Invertebrate Diversity under Artificial Cover in Relation to Boreal Forest Habitat Characteristics

STEVEN H. FERGUSON[1] and DANIELLE K. A. BERUBE[2]

[1] Fisheries and Oceans Canada, Freshwater Institute, 501 University Crescent, Winnipeg, Manitoba R3T 2N6 Canada
[2] Department of Biology, Lakehead University, 955 Oliver Road, Thunder Bay, Ontario P7B 5E1 Canada

Ferguson, Steven H., and Danielle K. A. Berube. 2004. Invertebrate diversity under artificial cover in relation to boreal forest habitat characteristics. Canadian Field-Naturalist 118(3): 386-392

We investigated invertebrate diversity in boreal forests using an experimental design that consisted of counting soil invertebrates under artificial cover. The aim was to assess the utility of using soil invertebrate diversity as a measure of ecosystem health. The study area was grouped into five habitats: upland hardwood, lowland hardwood, conifer, shrub, and conifer-grass. Simpson's and Shannon's indices of invertebrate diversity were negatively correlated with percent herbaceous cover. Number of recognizable taxonomic units (RTU richness) was negatively correlated with percent litter cover. The number of individual invertebrates was positively correlated with soil moisture and negatively correlated with percent conifer cover. Invertebrate diversity varied among habitat types, with conifer forests (spruce, fir, pine) having the highest diversity and regenerating conifer-grass forests having the lowest diversity, suggesting that successional stages affect diversity. The most productive sites, upland and lowland hardwood habitats, had the highest abundance of soil invertebrates, although intermediate diversity compared to the other five habitats. The results are consistent with the view that diversity increases and then decreases with productivity and disturbance over succession (ca. 50-100 yr). Hence, maintenance of soil invertebrate diversity in managed boreal forests requires the provision of a varied landscape with a mosaic of disturbance regimes.

Key Words: arthropods, biodiversity, conifer, earthworms, indices of diversity, moisture, Ontario.

Concerns about the effects of the widespread loss of biodiversity have prompted many recent studies investigating the relationship between biodiversity and ecosystem function (Symstad et al. 2000). Invertebrates are important in the functioning of nearly all environments, with changes in species composition potentially reflecting changes in the ecosystem (Majer 1990; Madden and Fox 1997). Hence invertebrates are increasingly being viewed as reliable indicators to assess human impacts on the general level of disturbance of an ecosystem (Majer 1983; Greenslade 1984; Andersen 1990). Biodiversity includes all levels of natural variation and thus diversity indices provide a relative measure of variation within a community (Tilman and Pacala 1993). Monitoring diversity across spatial and temporal scales allows for measurement of system complexity, functionality, and stability. Knowledge of diversity helps in understanding changes in ecosystem complexity before and after disturbance. Information on the habitat characteristics that influence diversity at various levels and knowledge of habitat changes resulting from human disturbance are required for management and conservation (Madden and Fox 1997).

Forest managers can assess diversity changes associated with human disturbances that include various forestry practices through an understanding of the relationship between animal diversity and forest structure to determine ecosystem changes (Noss 2000). Animal diversity includes soil invertebrates commonly found under logs and rocks in managed forests (Kolstrom and Lumatjarvi 1999). Downed wood is important for organisms in providing shelter and moisture, and in preventing light penetration. The use of soil fauna diversity has the potential to act as a surrogate of forest biodiversity. A number of forest characteristics have been shown to relate to soil invertebrate diversity, including understorey vegetation and litter (Bird et al. 2000), plant functional diversity (Siemann et al. 1998), coarse woody debris (Marra and Edmonds 1998), conifer species composition (Lattin 1993), forest succession (Paquin and Corderre 1997), soil moisture (MacKay et al. 1986) and structural complexity (Ferguson 2001).

To further this research, we used a method of surveying invertebrate diversity under artificial cover and relate indices of invertebrate diversity to measured forest characteristics. The study design consisted of (1) surveys of soil invertebrates (springtails, beetles, centipedes, slugs, earthworms and isopods) found under sand-filled cardboard boxes placed on the forest floor; and (2) surveys of the sampled forest characteristics (snags, logs, soil moisture, overstorey, understorey, and ground cover). Forest characteristics were used to identify habitats within a boreal forest landscape, and diversity of soil invertebrates was measured. The goal was to relate forest habitat characteristics to soil invertebrate diversity to assess their utility as surrogate measures of ecosystem changes associated with forest management practices.

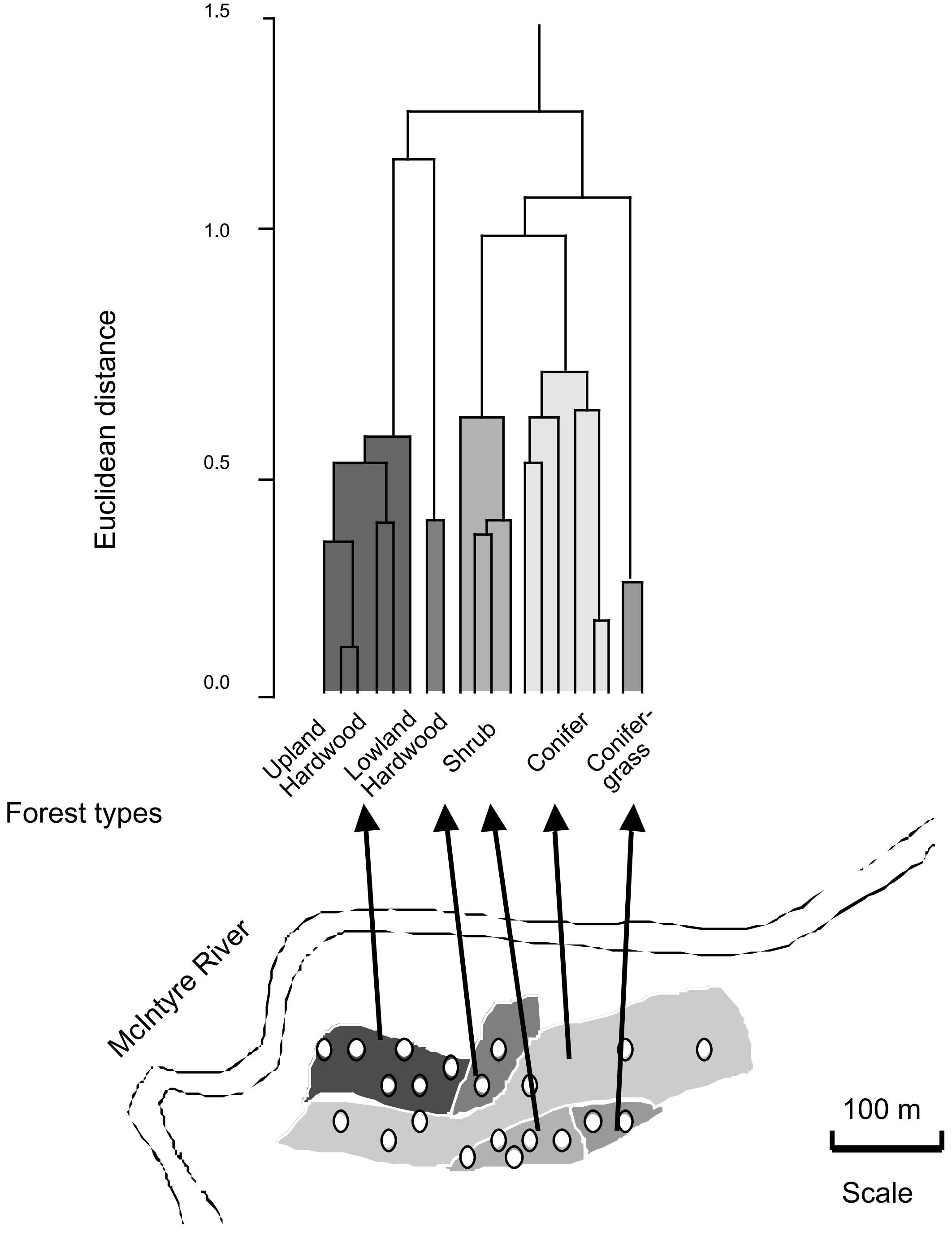

FIGURE 1. Location of study area in northwestern Ontario and dendrogram of 20 plots (0) located within a 1 km^2 stand of boreal forest grouped using cluster analysis based on forest characteristics (e.g., overstorey, understorey, ground cover, moisture, coarse-woody debris).

Study Area

The study area (Figure 1) was located in northwestern Ontario, Canada, and consisted of a 1 km^2 area of boreal forest located along the McIntyre River within Lakehead University's natural forest (48°22'N, 89°19'W). 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 (*P. 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 well-drained soils (Rowe 1972). The climate is humid continental with a mean minimum January air temperature of -15°C and a mean maximum daily air 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 air temperature (1961-1990 normals) varied from 9.0ºC in May to 17.7°C in July (annual mean = 2.4°C) and precipitation varied from 69.3 mm in May to 88.5 mm in August (annual mean = 58.6 mm) (Environment Canada 2001*).

Methods and Materials

Study design and sample plots

The sampling method was designed to assess soil invertebrate diversity under a standardized collection technique that optimized sampling replication, effort, and coarse taxonomic resolution. Coarse woody debris occurred in various shapes, sizes, and material. The use of cardboard boxes standardized the collection and reduced this variability while sampling a more diverse fauna than other methods such as pitfall traps. We decided to use a coarse taxonomic resolution (Bolger et al. 2000), thereby allowing inexperienced observers with minimal training to obtain reasonable survey counts efficiently. A trade-off associated with grouping invertebrates occurs between ease of surveys by observers with minimal taxonomic experience and the loss of more detailed guild and life history information related to individual species.

Twenty plots, each consisting of three adjacent boxes, were randomly distributed within the forest (minimum distance between plots was 5 m; Figure 1). Each box consisted of two 2-liter milk cartons with a plastic coating of red and white color. These were fitted one inside the other to create a solid box and filled with sand (approximately 2 kg) to create a footprint-sized depression 21 by 9.5 cm. Boxes depressed the leaf litter an average of 1.3 cm (Ferguson 2000), creating a microhabitat of increased humidity and decreased temperature similar to that beneath a log or rock resting on the forest floor.

Boxes were overturned and the numbers of all soil invertebrates (>1 mm) were visually counted. Boxes were lifted individually without disturbing adjacent boxes or the underlying litter. Twenty weekly surveys were conducted from 9 May to 24 September 2000 between the hours of 1100 to 1700. The survey numbers reflect a relative abundance of soil invertebrates. Observer bias was consistent across the landscape.

Recognizable Taxonomic Units (RTU; Bolger et al. 2000; Ferguson 2004) were used to group all macroinvertebrates (>3 mm) observed under boxes based on differences in size and feeding habits (Eisenbeis and Wichard 1987; Brock et al., 1994) and included springtails (Collembola), spiders (Araneae), ants (Formicidae), ant larvae, centipedes (Chilopoda), Diplura, adult flies (Diptera), phytophagous mites (Acarina: Oribatida), bugs (Hemiptera and Homoptera), Pseudoscorpionida, wasps (non-ant Hymenoptera), moth and butterfly larvae (Lepidoptera), Gastropoda (snails and slugs), Isopoda (woodlouse; *Tracheoniscus rathkei*), beetles (Coleoptera and Staphylinidae species – adults and larvae), millipedes (Diplopoda), and earthworms (Oligochaeta).

Forest characteristics measured

Site-specific habitat variables were measured 21-23 August 2000 using 5 × 5 m quadrats centered at three box plots. One quadrat was located at the centre of each plot. Four other quadrats were located 10 m from the centre in cardinal compass directions. A total of 100 quadrats were sampled for the following habitat characteristics: percent overstorey cover (>5 m), percent understorey cover (saplings and shrubs 0.5-5 m), percent herbaceous cover, percent litter cover, percent grass cover, percent moss cover, percent fern cover, number of snags (dead standing trees with dbh > 5 cm), number of decaying logs (> 5 cm diameter), percent cover by conifers, and a relative measure of soil moisture (i.e., xeric=1, mesic=2, hydric=3). Values for the five quadrats were averaged for each plot.

Measures of invertebrate diversity

Diversity of soil invertebrates was calculated for each plot across surveys using RTU richness (number of RTU at each site), Shannon-Wiener, and Simpson's Indices of Diversity (Ludwig and Reynolds 1988). Shannon's entropy (H) is a measure of species diversity used in relation to relative frequencies (probabilities) of the different species i of the sample and was calculated as:

$$H = - \sum [(n_i/n) \ln(n_i/n)] \text{, from } i=1 \text{ to } n \quad (1)$$

where n_i is the number of individuals belonging to the ith RTU in the sample and n is the total number of individuals in the sample. $H = 0$ (minimum value) when the sample contains only a single RTU, whereas diversity H increases with the number of RTUs. H is maximum when all RTUs are equally distributed in the sample. The Shannon-Wiener index of diversity is sensitive to changes in the rare species in a community sample (Pielou 1966). Invertebrate diversity was also measured by Simpson's index of diversity (Simpson 1949), which is sensitive to changes in the more abundant species and was measured as:

$$\lambda = 1- \sum n_i(n_i - 1)/n(n -1) \quad (2)$$

Simpson's index varies from 0 to 1, and gives the probability that two individuals drawn at random from a population belong to the same RTU. If the number approaches 0 then individuals belong to the same RTU and the diversity of the community sample is low. These diversity measures were calculated using the minimum number of invertebrates observed for the RTU in a given sampling period and were represented by an average value for each survey.

Statistical analysis

We performed a cluster analysis of the 11 forest measures to group the 20 sampling sites into forest habitats. Classification of habitats types was conducted by the average-linkage clustering method using a Euclidean distance similarity index (Romesburg 1984). All variables were standardized between 0 and 1.

Many (8 of 17) forest and soil invertebrate variables were not normally distributed (Wilk's statistic) and transformations (e.g., log, arc-sine) failed to normalize all variables. Therefore, we used nonparametric analyses by ranking nonparametric data before correlation analyses (Conover and Iman 1981). Measures of diversity (Simpson's and Shannon's), RTU richness, and number of individuals were normally distributed and did not require transformations. We report untransformed means in the Figures and Tables in the Results section to simplify presentations.

Analyses were performed to determine the relationship between (1) soil invertebrate diversity indices and forest characteristics, and (2) soil invertebrate numbers for each of the abundant RTU (springtails, beetles, centipedes, slugs, earthworms, and isopods) and forest characteristics. We tested for significant effects of forest characteristics on dependent measures (e.g., diversity) with Spearman's correlations and partial correlation analyses (i.e., multiple regression of ranked data without replacement). ANOVA was used to compare forest characteristics, indices of diversity, and soil invertebrate abundance relative to forest types, followed by a Tukey multiple range test if the ANOVA was significant. Spearman correlations for nonparametric data and Pearson's correlations for parametric data compared RTU abundance with forest characteristics. Sample units were the 3-box groups (n = 20) sampled every week (n = 20). All statistical analyses were done using SAS (SAS Institute Inc., Cary, North Carolina 1987) statistical software for microcomputers.

Results

Both indices of soil invertebrate diversity (Shannon's and Simpson's) were negatively related to percent herbaceous cover ($R^2 = 0.32$, $F = 5.89$, $P = 0.01$, $n = 20$ and $R^2 = 0.35$, $F = 6.64$, $P = 0.01$ respectively; Table 1, Figures 2A, and 2B). RTU richness (number of RTU) was negatively correlated with percent litter cover, which explained 48.6% of the variance in the model ($F = 17.0$, $P = 0.001$, $n = 20$; Table 1, Figure 2C). Diversity indices were also related to litter cover as herbaceous cover and litter cover covaried ($r = -0.94$). Soil moisture (69.5% of variation explained) and percent conifer cover (9%; Figure 2D) best explained the number of individual invertebrates. Greater numbers of soil invertebrates occurred in wet habitats and with less conifer cover (Table 1).

The forest measures were grouped into five forest types defined as upland hardwood, lowland hardwood (mesic), shrub, conifer, and conifer-grass (Figure 1). The upland hardwood forest consisted primarily of Trembling Aspen, with little understorey (47% cover) and the most abundant herbaceous cover (90%; Table 2). The soil invertebrate community in the upland hardwood forest consisted of numerous individuals (mean = 24/plot), moderate RTU diversity, and large numbers of isopods (Table 2). The lowland hardwood habitat consisted of mixed hardwoods in a mesic site that included an intermittent stream with a deep humus layer. The soil invertebrate community

TABLE 1. Seven multiple regression results used to determine the significant effects of 11 forest characteristics on (1) Shannon's index of diversity; (2) Simpson's index of diversity; (3) RTU richness (where RTU = recognizable taxonomic units); (4) Number of individual invertebrates, (5) springtail abundance; (6) earthworm abundance; (7) isopod abundance. Of the 11 explanatory variables included (soil moisture, % overstorey, % understorey; % herb cover; % litter; % grass; % moss; % ferns; number of snags; number of logs; and % conifer cover), only those with significant ($P < 0.05$) relationships are shown.

Dependent variable	Independent variable	Coefficient direction	Partials R^2	Model R^2	P
(1) Shannon's diversity index	% herb cover	negative	0.318	0.318	0.008
(2) Simpson's diversity index	% herb cover	negative	0.349	0.349	0.006
(3) RTU richness	% litter cover	negative	0.486	0.486	0.001
(4) Number of RTU	Soil moisture	positive	0.695	0.695	0.0001
	% conifer cover	negative	0.087	0.782	0.02
(5) Springtail abundance	% conifer cover	negative	0.224	0.224	0.04
(6) Earthworm abundance	Conifer cover	negative	0.657	0.657	0.0001
	Number of logs	positive	0.100	0.757	0.02
(7) Isopod abundance	% conifer cover	negative	0.624	0.624	0.0001

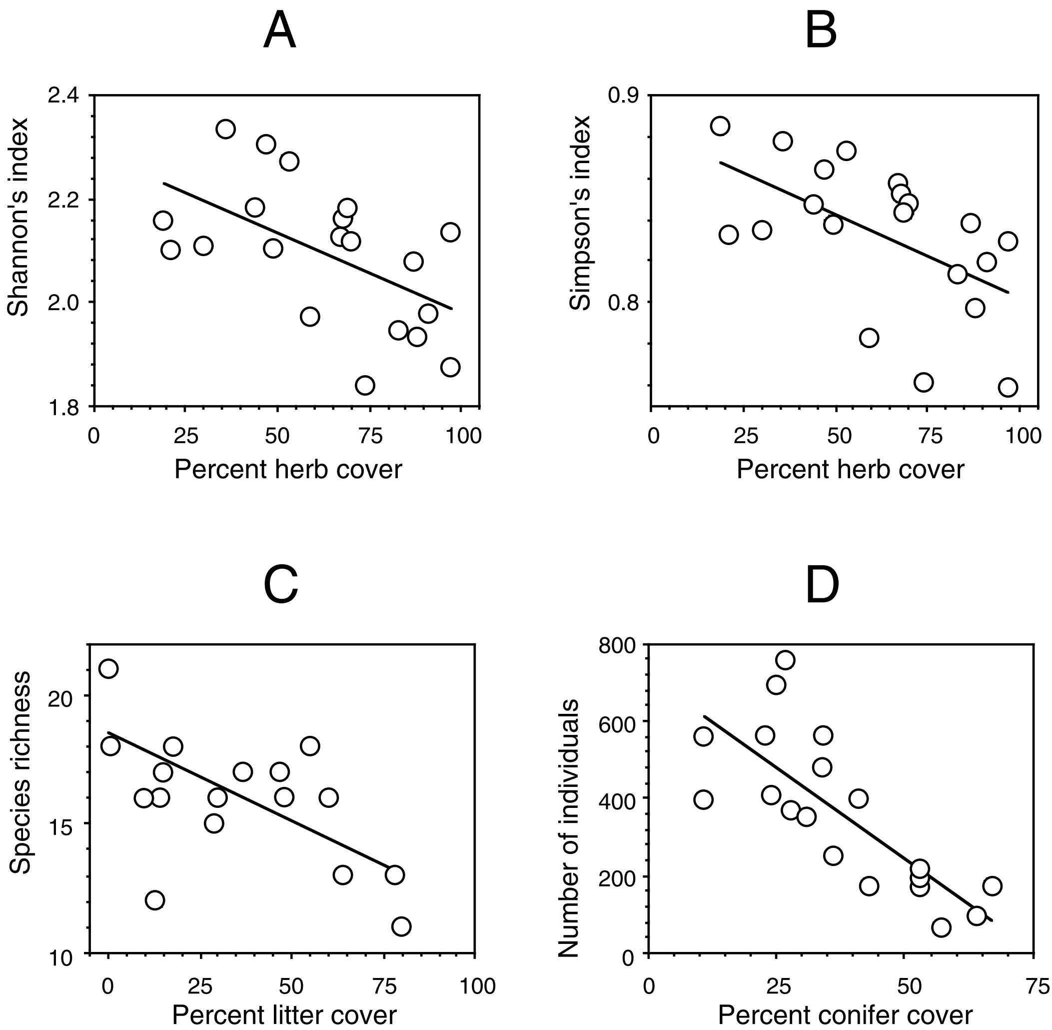

FIGURE 2. Bivariate relationships between two indices of diversity (Simpson's and Shannon's) of soil invertebrates and major explanatory habitat variables: (A) Shannon's index of diversity, and percent herbaceous cover ($y = -0.307x + 2.29$, $r^2 = 0.318$); (B) Simpson's index of diversity and percent herbaceous cover ($y = -0.0810x + 0.883$, $r^2 = 0.349$); (C) RTU richness (number of Recognizable Taxonomic Units) and percent litter cover ($y = -0.0692x + 18.6$, $r^2 = 0.486$); and (D) number of individual invertebrates and percent conifer cover ($y = -9.38x + 712$, $r^2 = 0.695$).

living in this forest consisted of moderate diversity, the greatest number of individuals (mean = 37/plot), and the most springtails and earthworms. The shrub habitat had the highest understorey cover (78%), lowest overstorey (34%), and moderate conifer and litter cover. The soil community in the shrub habitat was moderately diverse and consisted of a moderate number of individuals (mean = 16/plot). The conifer forest was the most extensive habitat and was composed of a mixed softwood/ hardwood (56/44%) forest with high overstorey cover (66%), high understorey cover (66%), low herb cover (33%), and high litter cover (64%). The conifer forest supported the highest soil invertebrate diversity although few RTU (low RTU richness) and few individuals (mean = 10/plot; Table 2). The conifer-grass forest type was represented by a relatively low overstorey (55%), intermediate understorey (56%), high conifer cover (53%) with the most grass (13%) and more herb than litter cover (66/22%). The soil invertebrate community in the conifer-grass habitat was the least diverse with the lowest RTU richness and fewest individuals per plot ($n = 9$).

The abundance of three out of the six most numerous RTU were significantly related to forest characteristics

TABLE 2. Comparison of forest and soil invertebrate characteristics for five forest types. Mean invertebrate abundances (numbers per m^2) are given for six of the more common invertebrates. Means with the same letters do not differ significantly according to Tukey's multiple range test.

			Forest types				
Variable	*F*	*P*	Upland hardwood (n = 6)	Lowland hardwood (n = 2)	Shrub (n = 4)	Conifer (n = 6)	Conifer-grass (n = 2)
Forest characteristics							
Snags	6.0	0.005	ab 13.3	a 16.0	b 4.3	ab 7.5	b 5.5
Logs	10.5	0.0003	ab 7.0	a 15.0	c 2.3	bc 2.7	c 2.0
Soil moisture	26.7	0.0001	b 0.6	a 1.4	c 0.0	c 0.1	c 0.0
Overstorey	5.1	0.008	ab 52.8	a 69.5	b 34.3	a 65.7	ab 54.5
Understorey	4.4	0.01	b 46.5	ab 54.5	a 77.8	ab 66.3	ab 56.0
Herb	28.3	0.0001	a 89.5	ab 68.5	bc 56.8	c 32.8	b 65.5
Litter	26.0	0.0001	c 2.8	cb 14.0	b 31.8	a 64.2	cb 21.5
Grass	25.7	0.0001	b 1.7	b 0.5	b 3.5	b 1.2	a 13.0
Conifer	19.0	0.0001	b 21.8	b 26.0	ab 36.0	a 55.8	a 53.0
Indices of diversity							
Shannon's	5.64	0.006	a 2.15	ab 1.99	a 2.17	a 2.19	b 1.90
Simpson's	7.37	0.002	ab 0.191	b 0.155	b 0.147	b 0.142	a 0.228
RTU richness	5.73	0.005	a 19.3	ab 17.0	ab 16.3	ab 14.5	b 14.0
Number of individuals	9.11	0.0006	ab 475	a 723	bc 313	c 190	c 179
Soil invertebrates							
Springtails	3.64	0.03	ab 67.8	a 120.5	ab 65.0	b 46.2	ab 76.5
Beetles	0.6	0.70	16.5	10.0	11.3	16.5	4.5
Centipedes	1.2	0.34	7.5	10.5	12.0	6.5	20.0
Slugs	0.8	0.52	4.0	6.0	5.3	6.3	6.0
Earthworms	8.8	0.002	a 54.5	a 116.5	ab 32.3	b 21.0	b 14.0
Isopods	5.9	0.005	a 127.3	ab 96.5	ab 64.5	b 25.3	b 14.5

(Table 1). Springtail abundance increased with greater litter cover (22.4% of variation explained; $F = 5.2$, $P = 0.04$). Earthworm abundance was negatively correlated with percent conifer cover (65.7% explained variance) and positively correlated with number of logs (10%; $F = 34.4$, $P < 0.001$). Isopod abundance was negatively related to percent conifer cover (62.4% of variation explained; $F = 29.9$, $P < 0.001$; Table 1). In contrast, beetles, centipedes, and slugs were relatively evenly distributed across forest types and their abundance was not significantly related to forest characteristics (not shown in Table 1).

Discussion

Our findings are consistent with the view that diversity is greater in the most common habitat within a varied landscape, such as a mixed-wood boreal forest (<80 y) and is often characterised by intermediate productivity and disturbance. Simpson's and Shannon's Indices of Diversity explained similar amounts of variation in the pattern of diversity of soil invertebrates with forest characteristics. Both found percent herbaceous cover the most important environmental factor explaining the pattern of soil invertebrate diversity among forest habitats. Also, both indices showed similar correlations, in magnitude and direction, such that as diversity increased the percentage of herbaceous cover decreased. In contrast to our findings, soil invertebrates from 27 orders did not differ significantly among five different landscapes (with the exception of earthworms) (Kalisz and Powell 2000).

We found a negative relation of soil invertebrate diversity with increasing composition of conifer vegetation. Few herbs and more litter are present under the conifer cover due to greater soil acidity (Kimmins 1997). Numbers of invertebrates were greater under herbaceous cover but diversity was reduced. Other studies have found invertebrates occurring in greater numbers under deciduous and herbaceous cover relative to conifer litter (Wallwork 1983; Paquin and Coderre 1997; Hammond 1997; Marra and Edmonds 1998). Within varied forest landscapes, the greatest diversity of soil invertebrates likely occurs for the most common (in time and space) successional community. In northern boreal forests this is likely for older conifer stands with greater overstorey and reduced ground vegetation understorey. Removal of conifers by natural disturbance or forest harvesting likely results in lower initial diversity with increasing diversity over time as other plants colonize the habitat (i.e., succession). We found greater invertebrate density under herbaceous cover associated with hardwood forest, but diversity was lower relative to the conifer forest. More research is required to explain these differences.

There are some limitations to the sampling methodology used in this study. Taxonomic levels lower than the one used here to identify invertebrates would certainly provide more detailed results though sampling efficiency would be reduced. Sampling was done around mid-day, which limits sampling to invertebrate groups that are active during the day (Eisenbeis and Wichard 1987). Results are limited to the invertebrates visually observed (i.e., >1 mm which may exclude arthropods such as small mites) found under boxes whereas smaller individuals and groups found in deeper soil are under-represented. Another potential concern is that ants, due to their clumped distribution and significant effects on community structure, may obscure patterns among other invertebrate groups (Madden and Fox 1997).

Diversity indices respond to both changes in species richness estimates and changes in species evenness. For example, the mesic lowland hardwood site recorded few RTU but high total density. Among those common taxa associated with the mesic lowland sites are springtails, earthworms, and isopods, which might be expected to be more abundant in moist soils. As a result, one problem with interpretation of diversity results is the possible relationship between measures of richness and diversity relative to measures of density. Both Shannon's and Simpson's indices are expected to be lowest when richness and evenness are low and to increase with richness and evenness. Shannon's index is more sensitive to richness and is impacted by the inclusion of rare taxa, while Simpson's index is more sensitive to evenness of the more common taxa. The result is usually that the two are generally correlated, although the relative ranking of sites may differ somewhat. Among the five forest types reported in Table 2, the two hardwood sites had the highest numbers of individuals. Both Shannon's and Simpson's indices are reported as moderate for these sites with higher estimates for both in the upland sites. The two conifer-grass sites yielded the lowest number of individuals. The Shannon's estimate is the lowest of the five sites while the Simpson's is the highest. Between the other two sites, which recorded somewhat higher numbers of individuals, the Shannon's estimates are the two highest while the Simpson's estimates are the two lowest. The net effect is that across all five habitat types the correlation coefficient between the Shannon and Simpson estimates for the forest stands arranged along a moisture gradient had a negative slope, although not significant, contrary to expectations. However, both indices were negatively correlated with % herb cover and positively correlated with each other. Greater replicates are required in various forest stands along environmental gradients to account for forest characteristics that covary.

Although increasing plant diversity significantly increases invertebrate diversity, local herbivore diversity is also maintained by a diversity of parasites (e.g., flies and nematodes) and predators (Siemann et al. 1998; Ferguson 2001). A community-level prediction is that invertebrate diversity increases with increasing plant species diversity, as many invertebrates forage on the leaves and litter of herbaceous plants (Symstad et al. 2000). However, if an entire functional group of plants, such as conifers, is absent from a habitat, then a landscape-level decrease in soil invertebrate diversity would occur, as many taxa are associated with the acidic soil and fungal hyphae characteristic of coniferous forest floors (Lattin 1993; Butterfield 1999). Alternatively, diversity is hypothesized to increase and decrease across the two dimensions of productivity and disturbance, respectively (Kondoh 2001). Our results conform to this view, as conifer cover had the highest diversity at the late successional stage but the lowest measure of diversity at the early conifer-grass stage. In contrast, more constant mesic hardwood habitats had high productivity and low disturbance, and showed intermediate indices of invertebrate diversity. Apparently, the pattern of invertebrate community diversity varied among habitat types according to productivity and disturbance gradients.

The decrease in soil invertebrate diversity with increasing grass cover may be due to the low nutritive value of grass and the microhabitat conditions of grassy areas. Low moisture, associated with dry grassy areas, has been found to have an adverse effect on soil invertebrate abundance due to a reduced oxygen level that degrades soil composition, increases erosion, and mobilizes carbohydrates and nutrients (Marra and Edmonds 1998). The majority of soil invertebrates are best suited to moderate moisture levels, as some species have little or no exoskeleton (e.g., earthworms) to protect against high and low soil moisture (Schaefer 1995; Ferguson 2004).

Soil invertebrate diversity was not significantly related to many of the forest characteristics. Still, the considerable diversity of invertebrates ensures that some species are adapted to many of the diverse conditions. For example, soil invertebrates did not show a relationship to the number of downed logs. This lack of a relationship with logs may have been related to the experimental technique of providing a similar microhabitat using boxes. Many soil invertebrates are known to depend on cover provided by coarse woody debris, such as downed logs, due to their provision of nutrients and protection from predators and stability of microclimatic conditions (Lattin 1993; Ferguson and Joly 2002). Slugs showed few relationships with forest characteristics and were found in a diversity of habitats. Slugs forage on larvae of beetles and flies and on cellulose and other plant polysaccharides (Port and Port 1986). Earthworms burrow in moist rich soil and feed on decaying organic matter from fallen leaves and vegetation (Edwards and Bohlen 1996). Earthworms were found to be positively associated with herbaceous cover, negatively associated with conifer cover, and positively associated with soil moisture. The major food items of centipedes are earthworms and small arthropods (Formanowicz and Bradley 1987). Although centipedes have been found to prefer moist habitats (Corey and Stout 1992), such as under logs, no significant relationships were found with the forest characteristics measured in this study.

Springtails are abundant in soil, and consume decomposing plant material and fungal hyphae (Hopkin 1997). Their abundance was negatively associated with litter cover, perhaps because it is living annual plants that provide the overwinter dead material that fungal hyphae provide as springtail food. The non-significant correlation ($P = 0.06$) of springtail abundance with herbaceous cover and the negative association with conifer composition contradicts other studies (Butterfield 1999; Paquin and Coderre 1997). A possible explanation for these differences is the differing sampling methodologies used whereby surface-dwelling springtails were sampled here, in contrast to sub-surface sampling from other studies.

Beetles showed little dependence on any of the measured forest characteristics in this study, in contrast to another study that found habitat dependencies (Fournier and Loreau 2001). Beetles are adapted to a wide range of environments partly due to their exoskeleton enabling life in a variety of moisture conditions (Eisenbeis and Wichard 1987). Isopods occur in greater abundance under stones and in damp environments (Sutton 1980), which is confirmed in this study by the positive association with relative soil moisture. Also, isopods were positively associated with herbaceous versus conifer cover, which is related to intolerance to acidic conditions of conifer soils and the greater food availability in deciduous and herbaceous forest cover (David et al. 2001). These findings differ with previous research that found isopod abundance unrelated to forest attributes (Bolger et al. 2000).

Forest management, with the goal of preserving forest biodiversity that includes soil invertebrates, needs to consider the requirements of individual taxa in boreal ecosystems by providing varied landscapes within a mosaic of forest stands. For example, climate change may profoundly influence boreal forest ecosystems and their management, via increased temperature and altered precipitation regimes (e.g., fires, etc.; Parker et al. 2000). In the boreal forest area studied here, conifer habitat had the highest diversity, although abundance and RTU richness were lower. However, our results need to be guardedly interpreted as they are based upon observations of a partly artificial system and our invertebrate diversity results are not sufficiently comprehensive to draw management conclusions. Still, monitoring soil invertebrate diversity can provide a means to assess changes in forest environments with climate warming as well as forest management practices that include silvicultural interventions to maintain forest health.

Acknowledgments

Students in the "Fish and Wildlife Practice" 4th year course offered at Lakehead University participated in data analysis. Financial support was provided by postdoctoral (SHF) and postgraduate (DKAB) funding from NSERC (Natural Sciences and Engineering Research Council) and Bowater Pulp and Paper Inc., Thunder Bay Woodlands Division.

Documents Cited (marked * in text)

Environment Canada. 2001. Canadian climate normals 1961-1990. http://www.cmc.ec.gc.ca/climate/normals/THBAY001.html. 13 February 2000.

Literature Cited

Andersen, A. N. 1990. The use of ant communities to evaluate change in Australian terrestrial ecosystems: a review and a recipe. Proceedings of the Ecological Society of Australia 16: 347-357.

Bird, S., R. N. Coulson, and **D. A. Crossley.** 2000. Impacts of silvicultural practices on soil and litter arthropod diversity in a Texas pine plantation. Forest Ecology and Management 131: 65-80.

Bolger, D. T., A. V. Suarez, K. R., Crooks, S. A. Morrsion, and **T. J. Case.** 2000. Arthropods in urban habitat fragments in southern California: area, age, and edge effects. Ecological Applications 10: 1230-1248.

Brock, T. E., M. T. Madigan, J. M. Martinko, and **J. Parder.** 1994. Biology of microorganisms, 7th ed. Prentice Hall, Englewood Cliffs, New Jersey.

Butterfield, J. 1999. Changes in decomposition rates and Collembola densities during the forestry cycle in conifer plantations. Journal of Applied Ecology 36: 92-100.

Conover, W., and **R. Iman.** 1981. Rank transformations as a bridge between parametric and nonparametric statistics. American Statistician 35: 124-129.

Corey, D. T., and **I. J. Stout.** 1992. Centipede and millipede (Chilopoda and Diplopoda) faunas in sandhill communities of Florida. American Midland Naturalist 127: 60-65.

David, J.-F., N., Malet, M.-M. Couteaux, and **J. Roy.** 2001. Feeding rates of the woodlouse *Armadillidium vulgare* on herb litters produced at two levels of atmospheric CO_2. Oecologia 127: 343-349.

Edwards, C. A., and **P. J. Bohlen.** 1996. Biology and ecology of earthworms. Wiley, New York. ISBN: 0-412-56160-3.

Eisenbeis, G., and **W. Wichard.** 1987. Atlas on the biology of soil arthropods. Springer-Verlag, Berlin. ISBN: 0-387-17764-7.

Ferguson, S. H. 2000. Predator size and distance to edge: 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. 2004. Does predation or moisture explain distance to edge distribution of soil arthropods? American Midland Naturalist 152:75-87.

Ferguson, S. H., and **D. O. Joly.** 2002. Dynamics of springtail and mite populations: the role of density dependence, predation, and weather. Ecological Entomology 27: 565-573.

Formanowicz, D. R., Jr., and **P. J. Bradley.** 1987. Fluctuations in prey density: effects on the foraging tactics of scolopendrid centipedes. Animal Behaviour 35: 453-461.

Fournier, E., and **M. Loreau.** 2001. Respective roles of recent hedges and forest patch remnants in the maintenance of ground-beetle (Coleoptera: Carabidae) diversity in an agricultural landscape. Landscape Ecology 16: 17-32.

Greenslade, P. J. M. 1984. Invertebrates and environmental assessment. Environmental Planning 3: 13-15.

Hammond, H. E. 1997. Arthropod biodiversity from *Populus* coarse woody material in north-central Alberta: a review of taxa and collection methods. Canadian Entomologist 129: 1009-1033.

Hopkin, S. 1997. Biology of springtails (Insecta: Collembola). Oxford University Press, Oxford. ISBN: 0198540841.

Kalisz, P. J., and **J. E. Powell.** 2000. Invertebrate macrofauna in soils under old growth and minimally disturbed second growth forests of the Appalachian Mountains of Kentucky. American Midland Naturalist 144: 297-307.

Kimmins, J. P. 1997. Forest ecology: a foundation for sustainable management. 2nd edition. Prentice-Hall, New Jersey. ISBN: 0-023-64071-5.

Kolstrom, M., and **J. Lumatjarvi.** 1999. Decision support system for studying effects of forest management on species richness in the boreal forest. Ecological Modelling 119: 43-55.

Kondoh, M. 2001. Unifying the relationship of species richness to productivity and disturbance. Proceedings of the Royal Society of London, Series B 268: 269-271.

Lattin, J. D. 1993. Arthropod diversity and conservation in old-growth northwest forests. American Zoologist 33: 578-587.

Ludwig, J. A., and **J. F. Reynolds.** 1988. Statistical ecology: a primer on methods and computing. John Wiley and Sons, New York. BN: 0-471-83235-9.

MacKay, W. P., S. Silva, D. C. Lightfoot, M. I. Pagani, and **W. G. Whitford.** 1986. Effect of increased soil moisture and reduced temperature on a desert soil arthropod community. American Midland Naturalist 116: 45-56.

Madden, K. E., and **B. J. Fox.** 1997. Arthropods as indicators of the effects of fluoride pollution on the succession following sand mining. Journal of Applied Ecology 34: 1239-1256.

Majer, J. D. 1983. Ants: bio-indicators of minesite rehabilitation, land-use and land conservation. Environmental Management 7: 375-383.

Majer, J. D. 1990. Rehabilitation of disturbed land: long term prospects for the decolonisation of fauna. Proceedings of the Ecological Society of Australia 16: 509-519.

Marra, J. L., and **R. L. Edmonds.** 1998. Effects of coarse woody debris and soil depth on the density and diversity of soil invertebrates on clearcut and forested sites on the Olympic Peninsula, Washington. Environmental Entomology 27: 1111-1124.

Noss, R. F. 2000. Ecological integrity: integrating environment, conservation, and health. Island Press, Washington. ISBN: 1-559-63808-7.

Paquin, P., and **D. Coderre.** 1997. Changes in soil macroarthropod communities in relation to forest maturation through three successional stages in the Canadian boreal forest. Oecologia 112: 104-111.

Parker, W. C., S. J. Colombo, M. L. Cherry, M. D. Flannigan, S. Greifenhagen, R. S. McAlpin, C. Papadopol, and **T. Scarr.** 2000. Third millennium forestry: what climate change might mean to forest and forest management in Ontario. Forest Chronicle 76: 445-454.

Pielou, E. C. 1966. The measurement of diversity in different types of biological collections. Journal of Theoretical Biology 13: 131-144.

Port, C. M., and **G. R. Port.** 1986. The biology and behaviour of slugs in relation to crop damage and control. Agricultural Zoology Review 1: 253-299.

Romesburg, H. C. 1984. Cluster analysis for researchers. Lifetime Learning Publications, Belmont, California. ISBN: 0-534-03248-6.

Rowe, J. S. 1972. Forest regions of Canada. Canadian Forestry Service, Department of the Environment Canadian Catalogue Number 47 – 1300. LC Control Number: 77375359.

SAS Institute. 1987. SAS/STAT Users Guide, Version 6, 4th edition, Volumes 1 and 2. SAS Institute, Inc. Cary, North Carolina.

Schaefer, M. 1995. Interspecific interactions in the soil community. Acta Zoological Fennica 196: 101-106.

Siemann, E., D. Tilman, J. Haarstad, and **M. Ritchie.** 1998. Experimental tests of dependence of arthropod diversity on plant diversity. American Naturalist 152: 738-750.

Simpson, E. H. 1949. Measurement of diversity. Nature 163: 688.

Sutton, S. L. 1980. Woodlice. Pergamon Press, Oxford. ISBN: 0-080-25942-1.

Symstad, A. J., E. Siemann, and **J. Haarstad**. 2000. An experimental test of the effect of plant functional group diversity on arthropod diversity. Oikos 89: 243-253.

Tilman, D., and **S. Pacala.** 1993. The maintenance of species diversity in plant communities. Pages 13-25 i*n* Species diversity in ecological communities. *Edited by* R. Ricklefs, and D. Schluter. University of Chicago Press, Chicago. ISBN: 0-226-71823-9.

Wallwork, J. A. 1983. Oribatids in forest ecosystems. Annual Review of Entomology 2: 1016-1023.

Received 16 April 2003
Accepted 23 November 2004