

# Changes in trophic abundance of soil arthropods along a grass–shrub–forest gradient

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**Abstract:** Ecological theory suggests that along productivity gradients, abundances of organisms within trophic levels will increase in a stepwise pattern from producers to consumers. To test this theory I investigated changes in abundance of soil arthropods at three trophic levels: microphytophages, represented by Collembola, predacious mites (Acari) that feed on Collembola, and three groups of macroarthropods (spiders, ants, and centipedes) that were observed to feed on mites. Changes in abundance were monitored along a gradient in vegetation structure from grass to shrub to forest in the Canadian prairies. I controlled for temporal variation in abundance among years and surveys within a year. As predicted, (i) numbers of Collembola did not change with increases in productivity; (ii) mite numbers were greatest in the shrublands; and (iii) numbers of macroarthropod predators increased from grassland to shrubland, and there was a nonsignificant increase in numbers of spiders and centipedes in forest habitat. Contrary to predictions, macroarthropod numbers were not significantly greater in forest habitat, and ant numbers actually declined. Possible explanations for the lack of increase in macroarthropod predator abundance in the forest habitat with the greatest productivity include decreased ground-level humidity and greater abundance of macroarthropod predators and parasites in forest environments.

**Résumé :** La théorie écologique veut que, le long de gradients de productivité, l'abondance des organismes des différents niveaux trophiques augmente en escalier, des producteurs aux consommateurs. Pour éprouver cette hypothèse, j'ai suivi les changements dans l'abondance des arthropodes du sol à trois niveaux trophiques : les microphytophages, représentés par les collemboles, les acariens prédateurs (Acari) qui se nourrissent de collemboles et trois groupes de macroarthropodes (araignées, fourmis, centipèdes) qui consomment des acariens. Les variations de l'abondance ont été enregistrées le long d'un gradient dans la structure de la végétation, des herbes aux buissons aux forêts dans les Prairies canadiennes. J'ai tenu compte de la variation temporelle de l'abondance d'une année à l'autre et d'un inventaire à un autre au cours d'une même année. Tel que prévu, (i) le nombre de collemboles n'a pas varié malgré l'augmentation de la productivité; (ii) le nombre d'acariens était maximal dans les zones buissonneuses; (iii) le nombre de macroarthropodes prédateurs était plus élevé dans la zone buissonneuse que dans la zone herbeuse et le nombre d'araignées et de centipèdes était plus élevé, mais pas de façon significative, dans la forêt. Contrairement aux prédictions, le nombre de macroarthropodes n'était pas significativement plus élevé en forêt et le nombre de fourmis était même inférieur. Parmi les raisons qui peuvent expliquer pourquoi l'abondance des macroarthropodes prédateurs n'augmente pas en milieu forestier où la productivité est maximale, il faut penser à la diminution de l'humidité au niveau du sol et à l'augmentation des macroarthropodes prédateurs et parasites en milieu forestier.

[Traduit par la Rédaction]

## Introduction

Over time and space, habitats change through predictable patterns (Clements 1916; Whittaker 1970; Connell and Slayter 1977). Increases in plant-species diversity or structural diversity are often correlated with an increase in species richness of animals (Southwood et al. 1979; Madden and Fox 1997) and energy availability (Hutchinson 1959; Connell and Orias 1964; Paine 1966). The gradient hypothesis for biological communities (Whittaker 1970) predicts that ecosystem gradients will vary in abundance of successive trophic levels (Hairston et al. 1960; Oksanen et al. 1981; Fretwell 1987). The trophic model (Power 1992; Oksanen and Oksanen 2000)

argues that accumulation of trophic levels along a productivity gradient results in an increase and then a plateau in successive trophic levels. This produces "stairsteps" of biomass and density along a productivity gradient (e.g., Kazinger and Morin 1998; Kaspari et al. 2000). Also, the general change in biological communities along the environmental gradient occurs gradually, from simple to complex (Naruhara et al. 1994). In contrast, both in donor-controlled chains and in situations with mixed bottom-up and top-down effects, the equilibrium abundances of all levels are expected to be positively correlated with the input at the bottom of the chain. However, few studies have investigated changes in taxon density in a detritus-based food chain along a terrestrial productivity gradient (Siemann et al. 1998; Kaspari et al. 2000).

When fire suppression is practiced, mesic prairie grassland communities change over long periods of time, litter accumulates, woody species invade, moisture level and nutrient availability increase, and eventually vegetation is distributed along an environmental gradient from grassland to shrubland to forestland (Bragg and Hulbert 1976; Petranka and McPherson

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1979; Delting 1998). However, invasion of grasslands by woody species is patchy (Knight et al. 1994), the patches changing from grassland to shrubland to woody species (Archer 1989). As a result of agricultural practices and natural fire cycles, prairie trembling aspen (*Populus tremuloides* Michx.) stands include small patches of vegetation in various stages (Knapp et al. 1998). For example, successional aging results in an increase in plant height and cover, a decrease in the proportion of grass, an increase in litter, and a more buffered microclimate (Majer 1990). Thus, a grass–shrub–forest gradient is created from a forested core with a natural grassland exterior (e.g., McDonnell and Pickett 1990). The grass–shrub–forest gradient relates to increasing litter fall, increasing complexity (Natuhara et al. 1994), and increasing net primary productivity (Wright et al. 1993; Hansen et al. 2000).

Here I test for differences in abundance of soil arthropods at three trophic levels with changes in vegetation structure in a prairie ecosystem. The experimental design used for studying trophic-level effects consisted of boxes distributed on the forest floor within a natural gradient from grassland to forest. The weight of the boxes depressed the litter layer like a rock on the forest floor. Differences in microclimate under the box included an increase in humidity and a decrease in temperature, offering a home to a diverse soil fauna community (Ferguson 2000). Boxes were overturned and numbers of individuals from taxonomic units were recorded during weekly surveys from May to September in 1997, 1998, and 1999. First, I objectively delineate the structural grades of habitat by grouping sites according to microclimatic and vegetation characteristics. Second, I control for temporal differences in soil arthropod abundance due to year effect and seasonal changes. Last, I test whether numbers of soil arthropods within the three trophic groups differed in abundance with vegetation type. The three trophic levels are Collembola that feed on fungi, mites (Acari) that feed on Collembola, and macroarthropod groups that were observed to feed on mites. Specifically, I test the following predictions: (i) there would be no change in numbers of Collembola along the productivity gradient; (ii) mite numbers would increase from grass to shrub stages; and (iii) numbers of macroarthropod predators would increase with each successive increase in productivity from grass to shrub to forest.

## Methods

### Description of the study area

The study area consisted of a 0.13-km<sup>2</sup> stand of undisturbed trembling aspen located within 1.5 km of the city of Saskatoon in the prairie region of south-central Saskatchewan, Canada (52°10'N, 106°41'W). Under suitable conditions, grassland prairies can succeed into shrub habitat that can succeed into small patches of forest (Collins 2000). The study site includes an overstorey canopy dominated by >40-year-old trembling aspen and an understorey of serviceberry (*Amelanchier* sp.). The contiguous vegetation patches had a variable 3- to 7-cm organic soil horizon (Ferguson 2000). Precipitation on dry-climate prairies is low and highly variable both within and between years, resulting in a moisture-limited ecosystem (Sala and Lauenroth 1982). The monthly mean daily temperature (1961–1990 normals) varied from 3°C in April to 18.6°C in July (annual mean 2.0°C) and precipitation varied from 19.7 mm in April to 63.4 mm in June (annual mean 28.9 mm) (Environment

Canada 2000). There was no evidence or known history of heavy grazing or other agricultural use of the site.

### Sampling

I randomly placed 24 groups of 5 contiguous boxes (120 boxes in total) within the grass–shrub–forest landscape. Each box consisted of two 2-L milk cartons fitted together to create a 21 × 9.5 × 9.5 cm box half-filled with sand and weighing about 2 kg. The boxes depressed the soil, on average, 1.3 cm (Ferguson 2000). I included time (week and year) as covariate in subsequent analyses to account for a possible colonization artefact due to the new artificial habitats.

To view the arthropod community I overturned individual boxes without disturbing the leaf litter and recorded numbers of all macroarthropods and microarthropods observed directly under them (i.e., on top of the litter). The sampling unit was each group of 5 boxes in a group and total numbers were summed. Twenty weekly surveys were conducted from 17 May to 4 October 1997, 25 from 4 April to 5 September 1998, and 20 from 17 April to 18 September 1999. Surveys were conducted between the hours of 11:00 and 17:00. The survey numbers do not reflect absolute abundance but rather are a relative measure of abundance of arthropods residing between the box and the leaf litter. It is likely that some small arthropods were overlooked; however, the bias should not affect the estimates of relative abundance by habitat type. The locations of all 5-box groups were recorded using distance measurements (in metres) and later digitized on GIS (SPANS™ GIS software, Intera Tydac Technologies, Inc., 1994) to calculate *x y* coordinates that were used to group sites into vegetation patches.

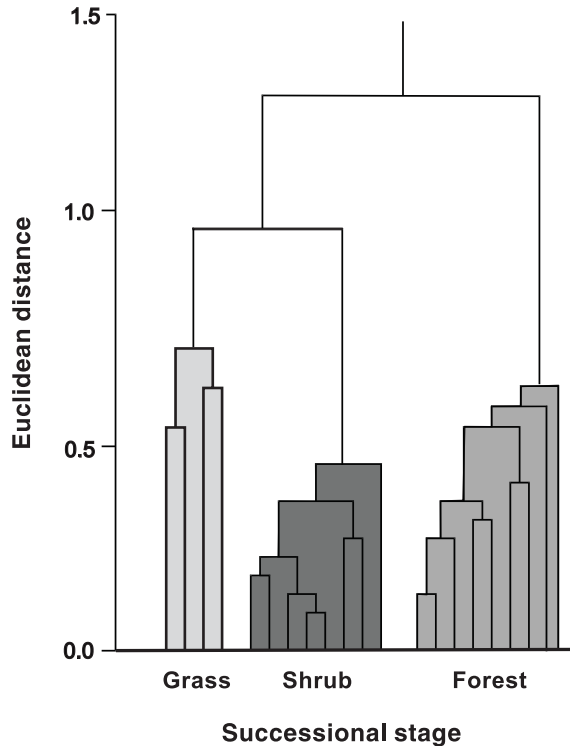
Arthropods observed under boxes were grouped into three trophic groups. All Collembola (springtails) were placed in one trophic group, as most species consume fungi (Hopkin 1997). Predatory mites (Acari: Gamasides; Krogh 1995) were placed in one trophic group, as most are nonspecific predators that commonly feed on Collembola (Hagvar 1995; Hamers and Krogh 1997; Rugusa and Tsolakis 2000). All macroarthropods (arthropods >1 mm and <5 cm long) were counted, but only data for spiders (Araneida), ants (Formicoidae), and centipedes (Chilopoda) are considered here. Seventeen occurrences of predation on mites were observed, including 7 by spiders and 4 by centipedes, and twice ants were observed carrying mites. Based on these observations I regard these three groups as major predators of mites. Other macroarthropod groups included Diplura, Diptera (flies; adults and larvae), phytophagous Acari (Oribatida), Hemiptera (bugs), Homoptera, Pseudoscorpionida, Lepidoptera (moths and butterflies; larvae), Anoplura, Gastropoda, Isopoda, Coleoptera (beetles; adults and larvae), Thysanoptera (thrips), and Psocoptera (bark lice).

I surveyed vegetation using point sampling positioned at the centre of each 5-box group. Percent cover of overstorey (>3 m), understorey (1–3 m), and ground vegetation (<1 m) was visually estimated to the nearest 10%. A 2 × 2 m plot at the northeast side of the 5-box group was used to visually estimate percent cover of grasses, forbs, and litter to the nearest 5%. As well, the trees (>3 m tall) and shrub stems (>1 cm diameter at breast height) within a 2-m radius of the box groups were counted.

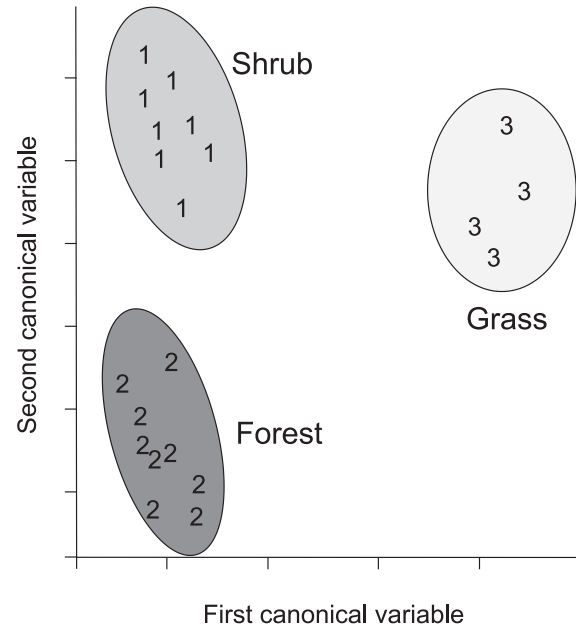
I measured relative humidity for each site (hereafter referred to as site-specific humidity) using an electric probe during four surveys in 1998. Two surveys were conducted following a recent rain (>1 cm during the previous 2 days) and two surveys during a dry period (no rain during the previous 4 days). The mean estimate from each of two surveys (wet and dry) was used in the following analyses.

Weather parameters for Saskatoon were measured daily at the Kernen Prairie weather station by the Agriculture Department, University of Saskatchewan. I used average soil temperature at 5 cm depth (°C), average relative humidity (dewpoint °C; hereafter

**Fig. 1.** Groupings of 21 sampled sites using cluster analysis of vegetation characteristics. Four sites grouped together as grass habitat, 8 sites as shrub habitat, and 9 sites as forest habitat.



**Fig. 2.** Discriminant analysis of 21 sampled sites according to vegetation characteristics. Results confirmed groupings into grass, shrub, and forest habitats from cluster analysis (see Fig. 1).



referred to as weekly humidity) at ground level, and total precipitation (mm) using daily values between surveys.

**Statistical analyses**

I used cluster analysis of vegetation characteristics measured at each 5-box group to delineate vegetation groups. Cluster analysis determined the groupings of box sites according to the following characteristics, deemed to be important in delineating vegetation type: percent cover of overstorey, understorey, and ground vegetation; percent cover of grass, forbs, and bare ground; number of trees and shrubs; and site-specific humidity. Sites were classified into vegetation groups by means of the average-linkage clustering method (Romesburg 1984). The similarity index was Euclidean distance. All variables were standardized to between 0 and 1. Canonical discriminant analysis was used for secondary validation of the classification of sites.

I tested for significant effects of year, week, and vegetation type on abundances of Collembola, mites, and macroarthropods by means of repeated-measures multiple analysis of variance (MANOVA) using Wilks'  $\lambda$  test statistic. Sample units were the 21 plots (5-box groups). The independent variables in the model were 3 years (1997, 1998, 1999), 20–25 weekly surveys, and three classes of vegetation complexity (grass, shrub, and forest). The repeated measure was week of survey. Year was a random variable. The dependent variables ( $n = 5$ ) were hypothesized to be related (trophic inferences) and included abundance of Collembola, mites, and macroarthropods. All dependent variables were square root transformed plot averages. I added 0.5 to all dependent values to allow transformation of zero values (Sokal and Rohlf 1981, pp. 421–423). I report untransformed means ( $\pm 1$  standard error) of these variables in the Results section. All analyses were conducted with SAS (SAS Institute Inc. 1990).

**Table 1.** Vegetation and climatic characteristics of the 21 sampled plots.

| Vegetation characteristic | Vegetation stage |     |       |     |        |     |
|---------------------------|------------------|-----|-------|-----|--------|-----|
|                           | Grass            |     | Shrub |     | Forest |     |
|                           | Mean             | SE  | Mean  | SE  | Mean   | SE  |
| % forb cover              | 19.9             | 1.4 | 26.5  | 2.8 | 17.8   | 1.7 |
| % grass cover             | 75.0             | 4.1 | 22.7  | 3.3 | 7.1    | 1.3 |
| % bare ground             | 16.3             | 3.8 | 59.6  | 5.1 | 91.0   | 3.2 |
| No. of shrubs             | 9.8              | 2.2 | 13.8  | 1.3 | 14.0   | 1.0 |
| No. of trees              | 0.3              | 0.1 | 2.9   | 0.4 | 2.1    | 0.4 |
| % humidity <sup>a</sup>   |                  |     |       |     |        |     |
| Wet                       | 85.1             | 1.6 | 76.6  | 1.7 | 61.6   | 1.4 |
| Dry                       | 60.2             | 1.7 | 71.4  | 1.7 | 53.2   | 1.1 |
| Overstorey                | 29.6             | 5.1 | 47.9  | 2.0 | 100.0  | 4.6 |
| Understorey               | 30.4             | 2.6 | 59.1  | 4.3 | 61.2   | 4.1 |
| Ground vegetation         | 100.0            | 5.3 | 90.1  | 3.9 | 24.6   | 4.3 |

<sup>a</sup>Site-specific measure of relative humidity (dewpoint °C).

**Results**

**Vegetation groups**

Box sites grouped into three stages of structural type according to cluster analysis (Fig. 1). Of the 24 box sites, 3 clustered as outliers and were not used in the following analyses.

Confirmation of the groupings was obtained using discriminant analysis (Fig. 2) with Wilks'  $\lambda$  indicating significant differences among the three clusters ( $F_{[3,48]} = 5.99$ ,  $P < 0.001$ ). The first discriminant function (linear combination of variables) explained 77% of the variation among sites and was positively correlated with percent grass cover ( $r =$

**Table 2.** Results of a repeated-measures MANOVA to determine the effects of vegetation type and time on abundance of soil arthropods.

| Source of variation | df | Collembola |          | Mites    |          | Spiders  |          | Ants     |          | Centipedes |          |
|---------------------|----|------------|----------|----------|----------|----------|----------|----------|----------|------------|----------|
|                     |    | <i>F</i>   | <i>P</i> | <i>F</i> | <i>P</i> | <i>F</i> | <i>P</i> | <i>F</i> | <i>P</i> | <i>F</i>   | <i>P</i> |
| Year                | 2  | 9.77       | 0.0004   | 29.16    | 0.0001   | 5.10     | 0.01     | 6.74     | 0.003    | 2.81       | 0.07     |
| Week                | 21 | 1.93       | 0.045    | 6.73     | 0.0001   | 1.93     | 0.045    | 0.47     | 0.96     | 1.57       | 0.12     |
| Vegetation stage    | 2  | 1.48       | 0.24     | 7.45     | 0.002    | 3.45     | 0.04     | 4.04     | 0.03     | 6.18       | 0.005    |
| Model               | 25 | 2.79       | 0.0003   | 6.46     | 0.0001   | 2.11     | 0.02     | 1.48     | 0.14     | 2.20       | 0.02     |

Note: Time (weekly surveys) was the repeated measure.

**Table 3.** Analysis of variance of differences among years in maximum relative humidity (weekly means of daily values), precipitation (weekly total), and temperature (mean).

| Year | <i>n</i> | Weekly humidity |      | Precipitation |      | Temperature |      | <i>F</i> | <i>P</i> |
|------|----------|-----------------|------|---------------|------|-------------|------|----------|----------|
|      |          | Mean            | SE   | Mean          | SE   | Mean        | SE   |          |          |
| 1997 | 20       | 77.8a           | 0.98 | 1.25a         | 0.36 | 17.6a       | 0.96 | 53.2     | 0.0001   |
| 1998 | 25       | 73.5a           | 1.57 | 1.22a         | 0.43 | 16.4a       | 1.25 | 0.31     | 0.74     |
| 1999 | 20       | 92.5b           | 1.41 | 1.62a         | 0.37 | 14.7a       | 1.15 | 1.51     | 0.23     |

Note: Means in a column followed by the same letter did not differ using Tukey's multiple-comparison test ( $\alpha = 0.05$ ).

0.87) and site-specific humidity ( $r = 0.92$ ) and negatively correlated with percent bare ground ( $r = -0.73$ ). The second discriminant function explained 16% of the variation and was correlated with overstorey ( $r = 0.83$ ) and forb cover ( $r = 0.84$ ).

The grass grouping was composed mostly of grass cover (75%) with few shrubs and trees (Table 1). The forest grouping was characterized by 100% overstorey and mostly bare ground (91%). The shrub grouping was intermediate in overstorey, grass, and bare ground but had the most forbs (27%) and highest site-specific humidity during dry periods. The grass grouping recorded the highest site-specific humidity during wet periods. During wet periods, percent grass cover was positively correlated with site-specific humidity ( $r = 0.48$ ,  $P = 0.02$ ) and the number of trees was negatively correlated with site-specific humidity ( $r = -0.49$ ,  $P = 0.02$ ). During dry periods, percent forb cover was positively correlated with site-specific humidity ( $r = 0.58$ ,  $P = 0.001$ ) and percent bare ground was negatively correlated with site-specific humidity ( $r = 0.41$ ,  $P = 0.03$ ).

### Temporal effects

Repeated-measures MANOVA indicated differences among years and weeks of surveys (Table 2). Weekly humidity was significantly higher in 1999, whereas temperature and precipitation did not vary among years (Table 3). Annual differences in Collembola and mite numbers matched similar changes in weekly humidity, with the highest measurements recorded in 1999 (Table 3). In contrast, centipede numbers did not increase with greater humidity in 1999, and spider and ant numbers declined (Fig. 3).

Of the three climate measures, weekly humidity had the greatest association with abundance among the trophic groups (Table 4). Changes in abundance of Collembola and mites were positively correlated with weekly humidity. Spider and ant abundance was negatively correlated with weekly humidity. Mite, spider, and ant numbers were positively correlated with temperature.

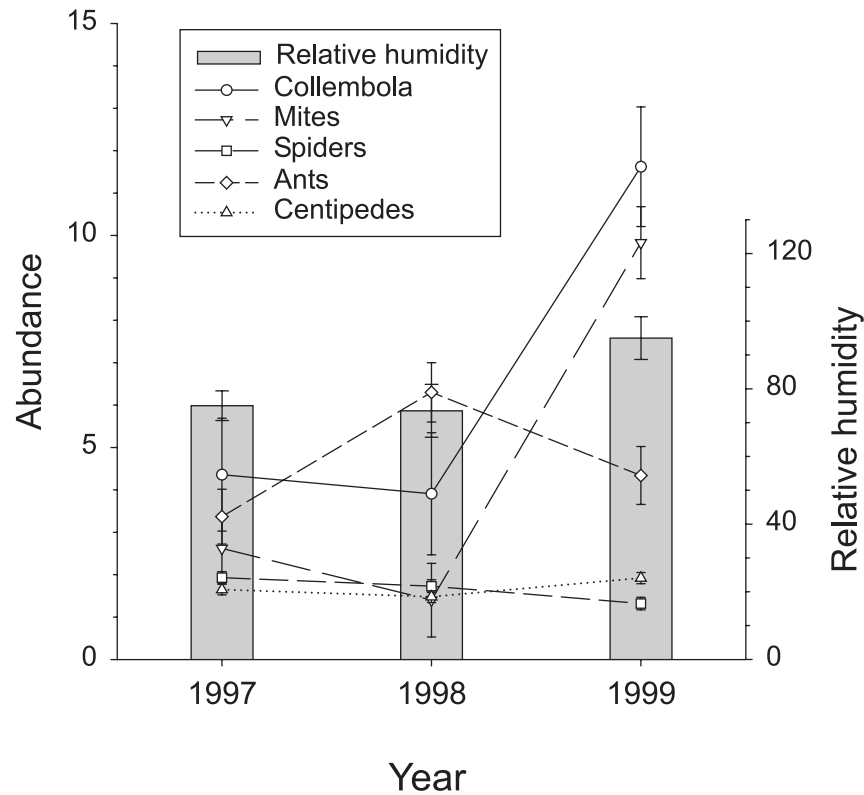
### Vegetation effects

Abundances varied with vegetation type and trophic level (temporal effects were controlled for using repeated-measures MANOVA; Table 5). Collembola numbers did not vary with vegetation ( $F_{[2,90]} = 1.48$ ,  $P = 0.24$ ). Mite numbers were lowest in grass habitat, increased in shrub habitat, and declined slightly in forested habitat ( $F_{[2,90]} = 7.45$ ,  $P = 0.002$ ). Abundances of all three macroarthropods were lowest in grass habitat and increased in shrub habitat ( $F_{[2,90]} > 3.45$ ,  $P < 0.04$ ). Spiders and centipedes were most abundant in forest habitat, although the increase was not significant. Ant numbers declined in forest habitat (Table 5).

### Discussion

This study revealed temporal and trophic differences in soil arthropod numbers between grass, shrub, and forest areas. Changes in composition and structure of vegetation may have affected the abundance at each trophic level. Increasing plant-species diversity and structural complexity can increase productivity (Tilman et al. 1996; Hooper and Vitousek 1997), although productivity gradients are strongly influenced by scale (Kaspari et al. 2000). Hence, the results of this study add to those of other correlative studies showing that the architectural or structural diversity of plants, which is likely correlated with both plant-species diversity and productivity, may be an important determinant of arthropod diversity and abundance at different trophic levels (Lawton 1983). It could be that trophic interactions do not play a key role in determining population densities in soil systems (Pimm 1982; Begon et al. 1996). Neither predator nor detritivore abundances were found to be strictly top-down-controlled, since both increased along a gradient of vegetative productivity. Whatever the actual length of the food chain, these results argue for at least some degree of bottom-up control of soil macroinvertebrate abundances. In this study, some patterns emerged when trophic interactions were considered, although the results are limited to a narrow variation and the small spatial scale of a 10-ha aspen stand.

**Fig. 3.** Changes in weekly humidity and abundance (square-root transformed) of three trophic groups of soil arthropods from 1997 to 1999. Abundance and weekly humidity in 1999 differed from those in 1997 and 1998. Error bars indicate  $\pm 1$  standard error.



The exploitation model (Oksanen and Oksanen 2000) argues that the accumulation of trophic levels along a productivity gradient results in an increase and then a plateau of successive trophic levels, with the following predictions for a soil-based system: (i) there will be no change in numbers of Collembola along the productivity gradient; (ii) mite numbers will increase from grass to shrub stages; and (iii) numbers of macroarthropod predators will increase with each successive increase in productivity from grass to shrub to forest. The results from this study generally support the prediction that the abundance of soil arthropod trophic groups will increase with productivity. Predictions of trophic-level abundance were corroborated for grass and shrub habitat, but the results for forest habitat were equivocal. Contrary to our predictions, abundance of the third trophic level did not increase significantly (spiders and centipedes) or declined (ants) in forest habitat relative to shrub habitat. Two possible explanations for the decrease in macroarthropod abundance in forest habitat include a decrease in humidity in the ground-level microclimate and an increase in macroarthropod predators.

First, abiotic factors such as pH, disturbance, and moisture level strongly influence the species composition and abundance of soil animal communities (Schaefer 1990; Andersen 1995; Schaefer 1995) and thus may explain the decreased abundance in forest habitat. Perhaps changes in the structure and composition of vegetation caused changes in the ground-level microclimate. Hence, environmental changes associated with vegetation type may have accounted for the greater numbers of soil arthropods in shrub habitat

**Table 4.** Correlations between abundances of Collembola, mites, and macroarthropods with relative humidity (weekly mean of daily values), precipitation (weekly total), and temperature (mean).

| Trophic group | Weekly humidity |          | Precipitation |          | Temperature |          |
|---------------|-----------------|----------|---------------|----------|-------------|----------|
|               | <i>r</i>        | <i>P</i> | <i>r</i>      | <i>P</i> | <i>r</i>    | <i>P</i> |
| Collembola    | 0.30            | 0.04     | 0.23          | 0.11     | -0.24       | 0.10     |
| Mites         | 0.29            | 0.04     | 0.26          | 0.07     | 0.40        | 0.004    |
| Spiders       | -0.29           | 0.03     | -0.26         | 0.06     | 0.35        | 0.01     |
| Ants          | -0.30           | 0.03     | -0.03         | 0.83     | 0.48        | 0.0003   |
| Centipedes    | 0.17            | 0.25     | 0.18          | 0.22     | -0.11       | 0.44     |

**Note:** The sampling unit is the total number of individual arthropods recorded during weekly surveys over 3 years ( $n = 65$ ).

than in grass and forest. Paquin and Coderre (1997) observed decreased abundance and diversity of macroarthropods with forest aging in the Canadian boreal forest and argued that these changes occur because of a decrease in pH, the complexity of the soil structure, and changes in the nature of dead plant matter. Soil moisture and rainfall are generally the strongest correlates of soil-surface arthropod abundance, particularly in grassland areas (Reddy and Venkataiah 1990). For grass habitat, the lack of understory vegetation results in less sheltering of the ground, thereby increasing insolation of the soil surface (Madden and Fox 1997). This is consistent with the finding of a lower litter moisture level in grass habitat following dry periods (Natuhara et al. 1994). Less vegetation and compaction of the litter layer in grass habitat may result in simpler structure and reduce the diver-

**Table 5.** Repeated-measures MANOVA of differences among vegetation types in abundances of Collembola, mites, and macroarthropods (spiders, ants, centipedes).

| Vegetation stage | <i>n</i> | Collembola        |      | Mites             |      | Spiders           |       | Ants               |      | Centipedes        |       |
|------------------|----------|-------------------|------|-------------------|------|-------------------|-------|--------------------|------|-------------------|-------|
|                  |          | Ls mean           | SE   | Ls mean           | SE   | Ls mean           | SE    | Ls mean            | SE   | Ls mean           | SE    |
| Grass            | 4        | 4.64 <sub>a</sub> | 2.15 | 1.79 <sub>a</sub> | 1.29 | 1.25 <sub>a</sub> | 0.23  | 4.25 <sub>ab</sub> | 1.04 | 1.29 <sub>a</sub> | 0.20  |
| Shrub            | 8        | 8.35 <sub>a</sub> | 0.88 | 6.93 <sub>b</sub> | 0.53 | 1.81 <sub>b</sub> | 0.094 | 5.80 <sub>a</sub>  | 0.43 | 1.88 <sub>b</sub> | 0.083 |
| Forest           | 9        | 6.90 <sub>a</sub> | 1.20 | 5.12 <sub>c</sub> | 0.72 | 1.91 <sub>b</sub> | 0.13  | 3.96 <sub>b</sub>  | 0.58 | 1.97 <sub>b</sub> | 0.11  |

**Note:** Means in a column followed by the same letter do not differ using Tukey's multiple-comparison test ( $\alpha = 0.05$ ). Ls mean, least-squares mean.

sity of the soil arthropod community (e.g., Bromham et al. 1999). Also, forest habitat had the greatest forb cover but relative humidity was lower, which may explain the smaller number of soil-surface arthropods. Lower humidity in forest habitat may result in greater numbers of microbial detritivores processing dead plant material, which would lead to a decrease in numbers of microarthropod detritivores (Berg and Wessén 1984; De Ruiter et al. 1994; Zheng et al. 1997; Polis 1999). Alternatively, lower humidity in forests may cause microarthropods to move deeper within the soil litter, resulting in a reduced estimate of abundance. The latter explanation would indicate a potential bias in the survey methodology if humidity was greater in grass and shrub than in forest habitat during dry periods, contrary to this study's findings (Table 1).

A second explanation for the decreased micro- and macroarthropod abundance associated with forest habitat relative to shrub habitat is that greater resources may be available in forest habitat, owing to greater structural heterogeneity and productivity. In shrub areas, representing intermediate vegetation complexity, there may have been an increase in numbers of micro- and macro-arthropods compared with the low-productivity grassland sites (e.g., Fraser and Grime 1997). In forest habitat, habitat with increased complexity may support greater densities of macroarthropod predators and parasites in forested areas, owing to changes in understorey vegetation and an increase in leaf litter. Hence, in forested areas, predator numbers increased substantially at high productivity, causing the abundance of micro- and macro-arthropods to level off. Comparable results were reported for succession in boreal forests, where a reduction in the proportion of decomposers was accompanied by an increase in numbers of macroarthropod predators (Paquin and Coderre 1997).

Although I did not assess their abundances, various vertebrate species that prey on invertebrate predators were recorded on the study site (personal observation), including blackbirds, shrews, voles, foxes, owls, and amphibians. Not all of these animals are specialized predators on soil invertebrates; they also prey on detritivorous invertebrates, on invertebrates belonging to the grazer food chain, on plant material, or even on one another. If vertebrate predation pressure is strong, and if the abundance of these predators increases with vegetation complexity, then they have to be taken into account as an additional trophic level (Ponsard et al. 2000).

Resource abundance may not necessarily be greater in forest habitat, but the structural complexity afforded by large vertical trees may provide more habitat for a more diverse and effective group of predators in lower trophic groups.

Previously, I found that a greater fractal dimension of box patterns (i.e., greater edge) afforded more opportunities for predators and resulted in decreases in prey density, particularly along edge (S.H. Ferguson, submitted for publication). Thus, because of their greater fractal dimension, the vertical tree structures associated with forest may have provided habitat for macroarthropod predators, leading to an increase in their diversity and density, as well as affording a greater amount of edge for foraging, thereby limiting micro- and macro-arthropod densities. Unfortunately, I did not survey vertebrate abundance to test this assumption.

Trophic dynamics that control population densities and community structure can be dominated by top-down forces (e.g., predation on herbivores) or bottom-up forces (e.g., primary productivity) (Hunter and Price 1992; Power 1992; Strong 1992). The results from this study generally support the prediction that the abundance of soil arthropod trophic groups will increase with the structural complexity of vegetation in a prairie landscape. However, trophic models have generally failed to allow accurate predictions to be made for more complex systems (Lundberg and Fryxell 1995; Polis and Strong 1996; Hansson et al. 1998). The critical challenges to trophic-model predictions have been posed by prey-size refuges (Mittelbach et al. 1988; Leibold 1989; Hambright et al. 1991; Mikola and Setälä 1998), spatial and temporal refuges (Sih 1987), and omnivory (Diehl 1993; Porter 1996).

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