

Microarthropod communities associated with biological soil crusts in the Colorado Plateau and Chihuahuan deserts

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ABSTRACT

Biological soil crusts provide habitat for microarthropods of various trophic groups in arid systems, but the community composition and functional role of microarthropods in these unique systems are not well characterized for many desert locations. This study examined the microarthropod community, including mites, collembolans, and tardigrades, associated with early- and late-successional stage biological soil crusts at two locations, Colorado Plateau (southeastern Utah) and Chihuahuan Desert (southern New Mexico). Most microarthropod groups were more abundant in Colorado Plateau than Chihuahuan Desert, and tardigrades were more abundant near the surface (0–10 cm) than at depth (10–30 cm). Although the microarthropod community composition differed between Colorado Plateau and Chihuahuan Desert, Aphelacaridae, Cosmochthoniidae, Micropsammidae, Nanorchestidae, Stigmaeidae, and Tydeidae were families common to both locations, both crust stages and both depths. Most families present were microphytophagous, either strictly or as facultative predators. These findings are compatible with the microfloral nature of biological soil crusts dominated by lichen, moss, and cyanobacteria. Occasional predation of nematodes and protozoa grazing on the crust flora is likely. Other groups identified included zoophages, necrophages and macrophytophages. Proposed is a ‘core community’ of five strict microphytophages, four facultative predators, two zoophages, and one necrophage family.

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1. Introduction

Arid and semiarid lands comprise almost 35% of all terrestrial lands. Biological soil crusts are diverse assemblages of bacteria, cyanobacteria, algae, fungi, lichens, and mosses that represent up to 70% of the living cover in arid and semiarid lands (Belnap and Lange, 2001). Biological soil crust formation begins with early-colonizing fungi and cyanobacteria that stabilize the soil surface and facilitate later-colonizing species. Subsequently, lichens, green algae, and mosses establish, representing a later stage of successional maturity. Distinct microflora and microfauna inhabit biological soil crusts along a gradient from early-successional, cyanobacteria-dominated crusts to late-successional, lichen- and/or moss-dominated crusts (Belnap and Lange, 2001; Darby et al., 2006, 2007).

Nematodes and protozoa comprise a large portion of total grazer biomass by feeding on fungi, bacteria, cyanobacteria, green algae,

plant roots, and other soil fauna (Clarholm, 1985; Freckman and Mankau, 1986). They inhabit water-filled pores and contribute to heterotrophic nitrogen mineralization. The dry air-filled pore spaces in biological soil crusts provide habitat for microarthropods in arid systems. Microarthropods are important for maintaining normal nutrient cycling by contributing to microbial turnover (Moore et al., 1988; Santos and Whitford, 1981; Santos et al., 1981; Parker et al., 1984). Several common families fragment detritus which enhances leaching of soluble materials and increases the surface area available for microbial colonization. Acari, especially Prostigmata, are prevalent microarthropod fauna in deserts (Noble et al., 1996; Shepherd et al., 2002; Whitford, 1996). Tardigrades, although less numerous than Acari, are tightly associated with moss and lichen patches in desert habitats (Beasley, 1978, 1988). Tardigrades probably affect surface microflora but are not typically credited as participants in nutrient cycling. The objective of this study is to meet a call for greater knowledge of biological soil crust-associated microarthropods (Shepherd et al., 2002) through comparative sampling of crust successional stages at two contrasting locations.

Multiple frameworks have been published describing the trophic groups and interactions among trophic groups for soil microarthropods. Elliott et al. (1988) proposed four groups of predatory microarthropods based on feeding behavior: 1) general

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predators of arthropods and nematodes, 2) specialists that feed exclusively on nematodes, 3) specialists that feed exclusively on arthropods, and 4) omnivores that feed primarily on microphytes. This was criticized as being too simplistic because it ignores facultative predation. Luxton (1972) provided initial insights on facultative predation and Walter and Proctor (1999) review the prevailing ambiguity of predation. Additionally, most engulfing detritivores are likely consuming protozoa along with microbes on detritus (Elliott et al., 1988). Based on published literature, we propose a preliminary classification for Acari following a mixture of Luxton (1972) and Walter and Proctor (1999) approaches, with application to soil biological crusts of the Colorado Plateau and Chihuahuan deserts, which contrast in summer temperature and time of year that precipitation occurs.

2. Materials and methods

2.1. Study sites

Two geographic locations were chosen for comparison, Canyonlands National Park (southeastern Utah, 38835.080N, 109849.160W), and the Jornada Experimental Range (southern New Mexico, 32831.800N, 106843.410W). Soils from Canyonlands, Utah, are classified as Rizo series loamy mixed, calcareous soil and soils at Jornada, New Mexico, are a Regan series clay loam. Both soils have pH of 7.5–8 and low organic matter (<1%) in plant interspaces. The Colorado Plateau is classified as a cool-desert as 65% of the precipitation occurs in winter while the Chihuahuan Desert is classified as a hot-desert as 65% of the precipitation occurs during summer (Havstad et al., 2006).

Areas of early- and late-stage successional crust were identified at each geographic location. The early-successional crust stage was dominated by filamentous, non-heterocystous cyanobacteria *Microcoleus vaginatus* at both sites. The late-successional stage crust in the Colorado Plateau was a more complex composition of cyanobacteria, lichen (predominantly *Collema tenax*), and moss (predominantly *Syntrichia ruralis*). Both cyanobacteria and lichens (predominantly *Placidium lachneum*, *Placidium squamulosum*, and *C. tenax*) dominated the late-successional maturity crust in the Chihuahuan desert. Late-successional stage crusts at both locations generally contain greater total microfloral diversity and biomass than early-successional stage crusts at both locations.

2.2. Sampling

Samples were collected in September 2002. At both sites, five replicate plots were chosen for each of the two stages of biological soil crust cover (early- and late-succession) and two depths (0–10 and 10–30 cm) for a total of 40 samples. Soil was excavated from 15-cm diameter and 30-cm deep holes and subsamples collected representing 0 to 10- and 10 to 30-cm depths for general microarthropods and tardigrades, separately. Both types of samples are from the same location but sampled at different times. For microarthropods, 1-kg samples were placed in 1 L, amber high-density polyethylene bottles to which 95% ethanol was added in the field and stored until processing. Tardigrade subsamples were 500-g and transported by 2-day delivery for immediate processing. All sample weights were corrected for gravimetric soil moisture determined by drying soil to equilibrium at 60 °C.

2.3. Extraction and identification

Microarthropods were extracted by heptane-flotation to allow immediate sample preservation, obtain both living and dead organisms, and eliminate biases of other microarthropod extraction

methods (Kethley, 1991). Voucher specimens of each family were mounted in Hoyer's fluid on glass slides for initial identification and subsequently archived. Subsequent specimens were cleared in lactic acid and placed in temporary mounts, consisting of disposable liquid-holding wells (Diversified Biotech, Boston, Massachusetts) attached to glass cover slips and filled with lactic acid, enumerated and archived in 70% ethanol. Collembolans were identified to genus (Christiansen and Bellinger, 1998) and mites were identified to family (Kethley, 1990; Krantz and Ainscough, 1990; Norton, 1990; Philips, 1990). Tardigrades were extracted in duplicate 200-g subsamples by Cobb's decanting and sieving method followed by a modified Oostenbrink cotton-wool filter extraction tray, and sucrose centrifugation (Darby et al., 2007). All tardigrades were counted from 10% of the entire recovery.

2.4. Feeding groups

Microarthropod feeding groups were assigned to each family based on reported feeding behavior of confamilials in the literature (Table 1). Feeding habit was based on five groups: macrophytophages, microphytophages, microphytophages that are facultative predators, zoophages and necrophages (Luxton, 1972; Walter and Proctor, 1999). Microphytophages were subdivided into two sub-groups, either 'strict microphytophages' or 'microphytophages that are facultative predators' (hereafter referred to as 'facultative predators'). The difference between the two sub-groups is that the latter has been reported to be significant predators of nematodes (Santos and Whitford, 1981; Santos et al., 1981; Walter, 1987, 1988). Unfortunately, there is a paucity of ecological information published on most soil microarthropods so feeding groups were based on multiple factors. Specifically, each microarthropod family was designated with a feeding group based on documented feeding behavior and prey types reported as "likely" or "probable" in the literature. When no information was available, feeding behavior was inferred based on feeding behavior of closely related taxa.

2.5. Statistical analysis

A three-way analysis of variance (ANOVA) or categorical analysis was performed to determine if total microarthropod abundance or family richness within trophic groups differed between location, crust stage, and vertical depth. Location, crust stage, and vertical depth were treated as main effects and were included in the mixed model. There was no significant statistical effect of interactions in preliminary analyses so we excluded them from the final model to optimize degrees of freedom. The 0 to 10- and 10 to 30-cm samples were dependent, so the factor experimental unit (each combination of location and crust) was treated as a random effect variable to compute the component of variance attributable to differences between experimental units prior to calculating the fixed effect of depth.

Canonical correspondence analysis (CCA) was performed to identify patterns of association between microarthropod community composition and environmental properties. Families occurring in at least 10% of samples were used as species variables and the eight treatment combinations were used as nominal environmental variables (i.e., 2 locations × 2 crust stages × 2 depths). Monte Carlo permutations were employed to test the significance of the first axis and the full model. CCA results are displayed graphically with bi-plot scaling focused on inter-species distances, where vectors depict environmental variables and taxa are represented as points. The result is a bi-plot that approximates the weighted averages of each taxon with respect to each of the environmental variables (location, crust stage, depth). Long vectors correlate more strongly with ordination axes than short vectors, and have greater reliability in predictive application. Ordination

Table 1
Occurrence of Acari and feeding habits in Colorado Plateau (CP) and Chihuahuan deserts (CD). Taxa are grouped alphabetically by suborder and family. Feeding habitats are indicated with dietary preferences within columns (a = algae, f = fungi, n = nematode, d = detritus, m = mammals, c = carrion, ar = arthropod, l = lichens, po = pollen, pl = plants). Feeding habits are defined according to Luxton (1972) and Walter and Proctor (1999): § denotes reported as “likely” or “probable” in the literature, ? denotes inferred based on feeding behavior of closely related taxa, and * denotes microphytophages that are facultative predators. Mean abundance is expressed as number per kg of dry soil (± 1 standard error, $n = 19$). Presence of families in early (E)- and late (L)-staged crusts at contrasting depths (0 = not present in any of the 5 reps, $s = 0$ –10 cm, $d = 10$ –30 cm) is recorded.

Suborder Family	Feeding habits					Colorado Plateau			Chihuahuan			References ^b
	obligate microphytophage	facultative predators	zoophage	necrophage	macrophage	no. kg ⁻¹	E	L	no. kg ⁻¹	E	L	
ASTIGMATA												
Saproglyphidae				m [§] ,c [§]		2.13 ± 0.881	sd	sd	0.1 ± 0.06	0	s	7
MESOSTIGMATA												
Ascidae			n,ar			0.09 ± 0.088			0.1 ± 0.06			8, 9, 22
ORIBATIDA												
Amerobelbidae	f [?]					0.05 ± 0.05	s	0	0.0 ± 0.0	0	0	
Aphelacaridae	a,f,c ^{§?}					2.9 ± 1.83	sd	sd	1.1 ± 0.34	sd	sd	15, 20
Brachychthoniidae	a,f					0.6 ± 0.28	sd	sd	0.2 ± 0.14	0	s	15, 17
Cepheidae				f,d		1.12 ± 0.563	s	sd	0.2 ± 0.07	sd	sd	7
Cosmochthoniidae	a					0.9 ± 0.28	sd	sd	0.6 ± 0.21	sd	sd	15
Ctenacaridae	a [?] f [?] c [?]					0.0 ± 0.0	0	0	0.1 ± 0.07	0	sd	
Cymbaeremaeidae	f,l					0.3 ± 0.19	0	s	0.1 ± 0.08	0	s	7, 15
Enarthranota ^a	a [?] f [?]					0.0 ± 0.0	0	0	0.04 ± 0.05	d	0	
Epilohmanniidae				d [?]		0.20 ± 0.092	sd	d	0.1 ± 0.09	0	d	
Gehyppochthoniidae				d [?]		0.29 ± 0.289	0	s	0.1 ± 0.06	d	s	9
Gymnodamaeidae	a,f					1.1 ± 0.41	s	sd	0.2 ± 0.09	0	sd	7, 15
Haplochthoniidae	a [?]					0.0 ± 0.0	0	0	0.05 ± 0.05	s	0	
Hydrozetidae	a,f,pl [?]					0.0 ± 0.0	0	0	0.05 ± 0.05	s	0	7, 15
Lohmanniidae				d		0.05 ± 0.049	s	0	0.3 ± 0.11	d	sd	14, 15
Mochlozetidae	a,f					1.2 ± 0.76	sd	sd	0.04 ± 0.04	0	s	15
Oppiidae		a,f,n				0.41 ± 0.228	sd	0	0.5 ± 0.21	d	sd	8, 9, 15, 17
Oribatulidae		a,f,po,n,ar,d				1.03 ± 0.467	sd	sd	0.4 ± 0.20	sd	sd	1,3, 5, 8, 15, 17
Parhyppochthonioidea				d		0.17 ± 0.077	0	sd	0.3 ± 0.20	0	sd	
Pediculochelidae	a [?]					0.5 ± 0.29	d	d	0.04 ± 0.04	0	s	
Scheloriobatidae		a,f,n,ar,d				0.53 ± 0.339	0	s	0.0 ± 0.0	0	0	9, 15, 17
Scutoverticidae	f [?]					0.0 ± 0.0	0	0	0.04 ± 0.04	0	s	
Sphaerochthoniidae	a [?]					0.1 ± 0.1	sd	sd	0.7 ± 0.1	sd	sd	
Trichthoniidae	a [?]					0.3 ± 0.19	s	s	0.0 ± 0.0	0	0	
unidentified nymphs ^a						1.02 ± 0.369	sd	sd	0.10 ± 0.097	s	0	
PROSTIGMATA												
Adamystidae			n,ar			0.0 ± 0.0	0	0	0.4 ± 0.30	sd	d	15, 20
Alicorhagiidae		a,f,n				0.60 ± 0.296	sd	sd	0.2 ± 0.12	d	s	17, 18, 22
Anystidae			n,ar			0.0 ± 0.0	0	0	0.04 ± 0.05	d	0	10, 15, 21
Bdellidae			n,ar			0.71 ± 0.334	s	0	0.7 ± 0.25	sd	s	6, 10, 21, 22
Bimichaeliidae		a [?] f [?] n [§]				0.18 ± 0.108	s	d	0.5 ± 0.17	d	sd	22
Caligonellidae			n [?] ,ar			0.56 ± 0.168	s	sd	0.6 ± 0.24	sd	sd	22
Calyptostomatidae			n,ar			0.16 ± 0.123	s	s	0.0 ± 0.0	0	0	7, 15
Cunaxidae			f,n,ar			0.10 ± 0.097	s	0	0.4 ± 0.20	sd	sd	8, 10, 19, 21, 22
Demodicidae			m			0.0 ± 0.0	0	0	0.1 ± 0.06	0	sd	7
Eupalopsellidae			n,ar			0.05 ± 0.050	s	0	0.04 ± 0.04	d	0	11, 21
Eupodidae		a,f,n				0.10 ± 0.066	sd	0	0.0 ± 0.0	0	0	8, 15, 17, 22
Micropsammidae	f					14.2 ± 6.96	sd	sd	1.0 ± 0.5	sd	sd	18
Nanorchestidae		a [§] ,f			pl	2.61 ± 0.747	sd	sd	6.8 ± 1.27	sd	sd	15, 17, 18
Paratydeidae			f [§] ,n,ar			0.31 ± 0.162	d	sd	0.1 ± 0.07	d	s	15, 21, 22
Proteonematalycidae ^a						0.32 ± 0.152	sd	s	0.52 ± 0.329	sd	s	
Psuedocheylidae			n,ar			0.04 ± 0.04	0	d	<0.01	0	0	7, 15, 21
Pygmephoridae	a,f					0.1 ± 0.08	0	d	0.04 ± 0.04	0	d	21
Raphignathidae			n,ar			0.0 ± 0.0	0	0	0.04 ± 0.04	0	s	12, 21
Rhagidiidae			n,ar			0.0 ± 0.0	0	0	0.04 ± 0.04	0	s	15, 22
Stigmaeidae			n,ar			2.63 ± 0.927	sd	sd	1.0 ± 0.46	s	sd	2,16, 21, 22
Stigmocheylidae			n [?] ,ar [?]			0.0 ± 0.0	0	0	0.5 ± 0.03	sd	sd	
Tenerifiidae			n,ar			0.27 ± 0.15	s	d	0.0 ± 0.0	0	0	7, 15, 21
Tenuipalpidae					pl	0.0 ± 0.0	d	d	0.08 ± 0.056	0	0	15
Terpnacaridae	f					0.2 ± 0.10	d	d	0.0 ± 0.0	0	0	18
Tydeidae		a,f,po,n,ar				6.83 ± 1.671	sd	sd	2.9 ± 0.8	sd	sd	2, 4, 10, 13, 17, 22

^a : Finest resolution possible for nymphs.

^b Numbered alphabetically, but ordered chronologically: (1) Behan and Hill, 1978, (2) de Vis et al., 2006, (3) Denmark and Woodring, 1965, (4) English-Loeb et al., 1999, (5) Hahem et al., 1993, (6) Ireson et al., 2002, (7) Krantz, 1978, (8) Mueller et al., 1990, (9) Muraoka and Ishibashi, 1976, (10) Petrova et al., 2004, (11) Rakha and McCoy, 1985, (12) Santos and Whitford, 1981, (13) Santos et al., 1981, (14) Schneider et al., 2004, (15) Smith et al., 1998, (16) Villanueva and Harmsen, 1988, (17) Walter, 1987, (18) Walter, 1988, (19) Walter and Kaplan, 1991, (20) Walter and Proctor, 1998, (21) Walter and Proctor, 1999, (22) Walter et al., 1988.

axes are presented in sequence of variance explained by a linear combination of environmental variables.

Abundance data were transformed as $\log(x + 1)$ prior to analysis to meet assumptions of distribution and variance. ANOVA and

categorical tests were computed using the mixed and catmod procedures, respectively, in SAS, Statistical Analysis Software, Release 8.00 (SAS Institute Inc., Cary, NC, USA) and CCA was analyzed using CANOCO Version 4.5 software (Wageningen, The Netherlands).

3. Results

Microarthropods were more abundant in the Colorado Plateau than Chihuahuan desert. The two groups that contributed to this difference ($p < 0.05$) were microphytophages and facultative predators but not zoophages, necrophages or tardigrades. There were no significant ($p > 0.05$) effects of crust stage, sample depth or interactions among main effects for total microarthropods, although they tended to be most abundant at 0 to 10-cm depth samples from the Colorado Plateau (Fig. 1). However, abundance of tardigrades was greater at 0–10 cm (mean of 54.8 and 9.9 per kg of dry soil in Colorado Plateau and Chihuahuan desert, respectively) than 10 to 30-cm deep (mean of 4.8 and 3.2 per kg of dry soil in Colorado Plateau and Chihuahuan desert, respectively, $p < 0.001$).

A total of 55 microarthropod families were observed in the two locations, 43 were found in Colorado Plateau and 44 in Chihuahuan desert (Tables 1, 2). The five most common families (Aphelacaridae, Cosmochthoniidae, Micropsammidae, Nanorchestidae, Stigmaeidae, and Tydeidae) occurred in all eight combinations of location, crust stage and depth (Table 1). All common families were Prostigmata except Aphelacaridae and Cosmochthoniidae which are oribatids. Prostigmata were the most common and diverse families in both locations, followed by Oribatida. Astigmata and Mesostigmata were neither common nor diverse. Four families of Collembola were observed in Colorado Plateau but only Isotomidae in Chihuahuan desert (Table 2). *Milnesium tardigradum* was the most abundant tardigrade from Chihuahuan desert, while the recently described species *Haplomacrobotus utahensis* (Pilato and Beasley, 2005) was common in Colorado Plateau.

Abundance and distribution of families were affected by geographic location, crust stage, and soil depth (Fig. 2). The first CCA axis represents a location gradient between microarthropods characteristic of Colorado Plateau and those characteristic of Chihuahuan desert. Although not statistically significant, CCA axis 2 tends to separate by depth in Colorado Plateau and crust type in Chihuahuan desert. Eigenvalues of CCA axis 1 (0.201, $p = 0.0020$) and 2 (0.143) explained 55.4% of the total species–environment variance. The species–environment correlations were large for both axis 1 (0.894) and 2 (0.789).

Microphytophagous microarthropods comprised the most common feeding group, representing 30 of the 55 microarthropod families collected at the two locations (Table 1). More of these families were found in early- than late-stage crusts at both depths in Colorado Plateau, but only in 0 to 10-cm depths in Chihuahuan desert (Table 1). The number of strict microphytophagous families exceeded those families known to be facultative predators, 20 and 10 respectively. Among the strict microphytophages, Aphelacaridae, Cosmochthoniidae and Micropsammidae were present at all eight site combinations. Facultative predators Tydeidae, Nanorchestidae, and Oribatulidae were present at all combinations of desert, crust stage and depth (Table 1). Zoophages were the second

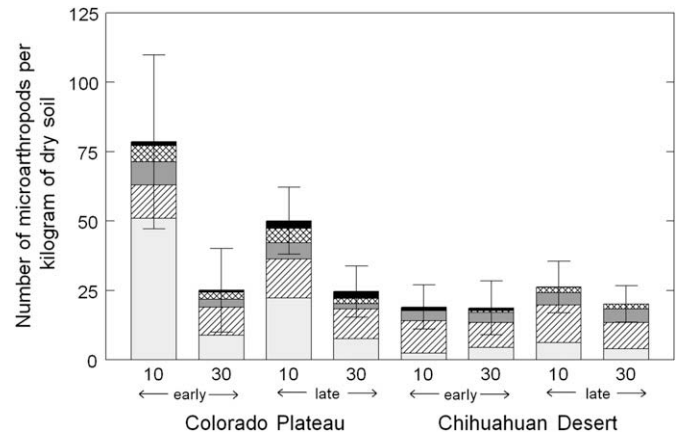


Fig. 1. Microarthropod abundance (number per kg dry soil, ± 1 standard error, $n = 5$) by location (Colorado Plateau, Chihuahuan Desert), crust stage (early-succession, late-succession) and depth (10: 0–10 cm, 30: 10–30 cm). The stacked-bar contrasting fill represents abundance of feeding groups: strict microphytophages (light gray), microphytophages that are facultative predators (diagonal hatch), zoophages (dark gray), necrophages (cross-hatched) and unknown (black).

most common feeding group, represented by 16 families. Caligonellidae and Stigmaeidae were present at all site combinations except beneath early-stage crusts at 10 to 30-cm depth in Colorado Plateau and Chihuahuan desert, respectively. The remaining 14 families were found among the other site combinations (Table 1). Less common were six necrophagous families, one macrophytophagous family, and two taxa designated as unknown (one family in which feeding behavior was neither reported in the literature nor was able to be inferred based on phylogeny, and one taxon that we could not identify). Necrophagous Cepheidae was present at all eight site combinations except in Colorado Plateau under early-stage crust at 10 to 30-cm depth. Numbers of families within each trophic group were not different statistically (Table 3).

4. Discussion

Microarthropod communities in our study were dominated by an ensemble of taxa capable of tolerating extreme abiotic conditions of the thermal and moisture extremes (Whitford, 1989) and limited nutrients. All site combinations included a community comprised of at least five strict microphytophage families (always including Aphelacaridae, Cosmochthoniidae, and Micropsammidae), four facultative predators (always including Nanorchestidae, Tydeidae, and Oribatulidae), two zoophages (usually including Caligonellidae and Stigmaeidae) and one necrophage (often Cepheidae). The specific composition varies by crust stage and geographic location that represent contrasting patterns of temperature, precipitation, and soil texture (Figs. 1, 2). Early-stage

Table 2

Occurrence of collembolans and feeding habits in Colorado Plateau (CP) and Chihuahuan deserts (CD). Taxa are grouped alphabetically by order. Feeding habitats are indicated with dietary preferences listed within cells (a = algae, f = fungi, n = nematode, d = detritus). Feeding habits are defined according to Luxton (1972) and Walter and Proctor (1999) Mean abundance is expressed as number per kg of dry soil (± 1 standard error, $n = 19$). Presence of families in early (E)- and late (L)-staged crusts at contrasting depths (0 = not present in any of the 5 reps, s = 0–10 cm, d = 10–30 cm) is recorded.

Family	Feeding habits					Colorado Plateau		Chihuahuan			References ^a	
	obligate microphytophage	facultative predators	zoophage	necrophage	macrophage	no. kg ⁻¹	E	L	no. kg ⁻¹	E		L
Hypogasturidae		a,f,n,d				0.04 ± 0.042	0	d	0.0 ± 0.0	0	0	2
Isotomidae		a,f,n,d				0.13 ± 0.095	0	sd	0.2 ± 0.14	s	sd	1,2
Onychiuridae	a,f					0.5 ± 0.23	0	sd	0.0 ± 0.0	0	0	1
Sminthuridae	f					0.1 ± 0.05	0	s	0.0 ± 0.0	0	0	1

^a : 1 = Walter (1987), 2 = Walter et al. (1988).

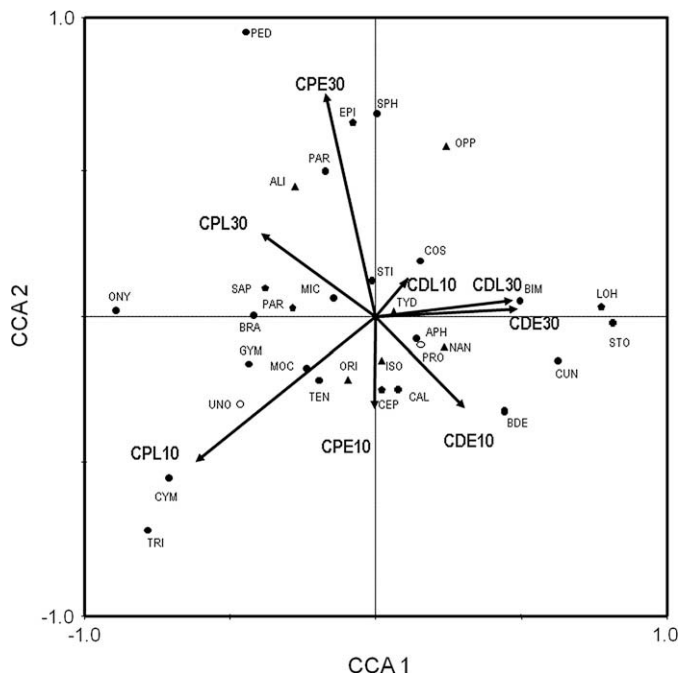


Fig. 2. Canonical correspondence analysis bi-plot of microarthropod families represented in at least 10% of samples (i.e., at least 4 of 40). Treatment combinations are nominal variables illustrated as vectors coded for location (CP = Colorado Plateau, CD = Chihuahuan Desert), crust stage (E = early-successional crust, L = late-successional crust) and depth (10: 0–10 cm, 30: 10–30 cm). Points indicate centroid abundance of each family. Feeding habits are coded by symbol shape (circle: microphytophage; triangle: facultative predator; pentagon: zoophages; x: necrophages; open: undetermined). Eigenvalues (λ) are 0.201 ($P=0.0020$), 0.143, 0.096, and 0.068 for first (horizontal), second (vertical), third and fourth axes, respectively. Families are abbreviated (ALI: Alicorhagiidae, APH: Aphelacaridae, BDE: Bdellidae, BIM: Bimichaeniidae, BRA: Brachychthoniidae, CAL: Caligonellidae, CEP: Cepheidae, COS: Cosmochthoniidae, CUN: Cunaxidae, CYM: Cymbaeremaeidae, EPI: Epilohmanniidae, GYM: Gymnodamaeidae, ISO: Isotomidae, LOH: Lohmanniidae, MIC: Micropsammidae, MOC: Mochlozetidae, NAN: Nanorchestidae, ONY: Onychiuridae, OPP: Oppiidae, ORI: Oribatulidae, PAR: Paratydeidae, PAR: Parhyphochthonioidae, PED: Pediculochelidae, PRO: Proteonematalycidae, SAP: Saprogllyphidae, SPH: Sphaerochthoniidae, STI: Stigmaeidae, STO Stigmocheyleidae, TEN: Teneriffidae, TRI: Trichthoniidae, TYD: Tydeidae and UNO: unidentified oribatid).

crusts contained more microphytophages, especially at the surface, and late-stage crusts tended to contain more families of necrophages. Furthermore, community composition contrasts with soil depth in the Colorado Plateau but not Chihuahuan desert. Strict microphytophages, Aphelacaridae and Micropsammidae, and tardigrades were more abundant at 0 to 10- than 10 to 30-cm soils in Colorado Plateau, where fungal and algal biomass is greatest.

Prostigmata were more abundant than Oribatida in the biological soil crusts of both Colorado Plateau and Chihuahuan desert. A combination of feeding habits and food preferences of the biological soil crusts may explain the abundance of prostigmatids over oribatids in these desert communities. The majority of prostigmatids feed by piercing and sucking cytoplasm from plant, fungal, bacterial and microfaunal cells, while oribatids ingest their litter and fungal food sources (Seastedt, 1984). Relative abundance of prostigmatids is also reported in other arid biomes, including alpine (O'Lear and Seastedt, 1994) and arctic tundra (Douce and Crossley, 1977). Despite being widespread, soil-inhabiting prostigmatids are often overlooked which underestimates their role in soil communities. This is primarily due to their small size and inefficiencies of active or expedient methods of extraction. As a result, many soil prostigmatids are as yet undescribed. For example, in this study, seven species in six genera belonging to the superfamily Tydeioidea were observed yet one genus and all species are undescribed.

Table 3

Number of Acari families per trophic group per site (Micro = microphytophage, F Pred = facultative predators, Zoo = zoophages, Necro = necrophages). Values in parentheses are the total number of families observed within a trophic group across the entire study. Three-way analysis of variance results are presented at the bottom of the table. F-statistics are illustrated for three main effects: desert (Colorado Plateau, Chihuahuan), crust stage (E = early, L = late-successional), and depth (0–10, 10–30 cm). Degrees of freedom were 1 and 32 as numerator and denominator, respectively.

Desert	Crust	Depth (cm)	Micro (20)	F Pred (10)	Zoo (16)	Necro (6)
Colorado Plateau	E	10	8	7	7	4
		30	8	6	2	2
	L	10	10	6	5	4
		30	11	7	5	4
Chihuahuan	E	10	5	4	6	1
		30	5	6	9	3
	L	10	11	7	9	5
		30	6	6	7	4
Main Effects						
Desert			2.89 ^{ns}	3.53 ^{ns}	0.09 ^{ns}	2.44 ^{ns}
Crust			1.64 ^{ns}	0.17 ^{ns}	0.24 ^{ns}	0.71 ^{ns}
Depth			1.21 ^{ns}	1.52 ^{ns}	2.58 ^{ns}	0.29 ^{ns}

^{ns} $p > 0.05$.

The prostigmatid groups, Nanorchestidae and Tydeidae, were among the most common families of the biological soil crusts of both Colorado Plateau and Chihuahuan desert. Nanorchestids and tydeids are also core members of other desert microarthropod communities, common in the Chihuahuan desert (Brantley and Shepherd, 2004; Santos et al., 1984; Shepherd et al., 2002), rangelands (Kay et al., 1999) and biological soil crusts of pinyon juniper (*Juniperus monosperma*) habitats in central Chihuahuan desert (Brantley and Shepherd, 2004; Vaculik et al., 2004) as well. Nanorchestids most likely feed on mosses, lichens, and cyanobacteria, but specific diet breadth and any prey preferences are poorly understood for desert species. Tydeidae are abundant to dominant in arid and semiarid temperate systems (André et al., 1997; Noble et al., 1996). Although classified as microbivorous (Kay et al., 1999; MacKay et al., 1986), there is uncertainty on whether cyanobacteria (specifically *Microcoleus*), lichens, and mosses (Ghabbour et al., 1980; Walter and Proctor, 1999), components of biological soil crust, form a direct portion of the diet of Tydeidae. Tydeidae are known to prey on nematodes (Santos et al., 1981) and nematode eggs (Santos and Whitford, 1981). Because microarthropods can be active even in dry conditions, anhydrobiotic nematodes may be a significant prey item for facultative predators. Furthermore, Tydeidae have been described as plant- and animal-parasites to predators and fungivores (Walter and Proctor, 1999). Walter (1987, 1988) suggests that *Tydeus* sp. and an unidentified microtydeid prefer to feed on fungi and algae in the presence of nematodes; *Paratydeus* sp. and isolates of Tydeidae from the Chihuahuan desert were both microbivorous and nematophagous. However, feeding rates of the isolates varied.

The role of microarthropods in decomposition and mineralization processes is deeply rooted in an evolution spanning 340 million years (Labandeira et al., 1997). Mites do not decompose or mineralize organic matter directly, they facilitate microbial turnover and fragment detritus through comminution, which enhances leaching of soluble materials and increases the surface area available for microbial colonization. Indirectly, they graze on saprobic and mycorrhizal fungi, stimulating their growth and decomposition (Moore et al., 1988). Fungivorous mites, not nematodes or protozoans, are primarily responsible for nitrogen mineralization of decomposing roots in the Chihuahuan desert (Whitford, 1989).

We propose a first approximation of feeding assignments, which have yet to be validated by direct observation, gut contents, morphology and/or phylogenetic relationships. Despite the

uncertainty of assignment to feeding habit, each community contains at least five strict microphytophages, four facultative predators, two zoophages, and one necrophage family. This 'core community' concept is analogous to that proposed by Bamforth (2008) for protozoa in these soils.

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