



## EFFECTS OF MANIPULATED SOIL MICROCLIMATE ON MESOFAUNAL BIOMASS AND DIVERSITY

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**Summary**—In experimentally heated plots, each spanning a microclimate and vegetation gradient within a subalpine meadow, heating enhanced both soil mesofaunal biomass and diversity in a cool, wet summer. In a warmer, drier summer, in contrast, heating depressed diversity and biomass in the drier zone of the plots and diversity in the moist zone, but enhanced biomass in the moist zone. Biomass and diversity were positively correlated across plots and, under conditions of moisture stress, both positively correlated with soil organic matter. Data from closed cores indicate that the effects of heating on mesofauna were due to in-plot effects of heating rather than to heating-induced movement of soil organisms. The sensitive response of soil mesofauna to altered microclimate and the dependence of that response on a variety of environmental factors suggest both promise and limitations in using either experimental manipulations or natural correlations between soil microclimate and mesofaunal populations to forecast effects of climate change.

### INTRODUCTION

Soil mesofauna exert strong regulatory control over the surface area and size distribution of soil particles (Kilbertus and Vannier, 1979; Werner and Dindal, 1987; Lee and Foster, 1991), the water holding capacity (WHC) and infiltration rate of soil (Lal, 1987; Anderson, 1988), the lability of organic compounds and the mineralization, immobilization, and availability of N and other nutrients (Elliot, 1970; Crossley, 1977; Petersen and Luxton, 1982; Ineson *et al.*, 1982; Teuben and Verhoef, 1992), the transport of chemical compounds (Anderson, 1988; Huhta *et al.*, 1988), and the composition, abundance, dispersal and activity of bacterial and fungal populations (Crossley, 1977; Hanlon and Anderson, 1979; Anderson and Bignell, 1980; Hanlon, 1981; Hassall *et al.*, 1983). Because these soil characteristics influence soil stability and fertility, and the composition of the plant communities that soil can sustain, environmental influences on soil mesofauna have a potentially large capacity to modify terrestrial ecosystems.

One such environmental influence on mesofaunal populations is soil microclimate, which is projected to be significantly altered under current scenarios of impending global warming (Schneider *et al.*, 1992; Harte *et al.*, 1995). We report here results on mesofaunal response to climate change from a controlled field manipulation designed to elucidate

vegetational and biogeochemical responses of a montane meadow to experimental warming. We focus here on two response variables: mesofaunal biomass and taxonomic diversity. Elsewhere we have described the dominant responses of soil microclimate and vegetation to the experimental warming (Harte and Shaw, 1995; Harte *et al.*, 1995).

Two experimental approaches to studying ecological responses to climate change are possible: analysis of ecosystem responses to manipulated microclimate (Billings *et al.*, 1983; Shaver *et al.*, 1986; Sturges, 1989; Peterjohn *et al.*, 1993; Van Cleve *et al.*, 1990; Harte *et al.*, 1995) and monitoring of ecological trends associated with natural climatic variation in space (Emmanuel *et al.*, 1985; Lashof, 1989) or over time (Overpeck *et al.*, 1991; Woodward, 1992; Webb, 1992). Investigations of effects of soil moisture and temperature on mesofauna have been largely confined to the latter approach—monitoring of mesofaunal responses to natural interannual or spatial microclimate variation (e.g. Reinecke, 1975; Takeda and Ichimura, 1983; Hassall *et al.*, 1983; Hutson, 1987; Sternberger *et al.*, 1990). Intercomparisons of these approaches and analysis of the validity of using natural spatial or temporal variations in soil microclimate to forecast effects of climate change on soil mesofauna is lacking.

We used both approaches in this investigation. We analyzed mesofaunal response to experimental heating and, in addition, we exploited the fact that our control and heated plots each span a microclimate gradient and were observed over a period of

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time in which significant interannual microclimate variation occurred. As reported here, analysis of mesofaunal response to the combination of controlled warming and natural microclimate variation provides considerably more insight into the strengths and weaknesses of each approach than would application of either of the two approaches in isolation.

## MATERIALS AND METHODS

### Site description

Our study site is a cattle-free subalpine meadow at the Rocky Mountain Biological Laboratory (RMBL), Gunnison County, CO, U.S.A. (38°53'N., 107°02'W., 2920 m). Annual precipitation has averaged 75 cm, with over 80% as snow, over the past several decades. During the two years of this study, 1992 and 1993, summer precipitation from June through August was 11 and 5 cm, respectively, while total snowfall the previous winter was 47 and 99 cm (water equivalent) respectively. Snowmelt typically concludes in May (Table 1). Mean daily summer air temperature is about 10°C. The magnitude of summer rainfall has a larger influence over midsummer soil moisture content than does the magnitude of total snowfall the previous winter or the timing of snowmelt (Harte *et al.*, 1995).

### Soil

Soil at the site is a cryoboroll consisting of deep, rocky, non-calcareous glacial till. Below a sparse litter layer, the soil is quite uniform in color and texture down to at least 50 cm. Organic C content averages approximately 4% of dry soil weight at a depth of 5 cm and drops to about 2.5% at 50 cm depth, as determined by weight loss upon combustion at 450°C and the assumption that the C content of the organic fraction was 40%. The soil has an average pH of 6.3, as measured potentiometrically in a 1 : 1 soil-water slurry.

### Plots

The experimental plots are 3 × 10 m, with the long dimension spanning an elevational, microclimatic and vegetational gradient from a dry ridge to a moist swale (Fig. 1). All our results below pertain to either the upper third of each plot, which we refer to as the "dry zone", or the lower third of each plot—the "moist zone". Five heated plots alternate with five controls. We heated the plots with IR radiators that have been on continuously, day and night, since January 1991. The heaters were suspended 2.6 m above the plots to provide a relatively uniform heat flux over the plots. In May of 1993, the output of the heaters was raised from 15 to 22 W m<sup>-2</sup>.

### Climate

Soil microclimate conditions and timing of snowmelt in heated and control plots during the 2 years of this study are summarized in Table 1. As shown there, heating resulted in roughly a 1°C increase in daily- and seasonally-averaged soil temperature and a 10% reduction in soil moisture in the dry zone. In the moist zone, in contrast, the effect of heating on soil temperature was negligible, but significant soil drying did occur. In both zones, the timing of snowmelt was advanced by warming. The daily-averaged soil temperature data obscure one important feature of the microclimate response, however. In particular, a strong diurnal cycle in incremental soil temperature was observed throughout the snowfree season in the dry zone, with the effect of heating (heated – control soil temperature) rising sharply to 4–8°C in early afternoon and dropping to nearly 0°C for much of the rest of the day and overnight. This sharp diurnal cycle in the treatment effect and the differences observed between the dry and moist zone responses to warming were due to interactions among soil moisture, soil temperature, and vegetation, as discussed in detail in Harte *et al.* (1995).

### Vegetation

Vegetation in the meadow consists of a diverse assemblage of forbs, graminoids and shrubs. Within each of our study plots, there are approximately 80 angiosperm plant species, most of which are long-lived perennials. Only two species of shrubs occur (*Artemisia tridentata* in the dry zone and *Pentaphylloides floribunda* in the moist zone of each plot).

### Sampling

Censuses of soil mesofauna were taken from soil cores taken from the dry and moist zones of each plot. The cores were 4.5 cm dia and taken to a depth of 9.5 cm. In 1992, we cored on 10 July in both the dry and moist zones; in 1993, we cored on 10 July in the dry zone, and 14 July in the moist zone. All cores

Table 1. Site characterization\*

	Dry Zone		Moist Zone	
	control plots	heated plots	control plots	heated plots
Soil temperature (°C)				
1992	12.6	13.5	12.1	12.2
1993	13.7	15.1	12.8	12.8
Soil moisture (% by wt)				
1992	28.4	25.7	38.0	36.4
1993	18.8	17.3	29.3	28.6
Date of snowmelt (calendar day)				
1992	118	112	119	113
1993	145	132	150	135

\*Soil temperature and moisture values are averages of measurements every 2 h over three depths (5, 12 and 25 cm), over day and night, and over the period from the end of snowmelt to mid August (110 days in 1992, 75 days in 1993). Statistical analysis of the treatment effects on microclimate and reasons for the much greater response of soil microclimate to heating is discussed in Harte *et al.* (1995). Date of snowmelt is defined to be the date on which the 5-cm soil temperature reaches + 1°C.

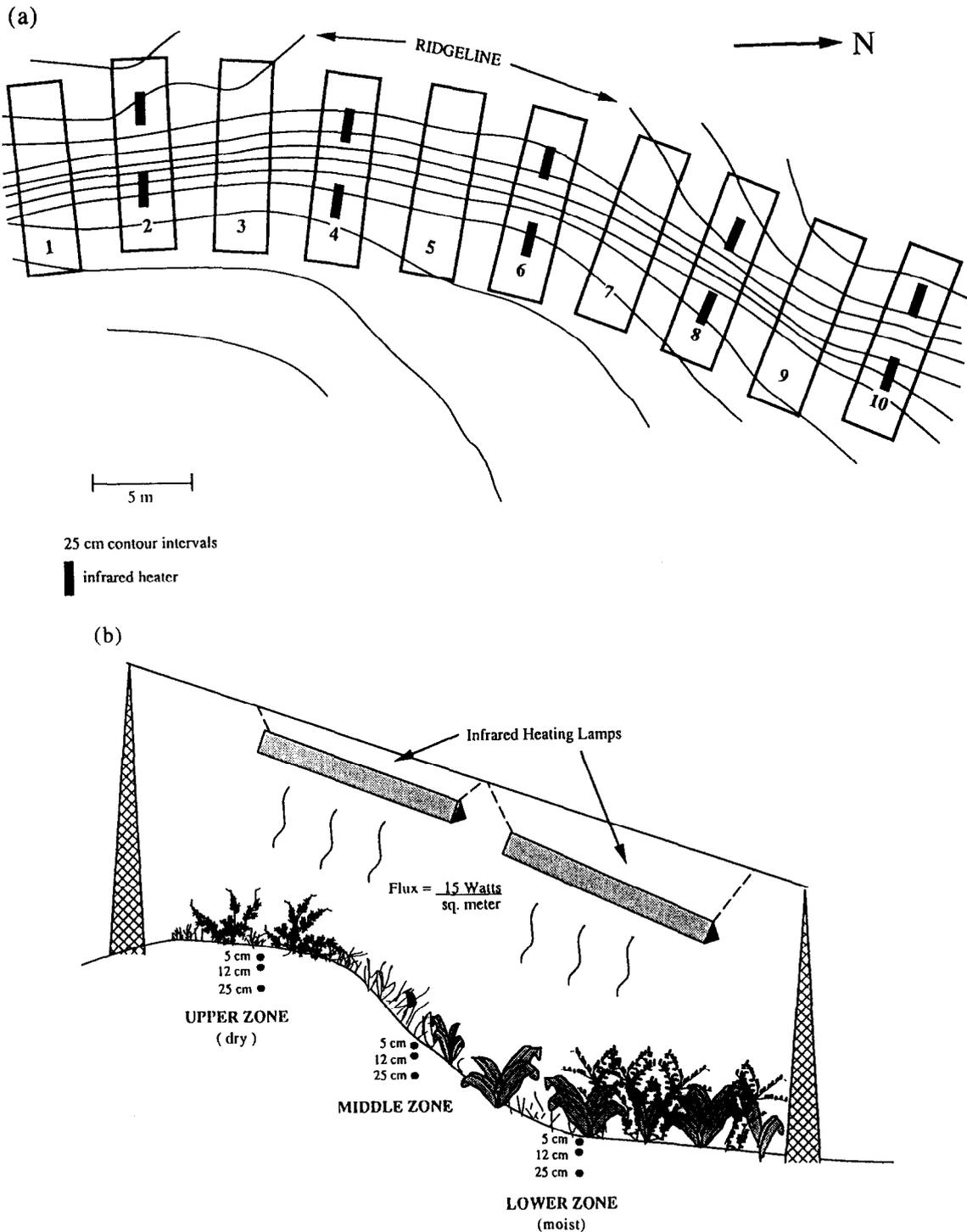


Fig. 1. Site and experimental design. (a) Arrangement of the plots. (b) Typical heated plot profile (not to scale); control plots are similar but lack the heaters.

were taken between 08.00 and 10.00 h. The cored samples included the sparse litter layer, which averaged  $70 \text{ g C m}^{-2}$  (compared with the organic content of the top 10 cm of soil, which averaged  $\sim 1100 \text{ g C m}^{-2}$ ). To obtain representative soil samples from each zone and plot, we took cores from five random locations and combined them prior to

extraction of animals. The rock-free (2 mm) weight of the five pooled soil samples for each plot averaged 220 g.

#### *Closed-core exposures*

In addition to these standard censuses, we also carried out closed-core field exposures to provide

insight into the mechanism by which heating affected mesofaunal biomass. In particular, we were interested in distinguishing between whether heating caused mesofauna to move preferentially in or out of the plots vs whether it affected in-plot growth, birth, and death. To this end, in June 1993, we cored to 10 cm and combined additional soil + litter samples from all 10 plots to obtain a representative pooled sample for each of the two zones. This soil was then apportioned into tubes of 15 cm length and 10 cm dia, one of which was placed in each plot in the zone of origin. The tubes were covered at both ends with three layers of fine nylon mesh to prevent migration of animals as small as the collembola in or out and placed in a vertical position with their tops flush with the soil surface. They remained in the plots from calendar day 171 to 211 (dry zone) and day 175 to 215 (moist zone) and were then removed from the plots for animal extraction.

#### Extraction of animals

From both the standard census cores and the exposed closed-cores, we extracted animals by placing the soil samples in Tullgren funnels (Woolley, 1982) for 96 h. Each funnel contained about 200 g of soil (oven-dried weight determined after extraction) spread over a 2 mm mesh plastic screen of area of 75 cm<sup>2</sup> and was subjected to a heat flux at the top of the funnels of about 500 W m<sup>-2</sup>. To prevent dehydration (which might hinder migration to the collection vial), we loosely covered the funnels with Saran Wrap. In addition, we sprinkled each soil sample with water 48 h after heating began. We placed a 100 ml plastic collection vial containing 20 ml of 70% ethanol under each Tullgren funnel.

#### Measurements

After extraction, we emptied the contents of each collection vial into a 3 cm Petri dish and examined them under a Leitz dissecting scope. We recorded the total number of organisms, the number of different taxa (see below), as well as the number of individuals within each taxa. To estimate our extraction

efficiency, we also examined under the microscope random soil samples that had been in the funnels for 96 h; extraction efficiencies were generally above 90%. To estimate the total mesofaunal biomass or volume, we assumed that each organism was a cylinder and measured the dimensions of representative organisms within each taxonomic category under the microscope. We used both the total number (*N*) of observed taxa and the Shannon-Weaver (*SW*) diversity measure (Pielou, 1966) to express mesofaunal diversity. After extraction of animals, the dry weight of each soil sample was obtained by drying the sample for 24 h at 60°C. We expressed mesofaunal biomass as volume of animals g<sup>-1</sup> (dry soil).

In 1992, we classified all observed animals into seven broad taxonomic categories: ants (Formicidae); centipedes and millipedes (Diplopoda and Chilopoda); springtails (Collembola); beetles (Coleoptera) and bugs (Hemiptera); flies (Diptera); mites (Acarina) and nematodes (Nematoda). In 1993, we made finer taxonomic distinctions (e.g. the Acarina were separated into seven distinct taxa; a total of 37 taxonomic categories were used). For comparison with the 1992 data, our diversity indices for 1993 are based on the seven categories used in 1992. We note that our use of the term mesofauna is more inclusive than that of some authors, who classify some of the above organisms as microfauna (e.g. nematoda) or macrofauna (e.g. coleoptera).

Throughout both years of our study, we monitored soil temperature and moisture in the experimental plots every 2 h using thermocouples and gypsum blocks wired to multiplexers and data loggers (Campbell Scientific Inc., CR10 data loggers). Temperature and moisture probes were located at depths of 5, 12 and 25 cm, in both the dry and moist zones of each plot, within 1 m of the site of core extraction.

#### Statistical treatment

To explore the patterns of dependence of plot-to-plot variation in the dependent variables, mesofaunal biomass and diversity, on possible

Table 2. Mesofaunal biomass, diversity and abundance\*

	Biomass (mm <sup>3</sup> kg <sup>-1</sup> )		SW-diversity		<i>N</i> -diversity		No. of individuals (No. kg <sup>-1</sup> )	
	Control	Heated	Control	Heated	Control	Heated	Control	Heated
1992 Census								
Moist zone	54 (17)	191 (53)	1.13 (0.07)	1.38 (0.01)	3.8 (0.4)	4.8 (0.4)	70 (12)	112 (17)
Dry zone	48 (18)	75 (20)	1.01 (0.14)	1.22 (0.14)	3.8 (0.9)	4.4 (0.4)	180 (36)	65 (14)
1993 Census								
Moist zone	181 (81)	329 (113)	0.67 (0.14)	0.71 (0.13)	2.4 (0.3)	2.8 (0.4)	30 (11)	49 (11)
	1.24 (0.10)	0.93 (0.14)	3.8 (0.7)	3.4 (0.7)				
Dry zone	115 (47)	24 (15)	0.45 (0.20)	0.11 (0.11)	2.0 (0.5)	1.2 (0.2)	57 (32)	9 (2)
	1.27 (0.19)	0.69 (0.19)	4.6 (0.9)	2.2 (0.4)				
1993 Closed cores								
Moist zone	284 (93)	368 (124)	0.70 (0.06)	0.63 (0.02)	2.4 (0.3)	2.2 (0.2)	66 (9)	90 (22)
Dry zone	760 (280)	287 (59)	0.63 (0.06)	0.68 (0.06)	2.4 (0.3)	2.4 (0.3)	205 (72)	88 (22)

\*Biomass is expressed in volumetric units (mm<sup>3</sup> kg<sup>-1</sup> o.d. soil), which can be approximately converted to mg o.d.w. m<sup>-2</sup> by multiplying by 10. Diversity is calculated both as a SW index (Pielou, 1966) and as the number of taxa (*N*). Diversity indices shown in italics for 1993 are based on the full set of 37 taxonomic categories, whereas the other diversity indices are based on 7 categories (see the text). SEs are given in parentheses, with *n* = 5 for all entries.

explanatory variables, we used analysis of covariance, with treatment as a categorical variable and three covariates: soil organic matter, soil temperature and soil moisture. The microclimate variables were taken to be averages of readings at 5 and 12 cm depth over the 20-day period prior to soil core extraction. These analyses were carried out separately for each zone and year because of the dramatic microclimate differences between years and between zones.

## RESULTS

Results of our standard censuses and the closed core experiments are shown in Table 2 and Fig. 2–4, with all data averaged over plots ( $n = 5$ ) within each year–zone–treatment combination.

### Standard census data

Numbers of individuals of the separate taxa per unit of soil volume were within, but at the low end of, the range of abundances typically observed in grassland or meadow habitat (Petersen and Luxton, 1982). Acarina and Collembola were the most abundant organisms, accounting for over 80% of the number of individuals in most zone–year–treatment combinations. In plot–zone combinations in which Formicidae, Coleoptera or Diptera were found, they generally contributed up to 80% of the total sample biomass.

*Comparison of years.* Both of the taxonomic diversity indices (SW and N) and the observed numbers of individuals were greater in 1992 than in 1993 for each of the four zone–treatment combinations ( $P > 0.05$ ,  $t$ -test). In contrast, 1993 biomasses exceeded those for 1992 (except in the heated plots of the dry zone), although these contrasting differences were not significant at  $P > 0.1$ . Acarina and Collembola were a proportionally larger component of total biomass in 1993 than in 1992.

*Comparison of zones.* In both years, biomasses in the moist zone exceeded those in the dry zone, with significant differences ( $P > 0.05$ ,  $t$ -test) only in the heated plots. Similarly, the diversity indices based on seven taxa and the total numbers of individuals for the moist zone exceeded those in the dry zone.

*Comparison of treatments.* In 1992, a relatively wet and cool year (Table 1), heating enhanced both mesofaunal diversity and biomass in both the dry and moist zones. In the relatively dry, hot year of 1993 heating also enhanced biomass and diversity in the moist zone, but it depressed mesofaunal biomass and diversity in the dry zone (Figs 2 and 3). Both measures of biodiversity (SW index and number of observed taxa) show the same effect of heating on diversity [Fig. 2(b) vs Fig. 2(c)]. By a  $t$ -test, the effect of heating on both biomass and diversity was statistically significant at  $P > 0.1$  in the moist zone of 1992 (biomass,  $P = 0.041$ ; SW-diversity,  $P = 0.008$ ; N-diversity,  $P = 0.095$ ) and in the dry

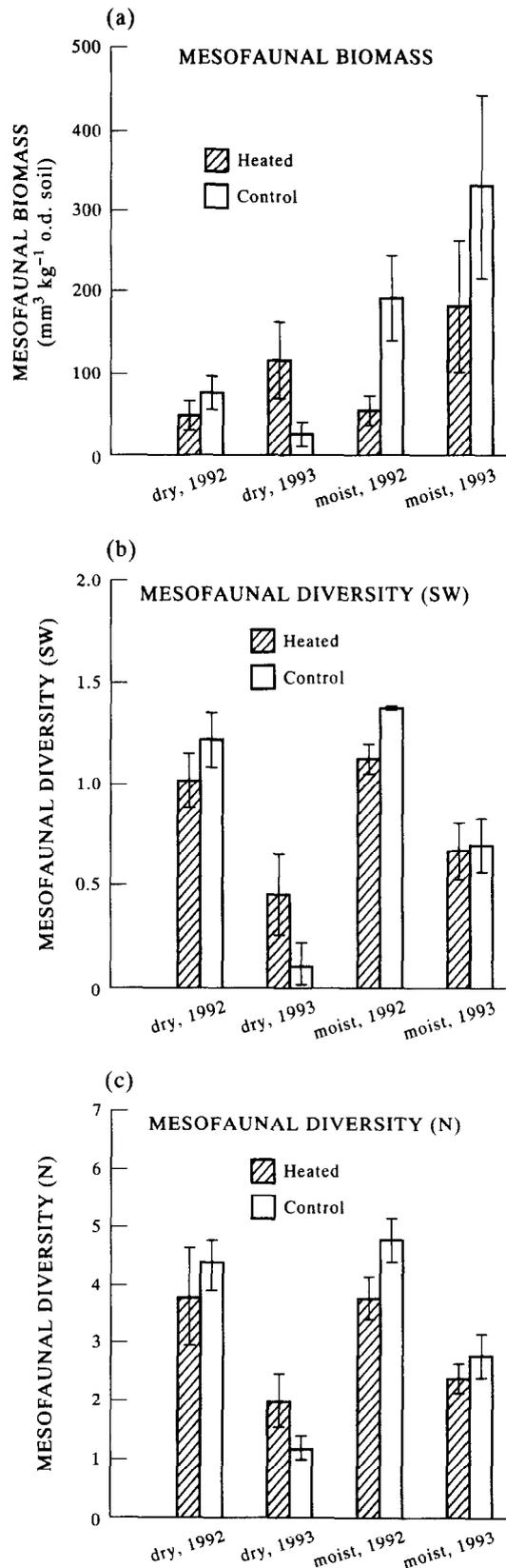


Fig. 2. Results of census data for each of the four zone-year combinations. (a) Mesofaunal biomass. (b) SW-diversity index. (c) Number of taxa. Error bars are SEs ( $n = 5$ ).

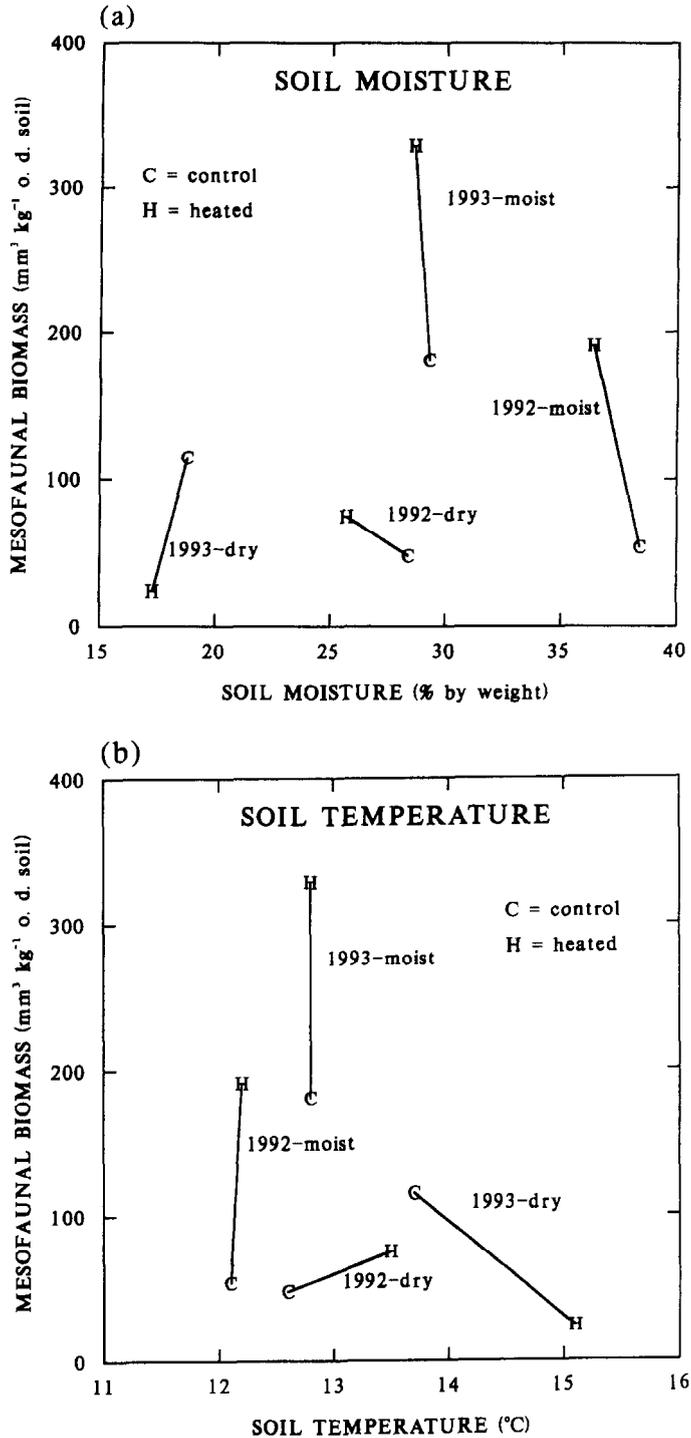


Fig. 3. Effect of experimental heating on mesofaunal biomass, for each zone-year combination, as a function of microclimate. (a) Dependence on moisture. (b) Dependence on temperature.

zone of 1993 (biomass,  $P = 0.098$ ; SW-diversity with 37 taxa,  $P = 0.061$ ;  $N$ -diversity with 37 taxa,  $P = 0.035$ ).

*Explanatory factors for plot-to-plot differences.* In 1992, in the dry zone, no combination of the covariates (soil organic matter, soil temperature and soil moisture) and the categorical variable (treatment)

explained more than 10% of the variance in the biomass data. In the moist zone, treatment, alone, was an explanatory factor ( $p = 0.04$ ) explaining 43% of the variance in the biomass data; none of the covariates was a significant factor. In 1993, in the dry zone, treatment ( $P = 0.033$ ) and organic matter ( $P = 0.001$ ) explained 90% of the variance in the

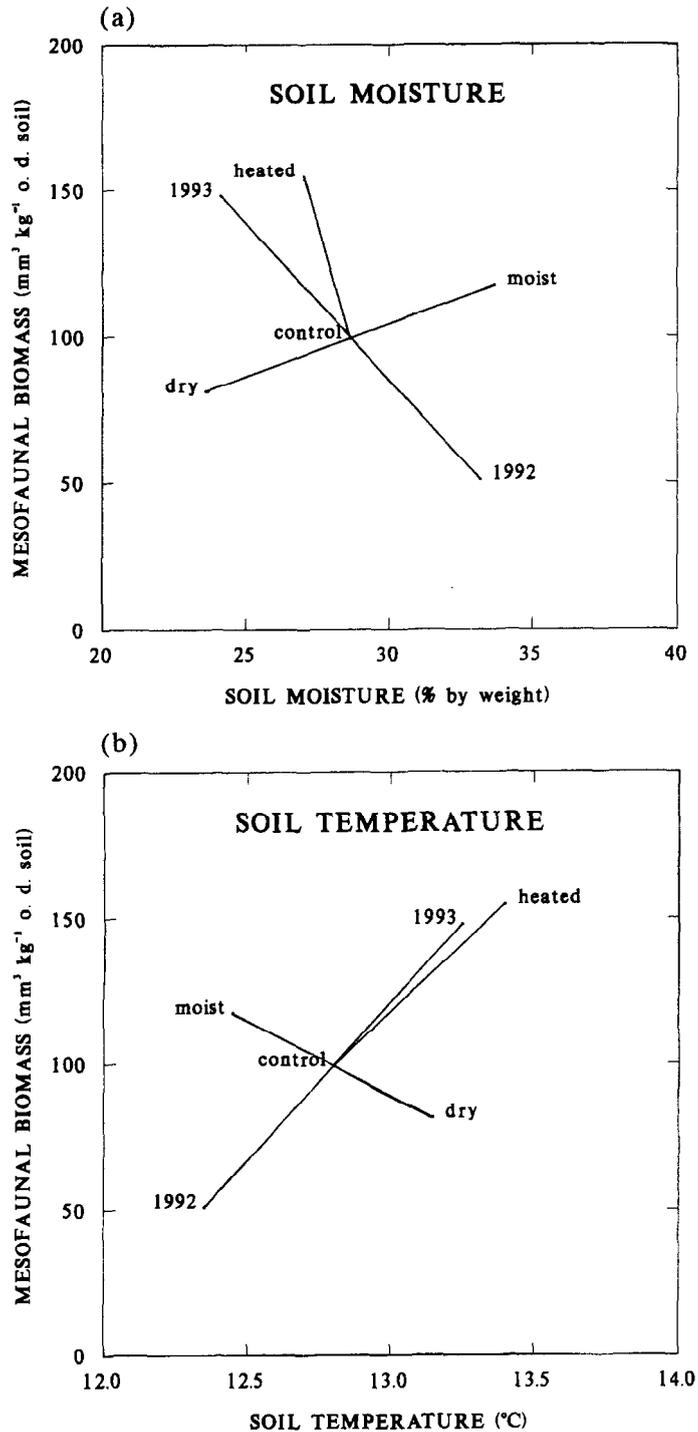


Fig. 4. Effect of changes in microclimate on mesofaunal biomass across three microclimate gradients: treatment (control vs heated); years (1992 vs 1993); zones (dry vs moist). (a) Dependence on moisture. (b) Dependence on temperature. Data for each year are control values averaged over both zones. Data for each zone are control values averaged over both years. Data for each treatment are averaged over both years and zones.

biomass data; in the moist zone, treatment ( $P = 0.074$ ), organic matter ( $P = 0.040$ ) and soil moisture ( $P = 0.090$ ) explained 68% of the variance. In neither year was temperature a significant explanatory factor. 1993 Mesofaunal biomass was

positively correlated with soil organic matter in the dry zone and negatively correlated with organic matter in the moist zone.

Analysis of covariance for the SW- and N-diversity data revealed only one qualitative difference from the

above results for the biomass data: organic matter was not a significant factor affecting response of diversity to warming.

*Relationships among measures of mesofauna.* We also calculated the pairwise correlation coefficients among biomass, SW diversity, and N diversity over all 10 plots in each zone. All three quantities were highly correlated. In the dry zone in 1993, and in both zones in 1992, SW-diversity, N-diversity, and biomass were all positively correlated with one another ( $r > 0.7$ ;  $P > 0.05$  by Bonferroni test). Only the moist-zone data for 1993 exhibited a low ( $r > 0.3$ ) correlation between biomass and either SW- or N-diversity, although the two diversity measures were positively correlated ( $r = 0.80$ ).

Dry-zone diversity measures based on 37 taxa showed the same response to the warming treatment as did those based on the aggregated 7 taxa. In the moist zone, the sign of the treatment effect on diversity depended on the level of aggregation, but for neither level was the treatment effect statistically significant at  $P > 0.1$ .

#### *Closed-core data*

In the moist zone, the closed cores in the heated plots had higher mesofaunal biomass than those in the control plots ( $368 \text{ mm}^3 \text{ kg}^{-1}$  in the heated plots vs  $284 \text{ mm}^3 \text{ kg}^{-1}$  in the controls). A comparison with the 1993 regular census data ( $329 \text{ mm}^3 \text{ kg}^{-1}$  in heated plots vs  $181 \text{ mm}^3 \text{ kg}^{-1}$  in the controls) indicates no significant difference between the two types of data ( $P > 0.1$  by *t*-test). In the dry zone, the effect of heating the closed cores ( $287 \text{ mm}^3 \text{ kg}^{-1}$  in the heated plots vs  $760 \text{ mm}^3 \text{ kg}^{-1}$  in the controls) was opposite to that in the moist zone, but again it was qualitatively similar to that observed in the 1993 standard census ( $24 \text{ mm}^3 \text{ kg}^{-1}$  in the heated plots vs  $115 \text{ mm}^3 \text{ kg}^{-1}$  in the controls). The closed-core dry-zone biomass values were significantly greater, however, than the biomass values from the standard census in both the heated plots ( $P = 0.01$ ) and the control plots ( $P = 0.05$ ).

Mesofaunal diversity in the closed cores exhibited no significant differences between heated and control plots. The moist-zone diversity indices did not differ from those observed in the 1993 standard census ( $P > 0.1$ ). In the dry zone, however, the closed core data from the heated plots indicated significantly higher diversity (both SW and N) than was observed in the standard census ( $P = 0.005$ ), whereas in the control plots the closed-core diversity data and the standard census data were statistically indistinguishable.

In contrast to the results from the standard censuses, pairwise correlations over plots between biomass and either index of diversity from the closed cores were not significant ( $P > 0.3$ ) but the two diversity measures were strongly positively correlated ( $r > 0.8$ ,  $P > 0.02$ ) in each zone.

## DISCUSSION

### *Patterns of response*

The following major qualitative patterns in our data were observed:

From 1992 (a cooler, wetter year) to 1993 (a warmer, drier year), mesofaunal biomass increased (except in the heated plots of the dry zone) and diversity decreased.

Mesofaunal biomass and, to a lesser extent, diversity was greater in the moist zone than in the dry zone.

Artificial soil heating generally increased mesofaunal biomass and diversity, the only exception being in the dry zone in the drier of the 2 years studied.

Only in the dry zone in the drier year was mesofaunal biomass highly correlated with soil organic matter; this correlation was positive.

Mesofaunal biomass and diversity (both SW and N) from the standard censuses were positively correlated across plots in all year-zone combinations.

Closed-core biomass and diversity data were generally statistically indistinguishable from the standard census data (closed-core data for 1993 only), except that both diversity and biomass in the heated plots of the dry zone were enhanced in the closed cores relative to the standard census. In the closed cores, artificial heating led to an increase in biomass in the moist zone and a decrease in the dry zone, just as it did in the standard census.

### *Optimal microclimate conditions*

Soil warming in the dry zone might have resulted in a biomass decline only in the second year of the study because of a cumulative effect of heating over an additional year. More likely, optimal soil microclimate conditions for mesofauna in the dry zone were intermediate between those in 1992 and in 1993. Thus, in the warm, dry year of 1993, heating created less favorable soil microclimate conditions for mesofauna, whereas in 1992, a cool, wet year, heating created more favorable conditions. Looking in more detail, Fig. 3(a) shows biomass declining under soil drying for control-plot moisture content  $\sim 20\%$  gravimetric and increasing for heated-plot moisture content at or greater than  $\sim 25\%$  gravimetric, suggesting a possible soil-moisture optimum for mesofaunal biomass between 20–25% gravimetric in the dry zone. Similarly, Fig. 3(b) suggests a temperature optimum in the dry zone of  $\sim 13.6^\circ\text{C}$ .

Further analysis of our observed patterns of contingent responses to heating, however, points to limitations in the applicability of the concept of "optimum microclimate". In particular, our data suggest that within the observed natural range of interannual and spatial microclimate variation, no unique (non-contingent) optimum set of microclimate condition exists. This is illustrated in Fig. 4, which shows that biomass response to a change in microclimate brought about by either the warming

treatment or by interannual variation is opposite to that in response to a change in microclimate across the zonal gradient. This mismatch between response to temperature or moisture variation across zone and across years or treatment may result from differences in the dominant species of vegetation found in the two zones (Koehler and Born, 1989; Harte *et al.*, 1995).

#### *Role of organic matter*

The correlation between soil organic matter and either mesofaunal biomass or diversity differed between the dry and moist zones, with a significant positive correlation observed only in the dry zone in 1993, the drier of the two study years. This may be due to increased WHC of organic matter in the soil of the dry zone. In particular, soil moisture was positively correlated with soil organic content in the dry zone in both 1992 and 1993 ( $r = 0.756$ ,  $P = 0.012$  and  $r = 0.660$ ,  $P = 0.038$ , respectively), whereas no significant correlation between soil moisture and soil organic matter was observed in the moist zone in either year. It is less likely that the observed dependence of mesofaunal biomass on organic matter reflects a substrate limitation on mesofaunal populations because the most significant positive relationship was observed only under the most moisture-stressed conditions (dry zone, drier year). Under these conditions, soil organic matter appears to buffer soil mesofauna against the stress of additional warming.

#### *Taxonomic measures of response*

The observed positive correlation, within each zone-year combination, between soil mesofaunal biomass and diversity, and between the various measures of diversity, points to the robustness and interchangeability of the different measures of response to warming that were estimated here. Nevertheless, because of experimental evidence that functional differences exist between taxonomically closely-related soil mesofauna (Faber and Verhoef, 1991), a more complete understanding of the ecological significance of mesofaunal response to warming will require future studies that, unlike this one, are designed to provide statistically valid information about responses of selected individual taxa to microclimate change.

#### *Migration vs in-plot responses*

Comparison of the 1993 census data and the closed-core data shows that the relative effect of artificial soil warming on mesofaunal biomass was qualitatively similar for both data types. This indicates that the effects of heating on mesofaunal biomass and diversity are not the result of heating-induced migration in or out of plots but rather due to in-plot effects of heating. Those differences that did show up between the closed-core and standard census data could have arisen because

we initially filled the closed cores with soil samples combined from both the heated and control plots.

#### *Summary*

In summary, four insights have emerged from this study:

The effects of manipulated soil microclimate on mesofaunal biomass and diversity are strongly contingent upon natural interannual climate variation and natural spatial inhomogeneity in soil microclimate conditions. Hence, the sign of the effect of climate change on the soil mesofauna is likely to vary considerably over space and time.

Attempts to forecast how mesofauna will respond to future warming by looking at patterns of response to natural spatial or temporal microclimate variations can yield answers at variance with each other and with results from a climate manipulation. Thus, such forecasting methods may yield misleading results.

The responses to soil warming that we observed in our experimental plots are most likely due to effects of warming on mesofaunal growth, birth, and death, rather than to heating-induced movement of animals in or out of the heated plots.

Soil organic matter buffered the effects of warming under the driest conditions studied, probably because of the enhanced water holding capacity of organically rich soils. Hence, long-term effects of climate warming on soil mesofaunal biomass and diversity could be mediated by effects of warming on plant litter production and on rates of soil decomposition. We conclude that our experimental climate manipulation of a terrestrial ecosystem has provided insight into the patterns and mechanisms of the responses of mesofaunal biomass and diversity to changes in soil microclimate, but the contingent nature of these responses implies the need for great caution in extrapolating information about their magnitude, and even their sign, over space and time.

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