *Dorymyrmex wolffhuegeli* Forel (13.2%), *Solenopsis geminata* group (13.2%) and *Camponotus punctulatus* Mayr (11.3%) as dominant in the ant assemblage (Table 2).

The assignment of the families and ants species to the trophic guilds and functional groups is shown in Tables 1 and 2, respectively. Predators were the most abundant trophic guild at family level (46.13%), followed in numerical importance by detritivores (38.63%) and herbivores (15.24%) (Table 1). At the same time, three functional groups dominated the assemblage of ants in similar proportions: generalized Myrmicinae (28.63%), hot-climate specialists (25.58%) and opportunists (25.25%) (Table 2).

Arthropod assemblages among plant communities

The NMDS ordination and the ANOSIM analysis showed that the structure of the arthropod assemblages was significantly different among plant communities for both taxonomic levels (arthropod families and ant species) (Fig. 2; Table 3). Meanwhile, all the R values for the three pair-wise comparisons were close to 1 (ranged from 0.74 to 1), indicating that each plant community was associated to a distinctive assemblage (Table 3).

Abundance of arthropod families and ant species

In general, the abundance of the dominant taxa (families and ant species with abundances higher than 1%), varied significantly among plant communities. The abundance of Machilidae and Lycosidae was the highest in the dwarf-shrub steppe (DS). Mummucidae dominated in shrub (SS) and grass (GS) steppes, whereas Tenebrionidae and Gryllidae were more abundant in DS and GS communities. Mutillidae and Blaberidae dominated in GS, while Liposcelididae did so in SS. Finally, the abundances of Elateridae, Bothriuridae, Salticidae, Ammotrechidae, and Theriididae were not significantly different among plant communities (Fig. 3a; Table 4).

In relation to the ant species, *D. wolffhuegeli* and *Forelius* sp1 were more abundant in DS, whereas *Dorymyrmex ensifer* Forel was least abundant in this plant community (Fig. 3b; Table 4). The abundances of *S. geminata* group and *Pheidole bergi* Mayr were greater in SS. *Dorymyrmex exsanguis* Forel, *Acromyrmex lobicorni*s Emery, *Acromyrmex* sp1 and *Solenopsis schilleri* Santschi dominated in the communities DS and GS. Finally, the abundance of *C. punctulatus* and *Pheidole* sp1 did not significantly differ among plant communities.

Abundance of trophic guilds and functional groups of ants

Abundance of trophic guilds also differed among plant communities. Predators and herbivores increased as SS < DS < GS, whereas detritivores showed a peak of abundance in DS (Fig. 4a; Table 4). Meanwhile, the group of generalized Myrmicinae was more abundant in SS than both DS and GS, while hot-climate specialists did so in DS. Opportunists, Attini and cryptics dominated in DS and GS (Fig. 4b; Table 4).

Richness and diversity of arthropod assemblages

The confidence intervals of the first Hill number (q = 0) of the three plant communities overlapped each other for both taxonomic levels, indicating not significant differences among plant communities in both richness of arthropod

Table 1 Number of individuals (N) and relative abundance (expressed as percentage) of ground-dwelling arthropod families in dwarf-shrub steppe (DS), grass steppe (GS) and shrub steppe (SS)

Order	Family	DS	GS	SS	Total	%	Trophic guild
Araneae	Amphinectidae	0	2	3	5	0.41	Predator
Araneae	Gnaphosidae	3	5	1	9	0.74	Predator
Araneae	Linyphiidae	1	2	0	3	0.25	Predator
Araneae	Lycosidae	35	20	15	70	5.76	Predator
Araneae	Philodromidae	0	0	1	1	0.08	Predator
Araneae	Prodidomidae	0	1	2	3	0.25	Predator
Araneae	Salticidae	10	8	3	21	1.73	Predator
Araneae	Sicariidae	0	0	2	2	0.16	Predator
Araneae	Sparassidae	0	0	1	1	0.08	Predator
Araneae	Theriididae	12	3	0	15	1.23	Predator
Araneae	Thomisidae	4	0	0	4	0.33	Predator
Araneae	Trachelidae	1	0	0	1	0.08	Predator
Araneae	Zodariidae	1	0	3	4	0.33	Predator
Archaeognatha	Machilidae	197	4	51	252	20.72	Detritivore
Blattodea	Blaberidae	7	24	6	37	3.04	Detritivore
Coleoptera	Carabidae	1	4	0	5	0.41	Predator
Coleoptera	Curculionidae	0	3	7	10	0.82	Herbivore
Coleoptera	Elateridae	16	29	0	45	3.7	Herbivore
Coleoptera	Histeridae	1	2	0	3	0.25	Predator
Coleoptera	Scarabaeidae	11	1	0	12	0.99	Detritivore
Coleoptera	Staphylinidae	5	4	3	12	0.99	Predator
Coleoptera	Tenebrionidae	69	54	3	126	10.36	Detritivore
Collembola	Sminthuridae	7	3	0	10	0.82	Detritivore
Hemiptera	Geocoridae	1	1	0	2	0.16	Predator
Hemiptera	Lygaeidae	0	0	4	4	0.33	Herbivore
Hemiptera	Reduviidae	1	3	3	7	0.58	Predator
Hemiptera	Rhyparochromidae	0	2	0	2	0.16	Herbivore
Hymenoptera	Mutillidae	45	72	16	133	10.94	Predator
Isoptera	Kalotermitidae	1	2	0	3	0.25	Herbivore
Mantodea	Mantidae	2	0	0	2	0.16	Predator
Orthoptera	Acrididae	7	1	3	11	0.9	Herbivore
Orthoptera	Gryllidae	34	62	3	99	8.14	Herbivore
Orthoptera	Proscopidae	0	0	3	3	0.25	Herbivore
Pseudoscorpiones	Indeterminate family	0	3	3	6	0.49	Predator
Psocoptera	Liposcelididae	1	5	19	25	2.06	Detritivore
Scorpiones	Bothriuridae	14	13	6	33	2.71	Predator
Siphonaptera	Indeterminate family	0	2	1	3	0.25	Predator
Solifugae	Ammotrechidae	6	10	2	18	1.48	Predator
Solifugae	Mummucidae	32	99	72	203	16.69	Predator
Thysanoptera	Phlaeothripidae	3	2	5	10	0.82	Herbivore
Thysanura	Indeterminate family	0	0	1	1	0.08	Detritivore

The assignment of taxa to each trophic guilds is also indicated

families and richness of ant species. Moreover, these results showed that the assemblages were adequately sampled (curves reaching an asymptote) (Fig. 5a, b). The exponential of Shannon entropy (q=1) differed among plant communities. The diversity of families was higher in GS that in DS (Fig. 5c), while SS showed intermediate values. The grass steppes displayed the highest diversity of ants (Fig. 5d).

Environmental characterization of plant communities

The three plant communities contrasted in several habitat variables. The shrub steppes had higher proportion of silt–clay content and higher soil compaction than the other two communities. Furthermore, SS exhibited higher number

Table 2 Abundance (number of individuals) of ant species in dwarf-shrub steppe (DS), grass steppe (GS) and shrub steppe (SS)

	DS	GS	SS	Total	%	Functional group
Acromyrmex lobicornis Emery	641	205	1	847	4.99	Attini
Acromyrmex sp1	100	56	14	170	1	Attini
Brachymyrmex patagonicus Mayr	36	72	3	111	0.65	Cryptic
Camponotus punctulatus Mayr	603	793	522	1918	11.3	Subordinate Camponotini
Dorymyrmex ensifer Forel	128	504	307	939	5.53	Opportunist
Dorymyrmex exsanguis Forel	373	547	68	988	5.82	Opportunist
Dorymyrmex silvestrii Gallardo	105	1	13	119	0.7	Opportunist
Dorymyrmex wolffhuegeli Forel	1325	562	353	2240	13.2	Opportunist
Forelius grandis Forel	2	1	4	7	0.04	Hot-climate specialists
Forelius sp1	2810	394	1114	4318	25.44	Hot-climate specialists
Forelius sp2	1	0	7	8	0.05	Hot-climate specialists
Pheidole aberrans Mayr	1	2	70	73	0.43	Generalized Myrmicinae
Pheidole bergi Mayr	30	427	1129	1586	9.34	Generalized Myrmicinae
Pheidole sp1	569	499	180	1248	7.35	Generalized Myrmicinae
Pheidole spininodis Mayr	0	3	15	18	0.11	Generalized Myrmicinae
Pogonomyrmex rastratus Mayr	0	8	0	8	0.05	Hot-climate specialists
Solenopsis geminata group	140	333	1461	1934	11.39	Generalized Myrmiciae
Solenopsis schilleri Santschi	112	314	15	441	2.6	Cryptic

The total number of individuals, the relative abundance (expressed as percentage) and the functional groups are also indicated

of plant species, shrub cover, proportion of desert pavement, number of interceptions in the 50–75 cm vertical stratum and bare soil cover (although this last variable was marginally significant) (Table 5). The grass steppes displayed the highest canopy cover, mainly concentrated in the lowest vertical stratum, and displayed higher percentage of sand and litter cover along with DS. Furthermore, DS showed the highest cover of dwarf-shrubs, intermediate cover of canopy and grasses, and a lower number of plant interceptions in the lower stratum than GS. Finally, the organic carbon content in the top soil and the cover of biological soil crusts did not significantly differ among plant communities (Table 5).

Relationship between arthropod assemblages and environmental variables

According to the set of criteria for selection of habitat variables, we included a subset of two soil (percentage of sand and soil compaction) and three vegetation variables (cover of grass, shrubs and proportion of bare soil) in the final models. The global models of db-RDA explained a significant proportion of the variation in the structure of the arthropod assemblages at both family (adjusted $R^2 = 51\%$, pseudo-$F = 2.66$, $p = 0.003$) and ant species level (adjusted $R^2 = 63\%$, pseudo-$F = 3.73$, $p = 0.001$). Twenty-one percent of the variation in arthropod families was explained by vegetation variables and only 8% was explained by soil variables, but this last fraction was not statistically significant (Fig. 6a). For the ant species assemblage, a high significant proportion of the

variation was explained exclusively by vegetation variables (44%), while soil variables had a unique contribution of 14% (marginally significant) (Fig. 6b).

Discussion

The assemblage of ground-dwelling arthropods found in this work was dominated by ants, representing more than 90% of the collected individuals. In addition, predators dominated the trophic structure. These results are in accordance with previous studies in Península Valdés (Cheli et al. 2010; Baldi et al. 2017). Furthermore, in accordance with our hypothesis, this study demonstrate that variation in the structure of the arthropod assemblage is associated with variability in vegetation and soil habitat variables, as we found distinct assemblages, at two different taxonomic levels, for three representative and contrasting vegetation units of Península Valdés. These results strongly suggest that the insect and arachnid assemblages of this region are heavily affected by the particular spatial configuration of the vegetation mosaic at intermediate spatial scales, as have been found in other regions (Schaffers et al. 2008; Cheli 2009; Werenkraut and Ruggiero 2012; Gessé et al. 2014; Staubus et al. 2015).

The higher diversity of arthropod observed at family level in grass and shrub steppes was mainly associated with changes in arthropod dominance that increased the evenness among taxa, as the richness of families was similar among plant communities (Magurran 2004).

Fig. 2 Non-metric multidimensional scaling ordination (NMDS) of the nine study sites based on **a** arthropod families (stress = 0.05) and **b** ant species (stress = 0.03)

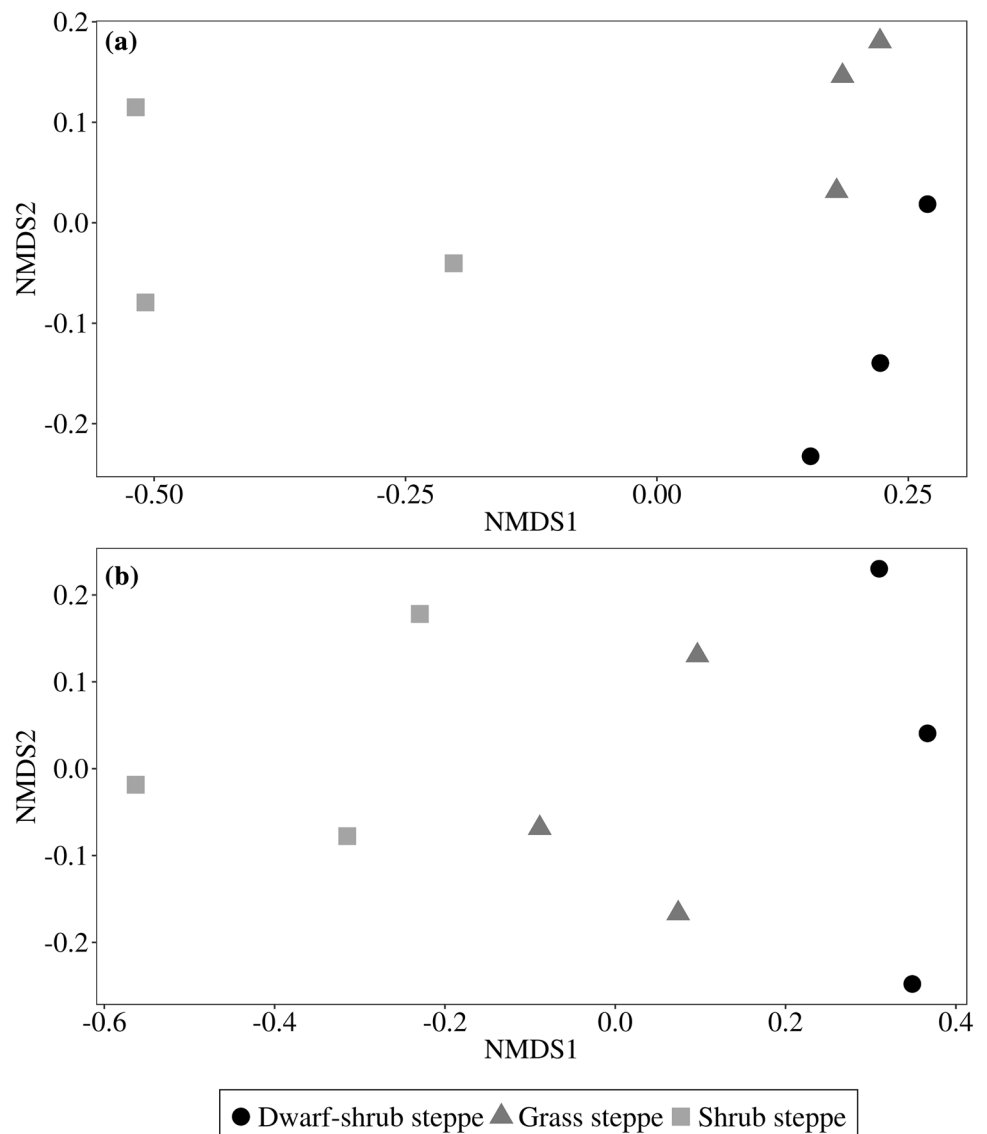● Dwarf-shrub steppe ▲ Grass steppe ■ Shrub steppe

Table 3 Results of the Analysis of similarity (ANOSIM) for the comparisons of the assemblages of families and ant species among plant communities (global and pair-wise comparisons)

	Families		Ant species	
	R	p	R	p
Global	0.802	0.006	0.884	0.005
DS vs. GS	0.740	0.357	0.852	0.294
DS vs. SS	1	0.387	1	0.357
GS vs. SS	0.963	0.51	0.852	0.369

The degree of dissimilarity (R) and significance level (p) are indicated

Furthermore, we found that habitat variables related to vegetation explained a significant percentage of the variation in the assemblages of families. This finding is important as large differences in soil characteristics also exist among the studied plant communities (Rostagno et al. 2017). The highest grass cover found in the grass steppes (which represent about 99% of the canopy cover in this plant community) could determine a more favorable microclimate to insects and arachnids by a reduction in soil surface temperature and higher conservation of soil moisture (de los Santos et al. 2002; Farji-Brener et al. 2008; Cheli 2009; Chenchouni et al. 2015), which could explain the high diversity of families. In the case of the shrub steppes, the heterogeneous spatial structure of vegetation associated with shrub patches immersed in a matrix of bare soil and sparse grasses may offer a large variety of niches for arthropod families (Schowalter 2016). Besides, plant species richness was the highest in this plant community, which could represent a higher diversity of food resources and microhabitats for arthropods, increasing the
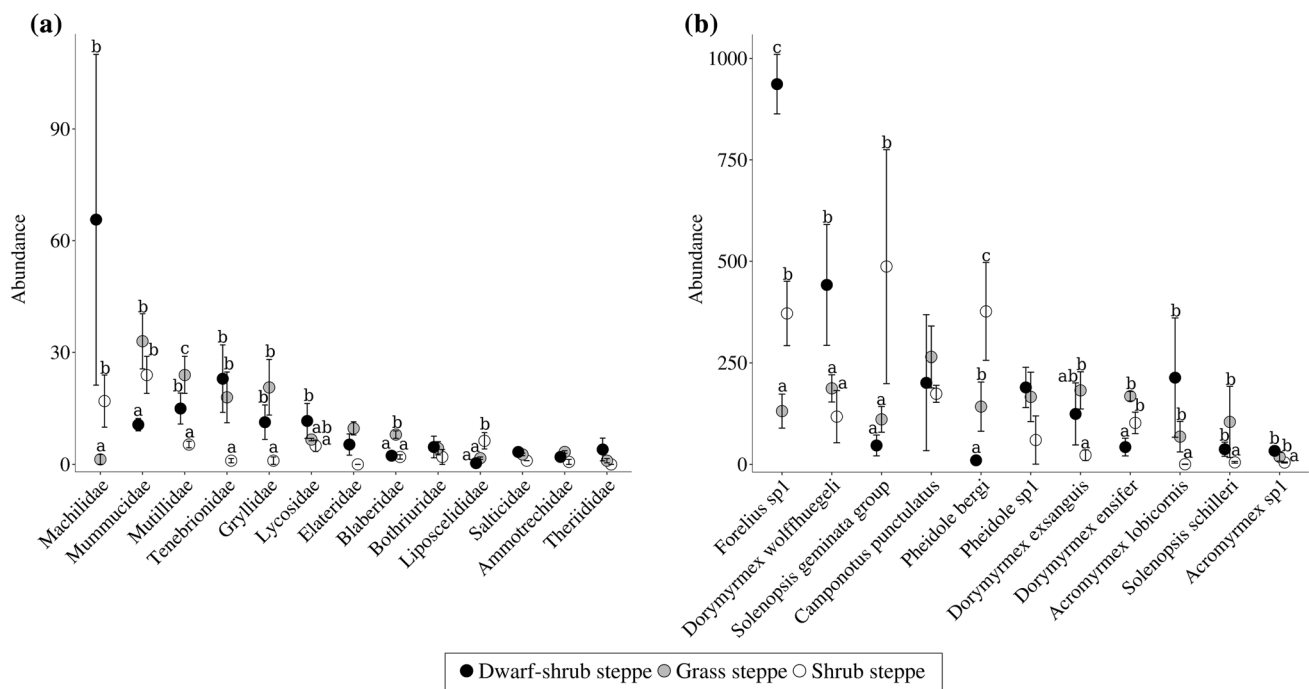
Fig. 3 Abundance (mean ± SE) of the **a** main arthropod families and **b** species of ants in the three plant communities. Significant differences are indicated by different letters

diversity of these organisms (Siemann 1998; Wenninger and Inouye 2008).

The lower diversity of arthropod families found in dwarf-shrub steppes was related to a marked dominance of a few taxa (e.g. Machilidae). According to Pazos et al. (2017) in long-term vegetation monitoring sites in the region, we found high cover of litter in the dwarf-shrub steppe, but with significantly lower grass and canopy cover than the grass steppe. Although the regional knowledge about the ecology of Machilidae is null and more specific analyses are needed to disentangle the probable causes, this pattern in the structure of vegetation may benefit Machilidae through increasing food availability and more favorable microenvironmental conditions.

In accordance with the results of Cheli et al. (2010) in other steppes of Península Valdés, we registered 18 ant species in our study area. This species richness well within the range of those reported for other arid regions of Argentina: ~ 30 for the central Monte Desert (Claver et al. 2014) and ~ 8 for the steppes of north-western Patagonia (Farji-Brener et al. 2002). Congruent with the patterns found for the family level, the diversity of ant species was also higher in the grass steppe. Considering the high importance of competitive interactions in the structuring of ant assemblages (Farji-Brener et al. 2002), the lower abundance in the grass steppes of those ant species that dominate the assemblages in shrub (e.g. *S. geminata* group and *P. bergi*) and dwarf-shrub steppes (e.g. *Forelius* sp1 and *D. wolffhuegeli*) could

favor the coexistence of species with a more homogeneous abundance distribution, leading to an increase in the evenness and diversity of ant assemblage in the grass steppes.

An important proportion of variation among the ant assemblages was explained exclusively by vegetation variables. This is not surprising since vegetation characteristics are one of the most important factors that determine the ant distribution at different spatial scales (Gotelli and Ellison 2002; Cheli et al. 2010; Chen et al. 2015). The higher proportion of grasses and the more closed canopy in the grass steppes could represent both greater resource availability for ants (Ríos-Casanova et al. 2015) and more favorable microclimate conditions (Chen et al. 2015). At the same time, in contrast with the analysis at family level, we found that soil variables explained an important variation among ant species assemblages. Less compacted soils of coarse granulometry in grass steppes may be particularly beneficial for ant species, facilitating the construction of tunnels and chambers (Boulton et al. 2005). This argument becomes more relevant especially in drylands, where most species of ants nest underground (Bestelmeyer and Wiens 2001). In conclusion, the combination of both vegetation and soil characteristics in grass steppes could be correlated to higher diversity of ants.

Grass steppes showed the highest abundance of both herbivores and predators arthropod trophic guilds. Perennial grasses are characterized by high relative concentration of nitrogen and low content of secondary metabolites (e.g.,

Table 4 Mean (SE) of abundance of the dominant taxa (families and ant species with abundances higher than 1%), trophic guilds, and ant functional groups in dwarf-shrub steppe (DS), grass steppe (GS), and shrub steppe (SS)

	DS	GS	SS	χ^2	p
Abundance of families					
Ammotrechidae*	2.00 (0.58)	3.33 (0.33)	0.67 (0.67)	5.82	0.05
Blaberidae*	2.00 (1.00)[a]	6.67 (1.86)[b]	2.00 (0.58)[a]	15.38	<0.001
Bothriuridae[#]	4.67 (2.91)	4.33 (1.76)	2.00 (2.00)	0.83	0.66
Elateridae*	5.33 (2.85)	9.67 (1.76)	0.00 (0.00)	3.65	0.16
Formicidae[#]	2325.33 (177.38)[b]	1573.67 (101.69)[a]	1758.67 (258.99)[a]	12.18	0.002
Gryllidae[#]	11.33 (4.63)[b]	20.67 (7.42)[b]	1.00 (1.00)[a]	17.73	<0.001
Liposcelididae*	0.33 (0.33)[a]	1.67 (0.33)[a]	6.33 (2.19)[b]	21.97	<0.001
Lycosidae*	11.67 (6.67)[b]	6.67 (0.33)[ab]	5.00 (1.53)[a]	8.96	0.01
Machilidae[#]	65.67 (44.38)[b]	1.33 (1.33)[a]	17.00 (7.00)[b]	19.93	<0.001
Mummucidae*	10.67 (1.67)[a]	33.00 (7.37)[b]	24.00 (4.93)[b]	36.36	<0.001
Mutillidae*	15.00 (4.16)[b]	24.00 (4.93)[c]	5.33 (0.88)[a]	38.56	<0.001
Salticidae*	3.33 (0.88)	2.67 (0.33)	1.00 (0.00)	4.19	0.12
Scarabaeidae*	6.33 (1.33)[b]	1.33 (0.67)[ab]	0.00 (0.00)[a]	29.28	<0.001
Tenebrionidae[#]	23.00 (9.02)[b]	18.00 (6.81)[b]	1.00 (0.58)[a]	22.04	<0.001
Theriididae*	4.00 (3.06)	1.00 (0.58)	0.00 (0.00)	1.79	0.41
Trophic guilds					
Detritivore[#]	100 (49.79)[b]	31.33 (9.06)[a]	26.67 (8.84)[a]	11.33	0.003
Herbivore*	20.33 (6.94)[b]	39.33 (7.31)[c]	3.00 (1.00)[a]	111.13	<0.001
Predator*	58.33 (8.01)[b]	88.33 (10.99)[c]	42.00 (2.31)[a]	52.02	<0.001
Abundance of ant species					
Acromyrmex lobicornis[#]	13 (21.66)[b]	45.67 (48.95)[b]	0.33 (0.58)[a]	15.88	<0.001
Acromyrmex sp1[#]	16.67 (22.03)[b]	29.67 (20.5)[b]	4.67 (2.31)[a]	14.82	<0.001
Camponotus punctulatus[#]	111.33 (83.07)	82.67 (85.62)	174 (36.37)	0.43	0.81
Dorymyrmex ensifer[#]	104 (44.8)[a]	61 (31.22)[b]	102.33 (45.88)[b]	16.63	<0.001
Dorymyrmex exsanguis[#]	26.33 (28.15)[ab]	32 (28.84)[b]	22.67 (22.5)[a]	6.89	0.03
Dorymyrmex wolffhuegeli[#]	339 (312.74)[b]	412.67 (304.02)[a]	117.67 (111.22)[a]	7.97	0.018
Forelius sp1[#]	566.33 (455.08)[c]	721.33 (444.57)[a]	371.33 (137.56)[b]	41.22	<0.001
Pheidole bergi[#]	327.33 (290.84)[a]	195 (312.97)[b]	376.33 (208.97)[c]	14.31	<0.001
Pheidole sp1[#]	72 (123..84)	158.33 (138.95)	60 (103.06)	1.24	0.54
Solenopsis geminata group[#]	166 (72.33)[a]	120 (112.62)[a]	487 (498.87)[b]	18.62	<0.001
Solenopsis schilleri[#]	19.33 (25.93)[b]	36.67 (31.37)[b]	5 (3.61)[a]	9.97	0.007
Ant functional groups					
Attini[#]	247 (239.98)[b]	87 (68.44)[b]	5 (2.65)[a]	25.38	<0.001
Cryptics[#]	49.33 (36.64)[a]	128.67 (134.44)[a]	6 (4.36)[b]	18.22	<0.001
Generalized Myrmicinae[#]	246.67 (111.45)[a]	421.33 (105.95)[a]	951.67 (407.13)[b]	24.76	<0.001
Hot-climate specialists[#]	937.67 (127.01)[c]	134.33 (70.22)[a]	375 (134.31)[b]	46.09	<0.001
Opportunists[#]	643.67 (165.89)[b]	538 (126.08)[b]	247 (149.29)[a]	14.57	<0.001
Subordinate Camponotini[#]	201 (289.64)	264.33 (131.5)	174 (36.37)	9.91	0.805

The χ^2 statistics and p values for the comparisons among plant communities are indicated. Different letters indicate significant differences among plant communities. Error distribution used in GLM models: *Poisson, [#]negative binomial

phenolics) (Campanella and Bertiller 2008). At the same time, the combination of these chemical characteristics is correlated with higher preference and consumption by herbivore insects (Pérez-Harguindeguy et al. 2003; Bisigato et al. 2015). Therefore, higher proportion of perennial grasses in this plant community with respect to shrub and dwarf-shrub steppes, may benefit herbivores. In accordance with previous studies in Península Valdés (Baldi et al. 2017), predators were the most abundant trophic guild with the arachnids as the dominant group. These arthropods increase their abundances in response to the higher density of prey (Wise 1993; Langellotto and Denno 2004), which could explain the similarity among the patterns showed for the abundances of predators and herbivores. As discussed above, the highest
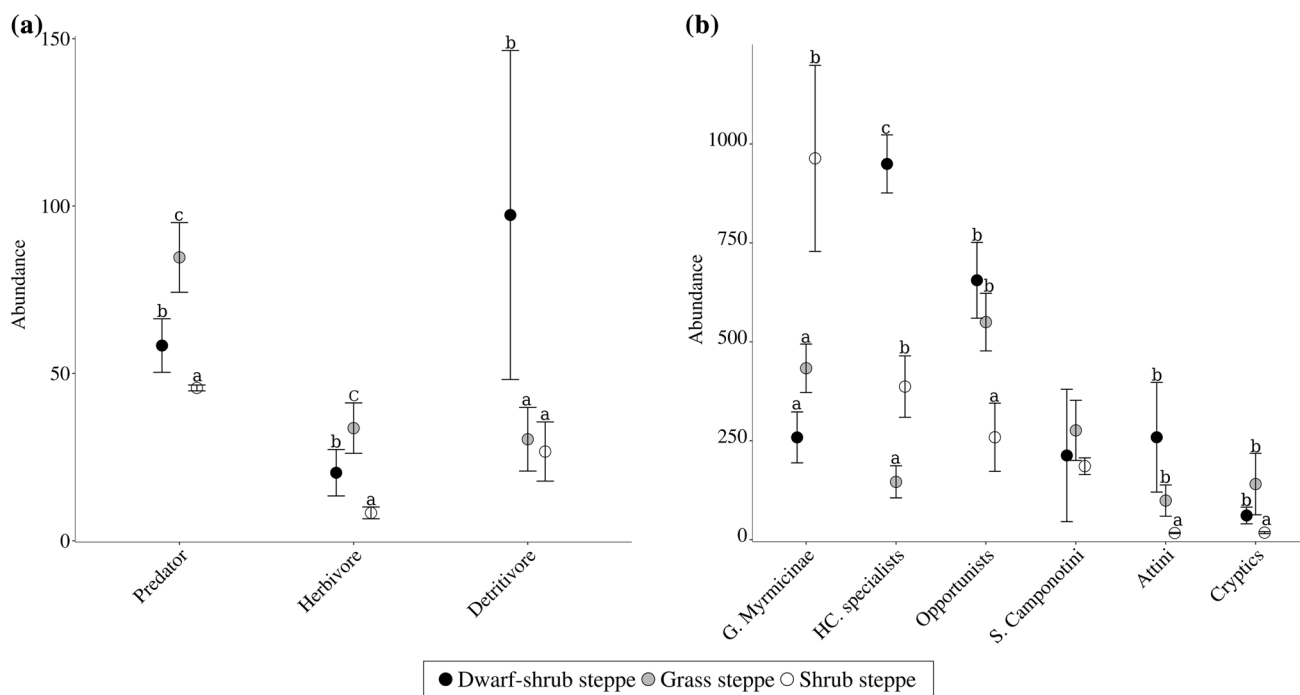
Fig. 4 Abundance (mean ± SE) of the **a** trophic guilds and **b** functional groups of ants in the three plant communities. Significant differences are indicated by different letters
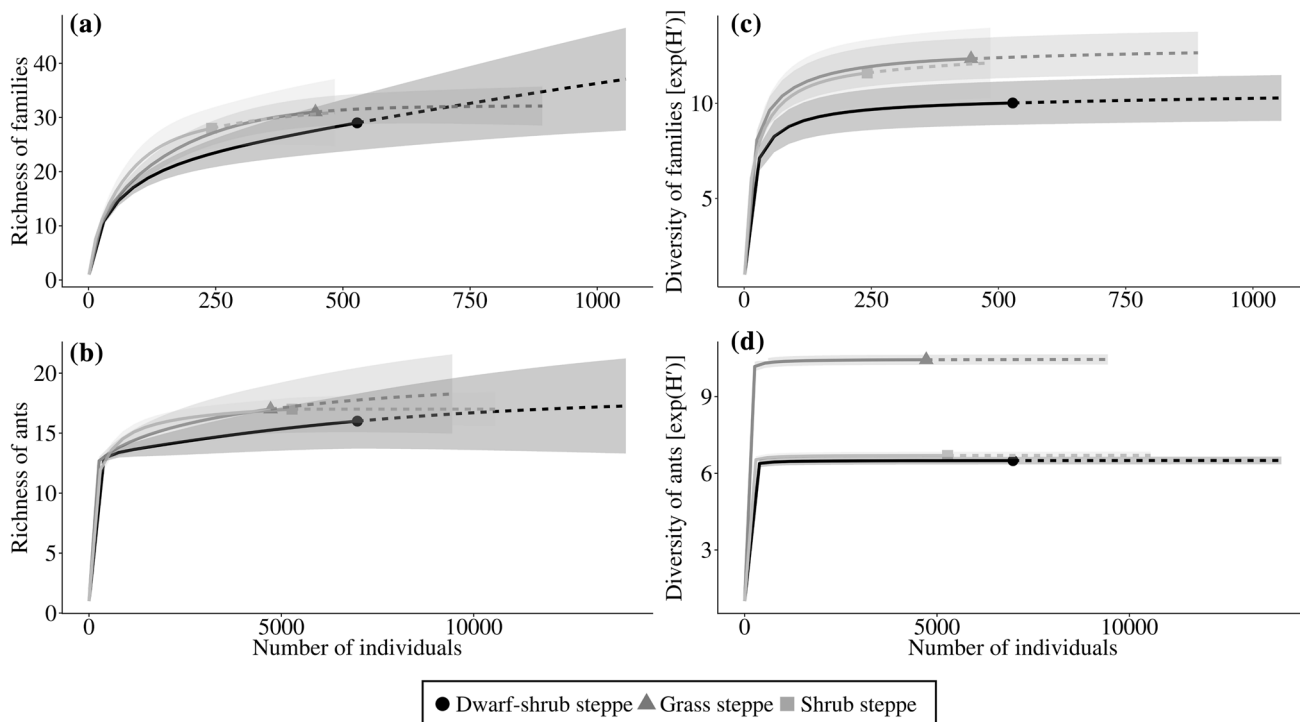

Fig. 5 Sample-size-based (number of individuals) rarefaction and extrapolation (R/E) curves for the richness (q = 0) and diversity (q = 1) of arthropod families (**a–c**) and ant species (**b–d**) among plant communities. Diversity indexes are expressed as exponential of the Shannon index. Symbols denote the observed values in each plant community and shaded areas give the 95% confidence interval of the estimates. Interpolation and extrapolation component of the analysis are represented by continuous and dotted lines, respectively

Table 5 Means (SE) of habitat variables measured in shrub steppe (SS), dwarf-shrub steppe (DS) and grass steppe (GS)

	DS	GS	SS	χ^2	p
Soil texture					
Sand (%)	92.86 (1.51)[b]	93.53 (0.08)[b]	72.57 (12.38)[a]	851.04	<0.001
Silt (%)	3.8 (0.63)[a]	3.07 (0.94)[a]	18.81 (11.39)[b]	54.95	<0.001
Clay (%)	3.34 (1.16)[a]	3.41 (1.03)[a]	8.62 (1.05)[b]	473.81	0.004
Soil compaction (kPa)	1077.85 (79.82)[a]	1017.69 (48.99)[a]	1232.13 (38.25)[b]	73,403	<0.001
Soil organic carbon (%)	0.42 (0.07)[a]	0.35 (0.13)[a]	0.68 (0.32)[a]	0.18	0.12
Cover (%)					
Canopy	70.44 (3.67)[b]	94.89 (2.34)[c]	59.56 (6.19)[a]	1964	<0.001
Litter	73.33 (8.33)[b]	72.44 (5)[b]	48.89 (6.68)[a]	1153	<0.001
Bare soil	18.22 (6.68)[a]	14.67 (7.69)[a]	27.11 (5.67)[a]	246.46	0.06
Biological soil crusts	3.11 (3.36)[a]	2.67 (0.67)[a]	6.00 (4.37)[a]	19.64	0.38
Desert pavement	0.00[a]	0.00[a]	8.89 (2.14)[b]	157.95	<0.001
Grass	59.56 (11.93)[b]	99.71 (0.51)[c]	42.43 (9.11)[a]	5185	<0.001
Shrubs	1.00 (1.74)[a]	0.29 (0.51)[a]	48.58 (12.76)[b]	4595	<0.001
Dwarf-shrubs	39.44 (10.95)[b]	0.00[a]	8.99 (3.66)[a]	2563	<0.001
Vertical complexity					
Stratum 0–25 cm (no. of interceptions)	108.11 (23.86)[a]	260.00 (43.99)[b]	92.00 (17.37)[a]	51,554	<0.001
Stratum 25–50 cm (no. of interceptions)	17.67 (7.77)[ab]	13.78 (3.24)[a]	25.89 (4.76)[b]	229.49	0.02
Stratum 50–75 cm (no. of interceptions)	0.89 (1.26)[a]	1.22 (1.58)[a]	5.78 (2.14)[b]	44.76	<0.001
Number of plant species	4.67 (0.88)[a]	4.78 (0.19)[a]	8.44 (0.84)[b]	27.69	<0.001

The χ^2 statistics and p values for the comparisons among plant communities are indicated. Different letters indicate significant differences among plant communities. All models were built based on Gaussian distribution
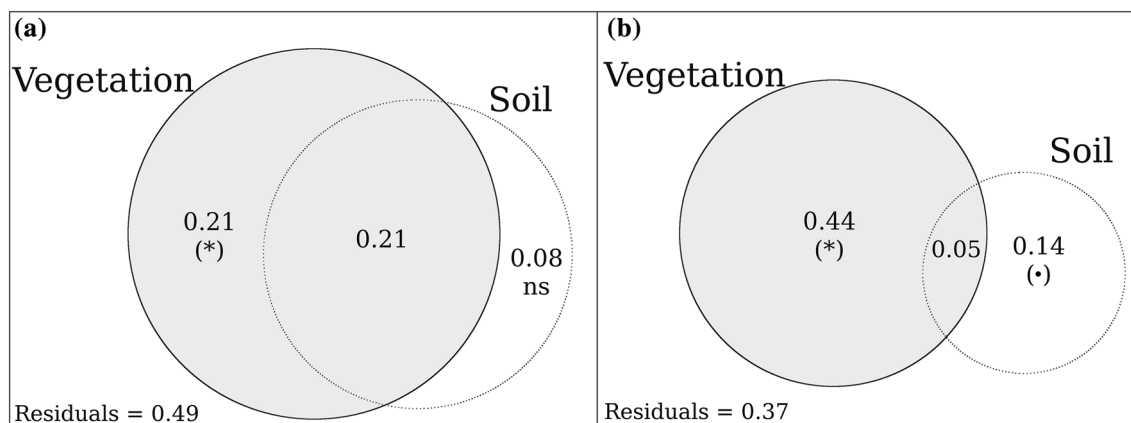

Fig. 6 Variation partitioning of db-RDA for the relationship between habitat variables and the arthropod assemblage at family (**a**) and ant species (**b**) taxonomic levels. Two sets of explanatory variables were included: Soil (percentage of sand and soil compaction) and Vegetation (cover of grass, shrubs and proportion of bare soil). The adjusted R^2 values and the significance of each testable fraction of the variation are indicated (*$p < 0.05$, •$p < 0.1$, *ns* non-significant)

abundance of detritivores in dwarf-shrub steppes was determined by the numerical dominance of Machilidae in this plant community.

We found generalized Myrmicine as clearly dominants in shrub steppes related to the higher abundance of *Solenopsis* spp. and *Pheidole* spp. Despite the fact that the generalized Myrmicine have flexible habitat requirements (Bestelmeyer and Wiens 1996), for the study area, this functional group seem to prefer shrub habitats since it is also dominant in other shrub steppes of Península Valdés (Cheli 2009). Moreover, although it has been suggested that sandy soils increase the abundance and diversity of ants (Boulton et al. 2005), some species of the genus *Pheidole* shows positive association with clay soils (Ríos-Casanova et al. 2015). Thus,

edaphic properties of the shrub steppes could also promote a higher abundance of generalized Myrmicine in this plant community. On the other hand, hot climate specialists were dominant in the dwarf-shrub steppe. The combination of sandy soils and an intermediate cover of vegetation in this plant community can be associated with higher soil surface temperatures (Akter et al. 2016). These characteristics could favor hot climate specialists (particularly *Forelius* spp.), which become more active and dominant when the soil-surface temperatures are higher (unfavorable conditions for other ants) (Bestelmeyer and Wiens 1996).

We are aware that the adopted number of replicates within each plant community was relatively low (n=3) and that statistical robustness of the analyses would increase with sample size. In spite of this, rarefaction curves flattened to the right confirmed that inventories were relatively complete, thus revealing that this sample size is appropriate to study arthropod assemblages in this plant communities, at least for late summer when sampling was carried out. Furthermore, due to logistical reasons, the sampling effort was concentrated in a single period of the year. However, it is known that abundance and composition of arthropod assemblages of the region fluctuate seasonally (Flores et al. 2004; Sola et al. 2016). Therefore it would be necessary include this seasonal variation in futures studies to check the constancy of the patterns observed in the present work.

This study demonstrated significant variations of the ground-dwelling arthropod assemblages of Península Valdés associated with natural heterogeneity of vegetation, highlighting the importance of each habitat types for the regional communities of insects and arachnids. Vegetation units of Península Valdés are affected by increased soil erosion, vegetation fragmentation and habitat loss associated with human activities, specially overgrazing (Blanco et al. 2008; Cheli et al. 2016; Baldi et al. 2017; Bertiller et al. 2017). Considering the key roles that arthropods play at ecosystem level (Prather et al. 2013), the preservation of the natural heterogeneity of this area is important not only for the conservation of insects and arachnids but also for regional ecosystem processes. Concerning this, the ability of arthropods to reflect the environmental variation present in Península Valdés found in this work and others regional backgrounds (Cheli et al. 2010; Baldi et al. 2017) could be a valuable tool to assist in future studies and management plans related to the conservation of terrestrial environments in north-eastern Patagonia.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

References

Akter M, Miah M, Hassan M et al (2016) Textural influence on surface and subsurface soil temperatures under various conditions. J Environ Sci Nat Resour 8:141. https://doi.org/10.3329/jesnr.v8i2.26882

Alvarez M, del P, Weiler, Hernández NE MA (2010) Linking geomorphology and hydrodynamics: a case study from Península Valdés, Patagonia, Argentina. Hydrogeol J 18:473–486. https://doi.org/10.1007/s10040-009-0528-x

Andersen AN, Majer JD (2004) Ants show the way Down Under: invertebrates as bioindicators in land management. Front Ecol Environ 2:291–298

Andersen AN, Fisher A, Hoffmann BD et al (2004) Use of terrestrial invertebrates for biodiversity monitoring in Australian rangelands, with particular reference to ants. Austral Ecol 29:87–92

Arias AM, Pazos GE, Udrizar Sauthier DE (2017) Introducción: contexto geográfico, historia y manejo para la conservación. In: Udrizar Sauthier DE, Pazos GE, Arias AM (eds) Reserva de Vida Silvestre San Pablo de Valdés 10 años. Conservando el patrimonio natural y cultural de Península Valdés Patagonia Argentina. Fundación Vida Silvestre Argentina & CONICET, Buenos Aires

Baldi R, Cheli G, Udrizar Sauthier DE et al (2017) Animal diversity, distribution and conservation. In: Bouza P, Bilmes A (eds) Late Cenozoic of Península Valdés, Patagonia, Argentina. Springer, Cham, pp 263–303

Battisti C, Poeta G, Fanelli G (2016) An introduction to disturbance ecology. Springer, Cham

Bertiller MB, Beeskow AM, Blanco PD et al (2017) Vegetation of Península Valdés: priority sites for conservation. In: Bouza P, Bilmes A (eds) Late Cenozoic of Península Valdés, Patagonia, Argentina. Springer, Cham, pp 131–159

Bestelmeyer BT, Wiens JA (1996) The effects of land use on the structure of ground-foraging ant communities in the Argentine Chaco. Ecol Appl 6:1225–1240

Bestelmeyer BT, Wiens JA (2001) Ant biodiversity in semiarid landscape mosaics: the consequences of grazing vs. natural heterogeneity. Ecol Appl 11:1123–1140

Bisigato AJ, Bertiller MB (1997) Grazing effects on patchy dryland vegetation in northern Patagonia. J Arid Environ 36:639–653

Bisigato AJ, Saín CL, Campanella MV, Cheli GH (2015) Leaf traits, water stress, and insect herbivory: is food selection a hierarchical

process? Arthropod-Plant Interact 9:477–485. https://doi.org/10.1007/s11829-015-9387-7

Blanco PD, Rostagno CM, del Valle HF et al (2008) Grazing impacts in vegetated dune fields: predictions from spatial pattern analysis. Rangel Ecol Manag 61:194–203. https://doi.org/10.2111/06-063.1

Borcard D, Gillet F, Legendre P (2011) Numerical ecology with R. Springer, New York

Boulton AM, Davies KF, Ward PS (2005) Species richness, abundance, and composition of ground-dwelling ants in northern California grasslands: role of plants, soil, and grazing. Environ Entomol 34:96–104

Bouyoucos GJ (1965) Hydrometer method improved for making particle size analysis of soils. Agron J 54:464–465

Bouza P, Bilmes A, del Valle H, Rostagno CM (2017a) Late Cenozoic landforms and landscape evolution of Península Valdés. In: Bouza P, Bilmes A (eds) Late Cenozoic of Península Valdés, Patagonia, Argentina. Springer, Cham, pp 105–129

Bouza P, Ríos I, Rostagno CM, Saín C (2017b) Soil–geomorphology relationships and pedogenic processes in Península Valdés. In: Bouza P, Bilmes A (eds) Late Cenozoic of Península Valdés, Patagonia, Argentina. Springer, Cham, pp 161–190

Campanella MV, Bertiller MB (2008) Plant phenology, leaf traits and leaf litterfall of contrasting life forms in the arid Patagonian Monte, Argentina. J Veg Sci 19:75–85. https://doi.org/10.3170/2007-8-18333

Chao A, Gotelli NJ, Hsieh TC et al (2014) Rarefaction and extrapolation with Hill numbers: a framework for sampling and estimation in species diversity studies. Ecol Monogr 84:45–67. https://doi.org/10.1890/13-0133.1

Cheli GH (2009) Efectos del disturbio por pastoreo ovino sobre la comunidad de artrópodos epígeos en Península Valdés (Chubut, Argentina). Universidad Nacional del Comahue Centro Regional Universitario Bariloche, Bariloche

Cheli GH, Corley JC (2010) Efficient sampling of ground-dwelling arthropods using pitfall traps in arid steppes. Neotrop Entomol 39:912–917

Cheli GH, Corley J, Bruzzone O et al (2010) The ground-dwelling arthropods community from Península Valdés (Patagonia, Argentina). J Insect Sci 10:50

Cheli GH, Pazos GE, Flores GE, Corley JC (2016) Efecto de los gradientes de pastoreo ovino sobre la vegetación y el suelo en Península Valdés, Patagonia, Argentina. Ecol Austral 26:200–211

Chen X, Adams B, Bergeron C et al (2015) Ant community structure and response to disturbances on coastal dunes of Gulf of Mexico. J Insect Conserv 19:1–13. https://doi.org/10.1007/s10841-014-9722-9

Chenchouni H, Menasria T, Neffar S et al (2015) Spatiotemporal diversity, structure and trophic guilds of insect assemblages in a semiarid Sabkha ecosystem. PeerJ 3:e860. https://doi.org/10.7717/peerj.860

Clarke KR, Warwick RM (2001) Change in marine communities: an approach to statistical analysis and interpretation. PRIMER-E, Plymouth

Claver S, Silnik SL, Campón FF (2014) Response of ants to grazing disturbance at the central Monte Desert of Argentina: community descriptors and functional group scheme. J Arid Land 6:117–127. https://doi.org/10.1007/s40333-013-0190-y

Colwell RK, Chao A, Gotelli NJ et al (2012) Models and estimators linking individual-based and sample-based rarefaction, extrapolation and comparison of assemblages. J Plant Ecol 5:3–21. https://doi.org/10.1093/jpe/rtr044

Coronato F, Pessacg N, Alvarez M, del P (2017) The climate of Península Valdés within a regional frame. In: Bouza P, Bilmes A (eds) Late Cenozoic of Península Valdés, Patagonia, Argentina. Springer, Cham, pp 85–104

Crawley MJ (2013) The R book, 2nd edn. Wiley, Chichester

Davidson DT (1965) Penetrometer measurements. In: Black CA (ed) Methods of soil analysis. Part 1. Physical and mineralogical properties, including statistics of measurement and sampling. ASA, Madison, pp 472–484

de los Santos A, de Nicolás JP, Ferrer F (2002) Habitat selection and assemblage structure of darkling beetles (Col. Tenebrionidae) along environmental gradients on the island of Tenerife (Canary Islands). J Arid Environ 52:63–85

Farji-Brener AG, Corley JC, Bettinelli J (2002) The effects of fire on ant communities in north-western Patagonia: the importance of habitat structure and regional context. Divers Distrib 8(4):235–243

Farji-Brener AG, Carvajal D, Gei MG et al (2008) Direct and indirect effects of soil structure on the density of an antlion larva in a tropical dry forest. Ecol Entomol 33:183–188. https://doi.org/10.1111/j.1365-2311.2007.00948.x

Feng Q, Li F-R, Liu J-L et al (2015) Ground-dwelling arthropod community response to native grassland conversion in a temperate desert of northwestern China. J Insect Conserv 19:105–117. https://doi.org/10.1007/s10841-014-9751-4

Fernández F (ed) (2003) Introducción a las hormigas de la región neotropical. Instituto de Investigación de Recursos Biológicos Alexander von Humboldt, Bogotá

Flores GE, Lagos SJ, Roig-Juñent S (2004) Artrópodos epígeos que viven bajo la copa del algarrobo (Prosopis flexuosa) en la Reserva Telteca (Mendoza, Argentina). MULTEQUINA 13:71–90

Gessé F, Monleón-Getino T, Goula M (2014) Biodiversity analysis of true bug assemblages (hemiptera, heteroptera) in four habitats in the Garraf Natural Park (Barcelona, Spain). J Insect Sci 14:1. https://doi.org/10.1093/jisesa/ieu145

Gibson DJ (2009) Grasses and grassland ecology. Oxford University Press, New York

González-Reyes AX, Corronca JA, Rodriguez-Artigas SM (2017) Changes of arthropod diversity across an altitudinal ecoregional zonation in Northwestern Argentina. PeerJ 5:e4117. https://doi.org/10.7717/peerj.4117

Gotelli NJ, Ellison AM (2002) Biogeography at a regional scale: determinants of ant species density in New England bogs and forests. Ecology 83:1604–1609

Hammer Ø, Harper DAT, Ryan PD (2001) Past: paleontological statistics software package for education and data analysis. Palaeontol Electron 4:1–9

Hoffmann BD, Andersen AN (2003) Responses of ants to disturbance in Australia, with particular reference to functional groups. Austral Ecol 28:444–464

Hothorn T, Bretz F, Westfall P (2008) Simultaneous inference in general parametric models. Biom J 50:346–363. https://doi.org/10.1002/bimj.200810425

Hsieh TC, Ma KH, Chao A (2016) iNEXT: an R package for rarefaction and extrapolation of species diversity (Hill numbers). Methods Ecol Evol 7:1451–1456. https://doi.org/10.1111/2041-210X.12613

Jost L (2006) Entropy and diversity. Oikos 113:363–375. https://doi.org/10.1111/j.2006.0030-1299.14714.x

Jung M, Kim S, Hunsung K, Joon-Ho L (2008) Biodiversity and community structure of ground-dwelling spiders in four different field margin types of agricultural landscapes in Korea. Appl Soil Ecol 38:185–195

Langellotto GA, Denno RF (2004) Responses of invertebrate natural enemies to complex-structured habitats: a meta-analytical synthesis. Oecologia 139:1–10. https://doi.org/10.1007/s00442-004-1497-3

Legendre P, Legendre L (2012) Numerical ecology, 3rd English edition. Elsevier, Amsterdam

Li F-R, Liu J-L, Liu C-A et al (2013) Shrubs and species identity effects on the distribution and diversity of ground-dwelling

arthropods in a Gobi desert. J Insect Conserv 17:319–331. https://doi.org/10.1007/s10841-012-9512-1

Magoba RN, Samways MJ, Simaika JP (2015) Soil compaction and surface-active arthropods in historic, agricultural, alien, and recovering vegetation. J Insect Conserv 19:501–508. https://doi.org/10.1007/s10841-015-9771-8

Magurran AE (2004) Measuring biological diversity. Blackwell Publishing, Oxford

Mazía NC, Chaneton E, Kitzberger T (2006) Small-scale habitat use and assemblage structure of ground-dwelling beetles in a Patagonian shrub steppe. J Arid Environ 67:177–194

Oksanen J (2015) Multivariate analysis of ecological communities in R: Vegan Tutorial

Oksanen J, Blanchet FG, Friendly M, Kindt R, Legendre P, McGlinn D, Minchin PR, O'Hara RB, Simpson GL, Solymos P, Stevens MH, Szoecs E, Wagner H.(2017). vegan: Community Ecology Package. R package version 2.4-1. http://CRAN.R-project.org/package=vegan

Passera CB, Dalmasso AD, Borseto O (1986) Método de "Point Quadrat" modificado. Subcomité Asesor del Árido Subtropical Argentino

Pazos GE, Ares JO, Bertiller MB (2010) Quantitative assessment of shrub–grass mosaic development in grazed shrublands: an example in the Patagonian Monte (Argentina). J Arid Environ 74:998–1002. https://doi.org/10.1016/j.jaridenv.2009.12.004

Pazos GE, Rodríguez MV, Blanco PD (2017) Vegetación terrestre. Descripción, monitoreo y relación con el clima y los herbívoros. In: Udrizar Sauthier DE, Pazos GE, Arias AM (eds) Reserva de Vida Silvestre San Pablo de Valdés 10 años. Conservando el patrimonio natural y cultural de Península Valdés Patagonia Argentina. Fundación Vida Silvestre Argentina & CONICET, Buenos Aires

Pérez-Harguindeguy N, Díaz S, Vendramini F et al (2003) Leaf traits and herbivore selection in the field and in cafeteria experiments: leaf traits, herbivory and preference. Austral Ecol 28:642–650. https://doi.org/10.1046/j.1442-9993.2003.01321.x

Prather CM, Pelini SL, Laws A et al (2013) Invertebrates, ecosystem services and climate change. Biol Rev 88:327–348. https://doi.org/10.1111/brv.12002

R Core Team (2015) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna

Ríos-Casanova L, Dávila P, Godínez-Alvarez H, Rico-Gray V (2015) Diversity of ants inhabiting a mosaic of environmental conditions in a semi-desert of Central Mexico. Southwest Entomol 40:307–322. https://doi.org/10.3958/059.040.0207

Roig-Juñent S, Claps LE, Morrone JJ (2014) Biodiversidad de Artrópodos Argentinos volumen 3. INSUE-UNT, San Miguel de Tucumán

Rostagno CM, Bouza PJ, Videla LS et al (2017) Suelos y geomorfología. In: Udrizar Sauthier DE, Pazos GE, Arias AM (eds) Reserva de Vida Silvestre San Pablo de Valdés 10 años.

Conservando el patrimonio natural y cultural de Península Valdés Patagonia Argentina. Fundación Vida Silvestre Argentina & CONICET, Buenos Aires

Samways MJ (1994) Insect conservation biology. Chapman and Hall, London

Schaffers AP, Raemakers IP, Sýkora KV, ter Braak CJF (2008) Arthropod assemblages are best predicted by plant species composition. Ecology 89:782–794. https://doi.org/10.1890/07-0361.1

Schowalter TD (2016) Insect ecology: an ecosystem approach, 4th edn. Elsevier Academic Press, San Diego

Scudder GGE (2009) The importance of insects. In: Foottit RG, Adler PH (eds) Insect biodiversity: science and society. Wiley, Chichester, pp 7–31

Siemann E (1998) Experimental tests of effects of plant productivity and diversity on grassland arthropod diversity. Ecology 79:2057–2070

Sola FJ, Peri PL, Huertas L et al (2016) Above-ground arthropod community structure and influence of structural-retention management in southern Patagonian scrublands, Argentina. J Insect Conserv 20:929–944. https://doi.org/10.1007/s10841-016-9918-2

Staubus WJ, Boyd ES, Adams TA et al (2015) Ant communities in native sage scrub, non-native grassland, and suburban habitats in Los Angeles County, USA: conservation implications. J Insect Conserv 19:669–680. https://doi.org/10.1007/s10841-015-9790-5

Tews J, Brose U, Grimm V et al (2004) Animal species diversity driven by habitat heterogeneity/diversity: the importance of keystone structures. J Biogeogr 31:79–92

Triplehorn CA, Johnson NF, Borror DJ (2005) An introduction to the study of insects, 7th edn. Thomson, Brooks/Cole, Australia

Venables WN, Ripley BD (2002) Modern applied statistics with S. Springer, New York

Walkley A, Black IA (1934) An examination of the Degjareff method for determinig soil organic matter and a proposed modification of the chromi acid titanion method. J Am Soc Agron 24:256–275

Wenninger EJ, Inouye RS (2008) Insect community response to plant diversity and productivity in a sagebrush–steppe ecosystem. J Arid Environ 72:24–33. https://doi.org/10.1016/j.jaridenv.2007.04.005

Werenkraut V, Ruggiero A (2012) Altitudinal variation in the taxonomic composition of ground-dwelling beetle assemblages in NW Patagonia, Argentina: environmental correlates at regional and local scales. Insect Conserv Divers 6:89–92

Whitford WG (2000) Keystone arthropods as webmasters in desert ecosystems. In: Coleman DC, Hendrix PF (eds) Invertebrates as webmasters in ecosystems. CABI Publishing, Wallingford, pp 25–42

Wickham H (2009) ggplot2. Springer, New York

Wise DH (1993) Spiders in ecological webs. Cambridge University Press, Cambridge

Zuur AF, Ieno EN, Walker N et al (2009) Mixed effects models and extensions in ecology with R. Springer, New York