

Original article

# Influence of edge on predator–prey distribution and abundance

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## Abstract

I investigated the effect of spatial configuration on distribution and abundance of invertebrate trophic groups by counting soil arthropods under boxes (21 × 9.5 cm) arranged in six different patterns that varied in the amount of edge (137–305 cm). I predicted fewer individuals from the consumer trophic group (Collembola) in box groups with greater amount of edge. This prediction was based on the assumption that predators (mites, ants, spiders, centipedes) select edge during foraging and thereby reduce abundance of the less mobile consumer group under box patterns with greater edge. Consumer abundance (Collembola) was not correlated with amount of edge. Among the predator groups, mite, ant and centipede abundance related to the amount of edge of box groups. However, in contrast to predictions, abundance of these predators was negatively correlated with amount of edge in box patterns. All Collembola predators, with the exception of ants, were less clumped in distribution than Collembola. The results are inconsistent with the view that predators used box edges to predate the less mobile consumer trophic group. Alternative explanations for the spatial patterns other than predator–prey relations include (1) a negative relationship between edge and moisture, (2) a positive relationship between edge and detritus decomposition (i.e. mycelium as food for the consumer group), and (3) a negative relationship between edge and the interstices between adjacent boxes. Landscape patterns likely affect microclimate, food, and predator–prey relations and, therefore, future experimental designs need to control these factors individually to distinguish among alternative hypotheses.

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## 1. Introduction

Landscape patterns affect animal distribution and play an important role in predator–prey interactions (Wiens, 1976; Turchin, 1991; Ferguson et al., 1998). The distribution of prey influences the movement and foraging behavior of predators (Kotliar and Wiens, 1990). Also, landscape features that affect predator foraging behavior will affect prey spatial distribution (Lima and Zollner, 1996). Edges can act as physical barriers (Bider, 1968) or as corridors for predator foraging (Dyer et al., 2001; Vistnes and Nellemann, 2001) and increase the vulnerability of prey located along edges (Orians and Wittenberger, 1991) or disturb prey resulting in fewer prey along edges (Lima and Zollner, 1996). The amount of edge increases with spatial complexity (e.g. fragmentation) and the fractal dimension of landscape patterns (Shorrocks et al., 1991) and, therefore, likely influences predator–prey relations (Ritchie and Olff, 1999).

I investigated the possible influence of edge on the spatial distribution of invertebrate predator–prey groups within a forest–soil ecosystem located in the American prairies. I defined edges as the linear place where a box ends and which is located farthest from the middle of a box. Irregular patterns are often associated with fragmentation and are portrayed in the experimental design as greater separation of individual boxes within five-box configurations. Soil arthropods include Collembola, predatory mites (Acari), and three groups of macroarthropods (spiders, ants, and centipedes). Collembola are a consumer trophic group with restricted mobility that often feed on stationary fungi (Hopkin, 1977). The more mobile predatory mites prey on Collembola (personal observations; Hagvar, 1995). The macroarthropods (spiders, ants, and centipedes) prey on both Collembola and mites (personal observations; Eisenbeis and Wichard, 1987; Kampichler, 1995; Paquin and Coderre, 1997). I predicted lower abundance of consumer prey and greater abundance of their predators in landscapes with greater edge as edge habitat may favor predation (Murcia, 1995).

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## 2. Materials and methods

### 2.1. Study site

The study area consisted of a 0.13 km<sup>2</sup> stand of undisturbed trembling aspen (*Populus tremuloides* Michaux) forest 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). Grassland prairies in this region include small patches of forest dominated by an aspen overstory. Precipitation on the dry-climate prairies is highly variable both within and between years (Sala and Lauenroth, 1982; Ferguson, 2001). Mean monthly daily temperature (1961–1990 normals) varied from 3.9 °C in April to 18.6 °C in July and precipitation varied from 19.7 mm in April to 63.4 mm in June (annual mean = 28.9 mm). There was no evidence or known history of grazing or other agricultural use of the site.

### 2.2. Sampling

Patterns were designed using six arrangements of five adjacent boxes (Fig. 1). Each box consisted of two 2-l milk cartons, one fitted inside the other (to create a solid box). The box was half filled with sand amounting to approximately 2 kg thereby creating a footprint-sized depression of area 21 × 9.5 cm. Boxes depressed the leaf litter to an average depth of 1.3 cm (Ferguson, 2000) creating a microhabitat island for soil arthropods similar to that beneath a rock resting on the forest floor. Measured microclimate differences under the boxes relative to outside of the boxes included increased humidity and decreased temperature (Fer-

guson, 2000) that offered a home to a diverse soil fauna community. I randomly placed four replicates of six patterns (minimum distance between patterns = 3 m) within the poplar stand.

Boxes were overturned and the numbers and size of all macroarthropods and most microarthropods (Collembola and mites) were visually counted. Arthropods that were observed by this method are active surface dwellers. An effort was made to lift individual boxes without disturbing adjacent boxes and the pattern of lifting each box in a pattern varied among surveys. A total of 20, 25, and 20 weekly surveys were conducted from May to October 1997, 1998, and 1999, respectively. I surveyed between the hours of 11:00 and 17:00 during daylight. Leaf litter was not moved and only arthropods directly under the box and located on top of the litter at the moment when the box was lifted were recorded. The survey numbers do not reflect absolute abundance but rather a relative measure of abundance of surface-dwelling soil arthropods. Time spent on watching overturned box was not standardized but approximated to 1–3 min.

Arthropods observed under boxes were grouped into one of three categories: Collembola, predatory mites, and macroarthropods. The trophic groups were based on differences in size and feeding habits. Collembola and predatory mites (Gamasides: Krough, 1995) were the most abundant microarthropods (<3 mm). All Collembolan species and stages of development were placed in one taxonomic group, as most species consume fungi (Hopkin, 1977). Observed Collembolan species were slow (no jumping species), small (length ranged from 0.2 to 2.6 mm), and soft-bodied. Predatory mites were identified according to their long legs and greater mobility (relative to phytophagous mites), and were placed in one taxonomic group since most are non-specific predators that commonly feed on the less-mobile Collembola (personal observations; Hagvar, 1995; Berg et al., 1998). All macroarthropods (>3 mm) were counted but only data for likely predators of Collembola were considered here: spiders (Araneida), ants (Formicoidae), and centipedes (Chilopoda). Seventeen occurrences of predation of mites were observed, seven by spiders, four by centipedes and twice ants were observed carrying mites. Based on these observations, I considered these three groups as predators of mites (Sabelis, 1992). Other macroarthropod groups included Diplura, Diptera (adult and larvae flies), phytophagous mites (Acari: Oribatida), Hemiptera (bugs), Homoptera, Pseudoscorpionida, Lepidoptera (moth and butterfly larvae), Anoplura, Gastropoda, Isopoda, beetles (Coleoptera and Staphylinidae, adults and larvae), Thysanoptera (thrips), and Psocoptera (barklice) (Ferguson, 2001).

Although biomass was estimated, all statistical analyses compared measures of abundance. To calculate biomass, I measured body lengths for a sample of 20 arthropods (four for each of five size classes) within each taxonomic category using callipers (for specimens greater than 5 mm) or an ocular micrometer on a dissecting binocular microscope (for

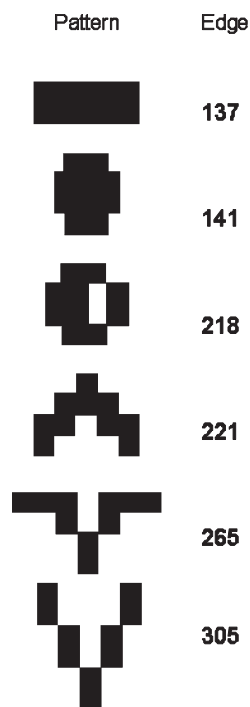


Fig. 1. Length of edge (cm) for six different arrangements of five boxes (21 × 9.5 cm) used to compare number of soil arthropods under boxes.

specimens less than 5 mm). Measurements were made to the nearest 0.1 mm from the most anterior part of the head to the anus but exclude appendages. For each taxonomic group, I used five categories to estimate body size in the field (categories 1–5 represented tiny, small, medium, large, and extra-large). Subsequently, I used mean values from each of these size categories to approximate individual body length. I derived biomass using power function regressions between body length and dry weight biomass (formulas from Ganihar, 1997).

### 2.3. Statistical analysis

The chief characteristic of each pattern was the total amount of edge. Also considered as biologically relevant was the total amount of interstices (defined as the narrow or small space between boxes) between adjacent boxes. The amount of interstices was measured as the distance (cm) of box edge next to box edge within patterns. Measures of interstices were negatively correlated with edge as the two summed to the total box perimeter (5 boxes  $\times$  21  $\times$  9.5 cm). Box patterns were chosen to obtain a range of total edge (Fig. 1). The amount of edge ( $L$ ) was calculated as the perimeter (cm) around patterns (total area = 998 cm<sup>2</sup>).

My goal was to test for relationships between spatial configuration and arthropod abundance. I used a mixed model (PROC MIXED in SAS Institute, 1996) to determine the spatial factors affecting arthropod abundance while controlling for the effect of time with repeated-measures analysis of variance (ANOVA; Sokal and Rohlf, 1981). The repeated measure was week of survey. Statistical interrelationships among the arthropod groups were not considered as the goal was to test for a relationship between abundance and edge for individual arthropod groups (Collembola, mites, spiders, ants, and centipedes). Here, the single response variable was the abundance of each of the five arthropod groups. The effect of two types of independent variables was examined on abundance of groups of arthropods: (1) time categorical variables (year and week of survey nested within year) and (2) the amount of edge in each box pattern as an interval variable. Sample units were the five-box groups that were arranged into six patterns and replicated four times ( $n = 24$  patterns). Sampling occurred every week ( $n = 20, 25, 20$ ) over 3 years, 1997–1999 ( $n = 1560$ ). For 1999 data, I excluded 12 of the 24 box patterns (two replicates of each of the six patterns) that may have been affected by a water addition experiment (Ferguson and Joly, 2002) leaving a total of 1320 samples. The counts included zero values and were not normally distributed; therefore, I used non-parametric analysis by ranking data (PROC RANK; SAS Institute, 1996) before ANOVA analyses (Conover and Iman, 1981). I report raw means for these variables in figures in Section 3.

Bivariate relationships were described using plots of abundance on the  $y$ -axis ( $\pm 1$  S.E.M.) against edge on the  $x$ -axis for four patterns with different edge amount. A second

order polynomial regression line was fit to the relationship to display the pattern as positive, negative, or uniform. I did not test the significance of the regression relationship as the ANOVA results are considered the relevant statistical test.

To test for differences in spatial distribution among arthropod groups under boxes, I used the coefficient of variation (CV) as a measure of the Poisson distribution (i.e. mean equals variance). Thus, the CV, given as variance/mean, will approach 1 in samples following a Poisson distribution,  $>1$  in clumped samples, and  $<1$  in uniform samples. CV was calculated for each arthropod group for each survey using box patterns as the sample unit. Thus, 24 box patterns estimated mean and variance for each survey. The Mann–Whitney test was then used to compare CVs of Collembola with arthropod predators ( $n = 65$  surveys).

### 3. Results

Collembola and mites were the most numerous arthropod groups, although due to small size, they contributed less to the total biomass than macroarthropods (Fig. 2). Of the macroarthropods groups, ants contributed the greatest number of individuals and the greatest biomass.

I will describe relationships between edge and abundance, although the same patterns exist for interstices. Edge and interstices are inversely related and, therefore, I consider interstices only as biologically relevant in the discussion.

Collembola abundance was not affected by edge (Fig. 3A). Collembola abundance increased within a year and more Collembola were recorded in later years of survey (Table 1).

Abundance of predatory mites varied with amount of edge of box groups (Fig. 3B), year and week of survey nested

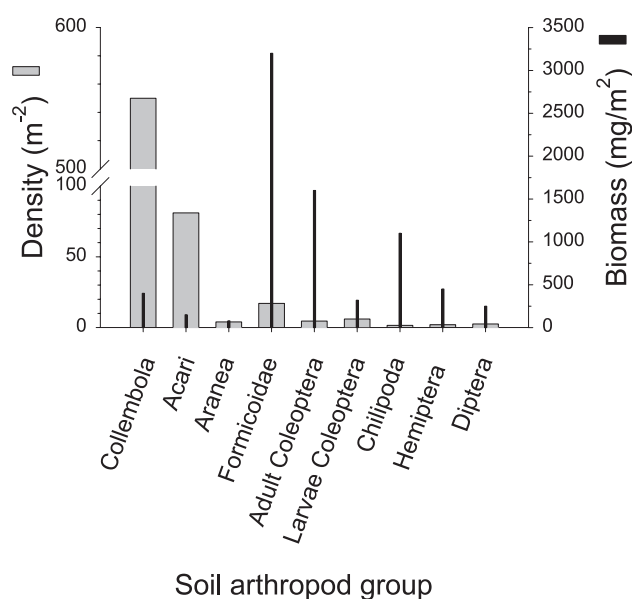


Fig. 2. Density (number m<sup>-2</sup>) and biomass (mg m<sup>-2</sup>) estimates for nine soil arthropod groups found under box groups.

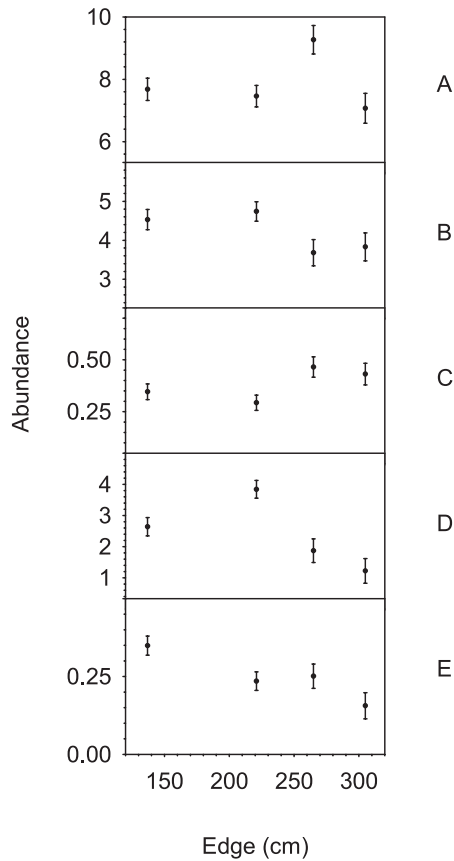


Fig. 3. Arthropod abundance ( $\pm 1$  S.E.M.) relative to length of edge. (A) Collembola abundance vs. amount of edge of box groups. (B) Abundance of predatory mites vs. amount of edge of box groups. (C) Abundance of spiders vs. amount of edge of box groups. (D) Abundance of ants vs. amount of edge of box groups. (E) Abundance of centipedes vs. amount of edge of box groups.

within year (Table 1). Mite abundance decreased under box groups with more edge. As with Collembola, mite abundance increased over time both within a year and among the 3 years surveyed.

Of the three-macroarthropod groups, ant and centipede abundance was negatively associated with amount of edge (Table 1). Greater ant (Fig. 3D) and centipede abundance (Fig. 3E) occurred in box sites with less edge. In contrast, spider abundance was not related to edge (Table 1). Abundance of all three macroarthropod groups varied with time of survey, however, only ants and spiders varied with year (Table 1).

Table 1

Results of analysis to determine the effects of year, week, and amount of edge on abundance of five groups of soil arthropods. Sample units were five-box groups (six patterns replicated four times,  $n = 24$ ) sampled during 20, 25, 20 weekly surveys in 1997, 1998, 1999, respectively ( $n = 1320$ )

Arthropod abundance	Response variables		Explanatory variables		Year, df = 2		Week (year), df = 62	
	Model, df = 67,1252		Edge, df = 3					
	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Collembola	76.7	0.0001	0.02	0.99	80.9	0.0001	80.3	0.0001
Acari	40.3	0.0001	2.7	0.046	72.0	0.0001	41.1	0.0001
Aranea	3.4	0.0001	1.3	0.28	5.5	0.004	3.4	0.0001
Formicoidae	8.5	0.0001	12.1	0.0001	6.6	0.001	8.3	0.0001
Chilopoda	2.6	0.0001	5.3	0.001	2.0	0.14	2.5	0.0001

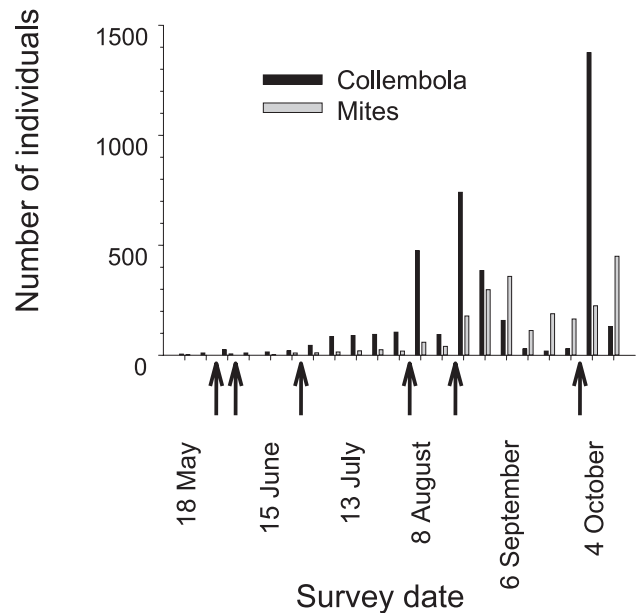


Fig. 4. Changes in abundance of Collembola and predatory mites over 20 weekly surveys from 18 May to 4 October 1997. Arrows indicate rainfall events.

During the short periods of significant precipitation, the abundance of Collembola near the surface leaf litter increased an average of 15 times relative to dry periods (Fig. 4). With the exception of ants (CV = 268), predators (mites CV = 79, spiders CV = 66, and centipedes CV = 32) were less clumped in distribution than Collembola prey (CV = 189;  $U = 3.1$ ,  $P < 0.01$ ).

#### 4. Discussion

The distribution and abundance of predators but not consumers was related to spatial pattern. I tested the prediction that prey would be distributed at higher density in more uniform patches of landscape that provided few 'navigation features' for predators that forage along linear features. In contrast, consumers (Collembola) were not noticeably affected by box patterns relative to edge. However, following wet periods and high humidity, Collembola abundance was large, a pattern noted by other researchers (Reddy and Venkataiah, 1990; Hijii, 1994). For the dry periods that followed wet periods, Collembola density was reduced

along edges (Ferguson, 2000). The experimental format did not account for changes in microclimate, such as humidity and, therefore, was unable to distinguish this alternative hypothesis. Previously, I found that arthropod predators were more abundant close to edge (Ferguson, 2000). In contrast to these findings, results of this experiment found that certain predators (ants, centipedes, and possibly mites) were more abundant in box patterns with less edge while others (spiders) were not affected. The observed spatial distribution of consumers and predator groups is not consistent with the view that some predator groups concentrated foraging efforts along box edges thereby reducing prey abundance in box patterns with greater edge. Unfortunately, the experimental design was unable to distinguish results from alternative explanation of the observed patterns. The center of boxes may act as a physical shelter from exterior microclimate (i.e. greater sunlight and reduced humidity), or shelter (i.e. reducing risk of predation), or boxes grouped together may provide more food (i.e. humid interstices).

Due to considerable differences in body size (two orders of magnitude), different arthropod groups likely perceive the spatial configuration of boxes differently. The small *Collembola* may have concentrated near the center of individual boxes where humidity was higher and all boxes may have been perceived as similar. In contrast, mites (small but more mobile than *Collembola*), ants, and centipedes may have perceived the larger uniform box groups as having favorable microhabitat characteristics. Previously, I found relatively constant humidity under boxes with distance to edge (Ferguson, 2001). However, I did not measure changes in humidity over time among the different box patterns. Abundance of predatory mites increased during dry periods, whereas *Collembola* prey abundance increased following precipitation events, as has been observed by other researchers (Stamou et al., 1993; Klironomos and Kendrick, 1995; Badejo et al., 1998; Detsis et al., 2000). Previously, we did not find evidence for regulation of *Collembola* by predatory mites (Ferguson and Joly, 2002), although mite predation of *Collembola* still occurred and may have been greater along edges. Consumer abundance was not affected by the complexity of the artificial landscape patterns, although I did not measure vertical or horizontal migration under box patterns that may have occurred during dry periods to avoid desiccation.

Of the predators of *Collembola*, none were more abundant with greater spatial complexity or greater amount of edge. Thus, edge may not influence the hunting behavior of predators. This result is surprising, as seven of the eight groups of soil arthropods were previously found closer to edge than expected (Ferguson, 2000). One explanation is that not all individuals along edges were foraging. For example, the movements of predators varied with time of day. Some individuals may have been inactive diurnally and located under boxes for protection from large arthropod or vertebrate predators. Proximity to edges may have occurred

if individuals did not move far under boxes. During nocturnal periods, they may forage beyond the boxes. Another consideration is that movements of individual predators, relative to the distribution of their prey, may be constrained to a home range. Thus, arthropod predator density may be relatively uniform across box groups and may not correlate with prey density. As well, predators and prey may interpret the landscape features of their shared environment differently. Predatory mites, ants, and centipedes did exhibit a spatial distribution negatively correlated with the amount of edge. Thus, amount of edge or the complexity of the landscape likely affects predator–prey spatial relations for some soil arthropod groups as has been shown for vertebrates (e.g. Russell et al., 1992).

Why are mites, ants, and centipedes found in greater numbers under box groups with less edge? Ants formed colonies that were more likely to occur in more uniform box patterns (unpublished data) that may have provided a larger undersurface relative to edge. Mites are small relative to ants, spiders, and centipedes, and, thus, may have been predated along edges by larger macroarthropod predators, thereby reducing their numbers or distribution along edges. Centipedes, by their large size, may require a larger uniform area due to their home range area requirements. Spiders were less affected by the availability of edges. Spiders may use box edges to construct their webs and there was some indication of greater abundance in box patterns with greater edge (Fig. 3C).

There are limitations of the sampling methodology used in this study. Taxonomic levels lower than the one I used to identify arthropods would certainly provide more detailed results. Results may vary with particular prey preference and foraging behavior within a taxonomic order. For example, springtail and mite populations appear to be regulated intrinsically by competition for food and secondarily by temperature rather than by predation (Ferguson and Joly, 2002). Sampling was done around mid-day which may bias results if certain arthropod groups follow a circadian cycle of activity (Eisenbeis and Wichard, 1987). Bias may result if the arthropods found under boxes over-represent and under-represent certain trophic groups that migrate to deeper soil-based ecosystem. Another concern is the large biomass of ants (Fig. 2) found in this study that may have the effect of obscuring patterns among other arthropod groups (Madden and Fox, 1997). Patterns of spatial distribution are influenced by temporal patterns, particularly time lags (Kareiva, 1990) making it difficult to detect spatial associations of predators and prey and separating alternative explanations. I suggest a revised sampling design that uses sheets of plywood cut to varying smooth shapes. The patterns could be designed to differ in the amount of edge and fractal dimension (Corbit and Garbary, 1995). The use of flat plywood would remove interstices as a confounding factor. Also, humidity could be measured over time to control for microclimatic variation. Alternatively, container experiments (Teuben and Verhoef, 1992) with linear sur-

face features could be monitored using video-recorders to assess predator–prey interactions relative to spatial distribution.

My findings could not distinguish between the alternate views that soil arthropod predators, food, and microclimate differences created a more clumped distribution pattern among consumer prey. This clumped distribution may have occurred as a result of predator searching behavior associated with edge that removed most prey along patterns with greater edge habitat. Alternatively, box patterns with different amount of edge may have provided different microenvironment that supported greater decomposition, and hence more detritivores. Nonetheless, the results of this experiment contradict other studies (Oehler and Litvaitis, 1996) that suggest consumers may concentrate in large blocks of uniform habitat as a result of use of edges by predators. Future research is required to control individually the spatial and temporal patterns of food, microclimate and landscape to better understand predator–prey relations.

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### References

- Badejo, M.A., Nathaniel, T.I., Tian, G., 1998. Abundance of springtails (Collembola) under four agroforestry tree species with contrasting litter quality. *Biology and Fertility of Soils* 27, 15–20.
- Berg, M.P., Kniese, J.P., Bedaux, J.J.M., Verhoef, H.A., 1998. Dynamics and stratification of functional groups of micro- and mesoarthropods in the organic layer of a Scots pine forest. *Biology and Fertility of Soils* 26, 268–284.
- Bider, J.R., 1968. Animal activity in uncontrolled terrestrial communities as determined by a sand transect technique. *Ecological Monographs* 38, 269–308.
- Conover, W., Iman, R., 1981. Rank transformations as a bridge between parametric and nonparametric statistics. *American Statistics* 35, 124–129.
- Corbit, J.D., Garbary, D.J., 1995. Fractal dimension as a quantitative measure of complexity in plant development. *Proceedings of the Royal Society of London B* 262, 1–6.
- Detsis, V., Diamantopoulos, J., Kosmas, C., 2000. Collembolan assemblages in Lesvos, Greece. Effects of differences in vegetation and precipitation. *Acta Oecologica* 21, 149–159.
- Dyer, S.J., O'Neill, J.P., Wasel, S.M., Boutin, S., 2001. Avoidance of industrial development by woodland caribou. *Journal of Wildlife Management* 65, 531–542.
- Eisenbeis, G., Wichard, W., 1987. *Atlas on the Biology of Soil Arthropods*. Springer, Berlin.
- Ferguson, S.H., 2000. Distance to edge and predator size: is bigger better? *Canadian Journal of Zoology* 78, 713–720.
- Ferguson, S.H., 2001. Changes in trophic abundance of soil arthropods along a grass–shrub–forest gradient. *Canadian Journal of Zoology* 79, 457–464.
- Ferguson, S.H., Joly, D.O., 2002. Dynamics of springtail and mite populations: the role of density dependence, predation, and weather. *Ecology and Entomology* 27, 565–573.
- Ferguson, S.H., Taylor, M.K., Born, E.W., Messier, F., 1998. Fractals, sea-ice landscape and spatial patterns of polar bears. *Journal of Biogeography* 25, 1081–1092.
- Ganihar, S.R., 1997. Biomass estimates of terrestrial arthropods based on body length. *Journal of Bioscience* 22, 219–224.
- Hagvar, S., 1995. Instability in small, isolated microarthropod communities. *Bulletin of Entomology Polone* 64, 123–133.
- Hijii, N., 1994. Abundance patterns of soil micro-arthropods at a *Pinus pumila* scrub in an alpine range of central Japan. *Ecological Researches* 9, 175–183.
- Hopkin, S.P., 1977. *The Biology of Springtails (Insecta: Collembola)*. Oxford University Press, New York.
- Kampichler, C., 1995. Biomass distribution of a microarthropod community in spruce forest soil. *Biology and Fertility of Soils* 19, 263–265.
- Kareiva, P., 1990. Population dynamics in spatially complex environments: theory and data. *Philosophical Transactions of the Royal Society of London, Series B* 330, 175–190.
- Klironomos, J.N., Kendrick, B., 1995. Relationships among microarthropods, fungi, and their environment. *Plant Soil* 170, 183–197.
- Kotliar, N.B., Wiens, J.A., 1990. Multiple scales of patchiness and patch structure: a hierarchical framework for the study of heterogeneity. *Oikos* 59, 253–260.
- Krough, P.H., 1995. Effects of pesticides on the reproduction of *Hypoaspis aculeifer* (Gamasida: Laelapidae) in the laboratory. *Acta Zoologica Fennica* 196, 333–337.
- Lima, S.L., Zollner, P.A., 1996. Towards a behavioral ecology of ecological landscapes. *Trends in Ecology and Evolution* 11, 131–135.
- Madden, K.E., Fox, R.J., 1997. Arthropods as indicators of the effects of floride pollution on the succession following sand mining. *Journal of Applied Ecology* 34, 1239–1256.
- Murcia, C., 1995. Edge effects in fragmented forests: implications of conservation. *Trends in Ecology and Evolution* 10, 58–62.
- Oehler, J.D., Litvaitis, J.A., 1996. The role of spatial scale in understanding responses of medium-sized carnivores to forest fragmentation. *Canadian Journal of Zoology* 74, 2070–2079.
- Orians, G.H., Wittenberger, F.F., 1991. Spatial and temporal scales in habitat selection. *American Naturalist* 137, S29–S49.
- Paquin, P., Coderre, D., 1997. Changes in soil macroarthropod communities in relation to forest maturation through three successional stages in the Canadian boreal forest. *Oecologia* 112, 104–111.
- Reddy, M.V., Venkataiah, B., 1990. Seasonal abundance of soil-surface arthropods in relation to some meteorological and edaphic variables of the grassland and tree-planted areas in a tropical semi-arid Savannah. *International Journal of Biometeorology* 34, 49–59.
- Ritchie, M.E., Olff, H., 1999. Spatial scaling laws yield a synthetic theory of biodiversity. *Nature* 400, 557–560.
- Russell, R.W., Hunt Jr, G.L., Coyle, K.O., Cooney, R.T., 1992. Foraging in a fractal environment: spatial patterns in a marine predator–prey system. *Landscape Ecology* 7, 195–209.
- Sabelis, M.W., 1992. Predatory arthropods. In: Crawley, M.J. (Ed.), *Natural Enemies: the Population Biology of Predators, Parasites and Diseases*. Blackwell Scientific Publications, London, pp. 225–264.
- Sala, O.E., Lauenroth, W.K., 1982. Small rainfall events: an ecological role in semiarid regions. *Oecologia* 53, 301–304.
- Institute, S.A.S., 1996. *The SAS System for Windows, version 6.12*. SAS Institute Inc., Cary, NC.
- Shorrocks, B., Marsters, J., Ward, I., Evennett, P.J., 1991. The fractal dimension of lichens and the distribution of arthropod body lengths. *Functional Ecology* 5, 457–460.

- Sokal, R.R., Rohlf, F.J., 1981. *Biometry*. second ed. W.H. Freeman & Company, New York.
- Stamou, G.P., Asikidis, M.D., Argyropoulou, M.D., Sgardelis, S.P., 1993. Ecological time versus standard clock time: the asymmetry of phenologies and the life history strategies of some soil arthropods from Mediterranean ecosystems. *Oikos* 66, 27–35.
- Teuben, A., Verhoef, H.A., 1992. Relevance of micro- and mesocosm experiments for studying soil ecosystem processes. *Soil Biology and Biochemistry* 24, 1179–1183.
- Turchin, P., 1991. Translating foraging movements in heterogeneous environments into the spatial distribution of foragers. *Ecology* 72, 1253–1266.
- Vistnes, I., Nellemann, C., 2001. Avoidance of cabins, roads, and power lines by reindeer during calving. *Journal of Wildlife Management* 65, 915–925.
- Wiens, J.A., 1976. Population responses to patchy environments. *Annual Review of Ecology and Systematics* 7, 81–120.