Arthropod diversity in necrotic tissue of three species of columnar cacti (Cactaceae)

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Abstract—We compared the insect and arachnid species found in spring and summer samples of necrotic tissue of three species of columnar cacti, cardón [*Pachycereus pringlei* (S. Watson) Britten and Rose], organ-pipe (*Stenocereus thurberi* Buxb.), and senita [*Lophocereus schottii* (Engelm.) Britten and Rose] (all Cactaceae), endemic to the Sonoran Desert of North America. A total of 9380 arthropods belonging to 34 species, 23 families, 10 orders, and 2 classes were collected in 36 samples. Arthropod communities differed in composition among host cacti, as well as between seasons. These differences may be a function of variation in host characteristics, such as chemical composition and abiotic factors, such as water content or temperature.

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Résumé—Nous comparons les espèces d'insectes et d'arachnides trouvées au printemps et à l'été dans des échantillons de tissus nécrotiques de trois espèces de cactus colonnaires, le cardón [*Pachycereus pringlei* (S. Watson) Britten et Rose], le « tuyau d'orgue » (*Stenocereus thurberi* Buxb.) et la senita [*Lophocereus schottii* (Engelm.) Britten et Rose], trois cactacées endémiques du désert de Sonora en Amérique du Nord. Au total, 9380 arthropodes appartenant à 34 espèces, 23 familles, 10 ordres et 2 classes ont été récoltés dans 36 échantillons. Les communautés d'arthropodes diffèrent par leur composition chez les trois espèces hôtes et varient d'une saison à l'autre. Ces différences sont sans doute fonction des variations des caractéristiques de l'hôte, telles la composition chimique et les facteurs abiotiques comme le contenu hydrique et la température.

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Introduction

Arms and stems of columnar cacti (Cactaceae) occasionally become necrotic and serve as feeding and breeding sites for a variety of arthropods. Several species of columnar cacti are endemic to the Sonoran Desert of North America. These cacti differ in size, density, and the frequency at which an arm or stem becomes necrotic (Breitmeyer and Markow 1998). Typically, necroses are initiated by some physical trauma or strain, after which, exposed cactus tissue is colonized by bacteria, yeasts, and various arthropods. Necroses differ in duration, depending upon the size of the cactus; the decay process lasts longer in species with larger arms and stems (Breitmeyer and Markow 1998). The senita cactus, *Lophocereus schottii* (Engelm.) Britton and Rose, has the highest density of necroses or "rots" (1.9/ha) but, owing to the thin arm diameter, they last only 1–3 months. Cardón, *Pachycereus pringlei* (S. Watson) Britton and Rose, is the largest cactus, especially in coastal Sonora, Mexico, and although necroses are infrequent

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(0.4/ha), they may last up to a year. Of intermediate size is the organ-pipe cactus, *Stenocereus thurberi* Buxb., which also has a low incidence of necroses (0.1/ha) that last many months.

The species of arthropods most widely studied in necrotic columnar cacti are those of the genus *Drosophila* Fallen (Diptera: Drosophilidae) that are endemic to the Sonoran Desert of North America (Heed 1978, 1982). These occur in large numbers at certain times of the year (Breitmeyer and Markow 1998). Several other species of insects and arthropods have also been reported to use these necroses. Two species, *Odontoloxozus longicornis* Coquillett (Diptera: Neriidae) and *Volucella isabellina* Wilson (Diptera: Syrphidae), were described from saguaro, *Carnegiea gigantea* Britton and Rose, and other columnar species (Mangan 1984). Saguaro is also host for *Dinocheirus arizonensis* (Pseudoscorpionida: Chernetidae) (Zeh and Zeh 1992) and *Macchrocheles subbadius* (Acari: Macchrochelidae) (Polak and Markow 1995). The composition and structure of the arthropod communities in which these species are found in columnar cacti have never been described. Whether the same communities are found in all cacti or if the specific characteristics of each species of cactus shape the diversity of arthropods utilizing them is therefore unknown.

In the study presented here, arthropod composition was determined for the necrotic tissues of three species of columnar cactus found together in the desert of coastal Sonora, Mexico: cardón, organ-pipe, and senita. We asked if different assemblages of arthropods were present in different cactus species and if communities were different in the spring compared with the summer. Two abiotic features of the necrotic material, pH and water content, were also characterized.

Materials and methods

Study sites

Samples of necrotic cacti were collected from two areas in the southern Sonoran Desert, both near Guaymas, Sonora, Mexico. The two areas are part of a long-term study of temporal and spatial variation in the incidence of cactus necroses and the population biology of *Drosophila* spp. that breed in them. The first area, El Sahuaral (28°00′N, 110°57′W), is a cactus forest of approximately 50 ha, in which a stand of exceptionally large cardón exists. These cacti can be up to 10 m high and weigh close to 5000 kg. The second site is on the Old Road to Algodones Beach (27°58′N, 110°05′W) and consists of a level valley of 70 ha surrounded by mountains of up to 500 m in elevation. All three cactus species are found at El Sahuaral, but no cardón exist on the Algodones site. Thus all samples of cardón were collected at El Sahuaral.

Field sampling

Twelve samples of necrotic tissue were collected for each species of cactus, six in April and six in August, for a total of 36 samples. Without being present at the inception of a necrosis, it is impossible to know its exact age. We attempted, however, to sample necroses of similar overall size and color. Given the large areas in which cacti are found and the relatively low incidence of necroses, this was the only viable sampling approach. Sampling was conducted in the mornings between 10:00 and 12:00. Before any material was collected, the pH of the necrosis was measured and insects observed flying around the necrotic tissue were collected for 30 min with a net or forceps. Insects were preserved in 70% ethanol in 2-mL plastic containers. Each piece of necrotic cactus, weighing about 1 kg, was placed in a preweighed glass jar for laboratory analysis.

Laboratory sampling

Each sample was weighed and assayed for water content. Water content was estimated using three subsamples of tissue of approximately 3 g each. These samples were weighed, desiccated in an incubator at 90°C for 24 h, and then weighed again. Insect communities within the necrotic tissue were sampled in two ways. First, the material was inspected visually and the largest insects were collected with forceps and preserved in 70% ethanol. Next, the necrotic material was divided in two and each subsample was extracted into 70% ethanol, using a modified 15-cm Berlese funnel with a 3-mm iron mesh and a 60-W bulb for 8 h, about 25 cm above the sample. Funnels were checked every 160 min, to retrieve any larvae before they could become desiccated and unidentifiable. All arthropods were retained in 70% ethanol in 2-mL plastic containers for identification. Voucher specimens were deposited in Instituto Tecnologico y de Estudios Superiores de Monterrey, Campus Guaymas, Sonora, México.

Data analyses

All specimens could be either identified to species or separated to morphospecies and, therefore, species frequency and number were used to compare diversity between cactus species and between seasons. Using orders or families, rather than species, would give an underestimate of biodiversity. The Shannon and Weaver index, expressed as

$$H' = \Sigma\ p_i \ln p_i \qquad [1]$$

where H' is biodiversity and p is the proportional abundance of each species, was selected for the analysis because it is the index most commonly used to express biodiversity richness and is moderately sensitive to sample size (Magurran 1988). The large number of individuals of some species found led us to use the Simpson index and the Shannon eveness index. The Simpson index, expressed as

$$D = \Sigma\ (n_i(n_i - 1)/(N(N - 1)) \qquad [2]$$

where n is the number of individuals per species and N is the total number of individuals, has moderate discrimination ability and a low sensitivity to sample size, making it a good index to express dominance in biodiversity (Magurran 1988). The Shannon eveness index, expressed as

$$E' = H'/\ln S \qquad [3]$$

where S is species number, has a low discrimination ability with regard to the size of the sample (Magurran 1988). Thus, in the present study, Shannon evenness should be interpreted with caution and viewed simultaneously with the Simpson index. Differences in the water content and pH of cacti were compared by factorial (cactus, season) ANOVA.

Results

The total number of organisms found was 9380, representing 34 species (Table 1). Species belonged to three orders of arachnids (four species) and seven orders of insects (30 species). Mites comprised the majority of all arthropods and Diptera the majority of the insects. Because tissue samples varied slightly in volume, the number of individuals is given per kilogram of necrotic material. The number of samples in which each arthropod species was found provides an indication of the variation among samples. Those

Table 1. Number of arthropod species found in necrotic tissue of three species of columnar cactus sampled in spring and summer 1995.

Order	Family	Species or morphospecies*	*Pachycereus pringlei*		*Stenocereus thurberi*		*Lophocereus schottii*	
			Spring	Summer	Spring	Summer	Spring	Summer
			Class Insecta					
Diptera (3961)	Cecidomyiidae	Morphospecies 1 (2945)		56 {4} A, L	1 {1} L	3 {1} L	133 {1} A, L	2752 {3} L
	Chironomidae	Morphospecies 2 (387)		229 {2} L			9 {1} L	149 {2} L
	Muscidae	*Muscina stabulans* (Fallen) (351)		2 {1} A		48 {2} L	7 {3} A	294 {5} A, L
	Drosophilidae	*Drosophila nigrospiracula* (Patterson and Wheeler) (111)	103 {3} A, L	8 {1} A				
	Drosophilidae	*Drosophila arizonae* Riuz Heed and Wasserman (100)		100 {1} A				
	Drosophilidae	*Drosophila mojavensis* (Patterson and Crow) (23)			23 {3} A, L			
	Drosophilidae	*Drosophila pachea* (Patterson and Wheeler) (22)					22 {3} A, L	
	Syrphidae	*Volucella isabellina* (15)		2 {1} L			8 {2} A, L	5 {1} L
	Chironomidae	Morphospecies 3 (3)		2 {2} L			1 {1} L	
	Sciaroidea	Morphospecies 4 (3)					3 {1} L	
	Culicidae	*Anopheles pseudopunctipennis* (Say) (1)		1 {1} A				
Coleoptera (483)	Histeridae	*Platydracus phoenicurus* (Nord) (152)	43 {6} A, L	3 {2} A	86 {4} A, L	8 {2} L	4 {1} A	8 {2} A, L
	Histeridae	Morphospecies 5 (113)	89 {4} L	23 {2} L	1 {1} L			
	Histeridae	*Platysoma* (species a) (96)	86 {3} A, L	1 {1} A	4 {2} A		5 {2} A	
	Histeridae	*Platysoma* (species b) (69)	20 {3} A		8 {1} A		1 {1} A	40 {3} A
	Nosodendronidae	*Nosodendron* sp. (27)	9 {6} A		18 {4} A			
	Histeridae	*Hololepta yucateca* Marseul (13)						13 {3} A, L
	Staphylinidae	*Tachyporus* sp. (12)	9 {3} A		3 {2} A			

	Tenebrionidae	*Centrioptera variolosa* Horn (1)			1 {1} A			
Isoptera (159)	Hodotermitidae	Morphospecies 6 (159)		159 {2} A				
Hymenoptera (135)	Formidae	*Crematogaster arizonensis* Wheeler (55)					55 {2} A	
	Formidae	*Pheidole* sp. (55)	24 {2} A		31 {2} A			
	Formidae	*Pseudomyrex* sp. (20)	2 {2} A		2 {1} A		16 {1} A	
	Chalcididae	*Brachymeria ovata* (Say) (3)				3 {1} A		
	Leucospididae	Morphospecies 7 (1)			1 {1} A			
	Leucospididae	*Leucospis* sp. (1)					1 {1} A	
Hemiptera (20)	Veliidae	*Microvelia* sp. (18)	1 {1} A				17 {2} A	
	Coreidae	Morphospecies 8 (2)					2 {1} A	
Dermaptera (1)	Chelisochidae	Morphospecies 9 (1)		1 {1} A				
Lepidoptera (1)		Morphospecies 10 (1)					1 {1} A	
		Class Arachnida						
Acari (4606)	Veigaiidae	Morphospecies 11 (4447)	212 {6} A, L	102 {2} A, L	8 {4} A		43 {1} A, L	4082 {5} A, L
	Macrochilidae	*Macchrocheles subbadius* (159)	18 {4} A	20 {2} A, L	9 {3} A			112 {4} A, L
Pseudoscorpionides (13)		*Dinocheirus arizonensis* (13)	4 {4} A	3 {2} A	1 {1} A			5 {1} A
Araneae (1)	Salticidae	Morphospecies 12 (1)					1 {1} A	
Total species			13	16	15	4	18	10
Total organisms			620	712	197	62	329	7460

NOTE: Values are the number of individuls of each taxon found in each cactus species for each season, with total number for each taxon given in parentheses; values in braces, { }, are the number of samples out of six in which each species was found; abbreviations: A, adults; L, larvae.

* The genus of all the morphospeciesis is unknown, but an exhaustive examination suggests a single species. Voucher specimens of all morphospecies are deposited in Instituto Tecnologico y de Estudios Superiores de Monterrey, Campus Guaymas, Sonora, México.

samples in which larvae were present indicate that the cactus tissue is the actual breeding site for these species.

The composition of the arthropod community differed among cactus species (Fig. 1). In cardón, Diptera, Coleoptera, and Acari were the dominant taxa, whereas the organ-pipe cactus had few Acari and senita hosted many Diptera and Acari but few Coleoptera. There were major seasonal shifts in arthropod-species composition in each cactus host (Fig. 2). In organ-pipe and senita, there was a reduction in the number of species from spring to summer. Both cardón and organ-pipe exhibited marked increases in Diptera and reductions in Coleoptera and Acari. In cardón, the increase was due to the abundance of larval rather than adult Diptera.

A comparison of the diversity indices among seasons revealed that species abundance declined in organ-pipe and senita from spring to summer, whereas in all three cactus species, the degree to which a small number of species dominated the community was greater in summer than spring (Table 2).

There were differences among cacti, by season for pH ($F_{5,25} = 5.46$, $P = 0.002$), and in water content ($F_{5,25} = 5.88$, $P = 0.001$). The highest pH values were observed in cardón and the lowest in organ-pipe, especially in the summer. Cardón had the highest water content in both seasons.

Discussion

Although we found a large number of arthropods utilizing necrotic columnar cacti, our survey results are probably an underestimate. Some arthropods, especially those at higher trophic levels or with a low reproductive output, may occur in small numbers and can be missed by such a survey. For example, Mangan (1984) quantified the occurrence of the dipterans *O. longicornis* and *V. isabellina* relative to *Drosophila nigrospiracula* Patterson and Wheeler in saguaro, and their numbers were low. At times other than during this survey, members of these species have been observed at cardón and organ-pipe necroses, although no *O. longicornis* and only 15 *V. isabellina* are among the organisms reported here.

Some arthropod species appear to be restricted to certain hosts and this restriction may reflect qualitative or quantitative properties of the specific cactus. Comparative chemical composition of columnar cacti has been extensively studied in the context of investigations of host specificity of *Drosophila* spp. (Kircher 1982). Some of the chemical constituents are toxic to most *Drosophila* spp. and their toxicity is an important factor in the specialization of *Drosophila* spp. on different columnar-cactus hosts. Either these compounds are not toxic to all other arthropods in the community or the position of some species in the trophic structure does not expose them to deleterious compounds. For example, lophocerine is a compound in senita that is toxic to eight species of southwestern *Drosophila* (Heed and Mangan 1986). The large number of Cecidomyiidae and Chironomidae in our sample suggests that the compound is not a problem for other Diptera. Also, overall host quality may differ among cactus species. organ-pipe appears less desirable as a resource than either senita or cardón (Heed and Mangan 1986), but the role of chemical differences, such as its comparatively lower water content and pH, is unknown.

Temporal and spatial differences in necroses among cacti may also underlie contrasts in arthropod communities between host species. The duration of necroses differs among cacti and, thus, in the length of time available for successional processes to occur (Breitmeyer and Markow 1998). Arthropod species with longer developmental times may not be able to colonize the necroses of smaller cacti, such as senita, that dry out more quickly. The number of dipteran larvae present may prolong the duration of the

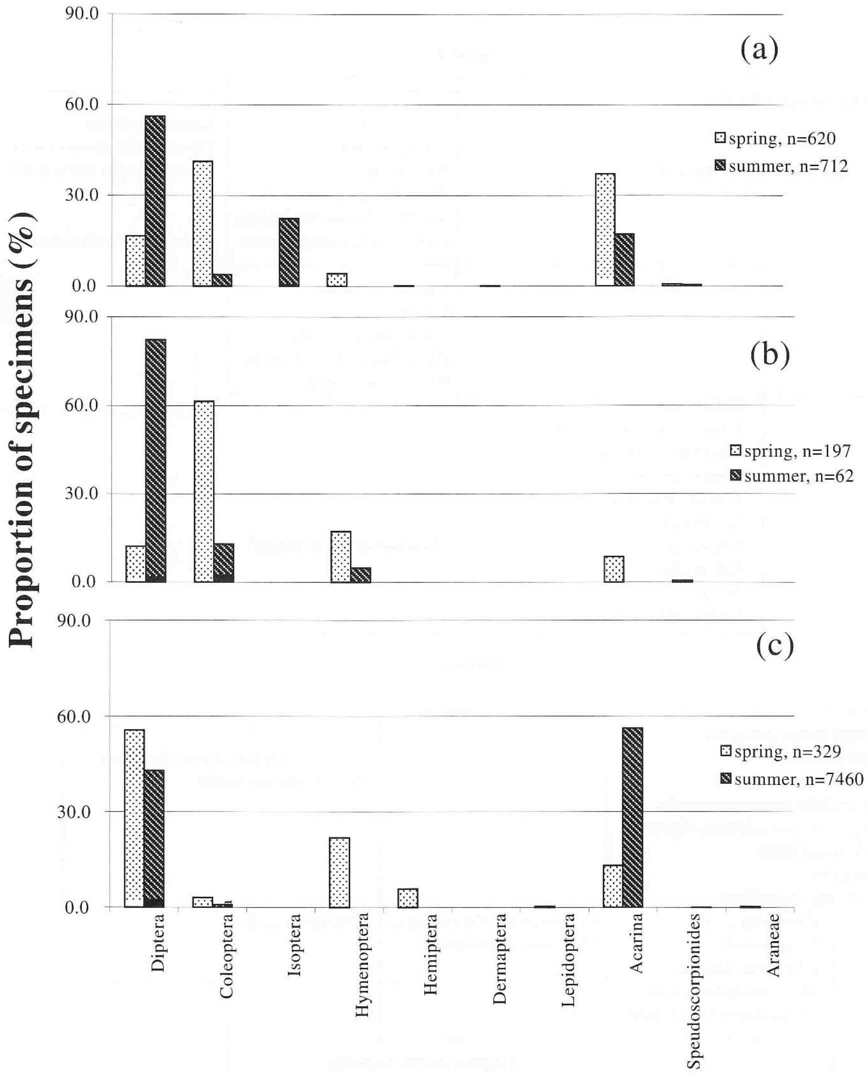

FIGURE 1. Proportions of total number of arthropods, by order, found in necrotic tissue of the columnar cacti *Pachycereus pringlei* (*a*), *Stenocereus thurberi* (*b*), and *Lophocereus schottii* (*c*) during spring and summer.

necrosis. Santana (1961) reported that, in another columnar cactus, *Carnegiea gigantea* Britten and Rose (Cactaceae), dipteran larvae congregated at the juncture between necrotic and healthy tissue, preventing the "corking-off" natural defense mechanism of the plant. Population sizes differ among species of the genus *Drosophila* (Breitmeyer and Markow 1998). Because *Drosophila* spp. are specific to particular host cacti, these differences may contribute to the host variability in necrosis duration. Finally, the niche breadth and dispersal ability of the arthropod species found in necrotic cacti may influence their appearance in different cactus hosts. For example, arthropod species that only live in cardón, patches of which are far apart, should be better dispersers than species inhabiting densely growing cacti such as senita.

Seasonal abiotic changes may also influence colonization of and succession within a necrotic patch. Summer in the Sonoran Desert brings temperatures of 50°C.

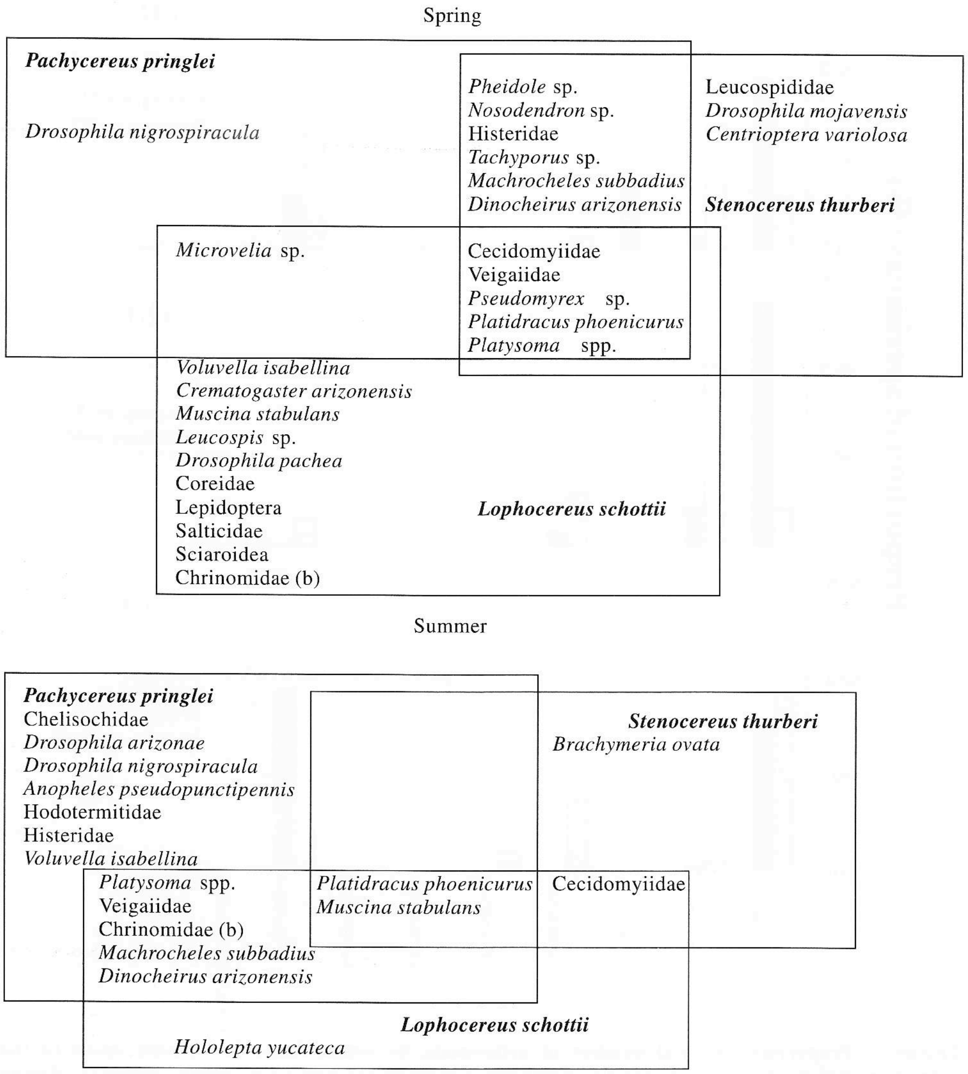

FIGURE 2. Arthropod-species distribution found in necrotic tissue of the columnar cacti *Pachycereus pringlei, Stenocereus thurberi,* and *Lophocereus schottii* during spring and summer.

Many microhabitats do not reach this temperature, but the summer heat is likely to be an important factor, direct or indirect, in the changes observed in species composition from spring to summer. Samples in this study were taken 3 months apart and from different cactus rots during each sampling period. It would be of interest to inventory the initial and successional colonizers in rots that start at different times of the year. Trophic structure also appears to change with season. In organ-pipe and cardón, the number of arthropods at higher trophic levels is always small but, in senita, there is an increase in the number of parasites and predators, mainly mites and beetles, in the summer. The Shannon evenness indices also reflect the tendency of certain species to dominate the community in the summer. Understanding the relationships among the

TABLE 2. Mean ± SE water content and pH of cacti necrotic tissue and diversity indices for arthropods found on three species of columnar cactus examined in spring and summer.

	Pachycereus pringlei		*Stenocereus thurberi*		*Lophocereus schottii*	
	Spring	Summer	Spring	Summer	Spring	Summer
Water content	84.0±1.0	83.6±2.2	77.0±2.1	72.8±3.8	78.1±2.8	67.8±3.3
pH	8.0±0.2	7.5±0.3	6.3±0.5	4.7±0.7	6.9±0.4	7.0±0.4
			Diversity index			
Simpson (1/*D*)	5.23	4.99	4.18	1.59	4.59	2.29
Shannon (*H*′)	1.93	1.84	1.85	0.73	1.96	1.02
Shannon (*E*′)	0.75	0.66	0.68	0.53	0.68	0.44

NOTE: See text for details of diversity indices.

arthropods and the relationship between different species of cacti and the arthropod communities residing in them can be better achieved by additional studies of the colonization and succession of cacti from the earliest signs of necrosis until the last organism emerges from the necrotic stem or arm.

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