Ecología Austral 33:938-949 Diciembre 2023
Asociación Argentina de Ecología
https://doi.org/10.25260/EA.23.33.3.0.2292

Ephedra shrubs facilitate local arthropod communities in the Andean Puna: Implications for conservation and habitat restoration

Natalia I. Yela; Javier Torréns; Antonella Y. Díaz Casas; Juca A. San Martín & Adriana Aranda-Rickert✉

Centro Regional de Investigaciones Científicas y Transferencia Tecnológica de La Rioja (CRILAR-CONICET). La Rioja, Argentina.

Abstract. In high-altitude deserts, the vegetation is spatially structured as a mosaic of patches with vegetation and interpatches of bare soil. Shrub patches create microhabitats that facilitate the persistence of other organisms by ameliorating climate extremes and increasing soil nutrients and moisture. Although this facilitative effect has been studied mainly on shrub understorey plants, the positive influence of desert shrubs may extend to the local arthropod community. In this study, we examined the hypothesis that plant facilitation by the desert shrub species *Ephedra multiflora* and *E. breana* positively influences the epigeal arthropod communities of the Andean Puna. We found that arthropod abundance, richness and diversity were all higher on *Ephedra* shrub microsites relative to paired open microsites. The harsh environmental conditions prevailing in the Puna ecosystems and the protection and resources provided by plants could jointly explain the positive influence of *Ephedra* shrubs over the arthropod community. The growth of tourism and the boom for lithium, as well as the increasing drought expected for the region under climate change scenarios, strengthens the importance of conserving shrub cover in these ecosystems to sustain biodiversity and ecosystem functioning. Our results are also relevant for restoration projects that consider the whole biological community, where using *Ephedra* as foundation shrubs to support desert endemics could be a strategy for land restoration.

[Keywords: shrub microhabitat, arthropod islands, high-mountain deserts]

Resumen. Los arbustos de *Ephedra* facilitan las comunidades locales de artrópodos en la Puna andina: Implicancias para la conservación y la restauración de hábitats. En los desiertos de altura, la vegetación se estructura espacialmente como un mosaico de parches de vegetación e interparches de suelo desnudo. Los parches con vegetación arbustiva crean microhábitats que facilitan la persistencia de otros organismos al suavizar las condiciones climáticas extremas y aumentar los nutrientes y la humedad del suelo. Aunque el efecto facilitador se estudió sobre todo en plantas que crecen bajo los arbustos, la influencia positiva podría extenderse a las comunidades locales de artrópodos. En este trabajo planteamos como hipótesis que la facilitación por las especies arbustivas *Ephedra multiflora* y *E. breana* tiene una influencia positiva sobre las comunidades de artrópodos epigeos de la Puna andina. Encontramos que la abundancia, la riqueza y la diversidad de artrópodos fue mayor en los micrositios con arbustos de *Ephedra* que en los micrositios pareados abiertos. Las duras condiciones ambientales de los ecosistemas de la Puna y la protección y los recursos que proporcionan las plantas pueden explicar la influencia positiva de los arbustos de *Ephedra* sobre la comunidad de artrópodos. El crecimiento del turismo y el auge del litio, así como el aumento de condiciones de sequía previsto para la región bajo escenarios de cambio climático, refuerzan la importancia de conservar la cubierta arbustiva en estos ecosistemas para mantener su biodiversidad y su funcionamiento. Nuestros resultados también son relevantes para proyectos de restauración que consideren al conjunto de las comunidades biológicas, en los que usar *Ephedra* como arbustos fundacionales podría ser una estrategia de restauración.

[Palabras clave: microhábitat arbustivo, islas de artrópodos, desiertos de alta montaña]

Editor asociado: Néstor Pérez Méndez

✉ ardrickert@gmail.com

Recibido: 4 de Agosto de 2023
Aceptado: 23 de Octubre de 2023

INTRODUCTION

In drylands, the vegetation is commonly arranged in a mosaic structure, where plants occur as well-defined vegetation patches surrounded by bare soil regions (Aguiar and Sala 1999; Gandhi et al. 2019). These vegetation patches are commonly founded by desert shrubs, which by means of their physical structure modify the surrounding environment and make it more habitable for other species (Stachowicz 2001; McIntire and Fajardo 2014). Once established, shrubs can create microrefugia within their canopy, allowing the colonization and persistence of other organisms. This process of ecological facilitation may result in a biased spatial distribution of organisms (Xu et al. 2015), where vegetation patches create 'islands of fertility' compared to unvegetated interspaces (Schlesinger et al. 1996).

Arthropods are the dominant component of biodiversity in drylands (Whitford 2000), and frequently used as bioindicators of environmental changes and ecosystem health (Kremen et al. 1993; Andersen and Majer 2004; Carvalho et al. 2020; Chowdhury et al. 2023). They sustain a variety of interactions and trophic connections, and play important roles as decomposers, herbivores, granivores, pollinators and predators, controlling the nutrient cycling and the energy flow through the different levels in the food chain (Ayal 2007; Noriega et al. 2018). Besides particular physiological adaptations, their persistence in deserts is conditioned to the existence of habitat structures that provide food, shelter or nesting sites.

Desert shrubs fulfil these habitat requirements, as they create milder microhabitats for arthropod communities by moderating solar radiation, changing soil moisture and temperature, and regulating extreme climatic factors (Brooker et al. 2008; Wright et al. 2021). They also provide key resources such as food (e.g., pollen, nectar, leaves, wood, prey/host), shelter, oviposition and mating places, affecting the longevity, reproduction and dispersion of arthropods (Gardarin et al. 2018). Arthropods, in turn, maintain a variety of interactions and trophic connections with shrubs, including those mutualistic such as pollination, seed dispersal, and herbivore predation (Scherber et al. 2010). The positive effect of shrub microhabitats on arthropod communities has been assessed in deserts around the world (e.g., Mazía et al. 2006; Li et al. 2013; Ruttan et al. 2016), and was found consistent with an 'arthropod island' effect when the abundance and diversity of arthropods is enhanced in shrub vegetation patches compared to bare soils (Sanchez and Parmenter 2002; Meloni and Martínez 2021; Braun et al. 2021). Therefore, shrubs have important implications for maintaining the biodiversity of desert arthropods, enhancing in turn the stability and complexity of arid ecosystems.

The Puna ('high and cold land' in Quechua) is part of the Andean plateau, the second largest in the world after the Tibet. It is located in the central Andes, and has an average altitude of 3500 m a. s. l. and peaks up to 6000 m a. s. l. A distinctive feature of the Puna is its arid climate, with low temperatures throughout the year, a large daily temperature range, and low rainfall. To this must be added a low air density (causing 'apunamiento'), high radiation and strong winds (Grau et al. 2019). It is also a biodiversity hotspot with high levels of endemism (Myers et al. 2000), and was declared by the UNESCO as one of the Global 200 priority conservation areas (Olson and Dinerstein 2002). Because life for humans in Puna is uneasy, for a long time their lands have been inhabited by few people, mainly descendents from indigenous populations, with a survival economy based on agriculture and camelids. During the last decades, the increasing tourism (so called 'adventure tourism') and, more importantly, the boom for lithium, have disrupted these remote landscapes (Izquierdo et al. 2015, 2018). To this must be added that future climate change scenarios identify high-elevation ecosystems among the most vulnerable (Beniston et al. 1997), while climate reconstructions show decreasing trends of precipitation for the area (Morales et al. 2015). This context of vulnerability highlights the urgency to understand the key factors that sustain the biodiversity in the Puna, in order to establish conservation recommendations.

In this study, we evaluate the facilitative effect of two species of *Ephedra* shrubs (*E. multiflora* and *E. breana*) on the epigeal arthropods of the desert Puna. *Ephedra* (Gymnospermae: Gnetales: Ephedraceae) are plants of ancient lineage distributed in semi-arid and arid habitats worldwide (Ickert-Bond and Renner 2016), known for some species that contain ephedrine alkaloids (not found as far in the South American species, Caveney et al. 2001). As gymnosperms, *Ephedra* are perennial, drought tolerant long-lived plants, and some species are used for ecological restoration and desertification control, mainly in the deserts of North America and Asia (Ackerman 1979; Derbel et al. 2010; Lortie et al. 2018; He et al. 2021). The *Ephedra* species of this study are common and dominant in the area, and found in plain steppes between 3300 and 3500 m a. s. l., where hydric stress and harsh climate impose particular adaptations for survival.

As a hypothesis, we establish that the epigeal arthropod community reflects the effects of plant facilitation. Therefore, we expect a higher abundance, species richness and diversity of arthropods in the *Ephedra* shrub microsites relative to paired non canopied (open) microsites.

Materials and Methods

Study area

We conducted this study in the Desert Puna of Catamarca Province, northwest Argentina (Carilla et al. 2019). This is a high-elevation cold desert (above 3000 m a. s. l.), where the dominant vegetation type is the shrub-steppe (Cabrera 1968). Climate is arid, with low temperatures, a large daily temperature range (more than 15 °C difference between day and night), and low rainfall concentrated in summer (<100 mm annually) (Morales et al. 2019). In addition to scarce rainfall, the combination of elevated evapotranspiration, strong winds and high solar radiation results in a negative water balance throughout the year (Izquierdo et al. 2018).

We selected two sampling sites based on the presence of each *Ephedra* species: 1) the *E. multiflora* site, near the town El Peñón (26°29′ S - 67°15′ W; 3400 m a. s. l.), and 2) the *E. breana* site, located 50 km apart to the east in the Reserva de la Biosfera Laguna Blanca, a protected natural area near the town of Laguna Blanca (26°43′ S - 66°55′ W; 3300 m a. s. l.) (Figure 1). Rainfall decreases in a Northeast-Southwest direction and, while both sites lie at similar elevations (3300-3400 m a. s. l.), they are separated by a mountain range with peaks as high as 6000 m a. s. l. (Cerro Laguna Blanca).

Preliminary site-level environmental characterization (climate, aridity index and soil properties) indicates that the *E. multiflora* site have more stressful environmental conditions than the *E. breana* site (Supplementary Material-Table S1). Indeed, all climatic parameters show a decrease in precipitation and temperature, as well as higher aridity for the *E. multiflora* site. Both sites have sandy soils with ~90% of sand, but in the *E. multiflora* site they have lower field capacity and organic matter. The vegetation of both sites is also quite different, since at the *E. multiflora* site the only other shrub found other than *E. multiflora* is *Aloysia deserticola,* while at the *E. breana* site, the plant community is more diverse and includes other shrub species such as *Fabiana densa*, *Junellia seriphioides* and *Adesmia horrida.*

Plant species

Ephedra shrubs are dioecious gymnosperms that produce seed cones, have small scale-like leaves, and photosynthetic stems. The two species of this study are easily differentiated because *E. multiflora* produce dry winged cone bracts and the seeds are wind-dispersed, while *E. breana* have succulent, brightly red coloured cone bracts (Hunziker 1995; Ickert-Bond and Renner 2016). During the pollination stage, the cones of female plants produce pollination drops rich in sugar that capture airborne pollen released from male plants (Gelbart and von Aderkas 2002). Both are conspicuous plants with a dense canopy (at maturity, they can reach more than 1 m in diameter and height). Besides their morphological differences, the two species do not coexist in the same plant communities. The actual distribution of *E. multiflora*, based on the collection sites found in the herbarium data, appears to be restricted to extreme arid habitats where very few other species grow. This suggests that *E. multiflora* occupies a narrow environmental niche, resulting in a relatively patchy distribution in the desert Puna. *Ephedra breana*, in turn, is widely distributed in the shrubland steppes of the Andean Puna from Ecuador to northwest Argentina (Hunziker 1995). We note that here we follow the *Ephedra* taxonomical classification of Hunziker (1995), where *E. breana* is considered a different species from *E. chilensis*.

Experimental setup

At each site, we established 30 replicate plots, each including a sampling *Ephedra* shrub. The distance between the plots was >15 m to ensure sampling independence. For each sampling plot, there were two paired sampling microsites: the shrub microsite, which includes both the canopy and the

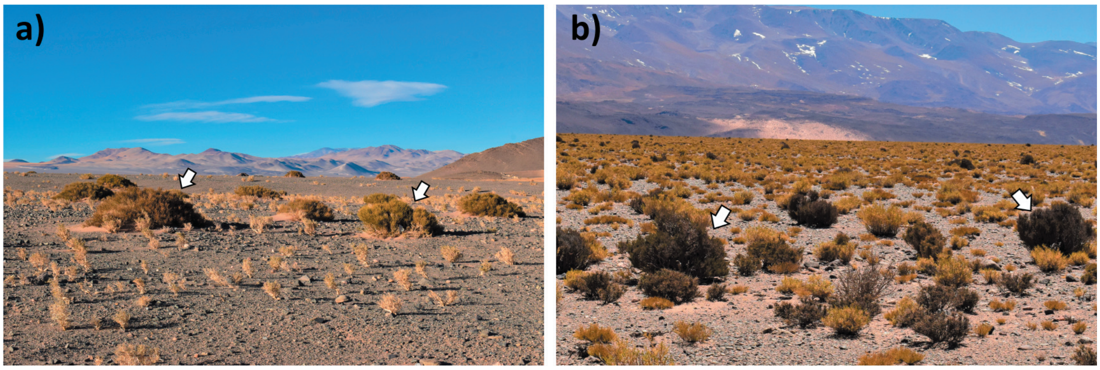

Figure 1. *Ephedra multiflora* (a) and *E. breana* (b) sampling sites in the Desert Puna of Catamarca, Argentina. Arrows show individual plants of each *Ephedra* species.

Figura 1. Sitios de muestreo de *Ephedra multiflora* (a) y *E. breana* (b) en la Puna desértica de Catamarca, Argentina. Las flechas indican individuos de cada especie de *Ephedra***.**

ground shrub understory, and the open microsite, randomly selected open spaces without vegetation placed at least 2 m away. Shrubs selected for sampling were of similar size and well-developed, and included both female (N=20) and male plants (N=10). We measured the dimensions of each sampling shrub (width at the widest point and height of the canopy) to account for a potential influence of the plant size on the arthropod assemblage.

Arthropod sampling

Samplings were carried out during late spring (November 2022), which corresponds to the pollination stage of both *Ephedra* species. At each site, we collected epigeal arthropods at each pair of microsites (shrub and open) using two sampling methods: pitfall traps and suction. While pitfall traps are expected to collect mainly ground-dwelling or near-ground arthropods, the suction method is more effective for flying insects or those associated to the shrub canopy. Pitfall traps consisted of plastic cups (8 cm upper diameter x 5.5 cm tall) filled with a 50% propylene glycol and water mixture; traps were active for three days. Suction sampling was done using a leaf blower set to suction mode (Lüsqtoff LSA-26), with a gauze-bag inserted into the suction tube. Each suction sample was defined as the suction during one minute over an area of one square metre placed on the ground, and up to 1.5 m height. Pitfall traps and suction methods were applied at both microsites (shrub and open), totalizing 60 samples for each method in 30 pairs of microsites at each site. Suction sampling at the shrub microsites was performed on the shrub canopy; at the open microsites suction was applied on the same area and height above ground but without vegetation. Collected samples were placed in containers with 70% ethanol and transported to the lab, where the arthropods were counted and sorted by order, family, genus, and species/morphospecies using available keys (Grissell and Schauff 1990; Acosta and Maury 1998; Fernández and Sharkey 2006; Brown et al. 2009; Fletcher 2009; Lawrence et al. 2010; Cigliano et al. 2023). Specimens that were identified up to family were sorted into putative species based on morphology, or morphospecies. Larval stages and hemipteran nymphs, as well as Acari and Collembola were excluded from the analyses. Collected specimens were deposited in the CRILAR Entomological Collection (CRILAR-En-Ar).

Data analyses

At each site, the arthropod community sampled was characterized by: 1) abundance (total number of arthropods); 2) species richness (total number of taxonomical groups), and 3) diversity, expressed by the Shannon diversity index. To test whether *Ephedra* shrubs facilitate arthropod communities, we analysed differences between microsites (shrub and open) by fitting Generalized Linear Mixed Models (GLMM) in R (function glmer.nb, package lme4). We performed three separate models, with 1) arthropod abundance; 2) species richness, and 3) Shannon diversity per sampling unit as response variables. Two analyses were performed: a) using as sampling unit the pooled data from the two sampling methods (pitfall and suction), and b) using only the data from pitfall traps. As predictor factors we used microsite (shrub and open), plant species, plant dimensions (plant height and width), plant sex (male and female), sampling unit (pitfall and suction) and their interactions. We treated plant ID as random effect. We used a negative binomial distribution because the arthropod abundance was represented by discrete counts that were overdispersed (Lindén and Mäntyniemi 2011). To analyse differences between the two sampling methods (pitfall traps and suction), we compared the arthropod abundance, species richness and Shannon diversity by fitting GLMMs for each response variable. The sampling method, plant species and their interaction were used as predictors, and plant ID as a random effect. Because suction sampling in the open microsites captured only one individual arthropod at each site, this analysis was performed only for shrub microsites. The best predictors for each model were selected based on Akaike's information criterion corrected for small samples (AICc) using the dredge function in the MuMIn package. Statistical analyses were performed in R version 4.2.2 (R Core Team 2022).

RESULTS

Overall, we recorded 2490 arthropods belonging to 130 species/morphospecies from 68 families distributed in 11 higher taxa (see Supplementary Material-Table S2 for full species list). The arthropod groups exhibiting the greatest abundance and species richness were dipterans (relative abundance 36.8% and 40 species) and hymenopterans (relative abundance 39.9% and 37 species), followed by arachnids (relative abundance 7.2% and 14 species), and coleopterans (relative abundance 6.4% and 12 species) (Table 1). Seven species of ants contributed to 80.46% of the total abundance within the hymenopterans.

Facilitative effect of Ephedra

Both *Ephedra* species have a positive effect on the arthropod communities at each site. When using the pooled data from pitfall trap and suction samplings as sampling unit, we found significantly higher abundance (29.26±12.30 vs. 13.14±4.15, P<0.001, means±S.D.), species richness (13.16±3.92 vs. 5.52±2.12, P<0.001) and Shannon diversity index (2.23±0.27 vs. 1.51±0.36, P<0.01) in shrub microsites compared to open microsites (Table 2, Figure 2). Females exhibited higher abundance (22.57±12.58 vs. 20.34±12.12, P<0.01, means±S.D.) and species richness (9.73±5.18 vs. 8.83±4.51, P<0.05) than male plants. The increase in the width of the shrub canopy had a positive influence only on the species richness (P<0.01), while the height of the canopy had no effect on the arthropod communities. This positive influence of *Ephedra* shrubs was also found with just the pitfall trap data (mainly ground-dwelling but also flying arthropods), with higher abundance (14.5±5.44 vs. 10.68±4.83, P<0.001, means±S.D.) and species richness (7.87±2.32 vs. 5.59±2.39, P<0.001) in shrubs compared to open microsites. The Shannon diversity index was also higher but only marginally significant (1.85±0.34 vs. 1.51±0.36, P=0.067) (Supplementary Material-Table S3).

The positive effect on the arthropod communities differed significantly between

Table 1. Total abundance (A), relative abundance (RA) and species richness (S) by higher taxa of arthropods collected in *E. multiflora* and *E. breana* sites.

Tabla 1. Abundancia total (A), abundancia relativa (RA) y riqueza de especies (S) por taxones superiores de artrópodos colectados en los sitios de *E. multiflora* y *E. breana*.

	E. multiflora			*E. breana*			*E. breana* + *E. multiflora*		
Higher taxa	A	RA (%)	S	A	RA (%)	S	A	RA (%)	S
Arachnida	65	6.62	8	114	7.56	12	179	7.19	14
Blattodea	1	0.10	1	0	0	0	1	0.04	1
Coleoptera	94	9.57	10	66	4.38	7	160	6.43	12
Diptera	365	37.17	33	551	36.54	34	916	36.79	40
Hemiptera	5	0.51	2	40	2.65	8	45	1.81	10
Hymenoptera	305	31.06	23	689	45.69	28	994	39.92	37
Lepidoptera	113	11.51	6	35	2.32	5	148	5.94	8
Neuroptera	4	0.41	1	3	0.20	1	7	0.28	1
Orthoptera	26	2.65	1	5	0.33	3	31	1.24	3
Siphonaptera	0	0	0	2	0.13	2	2	0.08	2
Thysanoptera	4	0.41	1	3	0.20	2	7	0.28	2
TOTAL	982	100	86	1508	100	102	2490	100	130

Table 2. Results of generalized linear mixed model selection testing for arthropod abundance, species richness and Shannon diversity index responses to *Ephedra* species (*E. breana* and *E. multiflora*), microsite (shrub and open), plant width and height (continuous variables), plant sex (male and female) and their interactions. Plant ID was modeled as random effect. Best model for each response variable was selected on AICc values. *P<0.05, **P<0.01, ***P<0.001, n.s.: non-significant, P>0.05. All models were run with a negative binomial error distribution. Sampling unit pooled the data from the two sampling methods (pitfall and suction).

Tabla 2. Resultados de la selección de modelos lineares generalizados mixtos analizando la respuesta de la abundancia, riqueza de especies e índice de diversidad de Shannon a la especie de *Ephedra* (*E. breana* y *E. multiflora*), micrositio (abierto y arbusto), ancho y alto de la planta (variables continuas), sexo de la planta (macho y hembra) y sus interacciones. La identidad de la planta fue incluida como efecto al azar. El mejor modelo para cada variable respuesta se seleccionó en base a los valores de AICc. *P<0.05, **P<0.01, ***P<0.001, n.s.: no significativo P>0.05. Todos los modelos se corrieron con una distribución de error binomial negativa. La unidad de muestreo es la suma de los datos obtenidos con los dos métodos de muestreo (trampas de caída y succión).

Response variable	Expl. variable	Est.	Std. error	Z-value	P	Variable effect
Abundance	Treatment***	0.9817	0.0633	15.504	<0.001	Shrub>open
	Ephedra species	-0.1336	0.1487	-0.899	0.3687	n.s.
	Plant sex**	-0.2863	0.0965	-2.967	<0.01	Female>male
	Plant width	0.0009	0.0005	1.592	0.1113	n.s.
	Plant height	0.0022	0.0014	1.525	0.1272	n.s.
	Ephedra species: treatment**	-0.3519	0.1104	-3.185	<0.01	Breana>multiflora
Species richness	Treatment***	1.0295	0.0953	10.793	<0.001	Shrub>open
	Ephedra species	-0.0949	0.1363	-0.696	0.4863	n.s.
	Plant sex*	-0.1829	0.0753	-2.430	<0.05	Female>male
	Plant width**	0.0011	0.0004	2.843	<0.01	Increase with width
	Plant height	0.0006	0.0011	0.517	0.605	n.s.
	Ephedra species: treatment*	-0.3440	0.1373	-2.505	<0.05	Breana>multiflora
Shannon index	Treatment**	0.3873	0.1324	2.925	<0.01	Shrub>open

the two *Ephedra* species (interaction term in the model species: treatment) for the response variables abundance and species richness (pitfall and suction data pooled). The shrub microsites of *E. breana* harbored a higher abundance (P<0.001) and species richness (P<0.05) of arthropods relative to the open microsites than the shrub microsites of *E. multiflora* (abundance shrub vs. open *E. breana*: 34.84±11.88 vs. 13.38±4.56, *E. multiflora*: 23.68±10.16 vs. 12.64±3.22; richness shrub vs. open *E. breana*: 15.25±3.85 vs. 5.66±2.04, *E. multiflora*: 11.18±2.84 vs. 6.04±1.95, means±S.D., Figure 2a, b). This higher positive effect was not found for the Shannon diversity index (shrub vs. open *E. breana*: 2.35±0.22 vs. 1.42±0.34, *E. multiflora*: 2.10±0.27 vs. 1.61±0.36) (Figure 2c).

Comparison between sampling methods

The absolute abundances and species richness of the arthropods collected by pitfall trap and suction sampling are shown in Supplementary Material-Table S4. In open microsites, the number of arthropods captured by suction was negligible (just one individual at each site). In shrub microsites, suction sampling contributed to approximately half of the collected arthropods (*E. multiflora:* 361 of 699 individuals, *E. breana:* 605 of 1120 individuals). We found no significant differences between the two sampling methods in terms of arthropod abundance (14.96±6.25 vs. 16.98±16.11, P=0.78, pitfall and suction, respectively, means±S.D.) and Shannon diversity index (1.85±0.34 vs. 1.31±0.59, P=0.24), though species richness was higher in pitfall traps (8±2.48 vs. 5.88±3.23, P<0.05).

Suction sampling yielded a number of species associated with the canopy that were captured solely by this collection method (19 species for *E. breana* and 17 species for *E. multiflora).* These included mainly dipterans (nine species at each site) and parasitoid wasps (seven species at each site). Certain species were particularly numerous in the suction samples, such as the parasitic wasp Ichneumonoidae sp. (189 individuals) in *E. multiflora*, and the dipteran *Olcella* sp. in *E. breana* (56 individuals). In contrast, all arachnids in the *E. multiflora* shrub microsites were collected with pitfall traps (scorpions, spiders, and camel spiders), while in *E. breana* this taxonomic group was dominated by jumping spiders (Salticidae) and was associated with the canopy. Ants were consistently more abundant in pitfall

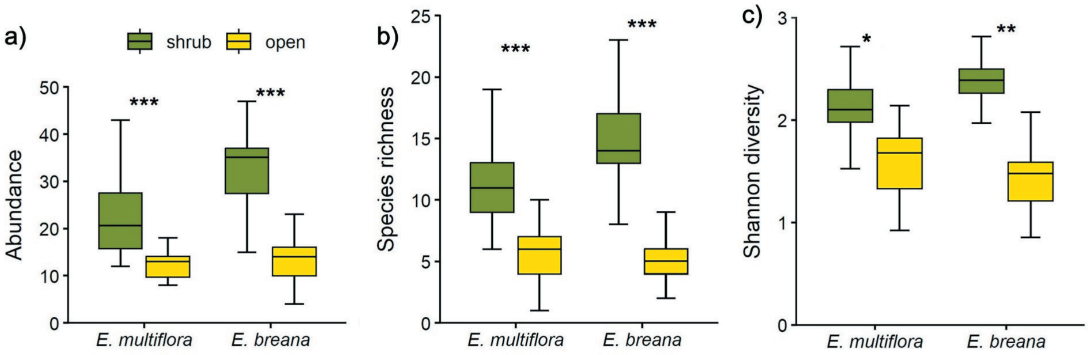

Figure 2. Abundance (a), species richness (b) and Shannon diversity index (c) in open and shrub microsites at *E. multiflora* and *E. breana* sites. Boxes show median (line), 25th and 75th percentiles of sampling units (N=30). Whiskers show maximum and minimum values. *P<0.05, **P<0.01, ***P<0.001. Sampling unit pooled the data from the two sampling methods (pitfall and suction).

Figura 2. Abundancia (a), riqueza de especies (b) e índice de diversidad de Shannon (c) en micrositios abiertos y arbustivos en los sitios de *E. multiflora* y *E. breana.* Las cajas muestran las medianas (línea), 0.25 y 0.75 percentiles de las unidades de muestreo (N=30). Las líneas verticales muestran los valores máximos y mínimos. *P<0.05, **P<0.01, ***P<0.001. La unidad de muestreo es la suma de los datos obtenidos con los dos métodos de muestreo (trampas de caída y succión).

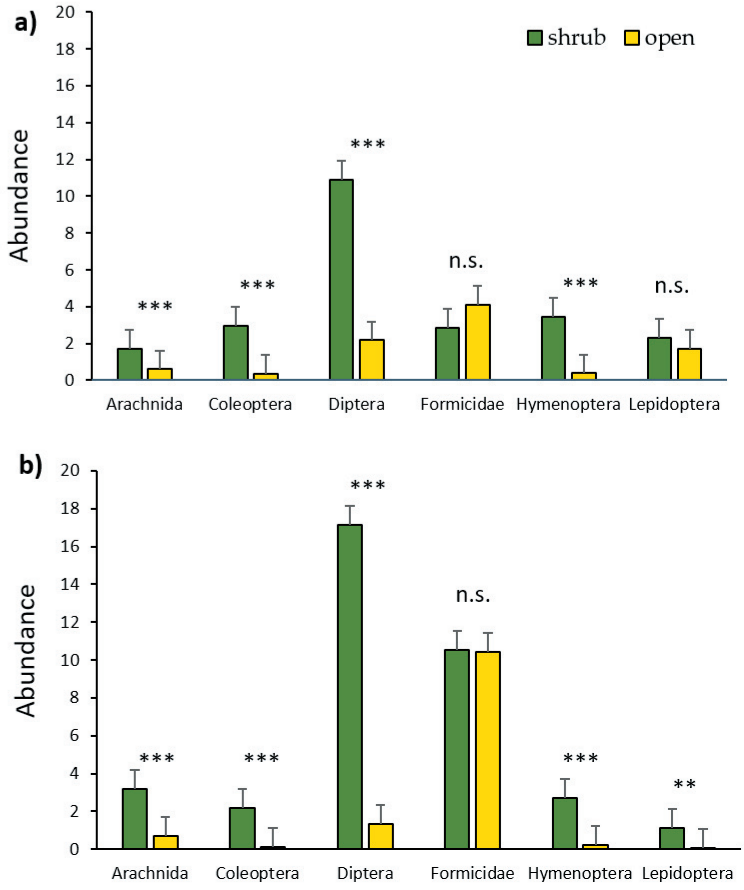

Figure 3. Abundance (means±S.D., N=30) of main arthropod taxonomical groups in open and shrub microsites in (a) *E. multiflora* and (b) *E. breana* sites. **P<0.01, ***P<0.001, n.s.: non-significant, P>0.05 (Kruskal-Wallis tests).

Figura 3. Abundancia (medias±D.E., N = 30) de los principales grupos taxonómicos de artrópodos en micrositios abiertos y arbustivos en los sitios de (a) *E. multiflora* y (b) *E. breana.* ** P<0.01, *** P<0.001, n.s.: no significativo, P>0.05 (pruebas de Kruskal-Wallis).

traps than in the suction samples, with the exception of *Brachymyrmex bruchi*, which was as numerous in the canopies of *E. breana* as on the ground.

Composition of the arthropod communities

When analyzing differences in abundance of the main taxonomical groups (Arachnida, Coleoptera, Diptera, Formicidae, Hymenoptera (excluding ants) and Lepidoptera) between microsites, in open microsites predominated ants (6.73±5, mean±S.D.), while in shrub microsites the most abundant group were dipterans (8.57±5.97) (Figure 3). The composition also differed between the microsites, where 38 species (44.2% of a total of 86 species, combined open and shrub) and 58 species (56.8% of 102 species) were collected exclusively in the shrub microsites of *E. multiflora* and *E. breana*, respectively. Hymenopterans (without ants) included overall 30 species of wasps, mainly parasitoids, predominantly captured in shrub microsites. This strong association with shrub patches was also found for some Coleopterans such as Coccinelidae (ladybugs) and Ptinidae, arachnids (scorpions, spiders and camel spiders [Solifugae]), as well as for the most abundant families among the collected dipterans (Ceratopogonidae, Chironomidae and Chloropidae).

Regarding differences in the composition of the arthropod communities between sites, 45 species (34.6% of 130 species, *E. multiflora* and *E. breana* sites combined) were found exclusively in the *E. breana* site and 27 (20.7%) exclusively in the *E. multiflora* site, while 58 (44.6%) were common to the two sites.

Discussion

We found that the abundance, species richness and diversity of epigeal arthropods were significantly higher in the *Ephedra* shrub microsites than in the open spaces between shrubs, thus supporting the hypothesis that the arthropod community reflects the effects of plant facilitation.

Many studies have addressed the effects of shrub microhabitats on arthropod communities and, as in our study, confirmed an 'arthropod island' effect generated by shrub cover on desert arthropods (e.g., Sanchez and Parmenter 2002; Mazía et al. 2006; Liu et al. 2013; Braun et al. 2021). The main underlying mechanism by which the shrub facilitative effect operates is the amelioration of the abiotic environmental conditions, this process resulting in a biased spatial distribution of arthropod individuals and species (Pugnaire et al. 2011). The microclimatic changes produced by vegetation benefit arthropods in both their mobility and foraging behavior, allowing them to thermoregulate better in relation to conditions outside of the vegetation (Molenda et al. 2012). Besides acting as a refuge, shrubs maintain soil moisture, incorporate organic matter into the soil, and provide an important source of food for pollinators, phytophagous, decomposers and predators (e.g., Whitford 2000; Rodríguez-Echeverría and Traveset 2015; Ruttan et al. 2021; Sagi and Hawlena 2021). The diversity of arthropods associated with the two species of *Ephedra* in our study shows that they support a wide range of arthropod groups that might provide a suite of ecosystem services locally, including those that contribute to the performance of plants. The harsh environmental conditions prevailing in the Puna ecosystems and the protection and resources provided by plants could jointly explain the influence exerted by shrubs over the arthropod community.

Shrub patches and bare soil interpatches can be seen as opposite sides of a continuous spatial system; therefore, it is expected to find arthropods in open spaces as a spillover effect of shrub facilitation (Michalet and Pugnaire 2016). Although the main benefits for arthropods would occur within the patch, the positive influence of shrub canopies could reach regions beyond the patch border, also affecting arthropods in bare soil (Meloni and Martínez 2021). Furthermore, while some arthropods are restricted to zones located under or very close to vegetation patches, other arthropods are relatively motile between microhabitats. Ants, for instance, were the most abundant group in open microsites. Desert ants possess mechanisms that allow them to cope with extreme temperatures, such as thermoregulatory nest architecture, time partitioning of activities to avoid extreme temperatures, and superorganism behaviors (Hölldobler and Wilson 1990; Yela et al. 2020). Therefore, in the open microsites there was an abundant but low diversity group of ants that live in bare soil but search for food in shrubs (such as invertebrate preys and pollination drops).

On the contrary, the dipterans were between five (for *E. multiflora*) and eleven times (for *E. breana*) more abundant in shrub microsites than in bare soils, suggesting that this group strongly depends on the habitat provided by *Ephedra* shrubs. Desert predators, represented mainly by spiders, scorpions, and camel spiders (Solifugae), as well as coleopterans and parasitoid wasps, were also more numerous in shrubs than in the open microsites. In this sense, the suction sampling methodology was proven to be useful in collecting arthropods strongly associated with the canopy that could not otherwise be collected by pitfall traps, thus providing a more complete picture of the entire arthropod community associated with *Ephedra* shrubs. The higher abundance and richness of arthropods in female plants compared to males could be explained by the pollination drops secreted by female cones (and absent in male cones), these representing a valuable food resource attractive to many arthropods (Aranda-Rickert et al. 2021) (Supplementary Material-Figure S1).

Although the two *Ephedra* species shared many species of the arthropod community, each had a particular species richness and assemblage exclusive to each site. For example, the most abundant parasitoid wasp in *E. multiflora* (Ichneumonidae sp.) was exclusively associated to the canopies of this species and absent at the *E. breana* site, suggesting that the local habitat or the identity of the plant species is of particular importance in determining the arthropod assemblage (Schaffers et al. 2008; Tobisch et al. 2023). Our results also show that the arthropod island effect was higher at the *E. breana* site, as shrub microsites differed from open microsites more strongly in terms of arthropod abundance (2.5 vs. 1.8 enhancement, *E. breana* vs. *E. multiflora*) and species richness (2.7 vs. 1.8) compared to the *E. multiflora* site. A possible explanation is that *E. breana*, which grows in relatively less stressful conditions and with higher plant cover and diversity, the increase in plant diversity should directly increase arthropod diversity (Borer et al. 2012). On the contrary, drought and stressful abiotic conditions, such as at the *E. multiflora* site, reduce plant and arthropod diversity, but also favor drought-adapted arthropods, thus facilitating a different arthropod assemblage (Prather et al. 2020). As the turnover of species at local sites within a given ecoregion significantly contributes to the full diversity in that ecoregion, our findings reinforce the importance of maintaining each of the different plant communities of the Desert Puna.

Future land management and restoration strategies for damaged natural habitats should consider the use of foundation shrubs such as *Ephedra* due to their positive effects on biodiversity, including their impacts on desert arthropods (Filazzola et al. 2019), as well as their tolerance to low water availability and preferences for well-drained soils. Differences in habitat requirements and plant characteristics between the two *Ephedra* species suggest that *E. multiflora* might be best suited for dune fixation and as foundation species in areas where environmental conditions are extremely harsh. On the other hand, *E. breana* is a valuable species for restoration because of its nutritional value as a forage resource for native fauna and livestock (Hunziker 1995); and has edible cones that are consumed by humans and native fauna (mainly birds) (Aranda-Rickert, unpublished). The lack of consumption of *E. multiflora* stems by native and exotic ungulates probably accounts for some kind of herbivore deterrent present in photosynthetic stems, which merits further study.

Many desert-adapted species of the *Ephedra* genus are currently used in desert restoration programs, such as *E. nevadensis* in the Mojave Desert, *E. trifurca* in the Sonoran Desert, and *E. californica* in the San Joaquin Desert of California (Ackerman 1979; Derbel et al. 2010; Lortie et al. 2018). In Argentina, *E. ochreata*, a species inhabiting the Patagonian steppes, has been also pointed out as a potential plant for productive (considering their value as food for livestock) restoration of degraded environments (Rodríguez-Araujo et al. 2019). In general, all these *Ephedra* species have high and homogeneous germination without pretreatments, and relatively high rates of establishment, with individuals that can reach an age greater than 50 years (Goldberg and Turner 1986). In California, *E. californica* is resilient to some herbivores during establishment, being able to recover quickly after significant removals of the shrub canopy (Lortie et al. 2018). As other desert foundation shrubs, *Ephedra* shrubs avoid growing under other shrub canopies and full-sun conditions promote their establishment rates and growth (Ji et al. 2019).

Final remarks

High-altitude deserts such as Puna are important ecological systems that support some of the highest levels of endemics relative to other ecosystems (Aagesen et al. 2012; Grau et al. 2019). Currently, climate change combined with growing tourism and an exponential growth of prospects and mining concessions for lithium exploitation are the main threats to biodiversity and hydrological function in Puna (Izquierdo et al. 2015). It can be expected that environmental pressures that lead to decreasing vegetation cover and/or connectivity of vegetation patches will result in additional indirect impacts on the arthropod community, amplifying the overall adverse effect on ecosystem functioning. Our study shows the positive effect of *Ephedra* shrubs on the arthropod fauna of the desert Puna, and stresses the importance of local and landscape conditions to maintain diverse arthropod communities. Given the crucial role played by arthropods in multiple ecosystem processes, a holistic approach that considers not only the plant species but also their associated arthropod communities is paramount for conservation and restoration strategies.

Acknowledgments. We are grateful to Virginia Cortés for assistance in the field, Carolina Rothen for soil analyses, and Segundo Núñez Campero, Gustavo E. Flores and Sergio A. Roig-Juñet for their help with the taxonomic identification of arthropods. Thanks are extended to the two anonymous reviewers that provided helpful comments on the earlier version of the manuscript. This research was funded by FONCYT (PICT-2019-1816 to AAR). NIY and AYDC were supported with postdoctoral and doctoral fellowships from CONICET, and JASM with a posdoctoral fellowship from FONCYT. JT and AAR are career researchers with CONICET. Field collection of entomological material in this study was carried out with the permission of the Secretaría de Medio Ambiente del Gobierno de la Provincia de Catamarca (Resol. No 905/15).

References

Aagesen, L., M. J. Bena, S. Nomdedeu, A. Panizza, R. P. López, and F. O. Zuloaga. 2012. Áreas de endemismo en los Andes centrales del sur. Darwiniana 50:218-251.

Ackerman, T. L. 1979. Germination and survival of perennial plant species in the Mojave Desert. Southwest Nat 24: 399-408. https://doi.org/10.2307/3671296.

Acosta, L., and E. A. Maury. 1998. Scorpiones. Pp. 545-558 *in* J. J. Morrone and S. Coscarón (eds.). Biodiversidad de Artrópodos Argentinos. Volumen I. Ediciones SUR, La Plata, Argentina.

Aguiar, M. R., and O. E. Sala. 1999. Patch structure, dynamics and implications for the functioning of arid ecosystems. Trends Ecol Evol 14:273-277. https://doi.org/10.1016/S0169-5347(99)01612-2.

Andersen, A. N., and J. D. Majer. 2004. Ants show the way down under: invertebrates as bioindicators in land management. Front Ecol Environ 2:291-298. https://doi.org/10.1890/1540-9295(2004)002[0292:ASTWDU]2.0.CO;2.

Aranda-Rickert, A., J. Torréns, N. Yela, M. M. Brizuela, and V. S. Di Stilio. 2021. Distance dependent contribution of ants to pollination but not defense in a dioecious, ambophilous Gymnosperm. Front Plant Sci 12. https://doi.org/10.3389/fpls.2021.722405.

Ayal, Y. 2007. Trophic structure and the role of predation in shaping hot desert communities. J Arid Environ 68:171-187. https://doi.org/10.1016/j.jaridenv.2006.05.013.

Beniston, M., H. Díaz, and R. Bradley. 1997. Climatic change at high elevation sites. An overview. Clim Change 36: 233-251. https://doi.org/10.1023/A:1005380714349.

Borer, E. T., E. W. Seabloom, and D. Tilman. 2012. Plant diversity controls arthropod biomass and temporal stability. Ecol Lett 15:1457-1464. https://doi.org/10.1111/ele.12006.

Braun, J., M. Westphal, and C. J. Lortie. 2021. The shrub *Ephedra californica* facilitates arthropod communities along a regional desert climatic gradient. Ecosphere 12:e03760. https://doi.org/10.1002/ecs2.3760.

Brooker, R. W., F. T. Maestre, R. M. Callaway, C. L. Lortie, et al. 2008. Facilitation in plant communities: the past, the present, and the future. J Ecol 96:18-34. https://doi.org/10.1111/j.1365-2745.2007.01295.x.

Brown, B. V., A. Borkent, J. M. Cumming, D. M. Wood, N. E. Woodley, and M. Zumbado. 2009. Manual of Central American Diptera: Volume I. NRC Research Press, Ottawa, Ontario, Canada.

Cabrera, A. L. 1968. Ecología Vegetal de la Puna. Pp. 91-116 *in* C. Troll (ed.). Geo-Ecology of the Mountain Regions of the Tropical Americas. Dümmler Verlag, Bonn, Germany.

Carilla, J., A. Grau, and S. Cuello. 2019. Vegetación de la Puna argentina. Pp. 143-156 *in* H. R. Grau, J. Babot, A. Izquierdo and A. Grau (eds.). La Puna Argentina: naturaleza y cultura. Serie Conservación de la Naturaleza 24. Fundación Miguel Lillo, Tucumán, Argentina. URL: tinyurl.com/2npaxj4k.

Carvalho, R. L., A. N. Andersen, D. V. Anjos, R. Pacheco, L. Chagas, and H. L. Vasconcelos. 2020. Understanding what bioindicators are actually indicating: Linking disturbance responses to ecological traits of dung beetles and ants. Ecol Ind 108:105764. https://doi.org/10.1016/j.ecolind.2019.105764.

Caveney, S., D. A. Charlet, H. Freitag, M. Maier-Stolte, and A. N. Starratt. 2001. New observations on the secondary chemistry of world *Ephedra* (Ephedraceae). Am J Bot 88:1199-1208. https://doi.org/10.2307/3558330.

Cigliano, M. M., H. Braun, D. C. Eades, and D. Otte. Orthoptera Species File. Version 5.0/5.0. URL: orthoptera.speciesfile.org.

Chowdhury, S., V. K. Dubey, S. Choudhury, A. Das, D. Jeengar, et al. 2023 Insects as bioindicator: A hidden gem for environmental monitoring. Front Environ Sci 11:1146052. https://doi.org/10.3389/fenvs.2023.1146052.

Derbel, S., B. Touzard, M. A. Triki, and M. Chaieb. 2010. Seed germination responses of the Saharan plant species *Ephedra alata* ssp. *alenda* to fungicide seed treatments in the laboratory and the field. Flora 205:471-474. https://doi.org/10.1016/j.flora.2009.12.025.

Fernández, F., and M. J. Sharkey. 2006. Introducción a los Hymenoptera de la Región Neotropical. Sociedad Colombiana de Entomología y Universidad Nacional de Colombia, Bogotá D. C., Colombia.

Filazzola, A., A. R. Liczner, M. Westphal, and C. J. Lortie. 2019. Shrubs indirectly increase desert seedbanks through facilitation of the plant community. PLoS ONE 14: e0215988. https://doi.org/10.1371/journal.pone.0215988.

Fletcher, M. J. 2009. Identification keys and checklists for the leafhoppers, planthoppers and their relatives occurring in Australia and neighbouring areas (Hemiptera: Auchenorrhyncha). URL: idtools.dpi.nsw.gov.au/keys/leafhop/index.html.

Gandhi, P., S. Iams, S. Bonetti, and M. Silber. 2019. Vegetation pattern formation in drylands. Pp. 469-509 *in* P. D'odorico, A. Porporato and W. C. Runyan (eds.). Dryland Ecohydrology. Springer International Publishing, Switzerland. https://doi.org/10.1007/978-3-030-23269-6_18.

Gardarin, A., M. Plantegenest, A. Bischoff, and M. Valantin-Morison. 2018. Understanding plant-arthropod interactions in multitrophic communities to improve conservation biological control: Useful traits and metrics. J Pest Sci 91:943-955. https://doi.org/10.1007/s10340-018-0958-0.

Gelbart, G., and P. von Aderkas. 2002. Ovular secretions as part of pollination mechanisms in conifers. Ann For Sci 59: 345-357. https://doi.org/10.1051/forest:2002011.

Goldberg, D. E., and R. M. Turner. 1986. Vegetation change and plant demography in permanent plots in the Sonoran Desert. Ecology 67:695-712. https://doi.org/10.2307/1937693.

Grau, H. R, J. Babot, A. Izquierdo, and A. Grau. 2019. La Puna Argentina: naturaleza y cultura. Serie Conservación de la Naturaleza 24. Fundación Miguel Lillo, Tucumán, Argentina. URL: tinyurl.com/bdemjkah.

Grissell, E. E., and M. E. Schauff. 1990. A Handbook of the families of Nearctic Chalcidoidea (Hymenoptera). Entomological Society of Washington, Washington, U.S.A.

He, P., J. Li, Y. Li, N. Xu, Y. Gao, L. Guo, T. Huo, C. Peng, and F. Meng. 2021. Habitat protection and planning for three Ephedra using the MaxEnt and Marxan models. Ecol Indic 133:108399. https://doi.org/10.1016/j.ecolind.2021.108399.

Hölldobler, B. and E. O. Wilson. 1990. The ants. Cambridge University Press, Cambridge, U.S.A. https://doi.org/10.1007/978-3-662-10306-7.

Hunziker, J. H. 1995. Ephedraceae. *In* A. T. Hunziker (ed.). Flora Fanerogámica Argentina 4:15-23.

Ickert-Bond, S. M., and S. S. Renner. 2016. The Gnetales: Recent insights on their morphology, reproductive biology, chromosome numbers, biogeography, and divergence times. J Syst Evol 54:1-16. https://doi.org/10.1111/jse.12190.

Izquierdo, A. E., H. R. Grau, J. Carilla, and E. Casagranda. 2015. Side effects of green technologies: The potential environmental costs of lithium mining on high elevation Andean wetlands in the context of climate change. GLP NEWS 12:53-56.

Izquierdo, A. E., H. R. Grau, C. J. Navarro, M. C. Castilla, and A. Grau. 2018. Highlands in Transition: Urbanization, Pastoralism, Mining, Tourism, and Wildlife in the Argentinian Puna. Mt Res Dev 38:390-400. https://doi.org/10.1659/MRD-JOURNAL-D-17-00075.1.

Ji, W., N. P. Hanan, D. M. Browning, H. C. Monger, D. P. C. Peters, et al. 2019. Constraints on shrub cover and shrub-shrub competition in a U.S. southwest desert. Ecosphere 10:e02590. https://doi.org/10.1002/ecs2.2590.

Kremen, C., R. K. Colwell, T. L. Erwin, D. D. Murphy, R. F. Noss, and M. A. Sanjayan. 1993. Terrestrial arthropod assemblages: their use in conservation planning. Conserv Biol 7:796-808. https://doi.org/10.1046/j.1523-1739.1993.740796.x.

Lawrence, J. F., A. M. Hastings, A. E. Seago, and S. A. Ślipiński. 2010. Beetles of the World. CSIRO Publishing, Clayton, Australia. URL: keys.lucidcentral.org/keys/v3/botw/.

Li, F., J. L. Liu, C. A. Liu, Q. J. Liu, and R. X. Niu. 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.

Lindén, A., and S. Mäntyniemi. 2011. Using the negative binomial distribution to model overdispersion in ecological count data. Ecology 92:1414-1421. https://doi.org/10.1890/10-1831.1.

Liu, R. T., F. Zhu, N. Song, X. Yang, and Y. Chai. 2013. Seasonal distribution and diversity of ground arthropods in microhabitats following a shrub plantation age sequence in desertified steppe. PLoS ONE 8:e77962. https://doi.org/10.1371/journal.pone.0077962.

Lortie, C. J., E. Gruber, A. Filazzola, T. Noble, and M. Westphal. 2018. The Groot Effect: plant facilitation and desert shrub regrowth following extensive damage. Ecol Evol 8:706-715. https://doi.org/10.1002/ece3.3671.

Mazía, C. N., E. Chaneton, and T. Kitzberger. 2006. Small-scale habitat use and assemblage structure of ground-dwelling beetles in a Patagonian shrub steppe. J Arid Environ 67:177-194. https://doi.org/10.1016/j.jaridenv.2006.02.006.

McIntire, E. J., and A. Fajardo. 2014. Facilitation as a ubiquitous driver of biodiversity. New Phytol 201:403-416. https://doi.org/10.1111/nph.12478.

Meloni, F., and A. S. Martínez. 2021. Soil arthropods indicate the range of plant facilitation on the soil of Mediterranean drylands. Theor Ecol 14:303-319. https://doi.org/10.1007/s12080-020-00498-z.

Michalet, R., and F. I. Pugnaire. 2016. Facilitation in communities: underlying mechanisms, community and ecosystem implications. Funct Ecol 30:3-9. https://doi.org/10.1111/1365-2435.12602.

Molenda, O., A. Reid, and C. J. Lortie. 2012. The Alpine Cushion Plant *Silene acaulis* as Foundation Species: A Bug's-Eye View to Facilitation and Microclimate. PLoS ONE 7: e37223. https://doi.org/10.1371/journal.pone.0037223.

Morales, M., J. Carilla, H. R. Grau, and R. Villalba. 2015. Multi-century lake area changes in the Southern Altiplano: a tree-ring-based reconstruction. Clim Past 11:1139-1152. https://doi.org/10.5194/cp-11-1139-2015.

Morales, M. S., D. A. Christie, R. Neukom, F. Rojas, and R. Villalba. 2019. Variabilidad hidroclimática en el sur del Altiplano: pasado, presente y futuro. Pp. 75-91 *in* H. R. Grau, J. Babot, A. Izquierdo and A. Grau (eds.). La Puna Argentina: naturaleza y cultura. Serie Conservación de la Naturaleza 24. Fundación Miguel Lillo, Tucumán, Argentina.

Myers, N., R. A. Mittermeier, C. G. Mittermeier, G. A. B. Da Fonseca, and J. Kent. 2000. Biodiversity hotspots for conservation priorities. Nature 403:835-858. https://doi.org/10.1038/35002501.

Noriega, J. A., J. Hortal, F. M. Azcárate, M. P. Berg, et al. 2018. Research trends in ecosystem services provided by insects. Basic Appl Ecol 26:8-23. https://doi.org/10.1016/j.baae.2017.09.006.

Olson, D. M, and E. Dinerstein. 2002. The global 200: priority ecoregions for global conservation. Ann Mo Bot Gard 89:199-224. https://doi.org/10.2307/3298564.

Prather, R. M., K. Castillioni, E. A. R. Welti, M. Kaspari, and L. Souza. 2020. Abiotic factors and plant biomass, not plant diversity, strongly shape grassland arthropods under drought conditions. Ecology 101:e03033. https://doi.org/10.1002/ecy.3033.

Pugnaire, F. I., C. Armas, and F. T. Maestre. 2011. Positive plant interactions in the Iberian Southeast: Mechanisms, environmental gradients, and ecosystem function. J Arid Environ 75:1310-1320. https://doi.org/10.1016/j.jaridenv.2011.01.016.

R Core Team. 2022. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Viena, Austria. URL: rproject. org.

Rodríguez-Araujo, M. E., C. Milano, and D. R. Pérez. 2019. Germinación de *Ephedra ochreata* Miers para la restauración de ambientes áridos en argentina. Agrociencia 53:617-629.

Rodríguez-Echeverría, S., and A. Traveset. 2015. Putative linkages between below- and aboveground mutualisms during alien plant invasions. AoB PLANTS 7:plv062. https://doi.org/10.1093/aobpla/plv062.

Ruttan, A., A. Filazzola, and C. J. Lortie. 2016. Shrub annual facilitation complexes mediate insect community structure in arid environments. J Arid Environ 134:1-9. https://doi.org/10.1016/j.jaridenv.2016.06.009.

Ruttan, A., C. J. Lortie, and S. M. Haas. 2021. Shrubs as magnets for pollination: A test of facilitation and reciprocity in a shrub-annual facilitation system. Curr Res Insect Sci 1:100008. https://doi.org/10.1016/j.cris.2021.100008.

Sagi, N., and D. Hawlena. 2021. Arthropods as the engine of nutrient cycling in arid ecosystems. Insects 12:726. https: //doi.org/10.3390/insects12080726.

Sánchez, B. C., and R. R. Parmenter. 2002. Patterns of shrub-dwelling arthropod diversity across a desert shrubland-grassland ecotone: a test of island biogeographic theory. J Arid Environ 50:247-265. https://doi.org/10.1006/jare.2001.0920.

Schaffers, A. P., I. P. Raemakers, K. V. Sýkora, and C. ter Braak. 2008. Arthropod assemblages are best predicted by plant species composition. Ecology 89:782-794. https://doi.org/10.1890/07-0361.1.

Scherber, C., N. Eisenhauer, W. W. Weisser, B. Schmid, et al. 2010. Bottom-up effects of plant diversity on multitrophic interactions in a biodiversity experiment. Nature 468:553-556. https://doi.org/10.1038/nature09492.

Schlesinger, W. H., J. A. Raikes, A. E. Hartley, and A. F. Cross. 1996. On the spatial pattern of soil nutrients in desert ecosystems. Ecology 77:364-374. https://doi.org/10.2307/2265615.

Stachowicz, J. 2001. Mutualism, Facilitation, and the Structure of Ecological Communities: Positive interactions play a critical, but underappreciated, role in ecological communities by reducing physical or biotic stresses in existing habitats and by creating new habitats on which many species depend. Bioscience 51:235-245. https://doi.org/10.1641/0006-3568(2001)051[0235:MFATSO]2.0.CO;2.

Tobisch, C., S. Rojas-Botero, J. Uhler, J. Müller, et al. 2023. Plant species composition and local habitat conditions as primary determinants of terrestrial arthropod assemblages. Oecologia 201:813-825. https://doi.org/10.1007/s00442-023-05345-6.

Whitford, W. G. 2000. Keystone arthropods as webmasters in desert ecosystems. Pp. 25-41 *in* D. C. Coleman (ed.). Invertebrates as webmasters in ecosystems. CABI Publishing, New York, U.S.A. https://doi.org/10.1079/9780851993942.0025.

Wright, A. J., K. E. Barry, C. J. Lortie, and R. M. Callaway. 2021. Biodiversity and ecosystem functioning: have our experiments and indices been underestimating the role of facilitation? J Ecol 109:1962-1968. https://doi.org/10.1111/1365-2745.13665.

Xu, C., M. Holmgren, E. H. Van Nes, F. T. Maestre, et al. 2015. Can we infer plant facilitation from remote sensing? a test across global drylands. Ecol Appl 25:1456-1462. https://doi.org/10.1890/14-2358.1.

Yela, N. I., L. A. Calcaterra, and A. Aranda-Rickert. 2020. Coping with temperature extremes: thermal tolerance and behavioral plasticity in desert leaf-cutting ants (Hymenoptera: Formicidae) across an altitudinal gradient. Myrmecol News 30:139-150. https://doi.org/10.25849/myrmecol.news_030:139.