REGULAR ARTICLE

Impact of biological soil crusts and desert plants on soil microfaunal community composition

Brian J. Darby · Deborah A. Neher · Jayne Belnap

Abstract Carbon and nitrogen are supplied by a variety of sources in the desert food web; both vascular and non-vascular plants and cyanobacteria supply carbon, and cyanobacteria and plant-associated rhizosphere bacteria are sources of biological nitrogen fixation. The objective of this study was to compare the relative influence of vascular plants and biological soil crusts on desert soil nematode and protozoan abundance and community composition. In the first experiment, biological soil crusts were removed by physical trampling. Treatments with crust removed had fewer nematodes and a greater relative ratio of bacterivores to microphytophages than treatments with intact crust. However, protozoa composition was similar with or without the presence of crusts. In a second experiment, nematode community composition was characterized along a spatial gradient away from stems of grasses or shrubs. Although nematodes generally occurred in increasing abundance nearer to plant stems, some genera (such as the enrichment-type *Panagrolaimus*) increased disproportionately more than others (such as the stress-tolerant *Acromoldavicus*). We propose that the impact of biological soil crusts and desert plants on soil microfauna, as reflected in the community composition of microbivorous nematodes, is a combination of carbon input, microclimate amelioration, and altered soil hydrology.

Keywords Colorado Plateau · Soil fauna · Desert · Soil food webs · Islands of fertility

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Introduction

Nutrients in desert soils can concentrate near desert shrubs due to shrubs relocating interspace soil nutrients to rhizosphere soil and trapping dust and plant litter (Schlesinger et al. 1996, Schlesinger and Pilmanis 1998). Shrubs and invasive bunchgrasses often replace native grasses in nutrient-poor soils, leading to further heterogeneity of soil resources and desertification of marginal lands (Schlesinger et al. 1990). However, Housman et al. (2007) demonstrate that not all nutrients concentrate consistently near plants. For example, calcium, copper, phosphorous, and zinc are often depleted under vascular plants relative to inter-space soils. In contrast to vascular plants that can be distributed sparsely, biological soil crusts can represent a continuous carpet, rather than islands, of nutrient fertility. Biological soil crusts form

when early-colonizing fungi and cyanobacteria stabilize the soil surface and facilitate later-successional stage crusts comprised of lichens, green algae, cyanobacteria, and mosses. Biological soil crusts increase the physical stability of surfaces and soil fertility through dust entrapment, photosynthesis, nitrogen fixation, and mineral chelation (reviewed in Belnap 2003). Thus, vascular and non-vascular plants, lichens, and cyanobacteria supply carbon for the desert soil food web, while nitrogen-fixing cyanobacteria and plant-associated rhizosphere bacteria supply nitrogen inputs.

Abundance of amoebae, flagellates, and ciliates, is similar among plant and interspace soils (Housman et al. 2007). In contrast, total abundance of nematodes declines progressively with increasing distance from stems of perennial grass and shrub stems (Housman et al. 2007). Furthermore, nematode communities are more abundant, diverse, and ecologically mature beneath late- than early-successional stage crusts (Darby et al. 2007). Biological soil crusts affect composition of soil nematode communities by both biotic and abiotic mechanisms. Greater diversity and biomass of prey resources are associated with a greater relative abundance of fast-growing micro-bivores. Abiotically, well-developed crusts physically and chemically alter the micro-environment resulting in increased infiltration, nutrient availability, and surface soil stability.

The objective of this study was to compare the relative influence of vascular plants and biological soil crusts on desert soil nematode and protozoan abundance and community composition. Two experiments were conducted. The first experiment sought to determine how removal of late successional biological soil crust, by a moderate level physical disturbance (i.e., annual trampling), affects the associated soil nematode and protozoan communities. The second experiment examined nematode community composition in a spatial gradient away from stems of grasses and shrubs surrounded by early and late successional stage crusts.

Methods

Crust removal experiment

Three representative cool desert sites were selected with different soil depths, a shallow (i.e., 10 cm to

bedrock), medium (i.e., 20 cm to bedrock), and deep (i.e., 30 cm to bedrock) site. The shallow and medium soil sites were located in the Island in the Sky (ISKY) district of Canyonlands National Park and the deep soil site was located in Arches National Park, both near Moab, Utah. These parks represent the cool desert environment of the Colorado Plateau (Rosentreter and Belnap 2001). The shallow, medium, and deep sites represent the range of Colorado Plateau soils and were selected in this study to more completely capture the effect of crust removal by physical trampling. Average annual precipitation and temperatures at ISKY and Arches are 229 mm and 219 mm, respectively, whereas annual average temperature is 11.5°C and 14.1°C, respectively. Soils at all sites are loamy fine sands. Untrampled lichen/moss cover at ISKY (shallow) was 7.1% (± 0.15), at ISKY (medium) was 4.4% (± 0.12), and at Arches (deep) was 17.2% (± 0.35).

At each site, ten plots of 10 m^2 area were delineated and five plots were trampled since May 1995 while five plots left untrampled. Each spot in the trampled plots was lightly and carefully stepped on twice in succession, annually, in spring, to remove biocrust organisms with the minimum disturbance possible. Soil from each plot was sampled in April 2004 (nematodes) and May 2004 (protozoa) at 10 cm sampling increments: 0 to 10 cm from the shallow, medium, and deep sites, 10 to 20 cm from the medium and deep sites, and 20 to 30 cm from the deep site, resulting in 60 total samples, trampled and untrampled.

Plant experiment

Soil was collected from two locations near Moab, Utah, in September 2003. The first location was just outside ISKY, and the second in the Needles district of the same park (referred to as "Needles"). Within each location, one area was identified that was dominated by the grass *Stipa hymenoides* and a second area dominated by the shrub *Coleogyne ramosissima* (Welsh et al. 2008). Portions of the biological soil crust cover were identified as belonging to one of two categories of crust cover within each combination of plant type and geographic location. The first category was defined as crust that is dominated by the cyanobacterium *Microcoleus vaginatus*, representing a relatively early successional stage, and hereafter called "cyanobacterial crusts". The second category of crust contains a more diverse floral

assemblage including the cyanobacteria *M. vaginatus*, *Scytonema myochrous*, and *Nostoc commune*, the lichens *Collema tenax* and *C. coccophorum*, and the moss *Syntrichia canninervis*. These represent a relatively late-successional stage and are hereafter called "cyano/lichen/moss crusts". At both locations, six plots were identified within each plant area for a total of three replicate plots for each crust type. Each plot consisted of three plants of the same species and associated with the same crust type. Soil cores (2.2 cm dia.) were collected from the top 0 to 10 cm in each of the four cardinal directions around each plant at five microsites: stem, dripline, close (3 cm), mid (10 cm), and far (35 cm) interspaces (measured from the edge of the canopy dripline). Cores from the four cardinal directions of the same microsite were pooled from all three plants within a plot. Thus, the sampling design included two locations, two plant types, two crust types, three replicate plots of each location, plant and crust combination, and five microsites per plot. Total abundance of microfauna and trophic groups were analyzed elsewhere, along with soil chemistry and microflora (Housman et al. 2007), and only nematode community composition at the genus level is addressed here.

Estimation of nematode and protozoa abundance

In both experiments, nematodes were extracted from 250 g soil samples with Cobb's decanting and sieving with cotton milk filter trays (Whitehead and Hemming 1965). Briefly, soil was decanted with duplicate passes over 600, 250, 150, 75, and 44 μm sieves. Nematodes and organic debris collected on the sieves were backwashed into a common basin and poured onto a cotton filter suspended above a collecting tray. After 48 h, the cotton filter was removed and the nematodes were collected for a counting of 10 % of the initial sample. Abundance of nematodes is expressed on a dry mass basis. Nematodes were then heat relaxed and fixed in warm 8% formalin prior to enumeration of a representative selection of nematodes to genus (Thorne 1974a, b, Jairajpuri and Ahmad 1992, Hunt 1993, Bongers 1994, Siddiqi 2000, and De Ley et al. 2003), 150 individuals per sample in the Crust Removal Experiment and 250 individuals per experimental unit in the Plant Experiment. A collection of the semi-permanent voucher specimens are stored in the DA Neher lab in the

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Protozoa were enumerated from soils using a most probable number technique according to Darbyshire et al. (1974) with the following modifications (Darby et al. 2006). Sterilized soil extract (6% w/v) was used as the diluent for MPN dilutions. Nine grams of the original soil sample were mixed in 80 ml of sterile DI water and agitated on a rotary shaker for 5 min at room temperature. Five milliliters of this dilution was diluted 3-fold, seven times (in serial dilutions), and homogenous 1-ml aliquots of each of the final six dilutions were placed in each of eight wells across a 48-well Falcon® tissue culture plate row, one dilution per row. Wells positive for protozoa were recorded for each plate after 3, 10, 17, and 24 d of incubation at room temperature using an inverted microscope with phase contrast at 100×, 200×, and 400× magnification. Repeated observations were necessary to observe the natural ecological succession in protozoan communities that develop in culture. Approximately 1 min per well per week was spent seeking each motility group throughout the entire well, resulting in a search effort of about 30 to 60 min per plate per week. The most probable number of each motility group (amoebae, flagellates, and ciliates) was calculated according to Cochran (1950). The minimum detection limit for this dilution series was estimated to be 7 cells g^{-1} dry soil by calculating a hypothetical most probable number from a standard 3-fold dilution series initiated by 9.0 g soil that would contain a single positive well at the most concentrated dilution.

Computation community indices

Abundance of microfauna was expressed as individuals per gram dry soil based on gravimetric determination of soil moisture at time of sample processing. Diversity at the genus level was computed as $\Sigma p_i*\ln(p_i)$, where p_i is the proportion of each genus i (n_i/N) (Shannon 1948). Finally, the combined Maturity Index was computed as the weighted mean of colonizer-persistor (cp) values: Σp_i*cp_i, where p_i is the proportion of the genus i and cp_i is the cp-value of genus i (Bongers 1990, as modified by Yeates 1994). Genera from families believed to represent faster-growing, colonizer-type individuals are assigned a low cp-value (1 or 2) and genera from families thought to

represent slower-growing, persister-type individuals are assigned a high *cp*-value (4 or 5). Consequently, low maturity values represent a community dominated by fast-growing, colonizer-type individuals while high maturity values represent a community with relatively more slow-growing, persister-type individuals (Bongers 1990).

Statistical analysis

Crust removal experiment

Univariate procedures were employed to analyze the dependent variables including nematode, amoebae, flagellate, and ciliate abundance, and the indices of richness, diversity, maturity, and bacterivore proportion of nematodes. Independent variables included site (shallow, medium, or deep), trampling (with or without) and the interaction between site and trampling. Data were analyzed using the MIXED procedure of SAS Version 9.1 (SAS Institute, Inc., Cary, NC) in two phases. First, site and treatment were tested as completely randomized for 0 to 10-cm samples only. This allowed for comparison across all three sites. Secondly, the effect of sampling depth was compared between all three sites, excluding the effect of trampling. This tested how communities changed with depth within a soil. Comparisons among means for treatments that were statistically significant ($p < 0.05$) were made by Fisher's protected Least Significant Difference (LSD) Test. Prior to analysis, nematode, amoebae, flagellate, and ciliate abundances were $\log_{10}$–transformed [$\log_{10}(x)$], and bacterivore nematodes as a proportion of all nematodes was arcsine of square-root transformed [$\sin^{-1}(\sqrt{(p)})$] to meet assumptions of Gaussian distribution. Diversity and maturity index values met assumptions without transformation.

Composition of nematode community at 0–10 cm was analyzed using a direct gradient canonical correspondence analysis (CCA) to identify patterns of association between nematode community composition, physical trampling, and sites. All genera were regarded as species variables and the six treatment combinations (i.e., factorial combination of three sites and two trampling treatments) were coded as nominal environmental variables (0, 1). Data were $\log_e$–transformed prior to analysis and CCA was computed using CANOCO software Version 4.5 (Biometris,

Wageningen, The Netherlands). The significance of the first axis and full model was tested against 499 unrestricted Monte Carlo permutations and the resulting *p*-value represents the proportion of models with permutated data that described more species-environment variation than actual data along the first axis or full model.

Plant experiment

Total abundance of nematodes was analyzed by mixed model ANOVA followed by Dunnett's multiple comparison tests using 'stem' samples tested against all other microsites of the same location, plant type, and crust type. Protozoa were analyzed elsewhere (Housman et al. 2007) and found to be distributed evenly across the microsites for all locations, plant types, and crust types. Multivariate analysis of nematode community composition from the Plant Experiment used a modification of the Principal Response Curves (PRC) approach of Van den Brink and ter Braak (1998, 1999). The PRC method is a multivariate ordination approach that modifies Redundancy Analysis (RDA) to accommodate repeated measures data and visualize community composition through time. Typically, PRC diagrams compare composition of treatment communities versus some control community over time using least-squares species weights obtained from the RDA. The present application used 'space' in place of the 'time' as the *x*-axis. The 'control' was defined as far inter-space microsites pooled from both crust types and represented as 'aggregate far inter-space community'. This represented a site without vascular plants or biological crust. Crust types were compared at each microsite (stem, dripline, 3, 10, and 35 cm from stems). The resulting diagram illustrates community response as a function of species composition across microsites in comparison to the aggregate far inter-space community. We believe this novel application of the PRC approach is necessary to fully account for the high-dimensional nature of this community composition data at the resolution of taxonomic genera. Quantitatively, the formula $f_{kt}=c_{dt} \cdot b_k$ fits the modeled abundance of species k at microsite t as a fraction f_{kt} of the log-abundance of species k relative to the control (pooled far inter-space samples) where c_{dt} is the overall community response of treatment d at microsite t and b_k is the weighting

factor for species k. Similarly, $f_{kt}=\exp\left(c_{dt}\cdot b_k\right)$ quantifies the fraction f_{kt} of the geometric mean of non-transformed original abundance to the same parameters as above. Data were $\log_e$-transformed prior to analysis and the initial RDA was computed using CANOCO software Version 4.5. The significance of the first (and only visualized) axis of the RDA model was tested against 499 unrestricted Monte Carlo permutations.

Results

Crust removal experiment

Only nematodes, but no protozoan groups, were affected negatively by trampling (Table 1). Richness of nematode genera was greater beneath non-trampled than trampled plots. The opposite pattern was true for the proportion of bacterivorous nematodes, which was higher beneath trampled than non-trampled plots. Values of the Maturity Index were similar between trampled and non-trampled plots. Nematodes were most abundant, and flagellates were least abundant, at the Arches deep site. Furthermore, richness and diversity of nematode communities were greatest in the Arches deep site, and while values of maturity indices were smallest

at the deep site relative to either the ISKY medium or shallow site.

Nematodes and flagellates at the surface (0 to 10 cm) were more abundant at the Arches deep site than at the surface of the ISKY medium or shallow site. Generally, nematodes and protozoa were more abundant at the surface (0 to 10 cm) than at depth (10 to 20 cm and 20 to 30 cm) (Table 2). However, amoebae at the surface (0 to 10 cm) tended to be less abundant than subsurface (10 to 20 cm) in the ISKY medium depth site (Table 2). Richness, diversity, ecological maturity, and bacterivore proportion were greater at the surface than at depth for both the ISKY medium and Arches deep sites (Table 2). Nematode composition of the three sites was diametrically opposed to each other in the first two CCA axes (Fig. 1). Eigenvalues of CCA axis 1 (0.176, $p=0.0020$) and axis 2 (0.083) explained 75.6 % of the total species-environment variance. The species-to-environment (site) correlations were large for axis 1 (0.975) and axis 2 (0.919).

Plant experiment

Nematodes were more abundant at ISKY than Needles and more abundant associated with cyano/lichen/moss crusts than with cyanobacteria crusts at intermediate microsites in ISKY. Furthermore, nematodes when

Table 1 Treatment Analysis of Microfauna from Crust Removal Experiment. (A) F-values from analysis of site, disturbance treatment, and the site*treatment interaction, on $\log_{10}$ transformed abundance of amoebae, flagellates, ciliates, and nematodes (individuals g^{-1}) and nematode community indices (Shannon's diversity, richness, Maturity Index, and angular-transformed bacterivore proportion) at 0 to 10 cm, followed by (B) comparison of back-transformed least-squares means between the three sites (0 to 10 cm) and (C) trampled and control (non-trampled) treatments (0 to 10 cm)

(A)	Effect	df	Amoebae	Flagellates	Ciliates	Nematodes	Diversity	Richness	Maturity	Bacterivores
	Site	2, 24	0.97	4.95*	3.09	6.22**	10.26***	10.36***	9.40**	4.72*
	Treatment	1, 24	2.20	0.31	2.54	4.81*	4.00	6.37*	2.15	11.85**
	Site*Treatment	2, 24	2.11	0.08	1.08	2.05	.67	0.73	1.08	0.96
(B)	Site		Amoebae	Flagellates	Ciliates	Nematodes	Diversity	Richness	Maturity	Bacterivores
	Arches Deep		2524	592[A]	188	4.65[A]	2.39[A]	22.7[A]	2.37[A]	0.65[A]
	ISKY Medium		1987	1155[B]	375	2.58[B]	2.21[B]	18.6[B]	2.60[B]	0.55[B]
	ISKY Shallow		2998	1423[B]	132	2.54[B]	2.00[C]	16.3[B]	3.32[A]	0.55[B]
(C)	Treatment		Amoebae	Flagellates	Ciliates	Nematodes	Diversity	Richness	Maturity	Bacterivores
	Trampled		2063	927	159	2.62[A]	2.13	17.7[A]	2.39	0.64[A]
	Control		2953	1058	278	3.72[B]	2.27	20.7[B]	2.47	0.53[B]

*$p<0.05$, **$p<0.01$, ***$p<0.001$. Means with contrasting letter (within a column) indicate contrasting means within an organism group ($p<0.05$). Means without a letter indicate a non-significant effect and no comparisons were made

Table 2 Sampling Depth Analysis of Microfauna from Crust Removal Experiment. (A) F-values from nested analysis of variance of trampling experiment comparing the effect of sampling depth on log_{10}-transformed abundance of amoebae, flagellates, ciliates, and nematodes (individuals g^{-1}) and nematode community indices (Shannon's diversity, richness, Maturity Index, and angular-transformed bacterivore proportion), and (B) comparison of back-transformed least-squares means from (A) between multiple sampling depths for the deep, medium, and shallow sites

(A)	Effect	df	Amoebae	Flagellates	Ciliates	Nematodes	Diversity	Richness	Maturity	Bacterivores
	Depth(Site)	5, 45	15.37**	15.83**	15.07**	14.92**	5.12**	12.15***	12.26***	5.85***
(B)	Depth(Site)		Amoebae	Flagellates	Ciliates	Nematodes	Diversity	Richness	Maturity	Bacterivores
(Arches Deep site)										
	0 to 10 cm		2524[A]	592[AB]	188[A]	4.65[A]	2.39[A]	22.7[A]	2.37[B]	0.94[A]
	10 to 20 cm		1120[B]	141[C]	11[C]	1.49[BC]	2.14[BC]	16.7[B]	2.29[BC]	0.82[B]
	20 to 30 cm		438[C]	106[C]	4[C]	0.68[D]	1.96[D]	13.0[C]	2.23[C]	0.81[B]
(ISKY Medium site)										
	0 to 10 cm		1987[A]	1155[A]	375[A]	2.58[B]	2.21[B]	18.6[A]	2.60[A]	0.84[B]
	10 to 20 cm		2471[A]	325[B]	46[B]	1.11[CD]	1.92[CD]	14.2[B]	2.20[C]	0.70[C]
(ISKY Shallow site)										
	0 to 10 cm		2998[A]	1423[B]	132[AB]	2.54[B]	2.00[C]	16.3[B]	3.32[A]	0.84[B]

$*p<0.05$, $**p<0.01$, $***p<0.001$. Means with contrasting letter (within a column) indicate contrasting means ($p<0.05$)

associated with all locations, plant types, and crust types declined in abundance with increasing distance from plant stems, but the decline was more dramatic at ISKY than at Needles (Fig. 2). The proportion of the bacterivore trophic group (those not possessing piercing stylets) remained relatively constant across distance microsites regardless of plant or crust type.

Nematode community composition shifted between the plant stem and interspace soils as a result of the increase in relative abundance of some genera and a decrease in the relative abundance of other genera (Fig. 3). Most genera increased in abundance from the interspace toward the plant stem; *Acrobeles, Aphelenchoides, Carcharolaimus, Chiloplacus, Eudorylaimus, Panagrolaimus* and *Tylencholaimus* were among the genera with weightings greater than 0.5 for at least three of the four location*plant type combinations and these genera were relatively more abundant near plant stems than at interspaces. *Acromoldavicus* was the only genus with a weighting less than 0.5 in three of the four location*plant type combinations, and *Stegellata* was the only genus with a weighting less than 0.5 around ISKY shrubs. The difference in community composition between crust types was greatest around shrubs at ISKY, and was nearly absent in communities at Needles. The full model was able to describe significantly more species-environment variance for original than permutated data for three of the four locations and plant types, including shrubs at ISKY ($p=0.0020$), shrubs at Needles ($p = 0.0300$), and grasses at Needles ($p = 0.0160$), but not grasses at ISKY ($p = 0.4600$).

Discussion

In this study, nematodes were 1.4-fold more abundant in non-trampled plots than in trampled plots (Table 1) and 2- to 4-fold more abundant at plant stems than in interspace soils in similar Colorado Plateau soils (Fig. 2). Darby et al. (2007) suggested that greater carbon input into the soil food web was one possible explanation for greater nematode abundance in late- than early successional stage crusts, and increased carbon input from plants (near stems) and crust photosynthesis (beneath non-trampled crusts) may similarly explain part of the increase in total microfaunal abundance. For example, the fast-growing bacterivore *Panagrolaimus* consistently increased in abundance close to plants disproportionately more than most other genera (Fig. 3), and this is likely the result of increased bacterial biomass near plant stems. The other genera that were found to be relatively more abundant near plant stems than interspaces,
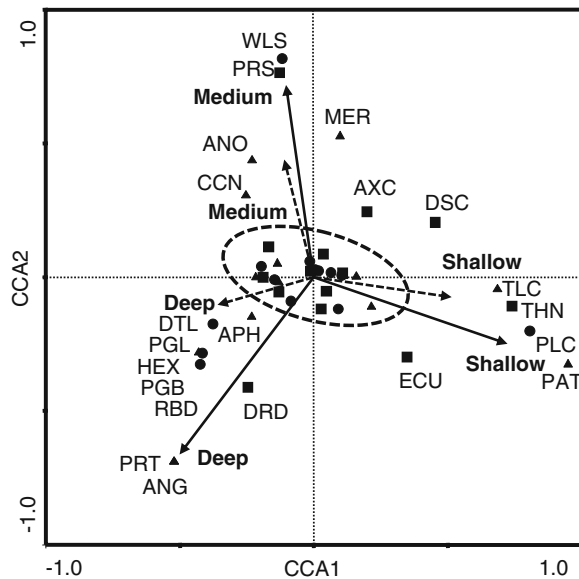
Fig. 1 Nematode Community Composition from Crust Removal Experiment. Canonical Correspondence analysis of 0 to 10 cm nematodes with environmental vectors representing treatment combinations of site (ISKY shallow, ISKY medium, or Arches deep), and physical disturbance (trampled, dashed lines, or non-trampled, solid lines). Points represent relative abundance of tylenchid piercers (triangles), dorylaimid piercers (squares), and ingesting bacterivores (circles). Genera within the dashed circle were unlabeled for clarity, remaining genera include: ANG, *Anguina*; ANO, *Anomyctus*; APH, *Aphelenchus*; AXC, *Axonchium*; CCN, *Criconemella*; DRD, *Dorydorella*; DSC, *Discolaimium*; DTL, *Ditylenchus*; ECU, *Ecumenicus*; HEX, *Hexatylus*; MER, *Merlinius*; PAT, *Paratylenchus*; PGB, *Panagrobelium*; PGL, *Panagralaimus*; PLC, *Plectus*; PRS, *Prismatolaimus*; PRT, *Pratylenchus*; RBD, *Rhabdolaimus*; THN, *Thonus*; TLC, *Tylenchus*; WLS, *Wilsonema*

including *Acrobeles, Aphelenchoides, Carcharolaimus, Chiloplacus, Eudorylaimus* and *Tylencholaimus,* may be candidate indicators of desert rhizosphere-like soil conditions. However, *Acromoldavicus* was the genus that was relatively more abundant in interspace soils than near plant stems. *Acromoldavicus mojavicus*, the main and perhaps only species of this genus in western US, is common in many cool deserts (Baldwin et al. 2001) and is known to tolerate desiccation by entering a dormant state called anhydrobiosis (Demeure et al. 1979). In a previous study (Housman et al. 2007), rotifers, typical of mesic or ephemerally wet soils, were found almost exclusively adjacent to plant stems, suggesting that the hydrology of rhizosphere soil or the plant microclimate facilitates water-film fauna that do well in more mesic soils. Thus, additional research should investigate how soil processes like hydraulic

lift, texture, and aggregate structure affect soil hydrology at scales relevant to individual microfauna. The hypothesis that small differences in fine-scale hydrology between rhizosphere and interspace soil could facilitate niche separation of desiccation tolerant and intolerant nematodes should also be further tested.

Not only did crust removal by physical trampling decrease nematode abundance, richness, and diversity, but also shifted the nematode microbivore trophic structure towards a greater dominance of bacterivores. In our study, bacterivores represented 53% of the community in non-trampled plots and up to 64% of the community in trampled plots (Table 1). This supports Belnap (1995), who found that a similar trampling disturbance resulted in a 40 to 60 % decrease in the ratio of total fungi to total bacteria. In the same study, trampling disturbance reduced the abundance of fungivorous nematodes more than bacterivorous nematodes and, thus, increased the ratio of bacterivores to fungivores. A shift in microbivorous nematodes from fungivores to bacterivores mirrors the shift in energy channels observed in agricultural food webs after other physically disruptive management practices. For example, annual tillage practices led to a dominance of bacterial energy channels over fungal channels in comparison to no-till (Hendrix et al. 1986) or integrated management (Moore and De Ruiter 1991) practices. This is important because the bacterial decomposition channel is thought to be faster and associated with greater nitrogen mineralization than the fungal decomposition channel (Ingham et al. 1985). Greater rates of nitrogen mineralization could lead to large losses of total nitrogen in a system prone to losses of gaseous and liquid nitrogenous compounds (Peterjohn and Schlesinger 1990).

In the crust removal experiment we did not find that crust removal by physical trampling systematically altered nematode community composition at the genus level other than by reducing overall richness (Fig. 1). Instead, the composition of genera reflected inherent differences of the three sites chosen for the crust removal experiment. The shallow, medium, and deep site were selected in this study to represent the range of Colorado Plateau soils to more completely capture the effect of crust removal by physical trampling. However, multiple confounding environmental effects differ among the sites selected. The deep site from Arches, where nematodes were most
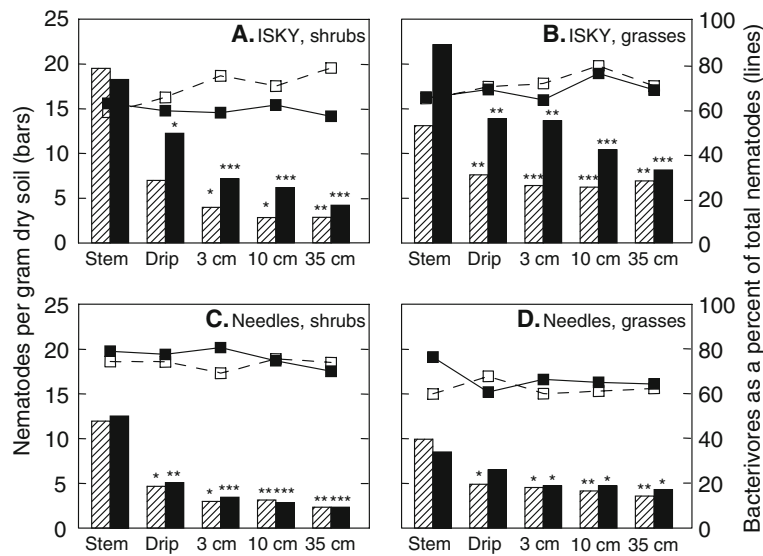
Fig. 2 Nematode Abundance and Trophic Composition around Plants. Nematode abundance (left axes, bars) and bacterivorous nematode proportion (right axes, lines) surrounding a shrub (*Coleogyne*, A, C) and a grass (*Stipa*, B, D), in the Island in the Sky (A, B) and Needles (C, D) region of Canyonlands National Park. Populations were enumerated from five microsites away from the plant (stem, dripline, and 3, 10, and 35 cm from dripline) for two crust types, cyanobacteria crusts (striped bars and dashed lines with open markers) and cyano/lichen/moss crusts (solid bars and solid lines with solid markers). Astrices above individual bars represent means significantly different from the stem microsite (*$p<0.05$, **$p<0.01$, ***$p<0.001$, Dunnett's multiple comparison)

abundant, had greater lichen/moss cover than the shallow and medium site of ISKY, and the deep site at Arches has less total phosphorous, Ca, N, and clay content than either site at ISKY. Thus, additional research is needed to explain the contrasting community composition among these sites, and at least three hypotheses can be tested. First, late-successional stage crusts have greater lichen and moss content than early succesional stage crusts as well as greater carbon and nitrogen inputs. Because lichen and moss cover were inadvertently confounded with site, nematode abundance, richness, and diversity were greater at the deep site due to the greater photosynthetic carbon and biologically fixed nitrogen from biological soil crusts at deep sites. Second, perhaps deeper soil profiles serve an 'innoculum' effect by supplying a reservoir to replace surface taxa. Third, nematode communities could differ as a result of one of the contrasting abiotic soil factors such as nutrient content, soil texture, or mineralogy (Housman et al. 2007). Currently, the first hypothesis (of contrasting biological soil crust composition) is best supported by the literature and is congruent with observations by Darby et al. (2007) and Housman et al. (2007).

A common theme from the present study, Darby et al. (2006, 2007), and Housman et al. (2007), is that the effects of crust removal, distance from plants, and crust age, appear to affect the protozoan groups — amoebae, flagellates, and ciliates — less dramatically, or not at all, compared to nematodes. It is not known if this pattern is an artifact of the precision of contrasting methodology, soils, climate, or whether soil nematodes are genuinely affected more than protozoans by the presence of vascular and non-vascular plants in these desert soils. Protozoa are smaller than nematodes and can access smaller soil pores than nematodes (Elliott et al. 1980). Thus, nematodes may have less access to prey than protozoa, making them more vulnerable to alterations in crust habitat. Furthermore, the physical trampling employed here may have increased bulk density, reduced porosity, and constricted the habitable pore spaces available to nematodes more than to protozoa.

In conclusion, experimental removal of biological soil crust reduced the abundance of nematodes and shifted the composition to a greater proportion of bacterivores than microphytophages. The overall affect of crust removal on total abundance was
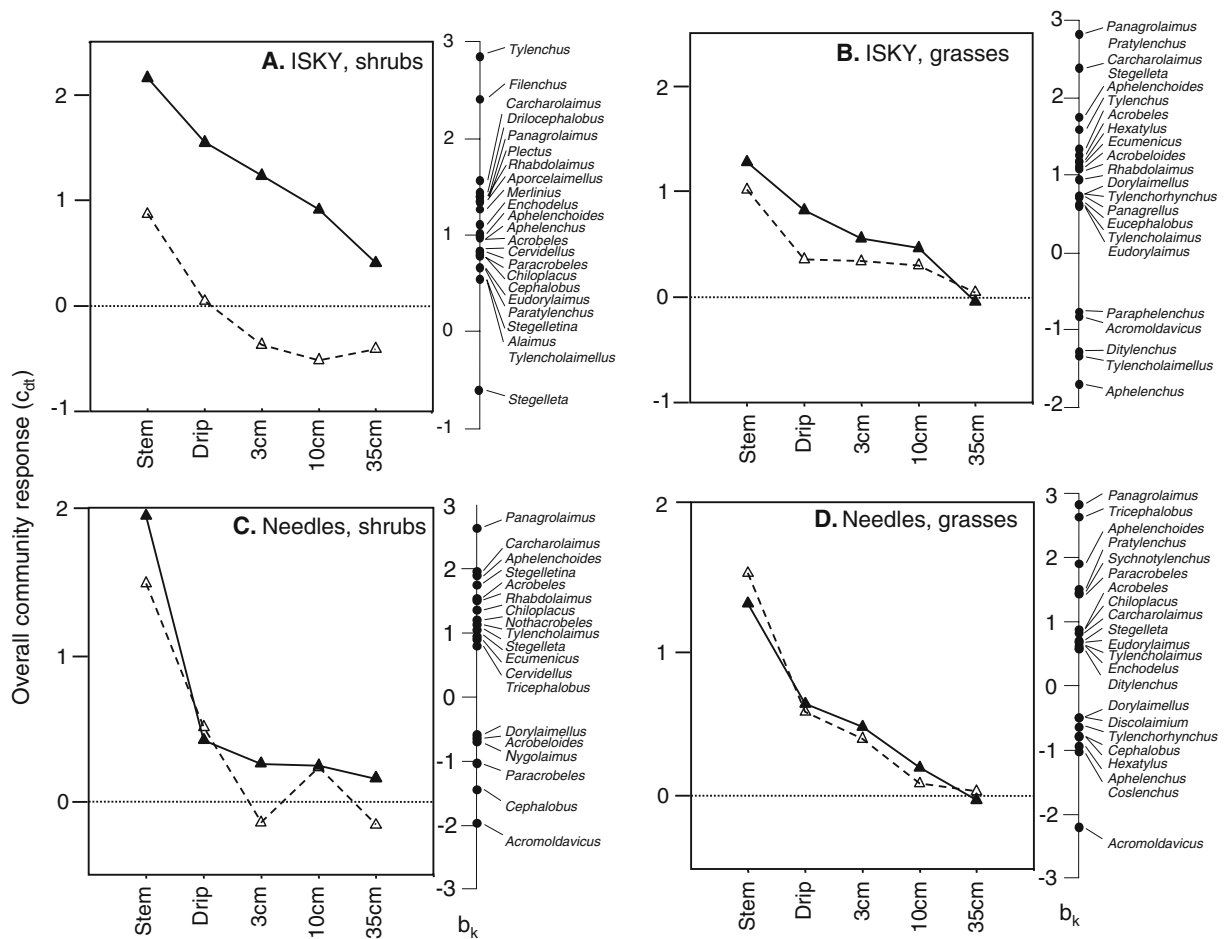
Fig. 3 Community Composition around Plants. Principal Response Curves of genera surrounding the shrub *Coleogyne* (A, C) and grass *Stipa*, (B, D), in the Island in the Sky (A, B) and Needles (C, D) region of Canyonlands National Park. Solid lines depict communities associated with late-successional cyano/lichen/moss crusts, while broken lines depict communities associated with early-successional cyanobacteria crusts.

Sites with high overall community response index (c_{dt}) values, such as near plant stems, contained disproportionately more genera with positive weights (b_k), while sites with low c_{dt}, such as near interspaces, contain disproportionately more genera with negative weightings. Genera with weights between −0.5 and 0.5 were removed for clarity

comparable to a previous comparison of early and late successional crusts, demonstrating the importance of biological soil crusts on nematode abundance. We propose that the impact of biological soil crusts and desert plants on soil microfauna, as reflected in the community composition of microbivorous nematodes, is a combination of carbon input, microclimate amelioration, and altered soil hydrology. Furthermore, as protozoa were unaffected by crust removal in this experiment, we can speculate specific scenarios of microfaunal community changes that have already been documented, such as changes in nematode abundance and composition, but not of protozoa.

Nematodes are an order of magnitude larger in body size than protozoa and are expected to respire less per biomass than protozoa. Stoichiometrically, bacterivorous microfauna are thought to contribute more to nitrogen cycling than fungivorous microfauna because of a relatively low carbon:nitrogen content of their respective prey (Hunt et al. 1987). Thus, we propose the hypothesis that a shift in community composition toward more bacterivores or a decline in nematode but not protozoan abundance, could result in greater rates of nitrogen cycling relative to microfaunal consumption. The implications of microfaunal nitrogen cycling to the whole desert soil food web will

depend on the spatial and temporal dynamics of microfaunal activity. Although nitrogen is often considered a limiting nutrient in deserts, arid lands can still lose significant amounts of nitrogen if the supply of nitrogen is timed with leaching and volatilization processes. Thus accelerated nitrogen mineralization in the soil food web could result in net ecosystem losses if microfaunal-mediated mineralization is spatially or temporally decoupled from the growth of plants and other members of the soil food web that utilize inorganic nitrogen.

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