



Brood chambers of a stem borer beetle modify arthropod functional diversity on its cactus host

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Abstract

Phenotypic variation in plants induced by biotic stressors can have cascading effects throughout arthropod communities. Habitat modifiers increase habitat complexity, which may promote species diversity and change arthropod species composition. A taxonomic approach to describe arthropod communities together with a trait-based approach might reveal mechanisms behind taxonomic changes and consequences for ecological processes. We previously found that the mistletoe *Tristerix aphyllus* induces susceptibility in the cactus *Echinopsis chiloensis* to the stem-borer beetle *Xyletomerus* sp., a habitat-modifier that drills brood chambers on cactus. Further, the community of arthropods that colonized chambers on parasitized cacti was more diverse and was different in composition compared to that found in chambers of non-parasitized cacti. We do not know whether the effects of brood chambers extend to the whole mistletoe-cactus system and how the arthropod community responds to seasonal phenology of mistletoe. Here we experimentally reduced the number of brood chambers and examined the effects on taxonomic and functional richness and composition, considering mistletoe seasonal phenology. We found a positive relationship between the number of chambers and arthropod species richness, abundance and functional richness. Arthropod taxonomic and functional richness were generally higher at mistletoe flowering compared to fruiting or mistletoe senescence/cactus flowering stages. Species composition varied with chamber number and changed with mistletoe seasonal phenology. Functional composition changed with mistletoe phenology. Functional richness and species richness were positively correlated, yet, functional redundancy is likely to occur. We conclude that cascading effects initiated by mistletoe extends beyond the chamber scale, up to the plant scale.

Keywords Arthropods · Cactus · Functional diversity · Mistletoe non-trophic indirect effects · Seasonal phenology

Introduction

Phenotypic variation in plants induced by biotic stressors can have cascading effects throughout arthropod communities (Callaway et al. 2003; Agrawal 2005; Denno and Kaplan

2007; Ohgushi et al. 2007; Ohgushi 2012, 2016; Ohgushi and Hambäck 2015). These bottom-up impacts over higher trophic levels may result from changes in plant nutritional quality, defensive traits and plant structure (Utsumi and Ohgushi 2009; Ohgushi 2012; Schoener and Spiller 2012; Ohgushi and Hambäck 2015). Trophic and non-trophic linkages caused by habitat modifiers may promote an increase in taxonomic diversity and generate changes in species composition (Bruno et al. 2003; Wright and Jones 2004; Hastings et al. 2007; Romero et al. 2015). Studies on plant trait-mediated indirect effects induced by biotic agents have mainly focused on changes in taxonomic diversity and species composition, but functional diversity parameters are seldom included. While a taxonomic approach describes changes in community structure based on species identity, a trait-based approach focuses on mechanisms behind these changes and their consequences on ecological processes (Hooper et al. 2002; Mouchet et al. 2010; Wong et al. 2019).

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Incorporating a trait-based approach in studies of plant trait-mediated indirect effects induced by biotic stressors may allow the development of a mechanistic framework linking traits and biotic stressors.

Parasitic plants may influence arthropod community parameters (Pennings and Callaway 2002; Mooney et al. 2006; Lázaro-González et al. 2019; Guerra et al. 2022). The development of broom-like branches in *Pinus ponderosa* P. Lawson & C. Lawson (Pinaceae) after infection by the mistletoe *Arceuthobium vaginatum* (Humb. & Bonpl. Ex Willd.) J. Presl (Santalaceae) had a positive indirect effect on predator abundance (Mooney et al. 2006). A reduction in tissue quality induced by the mistletoe *Viscum album* L. (Santalaceae) in *Pinus* needles had a negative indirect effect on the abundance of insect folivores (Lázaro-González et al. 2019). Habitat modifiers (also known as ecosystem engineers; Jones et al. 1994) increase structural complexity of their host plants, which might indirectly increase arthropod diversity and change community composition (Crain and Bertness 2006). In leaf rolls, galls and cavities made by habitat modifiers, it has been reported increased arthropod species richness (Johnson et al. 2002; Fournier et al. 2003; Vieira and Romero 2013; Calderón-Cortés et al. 2016; Pereira et al. 2021; Priest et al. 2021; Guerra et al. 2022). Furthermore, local effects of habitat modification can extend to the entire host plant (plant scale) (Lill and Marquis 2003; Vieira and Romero 2013).

To better understand how those changes in plant phenotype influence arthropod communities, it is useful to include a trait-based approach, which may provide mechanistic explanations on arthropod performance (Violle et al. 2007; Teittinen and Virta 2021). Studies including functional traits have mostly classified arthropod communities in terms of functional groups, with effect traits (i.e., traits that affect ecosystem processes) being rarely considered. For example, the abundance, richness and biomass of predators, herbivores and detritivores was higher in shrubs of *Croton fluribundus* Spreng. (Euphorbiaceae) with rolled leaves compared to shrubs with extended leaves (Vieira and Romero 2013). Effect traits might explain the impact of an organism on the system (Díaz and Cabido 2001). Thus, body length may characterize the ability of arthropods to use –and succeed on– different resource types, i.e., resource partitioning (Hoehn et al. 2008; Munyuli 2014), and head width may characterize resource use as wider heads accommodate larger mandibular muscles for chewing food (Silva and Brandao 2010; Gerisch et al. 2012). Trait-based studies often measure functional diversity and composition to describe functions within the system (Villéger et al. 2008; Mouchet et al. 2010). An index commonly used to describe functional diversity is functional richness (Mason et al. 2005; Mouillot et al. 2005; Villéger et al. 2008), which is defined by the amount of niche space filled by species in a community.

Analysis of the community-weighted mean (CWM), which is defined as the mean value of the trait in the community weighted by species relative abundance, is another approach to address trait-environment relationships and summarizes the community functional composition (Garnier et al. 2004; Lavorel et al. 2007; Ricotta and Moretti 2011). Functional richness is expected to decrease with decreasing species richness (Díaz and Cabido 2001; Guillemot et al. 2011). The positive association between species richness and functional richness may be explained by the selection effect, which assumes that species loss at random in a system would also decrease the range of trait values, and thus functional richness (Tilman et al. 1997). However, if there are functionally redundant species in the system then species loss would not significantly affect functional richness (Flynn et al. 2009; Mayfield et al. 2010). Communities resilient to disturbance and environmental change are characterized by a high functional redundancy (McCann, 2000).

The leafless mistletoe *Tristerix aphyllus* Ex. Barlow & Wiens (Loranthaceae) is a holoparasitic plant endemic to semiarid Chile that infects columnar cacti of the genera *Echinopsis* and *Eulychnia* (Cactaceae) (Silva and Martínez del Río 1996; Medel et al. 2002). Mistletoe flowering begins at the onset of fall (late March) and peaks between April–June (Medel et al. 2002). The peak of fruit production occurs during late winter–early spring (Medel et al. 2002). We recently found that *T. aphyllus*, by reducing cactus tissue toughness, induces susceptibility in *Echinopsis chiloensis* (Colla) Schlump. To the stem borer beetle *Xyletomerus* sp. (Coleoptera: Anobiidae), a habitat modifier that drills more brood chambers in parasitized compared to non-parasitized cacti (Guerra et al. 2022). Brood chambers in parasitized cacti were larger (over 35% more volume) than those in non-parasitized cacti (Guerra et al. 2022). The community of arthropods that colonized beetle brood chambers of parasitized cacti was richer in species, higher in abundance and different in composition compared to the arthropods community in chambers of non-parasitized cacti (Guerra et al. 2022). Those changes in the arthropod community were described in terms of species diversity and composition at chamber scale. Arthropods within the chambers might interact with arthropods on cactus surface or on mistletoe, likely modifying taxonomic and functional richness throughout the whole mistletoe–cactus system (plant-level). Mistletoe flowering begins at the onset of fall (late March) and peaks between April–June (Medel et al. 2002). The peak of fruit productions occurs during late winter–early spring (Medel et al. 2002). This winter-flowering mistletoe may provide food resources (nectar and fruits) for arthropods during seasons with food scarcity (fall and winter) (Olivares and Squeo 1999). Most shrubs at the coastal desert of Chile initiate flowering at early spring (late September) and produce fruits at mid-October (Olivares and Squeo 1999). The mistletoe

gradually dries up during late spring and emerges (or resprouts) by the end of summer, when *Echinopsis* is flowering (early October), thus mistletoe senescence and cactus flowering stages overlap. At a broader scale, i.e., the whole mistletoe-cactus system, an adequate use of resources provided by these plant species (e.g., nectar and fruits) across seasons may depend on the feeding strategies and morphological traits that arthropods show. Thus, different arthropod species, with different traits, would be expected depending on the available resources. Studies on arthropod interactions in the mistletoe-cactus system are scarce, but nectar-robbing ants (*Camponotus morosus* Smith, *Conomyrma goetschi* Goetsch and *Solenopsis gayi* Spinola; Hymenoptera, Formicidae) have been reported (Caballero et al. 2013).

The aim of this study was to evaluate the effects of brood chamber number on taxonomic and functional richness of the arthropod community at the plant scale (mistletoe-cactus system), further considering seasonal phenology (mistletoe flowering, mistletoe fruiting, and mistletoe senescence/cactus flowering). We performed a manipulative field experiment, reducing the number of chambers built by the stem-borer beetle on cactus surface. We hypothesized that a decreased chamber number would negatively affect arthropod taxonomic and functional richness and modify taxonomic and functional composition. Further, we expected that resources offered by the mistletoe and the cactus at different seasons would attract distinct arthropod assemblages with different identities and trait values, thus modifying taxonomic and functional richness and composition. We expected: (1) a decrease in species diversity and a change in species composition with decreasing chamber number as consequence of the loss of interactions between arthropods within and outside chambers, (2) that prevailing arthropod assemblages and specific traits would vary with resources offered by mistletoe and cactus at different seasons (e.g., nectarivorous prevailing at flowering season); (3) a decrease in functional richness and a change in functional composition with decreasing chamber number; and (4) a positive relationship between arthropod species richness and functional richness.

Methodology

Study site

We carried out a field experiment in the buffer zone of Fray Jorge National Park, located at the southern edge of the Atacama Desert in Chile (30°23'S; 71°23'W). The climate is semiarid Mediterranean, with warm dry summers (December–February) and mean annual precipitation of 125 mm mainly occurring during winter months (May–September) (Squeo et al. 2015). Mean monthly temperatures range from 24 °C (January) to 4 °C (July) (Gutierrez et al.

2010). Columnar cacti of the genera *Eulychnia* and *Echinopsis*, host plants of the mistletoe *T. aphyllus*, can be found in association with shrubs such as *Flourensia thurifera* Molina, *Gutierrezia resinosa* Hook. & Arn. and *Cordia decandra* Hook. & Arn., and the bromeliad *Puya chilensis* Molina (Squeo et al. 2015).

Manipulative experiment

A manipulative experiment was carried out in an area of 21.4 ha, where we chose a total of 40 parasitized cacti. Cacti were of 1.4–3.0 m height, similar in architecture and separated at least 5 m. We counted the total number of chambers in each cactus and implemented three treatments, closing 80%, 40% and 0% of the chambers. Thus, cacti resulted with 20% (average number of open chambers: 70.2 ± 8.3), 60% (average number of open chambers: 209.5 ± 19.1) and 100% (average number of open chambers: 442.6 ± 42.8) of their chambers opened. Chambers were closed with soft modeling clay. We further considered a control treatment that examined whether modeling clay for walls (Lanco-Chile) had any influence on arthropod behavior (average number of open chambers: 371.1 ± 35.6). This treatment consisted in placing a small piece of clay in close proximity to 100% of the chambers, without closing them. Sample size for each of the four treatments was ten.

Arthropod sampling

Arthropods were sampled from late April 2019 (beginning of mistletoe flowering) to early December 2019 (mistletoe senescence stage), and from late February 2020 to March 2020 (mistletoe bud production). The cactus flowering period overlaps with the end of mistletoe senescence during early October. Arthropods were sampled with water traps, consisting of plastic glasses (250 ml) filled with 200 ml of a solution of water, neutral soap and salt (0.5 ml of soap and 1 g NaCl per L H₂O). We attached traps to cacti stems (one glass per cactus) after removing spines from a 400 cm² area. Traps were strategically located 10 cm below *T. aphyllus*. This allowed to capture mistletoe arthropods and cactus arthropods during fall-winter (mistletoe flowering, fruiting and cactus vegetative stages) and arthropods at flowering stage of cactus (end of spring–summer months) when mistletoe dries (senescence stage). We collected arthropods in the traps every two weeks and refilled them with the solution after each collection event. Collected arthropods were stored in sealed Ziploc bags with ethanol 70%. Bags were immediately transported to the lab for species identification. Three sampling dates (March 2019, July 2019 and November 2019) were not considered in the analysis because foxes and guanacos dislodged 60% of traps.

Arthropod taxonomic identification

Arthropod specimens were sorted according to chamber closure treatments and sampling dates. Arthropods were identified to species or morphospecies, counted and morphological traits were measured. We pinned around 100 individuals as a reference collection for arthropod fauna associated with the mistletoe-cactus system. Identification was carried out in the Ecological Entomology Lab at Universidad de La Serena and the Laboratorio de Control Biológico at Universidad de Talca. Only adult individuals were considered in the identification. All specimen vouchers were deposited in the Ecological Entomology Lab at Universidad de La Serena, Chile.

Trait definition and measurement

We classified arthropods considering the following traits: (1) functional guild: nectarivores, omnivores, herbivores and predators (Wong et al. 2019), (2) oral apparatus/feeding type: chelicerae, chewers, chewers-suckers and suckers (Wong et al. 2019), and (3) morphometry: body length (measured from the head tip to the posterior abdominal tergum edge), head width (measured across the eyes), and thorax width (measured across the wings). In the case of spiders, because their body presents two segments (cephalothorax and abdomen), we considered the following measurements: body length, cephalothorax width and abdomen width (Brousseau et al. 2018). For statistical analysis we considered spider abdomen width analogous to insect thorax width. Measurements were performed following Moretti et al. (2017). All morphological measurements were carried out using a micrometer ruler coupled to a stereoscopic microscope.

Data analysis

All analyses were performed using the statistical package R ver. 3.3.2 (R Development Core Team, 2020).

Arthropod diversity and species composition vs beetle chamber number

To identify the relationship between chamber number and species richness and abundance, we conducted separated general linear analyses of covariance (GLM, ANCOVA design). We used as covariate mistletoe/cactus phenological stages (mistletoe flowering, mistletoe fruiting and mistletoe senescence/cactus flowering). For species richness and abundance (count data) we used a Quasi-Poisson distribution linked to a log function. In the case of species diversity (continuous data) we used a Gaussian distribution linked to an identity function. Statistical significance of GLM ANCOVA

was determined using Wald chi-square tests. To evaluate differences between phenological stages, we performed post-hoc multiple comparisons of means using the *lsmean()* function from the LSMEANS package.

We performed a non-parametric permutation multivariate analysis of variance (PERMANOVA) and regression to evaluate the association between chamber number and species composition of arthropods depending on mistletoe/cactus phenological stages. We used the *Adonis()* function from the VEGAN package to estimate a *P*-value ($\alpha=0.05$). Pairwise differences were tested using the *adonis.pair()* function from the ECOLUTILS package. We plotted community composition using the first two axis of a three-dimensional non-metric multidimensional scaling (NMDS) based on Euclidean distances. To assess whether there was a significant relationship ($P < 0.05$) between ordination axis scores and increased chamber number we used the *envfit()* function with 999 permutations. To evaluate the degree of association of arthropod species with phenological stages, we calculated indicator taxa values for each species, using *inval()* function from LABDSV package. We only report species with significant associations with the phenological stages.

Arthropod functional richness and composition vs beetle chamber number

We used *dbDF()* function from the FD package to calculate functional richness (FRic) and community-weighted mean (CWM). To identify the relationship between chamber number and FRic depending on mistletoe/cactus phenological stages, we conducted a GLM ANCOVA test. As FRic data are continuous, we used a Gaussian distribution linked to an identity function. Post-hoc multiple comparisons were performed using the *lsmeans()* function from the LSMEANS package.

To evaluate the effect of chamber number on functional composition (community-weighted mean, CWM) depending on mistletoe/cactus phenological stages, we conducted a non-parametric permutation multivariate analysis of variance (PERMANOVA) and regression. We used the *Adonis()* function from the VEGAN package to estimate a *P*-value ($\alpha=0.05$). Pairwise differences were tested using the *adonis.pair()* function from the ECOLUTILS package. We plotted community composition using the first two axis of a three-dimensional non-metric multidimensional scaling (NMDS) based on Euclidean distances. To assess whether there was a significant relationship ($P < 0.05$) between ordination axis scores and increased chamber number, we used the *envfit()* function with 999 permutations. In addition, to better understand the relationship between chamber number and functional traits (functional guilds and morphological

traits) at different phenological stages of mistletoe/cactus, we performed univariate GLM ANCOVAs.

Relationship between arthropod species richness and functional richness

To assess the relationship between species richness and functional richness, we used pooled functional diversity as dependent variable and pooled species richness as independent variable in a scatter plot. Then we fitted the curve by linear regression, asymptotic and logistic models using GLMs. The highest R^2 among the models was chosen as the best fit.

Results

Throughout 16 samplings 2019–2020, we collected a total of 10,159 arthropod specimens associated with the mistletoe-cactus system, belonging to 76 species (Supplementary data Table S1). Specifically, we conducted five samplings during mistletoe flowering, five during mistletoe fruiting and six during mistletoe senescence/cactus flowering periods, including a total of 40 plants (mistletoe-cactus) and approximately 40 traps. Morphological traits were measured in 3704 arthropod specimens that were sorted according to chamber closing treatments and mistletoe/cactus phenological stages (Supplementary data Table S1). The most abundant species belonged to the order Hymenoptera, which included solitary and eusocial bees from the family Halictidae (64.7%), mostly represented by the genus *Caenohalictus* (28.6%). Ants, represented by *Camponotus morosus* (9.3%) and *Dorymyrmex goetschi* (6.2%), were the second most abundant group within Hymenoptera. In the case of Diptera, the most representative flies were *Phthiria* sp. (Bombyliidae) (81.2%) and a hoverfly from the genus *Copestylum* (6.7%). Coleopterans were represented by the stem borer beetle *Xyletomerus* sp. (Anobiidae) (26.8%) and the click beetle *Conoderus* sp. (Elateridae) (21.2%). The order Aranea was mainly represented by the ghost spiders of the family Anyphaenidae (39.3%), which included the genera *Oxysoma* (24%) and *Gayennoides* (8%). The jumping spiders of the family Salticidae (37%), represented by the genera *Admesturius* (24.7%) and *Menemerus* (5.3%), were the second most abundant group within Aranea. Lepidoptera was mainly represented by Gelechiidae moths (84.2%), with caterpillars generally observed feeding on mistletoe fruits.

Arthropod diversity and species composition vs beetle chamber number

We found no differences in taxonomic or functional richness parameters between the control treatment (clay placed outside the chambers) and 0% closure treatment ($P > 0.05$;

data not shown). Therefore, we included the control treatment in the GLM ANCOVAs analyses.

Species richness (Fig. 1a; Table 1) and abundance (Fig. 1b; Table 1) were positively associated with chamber number, and both parameters varied with mistletoe/cactus phenological stages. Species richness was 20% greater during mistletoe flowering (MFI) compared to mistletoe fruiting (MFr) or mistletoe senescence/cactus flowering stages (MSe/CFl) (Fig. 1a). Species abundance was 67% higher during MFI than at MSe/CFl stages, while abundance during MFr did not differ from those at MFI or MSe/CFl stages (Fig. 1b).

Species composition changed with the chamber number (PERMANOVA: $F = 6.25$, $R^2 = 0.04$, $P < 0.05$) and differed among mistletoe/cactus phenological stages (PERMANOVA: $F = 18.36$, $R^2 = 0.24$, $P < 0.001$; Fig. 2)

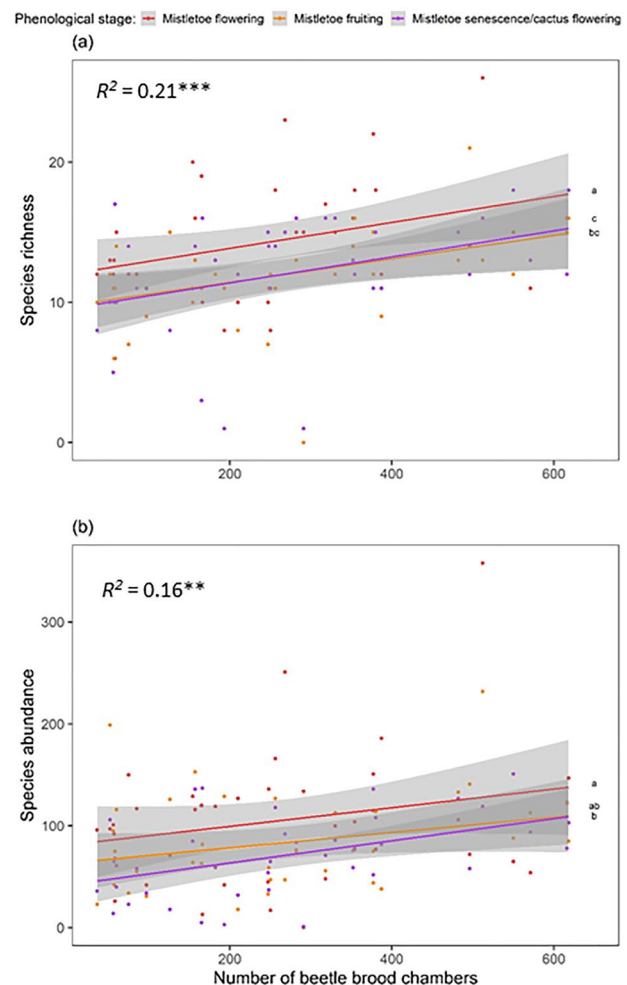


Fig. 1 Relationship between number of beetle brood chambers and species richness (a) and species abundance (b) of the arthropod community at mistletoe flowering, mistletoe fruiting and mistletoe senescence/cactus flowering phenological stages. Regression lines showing a different letter are statistically different ($P < 0.05$). R^2 of the general regression is shown (* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$)

Table 1 Results of GLM ANCOVA relating community parameters, brood chamber number (number of chambers per cactus) and phenological stages of the mistletoe *Tristerix aphyllus* (flowering, fruiting and senescence) and the cactus *Echinopsis chiloensis* (flowering)

Community parameters	Chamber number		Phenological stage		Chamber number x pheno- logical stage	
<i>Taxonomic diversity</i>						
Species richness	$X^2_{(1,115)} = \mathbf{20.38}$	$P < \mathbf{0.001}$	$X^2_{(2,113)} = \mathbf{12.16}$	$P = \mathbf{0.003}$	$X^2_{(2,111)} = 0.12$	$P = 0.94$
Species abundance	$X^2_{(1,115)} = \mathbf{314.26}$	$P < \mathbf{0.001}$	$X^2_{(2,113)} = \mathbf{274.51}$	$P = \mathbf{0.007}$	$X^2_{(2,111)} = 22.25$	$P = 0.67$
Simpson diversity index	$X^2_{(1,115)} = 0.004$	$P = 0.20$	$X^2_{(2,113)} = 0.04$	$P = 0.48$	$X^2_{(2,111)} = 0.04$	$P = 0.49$
<i>Functional diversity</i>						
Functional richness	$X^2_{(1,115)} = \mathbf{0.21}$	$P < \mathbf{0.01}$	$X^2_{(2,113)} = \mathbf{0.17}$	$P < \mathbf{0.01}$	$X^2_{(2,111)} = 0.03$	$P = 0.12$
<i>Community weighted mean</i>						
Functional guild						
Nectarivores	$X^2_{(1,114)} = 0.08$	$P = 0.07$	$X^2_{(2,112)} = \mathbf{0.38}$	$P < \mathbf{0.001}$	$X^2_{(2,110)} = 0.02$	$P = 0.64$
Omnivores	$X^2_{(1,114)} = \mathbf{0.18}$	$P = \mathbf{0.007}$	$X^2_{(2,112)} = \mathbf{0.43}$	$P < \mathbf{0.001}$	$X^2_{(2,110)} = 0.06$	$P = 0.32$
Herbivores	$X^2_{(1,114)} = \mathbf{0.007}$	$P = \mathbf{0.002}$	$X^2_{(2,112)} = 0.004$	$P = 0.053$	$X^2_{(2,110)} = 0.001$	$P = 0.42$
Predators	$X^2_{(1,114)} = 0.003$	$P = 0.30$	$X^2_{(2,112)} = 0.02$	$P = 0.052$	$X^2_{(2,110)} = 0.004$	$P = 0.55$
Type of oral apparatus						
Chelicerae	$X^2_{(1,114)} = 0.002$	$P = 0.41$	$X^2_{(2,112)} = 0.002$	$P = 0.71$	$X^2_{(2,110)} = 0.004$	$P = 0.49$
Chewer	$X^2_{(1,114)} = \mathbf{0.12}$	$P = \mathbf{0.03}$	$X^2_{(2,112)} = \mathbf{0.40}$	$P < \mathbf{0.001}$	$X^2_{(2,110)} = 0.04$	$P = 0.40$
Chewer-sucker	$X^2_{(1,114)} = 0.01$	$P = 0.49$	$X^2_{(2,112)} = \mathbf{1.34}$	$P < \mathbf{0.001}$	$X^2_{(2,110)} = 0.07$	$P = 0.30$
Sucker	$X^2_{(1,114)} = 0.03$	$P = 0.11$	$X^2_{(2,112)} = \mathbf{0.70}$	$P < \mathbf{0.001}$	$X^2_{(2,110)} = 0.02$	$P = 0.49$
Morphology						
Body size	$X^2_{(1,114)} = 0.25$	$P = 0.59$	$X^2_{(2,112)} = \mathbf{26.40}$	$P < \mathbf{0.001}$	$X^2_{(2,110)} = 2.11$	$P = 0.30$
Head width	$X^2_{(1,114)} = 0.005$	$P = 0.86$	$X^2_{(2,112)} = \mathbf{1.24}$	$P = \mathbf{0.03}$	$X^2_{(2,110)} = 0.21$	$P = 0.54$
Thorax width	$X^2_{(1,114)} = 0.08$	$P = 0.54$	$X^2_{(2,112)} = \mathbf{2.74}$	$P = \mathbf{0.002}$	$X^2_{(2,110)} = 0.40$	$P = 0.30$

Statistically significant effects ($P < 0.05$) are in bold

(Supplementary data Table S2). Arthropod community composition during MFI was different from those at MFr and MSe/CFI stages, while it differed between MFr and MSe/CFI stages (Supplementary data Table S2). Community composition changed with the chamber number (ENVFIT: $R^2 = 0.07$, $P < 0.018$; vector in Fig. 2). The indicator value for the degree of association showed that a total of 26 arthropod species displayed a significant association with a particular mistletoe/cactus phenological stage: 14 species for MFI, 9 species for MFr and 3 species for MSe/CFI (Table 2).

Arthropod functional richness and composition vs beetle chamber number

Functional richness (FRich) was positively correlated to chamber number and differed across mistletoe phenological stages (Fig. 3a; Table 1). FRich was 21% greater at MFI than at MFr and 24% greater than at MSe/MFI stages (Fig. 3a), while it was similar at MFr and MSe/CFI stages (Fig. 3a).

Trait composition (CWM) did not change with chamber number, but it differed among all three phenological stages (PERMANOVA: $F = 13.04$, $R^2 = 0.19$, $P < 0.001$) (Fig. 4; Supplementary data Table S3). A univariate analysis showed a marginally non-significant relationship between relative

abundance of nectarivores and chamber number (Fig. 5a; Table 1). Abundance of nectarivores varied with mistletoe/cactus phenological stage (Fig. 5a). Nectarivores were 16% more abundant at MFI compared to MFr (Fig. 5a) and showed a similar abundance at MFr and MSe/CFI stages (Fig. 5a). Conversely, abundance of omnivores was negatively related to chamber number and differed with mistletoe phenology (Fig. 5b; Table 1). Omnivores during MSe/CFI were 50% and 59.5% more abundant than at MFr and MFI, respectively (Fig. 5b), and were equally abundant at MFI and MFr. Herbivore abundance was positively associated with chamber number (Fig. 5c; Table 1). We found that herbivore abundance was marginally different across mistletoe phenological stages (Fig. 5c; Table 1). Abundance of predators was not related to chamber number and was marginally different with mistletoe phenology (Fig. 5d; Table 1).

Chelicerata abundance was related neither to chamber number nor mistletoe phenology (Fig. 5e; Table 1). Relative abundance of chewers showed a negative relationship with number of chambers and differed among mistletoe phenological stages (Fig. 5f; Table 1). Chewers during MSe/CFI were 60% and 30% more abundant than at MFI and MFr stages, respectively (Fig. 5f). Abundances of arthropods with chewer-sucker and sucker oral apparatus were not significantly related

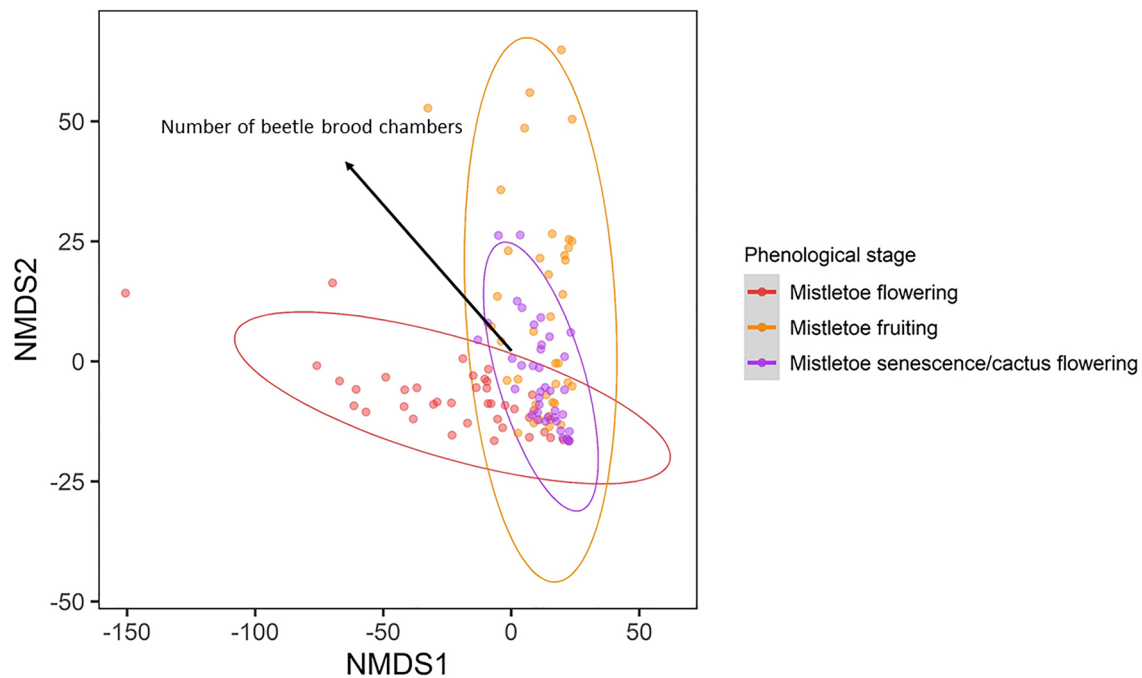


Fig. 2 Changes in arthropod species composition along a gradient of beetle brood chambers on cactus areoles (PERMANOVA: $F=6.25$, $R^2=0.04$, $P<0.05$ at mistletoe flowering (brown), mistletoe fruiting (orange) and mistletoe senescence/cactus flowering (purple) stages of mistletoe (PERMANOVA: $F=18.36$, $R^2=0.24$, $P<0.001$, final

stress=0.11). Patterns are based on global non-metric multidimensional scaling (NMDS) analysis. The vector represents the correlation between beetle brood chamber number and species composition in multidimensional space (ENVFIT: $R^2=0.07$, $P<0.018$)

to chamber number but did differ across mistletoe phenological stages (Fig. 5g, h; Table 1). Chewer-suckers were 31.3% more abundant at MFI than at MFr and 24.2% more abundant at MFI than at MSe/CFI (Fig. 5g). Suckers during MFr were 73.4% and 53.8% more abundant than at MFI and MSe/CFI stages, respectively. Sucker abundance was the same at MFI and MSe/CFI stages (Fig. 5h).

Whereas morphological traits (body length, head width and thorax width) were not statistically associated with chamber number, they varied with mistletoe phenological stage. Body size of arthropods found during MFI was 17% and 8% larger than those sampled at MFr and MSe/CFI stages, respectively; arthropods were 10% larger at MSe/CFI compared to MFr (Fig. 5i). Head width of arthropods found during MSe/CFI was 12.9% larger to those found at MFr and did not differ from those found at MFI (Fig. 5j). Head width of arthropods was the same at MFI and MSe/CFI stages. Finally, thorax width of arthropods at MFI was 18.4% larger than those at MFr and similar to those sampled during MSe/CFI (Fig. 5k).

Relationship between species richness and functional richness

The relationship between species and functional richness was linear and positive (Spearman $R=0.58$, $R^2=0.34$,

$P<0.001$; Fig. 6). We compared the slopes of this relationship (0.58) with the $y=x$ function with a 'ltest()' function (LMTEST package), and slope were significantly different ($P<0.001$).

Discussion

In a previous study on this mistletoe-cactus system, we found that mistletoe initiated cascading effects by reducing cactus tissue toughness, which facilitated the construction of brood chambers by the stem borer *Xyletomerus* sp., a habitat modifier. Beetle brood chambers were inhabited by a community of arthropods greater in diversity and different in composition from those in chambers of cacti not parasitized with mistletoe (Guerra et al. 2022). Here, after conducting a field experiment, we found that cascading effects initiated by mistletoe extend beyond the chamber scale, up to the plant scale. Furthermore, we found that the experimental reduction of brood chamber decreased both taxonomic (species richness and abundance) and functional diversity (functional richness) and changed taxonomic composition along the chamber gradient. Resources offered by mistletoe and cactus at different seasons likely influenced both taxonomic and functional richness and composition of arthropods. Species

Table 2 Arthropod species or morphospecies showing significant associations (indicator value) of arthropods with mistletoe/cactus phenological stages (mistletoe flowering = MFl, mistletoe fruiting = MFr, and mistletoe senescence/cactus flowering = MSe/CFI)

Species/Morphospecies	Family	Functional guild	Phenological stage	Indicator value	P
<i>Caenohalictus</i> sp. 1	Halictidae	Nectarivore	MFl	0.685	0.001
<i>Copestylum</i> sp. 1	Syrphidae	Nectarivore	MFl	0.494	0.001
Diptera sp. 3		Nectarivore	MFl	0.308	0.001
<i>Chilicola</i> sp. 1	Colletidae	Nectarivore	MFl	0.291	0.028
Diptera sp. 4		Nectarivore	MFl	0.253	0.001
Diptera sp. 5		Nectarivore	MFl	0.198	0.006
Syrphidae sp. 2	Syrphidae	Nectarivore	MFl	0.195	0.002
<i>Melectoides</i> sp. 1	Anthophoridae	Nectarivore	MFl	0.190	0.001
Geometridae sp. 1	Geometridae	Nectarivore	MFl	0.179	0.002
Hymenoptera sp. 1		Nectarivore	MFl	0.163	0.002
Geometridae sp. 2	Geometridae	Nectarivore	MFl	0.154	0.004
Sphecidae sp. 1	Sphecidae	Nectarivore	MFl	0.154	0.008
Diptera sp. 6		Nectarivore	MFl	0.128	0.019
Syrphidae sp. 3	Syrphidae	Nectarivore	MFl	0.103	0.039
<i>Phthiria</i> sp. 1	Bombyliidae	Nectarivore	MFr	0.689	0.001
Coccinellidae sp. 1	Coccinellidae	Predator	MFr	0.378	0.001
<i>Megachile</i> sp. 1	Megachilidae	Nectarivore	MFr	0.352	0.002
<i>Conoderus</i> sp. 1	Elateridae	Herbivore	MFr	0.265	0.002
<i>Megachile</i> sp. 2	Megachilidae	Nectarivore	MFr	0.219	0.001
<i>Svastrides</i> sp. 1	Apidae	Nectarivore	MFr	0.211	0.001
<i>Centris cinerea</i>	Apidae	Nectarivore	MFr	0.176	0.049
<i>Solenopsis</i> sp. 1	Formicidae	Omnivore	MFr	0.132	0.005
<i>Astylus</i> sp. 1	Merylididae	Herbivore	MFr	0.124	0.039
<i>Dorymyrmex goetschi</i>	Formicidae	Omnivore	MSe/CFI	0.575	0.001
<i>Apis mellifera</i>	Apidae	Nectarivore	MSe/CFI	0.469	0.001
<i>Lonchopria</i> sp. 1	Colletidae	Nectarivore	MSe/CFI	0.417	0.002

Functional guild of each species is shown

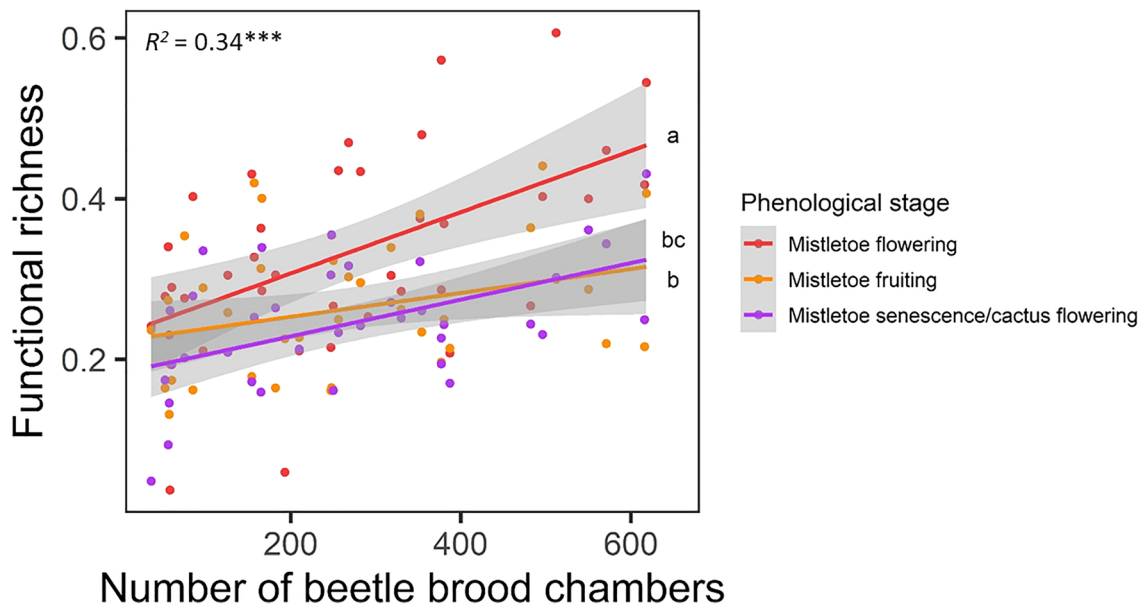


Fig. 3 Relationship between the number of beetle brood chambers on cactus and functional richness at mistletoe flowering, mistletoe fruiting and mistletoe senescence/cactus flowering phenological stages.

Regression lines showing a different letter are statistically different ($P < 0.05$). R^2 of general regression is shown (* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$)

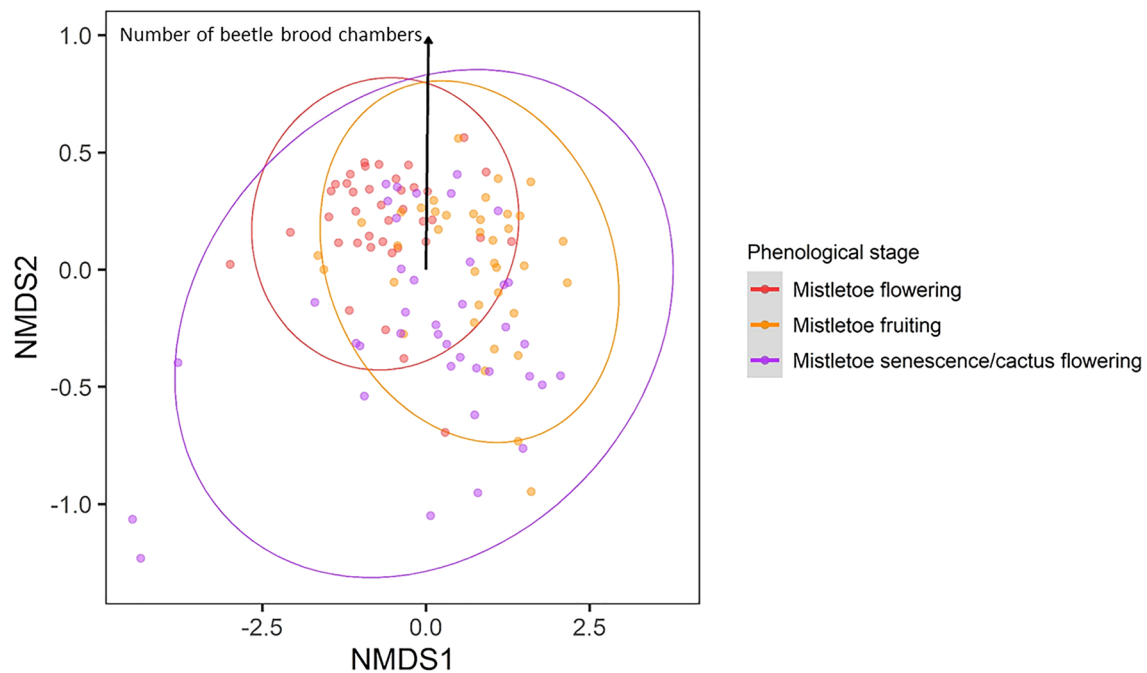


Fig. 4 Changes in trait composition along a gradient of beetle brood chambers in the cactus areoles at mistletoe flowering (brown), mistletoe fruiting (orange) and mistletoe senescence/cactus flowering (purple) phenological stages (PERMANOVA: $F=13.04$, $R^2=0.19$,

$P<0.001$; final stress=0.03). Patterns are based on global non-metric multidimensional scaling (NMS) analysis. The vector represents the correlation between chamber number gradient and trait composition in multidimensional space (ENVFIT: $R^2=0.02$, $P=0.22$)

richness, functional richness and species abundance were higher at MFI (fall) compared to MSe/CFI (spring–summer). Functional composition differed at all phenological stages. Nectarivores and chewing-suckers were more abundant at MFI, while omnivores were more abundant at MSe/CFI. The abundance of suckers was higher at MFr. Arthropods found during MFI were the largest.

Overall, arthropod species richness and abundance were favored by brood chamber presence across seasons, with values during mistletoe flowering being always highest. In general, the flowering period of bushes and herbs in north-central Chile begins in spring, after the (short) winter rains (Olivares and Squeo 1999), which coincides with the peak of abundance of terrestrial and flying arthropods (Meserve et al., 2016). However, arthropods that develop between fall and winter may be favored by winter-flowering plants such as mistletoe. Mistletoe's peak of flowering is in fall and it can partially extend over the rainy season (Medel et al. 2002). Arthropod species that feed on nectar (e.g., halictid bees and bombyliid flies) are the most abundant during mistletoe peak of flowering. The abundance of herbivores was not significantly associated with phenological stages of mistletoe but was positively associated with brood chamber number. This pattern suggests that this guild is the most functionally dependent on habitat modification, and hence should be conceived as the basis of the cascade of trophic and non-trophic interactions triggered by mistletoes.

Few studies have reported positive indirect effects of habitat modifiers on diversity and composition of arthropod communities at the plant scale considering the seasonal context (Lill and Marquis 2003; Vieira and Romero 2013; Novais et al. 2022). Leaf ties built by the moth *Pseudotelphusa* sp. (Lepidoptera: Gelechiidae) were removed or artificially added in saplings of *Quercus alba* L. (Fagaceae) to evaluate the effects of leaf shelter construction on seasonal patterns of herbivore recruitment at the plant scale (Lill and Marquis 2003). Removal of leaf ties had a negative effect on species richness of herbivores compared to saplings where ties were added, and construction of leaf shelters at early season (summer) had a persistent and large effect on seasonal patterns of herbivore community (Lill and Marquis 2003). Vieira and Romero (2013) surveyed associated arthropods on fully extended and artificially rolled leaves (similar to those rolled by caterpillars) in *Croton floribundus* Spreng. (Euphorbiaceae) in dry and rainy seasons, and after rainfall. Species richness and abundance of arthropods was higher in shrubs with artificially rolled leaves compared to shrubs with fully extended leaves. Richness of predators, herbivores and detritivores at the plant scale were higher in shrubs with rolled leaves during the dry season, when temperature is high and humidity is low (Vieira and Romero 2013). Only a few plant species bloom or produce fruits during fall and winter in arid zones of Chile (e.g., the shrub *Porlieria chilensis* I.M. Johns) (Moreno-Chacón 2015).

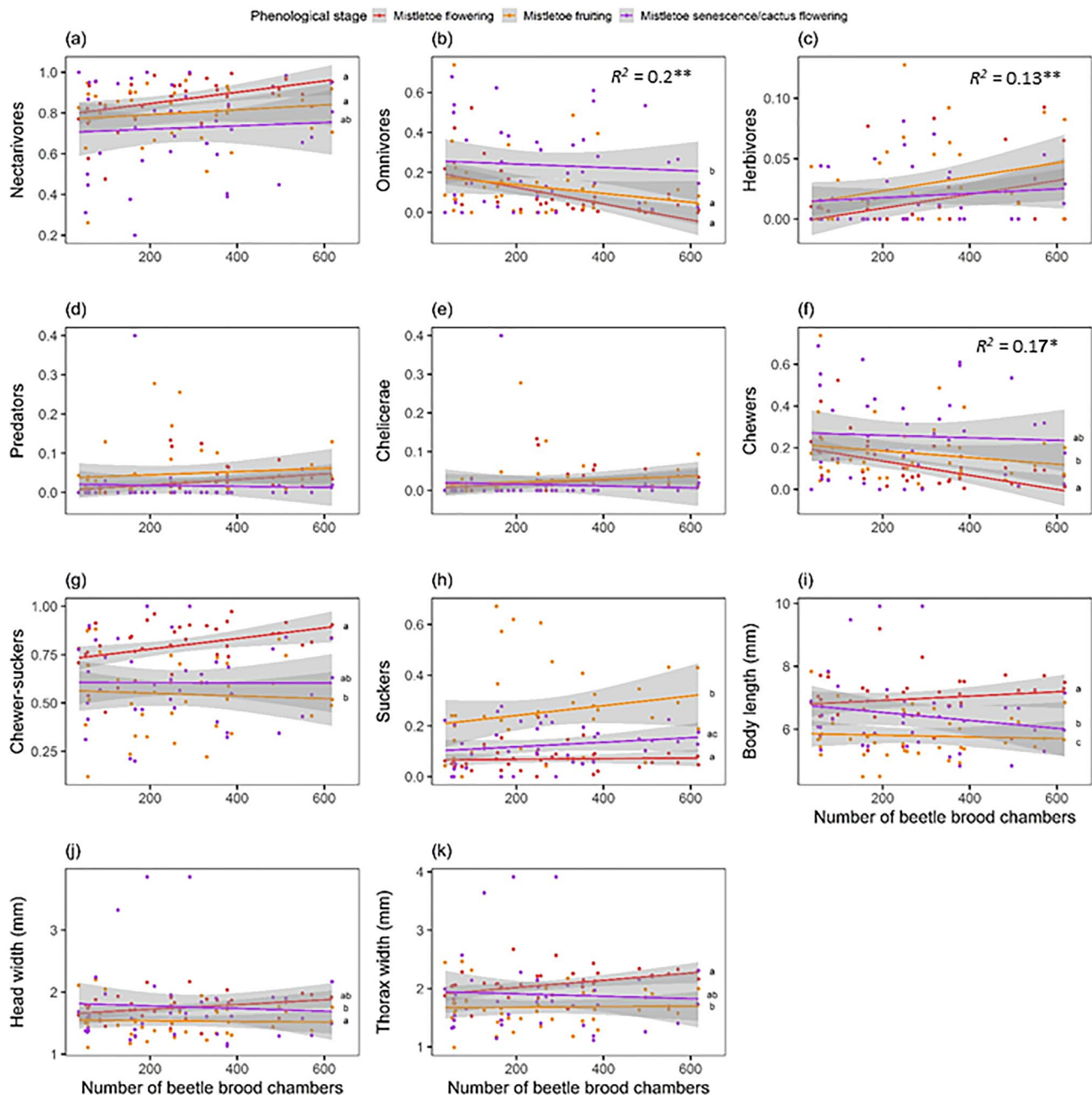


Fig. 5 Relationship between the beetle brood chamber number on cactus and univariate CWM (community weighted means) of nectarivores (a), omnivores (b), herbivores (c), predators (d), chelicerae (e), chewers (f), chewing-sucking (g), suckers (h), arthropod body length (i), head width (j) and thorax width (k) at mistletoe flowering, mis-

tletoe fruiting and mistletoe senescence/cactus flowering phenological stages. Regression lines sharing a different letter are statistically different ($P < 0.05$). R^2 of general regression is shown (* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$)

Therefore, the mistletoe may be an important species for arthropods, since it indirectly leads to the provision of refuges (e.g., chambers) and produces food resources for nectarivores, herbivores and omnivores.

Beetle chamber resources offered by mistletoe and cactus (nectar and fruit) sustain different functional groups with different requirements (e.g., shelter and/or food). The arthropod

community differed in composition through mistletoe seasonal phenology. The relative abundances of nectarivores, chewer-suckers and suckers were not associated with chamber number but varied with mistletoe phenology, being most abundant at mistletoe flowering (MFL). Bees belonging to the Halictidae family frequently visit mistletoe flowers (Guerra,

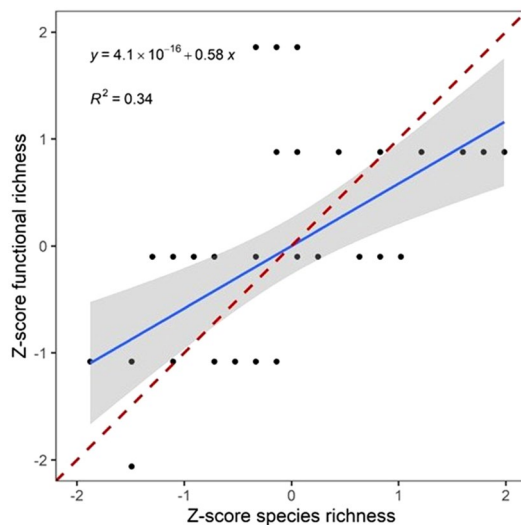


Fig. 6 Relationship between standardized values of species richness and functional richness (the amount of niche space filled by species in a community) in the mistletoe-cactus system. Best linear model is shown (blue line, the shade corresponds to the confidence interval). The dotted red line represents the $y=x$ function. The linear regression equation shows the positive association between species richness and functional richness ($P < 0.001$). Z score values are shown in the axes

personal observations). Arthropods at MFI stage tended to have longer (body length = 6.97 ± 0.14 mm; mean \pm se) and wider bodies (thorax width = 2.06 ± 0.07 mm) compared to those at MFr. These characteristics are similar to morphological characteristics of Halictid bees (i.e., *Caenohalictus* sp., *Corynura* sp.). The average width of mistletoe inflorescences is 3.5 mm (Medel et al. 2002), which might allow halictid bees to reach nectar. Although the hummingbird *Sebanoides sebanoides* Lesson, RP & Garnot (Apodiformes, Trochilidae) is considered the effective pollinator of this mistletoe (Medel et al. 2002), halictid bees might be important floral visitors. There is evidence that flower visitors can act as effective pollinators (Waser et al. 1996; Fumero-Cabán and Meléndez-Ackerman 2017). Further studies should be undertaken to test the effectiveness of halictid bees on mistletoe pollination.

The relative abundance of omnivores, represented by the ants *Camponotus morosus*, *Dorymyrmex goetschi*, *Pseudomyrmex linceus* Spinola and *Solenopsis gayeri*, was negatively associated with chamber number, and omnivores were more abundant at MSe/CFI stages. The ants *D. goetschi* and *S. gayeri* have been reported transporting seeds or feeding on pulp from fruits of *Echinopsis chiloensis* (Cares et al. 2013). The ants *C. morosus*, *D. goetschi* and *Solenopsis gayeri* are considered nectar-robbing ants in this mistletoe, yet damage inflicted on flowers seemingly does not affect mistletoe fruit set (Caballero et al. 2013). The presence of brood chambers could regulate the abundance of omnivores in the system, as

chambers are mainly inhabited by predators (e.g., spiders) (Guerra et al. 2022) that might prey upon or chase away ants.

Abundance of herbivores was positively related to brood chamber number. Herbivores were represented by beetles such as the stem-borer *Xyletomerus* sp., the habitat modifier that created chambers on cactus. Chewers, whose abundance was negatively associated with chamber number, included herbivores, predators and omnivores. Chewers comprised species present at the chamber and plant scales (*Xyletomerus* sp. and *Camponotus morosus*). These were the only arthropods shared between the chamber and plant scales (Fig. 7); 74 species were exclusively present at the plant scale and 7 at the chamber scale (Fig. 7). Most of the arthropods only found at the plant scale were nectarivores. Therefore, mistletoe, which mainly attracts arthropods from this guild, plays an important role in the system.

Relationships between species richness and functional richness are expected to be positive due to “selection effects” (Hooper et al. 2002; Gamfeldt et al. 2008; Sasaki et al. 2009; Guillemot et al. 2011; Song et al. 2014), which assumes that species loss results in the reduction of functional richness when functional species play a unique functional role in the system (Tilman et al. 1997). It has been suggested that functional redundancy in a system depends on the ratio between species diversity and functional diversity (Micheli and Halpern 2005; Guillemot et al. 2011). The steeper the slope, the faster the emergence of functions. Therefore, a moderate slope (< 1) suggests the occurrence of functional redundancy because in this scenario species loss occurs at a lower rate than function loss. We found a positive linear relationship between species and functional richness with a slope 0.58 (Fig. 6). Therefore, functionally redundant species might be lost when the number of chambers in cacti surface decreases, which suggest that the community would be to some extent protected from functional diversity decline. Functionally redundant species in our system might be represented by bees (nectarivores) that perform similar roles in the system. We identified 76 species of arthropods, 23 of which were likely flower visitors: bees from the Halictidae, Colletidae, Apidae, Andrenidae, Megachilidae and Anthophoridae families, and flies from the Bombyliidae and Syrphidae families. Bees, the most abundant arthropods collected during field work, were particularly found during mistletoe flowering.

We experimentally showed that stem borer beetles, being habitat modifiers play an important role in the mistletoe-cactus system as they affect taxonomic and functional diversity and change the arthropod community composition. These habitat modifiers has been shown to influence arthropod community structure at the chamber level (Guerra et al. 2022), and here we showed that such an effect is observed at a larger spatial scale, the plant level. Moreover, arthropod community structure is affected by seasonal phenology of mistletoe and the cactus host, with arthropod

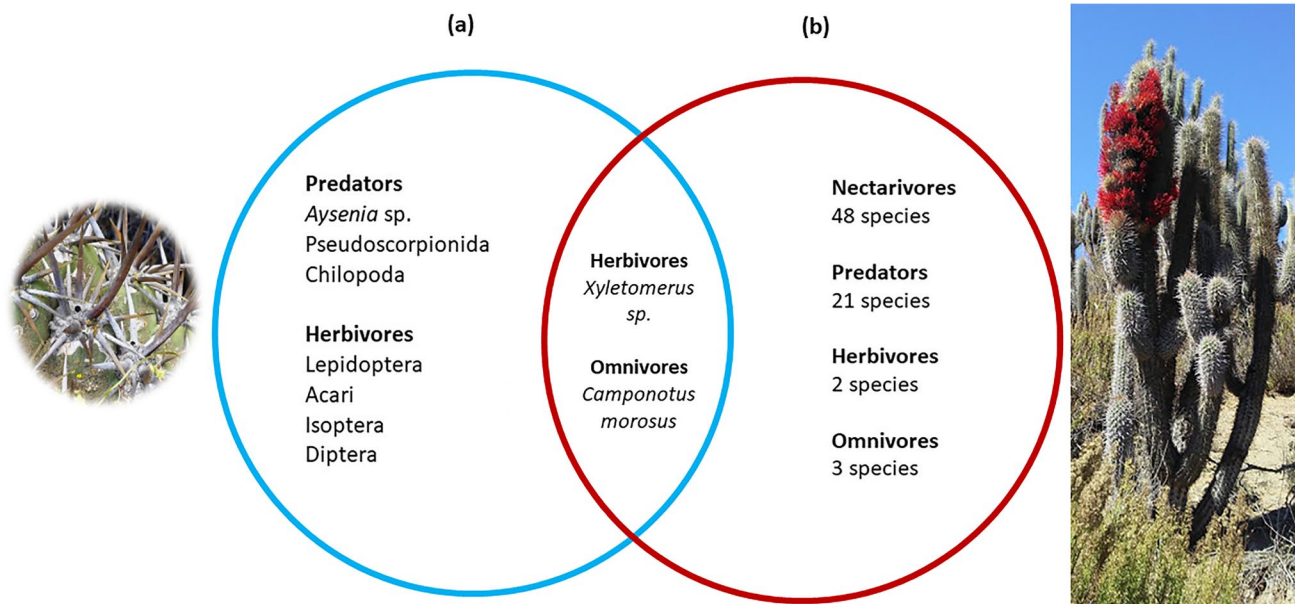


Fig. 7 Venn diagram showing exclusive and shared arthropod species at the beetle brood chamber scale (a) and plant scale: mistletoe-cactus system (b)

guilds and traits with resources offered by these plant species at different seasons. Mistletoe likely plays an important role in the system since a high number of species, mainly nectarivores, are attracted to flowers during a flower-scarce season. Brood chambers constructed on long-lives species, such as cacti, last longer than ephemeral shelters, such as leaf ties or leaf rolls. Thus, their impact on arthropods in brood chambers or the whole system (mistletoe-cactus) would span several generations. In sum, chambers built by stem borer beetles on cacti may have a positive impact on arthropod diversity in arid zones, where environmental conditions often limit arthropod abundance.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s11829-022-09930-z>.

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Author contribution PCG and EG designed the experiment. PCG and VME analyzed the data in consultation with EG. PCG and GOG carried out fieldwork. JPA and PGB identified arthropods. PCG and EG wrote the manuscript with VME and GOG input.

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Declarations

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

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