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# Habitat islands, forest edge and spring-active invertebrate assemblages

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**Abstract.** Forest management results in forest patches of varying sizes within a clearcut matrix. The result is a large amount of edge habitat and many small patches across the landscape. Here we describe the spring-active epigeal spider and carabid fauna found at the forest-clearcut edge of spruce forest in northern Ontario, Canada. We include two types of edge: the forest-clearcut interface and the small habitat patches formed by forest residuals within the clearcut. Spring-active forest spiders and carabids appear little affected by adjacent clearcutting activity, and some forest species, such as *Agyneta olivacea* (Emetron), *Diplocentria bidentata* (Emetron) and *Microneta viaria* (Blackwall), are more prevalent at the forested edge. Common and abundant spider species were equally recorded in forest interior and forest edge. Generally, no invasion of open-habitat species was observed within the forest, although smaller forest patches may be at higher risk.

## Introduction

Forest management has altered the natural process of stand development and patterns across the landscape due to clearcut logging pratices and fire suppression (Gluck and Rempel 1996; Johnson and Elliot 1996). In recognition of this, forest managers are moving to a paradigm of 'natural disturbance emulation' to try to maintain forest processes and biodiversity, by preserving the structural complexity of the forest and similar vegetation patterns across the landscape (Euler and Epp 2000; OMNR 2001; Lindenmayer and Franklin 2002). In practice, in the boreal forest of Canada, this approach includes cutovers varying in size from very small to over 260 ha and leaving habitat residuals within the cutovers to mimic the islands of forest left by wildfire (OMNR 2001). These patches are generally considered to be refuges for forest species. Fragmentation theory suggests that edge effects may be significant at the transition zone between forest (both fragments and the residual forest), and the clearcut habitat (Ranney et al. 1981; Murcia 1995).

Many invertebrate species respond to clearcut logging, with forest species declining on the clearcut habitat, often being replaced by open habitat species

(Huhta 1971; Coyle 1981; Klein 1989; Niemelä et al. 1993; Buddle et al. 2000). The forest-clearcut edge, therefore, provides a distinct boundary between two very different invertebrate assemblages, with high potential for the existence of edge effects. Invertebrate response to edge effects appears to vary according to the physical characteristics of the boundary between the contrasting habitats. For example, there is often an increase in species numbers as the contrasting habitats intergrade (Klein 1989; Bedford and Usher 1994) but not when the boundary is sharp (Ingham and Samways 1996; Martin and Major 2001). A more gradual gradient seems to increase the permeability of the edge.

We know from studies undertaken in urban agricultural landscapes that two invertebrate groups, carabid beetles and spiders, are sensitive to edge effects, patch size effects and landscape isolation effects (e.g., Báldi and Kisbenedek 1994; Burke and Goulet 1998). Overall species richness increases with decreased patch size, as open habitat species move into the patch (Jennings et al. 1986; Niemelä et al. 1988; Halme and Niemelä 1993; Usher et al. 1993) and forest species decline. These declines may be due to the fragment being too small to maintain viable populations, too isolated to allow effective dispersal, or the physical and biological changes associated with the creation of edges, resulting in habitat that is all edge (Niemelä et al. 1993; Ås 1993), and therefore less suitable.

However, it is not clear whether invertebrate groups such as carabids and spiders respond to fragmentation in forested landscapes. Niemelä et al. (1993) found that carabid diversity was lower in a fragmented forest landscape subject to 30 years of logging than forest on the edge of the active logging zone where mature stands were still connected to continuous old forest. However their landscape was not replicated, therefore, it is not clear whether these differences were simply a function of the high regional variability inherent in carabid (and spider) assemblages.

In forest areas, no effect of patch size has been found for carabids and spiders, unless the patches of residual forest were particularly small i.e., $< 5$ ha (Niemelä et al. 1988; Pajunen et al. 1995; Davies and Margules 1998). There is also little evidence to suggest that forest populations are adversely affected by the creation of edge (Heliölä et al. 2001). Some forest species may increase in abundance at the edge, while no forest species appear to avoid the edge. This response is contrary to that found at a forest–grassland interface in Hungary (Mágura and Tóthmérész 1997; Magura et al. 2001; Magura 2002), and may be due to the sharpness and temporary nature of the edge in production forest. In forested landscapes, the habitat at the boundary is little modified (Heliölä et al. 2001), although Harper and Macdonald (2002) observed some structural changes following edge creation. Forest–grassland ecotones, however, are less abrupt and contain a mixture of vegetation types at the edge zone (see Kotze and Samways 1999; Magura 2002). In Finland, Pajunen et al. (1995) found that young forest – old forest edges differed in ground spider species composition to interior old forest, with the diurnal hunting families (Lycosidae and Salticidae) colonising the edge but not the interior. In Maine, Jennings et al. (1988)

compared the spiders of strip clearcut habitats to intact forest. They found that no species were more prevalent within interior forest compared with residual forest in strip clearcuts although *Bathyphantes pallidus* (Banks) and *Diplocentria bidentata* (Emerton) were more abundant at the edge.

In Canada, the response of carabid and spiders to the creation of habitat edges in forested landscapes has not been previously examined. We explore whether these general responses to edge creation exist in timber production landscapes in Ontario. Here we present the results of a brief study undertaken in northwestern Ontario in spruce *Picea mariana* Mill (Pinaceae) forest. In particular we explore the questions: (1) are carabid and spider assemblages 10 and 100 m from an edge similar, and (2) are the carabid and spider assemblages within small forest remnants similar to those of intact forest?

## Method

This study was undertaken at the Rinker Lake research area (49°10′N, 89°20′W, Figure 1), about 120 km north of Thunder Bay in northwestern Ontario, Canada, in conjunction with a study by Pearce et al. (2003, 2004). They describe the spring-active carabids and spiders of this area within different stand types. Five stands within each of the spruce forest and clearcut habitats described by Pearce et al. (2004) were paired to examine the change in species composition that occurs across the edge of spruce forest following harvesting (Figure 1b, ‘E’). At each stand we established a series of four plots, one plot in each of: (1) spruce forest interior at least 100 m from the edge, (2) spruce forest 10–30 m from the edge, (3) clearcut 10–30 m from the edge, and (4) clearcut at least 100 m from the edge (Figure 2). This resulted in a total of 20 plots.

To examine the effect of creating islands of spruce forest within a clearcut landscape on carabid and spider populations, we established a single plot within each of 10 patches of spruce forest (Table 1) located throughout the study area (Figure 1b, ‘LP’, ‘SP’). All patches were entirely surrounded by clearcut.

The spruce forest stands and patches were pure black spruce on both wet and dry soils in mature previously unharvested forest with an average age of 88 years post-fire disturbance. Although the vegetation of the forest edge and interior were similar, we observed the edge environment to be lighter and the moss layer drier than the interior spruce forest. The forest patches were generally dominated by sphagnum ground cover to a much greater extent than the intact forest stands.

The clearcut plots were formerly mixed forest (5–10 years post-harvested) composed predominantly of aspen and jack pine, with lesser amounts of black spruce and balsam fir. The structure and floristic composition of the edge sites were similar to those in the clearcut interior. Generally the ground layer contained humus, bare soil and coarse woody debris, often with sporadic low shrubs present.

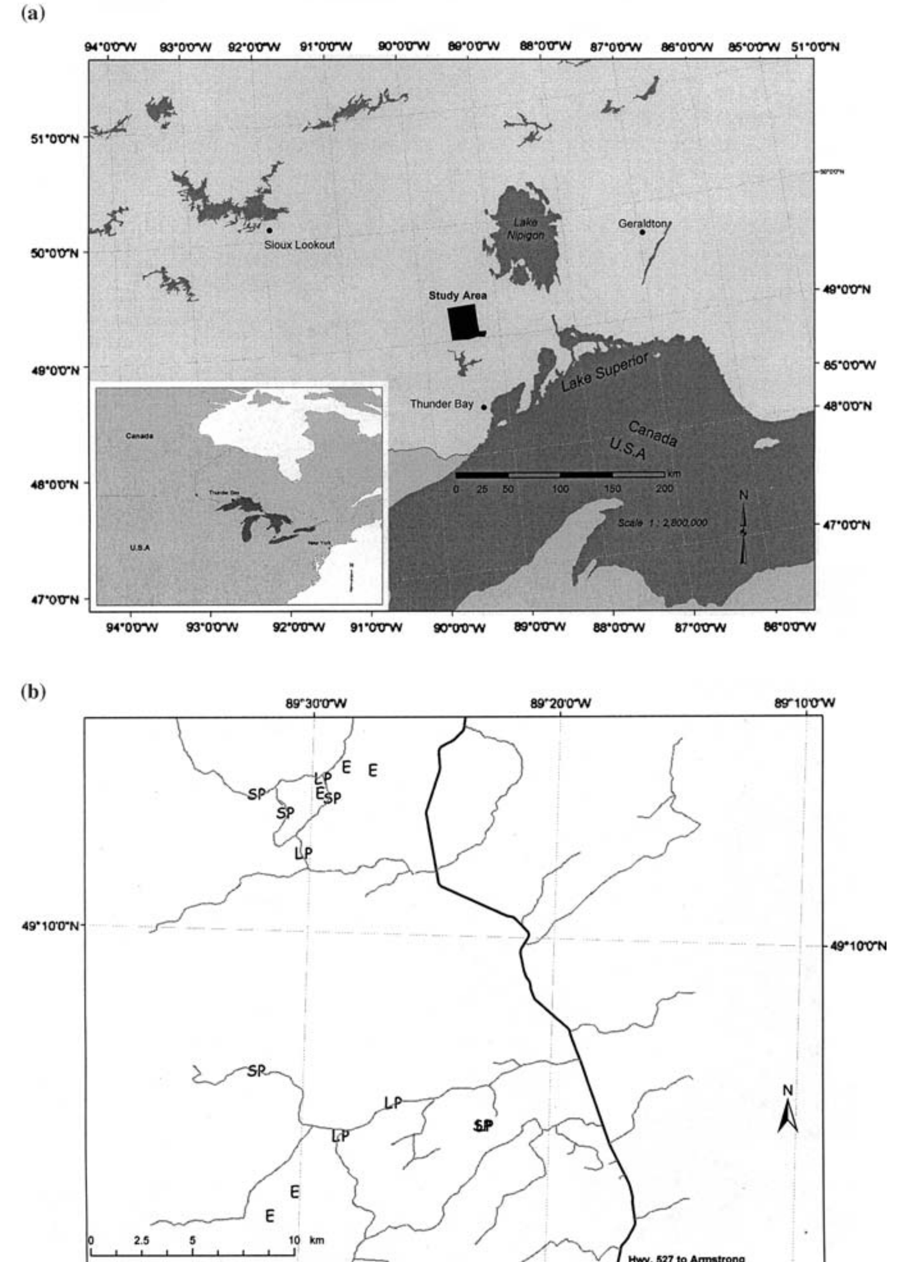


*Figure 1.* (a) Location of the Rinker Lake study area in northwestern Ontario; (b) location of each survey plot in the Rinker Lake study area.

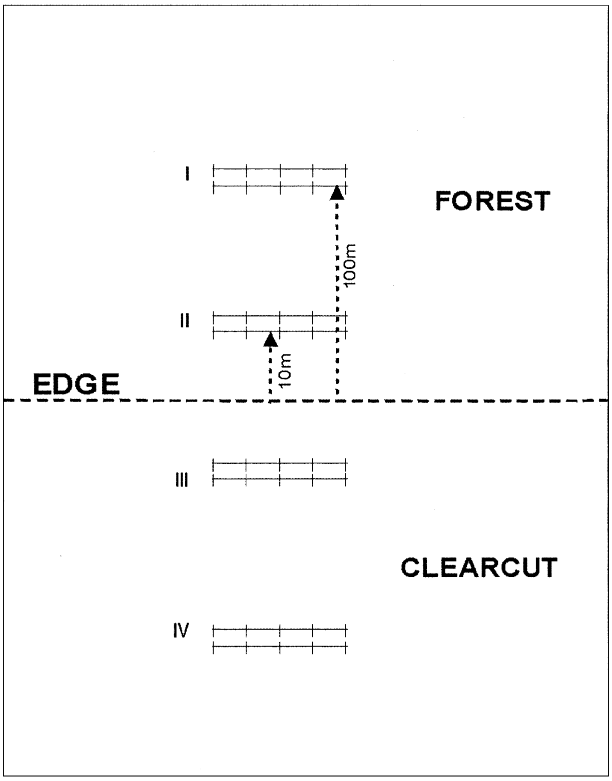


*Figure 2.* The layout of plots across each of the five spruce forest–clearcut edge habitats examined. Plots I and II are comprised of two pitfall lines located 100 and 10 m, respectively, from the forest edge in spruce forest. Plots III and IV are comprised of two pitfall trap lines located 10 and 100 m, respectively, from the forest edge in clearcut habitat.

Invertebrates were sampled at each site using pitfall traps for a total of 21 days from 6/7 June to 27/28 June 1999 and identified to species level, following the methods outlined in Pearce et al. (2003, 2004). At each plot, two parallel lines 20 m apart were installed. Each line had five traps 10 m apart, although small forest patches contained fewer traps, as they would not all fit into the forest area available (Table 1). Within patches, traps were placed at least 10 m from an edge. Due to the large number of spiders captured, only spiders from even numbered traps were identified to species level.

The spider and carabid data were standardised to number of individuals per 21 trap days (spiders: 105 trap days per plot; carabids: 210 trap days per plot) to account for trap losses and unequal sampling among stand types. Rarefaction was used to standardise the number of species recorded within each of the stand types to 39 individuals for spiders and 27 individuals for carabid beetles (Heck et al. 1975). For the most abundant species differences in mean

*Table 1.* Approximate area of the 10 forest patches and the number of traps able to be installed in each patch. na = not approximated.

| Patch | Area (ha) | Length (m) | Width (m) | Perimeter (m) | Distance to forest (m) | Total traps | Total species | Total Individuals |
|---|---|---|---|---|---|---|---|---|
| 1 | 10.8 | 223 | 52 | 522.47 | 32 | 10 | 25 | 52 |
| 2 | 3.6 | 86 | 65 | 244.20 | 27 | 10 | 29 | 90 |
| 3 | ~4 | 80 | 50 | na | 161 | 10 | 31 | 97 |
| 4 | 3.1 | 90 | 40 | 248.11 | 375 | 10 | 26 | 95 |
| 5 | 11.2 | 261 | 70 | 601.67 | 405 | 10 | 18 | 70 |
| 6 | 1.0 | 49 | 24 | 128.59 | 50 | 4 | 19 | 46 |
| 7 | ~0.7 | 60 | 20 | na | na | 4 | 19 | 80 |
| 8 | 0.5 | 24 | 20 | 78.99 | 161 | 2 | 10 | 23 |
| 9 | 3.0 | 87 | 47 | 227.83 | 77 | 7 | 30 | 54 |
| 10 | 2.5 | 63 | 44 | 197.41 | 224 | 5 | 15 | 46 |

abundance between treatments were tested using ANOVA and subsequent Scheffé multiple comparison test (of standardised abundance per plot) with an experimentwise error rate of 0.05 (Day and Quinn 1989). Species that were strongly associated with each habitat type were also identified using the indicator methods of Dufrêne and Legendre (1997), as implemented in PC-ORD (McCune and Mefford 1999). To summarise the assemblage composition of each of the stand types, the Bray–Curtis dissimilarity measure (Bray and Curtis 1957) was used to calculate a dissimilarly matrix between treatments, and isotonic non-metric-multi-dimensional scaling used to display the data (Venables and Ripley 2002).

All of the data in this study can be obtained from Venier et al. (2003).

## Results

In total 5764 individual spiders were recorded over a total of 2821 trap days, of which 87% were adults and could, therefore, be identified to species. We recorded 115 species from 13 families (Table 2). Of the carabid beetles, we recorded 670 individuals of 43 carabid species over 6643 trap days (Table 3). Of these, eight spider species (*Pardosa moesta* Banks, *Pa. mackenziana* (Keyserling), *Pirata insularis* Emerton, *Pa. hyperborea* (Thorell), *Pa. xerampelina* (Keyserling), *Pa. uintana* Gertsch, *Alopecosa aculeata* (Clerck), *Agyneta olivacea* (Emerton)) and four carabid species (*Agonum gratiosum* (Mannerheim), *Pterostichus adstrictus* Eschscholtz, *P. pensylvanicus* LeConte, *Sytomus americanus* Dejean) were abundantly recorded. Nineteen spider species (Table 3) and three carabid species (*Elaphrus clairvillei* Kirby, *Loricera pilicornis pilicornis* (Fabricius), *Pterostichus femoralis* (Kirby)) were new to the area, and were not recorded by Pearce et al. (2003, 2004).

*Table 2.* Total number of spiders recorded within each spruce-clearcut edge stand type and each spruce patch type, standardised to 105 trap days.

| Species | Family | Habitat | Forest edge study | | | | Spruce patch size study |
|---|---|---|---|---|---|---|---|
| | | | Forest–100 m | Forest–10 m | Clearcut–10 m | Clearcut–100 m | Spruce patch |
| **Forest–10 m to edge** | | | | | | | |
| *Agyneta olivacea* (Emerton) | Linyphiidae | Bogs | 12.50 | 52.50 | 10.00 | 1.00 | 140 |
| *D. bidentata* (Emerton) | Linyphiidae | Generalist | 6.00 | 17.00 | 1.00 | 4.00 | 25.17 |
| *Microneta viaria* (Blackwall) | Linyphiidae | Deciduous forest | 8.00 | 24.00 | 4.00 | 0.00 | 23.5 |
| **Clearcut–10 m to edge** | | | | | | | 0 |
| *Eperigone trilobata* (Emerton) | Linyphiidae | Generalist | 0.00 | 0.00 | 6.00 | 4.00 | 1 |
| *Haplodrassus hiemalis* (Emerton) | Gnaphosidae | Grass | 1.00 | 1.00 | 8.00 | 0.00 | 16.67 |
| *Micaria pulicaria* (Sundevall) | Gnaphosidae | Grass | 1.00 | 0.00 | 15.00 | 8.00 | 3 |
| *Neoantistea agilis* (Keyserling) | Hahniidae | Deciduous or mixed forest | 1.00 | 0.00 | 86.00 | 23.00 | 2 |
| *Zelotes puritanus* Chamberlin | Gnaphosidae | – | 0.00 | 0.00 | 6.00 | 2.00 | 0 |
| **Clearcut–100 m to edge** | | | | | | | 0 |
| *Drassodes neglectus* (Keyserling) | Gnaphosidae | Fields | 0.00 | 0.00 | 6.00 | 11.00 | 1 |
| *Gnaphosa parvula* Banks | Gnaphosidae | Fields | 0.00 | 0.00 | 1.00 | 10.00 | 3 |
| *Haplodrassus signifer* (C.L. Koch) | Gnaphosidae | Meadows | 0.00 | 4.50 | 5.00 | 13.50 | 7.5 |
| *Pardosa moesta* Banks | Lycosidae | Meadows | 1.00 | 11.75 | 408.00 | 993.00 | 52.17 |
| *Pirata minutus* Emerton | Lycosidae | Meadows | 0.00 | 0.00 | 4.00 | 17.00 | 0 |
| *Walckenaeria spiralis* (Emerton) | Linyphiidae | Bogs | 0.00 | 0.00 | 0.00 | 3.00 | 7 |
| **No clear relationship** | | | | | | | 0 |
| **Agelenopsis utahana* (Chamberlin & Ivie) | Agelenidae | Mixed forest | 0.00 | 1.00 | 0.00 | 0.00 | 0 |
| *Agroeca ornata* (Emerton) | Clubionidae | Generalist | 3.00 | 2.00 | 2.00 | 6.00 | 2.5 |
| *Alopecosa aculeata* (Clerck) | Lycosidae | Generalist | 14.50 | 31.25 | 66.00 | 54.00 | 1.5 |
| *Amaurobius borealis* Emerton | Amaurobiidae | Deciduous forest | 6.50 | 6.50 | 0.00 | 0.00 | 8.5 |
| **Antistea brunnea* (Emerton) | Haniidae | Bogs | 0.00 | 0.00 | 0.00 | 0.00 | 4 |

*Table 2.* Continued.

| Species | Family | Habitat | Forest edge study | | | | Spruce patch size study |
|---|---|---|---|---|---|---|---|
| | | | Forest–100 m | Forest–10 m | Clearcut–10 m | Clearcut–100 m | Spruce patch |
| *Aphileta misera* (O.P.-C) | Linyphiidae | Grass | 0.00 | 0.00 | 0.00 | 1.00 | 2 |
| *Arctosa raptor* (Kulczynski) | Lycosidae | Bogs | 0.00 | 0.00 | 2.00 | 3.00 | 0 |
| *Bathyphantes pallidus* (Banks) | Linyphiidae | Forest | 6.00 | 5.50 | 12.00 | 6.00 | 18.33 |
| *Callobius bennetti* (Blackwall) | Amaurobiidae | Forest | 3.00 | 1.00 | 0.00 | 0.00 | 1 |
| **Carorita limnaea* (Bishop & Crosby) | Linyphiidae | Mixed forest | 0.00 | 0.00 | 0.00 | 0.00 | 1 |
| *Centromerus furcatus* (Emerton) | Linyphiidae | – | 8.50 | 13.50 | 1.00 | 7.00 | 32.5 |
| *Ceraticelus laetabilis* (O.P.-C) | Linyphiidae | Mixed forest | 0.00 | 0.00 | 2.00 | 2.00 | 0 |
| *Ceraticelus laetus* (O.P.-C) | Linyphiidae | Deciduous forest | 0.00 | 1.25 | 2.00 | 0.00 | 0 |
| *Ceraticelus* sp. A | Linyphiidae | – | 0.00 | 0.00 | 0.00 | 1.00 | 0 |
| *Ceratinella brunnea* Emerton | Linyphiidae | Bogs | 1.00 | 1.50 | 2.00 | 1.00 | 3 |
| *Ceratinops inflatus* (Emerton) | Linyphiidae | – | 0.00 | 1.25 | 1.00 | 1.00 | 0 |
| *Ceratinopsis stativa* (Simon) | Linyphiidae | Generalist | 0.00 | 1.25 | 2.00 | 1.00 | 2.67 |
| *Cicurina brevis* Emerton | Agelenidae | Generalist | 0.00 | 1.00 | 0.00 | 1.00 | 2.5 |
| **Clubiona bryantae* Gertsch | Clubionidae | Meadows | 0.00 | 0.00 | 1.00 | 0.00 | 0 |
| *Clubiona canadensis* Emerton | Clubionidae | Forest | 3.00 | 5.50 | 0.00 | 0.00 | 3 |
| *Clubiona kastoni* Gertsch | Clubionidae | Forest | 0.00 | 0.00 | 0.00 | 2.00 | 1 |
| *Clubiona kulczynskii* Lessert | Clubionidae | Forest | 0.00 | 3.50 | 4.00 | 4.50 | 4.5 |
| **Cnephalocotes obscurus* (Blackwall) | Linyphiidae | Conifer forest | 0.00 | 0.00 | 1.00 | 0.00 | 0 |
| *Coriarachne utahensis* (Gertsch) | Thomisidae | Forest | 1.00 | 0.00 | 0.00 | 0.00 | 0 |
| *Cryphoeca exlineae* Roth | Agelenidae | – | 0.00 | 0.00 | 0.00 | 0.00 | 1 |
| *Cybaeopsis euoplus* (Bishop & Crosbie) | Amaurobiidae | Deciduous forest | 22.50 | 10.75 | 11.00 | 10.00 | 28.67 |
| *Cybaeopsis tibilis* (Emerton) | Amaurobiidae | Forest | 4.00 | 1.00 | 0.00 | 1.00 | 11.33 |
| **Dicymbium elongatum* Menge | Linyphiidae | Bogs | 0.00 | 0.00 | 0.00 | 0.00 | 7.33 |
| *Diplocephalus subrostratus* (O.P.-C) | Linyphiidae | – | 0.00 | 0.00 | 1.00 | 0.00 | 0 |
| *Dolomedes striatus* Giebel | Pisauridae | Bogs | 1.00 | 0.00 | 1.00 | 1.00 | 2 |

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| *Drassyllus depressus* (Emerton) | Gnaphosidae | Open | 0.00 | 0.00 | 1.00 | 2.00 | 0 |
| *Drassyllus niger* (Banks) | Gnaphosidae | Open | 0.00 | 0.00 | 4.00 | 2.00 | 0 |
| **Enoplognatha intrepida* (Sorensen) | Theridiidae | – | 0.00 | 0.00 | 0.00 | 0.00 | 1 |
| *Eperigone maculata* (Banks) | Linyphiidae | – | 1.00 | 0.00 | 0.00 | 0.00 | 0 |
| **Erigonine* sp. A | | – | 0.00 | 2.25 | 0.00 | 0.00 | 0 |
| **Erigonine* sp. B | | – | 0.00 | 0.00 | 0.00 | 0.00 | 1 |
| *Erigonine sp. D* | | – | 0.00 | 0.00 | 0.00 | 1.00 | 0 |
| *Euryopis argentea* Emerton | Theridiidae | Deciduous leaf Litter | 0.00 | 0.00 | 2.00 | 2.00 | 1 |
| *Evarcha hoyi* Peckham & Peckham | Salticidae | Generalist | 0.00 | 0.00 | 0.00 | 1.50 | 0 |
| **Gnaphosa brumalis* Thorell | Gnaphosidae | Bogs | 0.00 | 0.00 | 0.00 | 0.00 | 2.5 |
| *Gnaphosa muscorum* (L. Koch) | Gnaphosidae | Meadow | 0.00 | 3.75 | 26.00 | 27.00 | 0 |
| *Grammonota gigas* (Banks) | Linyphiidae | Bogs, meadows | 0.00 | 0.00 | 3.00 | 0.00 | 3 |
| *Hahnia cinerea* Emerton | Hahniidae | Mixed forest | 1.00 | 1.00 | 0.00 | 1.00 | 0 |
| *Haplodrassus eunis* Chamberlin | Gnaphosidae | Meadows | 0.00 | 0.00 | 1.00 | 0.00 | 8.5 |
| *Lepthyphantes alpinus* (Emerton) | Linyphiidae | Mixed forest | 1.00 | 1.00 | 0.00 | 0.00 | 0 |
| *Lepthyphantes complicatus* (Emerton) | Linyphiidae | Leaf litter generalist | 2.00 | 1.00 | 1.00 | 0.00 | 4 |
| *Lepthyphantes intricatus* Emerton | Linyphiidae | Deciduous forest | 0.00 | 6.00 | 4.00 | 6.00 | 9.17 |
| **Lepthyphantes turbatrix* (O.P.-C) | Linyphiidae | Bogs | 0.00 | 0.00 | 1.00 | 0.00 | 0 |
| **Lepthyphantes* sp. A | | – | 0.00 | 0.00 | 0.00 | 0.00 | 1 |
| *Lepthyphantes zebra* (Emerton) | Linyphiidae | Mixed forest | 0.00 | 0.00 | 0.00 | 0.00 | 1.67 |
| *Meioneta* sp. A | | – | 0.00 | 0.00 | 0.00 | 2.00 | 0 |
| *Metaphidippus* sp. A | | – | 1.50 | 0.00 | 0.00 | 0.00 | 0 |
| *Micaria aenea* Thorell | Gnaphosidae | Grass | 2.00 | 2.25 | 1.00 | 2.00 | 3.5 |
| *Micrargus longitarsus* (Emerton) | Linyphiidae | – | 2.00 | 0.00 | 0.00 | 0.00 | 0 |
| *Neoantistea magna* (Keyserling) | Hahniidae | Mixed forest | 0.00 | 0.00 | 1.00 | 4.00 | 0 |
| *Neon nellii* (Peckham & Peckham) | Salticidae | Mixed forest | 2.50 | 2.00 | 2.00 | 2.00 | 3.5 |
| *Neriene clathrata* (Sundevall) | Linyphiidae | Mixed forest | 0.00 | 1.00 | 0.00 | 2.00 | 1 |
| **Oedothorax trilobatus* (Banks) | Linyphiidae | Bogs | 0.00 | 0.00 | 0.00 | 0.00 | 8.33 |
| *Oreonetides recurvatus* (Emerton) | Linyphiidae | – | 0.00 | 0.00 | 0.00 | 0.00 | 1 |

*Table 2.* Continued.

| Species | Family | Habitat | Forest edge study | | | | Spruce patch size study |
|---|---|---|---|---|---|---|---|
| | | | Forest–100 m | Forest–10 m | Clearcut–10 m | Clearcut–100 m | Spruce patch |
| *Oreonetides vaginatus* (Thorell) | Linyphiidae | Coniferous leaf litter | 1.00 | 0.00 | 0.00 | 0.00 | 1 |
| *Orodrassus canadensis* Platnick & Shadab | Gnaphosidae | Conifer forest | 1.00 | 1.00 | 0.00 | 0.00 | 0 |
| *Ozyptila sincera canadensis* Dondale and Redner | Thomisidae | Forest | 13.00 | 12.75 | 14.00 | 16.00 | 20.5 |
| *Pardosa fuscula* (Thorell) | Lycosidae | Bogs | 0.00 | 0.00 | 6.00 | 8.00 | 0 |
| *Pardosa hyperborea* (Thorell) | Lycosidae | Sphagnum | 24.00 | 32.50 | 95.00 | 84.50 | 113.67 |
| *Pardosa mackenziana* (Keyserling) | Lycosidae | Conifer forest | 47.50 | 95.25 | 79.00 | 107.00 | 30.5 |
| *Pardosa* sp. | Lycosidae | – | 0.00 | 0.00 | 0.00 | 2.00 | 0 |
| *Pardosa uintana* Gertsch | Lycosidae | Spruce forest | 51.00 | 112.25 | 4.00 | 8.00 | 42.5 |
| *Pardosa xerampelina* (Keyserling) | Lycosidae | Open | 1.00 | 1.00 | 137.00 | 138.00 | 0 |
| *Pellenes montanus* Simon | Salticidae | – | 0.00 | 0.00 | 0.00 | 2.50 | 0 |
| *Pirata bryantae* Kurata | Lycosidae | Sphagnum | 6.00 | 11.50 | 7.00 | 14.00 | 12 |
| *Pirata canadensis* Dondale & Redner | Lycosidae | – | 0.00 | 0.00 | 0.00 | 1.00 | 3 |
| *Pirata insularis* Emerton | Lycosidae | Sphagnum | 32.00 | 68.00 | 16.00 | 68.00 | 119.67 |
| *Pirata montanus* Emerton | Lycosidae | Sphagnum | 17.00 | 14.00 | 1.00 | 6.00 | 9.5 |
| *Pirata zelotes* Wallace & Exline | Lycosidae | Bogs | 0.00 | 6.00 | 0.00 | 0.00 | 7 |
| *Pityophantes costatus* (Hertz) | Linyphiidae | Conifer foliage | 0.00 | 0.00 | 0.00 | 0.00 | 1 |
| *Pityophantes subarcticus* Chamberlin & Ivie | Linyphiidae | – | 1.00 | 0.00 | 0.00 | 0.00 | 0 |
| *Pocadicnemis americana* Milledge | Linyphiidae | Mixed forest bogs | 16.00 | 20.50 | 21.00 | 51.50 | 35.67 |
| *Robertus fuscus* (Emerton) | Theridiidae | Mixed forest | 0.00 | 0.00 | 0.00 | 0.00 | 1 |
| *Robertus riparius* (Keyserling) | Theridiidae | Deciduous leaf litter | 2.00 | 6.25 | 8.00 | 16.00 | 4.67 |
| **Sciastes* sp. | Linyphiidae | – | 0.00 | 0.00 | 0.00 | 0.00 | 20 |

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| *Sciastes truncatus* (Emerton) | Linyphiidae | Bogs, mixed forest | 4.00 | 4.25 | 0.00 | 0.00 | 5 |
| *Scotinotylus montanus* Milledge | Linyphiidae | – | 0.00 | 0.00 | 0.00 | 1.00 | 0 |
| **Scotinella pugnata* (Emerton) | Clubionidae | – | 0.00 | 0.00 | 0.00 | 0.00 | 1 |
| **Scotinotylus sacer* (Crosby) | Linyphiidae | Bogs | 0.00 | 4.00 | 0.00 | 0.00 | 6 |
| *Scyletria inflata* Bishop & Crosby | Lmyphiidae | Bogs | 0.00 | 0.00 | 0.00 | 1.00 | 0 |
| *Sergiolus montanus* (Emerton) | Gnaphosidae | Bogs | 0.00 | 1.00 | 0.00 | 0.00 | 0 |
| *Sisicottus montanus* (Emerton) | Linyphiidae | Generalist | 5.00 | 0.00 | 1.00 | 0.00 | 1 |
| *Theridion aurantium* Emerton | Theridiidae | Deciduous plants | 0.00 | 1.50 | 0.00 | 0.00 | 1 |
| **Theridion sp.* A | Theridiidae | – | 0.00 | 0.00 | 0.00 | 0.00 | 2 |
| **Theridion* sp. B | Theridiidae | – | 0.00 | 1.25 | 0.00 | 0.00 | 0 |
| **Theridion* sp. C | Theridiidae | – | 0.00 | 1.00 | 0.00 | 0.00 | 0 |
| *Tibellus oblongus* (Walckenaer) | Philodromidae | Tall grass | 0.00 | 0.00 | 0.00 | 1.00 | 0 |
| *Trochosa terricola* Thorell | Lycosidae | Meadows | 5.00 | 3.50 | 10.00 | 12.00 | 4 |
| *Tunagyna debilis* (Banks) | Linyphiidae | Generalist | 1.00 | 0.00 | 5.00 | 8.00 | 3 |
| *Walckenaeria atrotibialis* O.P.-C | Linyphiidae | Generalist | 5.00 | 9.50 | 6.00 | 4.00 | 3.5 |
| *Walckenaeria castanea* (Emerton) | Linyphiidae | Mixed forest | 0.00 | 0.00 | 0.00 | 3.00 | 2 |
| *Walckenaeria communis* (Emerton) | Linyphiidae | Generalist | 0.00 | 2.00 | 0.00 | 0.00 | 3 |
| *Walckenaeria directa* (O.P.-C) | Linyphiidae | Generalist | 2.00 | 5.25 | 4.00 | 3.00 | 6.5 |
| *Walckenaeria exigua* Milledge | Linyphiidae | Deciduous and mixed forest | 2.00 | 1.00 | 3.00 | 0.00 | 8.5 |
| *Walckenaeria lepida* (Kulczynski) | Linyphndae | Bogs, conifer litter | 1.00 | 0.00 | 0.00 | 0.00 | 1 |
| *Walckenaeria minuta* (Emerton) | Linyphiidae | – | 2.00 | 1.00 | 3.00 | 3.00 | 1 |
| *Walckenaeria pallida* (Emerton) | Linyphiidae | Deciduous and mixed forest | 0.00 | 0.00 | 0.00 | 0.00 | 2 |
| *Walckenaeria tricornis* (Emerton) | Linyphiidae | – | 17.00 | 15.75 | 3.00 | 4.50 | 28.5 |
| *Xysticus britcheri* Gertsch | Thomisidae | Forest | 1.00 | 1.00 | 2.00 | 0.00 | 2.5 |
| *Xysticus canadensis* Gertsch | Thomisidae | – | 5.50 | 5.00 | 0.00 | 0.00 | 0 |
| *Xysticus emertoni* Keyserling | Thomisidae | Fields | 0.00 | 0.00 | 7.00 | 8.00 | 0 |
| *Xysticus luctuosus* (Blackwall) | Thomisidae | Forest | 2.00 | 1.00 | 1.00 | 4.00 | 4 |
| *Xysticus obscurus* Collett | Thomisidae | Conifer forest | 3.00 | 3.00 | 0.00 | 1.00 | 1 |

*Table 2.* Continued.

| Species | Family | Habitat | Forest edge study | | | | Spruce patch size study |
|---|---|---|---|---|---|---|---|
| | | | Forest–100 m | Forest–10 m | Clearcut–10 m | Clearcut–100 m | Spruce patch |
| *Xysticus triguttatus* Keyserling | Thomisidae | Meadows | 0.00 | 0.00 | 0.00 | 2.50 | 0 |
| *Zelotes fratris* Chamberlin | Gnaphosidae | Generalist | 6.00 | 2.25 | 11.00 | 8.50 | 2 |
| Total number individuals | | | 381 | 602 | 1162 | 1788 | 653 |
| Mean number individuals per plot[a] | | | $78^{A}$ | $132^{AB}$ | $232^{BC}$ | $367^{C}$ | 98 |
| Total number species | | | 56 | 61 | 64 | 70 | 83 |
| Mean number of species per plot[b] | | | 54.4 | 28.4 | 32.8 | 32.6 | 22.5 |
| Expected number species[c] | | | $17.01^{A}$ | $15.35^{A}$ | $13.42^{AB}$ | $10.14^{B}$ | 16.14 |

Typical habitat information is derived from the taxonomic literature (Levi 1957; Leech 1972; Opell and Beatty 1976; Dondale and Redner 1978; Platnick and Dondale 1992) and Aitchison-Benell and Dondale (1990). Species not previously recorded in the study area are marked with an asterik.

[a] $F_{3,\,16} = 14.23$, $p < 0.001$.

[b] $F_{3,\,16} = 2.76$, $p < 0.076$.

[c] $F_{3,\,16} = 9.49$, $p < 0.001$.

*Table 3.* Total number of carabids recorded within each spruce-clearcut edge stand type and each spruce patch type, standardised to 210 trap days. Typical habitat information is derived from Lindroth (1961–1969). Species not previously recorded in the area are marked with an asterisk.

| Species | Habitat | Forest edge study | | | | Forest patch study |
|---|---|---|---|---|---|---|
| | | Forest −100 m | Forest −10 m | Clearcut −10 m | Clearcut −100 m | Spruce patch |
| **Clearcut** | | | | | | |
| *Harpalus solitaris* Dejean | Open | 0.00 | 0.00 | 2.00 | 11.17 | 0.00 |
| **Exterior (clearcut) edge** | | | | | | |
| *Syntomus americanus* (Dejean) | Open | $0.00^{A}$ | $1.00^{A}$ | $37.28^{B}$ | $8.03^{AB}$ | 0.00 |
| **No clear relationship** | | | | | | |
| *Agonum cupripenne* (Say) | Open | 0.00 | 0.00 | 2.03 | 2.03 | 0.00 |
| *Agonum gratiosum* (Mannerheim) | Open/peat | $6.17^{A}$ | $27.38^{A}$ | $35.00^{A}$ | $23.00^{A}$ | 41.25 |
| *Agonum retractum* LeConte | Mixedwood | 0.00 | 1.03 | 11.00 | 5.00 | 6.43 |
| *Agonum superioris* Lindroth | Open | 0.00 | 0.00 | 0.00 | 2.00 | 0.00 |
| *Amara lunicollis* Schiodte | Open | 0.00 | 0.00 | 0.00 | 1.00 | 0.00 |
| *Badister obtusus* LeConte | Open | 0.00 | 0.00 | 1.00 | 11.00 | 0.00 |
| *Bembidion fortestriatum* (Motschulsky) | Swamp | 0.00 | 0.00 | 0.00 | 5.00 | 0.00 |
| *Bembidion grapii* Gyllenhal | Open | 0.00 | 0.00 | 0.00 | 1.00 | 0.00 |
| *Bembidion mutatum* Gemminger & Harold | Open | 0.00 | 0.00 | 5.03 | 12.31 | 0.00 |
| *Bembidion quadrimaculatum oppositum* Say | Open | 0.00 | 0.00 | 4.14 | 0.00 | 0.00 |
| *Bembidion muscicola* Hayward | | 0.00 | 0.00 | 0.00 | 1.00 | 0.00 |
| *Bembidion transparens* (Gebler) | Swamp | 0.00 | 0.00 | 0.00 | 1.00 | 0.00 |
| *Bradycellus lugubris* (LeConte) | Open | 0.00 | 0.00 | 1.00 | 34.00 | 0.00 |
| *Bradycellus neglectus* (LeConte) | Open | 0.00 | 0.00 | 0.00 | 1.00 | 0.00 |
| *Calathus ingratus* Dejean | Deciduous forest | 0.00 | 1.03 | 1.00 | 0.00 | 0.00 |
| *Carabus serratus* Say | Open | 0.00 | 0.00 | 0.00 | 2.03 | 0.00 |
| *Cicindela longilabris longilabris* Say | Open | 0.00 | 0.00 | 2.03 | 5.07 | 0.00 |
| *Clivina fossor* (Linné) | Open | 0.00 | 0.00 | 0.00 | 3.00 | 0.00 |
| *Cymindis cribricollis* Dejean | Open | 0.00 | 0.00 | 1.00 | 0.00 | 0.00 |
| **Elaphrus clairvillei* Kirby | Riparian | 0.00 | 1.07 | 0.00 | 0.00 | 0.00 |
| *Harpalus fulvilabrus* Mannerheim | Open/deciduous forest | 0.00 | 0.00 | 2.00 | 0.00 | 0.00 |

*Table 3.* Continued.

| Species | Habitat | Forest edge study | | | | Forest patch study |
|---|---|---|---|---|---|---|
| | | Forest −100 m | Forest −10 m | Clearcut −10 m | Clearcut −100 m | Spruce patch |
| *Harpalus innocuus* LeConte | Open | 0.00 | 0.00 | 5.00 | 5.00 | 0.00 |
| *Harpalus laticeps* LeConte | Open | 0.00 | 0.00 | 0.00 | 1.00 | 0.00 |
| *Harpalus megacephalus* LeConte | Forest | 0.00 | 0.00 | 0.00 | 1.00 | 0.00 |
| *Harpalus pensylvanicus* (DeGeer) | Open | 0.00 | 0.00 | 0.00 | 1.00 | 0.00 |
| *Harpalus somnulentus* Dejean | Open | 0.00 | 0.00 | 0.00 | 4.00 | 0.00 |
| **Loricera pilicornis pilicornis* (Fabricius) | Open | 0.00 | 0.00 | 1.00 | 0.00 | 0.00 |
| *Patrobus foveocollis* (Eschscholtz) | Forest | 0.00 | 0.00 | 0.00 | 1.00 | 0.00 |
| *Platynus decentis* (Say) | Forest | 1.03 | 2.07 | 1.00 | 0.00 | 1.00 |
| *Platynus mannerheimi* (Dejean) | Sphagnum forest | 3.21 | 2.14 | 3.00 | 0.00 | 1.00 |
| *Poecilus lucublandus lucublandus* (Say) | Open | 0.00 | 0.00 | 10.07 | 13.17 | 0.00 |
| *Pterostichus adstrictus* Eschscholtz | Generalist | $5.18^{A}$ | $7.17^{A}$ | $10.10^{A}$ | $12.03^{A}$ | 0.00 |
| *Pterostichus brevicornis* (Kirby) | Forest | 0.00 | 2.07 | 0.00 | 0.00 | 0.00 |
| *Pterostichus coracinus* (Newman) | Forest | 0.00 | 0.00 | 0.00 | 1.00 | 0.00 |
| * *Pterostichus femoralis* (Kirby) | Open | 0.00 | 0.00 | 1.00 | 0.00 | 0.00 |
| *Pterostichus pensylvanicus* LeConte | Forest | $2.03^{A}$ | $1.00^{A}$ | $19.03^{A}$ | $12.07^{A}$ | 4.07 |
| *Pterostichus punctatissimus* (Randall) | Conifer forest | 5.21 | 1.00 | 0.00 | 0.00 | 1.00 |
| *Sphaeroderus nitidicollis brevoorti* LeConte | Forest | 0.00 | 0.00 | 0.00 | 0.00 | 1.00 |
| *Synuchus impunctatus* (Say) | Open | 0.00 | 0.00 | 9.00 | 10.00 | 1.43 |
| *Trechus apicalis* Motschulsky | Swamp | 3.21 | 0.00 | 1.00 | 5.00 | 2.73 |
| *Trechus crassiscapus* Lindroth | Swamp | 3.10 | 1.00 | 1.00 | 0.00 | 3.00 |
| Total number individuals | | 27 | 45 | 165 | 192 | 42 |
| Mean number individuals per plot[a] | | $5.40^{A}$ | $9.07^{A}$ | $33^{B}$ | $38.47^{B}$ | 0.61 |
| Total number of species | | 7 | 12 | 24 | 30 | 11 |
| Mean number species per plot[b] | | $2.6^{A}$ | $4^{A}$ | $10^{B}$ | $11.6^{B}$ | 0.42 |
| Expected number species | | 7 | 8.74 | 11.13 | 14.14 | – |

[a] $F_{3,16} = 9.52$, $p = 0.001$.
[b] $F_{3,16} = 9.52$, $p = 0.001$.

*Edge effects*

Within the spruce forest, the spider and carabid assemblages were similar at 10 m from the edge and 100 m from the edge (Figure 3). Both forested habitats were characterised by high spider diversity, with 73% of species represented by less than 10 individuals, and very low carabid diversity. In both groups, species were almost exclusively forest-inhabiting or generalist species (Tables 2 and 3).

Similar numbers of spider individuals and species were recorded at the forested edge and the forest interior, with three Linyphiid species significantly associated with edge forest: *Agyneta olivacea* (indicator value = 69.1, $p = 0.006$), *Microneta viaria* (Blackwall) (indicator value = 53.3, $p = 0.034$) and *D. bidentata* (indicator value = 48.6, $p = 0.045$) (Table 2). No carabid species were significantly associated with the edge habitat although more individuals and species were recorded there compared to the interior forest (Table 3).

Within the clearcut habitats the spider species composition was highly similar (Figure 3) and dominated by *Pardosa moesta* ($F_{3,\ 16} = 61.8$, $p < 0.010$) and *P. xerampelina* ($F_{3,\ 16} = 15.94$, $p < 0.010$) (Table 2). *Pardosa moesta* was more prevalent at clearcut habitats 100 m from the edge (indicator value = 70.2, $p = 0.004$), as were *Drassodes neglectus* (Keyserling) (indicator value = 51.8, $p = 0.032$), *Gnaphosa parvula* Banks (indicator value = 90.9, $p = 0.002$), *Haplodrassus signifer* (CL Koch) (indicator value = 58.7, $p = 0.016$), *Pirata minutus* Emerton (indicator value = 64.8, $p = 0.027$) and *Walckenaeria spiralis* (Emerton) (indicator value = 60.0, $p = 0.041$) (Table 3). These species have all been identified as open habitat species elsewhere (Table 2). A similar assemblage of families, but different species, were identified through indicator analysis as significantly associated with clearcut habitat 10 m from the edge, although only a few individuals of each species were recorded: *Haplodrassus hiemalis* (Emerton) (indicator value = 64.0, $p = 0.031$), *Micaria pulicaria* (Sundervall) (indicator value = 62.5, $p = 0.009$), *Zelotes puritanus* Chamberlin (indicator value = 60.0, $p = 0.019$), *Eperigone trilobata* (Emerton) (indicator value = 48.0, $p = 0.045$), and *Neoantistea agilis* (Keyserling) (indicator value = 78.2, $p = 0.007$) (Table 3). These species have been identified associated with various forested and non-forested habitats elsewhere (Table 2).

Within the clearcut habitat, some differences in species composition were observed for carabid beetles between 10 and 100 m from the edge, although the number of species and inviduals recorded was similar (Table 3). *Syntomus americanus* was identified as associated with habitat 10 m from the forest edge, forming a greater proportion of the carabid sample at these locations ($H_3 = 16.79$, $p < 0.001$; indicator value = 80.5, $p = 0.002$). *Harpalus solitaris* Dejean was almost exclusively recorded within clearcut habitat 100 m from the edge (indicator value = 67.9, $p = 0.015$). Other species such as *Bradycellus lugubris* and *Badister obtusus* were also predominantly recorded within clearcut 100 m from the edge, although they were only recorded at a few plots. Across the edge from the forest interior to the clearcut, there was a linear increase in the number of species and individuals (Table 3). There were more forest

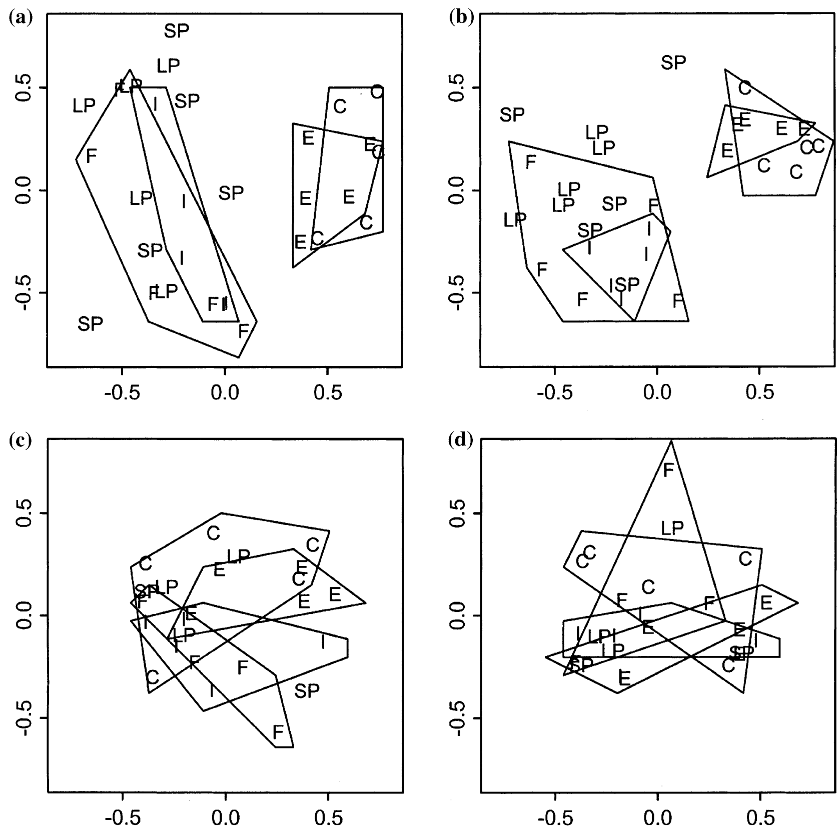

*Figure 3*. Non-metric multidimensional scaling ordination of spider assemblage (a) in 1st and 2nd and (b) 1st and 3rd dimensions, and carabid assemblage in (c) 1st and 2nd dimension and (d) 1st and 3rd dimensions. The symbols refer to each plot type: C = clearcut 100 m from edge, E = clearcut 10 m from edge, I = forest 10 m from edge, F = forest 100 m from edge, LP = the five largest patches and SP the five smallest patches. In the carabid ordination, 5 patches and 1 forest site 100 m from edge recorded only a single species and so were not considered in the ordination. Polygons enclosing each of the four edge treatments are overlain on each ordination graph.

specialists (10 m 21%, 100 m 9%) and more habitat generalists (10 m 28%, 100 m 19%) at 10 m, than at 100 m from the edge. Open habitat specialists dominated the clearcut 100 m from the edge (66% of individuals).

## *Patch size*

Similar numbers of spider individuals and species were recorded within the spruce forest patches and intact forest, although the smaller spruce patches contained more open habitat spiders, such as *Pardosa hyperborea, P. moesta* and *Haplodrassus hiemalis*, than the other forested habitats. *Pardosa hyperborea* has been predominantly described from *sphagnum* habitats elsewhere (Dondale and Redner 1990), but was most abundant in the study area within clearcut habitats (Pearce et al. 2004). However, other abundant open-habitat spiders such as *Pardosa xerampelina* and *Neoantistea agilis* were absent within the patches.

Very few carabid beetles were recorded in the spruce patches, with similar numbers of individuals and species recorded among all spruce habitat types (Table 3). The intact forest sites (100 m from the edge) were characterised by greater proportions of *Pterostichus punctatissimus* and *Platynus mannerheimi* than the forest patches, and *Pterostichus adstrictus* was absent from the patches.

## Discussion

Clearcutting appears to have little negative impact on the spring-active spider assemblage occupying the remaining spruce forest. Forest spiders did not appear to be excluded from the spruce forest edge environment and no invasion of species from the adjacent open habitat was observed, except within very small forest patches. Some forest spider populations were more abundant 10 m from the forest edge (e.g., *Agyneta olivacea, D. bidentata, Microneta viaria)*, although most forest species were equally prevalent in all spruce habitats with no species restricted to any particular forest habitat. Jennings et al. (1988) have also identified *D. bidentata* as more prevalent at forest edges than interior forest.

Within the carabid assemblage, so few carabids were recorded in the spruce forest that it was difficult to compare edge and interior sites within the forest. However, *Pterostichus punctatissimus* may be more prevalent within the interior forest. No carabid species were clearly identified as edge specialists, although a few sites contained greater numbers of *Agonum gratiosum* at the edge. A larger study would be required to confirm both these relationships and to examine their occurrence in relation to microclimatic factors such as temperature and humidity that may be altered at the edge.

Edge effects were more apparent within the clearcut habitats for carabid beetles, with a greater proportion of habitat generalists and forest species occurring at the clearcut edge, in contrast to a greater proportion of open habitat species in the clearcut interior. Koivula (2002) also found a gradient in species composition occurring with increased distance from a forested edge in Finland. The clearcut edge may provide a less harsh environment due to shading from the adjacent forest. Smaller differences in spider assemblages were found within the clearcut habitats 10 and 100 m from the edge, although five spider species were associated with the clearcut edge in small numbers. The most abundant of these, *Neoantistea agilis*, was described by Opell and Beatty (1976) as typically associated with deciduous or mixed forest. However, in the study area it was abundantly recorded only within the clearcut habitats (Pearce et al. 2004).

Small patches are more likely to have fewer species and individuals than nearby contiguous forest because: (1) as area increases, the range of microhabitats present is also likely to increase, (2) in a large area it is more likely that uncommon species that live at low densities will be encountered, and (3) large habitats will on average support larger populations, and species are thus less likely to go extinct. Given these conditions, the invertebrate fauna of the spruce forest patches within the clearcut matrix appeared similar to that of interior spruce forest. Leaving larger spruce forest patches is preferable, as these were more likely to contain a greater complement of the spruce forest fauna. Small forest patches tended to maintain common and abundant species only, and within the spider fauna at least, were more likely to be occupied by species from the clearcut matrix. Patches less than 3 ha in size may be too small to function effectively, unless very close to other forest patches.

Although edge effects can influence both adjoining ecosystems, only the effect on the remnant forest patch is of concern to forest managers (Murcia 1995). We know that clearcutting creates increased habitat diversity within a landscape and supports a wide range of open habitat carabid and spider species (Duchesne and McAlpine 1993; Niemelä et al. 1993; Beaudry et al. 1997). However, increasing diversity should not be the goal of forest management. The goal should be maintaining forest ecosystem processes and functions, and thus biodiversity. Edge effects within the forest ecosystem that negatively impact on the forest populations may indicate a detrimental impact of management on the forest ecosystem.

As found in European studies (Niemelä et al. 1988; Pajunen et al. 1995; Heliölä et al. 2001) spring-active carabid and spiders in the study area appear quite plastic to small changes within their forested environment. They appear able to persist within forest edges or remnants, and some species may be particularly associated with these environments. This study adds to the larger body of evidence suggesting that forest populations of spiders are not adversely affected by the creation of edge in forested landscapes. A larger study within a more productive habitat type (such as aspen or mixedwood types, Pearce et al. 2003) is required to confirm these results for carabid beetles. Sample sizes and species diversity here, were too small for differences to be reliably detected.

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## References

Aitchison-Benell C.W. and Dondale C.D. 1990. A checklist of Manitoba spiders (Araneae) with notes on geographic relationships. Le Naturaliste Canadien 117: 215–237.

Ås S. 1993. Are habitat islands islands? Woodliving beetles (Coleoptera) in deciduous forest fragments in boreal forest. Ecography 16: 219–228.

Báldi A. and Kisbenedek T. 1994. Comparative analysis of edge effect on bird and beetle communities. Acta Zoologica Academiae Scientiarum Hungaricae 40: 1–14.

Beaudry S., Duchesne L.C. and Côté B. 1997. Short-term effects of three forestry practices on carabid assemblages in a jack pine forest. Can. J. Forest Res. 27: 2065–2071.

Bedford S.E. and Usher M.B. 1994. Distribution of arthropod species across the margin of farm woodlands. Agr. Ecosys. Environ. 48: 295–305.

Bray J.R. and Curtis J.T. 1957. An ordination of the upland communities of southern Wisconsin. Ecol. Monogr. 27: 325–349.

Buddle C.M., Spence J.R. and Langor D.W. 2000. Succession of boreal forest spider assemblages following wildfire and harvesting. Ecography 23: 424–436.

Burke D. and Goulet H. 1998. Landscape and area effects on beetle assemblages in Ontario. Ecography 21: 472–479.

Coyle F.A. 1981. Effects of clearcutting on the spider community of a southern Appalachian forest. J. Arachnol. 9: 285–298.

Davies K.F. and Margules C.R. 1998. Effects of habitat fragmentation on carabid beetles: experimental evidence. J. Animal Ecol. 67: 460–471.

Day R.W. and Quinn G.P. 1989. Comparison of treatments after an analysis of variance in ecology. Ecol. Monogr. 59: 433–463.

Dondale C.D. and Redner J.H. 1978. The Insects and Arachnids of Canada. Part 5. The Crab Spiders of Canada and Alaska (Araneae: Philodromidae and Thomisidae). Agriculture Canada. Publication No. 1663, Ottawa, Canada.

Dondale C.D. and Redner J.H. 1990. The Insects and Arachnids of Canada. Part 17. The Wolf Spiders, Nurseryweb Spider, and Lynx Spiders of Canada and Alaska (Araneae: Lycosidae, Pisauridae, and Oxyopidae). Agriculture Canada. Publication No. 1856, Ottawa, Canada.

Duchesne L.C. and McAlpine R.S. 1993. Using Carabid Beetles (Coleoptera: Carabidae) as a Means to Investigate the Effect of Forestry Practices on Soil Diversity. Forestry Canada Petawawa National Forestry Institute: Chalk River, Ontario, Canada, Report No. 16.

Dufrêne M. and Legendre P. 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. Ecol. Monogr. 67: 345–366.

Euler D.L. and Epp A.E. 2000. A new foundation for Ontario forest policy for the 21st century. In: Perera A.H., Euler D.L. and Thompson I.D. (eds), Ecology of a Managed Terrestrial Landscape: Patterns and Processes in Forest Landscapes in Ontario. Vancouver, British Columbia, pp.276–294.

Gluck M.J. and Rempel R.S. 1996. Structural characteristics of post wildfire and clearcut landscapes. Environ. Monit. Assess. 39: 435–450.

Halme E. and Niemelä J. 1993. Carabid beetles in fragments of coniferous forest. Ann. Zool. Fenn. 30: 17–30.

Harper K.A. and Macdonald S.E. 2002. Structure and composition of edges next to regenerating clear-cuts in mixed-wood boreal forest. J. Veg. Sci. 13: 535–546.

Heck K.L. Jr., van Belle G. and Simberloff D. 1975. Explicit calculation of the rarefaction diversity measurement and the determination of sufficient sample size. Ecology 56: 1459–1461.

Heliölä J., Koivula M. and Niemelä J. 2001. Distribution of carabid beetles (Coleoptera, Carabidae) across a boreal forest-clearcut ecotone. Conserv. Biol. 15: 370–377.

Huhta V. 1971. Succession in the spider communities of the forest floor after clear-cutting and prescribed burning. Ann. Zool. Fenn. 8: 483–542.

Ingham D.S. and Samways M.J. 1996. Application of fragmentation and variegation models to epigaeic invertebrates in South Africa. Conserv. Biol. 10: 1353–1358.

Jennings D.T., Houseaert M.W., Dondale C.D. and Redner J.H. 1988. Spiders (Araneae) associated with strip-clearcut and dense spruce-fir forests of Maine. J. Arachnol. 16: 55–70.

Jennings D.T., Houseweart M.W. and Dunn G.A. 1986. Carabid beetles (Coleoptera: Carabidae) associated with strip clearcut and dense spruce-fir forests of Maine. Coleopts. Bull. 40: 251–263.

Johnson M.H. and Elliot J.A. 1996. Impacts of logging and wildfire on an upland black spruce community in northwestern Ontario. Environ. Monit. Assess. 39: 283–297.

Klein B.C. 1989. Effects of forest fragmentation on dung and carrion beetle communities in central Amazonia. Ecology 70: 1715–1725.

Koivula M. 2002. Boreal carabid beetles (Coleoptera, Carabidae) assemblages in thinned unevenaged and clearcut spruce stands. Ann. Zool. Fenn. 39: 131–149.

Kotze D.J. and Samways M.J. 1999. Invertebrate conservation at the interface between the grassland matrix and natural Afromontane forest fragments. Biodiv. Conserv. 8: 1339–1363.

Leech R. 1972. A revision of the nearctic Amaurobiidae (Arachnida: Araneida). Mem. Entomol. Soc. Can. 84: 1–182.

Levi H.W. 1957. The spider genera Enoplognatha, Theridion and Paidisca in America north of Mexico (Araneae, Theridiidae). Bull. Am. Mus. Nat. Hist. 112: 1–123.

Lindenmayer D.B. and Franklin J.F. 2002. Conserving Forest Biodiversity: A Comprehensive Multiscaled Approach. Island Press, Washington.

Lindroth C.H. 1961–1969. The Ground-Beetles (Carabidae, excl. Cicindelinae) of Canada and Alaska. (Suppl.) 20 (1961), 24 (1963), 29 (1966), 33 (1968), 34 (1969), & 35 (1969). Opuscula Entomologica, Lund University, Sweden.

Magura T. 2002. Carabids and forest edge: spatial pattern and edge effect. Forest Ecol. Manag. 157: 23–37.

Mágura T. and Tóthmérész B. 1997. Testing edge effect on carabid assemblages in an oak-hornbeam forest. Acta Zool. Acad. Sci. Hun. 43: 303–312.

Magura T., Tóthmérész B. and Molnár T. 2001. Edge effect on carabid assemblages along forest-grass transects. Web Ecol. 2: 7–13.

Martin T.J. and Major R.E. 2001. Changes in wolf spider (Aranae) assemblages across woodland-pasture boundaries in the central wheat-belt of New South Wales, Australia. Austral Ecol. 26: 264–274.

McCune B. and Mefford M.J. 1999. PC-ORD. Multivariate Analysis of Ecological Data, Version 4. MjM Software Design. Gleneden Beach, Oregon, USA.

Murcia C. 1995. Edge effects in fragmented forests: implications for conservation. Trends Ecol. Evol. 10: 58–62.

Niemelä J., Haila Y.H.E., Lahti T., Pajunen T. and Punttila P. 1988. The distribution of carabid beetles in fragments of old coniferous taiga and adjacent managed forest. Ann. Zool. Fenn. 25: 107–119.

Niemelä J., Langor D. and Spence J.R. 1993. Effects of clear-cut harvesting on boreal ground-beetle assemblages (Coleoptera: Carabidae) in western Canada. Conserv. Biol. 7: 551–561.

OMNR 2001. Forest Management Guide for Natural Disturbance Pattern Emulation, Version 3.1. Ontario Ministry of Natural Resources. Queen's Printer for Ontario, Toronto.

Opell B.D. and Beatty J.A. 1976. The nearctic Hahniidae (Arachnida: Araneae). Bull. Mus. Compar. Zool. Harvard Univ. 147: 393–433.

Pajunen T., Haila Y., Halme E., Niemelä J. and Punttila P. 1995. Ground-dwelling spiders (Arachnida, Araneae) in fragmented old forests and surrounding managed forests in southern Finland. Ecography 18: 62–72.

Pearce J.L., Venier L.A., Eccles G., Pedlar J. and McKenney D. 2004. Influence of habitat and microhabitat on epigeal spider (Araneae) assemblages in four stand types. Biodiv. Conserv. 13: 1305–1334.

Pearce J.L., Venier L.A., McKee J., Pedlar J. and McKenney D. 2003. Influence of habitat and microhabitat on carabid (Coleoptera: Carabidae) assemblages in four stand types. Can. Entomol. 135: 337–357.

Platnick N.I. and Dondale C.D. 1992. The insects and arachnids of Canada. Part 19. The ground spiders of Canada and Alaska (Araneae: Gnaphosidae). Agriculture Canada Publication No. 1875, Ottawa, Canada.

Ranney J.W., Bruner M.C. and Levenson J.B. 1981. The importance of edge in the structure and dynamics of forest stands. In: Burgess R.L. and Sharpe D.M. (eds), Forest island dynamics in man-dominated landscapes. Springer-Verlag, New York, pp. 67–95.

Usher M., Field J.P. and Bedford S.E. 1993. Biogeography and diversity of ground-dwelling arthropods in farm woodlands. Biodiv. Lett. 1: 54–62.

Venables W.N. and Ripley B.D. 2002. Modern applied statistics with S. 4th ed.. Springer-Verlag, New York.

Venier L., Pearce J., Pedlar J. and McKenney D. 2003. Multi-scale Habitat Relationships in a Managed Landscape at the Rinker Lake Study Area [online]. Available from http://www.glfc.cfs.nrcan.gc.ca/landscape/rinkerlake_e.html..