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Soil Microarthropods and Their Relationship to Higher Trophic Levels in the *Pedregal de San Angel* Ecological Reserve, Mexico

Alicia Callejas-Chavero,[1,2] Gabriela Castaño-Meneses,[2,3,4] María Razo-González,[2] Daniela Pérez-Velázquez,[2] José G. Palacios-Vargas,[2] and Arturo Flores-Martínez[1]

[1]Ecología Vegetal, Departamento de Botánica, Escuela Nacional de Ciencias Biológicas, Instituto Politécnico Nacional, México DF, México
[2]Ecología y Sistemática de Microartrópodos, Departamento de Ecología y Recursos Naturales, Facultad de Ciencias, Universidad Nacional Autónoma de México, México DF, México
[3]Ecología de Artrópodos en Ambientes Extremos, UMDI-Facultad de Ciencias, Campus Juriquilla. Universidad Nacional Autóma de México, Querétaro, México
[4]Corresponding author, e-mail: gabycast99@hotmail.com

ABSTRACT. Soil fauna is essential for ecosystem dynamics as it is involved in biogeochemical processes, promotes nutrient availability, and affects the animal communities associated with plants. In this study, we examine the possible relationship between the soil micro-arthropod community on foliage production and quality of the shrub *Pittocaulon praecox*. We also examine the arthropods associated to its foliage, particularly the size of the main herbivores and of their natural enemies, at two sites with contrasting vegetation cover and productivity. The diversity of soil microarthropods was assessed from soil samples collected monthly under *P. praecox* individuals over 13 mo. Specimens collected were identified to species or morphospecies. Shrub foliage productivity was evaluated through the amount of litter produced. Resource quality was assessed by the mean content (percentage by weight) of N, C, S, and P of 30 leaves from each shrub. The mean size of herbivores and their natural enemies were determined by measuring 20 adult specimens of each of the most abundant species. We found a higher species richness of soil microarthropods and foliar arthropods in the open site, although the diversity of foliage arthropods was lower in the closed site. Shrubs growing in the closed site tend to produce more, larger, and nutritionally poorer (lower nitrogen content) leaves than open site. Herbivores and their natural enemies were also larger in the closed site. We found a significant positive relationship between the diversity and species richness of foliar arthropods and the nitrogen content of leaves. In general, species richness and diversity of both the foliar and soil fauna, as well as the size of organisms belonging to higher trophic levels, were affected by vegetation cover and primary productivity at each site. These findings highlight the need to simultaneously consider at least four trophic levels (soil organisms, plants, herbivores, and natural enemies) to better understand the functioning of these systems and their responses to environmental changes.

Key Words: diversity, herbivores, multitrophic interactions, natural enemies

Despite the high biological diversity and the functional importance of soil fauna at the community and ecosystem levels, most studies dealing with plant–animal interactions have focused primarily on the relationships occurring in the plant shoot. However, several studies published during the last decade have shown that a full understanding of what happens in plant communities requires considering also the soil fauna and its effects on the interactions that take place above the ground (Bever et al. 1997, Bardgett et al. 1998, Van der Putten et al. 2001, Kostenko et al. 2012).

Trophic interactions play a key role in both evolutionary (Wardle 2006, Dyer et al. 2010) and ecological processes, due to their effects on the occurrence and performance of many organisms at the individual, population, community, and ecosystem levels (Mulder 1999, Thébault and Loreau 2006), even if environmental characteristics of systems and habitats can also have a major effect on community structure, species combinations of traits, and life history tactics among invertebrate assemblages [see the habitat templet of Southwood 1977, 1988 and its adaptation to running waters by Townsend (1989) and Townsend and Hildrew (1994)]. Interaction studies that only consider two species or trophic levels (e.g., plant–herbivore and herbivore–natural enemy) might be insufficient for understanding the behavior of such species. Hence, to gain a deeper insight into the systems' functioning requires encompassing several trophic levels, i.e., three or more species (multitrophic interactions; Van der Putten et al. 2010, Van Dam and Heil 2011).

Soil is essential for terrestrial ecosystems, as soil fauna influences organic matter degradation processes and primary productivity (Bardgett 2002, Allison 2006), and plays a key role in the structure, composition, and dynamics of plant communities (Wardle 2002, De Deyn et al. 2003, Arim and Jaksic 2005, Bedano et al. 2005), which, in turn, influence higher trophic levels such as foliar herbivores, pollinators, predators, parasitoids, and hyperparasitoids (Van der Putten et al. 2001, Bezemer et al. 2003, Wardle et al. 2004, Moreau et al. 2006, Morris et al. 2007, Kostenko et al. 2012). For example, Soler et al. (2012) reported that root herbivores can influence the nutritional quality of leaves and the concentration of secondary metabolites in plant foliage which, in turn, affects the growth, development, and survival of foliar insects and their natural enemies. Hooper et al. (2000) and De la Peña (2009) found a positive correlation between the diversity of soil organisms and the diversity of plant species growing on those soils.

Among soil microarthropods, springtails and mites play a primary role in organic matter breakdown and its incorporation to the soil system (Hooper et al. 2000). The ingestion and subsequent excretion of dead plant material accelerate plant material decomposition, thus facilitating the colonization of plant material by fungi and other microorganisms by increasing interfacial contact (Van Vliet and Hendrix 2007, Siddiky et al. 2012). They also redistribute spores and bacteria across the soil layers (Palacios-Vargas et al. 2000). Springtails are also involved in the mycorrhizal infection of some plants (Endlweber and Scheu 2007, Steinaker and Wilson 2008) and the recycling of organic

matter and nutrients in soil (Palacios-Vargas 1985, Luciáñez and Simón 1991, Van Straalen 1998, De la Peña 2009).

The composition and abundance of the soil microarthropod assemblage is determined by several factors, including interactions with other soil inhabitants (nematodes, enchytraeids, fungi, and bacteria), and soil organic matter content (Eaton et al. 2004), temperature, moisture, pH, (De la Peña 2009), and compaction (Cutz-Pool et al. 2006). Thus, changes in these conditions might affect the abundance and distribution of soil microarthropods (Filser et al. 2002).

Understanding the relationship between the diversity of organisms above and below the ground is necessary to infer the processes determining the structure and functioning of communities, both locally and regionally (Hooper et al. 2000, Soler et al. 2005, Moreau et al. 2006, González and Muller 2010, Kostenko et al. 2012). This knowledge can also provide useful information for better understanding the between-species dynamics, which can support the formulation of successful ecosystem conservation and restoration programs.

The *Pedregal de San Angel* Ecological Reserve (REPSA, Spanish) is located in the Southern part of Mexico City, and is home to many plants and animal species, including a large number of endemic species (Rzedowski 1954, Siebe 2009). However, given its proximity to the city, it is constantly exposed to a number of pressures that jeopardize its biodiversity (Juárez and Cano-Santana 2007, Meza and Moncada 2010). Although several studies have been conducted on the arthropods of REPSA, most of them have only focused on describing the composition or the spatial and temporal variation of arthropod communities (Cutz-Pool et al. 2006, Arango-Galván et al. 2007, Palacios-Vargas et al. 2009, Ríos-Casanova et al. 2010). Few of them have explored the interactions between different trophic levels (Martínez 2002, Carmona 2004, Blanco-Becerril et al. 2010, Razo-González et al. 2014). So far, no study has examined the interactions between soil microarthropods and other trophic levels (plants, foliar herbivores, and their natural enemies) in this area.

In this work, we examined 1) the relationship between the diversity of soil microarthropods, the foliage productivity, and the quality of the shrub *Pittocaulon* (*Senecio*) *praecox* H.Rob. and Brettell, and 2) the size and diversity of herbivores associated with the shrub and their natural enemies, at two contrasting sites (open and closed).

Materials and Methods

Study Sites. The *Pedregal de San Angel* Ecological Reserve (REPSA) is located southeast of Mexico City (19°14′–19°25′ N–99°08′–99°15′ W) and comprises 237 ha. Soils are mostly sandy loam with high organic matter and calcium content, and low levels of usable nitrogen and potassium (Rzedowski 1954), albeit with significant variations in vegetation cover within the Reserve. The climate is temperate subhumid with a summer rainy season [Cb (w1) (w)] (García 1988). The mean annual temperature is 15.5°C, ranging from 6°C to 34.6°C. Rainfall averages 870 mm/yr (Valiente-Banuet and Luna 1990), with two well-defined seasons: rainy, from June to October; and dry, from November to May (Rzedowski 1954).

REPSA's rough topography determines significant variations in the vegetation. Flat sites have a very open vegetation cover dominated by grasses and small shrubs, whereas the steep slopes display a closed vegetation dominated by trees and shrubs, with *P. praecox*, *Buddleja cordata* Kunth, *Wigandia urens* Kunthand *Bursera fagaroides* Engl. as the most conspicuous species (Castillo et al. 2007). Two sites of about 0.5 ha were selected. The "closed site" is characterized by a dense vegetation cover and high productivity compared to the "open site," with sparser vegetation cover and lower productivity (Cano-Santana 1994, Ríos-Casanova et al. 2010). The density of the shrub *P. praecox*, is higher in the closed site (18.65–3.41 ind/m²) than in the open site (12.99–2.41 ind/m²).

Both sites also differ in the physical and chemical characteristics of soil, e.g., absolute and relative moistures, as well as organic matter,

carbon and nitrogen contents, were higher in the closed site. In contrast, temperature, pH, and phosphorus content were higher in the open site (for further details see Razo-González et al. 2014).

Diversity of Soil Microarthropods. Three *P. praecox* shrubs were randomly chosen at each site, each shrub being at least 1.50 m tall and having a crown projection of about 3 m². Distance between both sites is about 1.5 km. Shrubs were separated from each other by approximately 100 m. The first week of each month, from March 2008 to March 2009, four soil subsamples per shrub (484 cm²) of the uppermost 10 cm were collected at 10 cm from the base of each plant and placed in a plastic container for transportation to the laboratory analyses were applied on the assemblages provided by the sum of the four subsamples per shrub (3) × site (2) × monthly campaigns (13) = 78 samples. Soil microfauna were extracted using Berlese–Tullgren funnels for 6 days. The organisms obtained were counted and sorted by species (or morphospecies when full identification was not possible). As needed (for mites, springtails, and diplurans), semipermanent slides were prepared for identification (Palacios-Vargas and Mejía-Recamier 2007). Soil microarthropod community structure was described in terms of species richness, diversity (Shannon index), the corresponding confidence intervals were calculated with Bootstrap estimator (Smith and van Belle 1984). The bootstrapping option (giving a 95% confidence interval) is based on 1,000 permutations. Evenness (Pielou index) was also calculated. Site community structure indices were calculated considering the 13 monthly campaigns. We used two tests for between-site differences in diversity index, first by calculation of delta index (Solow 1993) by Species Diversity and Richness ver. 3.0.3 software (Henderson and Seaby 2002) considering data set of 13 m campaigns by site. Second test was a nonparametric Wilcoxon-signed rank test, for that we use the diversity calculated for each site for each month obtained by considering the three shrubs together (2 sites × 13 monthly campaigns). This analysis would examine whether regardless of monthly variations, one of the communities is consistently more diverse than the other throughout the study period. Additionally, the taxonomic similarity between sites was calculated with the Sörensen index. The last two tests were performed with the Past Ver. 2.13 (Hammer et al. 2001) software.

The species recorded were categorized into trophic guilds according to the criteria proposed by several authors (Blanco-Becerril et al. 2010, Oelbermann and Scheu 2010, Palacios-Vargas et al. 2011, Sabais et al. 2011, Razo-González et al. 2014).

Growth, Productivity, and Nutritional Quality of *P. praecox* Leaves, and Relationship With Soil Microarthropods. The growth and productivity of *P. praecox* were evaluated for a year in terms of branch growth, number and size of leaves produced by three individual shrubs at each site. The crown of each shrub was subdivided into four quadrants; five branches of similar size were chosen from each quadrant, individually tagged and measured, providing a total of 60 branches by site. The length of each tagged branch was measured monthly and the presence of new leaves was noted. In this case, the length of the leaf was recorded. The growth of each branch was estimated as the difference between the final and initial lengths. To estimate litter productivity, a 1 by 1 m, 0.1 mm mesh size net was placed 50 cm above the ground under the center of each shrub to collect the litter shed throughout 13 mo. The litter collected was weighed fresh and then oven-dried at 40°C for 48 h.

To test for between-site differences in branch growth, leaf size, and leaf production over the year, generalized linear mixed models were used considering "Site" as a fixed factor, and "Shrub" (nested within Site), "Quadrat" (nested within Shrub), and "Branch" (nested within Quadrat) as random factors. Litter production was analyzed with repeated measures of analysis of variances (ANOVAs). All analyses were performed with the Systat V.13 software (Systat Software Inc. 2009).

To evaluate the quality of the host plant (*P. praecox*), 30 randomly chosen leaves were collected from each shrub in July, September, and December 2009. Thus, we have three samples by site by month. Leaves

were stored in paper bags, dehydrated and ground, and the nitrogen, carbon, sulphur, and phosphorus content (as percentage by weight) was determined using a Perkin Elmer PE2400 analyzer. Phosphorus content was determined using X-ray fluorescence. All tests were conducted at the Elemental Analysis Laboratory, Facultad de Química (Chemistry Faculty), UNAM.

To test for between-site differences in leaf nutritional quality, repeated measures ANOVAs were run (factor site (2) and time (3 mo), and three shrubs as replicate within each site). Lastly, to examine the relationship between soil microfauna diversity and both shrub productivity and leaf quality, simple linear correlations were calculated. Both analyses were made using the Systat V.13 software (Systat Software Inc. 2009).

Species Richness and Diversity of Arthropods Associated with *P. praecox*. The species richness and taxonomic diversity of arthropods associated with *P. praecox* leaves were evaluated based on monthly samples collected from March 2009 to 2010. We analyzed this association with a 1 yr lag because we want to be sure that the edaphic fauna shows differences between sites, in order to evaluate that differences between the plant quality and their associated herbivorous. Acording with Decaëns and Rossi (2001) the structured spatial patterns in the soil fauna ramin stable in time at scales of 1 or 2 yr, if there are no important disturb. Thus, we suppose that edaphic fauna community structure was maintained similar during our study period and the effect on the high trophic guilds can be evaluated. For collecting herbivorous insects, we used a Model 24 D-VAC vacuum insect sampler. The crown of each shrub was subdivided into four quadrats and insects were collected by applying the D-VAC for 5 min in each quadrat (total 20 min per shrub). Sampling took place between 11:00 a.m. and 01:00 p.m. The first site sampled was changed each month. Samples obtained were kept in jars with 70% alcohol; in the laboratory, specimens were identified to species and the abundance of each species was determined. Diversity indices (species richness, Shannon index, and Pielou's evenness index) and composition similarity (Sorensen similarity index) were calculated. Species were gathered into trophic guilds applying the same criteria as for the soil fauna. Then, to examine the relationship between plant quality and the species richness and diversity of foliage arthropods, and both shrub productivity and leaf quality, simple linear correlations were calculated. The analyses were made using the Systat V.13 software (Systat Software Inc. 2009).

Relationship Between *P. praecox* Leaf Quality and the Size of Herbivores and Their Natural Enemies. To determine whether the size of herbivores, predators, and parasitoids varied between sites, and whether this feature is affected by resource quality, 20 adult specimens of each of the most abundant species were randomly chosen. These species were three herbivore insects: *Asphaera abdominalis* (Chevrolat) (Coleoptera), *Eupterycyba* sp. (Hemiptera: Cicadellidae) and *Sphenarium purpurancens* (Charpentier) (Orthoptera); three predatory spiders *Neoscona oaxacensi* (Keyserling) (Araneidae), *Misumenoides* sp. (Thomisidea) and Salticidae, which, according to Martínez (2002) and Carmona (2004), prey on the herbivorous species mentioned above; and three parasitoids belonging to the families Eulophidea and Pteromalidae (both being generalist parasitoids of Coleoptera and Homoptera; Fowler et al. 1991, Olivares et al. 2000), and Diapriidae (parasitoid of various species of Hemiptera and Coleoptera; Triapitsyn et al. 2010, Loiácono and Margaría 2011). These species were mainly collected in rainy season (June–October) when they were present and interacting. Herbivores of different species were collected randomly at the same time and using the same sampling effort, in order to avoid size variability only related to life history (and not to between-site difference in biotic or abiotic conditions).

On each specimen, the structures that best depict body size for each corresponding taxon were measured under a stereoscopic microscope; i.e., body length and width for *A. abdominalis* (Zaragoza-Caballero 2008); femur length of the third pair of legs for *Eupterycyba* sp. (Malcolm 2007); and femur length of the third pair of legs, as well as

head width and length for *S. purpurancens* (Cepeda-Pizarro et al. 2003). For parasitoids, the tibia length of the third pair of legs was measured (Ríos-Casanova 1998). The *t*-test was run to find between-site differences in mean body size. Tests were run with the Systat V.13 software (Systat Software Inc. 2009). To relate prey size with body size of their natural enemies, the ratio of the mean size of each predator or parasitoid to the mean prey size was calculated separately for each site, taking into account only the interactions that have been already documented in the literature. Then, for each natural enemy–prey combination, the between-site (closed vs. open) ratio predator size/prey size was calculated. In order to explore, if the relationship between the size of natural enemies (predators and parasitoids) and the size of their preys (herbivorous) show differences between sites, we calculated to each natural enemies–prey interaction, the ratio between the size average of natural enemy and size average of prey by site, with a total of 12 possible interactions (six by predator–herbivorous and six by parasitoid–host). Comparisons between the "size ratios" were analyzed by *t*-test paired using Systat v. 13 software (Systat Sofware Inc. 2009).

If the results of the test show significant differences and the ratios are consistently higher in some site than the other, then the result can be related with the prey quality in that site. Several studies have documented that parasitoid performance is directly related to prey size (Hunter 2003, Wang and Messing 2004, Florez et al. 2004, Berner et al. 2005, Powers and Avilés 2007, Boivin and Gauvin 2009). Similarly, it has reported a positive relationship between the size of predator and prey size (Lang et al. 1999, Brose et al. 2006, Nakazawa et al. 2013)

Results

Species Richness and Diversity of Soil Microarthropods. In total, 131,593 specimens, belonging to 14 different orders and 146 morphospecies, were recorded during the sampling design. The species richness of microarthropods in the open site (146) was slightly higher than in the closed site (143). In both sites, Collembola (open 40 species; closed 38 species), Cryptostigmata (34 and 33 species, respectively) and Prostigmata (25 and 24 species, respectively) were the species-richest taxa. The Order Protura was represented by a single specimen (Table 1).

Considering data cumulated on the whole study period, sites differ significantly in terms of species diversity ($\delta = 0.09691$; $P = 0.005$) (open site: $H' = 3.54$ (3.49 ± 3.51), closed site: $H' = 3.61$ (3.58 ± 3.61)). The microarthropod communities of the two sites are remarkably similar. They shared 140 of the 151 recorded species (~93%).

Detritivores and predators were the guilds that included the largest numbers of species and individuals, while herbivores were poorly represented. Although this pattern was similar in both sites, the proportion of herbivores in the closed site was twofold higher than in the open area.

Figure 1 depicts monthly variation in morphospecies richness and taxonomic diversity in the two sites. In both sites, species richness and diversity were noticeably higher during the rainy season (July–November) relative to the cold, dry months of the year.

During the rainy season, the microarthropod communities of both sites were more similar (70–90% common species) than during the cold, dry months of the year, when common species did not exceed 60%.

However, according to the nonparametric Wilcoxon-signed rank test, the sites did not differ significantly in terms of species richness ($W = 53.5$; $P = 0.575$) and diversity ($W = 64$; $P = 0.196$).

Growth, Productivity, and Nutritional Quality of *P. praecox* Leaves and Their Relationship With Soil Microarthropods. The generalized linear mixed models showed that shrubs growing at the closed site produced, on average, more leaves than those at the open site (Table 2), but this difference was not statistically significant ($F_{1,97} = 2.97$, $P = 0.088$). Mean leaf size was significantly higher in the

Table 1. Species richness (S), absolute abundance (number of individuals), relative abundance (%) of soil arthropods associated to *P. praecox* in REPSA and their distribution in main trophic guilds

Group	Guild	Richness		Absolute abundance		Relative abundance	
		O	C	O	C	O	C
Astigmata	Predators	6	6	391	328	0.65	0.81
Chilopoda	Predators	4	3	55	25	0.09	0.06
Mesostigmata	Predators	19	19	9,468	4,923	15.82	12.09
Prostigmata	Predators	25	24	16,450	11,468	27.49	28.18
Pseudoscorpionida	Predators	3	3	141	101	0.23	0.25
Diplura	Predators-Detritivores	2	2	98	61	0.16	0.15
Collembola	Detritivores	40	38	4,676	4,151	7.81	10.2
Diplopoda	Detritivores	4	3	205	194	0.34	0.48
Pauropoda	Detritivores	1	1	41	1	0.06	0.01
Cryptostigmata	Fungivores–Detritivores	29	30	25,981	15,161	43.41	37.25
Protura	Herbivores	1	1	2	1	0.01	0.01
Psocoptera	Herbivores	2	2	198	194	0.33	0.48
Symphyla	Herbivores	1	1	77	45	0.13	0.11
Thysanoptera	Herbivores	4	4	212	146	0.35	0.36
Hemiptera	Herbivores	7	6	1,847	3,897	3.09	9.57
	Detritivores	45	42	30,903	19,507	44.28	41.39
Main guilds	Predators	57	55	26,505	16,845	8.21	10.69
	Herbivores	15	14	2,336	4,283	3.91	10.53
		Open	Closed				
	Richness (S)	146	143				
	Diversity (H′)	3.54	3.61				
	Evenness (J′)	0.70	0.72				
	Similarity	0.96					

Shannon–Wiener diversity (H′) and Pielou's Evenness (J′) indices at the open (O) and closed (C) sites are given.
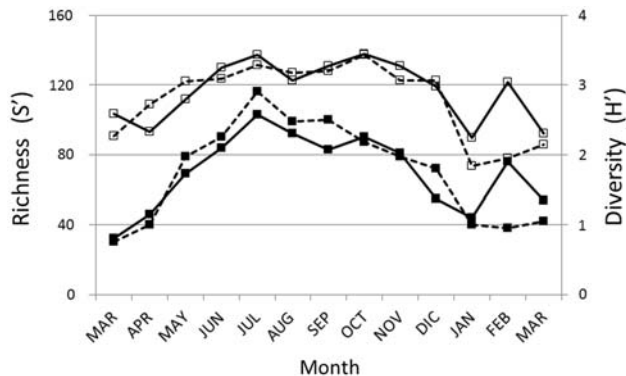
Fig. 1. Temporal variations in species richness (S) and Shannon–Wiener diversity index (H′) of the soil microarthropods at closed and open sites in the *Pedregal de San Angel* Ecological Reserve (REPSA). Solid lines: closed site; dashed lines: open site. Solid symbols: S; empty symbols: H′.

closed site ($F_{1,97} = 14.02, P = 0.0003$), but branch growth was significantly lower in the open site ($F_{1,97} = 16.81, P = 0.0001$).

The repeated measures ANOVAs showed significant differences in litter production between months ($F_{9,36} = 8.006, P < 0.001$), but no significant difference between sites. Although litter production was consistently higher in the closed site, it was not significantly different from production recorded in the open site ($F_{1,4} = 1.38, P = 0.305$, Fig. 2).

The repeated measures ANOVAs showed that nitrogen, carbon, sulphur, and phosphorus content in leaves was generally higher in shrubs growing in the open site than in those located in the closed site, but these differences were not statistically significant. Only nitrogen and sulphur content showed significant differences between sampling dates ($F_{2,8} = 34.55, P < 0.001, F_{2,8} = 6.053, P = 0.025$, respectively). For all these elements, leaf content tended to decrease as the foliage-shedding season approached (Table 3).

We found a significant positive correlation between litter production and microarthropod diversity in both sites ($R = 0.587, P < 0.001, R = 0.527, P < 0.001$; for the closed and open sites, respectively): The greater the amount of litter, the higher the diversity of microarthropods.

Table 2. Mean ± SE of the number of leaves, leaf length (cm) and branch length increase (cm) in *P. praecox* shrubs growing at two contrasting sites in REPSA

Variable	Closed site	Open site
Number of leaves	26.50 ± 1.21	23.58 ± 1.19
Leaf length	19.66 ± 0.60*	16.48 ± 0.60*
Branch length increase	0.45 ± 0.07*	0.88 ± 0.07*

*Statistically significant differences ($P < 0.05$) between sites.

Of all the nutrients examined, only the N and S leaf contents showed a significant positive correlation with the diversity of soil microarthropods ($R = 0.532, P < 0.022, R = 0.540, P < 0.020$, respectively).

Species Richness and Diversity of Arthropods Associated With the Foliage of *P. praecox*. In the open site, the community of arthropods associated with the foliage of *P. praecox* included 113 species belonging to 18 Orders, with Hymenoptera, Hemiptera, and Coleoptera exhibiting the highest abundance and species richness. In the closed site, 87 species belonging to 16 Orders were recorded, with Hymenoptera and Hemiptera having the highest species richness (Table 4). The total abundance of arthropods was higher in the open than in the closed site (1535 vs. 974 individuals, respectively).

The mean diversity of the two sites was significantly different ($\delta = 0.22177; P = 0.000$). The open site showed a higher mean diversity ($H′ = 3.91$ (3.79 ± 3.92)) than the closed site ($H′ = 3.65$ (3.55 ± 3.70)). Both sites shared 34% of the 190 species recorded.

Herbivore abundance was higher in the open than in the closed site (1,069 and 632 individuals, respectively). The most abundant herbivore species were *Eupterycyba* sp. (O = 352, C = 211 individuals), *Sphenareum purpurancens* (O = 62, C = 32), and *Asphaera abdominals* (O = 60, C = 30). As for as their relative abundance in the open site, herbivores accounted for 67.8% of all the individuals collected and predators for 25.8%. These figures are slightly higher than those observed in the closed site, where they only accounted for 64.5 and 23.7%, respectively.

Predator (spiders and parasitoids) abundance was higher in the open than in the closed site (95 and 252 vs. 71 and 162 individuals, respectively).

As for the relationship between plant quality and the species richness and diversity of foliage arthropods, only nitrogen content showed a significant correlation ($R = 0.471$, $P < 0.001$ and $R = 0.530$, $P < 0.001$, respectively). The higher the foliage concentration of nitrogen, the higher the number of species and diversity of arthropods found
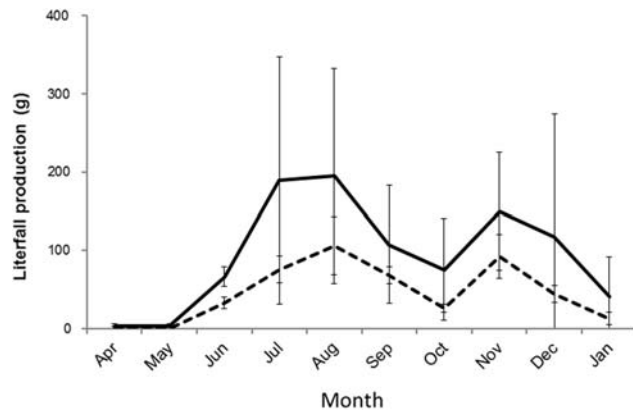

Fig. 2. Temporal variations in litterfall production at closed and open sites in REPSA. Solid lines: closed site; dashed lines: open site. Vertical lines represent one standard error.

in the foliage. Sulphur, carbon, and phosphorus content showed no statistically significant relationship with taxonomic structure of foliage microarthropod assemblages.

Relationship Between *P. praecox* Foliage Quality and Size of Its Herbivores and Their Natural Enemies. In general, both the herbivores and predators (spiders and parasitoids) had larger body sizes in the closed site than in the open site. A statistically significant effect of site on body size was found for the three herbivore species considered (*A. abdominalis*: $t_{38} = 4.92$, $P < 0.0001$; *S. purpurancens*: $t_{38} = 4.24$, $P < 0.0001$; *Eupterycyba* sp.: $t_{38} = 6.22$, $P < 0.0001$) (Table 5).

Arachnids preying on the herbivores mentioned above were significantly larger in the closed than in the open site (*Neoscona oaxacensis* $t_{38} = 4.88$, $P < 0.0001$; Salticidae $t_{38} = 3.25$, $P < 0.0001$; *Misumenoides* sp.: $t_{38}4.91$, $P = 0.0001$) (Table 5).

Parasitoids belonging to the families Pteromalidae, Eulophidae, and Diapriidae, which are natural enemies of the herbivores *A. abdominalis* and *Eupterycyba* sp., were significantly larger ($t_{38} = 6.94$, $P < 0.0001$, $t_{38} = 2.02$, $P = 0.0001$, $t_{38} = 5.98$, $P < 0.0001$) in the closed than in the open site (Table 5).

The size average ratio of predators and parisitods in relation to their preys shown significant differences between sites ($t_{11} = 2.428$, $P = 0.03$). The closed site shows higher values in the ratio than the open site. Thus, predators and parasitoids show higher size in the closed site and their size are proportionally greater to the closed site, probably because used preys of high size too.

Table 3. Chemical composition of *P. praecox* leaves

	Closed site			Open site		
	July	September	December	July	September	December
Nitrogen	3.64 (0.16)	1.66 (0.10)	1.63 (0.21)	3.77 (0.24)	2.11 (0.02)	1.59 (0.49)
Carbon	45.37 (0.33)	45.12 (0.20)	44.35 (0.42)	46.44 (0.78)	44.63 (0.30)	45.42 (1.44)
Sulphur	0.09 (0.01)	0.05 (0.04)	0.01 (0.01)	0.10 (0.02)	0.03 (0.03)	0.01 (0.01)
Phosphorus	1.98 (0.28)	1.66 (0.48)	1.06 (0.02)	1.99 (0.61)	0.90 (0.02)	1.60 (0.27)

Mean percentages of each element (in terms of weight) in both sites. The value in parentheses is the standard error.

Table 4. Species richness (*S*), absolute (number of individuals), relative abundance (%) of foliage arthropods associated to *P. praecox* in REPSA and their distribution in main trophic guilds

Group	Guild	Richness		Absolute abundance		Relative abundance	
		Open	Closed	Open	Closed	Open	Closed
Araneae	Predator	4	3	95	71	7.24	6.04
Hymenoptera	Predator	24	21	252	162	16.53	16.02
Neuroptera	Predator	1	1	18	15	1.53	1.14
Pseudoscorpionida	Predator	1	1	2	2	0.2	0.13
Dermaptera	Detritivore	1	1	2	4	0.13	0.4
Diplopoda	Detritivore	1	0	9	0	0.57	0
Isopoda	Detritivore	1	1	3	8	0.19	0.82
Diptera	Phytophagous and parasite	9	8	65	77	4.13	7.85
Isoptera	Phytophagous	1	1	16	3	1.01	0.31
Mollusca	Herbivore	1	1	58	76	3.68	7.75
Coleoptera	Herbivore	25	20	121	110	7.69	11.22
Lepidoptera	Herbivore	12	3	55	34	3.49	3.46
Orthoptera	Herbivore	1	1	62	32	3.94	3.26
Psocoptera	Herbivore	1	1	146	43	9.28	4.38
Hemiptera	Herbivore	29	24	627	337	39.86	34.88
Blattodea	Omnivore	1	0	4	0	0.25	0
Main Guilds	Predator	32	27	405	256	25.50	23.33
	Herbivore	68	49	1069	632	67.94	64.95

	Open	Closed
Richness (*S*)	113	87
Diversity (*H′*)	3.91	3.65
Evenness (*J′*)	0.81	0.78
Similarity	0.34	

Shannon-Wiener diversity (*H′*) and Pielou's Evenness (*J′*) indices at the open (O) and closed (C) sites are given.

Table 5. Average of morphological metrics of the most abundant herbivores of *P. praecox*, their predators and parasitoids at two contrasting sites within REPSA

	Open Mean (SE)	Closed Mean (SE)
Herbivores		
Asphaera abdominalis (body length; mm)	8.46 (0.16)	9.31 (0.05) *
Eupterycyba sp.(femur length; mm)	2.39 (0.06)	2.77 (0.06)*
Sphenareum purpurancens (femur length/head width)	3.19 (0.04)	3.72 (0.07)*
Predators (Arachnids) (Prosoma length, mm)		
Neoscona oaxacensis (Araneidae)	2.88 (0.07)	3.65 (0.13)*
Salticidae	1.83 (0.07)	2.47 (0.18)*
Misumenoides sp. (Thomisidae)	1.95 (0.03)	2.21 (0.05)*
Parasitoids (Tibia length, mm)		
Pteromalidae	0.70 (0.02)	1.01 (0.03)*
Diapriidae	0.67 (0.01)	0.72 (0.02)*
Eulophidae	1.06 (0.04)	1.30 (0.02)*

Discussion

Each trophic level involved in an interaction is influenced by biotic and abiotic factors acting together in a complex fashion and with varying relative weights depending on the particular community (William and Travis 1991).

Authors as Razo-González et al. (2014) has found that the vegetation cover at the REPSA not only affects soil characteristics at a given site (open vs. closed), but can also influence the diversity and composition of soil microarthropod community, that the dense vegetation cover at closed sites creates a more stable environment, with higher soil moisture and less temperature variations. Van Straalen (1998) and Cutz-Pool et al. (2006) reported a higher diversity for the arthropod community inhabiting the soil of closed sites. However, no significant difference was observed in the taxonomic diversity of the microarthropod community of the open versus closed site, even if the mean value of the Shannon–Wiener index was slightly higher in the closed site. The composition of the microarthropod community also reflects micro environmental conditions. At the closed site, we found a higher richness of Collembola and immature stages of various Hemiptera species which, by having relatively thin cuticles, are more sensitive to moisture and temperature variations. By contrast, the sparse vegetation cover, larger temperature variations, and lower soil moisture at the open site led to the dominance of Cryptostigmata and Prostigmata mite species, which possess specialized morphological adaptations such as thick cuticles (e.g., Cryptostigmata) and very broad tolerance limits (Eisenbeis 2006) enabling them to thrive in environments that seem to be adverse for other groups (Villani et al. 1999).

Several authors have pointed out that the diversity of—and interactions between—soil-dwelling organisms have a major influence on plants settled on the site, and might account for the higher productivity and quality (e.g., higher nutrient content) of plants in some cases (De Deyn et al. 2003, Wurst et al. 2004, Wardle 2006, Bliss et al. 2010, Van Dam and Heil 2011). Our findings also suggest that soil fauna is related to plant performance in the closed site, where a higher productivity and better growth of *P. praecox* were observed. Although various mechanisms have been suggested to explain plant performance improvement by soil microarthropod community (e.g., increased water channelization and uptake, increased soil fertility through fragmentation of organic matter, Bedano et al. 2005, Prieto et al. 2005), experiments under controlled conditions are needed to determine the magnitude of these effects and their mechanisms of action.

Interactions between soil-dwelling organisms and plants not only affect plant growth, but also influence higher trophic levels such as foliar herbivores, parasitoids, hyperparasitoids, and pollinators (Morris et al. 2007, Kostenko et al. 2012). In many cases, the interaction between the plant and soil fauna triggers a metabolic response in the former that affects either its interaction with foliar herbivores through changes in the production and distribution of carbon compounds from photosynthetic activity, or the production and mobilization of secondary metabolites that directly or indirectly protect the plant from foliar herbivores and other pathogens (Núñez-Farfán et al. 2007, Kaplan et al. 2008, Bukovinszky et al. 2008, De la Peña 2009, Soler et al. 2012). In the particular case of the genus *Pittocaulon*, Gómez et al. (2003) reported an increased production and concentration of alkaloids and other elements in leaves in response to herbivory. Although the effect of soil herbivores on plant quality has not been directly assessed in our study, our results suggest that they might play an important role, especially in the closed site where plant quality (e.g., nitrogen content) was lower and the number of soil herbivores was 2.5 times higher than in the open site. Awmack and Leather (2002), Dugravot et al. (2005), and Berner et al. (2005) already reported that nitrogen is an essential element for insect development and size, while sulphur acts as an inhibitor to prevent herbivory. The higher sulphur concentration recorded in the closed site might be a plant response to the pressure of soil herbivores. Indeed, the abundance of foliar herbivores in the open site, where leaves had a higher quality (i.e., higher nitrogen content) and lower defences (i.e., lower sulphur content), was 46% higher than in the closed site. The differences observed in the composition of herbivore communities could be related to the presence of human activities in the open site, as its surroundings are used as recreational areas and jogging paths, which facilitate the entry of exotic species. In this open site, some Diptera, Blattodea, and Hymenoptera species (e.g., *Apis mellifera* L., *Musca domestica* L., *Periplaneta americana* L.) usually associated with disturbed sites or human settlement, were recorded.

The abundance and body size of foliar herbivores seem to be more closely related to the amount of resources available than to their quality. In the closed site, shrubs produced more and larger leaves and, although fewer organisms were recorded, these had larger body sizes than at the open site. Dicke (2000), Awmack and Leather (2002), and Sayer et al. (2010) already noted the importance of the amount of available resources, rather than their quality, for insect development and fecundity. More resources could offset the nitrogen deficit. This observation has been already reported for other systems. For example, when grass species exhibit low nitrogen concentration, Díaz et al. (2001) and Berner et al. (2005) found that herbivores tend to compensate this deficit by consuming larger amounts of the available resource or, in the case of generalists, by consuming other plant species as well.

It has been reported that a larger size of natural enemies is related to a larger prey size and, possibly, to a higher prey quality (Denno et al. 2002, Hunter 2003, Berner et al. 2005). The size of natural enemies (spiders and parasitoids) observed in this study at the closed site might be related to prey quality. Consistently, predators and parasitoids from the closed site were 10–30% larger to those from the open site.

In most cases, the predator/prey size ratio was larger in the closed site. Consequently, predators at the closed site had a proportionally larger body size for a given prey size, supporting the idea of a better prey quality at the closed site than at the open site.

However, further research is needed on other physical and chemical factors that might contribute to the performance (size or fitness or both) of natural enemies under natural conditions.

In summary, the characteristics of soil microarthropod communities, plants, herbivores, and their natural enemies suggest complex relationships involving numerous direct and indirect, positive and negative effects between them, mediated primarily by the quantity and quality of the available plant resources. Site conditions directly affect the diversity of soil microarthropods which, in turn, can affect the quality and quantity of resources provided by plants to herbivores, influencing the performance of organisms at higher trophic levels (predators and parasitoids).

However, a precise definition of which trophic level is the key driver of the structure and dynamics of communities under natural conditions is still an unsolved challenge. Controlled experiments are required,

including as many trophic levels as possible, coupled with the control of physical and chemical factors.

Gaining deeper insight into the functioning and interactions of the different trophic levels in ecosystems will facilitate understanding of the consequences of disturbances and address the challenge of restoring and recovering disturbed sites. Descriptive studies under natural conditions may provide important clues about the nature and complexity of trophic interactions in ecosystems, as well as on the multiple factors that influence species performance.

Acknowledgments

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