

Does Predation or Moisture Explain Distance to Edge Distribution of Soil Arthropods?

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ABSTRACT.—Ecological trap theory suggests that greater predator activity occurs along edge habitat, thereby reducing prey abundance. Alternatively, environmental gradients associated with edge habitat may be responsible for changes in prey abundance irrespective of predator spatial distribution. To test these alternative hypotheses, I measured the distance soil arthropods were to edge of boxes (21×9.5 cm) placed on the forest floor of prairie (precipitation-limited; 1977–1999) and boreal forest (moderate precipitation; 2000–2001) sites. Predator theory predicted that in either environment predatory groups would be located close to edge and herbivore/detritivore groups would not be distributed different from random. In support of this hypothesis, in the precipitation-limited environment 7 of 11 soil arthropod groups were distributed as predicted; however, only 7 of 13 groups followed predator predictions in the moderate-precipitation environment. In support of the environmental gradient hypothesis, 22 of 24 soil arthropod groups were distributed as predicted. Here, all hard-bodied groups, with the exception of snails, were located closer to edge than expected and all soft-bodied groups, with the exception of slugs, were not located closer to edge than expected indicating possible avoidance of external dryness. Tests of these two hypotheses were confirmed with similar results using a regression method to determine if distribution declined from edge to interior. In conclusion, the results did not support the predation hypothesis and instead supported the environmental gradient hypothesis with moisture the likely explanation for the distribution pattern of soil arthropods.

INTRODUCTION

Increasing recognition of the importance of edges has led many researchers to call for studies of the functional links between habitat edges and community dynamics (Murcia, 1995; Didham *et al.*, 1996; Fagan *et al.*, 1999; Heliöitä *et al.*, 2001). One approach to studying ecological edges is to focus on the abiotic edge effects (*i.e.*, environmental conditions that change from proximity to a dissimilar ecotone) that link edges to community structure (*e.g.*, Chen *et al.*, 1995; Lövei and Sunderland, 1996; Magura *et al.*, 2001). Another approach emphasizes direct biotic interactions resulting from edge, including disease, parasites, competition and predation and their trophic consequences (Kareiva, 1987; Roland and Taylor, 1997; Kotze and Samways, 1999). Understanding the functional roles of edges relative to biotic and abiotic interactions is important as human activities are resulting in the creation of more edges on Earth (Brooks, 2000).

The objective of this study was to test between the two hypotheses explaining soil arthropod distribution under box edges relative to soil arthropod trophic groups (*e.g.*, predation) and environmental differences (*e.g.*, moisture). Edges are transition zones between adjacent habitats, often created by fragmentation due to increased human activity, that increase the risk of local extinctions (Wiens *et al.*, 1985). Changes in biotic conditions in edge compared with exterior habitat include predation, parasitism and species interactions (Saunders *et al.*, 1991; Andrén, 1995). The predation hypothesis predicted that predatory arthropod groups would be located closer to edge in both habitats, whereas herbivore/detritivore arthropod groups would be distributed randomly under boxes. Predation at

edges (Ferguson and Joly, 2002) and greater abundance of larger predators has been observed near box edges and may explain soil arthropod distribution (Ferguson, 2004a).

Edges have distinctive microclimates, with abrupt changes in light, substrate, water conditions and complexity (Murcia, 1995). These factors are highly significant for small animals such as soil arthropods (Lövei and Sunderland, 1996). Soil arthropods are commonly found under logs (Kolstrom and Lumaajarvi, 1999) and the sheltered environment under boxes provided a similar microenvironment that included less variable temperatures, greater moisture and reduced light (Ferguson, 2000). Drying out under boxes from the outside edge to the centre has been reported for precipitation-limited prairie environments during periods without rain (Ferguson, 2000) and changes in abundance of smaller arthropods has been reported with changes in humidity, precipitation and temperature (Ferguson, 2001). The environmental gradient hypothesis predicted that hard-bodied arthropods that can withstand desiccation would be located closer to box edges than at random, whereas soft-bodied arthropods that are more susceptible to desiccation would be distributed randomly with respect to edge habitat. Also, the environmental gradient hypothesis predicted that soft-bodied arthropods would be more likely to be located closer to the centre of boxes in the precipitation-limited environment relative to the moderate-precipitation environment because the boreal forest provided more humid conditions.

To test the alternative explanations for the distribution of soil arthropods, I surveyed arthropods under milk carton boxes (21 × 9.5 cm) placed on the forest floor. The side of the box created a linear discontinuity (*i.e.*, edge) between the under surface of the box and 'outside' forest floor. First, I tested whether density or biomass varied with distance to edge for soil arthropods located under boxes in a precipitation-limited prairie (summer 1997–1998) and a moderate-precipitation forest (summer 2000–2001) environment. Next, I tested which arthropod groups were located closer to edge than at random according to the predictions for the predation and environmental-gradient hypotheses. Last, I tested the alternative predictions using a regression of distance to edge and density of arthropods between the two environments.

STUDY AREA AND METHODS

Study area.—Two study sites were surveyed. The first study area occurred in the precipitation-limited prairie environment and consisted of a 0.13 km² stand of undisturbed trembling aspen (*Populus tremuloides* Michaux) forest located within 1.5 km of the city of Saskatoon (elevation 504 m) in the prairie region of southcentral 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 11.5 C in May to 18.2 C in July (annual mean = 2.2 C) and mean monthly precipitation varied from 29.0 mm in Sept. to 61.1 mm in June (annual mean = 29.2 mm). There was no evidence or known history of grazing or other agricultural use of the site.

The second study area occurred in a moderate-precipitation environment and consisted of a 1 km² stand of boreal forest located along the McIntyre River within the city of Thunder Bay, Ontario, Canada (48°22'N, 89°19'W; elevation 199 m). The mixed boreal forest consisted of jack pine (*Pinus banksiana* Lamb.), black spruce [*Picea mariana* (Mill.) B.S.P.], balsam fir [*Abies balsamea* (L.) Mill.], white spruce [*Picea glauca* (Moench) Voss], white birch (*Betula papyrifera* Marsh.) and trembling aspen (*Populus tremuloides* Michx.). The study site lies within the Boreal Ecosystem that consists of rolling rocky uplands with coarse

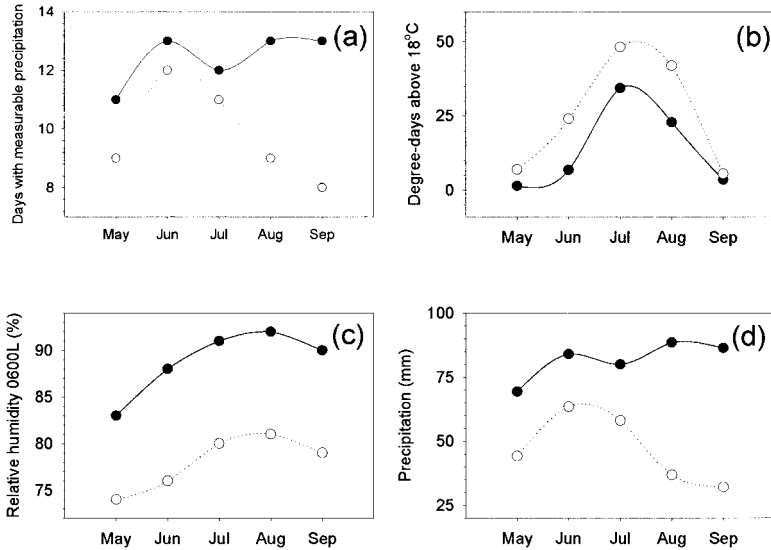


FIG. 1.—Comparison of weather between precipitation-limited environment (Saskatoon, SK) (○) and moderate-precipitation environment (Thunder Bay, ON) (●) for (a) days with measurable precipitation, (b) degree-days above 18 C, (c) relative humidity (0600L%), and (d) precipitation (mm) over the study season, May–September

well-drained soils (Rowe, 1972). The climate is humid continental with a mean minimum January temperature of -15 C and a mean maximum daily temperature for July of 18 C (Environment Canada, 2001). Mean annual precipitation is approximately 700 mm, including a mean winter snowfall of 196 cm (Environment Canada, 2001). For the study period (May to September), mean monthly daily temperature (1961–1990 normals) varied from 9.0 C in May to 17.7 C in July (annual mean = 2.4 C) and mean monthly precipitation varied from 69.3 mm in May to 88.5 mm in August (annual monthly mean = 58.6 mm) (Environment Canada, 2001).

In comparing the two study sites, the precipitation-limited study site (Saskatoon) received considerably less precipitation than the moderate-precipitation environment (Thunder Bay), particularly during the field season (May–September), and also had fewer days with precipitation (*i.e.*, longer dry periods; Fig. 1a). Saskatoon was not only hotter (Fig. 1b) and received less rainfall (Fig. 1d), but also the combination of hot days with little moisture resulted in lower relative humidity (Fig. 1c).

Sampling.—Twenty plots, consisting of three adjacent boxes, were randomly distributed within each of the two forests (not along the forest edge) with a minimum distance between plots of 5 m. Each cardboard box consisted of two 2-liter milk cartons, fitted inside the other (to create a solid box) and filled with sand (ca. 2 kg). Boxes placed on the leaf litter created a footprint-sized depression 21 by 9.5 cm. Boxes were initially placed in the field 3 wk before surveys commenced for the first year at each study site and boxes were replaced as necessary 1 wk before the start of surveys each subsequent year. Boxes depressed the leaf litter creating a microhabitat island for a diverse soil fauna community similar to that beneath a rock resting on the forest floor. Casual inspection of rocks and fallen logs within each study area indicated that boxes supported similar soil fauna.

During count surveys, boxes were approached cautiously, overturned quickly and the numbers and size of all soil arthropods (>1 mm) directly under the box were visually counted. Individual boxes were lifted without disturbing adjacent boxes. Survey seasons began approximately 1 wk after snow had melted, typically in late April, and ended once daytime temperatures fell below zero, typically in late September. For the precipitation-limited environment, 23, 24 and 20 weekly surveys were conducted from May to October 1997, 1998 and 1999, respectively. After the third year of surveys on the Canadian prairies, the study site was changed to a boreal forest habitat to make comparisons of the associated soil fauna. For the moderate-precipitation environment, 20 and 11 weekly surveys were conducted from May to September 2000 and 2001, respectively. Thus, for all years between 20 and 24 weekly surveys were conducted, with the exception of the 2001 survey where a reduced sampling protocol was implemented to accommodate a different experiment (Ferguson, 2004b).

Soil arthropod groups (*see* Bolger *et al.*, 2000) were used to group all soil arthropods observed under boxes based on differences in size and feeding habits and included: springtails (Collembola), spiders (Arachnida), ant adults (Formicoidae), centipedes (Chilopoda), diplurans (Diplura), adult flies (Diptera), mites (Acari), bugs (Hemiptera), slugs and snails (Mollusca: Gastropoda), Isopods (woodlice), beetles (Coleoptera, adults and larvae) and earthworms (Annelida). Groups were distinguished as predators, herbivores/detritivores, hard-bodied or soft-bodied based on available information (Eisenbeis and Wichard, 1987; Brock *et al.*, 1994). Most of the soil-litter invertebrate community can be described as belonging to two trophic levels, one feeding on the superficial litter layers and a second trophic level feeding on the consumer group (Ponsard and Arditì, 2000). For centipedes a noticeable difference between large and small individuals occurred which may relate to their ability to endure desiccation. Therefore, I split the group into large (>2 cm) and small (<2 cm) individuals. Some minor arthropod groups (*e.g.*, moths) were excluded from the analyses if fewer than 20 distance measures were recorded during a field season.

For individual arthropods, I measured distance (mm) from the centre of locations prior to movements to the closest box edge (Ferguson, 2000). Once boxes were overturned, coloured toothpicks were placed where fast-moving arthropods were first observed. For ants, I only measured distance to edge if fewer than two ants were observed under an individual box, as large numbers of ants were associated with colonies. For comparison to random distances to edge, 100 random location points under a theoretical box were generated using a GIS algorithm (Ferguson, 2000). Random distances provided the available distribution to which observations could be compared relative to expected patterns. Measures of 0 cm distance were included in both observed and expected values as these indicated locations on the edge and sometimes arthropods actually attached to the box edge (*e.g.*, slugs).

Both density and biomass were calculated, as differences in size of individuals of the same group have been found to influence distance to edge (Ferguson, 2000). For each taxonomic group, five categories were used to estimate body size in the field with 1 as the smallest and 5 as the largest. I measured body lengths for a sample of 20 arthropods, 4 from each of the five size categories, within each taxonomic category. Body lengths were measured using calipers for specimens greater than 5 mm or an ocular micrometer on a dissecting binocular microscope for specimens less than 5 mm. Body length measurements were made to the nearest 0.1 mm from the most anterior part of the head to the anus but excluded appendages. Taking of individuals for measurements occurred during the first year and the first month for each study site and numbers removed were small relative to the total number of individuals available. Mean body length measurements by size category were used to

calculate biomass (dry weight per m²) for the various taxa via published regression equations (Edwards, 1967; Dotson and Kalisz, 1989; Ganihar, 1997).

Statistical analysis.—For comparative purposes, previously published data on distance to edge measurements for soil arthropods from the precipitation-limited environment (Ferguson, 2000) were included in this analysis. The differences from previous analyses include the addition of data on distance to edge for mites, dividing the centipedes into two groups (large and small) and using regression analysis to objectively compare distributions according to distance to edge.

Soil arthropod count and distance data were not normally distributed (Wilk's Shapiro normality test, $P > 0.05$) and transformations failed to normalize all variables. Therefore, I used nonparametric analyses by ranking data before correlation analyses (Conover and Iman, 1981). The sample units were measurements of distance to edge for individual arthropods. The measurements were randomly distributed among box sites so as to not predispose measurements to any site's microclimatic conditions. I report untransformed means ± 1 standard error. All statistical analyses were done using SAS (SAS, 1987) statistical software.

Analyses were performed to determine if density and biomass of arthropod groups varied with distance (ANOVA of ranked data). Seasonal differences were controlled by using a general linear model with survey as a repeated measure. Distance to edge for arthropod groups was compared with a random distribution of locations to determine if some groups were located closer to edge than expected. The null hypothesis is that there is no difference between the treatments. Predator-prey theory predicted that herbivore/detritivore groups would not be located closer to edge habitat than expected whereas predator groups would be closer to edge habitat relative to a random distribution. Here, I tallied the number of distance to edge relationships that followed predator/prey predictions in either environment (precipitation limited vs. moderate precipitation). Environmental gradient hypothesis predicted that hard-bodied groups would be located closer to edge than either soft-bodied groups or at random. Again, I compared the number of arthropod groups that were closer to edge than at random for either hard or soft bodied arthropod groups. As a secondary test, regression analysis was used to determine whether a significant relationship existed between density and distance according to the same predictions.

RESULTS

Comparison of distance to edge between sites.—In support of the environmental gradient hypothesis, density and biomass of soil arthropods was greater closer to edge within the precipitation-limited environment relative to the moderate-precipitation environments (Table 1). Overall, soil arthropods were closer to edge in the precipitation-limited environment (1.45 cm) versus the moderate-precipitation environment (1.87 cm) as well as for each month of surveys (Fig. 2).

Comparison of arthropod groups between sites.—For the precipitation-limited environment, spiders, bugs, adult flies, ants, beetles and large centipedes were located closer to edge than at random (Table 2). Beetle larvae, mites, small centipedes, diplurans, and springtails were not found closer to edge than at random. Only spiders were generally located within 1 cm of box edges.

For the moderate-precipitation environment, earthworms were found closer to the centre of boxes although distances were not significantly different from random (Table 2). Beetle larvae, snails, small centipedes, springtails and diplurans were found at distances not significantly different from random. Bugs, slugs, ants, isopods, spiders, and beetles were

TABLE 1.—Analysis of variance of ranked data to determine the effects of distance to edge on density and biomass of arthropod groups

Source of variation	Density (no./m ²)			Biomass (mg/m ²)		
	df	F	P	df	F	P
(A) Precipitation-limited environment:						
Arthropod group	8	6.9	0.0001	8	7.3	0.0001
Distance	5	38.7	0.0001	5	37.4	0.0001
Distance by group	14	5.1	0.003	14	3.1	0.005
Error	955			955		
(B) Moderate-precipitation environment:						
Arthropod group	9	5.8	0.0001	9	13.0	0.0001
Distance	5	6.8	0.0001	5	10.2	0.0001
Distance by group	15	3.2	0.008	15	2.9	0.006
Error	1292			1292		

found closer to edge than at random (Table 2). Bugs and slugs were generally observed within 1 cm of box edges.

Tests of the predator hypothesis using distance to edge.—Predator theory predicted that predatory arthropod groups would be located close to edge in either precipitation-limited or moderate-precipitation environment. In support of the predation hypothesis, in the precipitation-limited environment 7 of 11 soil arthropod groups were distributed as predicted: herbivore/detritivore groups were not located closer to edge habitat than expected and predator groups were closer to edge habitat relative to a random distribution (Table 2). However, only 7 of 13 groups matched predator predictions for the moderate-precipitation environment. In total 58% (14 of 24) of groups of arthropods followed predator predictions.

Tests of environmental gradient hypothesis using distance to edge.—In support of the environmental gradient hypothesis, 92% (22 of 24) of soil arthropod groups were distributed as predicted in either environment (Table 2). All hard-bodied groups, with the exception of snails, were located closer to edge than expected. In contrast, all soft-bodied groups, with the exception of slugs, were not located closer to edge than expected. The two exceptions occurred for the moderate-precipitation environment which followed predictions based on the environmental-gradient hypothesis that patterns would be less strong if moisture was not limiting.

Secondary test of predator hypothesis using linear relationship.—Next, I compared the soil arthropod groups from each site relative to the linear relationship between abundance and distance for the precipitation-limited and moderate-precipitation environments (Table 3). Predator theory predicted that predatory groups would be located close to edge in either forest, whereas herbivore/detritivore groups would not be located closer to edge habitat than expected relative to a random distribution. For the precipitation-limited environment, spiders, ants, adult beetles, large centipedes and bugs showed a linear decline in abundance with distance from edge. In contrast, small centipede, beetle larvae, dipluran, springtail and mite abundance showed no significant decline in abundance (slope not different from zero) with distance from edge. The tally indicated 6 of 10 predictions followed predictions based on the predator hypothesis.

For the moderate-precipitation environment, spiders, ants, adult beetles, large centipedes, bugs and snails declined in abundance with distance from edge (Table 3). Small centipedes, beetle larvae, diplurans, springtails, mites, slugs, earthworms and isopods

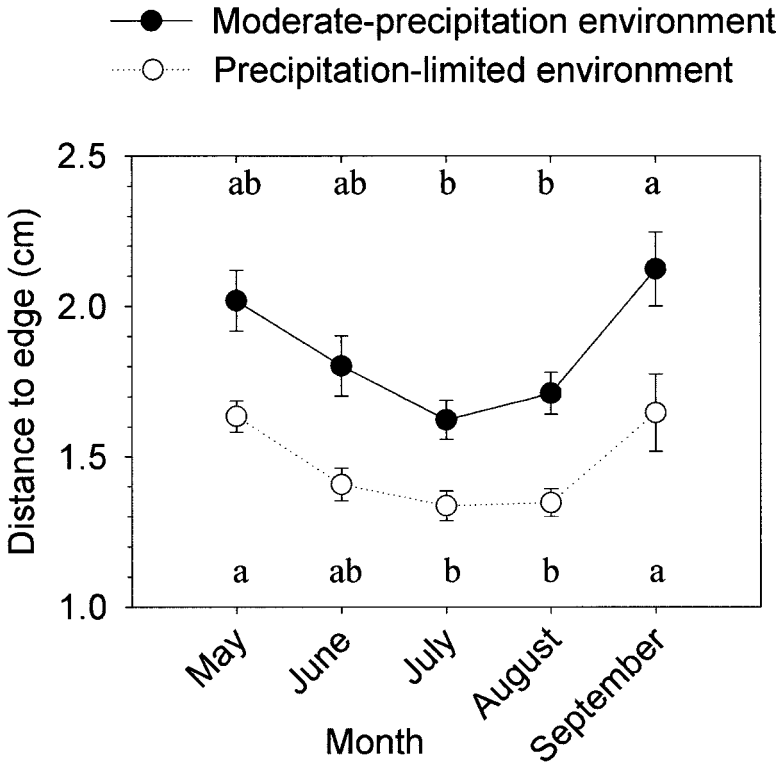


FIG. 2.—Comparison of monthly changes in distance to edge of soil arthropods between precipitation-limited environment (Saskatoon, SK) (○) and moderate-precipitation environment (Thunder Bay, ON) (●). Differences in monthly mean distance to edge (± 1 SE) were indicated if letters differ for the moderate-precipitation environment (top) and precipitation-limited environment (bottom)

showed no significant relationship with distance to edge. The tally for the moderate-precipitation environment was 8 of 13 followed predator predictions. In total only 54% (13 of 24) of groups followed predator predictions for either environment.

Secondary test of environmental-gradient hypothesis using linear relationship.—The environmental-gradient hypothesis predicted that hard-bodied groups would be located closer to edge than expected and soft-bodied groups would not be located closer to edge (because edges dry out sooner). In support of the environmental gradient hypothesis, all five hard-bodied soil arthropod groups in the precipitation-limited environment were negatively related to distance to edge as predicted, whereas none of the soft bodied ($n = 5$) were linearly related to edge (Table 3). For the moderate-precipitation environment, 6 of 7 hard-bodied arthropod groups were negatively related to distance to edge and 7 of 7 soft-bodied arthropod groups were not linearly related to edge. The only exception was for isopods in the moderate-precipitation environment, which were not negatively related to distance to edge ($P = 0.08$). In total, 96% (23 of 24) of arthropod groups followed the environmental-gradient predictions.

Of note, spiders and ants had greater negative slopes in precipitation-limited environment versus the moderate-precipitation environment for the linear regression between

TABLE 2.—Distance to box edge for soil-surface arthropod groups in a (A) precipitation-limited environment (prairie) and a (B) moderate-precipitation environment (boreal forest). Arthropod groups that are closer to edge than expected (above dashed line) do not share the same letter as random points (multiple comparison ANOVA test)

Arthropod group	Characteristics [%]	Multiple comparison*	Mean (cm)	Standard deviation	Sample size	Median	Mode
(A) Precipitation-limited environment:							
Spiders	Pred/Hard	<i>e</i>	0.80	0.94	174	0.5	0.0
Bugs	Herb/Hard	<i>e</i>	1.01	1.07	121	0.6	0.0
Adult flies	Pred/Hard	<i>de</i>	1.20	1.33	121	0.6	0.0
Ants	Pred/Hard	<i>cd</i>	1.2	1.17	302	0.8	0.0
Beetles	Pred/Hard	<i>cd</i>	1.35	1.17	179	1.0	0.0
Centipedes L [#]	Pred/Hard	<i>cd</i>	1.60	1.20	46	1.8	0.0
Beetle larvae	Pred/Soft	<i>abc</i>	1.69	1.16	114	1.7	2.0
Mites	Herb/Soft	<i>ab</i>	1.76	0.97	139	1.4	1.2
Centipedes S [#]	Pred/Soft	<i>ab</i>	1.91	0.88	60	1.8	1.4
Diplurans	Pred/Soft	<i>ab</i>	2.22	1.10	92	2.0	1.5
Springtails	Herb/Soft	<i>ab</i>	2.35	1.14	204	2.0	1.4
Random points [†]		<i>a</i>	2.43	1.35	100	2.5	1.5
(B) Moderate-precipitation environment:							
Bugs	Herb/Hard	<i>e</i>	0.91	0.76	38	0.8	0.2
Slugs	Herb/Soft	<i>e</i>	0.98	0.99	159	0.6	0.4
Ants	Pred/Hard	<i>de</i>	1.21	0.83	31	1.0	0.4
Isopods	Herb/Hard	<i>cde</i>	1.32	0.78	209	1.1	0.8
Spiders	Pred/Hard	<i>cde</i>	1.49	1.27	70	1.1	0.2
Beetles	Pred/Hard	<i>cde</i>	1.49	0.99	217	1.2	0.9
Centipedes L [#]	Pred/Hard	<i>cde</i>	1.50	0.90	46	1.2	0.8
Larvae	Pred/Soft	<i>bcd</i>	1.66	0.96	83	1.4	0.8
Snails	Herb/Hard	<i>bcd</i>	1.99	1.24	44	1.7	0.9
Centipedes S [#]	Pred/Soft	<i>abc</i>	2.05	1.10	159	1.7	1.4
Springtails	Herb/Soft	<i>ab</i>	2.35	1.22	46	2.5	1.4
Diplurans	Pred/Soft	<i>ab</i>	2.51	1.08	61	2.0	1.4
Earthworms	Herb/Soft	<i>a</i>	2.82	2.44	390	2.2	1.6
Random points [†]		<i>ab</i>	2.43	1.35	100	2.5	1.5

* Groups with the same letter did not differ using Tukey's multiple comparison test ($\alpha = 0.05$)

[†] One hundred points were randomly generated

[#] Large (>2 cm) and small (<2 cm) centipedes separated

[%] Hard = exoskeleton limits desiccation; Soft = soft body susceptible to desiccation; Pred = largely predaceous; Herb = largely herbivore/detritivore

density and distance to edge (Table 3). Thus, spider and ants were found closer to edge at both sites; however, the relationship was stronger in the precipitation-limited environment. No other arthropod groups differed in slopes between the two sites.

DISCUSSION

Within the two forest communities, soil arthropod abundance and distribution appeared to be influenced more by abiotic, environmental gradients than by biotic predation influences. In all, predation predictions were supported by 54–58% of the tests. In contrast, the environmental-gradient hypothesis explained 92–96% of the observed distance to edge

TABLE 3.—Regression statistics for density vs. distance from edge for soil arthropod groups measured in a precipitation-limited environment (Saskatoon, 1997–1999) and a moderate-precipitation environment (Thunder Bay, 2000–2001). Symbols as in Table 2

Arthropod group	Characteristics [%]	(A) Precipitation-limited environment			(B) Moderate-precipitation environment		
		Slope	P	r ²	Slope	P	r ²
Spiders	Pred/Hard	−27.4	0.026	0.85	−6.6	0.041	0.80
Ants	Pred/Hard	−41.9	0.006	0.94	−4.6	0.019	0.96
Beetles	Pred/Hard	−27.6	0.003	0.97	−23.4	0.006	0.94
Centipedes L [#]	Pred/Hard	−18.0	0.01	0.90	24.8	0.008	0.90
Centipedes S [#]	Pred/Soft	−16.1	0.25	0.58	15.2	0.94	0.15
Bugs	Herb/Hard	−18.2	0.002	0.97	−8.0	0.05	0.90
Larvae	Pred/Soft	−16.1	0.16	0.53	−16.9	0.38	0.51
Diplurans	Pred/Soft	−45.3	0.46	0.29	−81.7	0.41	0.57
Springtails	Herb/Soft	10.5	0.85	0.12	−0.5	0.99	0.07
Mites	Pred/Soft	5.8	0.95	0.09	−19.5	0.55	0.12
Slugs	Herb/Soft				−45.7	0.089	0.67
Snails	Herb/Hard				−3.0	0.046	0.78
Earthworms	Herb/Soft				174	0.66	0.07
Isopods	Herb/Hard				−63.5	0.078	0.70

patterns. In additional support of the environmental-gradient hypothesis, some of the linear relationships (ants and spiders) were stronger (steeper slope) within the precipitation-limited vs. moderate-precipitation environment, suggestive of a response to decreased humidity on the prairies. And of the few arthropod groups that did not follow environmental gradient predictions, all occurred in the moderate-precipitation environment where moisture limitation was considerably reduced. This study provides correlative evidence that soil arthropod distribution relative to edges is largely determined by moisture gradients at the scale of 21 × 9.5 cm boxes. However, biotic variables likely contributed to the spatial distribution of soil arthropods, although perhaps at a different temporal scale than that investigated.

Conclusive testing of these alternative explanations will require a more detailed experimental design that incorporates a more comprehensive understanding of individual species' life histories. Therefore, interpretations of the results of this study should be tempered by recognition of the limitations of the sampling methodology (André *et al.*, 2002) that includes the coarseness of taxonomic analysis and the general lack of knowledge of diets and resistance to desiccation of individual species. The experimental design did not properly control for annual variation as the two studies at different sites were conducted one after the other rather than at the same time. Still, the precipitation-limited environment was studied over 3 y and the moderate-precipitation environment over 2 y, which incorporated at least some annual variation. Changes in the distribution and abundance of particular species, genera or families of arthropods, relative to predation and moisture, may be more important in understanding distributional changes associated with edge habitat than the general grouping of arthropods used here. Another uncontrolled effect was differences in precipitation between study sites that resulted in differences in vegetation and subsequently differences in soil-arthropod community assemblages. Once again, species-specific responses to moisture changes associated with these different communities may have been obscured by the taxonomic scale used in this study. Research into community ecology requires balancing more simple studies of predator-prey perspectives and environmental influences with

ecological system analysis that accounts for the dynamic attributes of interacting species and their response to the details of habitat structure (*e.g.*, Roland and Taylor, 1997).

Effects of a moisture gradient under boxes were more extreme for the precipitation-limited environment relative to the moderate-precipitation environment. The precipitation-limited environment was representative of temperate prairie grasslands where it is known that water limits primary productivity (Knapp *et al.*, 2001), in part, due to extreme interannual variation (Frank and Inouye, 1994). Soil moisture and rainfall are generally the strongest correlates with densities of soil-surface arthropods in grassland areas (Reddy and Venkataiah, 1990; Ferguson and Joly, 2002). Prairie environments have greater temporal variability in precipitation, whereas boreal forests have greater primary production and less variability in precipitation (Knapp and Smith, 2001). Forests, with their relatively large plants, have high production from year to year, with grasslands coming in second and deserts third (Knapp and Smith, 2001). They found a different pattern in how these three biomes responded to *fluctuations* in precipitation. Forests, which receive fairly stable amounts of annual rainfall, grow roughly the same amount in wet or dry years. In contrast, grasslands proved more extreme in rainfall and four times more variable in year-to-year rainfall than forests. In this study, the precipitation-limited study site (prairie) received considerably less precipitation, particularly during the May–September field season, and had fewer days with precipitation that resulted in longer dry periods (Ferguson, 2004a). The combination of hot days with little moisture on the prairie site resulted in lower relative humidity which would have resulted in periods of drying-out under boxes. This pattern may explain the low numbers of earthworms, slugs and snails under boxes placed on the precipitation-limited environment relative to the moderate-precipitation environment.

Soil arthropods can survive drought by physiological tolerance to loss of body water (Crowe *et al.*, 1992), evolving lessened water permeability of their integument to resist desiccation (Vannier, 1983) or moving to moist microsites during drought periods, either vertically (Hågvar, 1983) or horizontally (Verhoef and Van Selm, 1983). This latter strategy could explain changes in distribution associated with edges. Migration may enable arthropods to survive transient drought spells, but longer-lasting or extreme drought is likely to incur physiological stress. Moreover, evapotranspiration by plants tends to dry out the soil in the whole root zone, leaving soil invertebrates living in precipitation-limited environments with no moist place in which to migrate (Holmstrup *et al.*, 2001).

Soil-dwelling arthropods living in precipitation-limited environments are, therefore, likely to be physiologically stressed during summer droughts that result in loss of body water. Springtails respond to light by moving away, which is likely a response to avoid the risk of desiccation (Salmon and Ponge, 1998). Changes in movement patterns are the simplest, and perhaps most widespread, edge-mediated effect (Kareiva, 1987; Henein and Merriam, 1990; Ims, 1995; Andreassen *et al.*, 1998). Also, microclimatic conditions differ greatly across edges (*e.g.*, Chen *et al.*, 1992, 1995), thereby influencing the survival of dispersing arthropods. Surface dispersal abilities may be important in environments where suitable habitats are patchy and individuals rely on dispersal between patches to reduce risk of desiccation (Hertzberg and Leinaas, 1998; Hertzberg *et al.*, 2000). The ability of soil arthropods to physiologically adapt to drought and behaviourally disperse will modify the distribution and abundance in edge habitats. Greater structural diversity characterizes edge habitats relative to interior habitat (Harper and Macdonald, 2001) and, therefore, affects soil arthropod distribution along the edge-to-interior gradient. Previous research in the precipitation-limited environment found soil-arthropod predators located closer to edge than small arthropod prey and large predators were located closer to edge than small predators (Ferguson, 2000).

The most studied edge mediated change in species interactions is the so-called ecological trap hypothesis (Gates and Gysel, 1972) whereby nesting passerine birds behaviourally favor the edges of forest patches at the risk of increased mortality from edge-foraging generalist predators and nest parasites (Pasitschniak-Arts and Messier, 1995; but *see* Larivière, 2003). Edges that act as biological barriers (*e.g.*, Wegner and Merriam, 1979) may increase animal movement parallel to edges resulting in “travel corridors” (Bider, 1968; Kaiser, 1983). Travel corridors generate a disproportionately high frequency of interspecific contacts at edges, including predation (Gates and Gysel, 1972; Angelstam, 1986; Patterson and Messier, 2000). Use of travel corridors by predators was the mechanism proposed to explain the spatial distribution of soil arthropod predators and prey in the precipitation-limited environment (Ferguson, 2000).

However, the research results reported here indicate that moisture gradients may be a more heuristic explanation of the distribution patterns of soil arthropods under boxes. Habitat edges are a principal component of fragmentation and patch patterns (Weathers *et al.*, 2001). Habitat fragmentation and patchiness have at least as much potential to affect species interactions and communities as they do to affect population dynamics. Therefore, understanding the impact of edges is key to deciphering how community dynamics change as functions of habitat structure and spatial scale. Future experimental efforts should focus on the community impacts of habitat edges that will help understand spatial dynamics by combining movement data with information on demographics and species interactions to obtain a more complete interpretation of overall biotic and abiotic effects of edges. Monitoring soil arthropod biodiversity will provide means to assess changes in forest environments due to global climate change and conserve biodiversity.

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