Heterogeneity of soil nutrients and subsurface biota in a dryland ecosystem

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Abstract

Dryland ecosystems have long been considered to have a highly heterogeneous distribution of nutrients and soil biota, with greater concentrations of both in soils under plants relative to interspace soils. We examined the distribution of soil resources in two plant communities (dominated by either the shrub *Coleogyne ramosissima* or the grass *Stipa hymenoides*) at two locations. Interspace soils were covered either by early successional biological soil crusts (BSCs) or by later successional BSCs (dominated by nitrogen (N)-fixing cyanobacteria and lichens). For each of the 8 plant type × crust type × locations, we sampled the stem, dripline, and 3 interspace distances around each of 3 plants. Soil analyses revealed that only available potassium (K_{av}) and ammonium concentrations were consistently greater under plants (7 of 8 sites and 6 of 8 sites, respectively). Nitrate and iron (Fe) were greater under plants at 4 sites, while all other nutrients were greater under plants at less than 50% of the sites. In contrast, calcium, copper, clay, phosphorus (P), and zinc were often greater in the interspace than under the plants. Soil microbial biomass was always greater under the plant compared to the interspace. The community composition of N-fixing bacteria was highly variable, with no distinguishable patterns among microsites. Bacterivorous nematodes and rotifers were consistently more abundant under plants (8 and 7 sites, respectively), and fungivorous and omnivorous nematodes were greater under plants at 5 of the 8 sites. Abundance of other soil biota was greater under plants at less than 50% of the sites, but highly correlated with the availability of N, P, K_{av}, and Fe. Unlike other ecosystems, the soil biota was only infrequently correlated with organic matter. Lack of plant-driven heterogeneity in soils of this ecosystem is likely due to (1) interspace soils covered with BSCs, (2) little incorporation of above-ground plant litter into soils, and/or (3) root deployment patterns.
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1. Introduction

Ecologists have long considered how the distribution of abiotic resources affects the structure and function of a given ecosystem and, conversely, how the structure of biotic components within a given ecosystem affects the distribution of abiotic resources (Lovett et al., 2005). At a large scale, abiotic factors (e.g., geology, climate) set limits on biotic components, but at the other end of the continuum, biotic factors can control the distribution of abiotic factors (Kratz et al., 2005). Feedbacks among abiotic and biotic components further complicate the matter. As ecosystem ecology concerns itself with the flow of energy and materials through organisms and their environment, understanding the controls on these dynamics is of essential importance in comprehending ecosystem structure and function, the response of that ecosystem to disturbance, and the overall landscape in which that ecosystem is embedded (Tongway and Ludwig,

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2005; Turner and Chapin, 2005). Heterogeneity is generally not random, in that landscapes have a characteristic patterning and scale over which resources are mobilized, transported, and deposited (Tongway and Ludwig, 2005). When the scale or the nature of the heterogeneity of a system is altered, degradation generally occurs and the nature of the source–sink relationship for different resources is then also changed.

Muller (1887) noted that dryland ecosystems were highly heterogeneous environments, characterized by greater concentrations of nutrients in soils under plant canopies compared to those in plant interspaces. Since then, there have been over 70 studies of this phenomenon in dryland ecosystems (e.g., Charley and West, 1975; Gallardo and Schlesinger, 1992; Whitford, 2002; Reeder et al., 2004; Schade and Hobbie, 2005; Stubbs and Pyke, 2005; Tongway and Ludwig, 2005). The formation of these resource islands, or "islands of fertility", is generally believed to result from the transfer of resources from interspace soils, via roots and soil movement, to soils under plant canopies, via litter fall and the capture of soils moved from the interspace. Through time, under-canopy soils are believed to accumulate resources at the expense of interspace soils. Indeed, the above-mentioned studies often report concentrations of N, P, available potassium (K_{av}), OM, microbial biomass, and nutrient transformations to be greater in soils under plant canopies vs. those in the interspace.

Despite the persuasive logic of resource island formation in dryland ecosystems, careful review of many past studies (spanning hot to cold deserts and grasslands to shrublands) shows that most soil nutrients do not have a consistent spatial distribution across ecosystems (Belnap, unpublished). Therefore, forces counteracting the formation of resource islands must also be present. However, the nature of these forces, and the conditions under which they operate, are poorly understood. Plant species differ greatly in many ways, including nutrient uptake rates, productivity, decomposition rates, tissue allocation, and root deployment patterns, and thus the strength of the resource island signal is likely to vary among plant growth forms, genera, and species (reviewed in Schenk and Jackson, 2002; Meinders and van Breemen, 2005). Animal activity (e.g., Titus et al., 2002) and the capture by plants of wind and water-eroded soils from the interspace can also increase nutrient accumulation under plants.

Biological soil crusts (BSCs) are a community of cyanobacteria, lichens, and mosses that cover interspace soils in dryland regions and that may counteract the formation of resource islands. BSCs stabilize and roughen the soil surface, thus reducing or preventing redistribution of soil, OM, and seeds from the interspace to nearby plants (Belnap and Lange, 2003). They also contribute newly fixed carbon (C) and N to interspace soils. In addition, the presence of BSCs increase abundance and richness of soil fauna in interspace soils (Belnap and Lange, 2003; Darby et al., 2007). The successional stage of the crust increases soil surface temperature and moisture, and thus they likely affect the rate at which soil processes occur. Mature soil crusts (hereafter referred to as "dark" crusts due to their dark color) harbor a greater abundance of lichens, mosses, and N-fixing microorganisms than early successional cyanobacterial crusts (hereafter referred to as "light" crusts due to their light color) dominated by cyanobacterial species (e.g., *Microcoleus*). Cyanobacteria stabilize soils and fix C and N at a lower level than lichens and mosses. Thus, dark BSCs, with greater biomass, fixation rates, and stabilizing ability, contribute more to soil fertility than light BSCs. Current soil food web theory predicts that soil biotic abundance is mostly determined by the availability of soil resources, especially OM (Wardle, 2002). Thus, if soil resources accumulate under plants, we would expect to find soil biota concentrated there. However, as protozoans, nematodes, and microarthropods ingest BSCs (reviewed in Belnap, 2003) that occur in the interspace, the presence of BSCs may counter the concentration of soil biota under plant canopies (Belnap, 2003).

We designed this study to address the following questions: (1) is the distribution of soil abiotic factors related to the distribution of biotic components (plants) within a dryland ecosystem? Is the strength of this relationship influenced by plant life form? (2) can the presence of a different biotic component (i.e., mature BSCs) counteract the influence of vascular plants? and (3) is the distribution of soil biotic (BSCs, plants) and abiotic resources related to the distribution of subsurface soil biota?

2. Materials and methods

2.1. Area of study and soil chemistry

Sites were located adjacent to the Island in the Sky (ISKY) and Needles (NDLS) districts of Canyonlands National Park, Utah, USA. These districts are ~45 km apart, and both have an average annual precipitation of 215 mm. Soils are a sandy loam covered by light or dark BSCs and dominated by the shrub *Coleogyne ramosissima* or the grass *Stipa hymenoides*. *Coleogyne* is a slow-growing C_3 shrub with both shallow and deep roots. It retains about 30% of its leaves throughout the year, although all leaves will fall during severe drought. *Stipa* is a shallow-rooted C_3 bunchgrass with high annual productivity and turnover of tissue. Plants at our sites were growing at least 70 cm apart, with the BSCs occurring right up to the stem of the plant.

At both locations, we sampled 3 plots, each containing 3 plants, within each plant type × crust type combination. At each plant, 2-cm dia soil cores (0–10 cm in depth) were collected from 5 microsites: plant stem; plant dripline (outer canopy edge); and close (3 cm from dripline), middle (10 cm from dripline) and far (35 cm from dripline) interspaces. At each of the 5 microsite types, we collected soil cores from the 4 cardinal directions around each plant. The 12 (4 directions × 3 plants) cores were composited into 1 sample per microsite per plot. Cover of BSCs was

estimated for a subset ($n = 8$) of each plant × crust × microsite in ISKY and NDLS by measuring 10 points at 1-cm intervals perpendicular to each cardinal direction. Abundance of late successional cyanobacteria *Nostoc* and *Scytonema* was measured with microscope counts.

Soil samples were mixed and divided into 3 subsamples. One subsample was used for soil biotic analyses. One subsample was field-extracted in 2 M KCl (Bremner and Keeney, 1966) and analyzed colorimetrically on a Lachat for NO_3 and NH_4. The third subsample was sifted to 2 mm and analyzed for soil texture (hydrometer method); OM (Walkley and Black method); P, available K (K_{av}), exchangeable K, Ca, Mg, and Na after extraction in NH_4OAc buffered to pH 8.5; and Cu, Fe, Mn, and Zn after extraction with diethylenetriaminepentaacetic acid (DTPA). Acid-neutralizing potential (ANP, the combination of soil constituents that neutralize acids, including $CaCO_3$ and oxides of Zn, Mn, Fe, and Mg) was measured by HCl neutralization (Allison and Moodie, 1965). In addition to analyzing the individual elements, we also looked at ratios where antagonistic relationships can influence nutrient availability (e.g., Mn can decrease P availability, Mg can decrease K availability).

2.2. Soil biota

Protozoa (amoebae, flagellates, and ciliates) were enumerated with a most probable number method adapted for protozoa (Darbyshire et al., 1974). Presence/absence data for each motility group were observed from 8 wells of 6 concentrations in a 3-fold serial dilution ranging from 1:80 through 1:19,440. The most probable number for each motility group was solved according to Cochran (1950). Nematodes (fungivores, bacterivores, omnivores/predators, and herbivores), tardigrades, and rotifers were extracted with Cobb's decanting and sieving method followed by the Oostenbrink cotton filter technique (Nicholas, 1975). Individuals were counted from duplicate 150 g subsamples. An average of 250 nematodes per sample was identified to trophic group based on Yeates et al. (1993).

Soil DNA was used as a relative measure of soil bacterial biomass and was extracted from 0.5 g of soil using the UltraClean-htp^{TM} 96 Well Soil DNA Isolation Kit (MoBio Labs, Solana Beach, California). Extracts were stored in 96 well plates at $-20\,^{\circ}C$, and DNA was quantified by densitometric analysis of ethidium bromide-stained, high molecular weight DNA in agarose gels. DNA stock solutions were diluted 10-fold, and aliquots were run alongside molecular mass standards on 3% agarose gels. Gels were stained with ethidium bromide, and high molecular weight band intensities were determined with Science Lab 99 Image version 3.3 software (Fuji Photo Film Co., Tokyo, Japan). Although the MoBio DNA soil isolation methodology has been developed to specifically extract DNA from microorganisms, the results still include a minor fraction of DNA contributed by other soil biota.

Partial *nifH* gene sequences were amplified from soil DNA using a nested PCR procedure and degenerate primers (Yeager et al., 2004). These primers universally amplified a 358 bp portion of *nifH* (Ueda et al., 1995; Zani et al., 2000). Species richness and relative abundance of the *nifH* sequence types amplified from each soil sample were analyzed using the terminal restriction fragment length polymorphism (T-RFLP) technique (Marsh, 2005). Three individual nested *nifH* PCRs (using a 5-carboxyfluorescein-labeled *nifH* 11 primer in the second reaction) were done for each sample, and the resulting PCR amplicons were pooled and concentrated using a speedvac. The PCR amplicons were purified using the QIAquick PCR purification kit (Qiagen, Chatsworth, California). Purified *nifH* amplicons (50 ng) were digested with 2.5 U of *Mae*III (Roche Diagnostics Co., Indianapolis, Indiana) at $55\,^{\circ}C$ for 4.5 h, and 1 μl of the restriction digest (30 μl total volume) was heated to dryness at $95\,^{\circ}C$. T-RFLP data were analyzed by converting each individual peak area within a given profile to a percentage of the total peak area (total fluorescence) of that profile. In this way, the relative abundance of each terminal restriction fragment (TRF) within a given sample was determined. Three replicates were used to determine relative TRF abundance. Expected TRF sizes of clones were determined using NEBcutter V2.0 (http://tools.neb.-com/NEBcutter2/index.php) to identify the presence and position of *Mae*III restriction sites. Clone libraries were generated from *nifH* amplicons with the TOPO TA cloning kit for sequencing and TOP10 chemically competent cells (Invitrogen, Carlsbad, California).

2.3. Statistical analyses

Soil chemistry and faunal data were analyzed separately using a fully nested 4-way ANOVA (SAS, 1989). We tested each dependent variable by location, plant type nested within location, crust type nested within location × plant type, and microsite nested within location × plant type-crust type. *A priori* orthogonal contrasts were used to identify significant interaction terms in soil chemistry and fauna analyses. Soil DNA concentrations were averaged among replicate samples and compared using a standardized *t*-test. T-RFLP profiles from each field variable combination (location, plant type, crust type, microsite) were each normalized to 100% peak fluorescence and averaged across 3 field replicates. Profile similarities were compared by generating Jaccard distance matrices (based on presence/absence of each peak in the comparison group) or Agnes distance matrices (based on the relative abundance of each peak in the comparison group), followed by cluster analysis using UPGMA. Prior to analysis, all data were checked and transformed if necessary to meet statistical assumptions. For graphical presentation, data were transformed into relative abundances to display proportions within microsites. We report $P < 0.05$ as significant and $P < 0.10$ as marginally significant.

3. Results

3.1. Characterization of the biological soil crust cover and soil chemistry

All light BSCs were cyanobacteria consisting of $>98\%$ *Microcoleus vaginatus* (data not shown). In dark BSCs, cover of the different components was generally similar among sites (Table 1). At the stem microsites, there was no difference in lichen or moss cover among sites. At the dripline microsites, lichen cover was greater at the ISKY *Coleogyne* sites, and moss cover lower at the NDLS *Stipa* site, when compared to other sites. Microscope cell counts showed that the cover of *Scytonema* plus *Nostoc* at all sites combined averaged 6% at the stem, 18% at the dripline, 19% at 3 cm, 15% at 10 cm, and 9% at the 35-cm interspace. *Stipa* interspace microsites at NDLS had greater abundance of *Nostoc* and *Scytonema* relative to other dark BSC sites (25% vs. 12%), but there was no difference among sites at the other microsites. *nifH* populations were Nostocales-type specimens, with some heterotrophic sequences present. Sequences were 65% *Nostoc commune*, 16% *Tolypothrix* spp., 7% *Scytonema* spp., 5% other cyanobacteria, and 7% other bacterial species. All the samples contained representatives in 5–7 of the 9 T-RFLP peak locations plus an 'others' category (data not shown). There was no significant difference in species richness between location, plant, or crust type, although variability was high in the relative abundance of peaks in the *nifH* T-RFLP profiles (Fig. 3). Only ISKY dripline samples were statistically distinct from NDLS microsites.

Most soil chemistry variables differed among plant type, crust type, and/or microsite (Table 2; Supplementary Appendices A and B). When we compared soil chemistry variables across the 5 microsites to test for resource islands, most differences in soil nutrients, OM, and soil texture from the plant stem outwards into the interspace were not consistent among sites, within or between plant types, nor within or between crust types (Fig. 1). At the *Coleogyne* sites, NH_4 was the only nutrient that was always greater at the plant stem compared to the interspace soils (Fig. 1). Values were greater at the plant stem for K_{av} at 3 of 4 sites; for NO_3 and OM, values were greater at the plant stem at only two of the 4 sites. In contrast, interspace microsites had greater Ca, Cu, and clay relative to the plant stem at 3 of the 4 sites, and greater P at two of the 4 sites. There were no differences for total N, Mn, pH, or silt at any site. Combined, there were differences (or resource island formation) in only 24 of 48 possible cases for soil elements (12 elements (thus excluding texture and pH) $\times$ 4 sites; Supplementary Appendix B). The presence of dark BSCs may have had some influence: the presence of dark BSCs at NDLS erased differences that were seen in OM and K_{av} when soils with light BSCs were present, where values were higher in canopy than interspace soils. While the presence of dark BSCs did not seem to affect the distribution of NH_4, the distribution of NO_3 and OM at NDLS and total N at both sites may have been affected, as these nutrients did not show any increased concentrations under the plant stem.

As with the *Coleogyne* sites, the *Stipa* sites showed resource island formation for few soil variables (Fig. 1). These included K_{av}, which was greater in stem than interspace (i.e., beyond dripline) soils at all 4 sites, and Mn, which was greater in soils at the plant stem at 3 of the sites. Values were greater at the stem at only 2 sites for Fe, NO_3, and NH_4, and only 1 site for P and OM (Fig. 1). In contrast, clay was greatest in the interspace at 3 of the 4 sites, Ca was greater at 2 of the 4 sites, and Cu was greater at 1 of the sites. As with the *Coleogyne* sites, there was no difference in total N, pH, or silt at any *Stipa* site. Combined, there was a resource island signal in only 20 of the 48 possible cases at *Stipa* sites. Dark crusts appeared to prevent the formation of NH_4 resource islands: at both *Stipa* sites, soils with light crusts had higher NH_4 under the plants than in the interspace, whereas dark-crusted soils showed no differences among the microsites. Similarly, dark BSCs appeared to reduce island formation for NO_3 at ISKY and P at NDLS.

When plant types and locations were combined, we saw the formation of resource islands in soils under plants only

Table 1
Percent cover of soil crust constituents in dark biological soil crusts (BSCs) around *Coleogyne ramosissima* and *Stipa hymenoides* at the Island in the Sky (ISKY) and Needles (NDLS)

Parameter	Microsite	ISKY		NDLS	
		Coleogyne	*Stipa*	*Coleogyne*	*Stipa*
Lichen	Stem	1 ± 1^b	0 ± 0^a	1 ± 1^a	0 ± 0^a
	Dripline	8 ± 2^a	0.2 ± 0.3^a	3 ± 2^a	0.6 ± 0.6^a
	3-cm interspace	6 ± 2^{ab}	0.6 ± 0.4^a	3 ± 2^a	0.6 ± 0.4^a
	10-cm interspace	6 ± 1.4^{ab}	0.6 ± 0.6^a	1 ± 0.4^a	0 ± 0^a
	35-cm interspace	3 ± 1^{ab}	0 ± 0^a	1 ± 1^a	0 ± 0^a
Cyanobacteria	Stem	69 ± 6^{ab}	90 ± 3^a	70 ± 4^{cb}	93 ± 2^a
	Dripline	63 ± 3^b	64 ± 5^b	58 ± 4^c	53 ± 5^c
	3-cm interspace	70 ± 6^{ab}	74 ± 3^{ab}	68 ± 5^{bc}	63 ± 6^c
	10-cm interspace	73 ± 4^{ab}	76 ± 6^{ab}	76 ± 3^{ab}	73 ± 5^b
	35-cm interspace	83 ± 4^a	79 ± 4^{ab}	87 ± 5^a	79 ± 4^{ab}
Moss	Stem	4 ± 3^a	5 ± 2^b	13 ± 5^{ab}	1.1 ± 0.7^{ab}
	Dripline	8 ± 4^a	18 ± 3^a	18 ± 4^a	3.9 ± 1.6^a
	3-cm interspace	5 ± 2^a	9 ± 3^{ab}	14 ± 3^{ab}	1.4 ± 0.7^{ab}
	10-cm interspace	2 ± 0.8^a	10 ± 4^{ab}	12 ± 2^{ab}	0.3 ± 0.3^b
	35-cm interspace	2 ± 1^a	6 ± 3^{ab}	3 ± 2^b	0 ± 0^b

Shown are means ($\pm$SEM) for BSCs around 8 plants. Superscripts indicate differences in cover for microsites around a given plant type ($P<0.05$).

Table 2
Soil chemistry by soil crust and microsite type for *Coleogyne ramosissima* and *Stipa hymenoides* at Island in the Sky (ISKY) and Needles (NDLS)

Comparison	df[a]	Ca	Clay	Cu	Fe	K_{av}	Mn	NH_4	NO_3	Total N	OM	P	Zn
ISKY dark^1 vs. light^2 crust around *Coleogyne*	1.80	2.74	17.58^2	15.23^1	0.37	9.26^1	0.08	8.00^2	0.02	0.94	17.37^1	4.57^2	0.09
ISKY dark^1 vs. light^2 crust around *Stipa*	1.80	1.33	12.68^2	0.76	12.26^2	38.50^1	5.90^2	25.14^1	18.63^1	1.83	3.75^2	18.29^1	0.21
NDLS dark^1 vs. light^2 crust around *Coleogyne*	1.80	0.03	4.71^2	12.70^2	12.18^1	46.18^2	2.37	0.00	3.99^1	0.60	13.73^1	0.07	2.47
NDLS dark^1 vs. light^2 crust around *Stipa*	1.80	12.43^1	0.89	24.03^2	7.82^1	12.23^2	0.39	0.59	0.21	0.02	0.36	1.02	1.90
ISKY, dark crust understory^1 vs. interspace^2 around *Coleogyne*	1.80	0.33	10.67^2	11.19^2	2.29	17.62^1	2.95^1	4.27^1	18.11^1	5.62	4.88^1	16.91^2	0.02
ISKY, light crust understory^1 vs. interspace^2 around *Coleogyne*	1.80	5.55^2	21.49^2	15.82^2	0.00	5.64^1	1.87	9.88^1	12.20^1	1.00	2.05	37.54^2	4.24^2
ISKY, dark crust, understory^1 vs. interspace^2 around *Stipa*	1.80	3.24^2	2.07	1.22	1.26	2.48	1.15	12.41^1	1.84	0.33	4.07^1	0.92	1.57
ISKY, light crust understory^1 vs. interspace^2 around *Stipa*	1.80	0.06	0.01	1.17	0.10	8.60^1	0.07	6.71^1	0.27	0.02	1.07	0.41	0.42
NDLS, dark crust understory^1 vs. interspace^2 around *Coleogyne*	1.80	9.59^2	8.04^2	1.34	49.05^1	2.65	0.29	13.82^1	10.42^1	1.59	3.67^2	4.37^1	1.36
NDLS, light crust understory^1 vs. interspace^2 around *Coleogyne*	1.80	2.83^2	0.90	1.79	8.30^1	14.50^1	0.85	20.72^1	5.98^1	6.31	5.40^1	3.80^2	2.09
NDLS, dark crust understory^1 vs. interspace^2 around *Stipa*	1.80	13.55^2	0.21	2.72	2.66	6.73^1	3.33^1	0.85	0.26	0.00	0.38	0.21	4.07^1
NDLS, light crust understory^1 vs. interspace^2 around *Stipa*	1.80	6.68^2	0.56	5.05^2	3.28^1	11.29^1	1.99	11.28^1	9.00^1	0.02	0.15	0.00	2.85^1

Superscripts indicate which variables are statistically distinct ($P < 0.05$) when the two sites listed in the first column are compared; this number also denotes which of the two sites had the higher value. Shown are degrees of freedom and F-values for comparisons of soil chemistry concentrations.

[a] Denominator degrees of freedom equal 79 for NO_3 and 65 for total N for all main effects, interactions, and contrasts.

46% of the time (44 of 96 possible cases). In addition, there was little evidence of resource island formation for the nutrients considered most likely to accumulate under the plant stem: total N was not greater under the plant canopy at any of the sites, P was only greater at one of the 8 sites, and OM was only greater at 3 of the 8 sites. Only K_{av} showed a strong and consistent increase in soils under plant stems relative to interspace soils, as it was greater at 7 of the 8 sites. There were slightly more cases of soil nutrient concentration under shrub sites (24/48) than grass sites (20/48).

3.2. Subsurface soil biota

Extracted DNA was significantly higher in the ISKY soils compared to the NDLS soils and in *Stipa* soils relative to *Coleogyne* soils. There was no significant difference in extracted DNA between crust types when all locations and plant types were pooled. Extracted DNA declined with distance from plants 50% of the time (Fig. 2), with a sizeable dip in values at the plant dripline (with the exception of dark-crusted ISKY soils).

Abundance of amoebae, ciliates, herbivorous and bacterivorous nematodes, and rotifers differed by plant type (Table 3; Supplementary Appendices C and D), while amoebae, flagellates, and all nematode categories varied with crust type. Total protozoa (amoebae + ciliate + flagellate) abundance was greater around *Stipa* than *Coleogyne* at ISKY, but showed no difference by plant type at NDLS. Additionally, total nematode abundance was greater around *Stipa* than *Coleogyne* at both sites.

In the *Coleogyne* community, there was no significant accumulation of protozoa in canopy soils vs. interspace soils (Fig. 2). Similarly, herbivorous nematodes and tardigrades showed little concentration under plant canopies (only 1 of 4 sites). Fungivorous nematodes were greater under plants than in interspaces at 3 of 4 sites, whereas rotifers and bacterivorous and omnivorous nematodes were consistently greater under the plant canopy. Combined, only 17 of 36 possible cases (9 faunal groups × 4 sites) showed greater values in soils under the plant canopy compared to interspace soils.

The *Stipa* community showed a distribution of soil fauna similar to the *Coleogyne* community (Fig. 2). Ciliates and flagellates showed no differences in numbers among the microsites. Amoebae, omnivorous and herbivorous nematodes, and tardigrades showed accumulation under plants at only one of 4 sites and fungivorous nematodes at 2 of 4 sites. Rotifers and bacterivorous nematodes were most often concentrated under plants (3 and 4 of 4 sites, respectively). The largest difference seen between *Coleogyne* and *Stipa* sites was in omnivorous nematodes: their abundance was significantly greater under *Coleogyne* at all 4 sites, whereas this occurred at only one *Stipa* site. Only 13 of 36 possible cases in the *Stipa* sites showed greater values in soils under plants than in interspace soils. Combined *Stipa* and *Coleogyne* sites showed soil fauna was concentrated under plant canopies only 42% of the time (30 of 72 possible cases). The *Coleogyne* shrub community showed a higher incidence of organisms accumulating under plants than did the *Stipa* grass community (47% vs. 36%).

Regression analyses were used to determine the relationships between soil chemistry and fauna. Models had low resolution when all data were combined (data not shown). For amoebae, protozoa, omnivorous/predator nematodes, and soil DNA, combining sites with plant and crust type kept separate produced the best models, although many were weak ($R^2 = 0.27$–0.34, 0.26–0.43, 0.47–0.87, 0–0.49, respectively; Supplementary Appendix E). We considered only models with $R^2 \geqslant 0.30$ and individual components $\geqslant 0.10$ as significant. Under those constraints, amoebae were associated with K availability (K, K/Mg); protozoa with K availability and silt; omnivorous/predator nematodes with P (P, P/Mn, ANP) and K availability, N (total
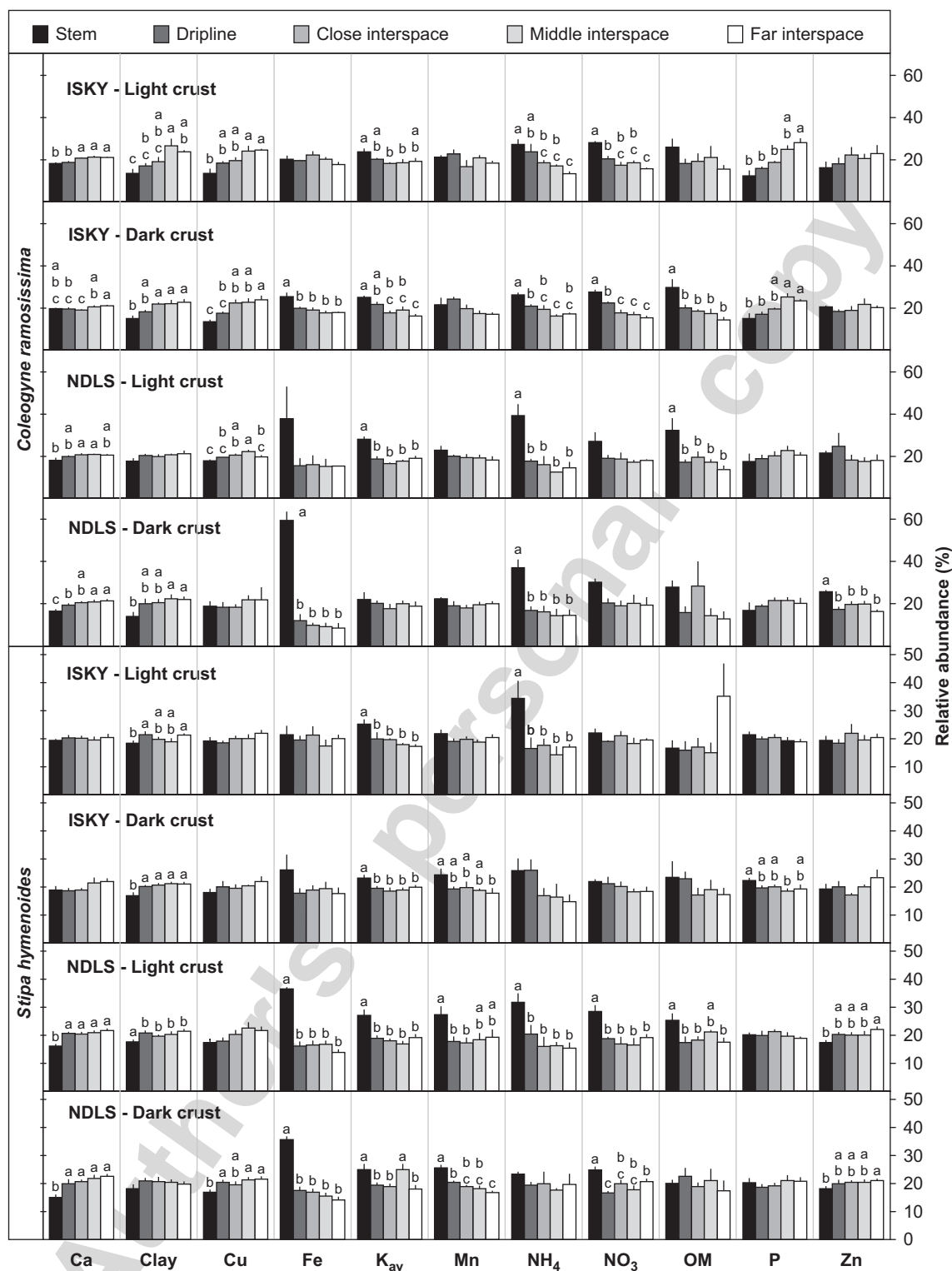
Fig. 1. Relative abundance of soil chemistry variables by microsite for *Coleogyne ramosissima* and *Stipa hymenoides* growing in conjunction with light and dark biological soil crusts near the Island in the Sky (ISKY) and Needles (NDLS). The relative abundance of each variable sums to 100% within a location by crust type. Shown are relative abundance means ($\pm$ SEM) for soil chemistry variables with significant differences indicated by letters; actual means are in (Supplementary Appendix A).

N, NO_3, NH_4), Ca, Mn, and OM; and soil DNA with P, OM, Na, clay, and pH. For the other faunal groups, model resolution was best and associations were often strong

(Table 4, Supplementary Appendix F) when location and plant and crust types were kept separate. Most groups were positively associated with N, P, and K availability. In
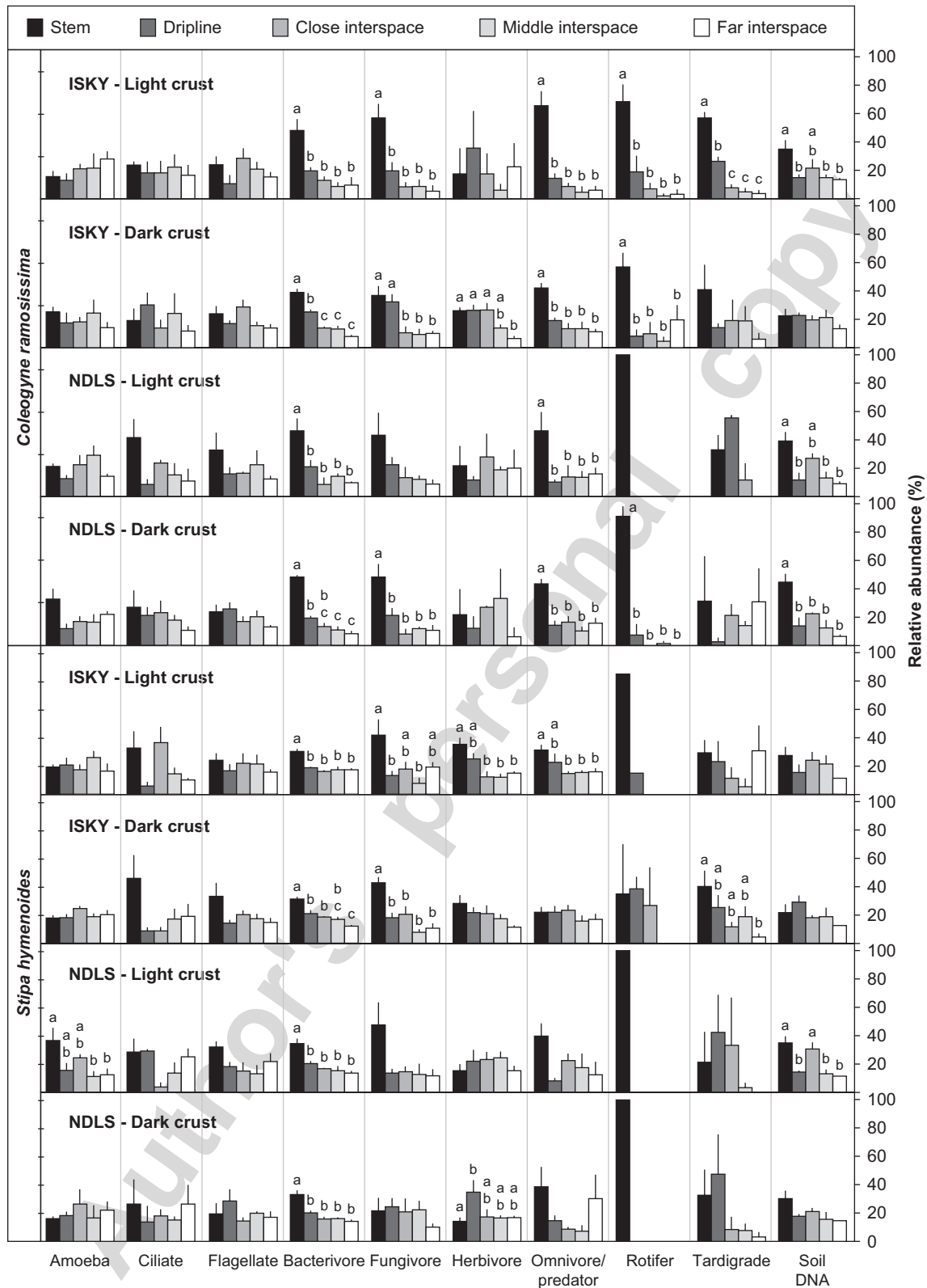
Fig. 2. Relative abundance of soil fauna by microsite for *Coleogyne ramosissima* and *Stipa hymenoides* growing in conjunction with light and dark biological soil crusts near the Island in the Sky (ISKY) and Needles (NDLS). The relative abundance of each variable sums to 100% within a location by crust type. Shown are relative abundance means (±SEM) for soil biota variables with significant differences indicated by letters; actual means are in (Supplementary Appendix C).

Table 3
Soil fauna by soil crust and microsite type for Coleogyne ramosissima and Stipa hymenoides at the Island in the Sky (ISKY) and Needles (NDLS)

Comparison	df[a]	Amoeba	Ciliate	Flagellate	Bacterivore	Fungivore	Herbivore	Omnivore/predator	Rotifer	Tardigrade
ISKY dark[1] vs. light[2] crust around Coleogyne	1.80	22.48[l]	0.01	15.62[l]	11.72[l]	1.34	55.68[l]	14.57[l]	0.07	0.33
ISKY dark[1] vs. light[2] crust around Stipa	1.80	2.82[l]	1.10	0.52	16.73[l]	11.83[l]	1.13	0.89	0.21	2.10
NDLS dark[1] vs. light[2] crust around Coleogyne	1.80	0.04	0.40	2.37	0.85	0.99	0.43	0.01	3.37[l]	1.03
NDLS dark[1] vs. light[2] crust around Stipa	1.80	0.00	0.04	0.31	1.92	0.68	0.06	3.03[l]	0.13	4.56[l]
ISKY, dark crust understory[1] vs. interspace[2] around Coleogyne	1.80	0.30	0.84	0.14	34.74[l]	15.52	0.74	3.46[l]	2.20	0.83
ISKY, light crust understory[1] vs. interspace[2] around Coleogyne	1.80	2.76	0.05	1.36	52.79[l]	29.43[l]	0.03	21.42[l]	18.67[l]	8.56[l]
ISKY, dark crust, understory[1] vs. interspace[2] around Stipa	1.80	0.36	0.41	0.66	8.26[l]	7.41[l]	0.29	0.13	2.82[l]	1.75
ISKY, light crust understory[1] vs. interspace[2] around Stipa	1.80	0.05	0.53	0.03	3.99[l]	3.00[l]	1.14	1.16	4.21[l]	0.78
NDLS, dark crust understory[1] vs. interspace[2] around Coleogyne	1.80	0.07	0.25	2.14	40.93[l]	13.14[l]	0.29	1.74	27.9[l]	1.05
NDLS, light crust understory[1] vs. interspace[2] around Coleogyne	1.80	0.57	0.31	1.03	29.46[l]	7.75[l]	0.66	0.47	10.41[l]	0.24
NDLS, dark crust understory[1] vs. interspace[2] around Stipa	1.80	0.05	2.97[l]	0.99	9.41[l]	0.78	0.11	2.51	0.44	3.91[l]
NDLS, light crust understory[1] vs. interspace[2] around Stipa	1.80	3.24[l]	4.31[l]	3.76[l]	11.14[l]	4.84[l]	0.08	1.16	1.69	2.54

Superscripts indicate which variables are statistically distinct ($P<0.05$) when the two sites listed in the first column are compared; this number also denotes which of the two sites had the higher value.
Shown are degrees of freedom and F-values for comparisons of soil fauna abundance.

[a] Denominator degrees of freedom for bacterivores, fungivores, herbivores, omnivores/predators, tardigrades, and rotifers equal 79.

addition, flagellates also responded to Fe, Cu, and silt; bacterivore nematodes to OM; fungivorous nematodes to OM and Cu; total nematodes to Cu, OM, and silt; rotifers Fe and OM; tardigrades to Cu; and soil DNA to OM. Combined, the soil factors that appeared in the models most often (having an $R^2 > 0.10$) when location, plant, and BSC types were kept separate (Supplementary Appendix F) were P availability [19 of the possible 72 (9 faunal groups $\times$ 8 groupings) cases; 24/72 if Fe is included with P availability], N (14/72 cases), and K availability (12/72 cases). Surprisingly, OM was important only in 9/72 cases, and 4 of these had low R^2 values (<0.15). Silt and Cu both appeared 5/72 times (Fig. 3).

4. Discussion

4.1. How did soil resource heterogeneity respond to vascular plants?

Contrary to our expectations, we found most soil nutrients had a relatively homogenous distribution in this ecosystem. We were especially surprised to find little or no heterogeneity in the distribution of total N, P, and OM, as these elements are used in large quantities (N and P) or produced (OM) by the plants and thus would be most likely to accumulate under them. We did see consistent accumulations of K_{av} and NH_4 under plants (7 and 6 of 8 cases, respectively). However, macronutrients and OM were more often evenly distributed across the landscape than concentrated under the plants (27 vs. 21 cases out of 48, respectively). Similar random patterns were seen in other cations and micronutrients. This was less surprising, as plants use these nutrients in small amounts, and thus these nutrients are less likely to accumulate due to plant litter accumulation under the canopy.

This same lack of consistent response among plant species and among sites can be seen in many past studies of resource islands. Total N is often reported higher under plants (e.g., Charley and West, 1975). However, other studies (e.g., Doescher et al., 1984; Herman et al., 1995; Schade and Hobbie, 2005) show a mixed response within and among plant species and sites. Similarly, although OM is most often greater under plants, there are exceptions (e.g., Charley and West, 1975; Titus et al., 2002; Reeder et al., 2004). Almost all studies show a mixed response in P distribution (e.g., Charley and West, 1975; Herman et al., 1995; Titus et al., 2002).

The presence of BSCs may have counteracted the formation of C and N islands at some sites. First, total N was evenly distributed at all sites, which may have resulted from equal N additions to the canopy and interspace soils by BSCs. While an accumulation of NH_4 under plants was observed in light-crusted Stipa soils, with few N-fixing organisms, this accumulation was not seen in dark-crusted Stipa soils. Secondly, there was no formation of OM islands at most sites, possibly due to C contribution by BSCs to interspace soils. Lastly, soil crust organisms also

Table 4
Relationship between soil chemistry and soil biota associated with light and dark biological soil crusts around *Coleogyne ramosissima* and *Stipa hymenoides* in Island in the Sky (ISKY) and Needles (NDLS)

	ISKY				NDLS			
	Coleogyne		*Stipa*		*Coleogyne*		*Stipa*	
	Light crust	Dark crust	Light crust	Dark crust	Light crust	Dark crust	Light crust	Dark crust
Amoeba	NS	NS	NS	NS	NS	0.32	NS	NS
Ciliate	0.62	NS	NS	0.53	NS	NS	0.73	NS
Flagellate	0.60	0.70	NS	0.80	0.38	NS	NS	NS
Total protist	NS	NS	NS	NS	NS	0.34	NS	NS
Bacterivore nematode	0.92	0.90	NS	0.62	0.78	0.68	0.75	0.86
Fungivore nematode	0.83	0.78	NS	0.49	NS	NS	0.78	0.34
Herbivore nematode	NS	0.85	0.30	0.75	NS	NS	NS	NS
Omnivore/predator nematode	NS	0.91	NS	NS	0.66	0.65	NS	NS
Rotifer	0.75	NS	NS	NS	0.84	0.49	0.79	0.50
Tardigrade	0.86	NS	0.38	NS	NS	NS	0.41	NS
Soil DNA	0.54	NS	NS	NS	NS	0.67	NS	NS

Only values statistically significant at $R^2 \geqslant 0.30$ are shown. For partial R^2 values for each model, see Appendix E. NS = not significant.
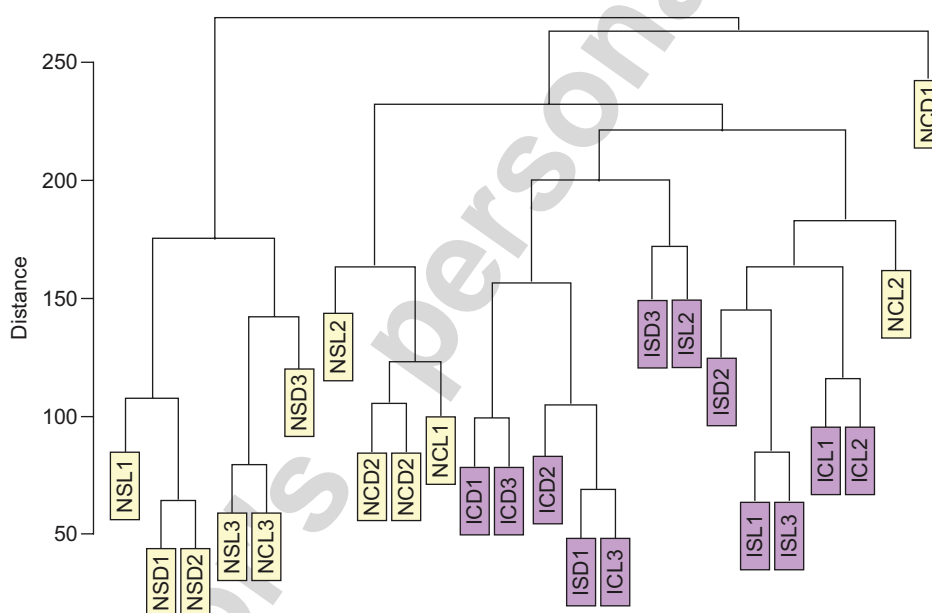

Fig. 3. A dendrogram of the composition of nitrogen-fixing bacteria generated from PCR amplifications of *nifH* DNA followed by T-RFLP analysis. Samples are from the dripline of two plant species from two locations as described in the text. Sample code: N/I = Needles/Isky, S/C = *Stipa hymenoides*/ *Coleogyne ramosissima*, D/L = Dark crust/Light crust, 1/2/3 = field replicate.

secrete compounds (e.g., citric and malic acid) that increase soil P concentrations (Gadd, 1999), which may explain why P did not accumulate under plants when dark BSCs were present. Additionally, soil surface structure also affects movement/retention of nutrients, and heterogeneity in surface roughness between BSCs (rough in dark crusts vs. more smooth in light crusts) may also explain differences between them.

Past studies have consistently predicted or reported that soil resources are more likely to be distributed heterogeneously in shrublands than grasslands (e.g., Smith et al., 1994, 2002). In this study, we saw little difference between

grasses and shrubs, as grasses accumulated resources under the plants 36% of the time, whereas shrubs accumulated them under the plants 43% of the time. Soil fauna appeared to concentrate somewhat more under shrubs than grasses.

4.2. What determined the distribution patterns in subsurface soil biota?

Based on previous studies in disparate ecosystems (reviewed in Wardle, 2002), we expected microbial biomass (i.e., soil DNA) values to follow plant distribution and OM values. We found 50% of the time the highest microbial

biomass was under the plant canopy, 75% in *Coleogyne*. We also expected microbial predators to be highest where their prey was located. However, we found only 2 (bacterivorous nematodes and rotifers) of 8 microbial predator groups concentrated under the plant canopy. The other groups, including amoebae, ciliates, flagellates, fungivores, and omnivorous nematodes and tardigrades, did not closely follow the distribution of their microbial prey. Thus it is likely they are feeding on other organisms that are found in soils both under the plant and soil crust in the interspace.

Flagellates, small ciliates and rotifers eat mostly bacteria and fine particulate organic matter (FPOM). Larger ciliates eat bacteria, FPOM, small ciliates, amoebae, small cyanobacteria, and possibly small nematodes and rotifers. Amoebae are very diverse trophically: while feeding primarily on bacteria and FPOM, they also prey on flagellates, ciliates, nematodes, rotifers, cyanobacteria and fungi. Tardigrades primarily eat cyanobacteria and fungi, but some also eat bacteria and FPOM. Nematodes feed on all the above groups. Thus, BSCs may contribute to the lack of soil faunal "islands", as the cyanobacteria may attract larger ciliates, amoebae, and tardigrades, as well as those organisms which feed on these predators (e.g., nematodes). In addition, the crusts contribute C to soils and thus can support FPOM-feeding organisms.

Our results both agree and disagree with the previous studies we could find. As in our study, most previous researchers found greater microbial abundance in soils under plants compared to interspace soils (e.g., Vollmer et al., 1977; Kieft, 1991; Gallardo and Schlesinger, 1992; Bolton et al., 1993). However, Herman et al. (1994) found no difference in bacterial assemblages when comparing canopy and interspace soils, and abundance was greater under plants only 50% of the time. In contrast to our findings, Robinson et al. (2002) found ciliates and amoebae greater under the canopy than in interspace soils, and Santos et al. (1978) concluded that the distribution of surface litter, not necessarily that of plants or soil OM, controlled microarthropod distribution in the Chihuahuan desert. Freckman and Mankau (1977) found that all nematode groups declined with distance from plant stems.

Our results also show soil chemistry can influence soil faunal distributions. Surprisingly, we seldom found soil faunal abundance correlated with OM, as commonly reported in the literature (e.g., Gallardo and Schlesinger, 1992; Smith et al., 1994; Wardle, 2002). Instead, the availability of N, P, and K_{av} were most often related to soil faunal abundance at our sites. This is similar to Gallardo and Schlesinger (1992), who also found microbial biomass to be related to soil N. We found no reported relationships between soil fauna and the availability of P or K_{av} in the literature.

4.3. Why are soil resources distributed more heterogeneously in some ecosystems than others?

There are several possible explanations as to why some dryland ecosystems show a fairly homogenous, rather than heterogeneous, distribution of soil resources. (1) Interspace condition: the "fertile island" signal may result more from the depletion of interspace soil resources than from an accumulation under plants. The interspace soils in our study were fairly undisturbed and covered with BSCs; in contrast, the classic studies of fertile islands occurred where interspaces were heavily degraded, BSCs absent, and large amounts of soil lost (e.g., Charley and West, 1975). Thus, land use history may determine nutrient and soil biota distribution patterns and thus the strength of the "island" signal. (2) Plant litter in soils: Whitford (2002) showed that most above-ground plant litter is lost via UV, wind, and water and does not enter the soil. We have seen this in cool deserts as well (Belnap, unpublished). Thus, the major mechanism thought to create heterogeneity in soil resources (i.e., plant litter accumulating in soils beneath plants) may not occur in many dryland ecosystems. Instead, litter incorporation may depend on whether a given plant species is utilized by soil fauna present at a specific site. (3) Plant and soil nutrient concentrations vary: plant species are differentially efficient in their uptake and resorption of nutrients. Plants that fix N have greater leaf N than non N-fixing plants. Thus, nutrient concentrations in litter from different plant species will vary (Crawford and Gosz, 1982), and this will affect the accumulation of specific nutrients under plants. Timing of measurements is also important, as Schade and Hobbie (2005) showed that soil N values varied seasonally. Biological activity may be more concentrated under plants in drier than in wetter sites (Stubbs and Pyke, 2005). Greater heterogeneity, and thus stronger island signals, may also be found in less fertile soils, as the same amount of resource transfer from interspace to plant canopy soils is proportionally greater at a less fertile than more fertile site. (4) Root deployment: rooting patterns vary among desert plant species and within species among sites (e.g., Schenk and Jackson, 2002). As most studies analyze soils at 0–20 cm depth, finding resource islands (e.g., nutrients, soil biota) may depend on where plants are rooted relative to where soils are collected.

5. Conclusions

Understanding the controls on the distribution of nutrients, soil C, and soil biota is essential for understanding ecosystem function, ecosystem condition, issues of scaling, and the resistance and resilience of that ecosystem to disturbance, whether it be from climate change or land use. Our results indicate a lack of plant-driven soil heterogeneity around the shrub and grass we investigated. This is likely due to the presence of interspace BSC's, little incorporation of aboveground plant litter into soils, and/or root deployment patterns. The results from the many studies in drylands regarding resource distribution patterns still appear contradictory, indicating that we currently lack sufficient knowledge or the proper viewpoint needed to

construct an underlying framework to accommodate currently existing data.

Concomitantly, although considerable speculation has focused on how resource islands form in dryland ecosystems, there are few studies that test these hypotheses directly. In addition, there has been little discussion on which variables might counteract the formation of resource islands. We propose that the condition of the interspace, including the presence or absence of BSCs, may be a key to understanding the processes that control resource island formation. We need studies that explicitly address these questions, including assessment of the condition of the interspace. Our understanding on controls of soil biota, and thus the rates and locations of nutrient inputs, transformations, and loss, is equally lacking, and will require much more future study.

Acknowledgments

Appendix A. Supplementary data

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.soilbio.2007.03.015.

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