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Native shrubs and their importance for arthropod diversity in the southern Monte, Patagonia, Argentina

Fernando J. Martínez[1,2] · Pablo M. Dellapé[3] · Alejandro J. Bisigato[1,2] · Germán H. Cheli[1,2]

Abstract

The Monte, one of the main arid regions in Argentina, is affected by degradation processes that impact the biological communities. Arthropods are the most diverse component of the Monte fauna and play important roles in several ecosystem processes. The study of interactions between native plants and arthropods, two key elements of the Monte biodiversity, contributes to our understanding of how this ecosystem functions. Our objective was to compare the plant-dwelling arthropod assemblages associated with representative shrub species of the southern Monte and to analyse the relationship between plant architecture and the assemblage structure. We sampled arthropods using the beating method on three evergreen shrub species (*Chuquiraga avellanedae*, *Schinus johnstonii* and *Larrea divaricata*) at six sites during two consecutive spring seasons. We recorded shrub height, canopy area, volume and an index of canopy openness. Our results showed that native shrub species host different arthropod assemblages, partially explained by both the shrub species identity and shrub architecture (mainly canopy openness). The arthropod assemblage that lives in *S. johnstonii* showed the highest diversity, probably related to the plant's intermediate canopy openness, which may determine favourable microhabitats that provide protection against adverse climatic conditions and predators. The assemblage in *C. avellanedae* had the lowest diversity. The closed canopy of *C. avellanedae* could be beneficial for a few very abundant taxa that dominate the assemblage associated with it.

Implications for Insect Conservation Our results show that these native shrubs support a wide range of arthropod taxa and guilds, contributing to maintaining the biodiversity in the southern Monte.

Keywords Insects · Arachnids · Plant canopy · Abundance · Richness · Trophic structure

Introduction

Spatial variation of biological communities has emerged as a topic of great interest in the development of current ecological studies (Magurran and McGill 2011; Dalerum et al. 2017). Particularly, diversity is a fundamental attribute of communities that plays a critical role in the functioning of all ecosystems (Hooper et al. 2005). In this regard, knowing the spatial variability of biodiversity and determining its causes are crucial to preserve ecosystem processes and services (Cardinale et al. 2012). Furthermore, this information will help to understand ecological consequences of current biodiversity loss caused by the impact of human activities (Loreau 2010), which has critical implications for developing suitable conservation strategies and management decisions in the context of habitat loss and environmental degradation (Gaston 2000; Samways 2018).

Arthropods are fundamental components of all land-associated ecosystems (Samways 2018). They are the most diverse animal group and play key roles in several ecosystem processes, such as pollination, seed dispersal and nutrient cycles (Prather et al. 2013). Moreover, they are important components of food chains and alter soil structure and fertility (Scudder 2009). Insects and arachnids are widely distributed, easy to sample, and respond more markedly to small habitat changes than other organisms (e.g. birds and

✉ Germán H. Cheli
  cheli@cenpat-conicet.gob.ar

1   Instituto Patagónico para el Estudio de los Ecosistemas Continentales (IPEEC-CONICET), Boulevard Brown 2915, Puerto Madryn, Chubut, Argentina

2   Universidad Nacional de la Patagonia San Juan Bosco, Sede Puerto Madryn, Boulevard Brown 3051, Puerto Madryn, Chubut, Argentina

3   División Entomología, Universidad Nacional de la Plata, CONICET, Museo de La Plata, Paseo del Bosque s/n, La Plata, Buenos Aires, Argentina

mammals) (Blaum et al. 2009; Hoffmann 2010; Bosc et al. 2018). As a result, they have been proposed as a suitable animal group for assessing ecological responses to environmental variation (Andersen and Majer 2004; Fartmann et al. 2012; Martínez et al. 2018).

In general, each plant species is inhabited by a particular arthropod assemblage (Rango 2005; Huffman et al. 2009; Kwok and Eldridge 2016). This assemblage is determined by, among other causes, the abundance of host plants, the evolutionary time of arthropod-plant coexistence, the efficiency of anti-herbivorous mechanisms, and the plant architecture (Forbes et al. 2017). Particularly, canopy architecture, commonly estimated from plant size and branching density (Bell et al. 1991; Gingras et al. 2002), has been identified as one of the key factors affecting the arthropod assemblage structure (Lawton 1983; Spears and MacMahon 2012). More complex plants provide diverse habitats and enable the coexistence arthropod taxa through vertical differentiation of ecological niches (Langellotto and Denno 2004; Obermaier et al. 2008). Moreover, canopy size is a characteristic which increases the probability that plants will be detected and colonized by insects, and reflects the availability of sources of food, oviposition sites and shelters (Spears and MacMahon 2012; Forbes et al. 2017; Vasconcellos-Neto et al. 2017). In this sense, larger and more complex plants are often associated with higher abundance and diversity of arthropods (Lawton, 1983; Denno and Roderick, 1991).

The Monte, one of the largest arid regions in Argentina, is a phytogeographical province that covers approximately 460,000 km^2 (Rundel et al. 2007). This region is severely affected by degradation processes, such as soil erosion, overgrazing and deforestation (Rostagno et al. 2006; Villagra et al. 2009). Human disturbances greatly influence the native flora and fauna of the Monte and ultimately their ecosystem dynamics (Rundel et al. 2007). Although arthropods are the most abundant and diverse animal component of the Monte (Roig et al. 2009), ecological studies on the interaction between vegetation and fauna in this region are greatly biased toward vertebrates (Bertiller et al. 2009; but see Debandi 1999; Cheli et al. 2009; Tadey 2015; Pol et al. 2017; Martínez et al. 2020). Considering the ecological importance of arthropods in arid environments, knowledge of their spatial structure and identification of their environmental determinants will greatly contribute to a comprehensive view of local ecosystem functioning (Pryke and Samways 2012). Including this theoretical knowledge in ongoing strategies in the region, such as ecological restoration and rehabilitation (Pérez et al. 2019), is relevant for the conservation of both arthropod diversity and ecosystem processes in which they are involved (Prather et al. 2013)

Larrea divaricata Cav., *Schinus johnstonii* Barkley and *Chuquiraga avellanedae* Lorentz are representative shrubs of the southern Monte (Bisigato et al. 2016). These species play important roles in the regional ecosystems, for example, by influencing the plant community structure (Bisigato and Bertiller 1997; Campanella and Bisigato 2019) and determining the availability of soil nutrients (Bisigato et al. 2008). However, practically nothing is known about the canopy arthropod assemblages associated with these three shrub species (but see Debandi 1999). Moreover, compared to other native plants, the three shrub species share similar chemical characteristics (Bertiller and Ares 2008; Campanella and Bertiller 2008). These focal species are therefore appropriate for studying the relationship between canopy arthropods and variations in shrub architecture.

The main objective of our study was to describe and compare the taxonomic and functional structure of arthropod assemblages inhabiting three native shrub species of the southern Monte. We also analyse the relationship between arthropod assemblages and architectural features of shrub canopies. In this study, we mainly addressed the following questions: (i) How similar are the shrub-dwelling arthropod assemblages associated with representative shrub species of the southern Monte? and (ii) Is the canopy architecture an important determinant of these arthropod assemblages?

Materials and methods

Study area

We conducted the study at six sampling sites located at a minimum distance of 300 m from each other, in an area with homogenous soil, floristic and topographical characteristics in the southern Monte district (León et al. 1998; Rundel et al. 2007), located in north-eastern Chubut Province, Argentina (42° 26′; 65° 59 W; 98 m a.s.l.). The climate is arid with mean annual temperature 13.4 °C and mean annual precipitation 236 mm (Bisigato et al. 2005). Precipitation events occur without a defined seasonal pattern, with a high intra- and interannual variation. The characteristic vegetation is shrubland with several strata. Vegetation covers 20% to 40% of the soil in a random, patchy structure formed by clumps of shrubs and perennial grasses on a matrix of bare soil or sparse vegetation. The upper canopy layer (1–2 m) is dominated by evergreen and deciduous shrubs of *Larrea divaricata* Cav., accompanied by *Schinus johnstonii* Barkley, *Lycium chilense* Miers ex Bert., *Prosopis alpataco* Phil. and *Prosopidastrum striatum* (Benth.) R.A. Palacios & Hoc. In the lower canopy layer (< 1 m), *Chuquiraga avellanedae* Lorentz is highly abundant with the co-occurrence of perennial grasses and dwarf shrubs (Bisigato and Bertiller 1997; Morello et al. 2018).

Focal plant species

We focused on arthropods inhabiting three common shrub species of the southern Monte (Bisigato et al. 2016): (1) *Larrea divaricata*, a shrub 3 m tall with open branching and an inverted cone shape; (2) *Schinus johnstonii*, a shrub 0.5 to 1.5 m tall, stocky shaped with thorny stems; (3) *Chuquiraga avellanedae,* a shrub 0.5 to 1 tall, with a hemispheric shape and coriaceous thorny leaves (Campanella 2009). These species are abundant, however *S. johnstonii* has a more heterogeneous spatial distribution and is less ubiquitous than *C. avellanedae* and *L. divaricata* (Bisigato et al. 2005). In fact, *C. avellanedae* and *L. divaricata* dominate the plant communities described in the area (Bisigato et al. 2016). Debandi (1999) analysed arthropod associated with the canopy of *Larrea* spp. in the central area of the Monte, finding assemblages dominated by herbivores (mainly sap-sucking insects), with highest diversity in the warm months, and strongly influenced by variations in temperature. There are no previous studies on the shrub-dwelling arthropod assemblages associated with *C. avellanedae* and *S. johnstonii*. Finally, chemical differences among the three focal plants are much smaller than those found among plant species of different functional groups. At a general level, these shrub species have higher lignin and phenol concentration, and lower nitrogen content than deciduous shrubs and perennial grasses growing in the same area (Bertiller and Ares 2008; Campanella and Bertiller 2008).

Arthropod and plant sampling

To obtain representative samples of the arthropod assemblages and based on a previous study in the same area (Martínez 2018), we selected five individuals of each shrub species per site. We collected the arthropods by the beating method, which is appropriate for sampling insects and arachnids living on shrub canopies (Triplehorn et al. 2005; Moir et al. 2010). We placed a 65 cm diameter net under each shrub and beat twenty times, distributed throughout the canopy area of the shrub. Arthropods were stored in a freezer chamber (− 18 °C) until processing time (no longer than 5 months). To avoid possible biases on sampling because of weather conditions, we took the samples only between 10 am and 5 pm on days with minimal wind speed (at most 5 m/s). Each shrub was sampled once. Each sampling event (5 individuals × 3 shrub species × 6 sites = 90 shrubs) was completed within a 15-day period in November of two consecutive springs (2014–2015). We selected spring because it is the season when the highest activity of shrub-dwelling arthropods in drylands is reported (Debandi 1999; Rango 2005; Sanford and Huntly 2010).

We measured the height of each shrub where arthropods were collected, and its canopy area was estimated by the crown diameter method (Mueller-Dombois and Ellenberg 1974). We estimated plant volume by using the half ellipsoid formula for *C. avellanedae* and *S. johnstonii,* and an inverted cone for *L. divaricata* (Ludwig et al. 1975; Spears and MacMahon 2012). We defined the index of canopy openness (ICO) as the mean distance needed to intercept 3 branches across the canopy. Using an iron rod (needle), we took this measurement on the three main dimensions of each shrub (length, width, and height) and averaged them for each individual.

We quantified and determined all insects and arachnids to the family taxonomic level using taxonomic keys (Triplehorn et al. 2005; Grismado et al. 2014) and consulting with specialists. The family level is appropriate for ecological studies based on arthropod communities, especially in regions where taxonomic knowledge is insufficient (Báldi 2003; Timms et al. 2013). Moreover, the family level is a reasonable predictor of the arthropod community structure at species level in north-eastern Patagonia (Cheli et al 2010). At the same time, we classified the arthropod families into four trophic guilds based on Triplehorn et al. (2005): detritivores, folivores, predators (including parasitoids), and sapsucking arthropods. Considering the difficulty of determining the Lepidoptera larvae at the family level, their high abundance, and their importance as folivores, we considered them only in the trophic guild analysis (Schoonhoven et al. 2005). We excluded ants from the trophic analysis because the family taxonomic level adopted in this study is not useful for this taxon since ants occupy a wider variety of trophic levels than other arthropod families (Hoffmann and Andersen 2003; Day et al. 2019). We deposited all arthropod specimens in the Entomological Collection of the Instituto Patagónico para el Estudio de los Ecosistemas Continentales (IPEEC-CONICET).

Statistical analysis

We used Hill numbers and rarefaction-extrapolation curves (Chao et al. 2014) to compare the richness and diversity of arthropods assemblages among shrub species. For this analysis, we pooled the abundance of the arthropod families of the six sites and 2 years per plant species. We derived two indices from Hill numbers: $q = 0$ (richness) and $q = 1$ (the exponential of Shannon entropy) (Jost 2006). We analysed the rarefaction/extrapolation curves using the iNEXT package (Hsieh et al. 2016) for R software version 3.4.3 (R Core Team 2017) in RStudio version 0.99.903 (RStudio Team 2015). Following the advice of the package authors, we extrapolated each curve twice the overall abundance (sample size). We built the 95% confidence intervals through the bootstrap method (100 replicates) (Hsieh et al. 2016). In addition, the observation of the rarefaction curves enables evaluation of the sampling effort (Chao et al. 2014).

To analyse the variation in trophic guild abundance (number of arthropods in each guild per sampled shrub) among plant species, we performed generalized linear mixed models (GLMM) by using the glmmTMB package for R (Brooks et al. 2017). We performed the models with shrub species as fixed factor, sampling sites as random factor, and negative binomial errors (link function = log) due to the high overdispersion of the data (Zuur et al. 2009). Based on the same model structure, we tested the variation in architectural variables (height, canopy area, shrub volume, and ICO). Because the plant variables are continuous, we built linear mixed models (Gaussian distribution) by using the lme4 package (Bates et al. 2015). Then we checked the model assumptions through the diagnostic residual plots generated by the DHARMa package (Hartig 2020). Finally, we used the anova function to test the significance of the fixed effect and post hoc Tukey pairwise comparisons to analyse differences among shrubs species, correcting p values for multiple comparisons with the Holm method (glht function of the multcomp package) (Hothorn et al. 2008).

To visualize the similarity between arthropod assemblages, we used non-metric multidimensional scaling (NMDS) to obtain an ordination of the samples (individual shrubs) as a function of the arthropod taxa captured on them (Clarke and Warwick 2001; Legendre and Legendre 2012). We performed the analysis based on a matrix of biological similarity, using the Bray–Curtis index as a measure of distance on taxa abundances (not transformed) (Legendre and Legendre 2012). We performed the NMDS with the function metaMDS of the vegan package (Oksanen et al. 2018).

We tested the relationship among the matrix of biological similarity (same data as used in NMDS), the host shrub species, and the architectural variables through a distance-based redundancy analysis (dbRDA) (Legendre and Anderson 1999; Legendre and Legendre 2012). The dbRDA technique is similar to redundancy analysis, but adapts to other distance measures that are more appropriate for community composition data (Legendre and Legendre 2012). Firstly, we proposed a general model including all plant variables and the sampling year as fixed effects. We also considered the study sites as a random factor. We performed a forward selection procedure based on permutation p-values (Oksanen et al. 2018), followed by assessment of multicollinearity among explanatory variables by VIF coefficients (variables with VIF > 10 were removed) (Legendre and Legendre 2012). As a result, the model selected was: similarity matrix ~ shrub species + shrub volume + ICO index + sites (random). We standardized the architectural variables before analyses and tested the significance of the global model and individual axes using a permutation procedure (999 iterations). Finally, we used partial dbRDA to identify the contribution of each explanatory variable using the others as covariables (Legendre and Legendre 2012). We performed

the dbRDA using decostand, ordistep, vif.cca and capscale functions of the vegan package. We made plots by utilizing the ggplot2 package (Wickham 2016).

Results

We collected 3386 arthropod specimens (2989 not including Lepidoptera larvae), belonging to 54 families. Psocidae (31.65%), Anyphaenidae (16.79%), Melyridae (9.47%) and Miridae (6.19%) were the dominant taxa (Table 1). Fifty-two percent of the catches were collected on *C. avellanedae*, with Psocidae (50.22%) and Anyphaenidae (19.12%) as the most abundant families. The fauna associated with *S. johnstonii* represented 24.05% of the collected individuals and was dominated by Melyridae (19.47%), Psocidae (17.80%) and Anyphaenidae (16.55%). Finally, 23.45% of the arthropods were collected on *L. divaricata*, where Miridae (17.12%), Melyridae (16.41%) and Psyllidae (14.69%) represented the most abundant families (Table 1).

Rarefaction/extrapolation curves showed that the assemblages were adequately sampled (curves reaching an asymptote in all cases, see Fig. 1); therefore, our diversity estimations are reliable. The assemblage associated with *S. johnstonii* presented the highest arthropod family richness (q = 0) (Fig. 1a). Furthermore, family diversity (q = 1) differed among the three shrub species, increasing as *C. avellanedae* < *L. divaricata* < *S. johnstonii* (Fig. 1b).

Considering the total number of arthropods, detritivores were the most abundant trophic guild (38.06%), followed by predators (28.52%), folivores (26.41%) and sap-sucking insects (13.01%). Detritivores and predators increased their abundance as *L. divaricata* < *S. johnstonii* < *C. avellanedae*. The sap-sucking insects showed a peak of abundance in *L. divaricata,* while the number of folivores was lower in *C. avellanedae* (Fig. 2; Table 2). Canopy architecture varied among the three shrub species. This was evidenced both in shrub height and the canopy openness (ICO index), which increased as *C. avellanedae* < *S. johnstonii* < *L. divaricata*. The canopy area showed the following trend: *C. avellanedae* < *L. divaricata* < *S. johnstonii*. Finally, the shrub volume was lower for *C. avellanedae* (Table 3).

The NMDS plot showed that *C. avellanedae* and *L. divaricata* individuals were arranged in different groups (Fig. 3). The clustering of the *S. johnstonii* samples was not so clear, displaying some overlap with the assemblages associated with the other two shrub species. The dbRDA analysis indicated that plant variables explained 33% of the total variability in the arthropod assemblages (pseudo-F = 9.26, p = 0.001, Fig. 4). The first axis of the ordination diagram explained 78% of the constrained variability (pseudo-F = 61.39, p = 0.001). The arthropod assemblage associated with *L. divaricata*, related to a higher volume

Table 1 Number of individuals and relative abundance (expressed as percentage in brackets) of arthropod families per shrub species. The global abundances and the assignment of taxa to each trophic guilds is also indicated

	C. avellanedae	*L. divaricata*	*S. johnstonii*	Global abundance	Throphic guild
Anyphaenidae	300 (19.12)	83 (11.84)	119 (16.55)	502 (16.79)	Predator
Aphididae	1 (0.06)	0	2 (0.28)	3 (0.10)	Sap-sucking
Araneidae	21 (1.34)	5 (0.71)	36 (5.01)	62 (2.07)	Predator
Bethylidae	0	0	1 (0.14)	1 (0.03)	Predator
Bostrichidae	2 (0.13)	0	0	2 (0.07)	Folivore
Braconidae	0	2 (0.29)	1 (0.14)	3 (0.10)	Predator
Caeculidae	2 (0.13)	0	0	2 (0.07)	Predator
Ceraphronidae	0	0	1 (0.14)	1 (0.03)	Predator
Ceratozetidae	10 (0.64)	0	2 (0.28)	12 (0.40)	Detritivore
Chrysomelidae	2 (0.13)	0	5 (0.70)	7 (0.23)	Folivore
Cicadellidae	66 (4.21)	3 (0.43)	8 (1.11)	77 (2.58)	Sap-sucking
Coccinellidae	3 (0.19)	0	16 (2.23)	19 (0.64)	Predator
Coccoidea	43 (2.74)	2 (0.29)	1 (0.14)	46 (1.54)	Sap-sucking
Curculionidae	2 (0.13)	75 (10.7)	30 (4.17)	107 (3.58)	Folivore
Dictyopharidae	1 (0.06)	0	0	1 (0.03)	Sap-sucking
Encyrtidae	7 (0.45)	0	6 (0.83)	13 (0.43)	Predator
Erythraeidae	17 (1.08)	1 (0.14)	22 (3.06)	40 (1.34)	Predator
Eulophidae	10 (0.64)	5 (0.71)	5 (0.70)	20 (0.67)	Predator
Eupelmidae	1 (0.06)	0	3 (0.42)	4 (0.13)	Predator
Flatidae	0	2 (0.29)	0	2 (0.07)	Sap-sucking
Formicidae	43 (2.74)	71 (10.13)	12 (1.67)	126 (4.22)	–
Hemerobiidae	0	6 (0.86)	0	6 (0.20)	Predator
Issidae	44 (2.8)	35 (4.99)	5 (0.70)	84 (2.81)	Sap-sucking
Liposcilididae	0	2 (0.29)	1 (0.14)	3 (0.10)	Detritivore
Lygaeidae	0	0	2 (0.28)	2 (0.07)	Sap-sucking
Mantidae	1 (0.06)	1 (0.14)	0	2 (0.07)	Predator
Meloidae	0	1 (0.14)	0	1 (0.03)	Folivore
Melyridae	28 (1.78)	115 (16.41)	140 (19.47)	283 (9.47)	Folivore
Miridae	55 (3.51)	120 (17.12)	10 (1.39)	185 (6.19)	Sap-sucking
Mordellidae	0	0	2 (0.28)	2 (0.07)	Folivore
Mymaridae	0	0	1 (0.14)	1 (0.03)	Predator
Neoliodidae	0	0	1 (0.14)	1 (0.03)	Detritivore
Oribatulidae	6 (0.38)	0	1 (0.14)	7 (0.23)	Detritivore
Oxycarenidae	1 (0.06)	0	1 (0.14)	2 (0.07)	Sap-sucking
Pentatomidae	2 (0.13)	5 (0.71)	1 (0.14)	8 (0.27)	Sap-sucking
Philodromidae	19 (1.21)	1 (0.14)	5 (0.70)	25 (0.84)	Predator
Phlaeothripidae	2 (0.13)	7 (1.00)	15 (2.09)	24 (0.80)	Sap-sucking
Platygastridae	0	3 (0.43)	1 (0.14)	4 (0.13)	Predator
Proscopidae	1 (0.06)	0	1 (0.14)	2 (0.07)	Folivore
Psocidae	788 (50.22)	30 (4.28)	128 (17.80)	946 (31.65)	Detritivore
Psyllidae	3 (0.19)	103 (14.69)	44 (6.12)	150 (5.02)	Sap-sucking
Pteromalidae	3 (0.19)	0	1 (0.14)	4 (0.13)	Predator
Reduviidae	0	4 (0.57)	0	4 (0.13)	Predator
Rhopalidae	0	0	1 (0.14)	1 (0.03)	Sap-sucking
Salticidae	39 (2.49)	7 (1.00)	50 (6.95)	96 (3.21)	Predator
Scutoverticidae	12 (0.76)	1 (0.14)	2 (0.28)	15 (0.50)	Detritivore
Sminthuridae	2 (0.13)	0	0	2 (0.07)	Detritivore
Tenebrionidae	1 (0.06)	4 (0.57)	3 (0.42)	8 (0.27)	Folivore
Tetragnathidae	10 (0.64)	0	0	10 (0.33)	Predator
Tettigoniidae	2 (0.13)	0	1 (0.14)	3 (0.10)	Folivore
Theridiidae	7 (0.45)	1 (0.14)	13 (1.81)	21 (0.70)	Predator

Table 1 (continued)

	C. avellanedae	*L. divaricata*	*S. johnstonii*	Global abundance	Throphic guild
Thomisidae	10 (0.64)	6 (0.86)	12 (1.67)	28 (0.94)	Predator
Uloboridae	2 (0.13)	0	7 (0.97)	9 (0.30)	Predator
Total	1569 (52.49)	701 (23.45)	719 (24.05)	2989	

Fig. 1 Sample-size-based (number of individuals) rarefaction and extrapolation (R/E) curves for the richness (q = 0) and diversity (q = 1) of arthropod families. Symbols denote the observed values in each shrub species and shaded areas show the 95% confidence interval of the estimates. Continuous and dotted lines represent the interpolation and extrapolation component of the analysis. Diversity indexes are expressed as exponential of the Shannon entropy
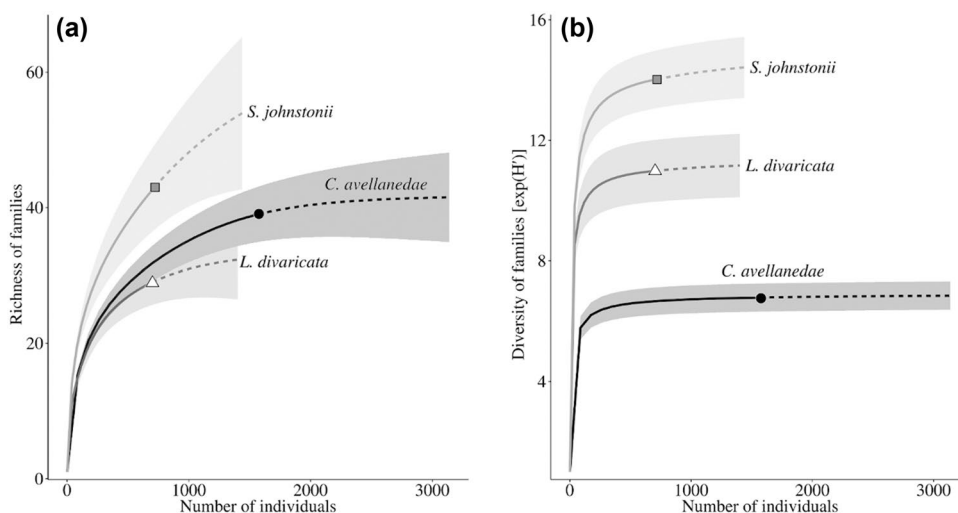
Fig. 2 Abundance (mean ± standard deviation) of the arthropod trophic guilds in the three shrub species. Different letters indicate significant differences in guild abundances (number of arthropods per sampled shrub) among plant species
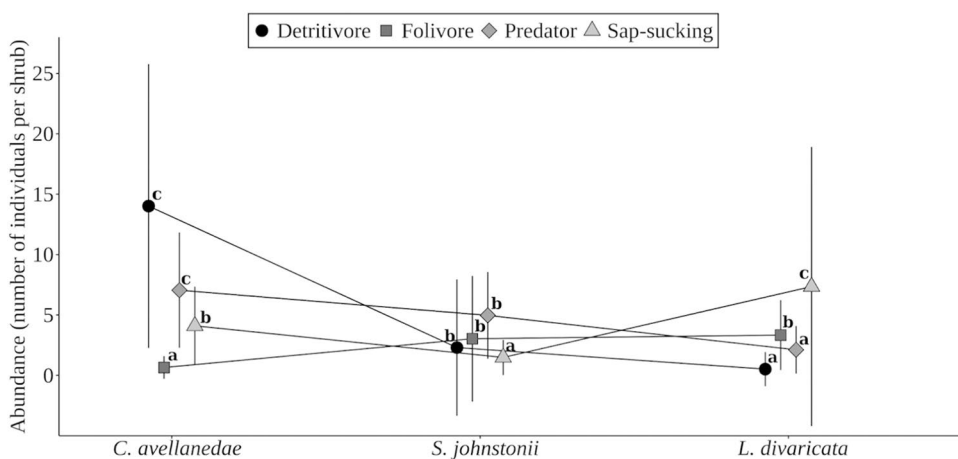

Table 2 Mean (standard deviation) trophic guild abundances per individual of each shrub species (N = 180). The statistics and the significances for the global test and pair-wise comparisons are indicated. Ca: *C. avellanedae*; Ld: *L. divaricata*; Sj: *S. johnstonii*. *p < 0.05; ***p < 0.001; ns: non-significant

Trophic Guild	Mean (SD) of abundance			Global test	Pair-wise tests (Z-statistics)		
	C. avellanedae	*S. johnstonii*	*L. divaricata*	$\chi^2_{(2, 177)}$	*Ca* vs. *Ld*	*Ca* vs. *Sj*	*Sj* vs. *Ld*
Detritivore	14.02 (11.75)	2.3 (5.64)	0.52 (1.41)	132.63***	12.81***	9.25***	5.51***
Folivore	0.65 (0.94)	3.03 (5.2)	3.33 (2.89)	45.25***	6.62***	6.16***	0.52 [ns]
Predator	7.05 (4.77)	4.97 (3.59)	2.12 (1.97)	64.03***	8.53***	2.81*	5.92***
Sap-sucking	4.1 (3.24)	1.48 (1.46)	7.35 (11.56)	58.30***	3.06***	5.32***	8.21***

Table 3 Mean (standard deviation) architectural variables per shrub species (N = 180). The statistics and the significances for the global test and pair-wise comparisons are indicated. Ca: *C. avellanedae*; Ld: *L. divaricata*; Sj: *S. johnstonii*. ***p < 0.001; ·p < 0.1; ns: non-significant

	Mean (SD) of vegetation variables			Global test	Pair-wise tests (Z-statistics)		
	C. avellanedae	*S. johnstonii*	*L. divaricata*	$F_{(2,177)}$	*Ca* vs. *Ld*	*Ca* vs. *Sj*	*Sj* vs. *Ld*
Height (m)	0.64 (0.11)	1.23 (0.27)	1.78 (0.19)	513.25***	32.03***	16.57***	15.48***
Canopy area (m²)	0.78 (0.29)	4.04 (2.09)	3.01 (1.31)	81.87***	8.54***	12.52***	1.15·
Volume (m³)	1.63 (0.52)	4.75 (2.28)	4.70 (1.99)	63.08***	9.66***	9.78***	0.11ns
Index of canopy openness (m)	0.32 (0.07)	0.59 (0.18)	0.85 (0.18)	195.39***	19.76***	10.13***	9.64***

Fig. 3 Non-metric multidimensional scaling ordination (NMDS) of the sampled shrubs (N = 180) based on the abundance of the arthropod families (stress 0.20). Dotted lines indicate the 95% confidence ellipses. Shrub species are shown with different shapes: circles = *C. avellanedae*; triangles = *L. divaricata*; squares = *S. johnstonii*
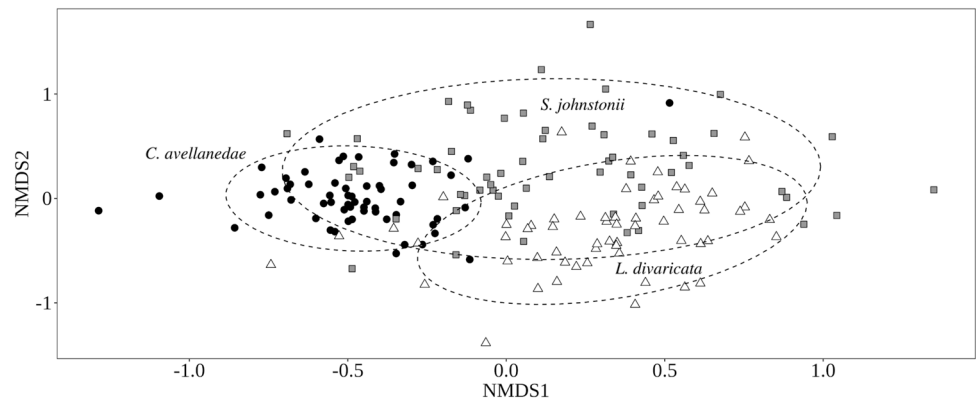
and more open canopy, was characterized by higher abundances of Psyllidae, Miridae, Curculionidae and Melyridae. On the other hand, the *C. avellanedae* assemblage, associated with lower volume and more closed canopy, was mainly characterized by higher abundances of Psocidae, Anyphaenidae, Cicadellidae, and Coccoidea. The arthropod assemblage associated with *S. johnstonii* was mostly differentiated by the second axis, as it explained 18% of the constrained variability (pseudo-F = 12.17, p = 0.003). This assemblage, mainly characterized by higher abundances of Salticidae and Araneidae, was positively correlated with shrub volume. The partial dbRDA analyses showed that the shrub species identity explained the highest proportion of the variability, followed in importance by the index of canopy openness and volume (Table 4).

Discussion

We found that each shrub species hosts a distinct arthropod assemblage. These assemblages varied not only in the abundances of families, but also in taxonomic diversity and trophic guild abundances. The general composition of the assemblages was similar to that found in previous studies carried out in other drylands (Debandi 1999; Rango 2005; Spears and MacMahon 2012; Whitford and Duval 2020), with a high proportion of herbivores (mostly represented

by families of Hemiptera and Coleoptera), and predators (mainly small spiders). A peculiarity of our study was the high abundance of Psocidae. However, these insects have been also recorded in large numbers in another semi-arid plant community in Argentina (Diodato and Fuster 2016). In accordance with other authors (Spears and MacMahon 2012; Kwok and Eldridge 2016; Forbes et al. 2017), our results showed that both the shrub species identity and variations in the canopy architecture are important drivers of the arthropod assemblages associated with dryland plants. Finally, our findings highlight the importance of the native shrub species in favouring the coexistence of arthropod assemblages and consequently, in maintaining arthropod biodiversity in the southern Monte and the and ecosystem processes in which arthropods are involved.

Larger plants generally provide more resources and enable the coexistence of insects and arachnids through vertical differentiation of ecological niches (Langellotto and Denno 2004; Obermaier et al. 2008). Some authors have found a positive relationship between plant size and arthropod diversity (Lawton, 1983; Denno and Roderick 1991; Spears and MacMahon 2012). In our study, *L. divaricata* was the tallest shrub with a high canopy volume (similar to *S. johnstonii*). However, we found that *L. divaricata* did not show the highest diversity of canopy arthropods. Other factors related to the plant size, such as complexity or diversity of aboveground structures, are
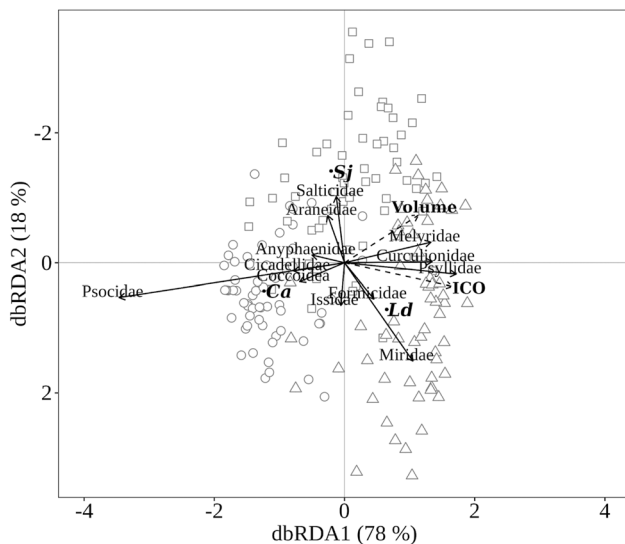
Fig. 4 Ordination resulting from the distance-based RDA analysis (dbRDA). Only the scores of the arthropod families with an abundance higher than 1% with respect to the total of individuals are shown (continuous lines). Dotted lines indicate the vegetation variables related to the architectural characteristics (ICO = index of canopy openness). The centroids of the categorical variable (shrub identity) and samples (shrubs) are shown in italics and different shapes respectively: *Ca* = *C. avellanedae* (circles); *Ld* = *L. divaricata* (triangles); *Sj* = *S. johnstonii* (squares). The variability explained by the first two axes is indicated in brackets. The plot was performed using the scaling 2 or "species" (species scores are scaled by eigenvalues)

Table 4 Response of arthropod assemblages to each plant variable (results of partial RDAs). Degree of freedom (df), statistic (Pseudo-F) and explained variability (R^2) are shown. *p < 0.05; **p < 0.01; ***p < 0.001

Plant variables	df	Pseudo-F	R^2
Shrub species	2	8.05***	13.28
Index of canopy openness (m)	1	5.01**	4.12
Volume (m^3)	1	2.65*	2.18

important for insects and arachnids (Derraik et al. 2002). In this regard, our results suggest that canopy openness could be a major determinant of shrub-dwelling arthropod assemblages. Canopy openness can modify the microclimatic conditions (e.g. temperature, relative humidity and radiation intensity) or biotic interactions (e.g. predation), influencing arthropod assemblages (Debandi 1999; Obermaier et al. 2008; Littlewood et al. 2012).

The arthropod assemblage on *L. divaricata* was characterized by a dominance of sap-sucking insects (mainly mirid bugs and psyllids). A similar pattern was found by Debandi (1999) in species of the genus *Larrea* in the central area of the Monte. As mentioned above, the diversity of arthropods

associated with *L. divaricata* was lower than expected. The open canopy of this shrub species, with well separated branches, could be disadvantageous for certain arthropod taxa of arid environments due to the high risk of desiccation (Obermaier et al. 2008; Chen and Robinson 2014). Moreover, it is known that insectivorous birds are important drivers of arthropod populations (Gunnarsson 2007; Barber and Wouk 2012; Cheli et al. 2019) and represent an important component within the southern Monte animal communities (Krapovickas et al. 2017). These birds prefer foraging in the canopy during spring and summer in response to the higher abundance of arthropods on the foliage (Blendinger 2005). Thus, the open canopy of *L. divaricata* could be disadvantageous for several arthropod families since they would be more exposed and accessible to insectivorous birds (Blendinger 2005; Dennis et al. 2007; Littlewood et al. 2012) and to other flying arthropod predators of the Monte desert (e.g. Asilidae) (Debandi 1999).

Although the assemblage associated with *C. avellanedae* had the lowest diversity, it displayed some interesting characteristics. Particularly, the high abundance of Anyphaenidae in *C. avellanedae* is remarkable. These foliage-runner spiders actively hunt their prey at short distance and prefer dense canopies because they allow them high mobility and offer a high number of shelters (Rodrigues and Mendonça 2012; Vasconcellos-Neto et al. 2017). This explains the higher abundance of predatory arthropods (per individual shrub) in *C. avellanedae*, and could be related to a decrease in diversity by top-down effects on prey populations (Symondson et al. 2002; Vasconcellos-Neto et al. 2017). Moreover, the high detritivore abundance in this shrub is mainly due to the large number of Psocidae in *C. avellanedae* (mostly nymphs). These findings are in agreement with some authors who claim that these insects, especially in their juvenile stages, display gregarious behaviour and prefer closed canopies (Requena et al. 2007; García-Aldrete et al. 2012). Our results suggest that *C. avellanedae* provides a crucial habitat for certain taxa and trophic guilds, which could be specialized to inhabit its canopy. This is reflected by the high abundance of these arthropods, which dominate the assemblage and determine a relatively low diversity (Marques et al. 2000). The specialization of arthropods according to their host plants has frequently been observed in deserts (Whitford and Duval 2020).

Schinus johnstonii supported the highest richness and diversity of arthropod families. In contrast to *C. avellanedae*, the assemblage associated with *S. johnstonii* did not show dominant taxa or guilds with very high relative abundances. In addition, *S. johnstonii* individuals evidenced intermediate characteristics in terms of canopy architecture, with a more closed canopy than *L. divaricata*. This could determine favourable conditions for insects and arachnids with respect to both microclimatic conditions and shelter from predators,

explaining the high arthropod diversity in *S. johnstonii*. Despite the low abundance of *S. johnstonii* compared to the other two plant species (Bisigato et al. 2005), our results would support the idea of *S. johnstonii* as a local example of "island of arthropod diversity" that facilitates the concentration and colonization of the surrounding habitats by insects and arachnids. This pattern has been observed in other drylands around the world (Sanchez and Parmenter 2002; Flores et al. 2004; Mazía et al. 2006; Zhao and Liu 2013).

Although the chemical characteristics of the three shrub species are similar to each other compared to other plant groups, the differences are not necessarily negligible. For example, *C. avellanedae* generally presents higher lignin concentration and lower nitrogen content than the other two species (Bertiller and Ares 2008; Campanella and Bertiller 2008). This could harm some arthropods, especially herbivore taxa (Lightfoot and Whitford 1989; Forbes et al. 2017), and help to explain the low diversity of the assemblage associated with *C. avellanedae*. Therefore, measuring and including certain plant chemical traits in future studies would provide more complete knowledge about the interaction between canopy arthropods and shrubs in the southern Monte.

This first approximation to the relationship between plant-dwelling arthropods and native vegetation in the southern Monte showed that each shrub species hosts a particular arthropod assemblage. One interesting point is that the assemblage differentiation occurred at the shrub scale even though these plant species coexist in the same area and often in the same vegetation patch (Bisigato and Bertiller 1997). Our study suggests that arthropods probably detect the mosaic generated by differences among shrub species which in turn generates a differentiation of their assemblages on small spatial scales (Whitehouse et al. 2002), increasing the diversity of insects and arachnids on a larger scale (Dalerum et al. 2017; González-Reyes et al. 2017; Gavish et al. 2019). Thus, the environmental heterogeneity generated by variations in the architecture of shrubs would be an essential environmental characteristic for the biodiversity of arthropods in the southern Monte.

Compliance with ethical standards

Conflict of interest The authors of the manuscript entitled "Native shrubs and their importance for arthropod diversity in the southern Monte, Patagonia, Argentina" declare that they have no conflict of interest.

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