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Few apparent short-term effects of elevated soil temperature and increased frequency of summer precipitation on the abundance and taxonomic diversity of desert soil micro- and meso-fauna

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ABSTRACT

Frequent hydration and drying of soils in arid systems can accelerate desert carbon and nitrogen mobilization due to respiration, microbial death, and release of intracellular solutes. Because desert microinvertebrates can mediate nutrient cycling, and the autotrophic components of crusts are known to be sensitive to rapid desiccation due to elevated temperatures after wetting events, we studied whether altered soil temperature and frequency of summer precipitation can also affect the composition of food web consumer functional groups. We conducted a two-year field study with experimentally-elevated temperature and frequency of summer precipitation in the Colorado Plateau desert, measuring the change in abundance of nematodes, protozoans, and microarthropods. We hypothesized that microfauna would be more adversely affected by the combination of elevated temperature and frequency of summer precipitation than either effect alone, as found previously for phototrophic crust biota. Microfauna experienced normal seasonal fluctuations in abundance, but the effect of elevated temperature and frequency of summer precipitation was statistically non-significant for most microfaunal groups, except amoebae. The seasonal increase in abundance of amoebae was reduced with combined elevated temperature and increased frequency of summer precipitation compared to either treatment alone, but comparable with control (untreated) plots. Based on our findings, we suggest that desert soil microfauna are relatively more tolerant to increases in ambient temperature and frequency of summer precipitation than the autotrophic components of biological soil crust at the surface.

1. Introduction

Desertification is the collective process of reduced productivity in arid and semi-arid lands that can result from long-term grazing, exotic shrub invasion, and extended drought (Schlesinger et al., 1990). The majority of global climate models used by the International Panel on Climate Change (IPCC) predict a transition to more arid conditions for much of the arid southwest US (Seager et al., 2007), in part due to projected increases of 2–4 °C by 2050 for Western North America. However, models differ in their predictions of drought through 1) reduced annual precipitation or 2) shifts toward precipitation in hot (summer) seasons. Biological soil crusts (comprised of cyanobacteria, lichens, green algae, and mosses) may slow desertification in many desert soils by increasing the physical stability of surfaces and improving soil fertility through dust entrapment, photosynthesis, nitrogen fixation, and mineral chelation (Belnap, 2003). However, rapid desiccation due to elevated temperatures after wetting events was found to adversely affect the autotrophic components of crusts because rapid wetting and drying cycles reduce quantum yield (an indication of radiation-induced damage to Photosystem II), chlorophyll content, and UV protective pigments of soil lichens (Belnap et al., 2004; Bowker et al., 2002), and high temperatures (>26 °C) inhibit nitrogen fixation (Belnap, 2002). Frequent small precipitation events in arid systems accelerate rates of carbon (C) and nitrogen (N) mineralization by increasing microbial respiration, death by membrane rupture, and release of intracellular solutes (Austin et al., 2004; Fierer and Schimel, 2003; Kieft et al., 1987; Miller et al., 2005). In the case of autotrophic components of desert biological soil crusts, rapid desiccation reduces their ability to conserve carbon by osmoregulation (Belnap et al., 2004). As a result, arid lands can

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experience significant losses of C and N by volatilization of gaseous compounds and leaching of aqueous compounds upon rewetting if nutrients are not immobilized by plant, microbial, or consumer uptake. To understand how changes in the climate of arid land regions affect the ability of soil food webs to mediate nutrient cycles, it is necessary to understand how the soil food web consumer groups themselves also respond to altered temperature and precipitation.

Previous studies have reported numerous impacts of altered temperature and precipitation on soil microfauna communities, but the changes documented appear to be idiosyncratic or without clear functional implications (Bakonyi and Nagy, 2000; Bakonyi et al., 2007; Sohlenius and Bostrom, 1999; Todd et al., 1999). Desert soil food webs are composed of multiple consumer groups that mobilize nutrients (Whitford, 1996), and various functional groups within these food webs contribute to different parts of the C and N cycle. For example, Santos et al. (1981) suggested that cephalobid nematodes in desert soils influence decomposition by regulating the population sizes and activity of their bacterial prey, while Santos and Whitford (1981) showed that microarthropods accelerated litter decomposition 200% in comparison to litter excluding microarthropods. Only 50% of nematodes in desert soils with similar texture and species composition were estimated to be metabolically active (Freckman and Mankau, 1986), with 30 °C representing an approximate threshold at which desert microfauna begin to die when hydrated and forced to be active (Darby et al., 2006).

The primary objective of this study was to determine the response of microfaunal groups of desert soil food webs to an annual scale elevated temperature and increase in frequency of summer precipitation. We conducted a two-year field experiment with treatments in a complete factorial combination with sampling in both spring and early fall to capture seasonal dynamics over a winter and summer period, respectively. It has been previously shown that the autotrophic components of crusts are sensitive to rapid desiccation due to elevated temperatures after wetting events (Belnap et al., 2004; Bowker et al., 2002), and that high temperatures (>26 °C) inhibit nitrogen fixation (Belnap, 2002). Consequently, we asked whether the microfaunal consumers of the desert soil food web (e.g., protozoa, nematodes, and microarthropods) are similarly sensitive to elevated temperature and increased frequency of summer precipitation. Desert microfauna are capable of tolerating considerable drought and temperature extremes by entering and exiting from the dormant state. However, such stress tolerance is metabolically costly (Crowe et al., 1977), so we hypothesized that microfauna would be affected adversely by the combination of elevated temperature and frequency of summer precipitation more than either factor alone. An additional objective of this study is to simply characterize the abundance of nematodes, protozoa, and microarthropods together from this cool-desert location in southeastern Utah, USA, as well as the composition of nematode and microarthropod taxa. For this reason, we report the major taxa found from each group, and suggest characteristics of the consumer portion of this desert food web that differ from temperate food webs and may be of functional significance.

2. Methods

2.1. Field experiment design

A study site (60 m by 60 m) was selected in fall of 2005 near Moab, Utah (38.67485 N, −109.4163 W, 1310 m.a.s.l.), representative of the Colorado Plateau, where about 65% of the precipitation occurs in winter. The soil at this site is classified as loamy, mixed (calcareous), mesic Lithic Ustic Torriorthent. Vascular plant vegetation at this site, comprising 5–20% of the total cover, is dominated by the grasses *Pleuraphis jamesii* (Torr.) (syn. *Hilaria jamesii*), *Achnatherum hymenoides* (Roem. & Schult.) (syn. *Stipa hymenoides*), and *Bromus tectorum* (L.) (Rosentreter and Belnap, 2001). Biological soil crusts at this site, comprising 70–90% of total cover, are dominated by the lichen *Collema tenax* (Sw.) Ach., the cyanobacterium *Microcoleus vaginatus* (Vauch.) Gomont, and the moss *Syntrichia caninervis* Mitt. Experimental field units were arranged in a randomized block design with five replicate blocks arranged perpendicular to a gradual slope. Each block contained five, 2-m by 2-m plots containing representative vegetative cover and composition. One of five treatments was applied randomly to each experimental unit within a block: 1) control, 2) lamp control, 3) elevated temperature, 4) elevated frequency of summer precipitation, and 5) both elevated temperature and frequency of summer precipitation. Control plots (1) had no lamp shell, while all other plots (2, 3, 4, 5) had a lamp shell 1.5 m above the soil; the plots without elevated temperature treatments (2, 4) included the lamp shell with no heating filament, whereas the plots with elevated temperature treatments (3, 5) included a working infrared heating filament (Model MRM-1208, 120 V, 800 W, 6.7 A, 35 in., Kalglo Electronics Co. Inc, Bethlehem, PA). The lamps add no photosynthetically active radiation and have been used successfully to warm soils in previous climate change experiments (Harte et al., 1995; Bridgham et al., 1999; Zavaleta et al., 2003). The heating lamps (active throughout the entire two-year experiment) provide greater warming at night than during the day, and greater warming in the winter than the summer which better mimics empirical climate change data than other warming technologies. The frequency of summer precipitation was increased to approximately twice the 40-year summer median with 2-mm artificial rainfall events (6 L of water per plot, or approximately the 40-year median event size) applied five times per two-week interval through summer (June, July, August, and September). Thus, both frequency of total summer precipitation was increased, but no individual rainfall event size was increased beyond ambient. Simulated rainfall was provided with a watering nozzle calibrated to supply raindrop sizes appropriate for this region. Thermopiles were constructed from 24 ga Type-T thermocouple wire (Omega Engineering, Inc., Stamford, CT) and installed in every plot of every treatment to record half-hourly temperature data at 1-, 5-, and 15-cm to confirm elevated temperature treatments. Campbell CS616 water content reflectometer probes (Campbell Scientific, Inc., Logan, UT) were installed in every plot of every treatment to measure volumetric water content at 5-cm depths every 30 min. In general, the field site experienced comparable climatic conditions for the region (Fig. 1) and experimental treatments elevated temperatures 2–3° for most of the year relative to control plots (Fig. S1). To assess vegetative cover for comparison with nematode and mite communities, we estimated percent cover at the final sampling date (September 2007) by visual inspection of each plot's sampling area for seven major cover-type groups: bare/rock, lichen, cyanobacteria, moss, *P. jamesii*, *A. hymenoides*, and *B. tectorum*.

2.2. Sampling

Sampling of all 25 plots for nematodes and protozoa occurred on rain-free days in March 2006, September 2006, May 2007, and September 2007. The spring and fall sampling dates were selected to be able to assess the population dynamics that occur between the two most contrasting seasons at this site, winter and summer respectively. Surface (0–10 cm depth) soil was collected with approximately 8–10 cores (2.5 cm diameter) to obtain at least 250 g soil for the nematode and protozoa assay. On each sampling date, cores were collected from within an 8-cm wide segment adjacent

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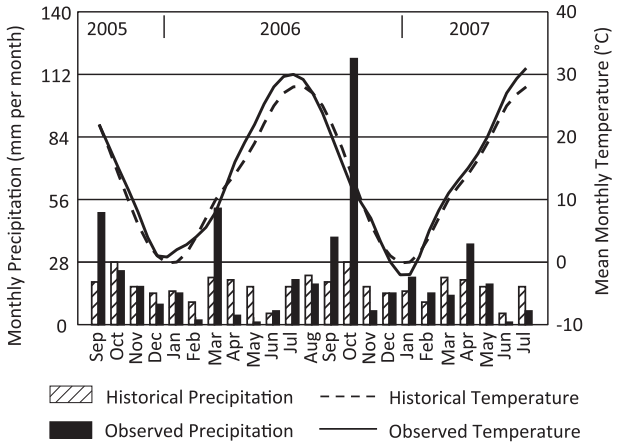

Fig. 1. Observed mean monthly air temperature and monthly natural precipitation collected from field site between September 2005 and July 2007. Additionally, historical mean monthly air temperature and historical median monthly natural precipitation are presented that were collected from 1971 to 2000 monthly records at Moab, UT (www.ncdc.noaa.gov).

to, but not overlapping, the previous sampling segment to avoid disturbed crust surfaces. Microarthropods were sampled in September 2006 and September 2007 from all 25 plots by collecting 8–10 cores amounting to 500 g soil from 0 to 20 cm soil depth, which was often the entire depth of the profile due to a shallow bedrock or caliche layer. All soil samples were shipped to Burlington, Vermont, by overnight courier, and soil for microarthropods was immediately preserved in 95% ethanol for later processing.

Nematodes were extracted from 200-g soil samples with Cobb's decanting and sieving with cotton milk filter trays (Whitehead and Hemming, 1965, with modifications by Darby et al., 2007, 2010). Nematodes were heat relaxed and fixed in warm 8% formalin prior to identification of a representative selection of 200 nematodes to genus. Genera were assigned to one of four nematode functional groups: bacterivores, herbivores, tylench-type omnivores, and dorylaim-type omnivores (Supplementary information Table S1). Protozoa were enumerated from soils using a most probable number technique (Darbyshire et al., 1974) with modifications optimized for these communities (Darby et al., 2006, 2010), and calculations of Cochran (1950). Microarthropods were extracted from 500-g samples by heptane flotation (Geurs et al., 1991) and mounted individually on microslides in Hoyer's solution for clearing and identification to family and one of three functional groups (Supplementary information Table S2): zoophagous prostigmatids, microphytophagous prostigmatids, and oribatids. The separation of zoophagous from microphytophagous prostigmatids was determined to be a functionally relevant distinction among species of Prostigmata informed by a literature review of the families' known feeding habits (as outlined in Neher et al., 2009).

2.3. Statistical analysis

Soil fauna were analyzed by univariate repeated measures mixed linear models (with plot as a random 'subject' variable) on three groups of dependent variables: 1) $\log_{10}$-transformed total abundance of total amoebae, flagellates, ciliates, nematodes, mites, and collembolans (expressed as individuals per mass of dry soil), 2) arcsine-transformed proportions of functional groups (bacterivore, tylench-type omnivore, herbivores, dorylaim-type omnivore nematodes and microphytophagous prostigmatid, zoophagous prostigmatid, and oribatid mites), and 3) Shannon diversity of nematode genera (and mite families), computed as $\Sigma[p_i{*}\log_e(p_i)]$, where p_i is the proportion of each nematode genus or mite family i (n_i/N) (Shannon, 1948). These dependent variables were tested against independent variables of sampling time (March 2006, September 2006, May 2007, September 2007), temperature (ambient or elevated), and precipitation (ambient or elevated) as fixed effects. All variables tested, with the described transformations, were found to satisfy assumptions of normality and homogenous variances prior to analysis. Treatment effects that were found to be statistically significant at $\alpha < 0.05$ are graphed and described in further detail. For presentation, proportions were back-transformed to percentages. Due to the short duration of the experiment and variable nature of microfaunal communities, statistical test with a p-value in the range of $0.05 < p < 0.1$ are noted in tables not as a conclusion but to alert future research of a potential effect that may prove more statistically significant if treatments are applied for longer periods of time. Although the lamp shell produces a shadow that passes over the plots and briefly reduces temperature and direct sunlight (<0.5 h shortly after sunrise), the presence or absence of a lamp shell had no other detectable affect on temperature or moisture. Thus, the analysis is an unbalanced model that includes five replicated plots for each treatment combination except ten replicate plots (five control and five lamp control) for the ambient temperature, ambient precipitation treatment. Analyses were performed using type III sums of squares test from the restricted maximum likelihood method of the MIXED procedure of SAS software (Statistical Analysis Systems Institute, Inc., Cary, NC).

Nematode and mite community composition (at the level of genus, and family, respectively) was also analyzed with multivariate ordination using Canonical Correspondence Analysis (CCA) with CANOCO Version 4.5A software (Wageningen, The Netherlands). In separate analyses, the relative abundance of all genera of nematodes (and all families of mites) were modeled against the four treatment combinations (control, elevated temperature, elevated frequency of summer precipitation, and combined elevated temperature and frequency of summer precipitation) as binary environmental variables. To test the relationship between fauna and vegetative cover at the conclusion of the experiment, we modeled the relative abundance of tylench-type omnivorous nematodes and microphytophagous prostigmatid and oribatid mites (those taxa most likely to prey on autotrophic components of the soil) against the percent cover as determined at the final fall 2007 sampling. The first canonical axis, and the full model, were both tested with 499 random Monte Carlo permutations of the data to assess statistical significance.

3. Results

3.1. Protozoa

In the absence of altered temperature or precipitation treatments, the total abundance of all protozoan groups differed between seasons, with a general increase in abundance throughout the two-year experiment (Fig. 2). Under control conditions, amoebae and ciliates increased in abundance between March and September, while flagellates increased between September 2006 and May 2007. Ciliates were affected by a significant interaction between sampling date and precipitation, but Amoebae were the only major faunal group to be affected by a significant three-way interaction between sampling date, temperature, and precipitation. Elevated temperature alone and increased frequency of summer precipitation alone both increased the abundance of amoebae in the final sampling interval (May 2007 to September 2007) to be greater than the previous September 2006 sampling. However, the increase in abundance of amoebae in the final sampling interval

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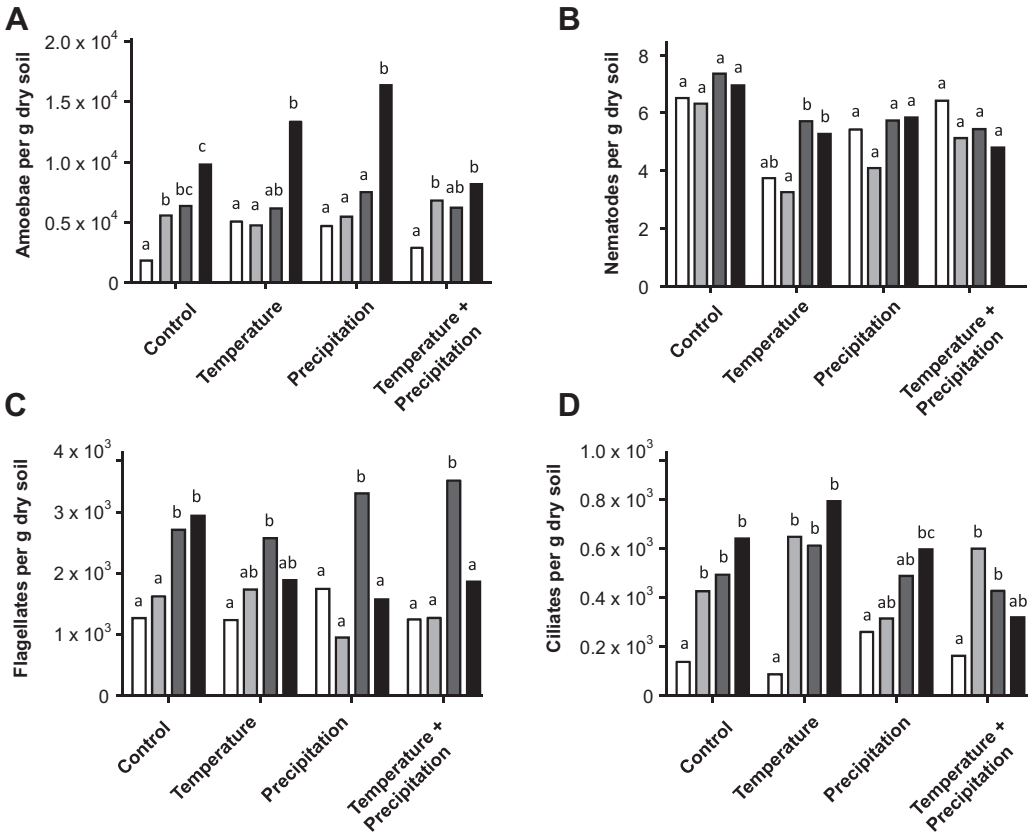

Fig. 2. Abundance of A) amoebae, B) nematodes, C) flagellates, and D) ciliates (individuals per gram dry soil) through four sampling events (shaded sequentially as March 2006 [white], September 2006 [light gray], May 2007 [dark gray], and September 2007 [black]), and from four treatments: ambient temperature and precipitation ('Control'), elevated temperature ('Temperature'), elevated frequency of summer precipitation ('Precipitation'), and elevated temperature and frequency of summer precipitation ('Temperature + Precipitation'). Contrasting letters represent significant changes between sampling dates within a treatment. Overall treatment effects for the change in abundance through time (repeated measures ANOVA, from Table 1) was significant for the three-way interaction of sampling date, temperature and precipitation for amoebae and by the two-way interaction of sampling date and precipitation for ciliates.

under both elevated temperature and frequency of summer precipitation together was similar to that of control plots.

3.2. Nematodes

At total of 47 genera in 24 families of nematodes (Supplementary information Table S1) were identified at this site over two years. The predominant functional guild of nematodes was bacterivores, ranging from 60 to 80% of the nematode community (Table 2). Tylench-type omnivores were second most abundant (20–37%), followed by dorylaim-type omnivores (1.5–20%), and finally those classified as strictly herbivores (0–3%). Among nematodes, bacterivores (predominantly Cephalobidae) were disproportionately most abundant at the September 2006 and September 2007 sampling events. No treatment effects other than sampling date were observed for any nematode functional group. The three-way interaction of sampling date, elevated temperature, and increased frequency of summer precipitation on diversity of nematode genera was marginally significant (ANOVA, $F_{4,63} = 2.20$, $p = 0.0790$) and graphed in Fig. 3A.

3.3. Microarthropods

A total of 35 families of mites (Supplementary information Table S2) were identified at this site over two years. The family Tydeidae comprised 60% of the microphytophagous prostigmatids, followed by Brachychthoniidae (15%). Only one collembolan genus (*Anurophorus*) was found during the two sampling events, but three additional genera (*Schaefferia*, *Tullbergia*, and *Bourletiella*) were found at the site in preliminary samplings. Among the microarthropods, Oribatida were most abundant in September 2006, while microphytophagous prostigmatids were most abundant in September 2007. Microphytophagous prostigmatids were the only mite functional guild to be significantly affected by a treatment (Fig. 3B), which was precipitation ($F_{2,21} = 7.63$, $p = 0.0032$). The proportion of mites that were microphytophagous remained constant between September 2006 and September 2007 for plots receiving increased frequency of summer precipitation, but increased for non-watered plots.

3.4. Multivariate ordination

Canonical Correspondence Analysis ordination of all mite families at the final sampling date of September 2007 modeled against treatments is illustrated with a bi-plot ordination (Fig. 4A). Although the first axis was not significant for all mite families included, the combined model was (Table 3). The first axis appears to be a gradient of heat tolerant taxa, while the second axis delineates the combined elevated temperature and elevated frequency of summer precipitation treatment. For mites, the first (dominant) axis is a gradient of heat tolerant-to-intolerant taxa. Neither the first axis (eigenvalue = 0.070, $F = 1.952$, $p = 0.3180$) nor the combined canonical axes (trace = 0.118, $F = 1.169$, $p = 0.260$) was significant with all nematode genera included, but the ordination of the nematode species most likely to prey on autotrophic components of the soil (tylenchid-type omnivore and strict

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Table 1
F-values from repeated measures analysis of variance (ANOVA) on microfauna from field experiment: abundance (individuals g^{-1} dry soil) of amoebae, flagellates, ciliates, nematodes, mites, and collembolans, proportions of nematodes that are tylench-type omnivores, tylench-type herbivores, bacterivores, or dorylaim-type omnivores (all nematodes), proportions of mites that are zoophagous prostigmata, microphytophagous prostigmata, or oribatida, and nematode and mite Shannon diversity. Variables are separated by sampling frequency, which results in differing degrees of freedom for nematode and protozoan variables (top) and microarthropod variables (bottom). Abundances were $\log_{10}$-transformed and proportions were arcsin of square-root transformed prior to analysis.

Effect	Sampling date	Temperature × sampling	Precipitation × sampling	Temperature × precipitation × sampling
df (n,d)	3,60	4,60	4,60	4,60
Amoebae	15.55***	0.45	0.28	3.27*
Flagellates	14.09***	0.51	2.25	0.79†
Ciliates	27.86***	2.48†	3.22*	0.97
Nematodes	2.84*	0.49	0.89	2.07†
Nematode diversity	18.27***	0.39	0.23	2.14†
Tylench-omnivores	2.13	0.99	0.54	0.03
Tylench-herbivores	16.12***	0.17	0.09	0.43
Bacterivores	8.71***	0.29	0.45	0.24
Dorylaim-omnivores	67.88***	1.51	0.07	2.40†
df (n,d)	1,18	4,18	4,18	4,18
Mites	22.13***	1.16	0.60	1.23
Collembola	4.08†	0.08	0.71	0.58
Mite diversity	5.77*	2.17	1.72	0.29
Zoophagous prostigmata	0.07	1.07	0.40	0.46
Microphytophagous prostigmata	8.07*	3.06†	7.70**	0.17
Oribatida	2.17	0.94	2.86	0.77

*$p < 0.05$, **$p < 0.01$, ***$p < 0.001$.
†$0.05 < p < 0.1$.

herbivore nematode genera) was (Table 3, Fig. 4B). The taxa included in the ordination are only those found at the final sampling data and are therefore fewer than the full list from Tables S1 and S2.

4. Discussion

4.1. Experimental effects

We hypothesized that the combination of elevated temperature and frequency of summer precipitation would adversely affect the total abundance and diversity of microfauna more than either elevated temperature or frequency of summer precipitation alone, as was found for the autotrophic components of the surface biological soil crusts. In contrast, the abundance of most microfaunal groups was relatively resistant to elevated temperatures of 2–3 °C throughout the year or a doubling of the frequency of summer precipitation. This observation is similar to the finding of Bakonyi et al. (2007) who found, in a comparable semi-arid shrubland, that total nematode density was not significantly affected by experimental warming or drying treatment. The only major group in our study affected by the treatments was amoebae. Generally, the increase of amoeba abundance through time was most pronounced under either elevated temperature or increased frequency of summer precipitation treatments, while abundance under the combination treatment was not greater than that of the control. This field experiment allows us to examine how soil microfauna are affected by contrasting climatic trajectories from

Table 2
Changes in nematode functional group composition (mean percentage ± SE) from field experiment control (non-treated) plots.

Sampling date	Bacterivores	Tylench-type omnivores	Dorylaim-type omnivores	Herbivores
March 2006	59 (5.3)	29 (4.9)	19 (2.1)	2.9 (0.7)
September 2006	76 (4.7)	29 (4.9)	1 (0.6)	0.0 (0.1)
May 2007	68 (5.1)	37 (5.3)	4 (1.0)	0.1 (0.2)
September 2007	79 (4.5)	22 (4.5)	3 (1.0)	0.3 (0.2)

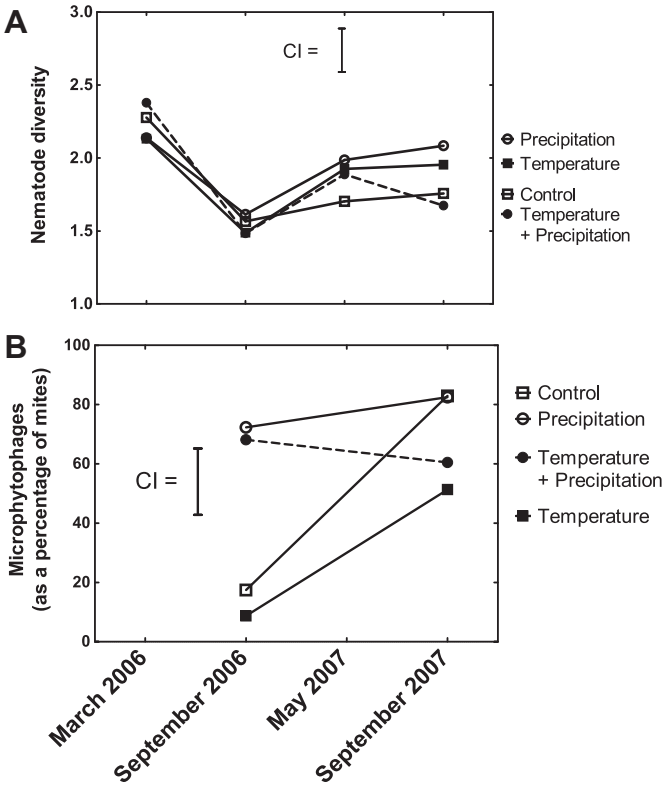

Fig. 3. A) Nematode genus diversity, and B) microphytophagous prostigmatids, as a proportion of total mites, from field experiment under four treatments: ambient temperature and precipitation ('Control', open squares), elevated temperature ('Temperature', filled squares), elevated frequency of summer precipitation ('Precipitation', open circles), or elevated temperature and frequency of summer precipitation ('Temperature + Precipitation' filled circles). In both graphs, straight lines are not meant to imply a known linear trend, but instead are a visual aid to connect markers of the same treatment.

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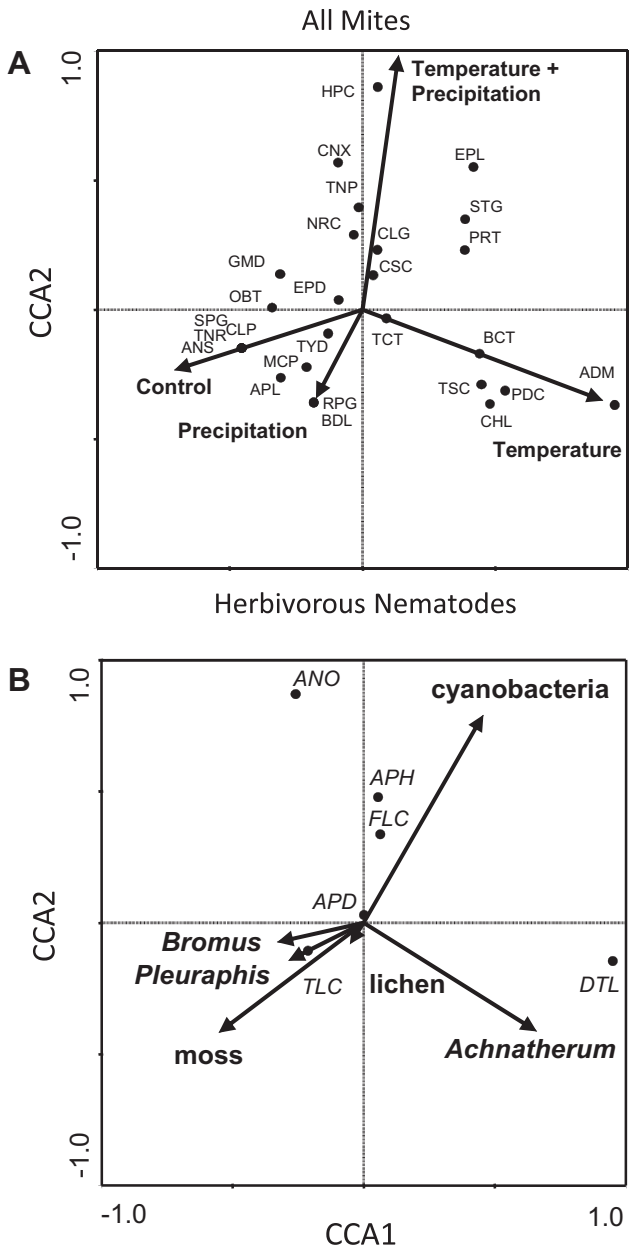

Fig. 4. Canonical Correspondence Analysis ordination of microfauna communities at the conclusion of the experiment in fall 2007. A) Mite families in relation to the field treatments: ambient temperature and precipitation ('Control'), elevated temperature ('Temperature'), elevated frequency of summer precipitation ('Precipitation'), and elevated temperature and frequency of summer precipitation ('Temperature + Precipitation'). B) Nematode genera in relation to vegetative cover classes: bare/rock, lichen, cyanobacteria, moss, *Pleuraphis*, *Achnatherum*, and *Bromus*. Species abbreviations for mites: EPL: Eupalopsellidae, HTS: Heterostigmatid, ADM: Adamystidae, ANS: Anystidae, BDL: Bdellidae, CLG: Caligonellidae, CLP: Calyptostomatidae, CHL: Cheyletidae, CNX: Cunaxidae, DMD: Demodicidae, EPD: Eupodidae, MCP: Micropsammidae, NRC: Nanorchestidae, PRT: Paratydeidae, RPG: Raphignathidae, STG: Stigmaeidae, TSC: Tarsocheylidae, TNR: Tenerifiidae, TNP: Tenuipalpidae, TPC: Terpnacaridae, TNC: Tetranychidae, TYD: Tydeidae, HPC: Haplochthoniidae, APL: Aphelacaridae, BCT: Brachychthoniidae, CPH: Cepheidae, CSC: Cosmochthoniidae, GMD: Gymnodamaeidae, OBT: Oribatulidae, PDC: Pediculochelidae, TCT: Trichthoniidae, SPG: Saproglyphiidae, ASG: Astigmatid. Species abbreviations for nematodes: TLC: *Tylenchus*, FLC: *Filenchus*, DTL: *Ditylenchus*, APH: *Aphelenchus*, APD: *Aphelenchoides*, ANO: *Anomyctus*.

a common beginning point, but the resulting population dynamics and any extrapolation into future potential climate scenarios must be put in the context of the abiotic conditions during the experiment. The general increase in abundance of faunal groups suggests that abiotic conditions during this experiment were adequate to promote population growth for most functional groups. However, the effects of increased temperature or frequency of summer precipitation may be more pronounced in years with more extreme summer temperatures. Studies performed in contrasting years, or for longer periods of time, would be advised to better characterize how elevated temperature and increased summer precipitation affect desert soil fauna in a broader range of yearly climate extremes.

Seasonal differences were observed for protozoa groups. Specifically, ciliates increased abundance between March 2006 and September 2006. In contrast, abundance of amoeba increased from September 2006 to May 2007. This result was surprising because, although amoebae and ciliates have relatively high thermal optima for population growth and are able to encyst (a temporary dormant stage) at high temperatures (Darby et al., 2006), we had expected that flagellates would increase in population sizes in the same climatic conditions as did amoebae and ciliates. Understanding seasonal dynamics of desert microfauna is important because any cumulative long-term effects of potentially altered climate on soil food webs will depend on whether the seasons that change are those in which different microfauna tend to increase or decrease in abundance.

Table 3
Results of multivariate Canonical Correspondence Analysis ordination at the final sampling date of all mites (modeled against field treatments) and of the microphytophagous nematode species most likely to feed on autotrophic soil flora (modeled against soil cover classification measured at the final sampling date).

	Axis 1	Axis 2	Axis 3	Axis 4	Full
Mites (all)					
Eigenvalues	0.162	0.132	0.064	0.418	
Species–environment correlations	0.648	0.792	0.596	0.000	
Cumulative percent variance of Species–environment relation	45.2	82.0	100.0	100.0	
F-ratio	2.036				1.704
p-value	0.1300				0.0240
Nematodes (microphytophagous)					
Eigenvalues	0.452	0.137	0.036	0.009	
Species–environment correlations	0.802	0.691	0.565	0.206	
Cumulative percent variance of species–environment relation	71.0	92.6	98.3	99.6	
F-ratio	8.865				2.604
p-value	0.0480				0.0440

4.2. Community composition

The soil food web beneath well-developed, undisturbed biological soil crust at this site retains many of the same major functional groups as the well-studied Central Plains Experimental Range (CPER) shortgrass prairie site (Hunt et al., 1987). However, two major ecological differences exist between the Colorado Plateau cool desert and Central Plains shortgrass prairie soil food webs that may affect their relative functioning. First, there are numerous microphytophagous omnivores with piercing mouthparts (i.e., tardigrades, nematodes, and microarthropods) or pseudopodia (i.e., filose amoebae) that are capable of feeding on the autotrophic, and sometimes diazotrophic, components of desert biological soil crusts. Wood (1973b) reported observations of some of these omnivores (including both the fine-apertured *Aphelenchus*, *Aphelenchoides*, and *Tylenchus* as well as some broad-apertured Dorylaimida) directly feeding on algae, cyanobacteria, or moss, but quantitative estimates of consumption and preferences remain scarce due to their small

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body size and opaque habitat. Thus, a significant portion of the cool-desert soil food web potentially feeds on relatively high-N content prey (such as moss or nitrogen-fixing cyanobacteria) than their temperate counterparts, who would otherwise feed on low-N content plant roots or fungal hyphae.

A second difference is that the bacterivorous energy channel in desert soil food webs is dominated by a greater abundance of amoebae relative to nematodes. Extraction and enumeration efficiency may contribute to this apparent difference, but we predict that the relative composition of bacterivorous consumers will be important because bacterivorous nematodes and protozoa differ in the way they forage and metabolize their diet. Most amoebae feed by phagocytosis and digest their prey enzymatically, while bacterivorous nematodes pass their prey through a crushing valve prior to exposing the consumed diet to a humification process in the intestines. Amoebae (0.0848 ng dry weight ind^{-1}) are expected to be active in smaller pore spaces with less available moisture than nematodes (100 ng dry weight ind^{-1}), causing nematodes to be restricted to periods of growth with greater levels of soil moisture than for amoebae. Nematodes in these desert soils are assumed to be mostly dormant in an anhydrobiotic state while volumetric water content is below 5% (Freckman and Mankau, 1986), but frequent small wetting events force near-surface nematodes to become active within hours and cause mortality to intolerant species in high temperatures. However, many protozoa remain in their dormant encysted state through high temperatures even when wetted (Darby et al., 2006). Bacterivorous amoebae can also consume prey in pore spaces smaller than their mean body diameter by extending flexible pseudopods. Additional research should address whether alterations in the relative abundance of these groups has a functional consequence in light of their contrasting size, motility and feeding habits.

The functional group classifications used here may differ from the groupings commonly used in temperate biomes (Yeates et al., 1993) for two reasons. Firstly, after examination of the taxa present at this site, there was relatively little diversity in colonizer–persister classifications (from Bongers, 1990), such as c–p = 2 for most of both bacterivores and tylench-type omnivores, and it was preferable to look at the communities in terms of integrated functional groups (taxa with similar feeding habits and life history traits) rather than as trophic groups and colonizer–persister classifications separately. Secondly, the uncertainty regarding feeding habits of nematodes (particularly with respect to the potential for herbivores to feed on lichens, moss, and cyanobacteria) is especially problematic in desert soils, where diverse microflora dominate the autotrophic food web. Nematode taxa that might have been classified as fungivores or fine root herbivores elsewhere (e.g., Tylenchidae, Anguinidae, Aphelenchida) are here considered 'omnivores' because they are known to potentially prey on cyanobacteria, moss and green algae (Wood, 1973b), which are significant components of the desert soil food web. These tylench omnivores have fine-apertured stylets that are used to pierce diverse filamentous material such as plant fine roots, fungal hyphae, and cyanobacteria. In contrast, dorylaim-type omnivores differ functionally by having broad-apertured stylets that are capable of feeding not only on fungi and cyanobacteria, but also other nematodes and micrometazoans. Additionally, the dorylaim omnivores tend to have a longer generation time, fewer progeny, and slower growth rates than the tylench omnivores (Bongers, 1990). With respect to predaceous nematodes, Diplogasteridae and Mononchidae were not detected, Nygolaimidae were rare (<0.5%), and the remaining piercing-type predators (e.g., *Aporcelaimellus*) are also known to prey on cyanobacteria, green algae, and fungi (Wood, 1973a). For this reason, we did not analyze predators separately but rather all non-herbivorous Dorylaimida together as omnivores.

5. Conclusion

In conclusion, the effect of elevated temperature and frequency of summer precipitation on abundance of most microfaunal groups was found to be not statistically significant and ultimately less than normal seasonal fluctuations in abundance. However, the seasonal increase in amoebae abundance was reduced with combined elevated temperature and increased frequency of summer precipitation compared to either treatment alone, but comparable with control (untreated) plots. Based on our findings, we suggest that desert soil microfauna are relatively more tolerant to increases in ambient temperature and frequency of summer precipitation than the autotrophic components of biological soil crust at the surface.

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Appendix. Supplementary information

Supplementary information related to this article can be found online, at doi:10.1016/j.soilbio.2011.03.020.

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