Spiders and Ants Associated with Fallen Logs in Forillon National Park of Canada, Quebec

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Canada

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

LIST OF APPENDICES

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PREFACE

This thesis is composed of four chapters.

Chapter 1

This chapter is a general introduction and literature review.

Chapter 2

This chapter is a manuscript in preparation for submission to *Biodiversity and Conservation.*

Varady-Szabo H. and Buddle C. M. Use of dead wood by generalist arthropod predators and their response to dead wood characteristics.

Chapter 3

This chapter is a manuscript in preparation for submission to *The Canadian Entomologist.*

Varady-Szabo H. and Buddle C. M. Effects of forest type on dead wood use by generalist arthropod predators.

Chapter 4

This chapter is a general conclusion.

CONTRIBUTION OF AUTHORS

Both authors designed the first experiment (Chapter 2) and H. Varady-Szabo designed the experiment outlined in Chapter 3. H. Varady-Szabo executed the experiments, collected all the data, completed analyses and presented the results. C. M. Buddle supervised this project and provided financial support. He gave advice on how to perform key elements of the project (design, statistics, identifications) and edited final drafts of all the chapters presented in this thesis.

ABSTRACT

Downed woody material (fallen logs) offers spiders (Araneae) and ants (Hymenoptera: Formicidae) ideal nesting and foraging sites. In a maple forest of Forillon National Park, I compared spider and ant assemblages on, adjacent to, and away from fallen logs, and on these I tested the effects of log type and decay stage. In a second study, spider and ant assemblages were compared on, adjacent to, and away from fallen logs in different forest types.

In the first experiment spiders were highly affected by trap placement, and diversity was highest on the wood surface compared to the forest floor. In contrast, wood type and decomposition stage of logs had few significant effects on spiders. Log type did not affect the estimated number of spider species nor the spider catch rates. Decomposition stage did not affect spider collections, but less decayed logs were more diverse in spider than heavily decayed logs.

The second experiment showed that use of dead wood by spiders depends on forest type. Ant diversity and abundance was generally low, making it difficult to offer concrete conclusions related to log use by ant assemblages. This work brings additional support for the important role of dead wood to forest arthropod biodiversity.

RÉSUMÉ

Le bois mort au sol (notamment les troncs d'arbres morts) offre aux araignées (Araneae) et aux fourmis (Hymenoptera: Formicidae) des habitats propices. Dans une érablière du parc national du Canada Forillon, j'ai comparé les communautés d'araignées et de fourmis présentes, dessus, adjacentes, et au loin des troncs d'arbres morts au sol, et j'ai testé l'effet du type des troncs d'arbres morts et leurs stades de décomposition sur ces communautés. Une deuxième expérience a permis de comparer les communautés d'araignées et de fourmis, dessus, adjacentes et au loin des troncs d'arbres morts au sol, au sein de différents couverts forestiers.

La première expérimentation a démontré que les araignées sont fortement affectées par l'emplacement des pièges, et que leur diversité est plus grande à la surface du bois comparativement au sol forestier. Le type et le niveau de décomposition des troncs d'arbres morts ont révélé relativement peu d'effets. Le type de bois mort n'a pas affecté le nombre estimé d'espèces d'araignées ni le nombre total d'araignées collectées. Le niveau de décomposition des troncs d'arbres morts n'a pas affecté le nombre total d'araignées collectées mais les troncs d'arbres morts de décomposition inférieure étaient plus divers en araignées que celles de décomposition plus avancée.

La seconde expérience a démontré que l'utilisation du bois mort par les araignées est dépendante du type forestier. La diversité et l'abondance des fourmis furent généralement faible, ce qui a rendu difficile de conclure qu'en à leur utilisation du bois mort. Cette étude apporte de nouveaux supports sur l'importance des troncs d'arbres morts pour la biodiversité des arthropodes forestiers.

CHAPTER 1: GENERAL INTRODUCTION AND LITERATURE REVIEW

Biodiversity, conservation and dead wood

Forest ecosystems cover about 40% of the earth's ice-free land surface (Waring and Running 1998). They are an important source of wood and cleanse the air and soil of many pollutants through plant respiration and soil organism biotic activity. Forests also help to stabilize the global carbon balance through carbon fixation, provide habitat for wildlife, and provide recreational opportunities for humans (Waring and Running 1998). As human population and standard of living increases, the demand for forested lands and products will also increase. Thus, proper management of forests is a priority for human well-being (Waring and Running 1998). The preservation of forest biodiversity, which is important to consider in resource management (Probst and Crow 1991; Burton et al. 1992), will become a challenge as a result of fewer forests and increased demands on resources. Knowledge of the forest flora and fauna will become essential to good management practices. Arthropods contribute significantly to overall forest biodiversity (Danks and Foottit 1989; Wilson 1992) and should, therefore, be a focal point for research concerned with forest conservation (Kremen et al. 1993). One approach towards conservation of biodiversity within forest ecosystems is to specifically target key habitat features (Berg et al. 1994), such as dead and decaying wood (i.e., coarse woody debris, CWD, including snags and downed woody material, DWM).

CWD (logs, large branches and stumps) has long been recognized as an essential element for the conservation of biodiversity and function of forest ecosystems (Harmon et al. 1986; Speight 1989; Caza 1993; Samuelsson et al. 1994; Vallauri et al. 2003). Dead wood creates organic matter accumulation (Lambert et al. 1980), its presence can help the natural regeneration of trees (Harmon et al. 1986), it can affect the carbon cycle by acting as sink for atmospheric carbon (Lambert et al. 1980; Vallauri et al. 2003) and dead wood is an important habitat for many parasitoids and predators (Ehnström 2001), which may in turn regulate populations of pest insects.

Dead wood can also change its surrounding environment by altering moisture regimes and microsite temperature, or by modifying the physical and chemical properties of the forest floor litter by adding woody fragments to the nearby litter and by affecting the surrounding litter accumulation (Evans et al. 2003). For example, Marra and Edmonds (1998) and Evans et al. (2003) found that soil moisture was higher close to logs than away from logs and that this change can alter the fauna and flora of the litter (Marra and Edmonds 1998). Jabin et al. (2004) showed that Opilionida, Araneida, Pseudoscorpionida, Isopoda, Diplopoda, Chilopoda and Coleoptera were all more abundant in litter close to logs than in litter further away from logs.

Dead wood also supports high plant and animal diversity, as documented for various groups: herbaceous plants (Zielonka and Grzegorz 2004), fungi (Lindblad 1998), bryophytes and lichens (Söderström 1988), birds (Torgersen and Bull 1995), small mammals (Mengak and Guynn 2003), amphibians (Butts and McComb 2000) and arthropods (Hamilton 1978; Hammond 1997; Buddle 2001; Siitonen 2001). Species which require dead wood during some stage of their life cycle are called 'saproxylic' (Speight 1989). These organisms use the dead wood habitat for nesting, feeding, hibernating, reproducing, or as shelter (Samuelsson et al. 1994; Irmler et al. 1996; Esseen et al. 1997; Hammond 1997; Jonsell et al. 1998). In certain ecosystems, notably the boreal forest, dead wood can be the manageable property that has the greatest influence on biodiversity (Samuelsson et al. 1994; Hanski and Hammond 1995; Huston 1996; Martikainen et al. 2000). In Sweden, for instance, for the 1487 threatened forest species studied by Berg et al. (1994), the three most important habitat elements were old living trees (critical for 26% of the threatened species), logs (26% of species) and snags (21% of species). Saproxylic organisms also play an important role in decomposition and nutrient recycling (Samuelsson et al. 1994), contributing significantly to these ecosystem processes.

Dead wood is of high value because many rare temperate and/or boreal forest species are known to be associated with it (Berg et al. 1994; Berg et al. 1995; Martikainen and Kouki 2003; Vallauri et al. 2003). The decreases of dead wood due to current forestry practices (Bader et al. 1995; Sippola et al. 1998; Siitonen 2001) correlate with disappearance of some arthropod species and the high reduction in abundance of others (Heliövaara and Väisänen 1984; Siitonen and Martikainen 1994; Kaila et al. 1994; Väisänen et al. 1993; Vallauri et al. 2003). As a result, saproxylic insects now form an enormous proportion of nationally rare and threatened species in Europe (Speight 1989;

Berg et al. 1994), making the maintenance of dead wood of critical importance. Since forest ecosystems have been altered by forestry activities and since forestry is a rapidly expanding global industry (Bryant et al. 1997), it is time to properly document and understand the arthropod fauna associated with dead wood. To achieve this goal, forest managers need to know the characteristics of dead wood and the variations in those characteristics that will allow conservation of arthropod biodiversity (Niemelä et al. 1996; Hagan and Grove 1999).

Dead wood characteristics and invertebrate assemblages

Several studies have investigated which dead wood characteristics best predict saproxylic arthropod diversity (e.g., Savely 1939; Irmler et al. 1996; Jonsell et al. 1998; Kruys and Jonsson 1999; Buddle 2001; Siitonen 2001; Lindgren and MacIsaac 2002; Simila et al. 2003). Having a high diversity of dead wood (i.e. dead wood of many different type) is one of the best predictors of high saproxylic species diversity (Esseen et al. 1997; Simila et al. 2003). However, Siitonen (2001) mentionned that that bole diameter, tree species, and decomposition stage of dead wood are the main factors determining saproxylic species composition in a dead bole.

Size of dead wood can directly affect some saproxylic organisms (Elton 1966). In general, wood of large diameter is associated with higher species richness and abundance of invertebrates and more frequent occurence of rare and threatened species (e.g. Bader et al. 1995; Kruys et al. 1999; Kolstrom and Lumatjarvi 2000; Simila et al. 2003; Hammond et al. 2004). There are several explanations for this trend: trees of larger diameter contain more microhabitats, take longer to decompose and house more species of fungi on which many saproxylics are dependent (Väisänen et al. 1993; Marra and Edmonds 1996; Kruys and Jonsson 1999; Kolstrom and Lumatjarvi 2000; Komonen 2003).

Diversity of decomposition stages of dead wood creates different microhabitats favouring high saproxylic insect diversity (Esseen et al. 1992; Kaila et al. 1994; Hammond et al. 2001; Siitonen 2001). Decomposition of dead wood has different phases, each of which contains its own fauna and flora (Savely 1939; Siitonen 2001). Speight (1989) recognized three distinct principal phases: 1- A phase of colonization in which, are present, animals that are able to penetrate the wood when it is still hard; 2- A longer decomposition phase where saproxylic animals base their feeding on the passage of the other animals or feed directly on them (predators); 3- A longer phase of humification where saproxylic organisms are slowly replaced by detritivorous animals (e.g., Collembola). Several studies have shown that decomposition stages of dead wood correlate with the number of species associated with it (Irmler et al. 1996; Kruys et al. 1999; Hammond et al. 2004). The middle decomposition stage seems to be the stage harboring the highest invertebrate diversity (Jonsell et al. 1998). This may be because this stage is intermediate between high presence of nutrients present for saproxylic insects to feed on (in early decomposition stage) and being similar to the forest floor habitat (in late decomposition stage) (Irmler et al. 1996). As the wood decays, the wood-dwelling fauna becomes more similar to the litter-dwelling fauna due to an increase in the number of species immigrating from the adjacent litter layer into the dead wood (Irmler et al. 1996).

Every tree species has a different mode of death that produces different dead wood qualities (Siitonen 2001). Such dissimilarity could result in different saproxylic species composition (Ehnström 2001). However, Irmler et al. (1996) found that only a few of the species associated with dead wood were typical of the wood of a particular tree species and that the different tree species seemed to contribute less to the species diversity of wood dwelling species than decomposition stage. Hamilton (1978) also found that at the species level, conditions of bark and wood and state of invasion by fungi were more important than tree species. In contrast, Savely (1939) found a difference between the fauna of hardwoods and that of soft woods and Hamilton (1978) found that in Britain, insect communities could be separated according to conifer or hardwood tree type. However, the specificity of saproxylic insects to wood type is weaker as decomposition progresse (Savely 1939; Irmler et al. 1996; Jonsell et al. 1998) and even when wood type has an effect on insect diversity, decomposition stage remains important (Harmon et al. 1986; Jonsell et al. 1998).

Effects of these dead wood qualities on invertebrate communities could be affected by forest type since they each harbour invertebrate communities which have different ecological needs (Anderson and Death 2000). Ehnström (2001) stated that insects that have different environmental preference are associated with dead wood of different tree species. In southern Sweden, beetles that were associated with dead oak were different than those associated with beech in that they preferred sunny and dry sites (Gardenfors and Baranowski 1992). Furthermore, the majority of insects associated with pine preferred open habitat while beetles associated with spruce generally preferred shady sites (Ehnström 2001). In North America, however, there are no published studies testing directly the effects of forest type on invertebrate communities associated with dead wood.

Presence of dead wood affects overall forest invertebrate diversity (Martikainen et al. 2000) as invertebrates using dead wood are affected by its presence, variation and diversity (Esseen et al. 1997). Size, species and decomposition stage of dead wood are three main characteristics affecting invertebrates (Siitonen 2001). Surrounding forest type also influence use of dead wood by invertebrates since it harbours different microclimate and invertebrate assemblages (Anderson and Death 2000), but this has not been adequately studied in North America. Therefore, when testing the effects of important features of dead wood on its associate invertebrate fauna, one should concentrate on the dead wood characteristics that mainly affect invertebrate assemblages (mentioned above) and should take into consideration the forest type in which the dead wood is found.

Dead wood characteristics and predator assemblages

Even though much research has been devoted to understanding dead wood characteristics important to saproxylic species, very little information exists on other groups associated with decaying wood. Saproxylic species are only a fraction of the species living in or on dead wood (Irmler et al. 1996) and many predators (such as spiders and ants) are also known to use the dead wood habitat (Wu and Wong 1987; Torgersen and Bull 1995; Buddle 2001; Ehnström 2001; Lindgren and MacIsaac 2002). Spiders (Araneae) might use the dead wood environment for feeding, mating, overwintering or oviposition site (Lowrie 1948; Buddle 2001) and ants (Hymenoptera: Formicidae) are mainly known to use dead wood for nesting (Sanders 1964; Letendre et al. 1971; Letendre and Pilon 1973a; Wu and Wong 1987; Torgensen and Bull 1995).

Very few studies have investigated the relationship between the dead wood habitat and spiders. There are scattered notes in various identification guides and faunistic surveys suggesting that many ground-dwelling spider species use the dead wood habitat (Dondale and Redner 1978, 1982; Platnick and Dondale 1992; Paquin and Duperre 2003) and some spiders (e.g., *Nuctenea umbratica* (Clerck), *Segestria florentina* (Rossi), *Coriarachne utahensis* (Gertsch), and *Coriarachne versicolor* Keyserling) have been defined as under-bark specialists (Lowrie 1948; Dondale and Redner 1978; Speight 1989). Lowrie (1948) suggested that there was a succession of ground-dwelling spiders associated with the decomposition of logs. He divided spiders into two ecological guilds, which relates to their food gathering strategy: the web-building spider species, which catch their prey by the use of webs, and the hunting spider species, which do not build snares to catch prey. According to Lowrie (1948) there are three stages of log decomposition that form the succession of spiders associated with dead wood: the first stage is characterized by both free-running and web-building spiders that use crevices and loose bark of the newly decayed log. In the second stage the larger cavities of the wood are used by some characteristic log dwellers. The last stage of log decay resembles the first stage with mainly free running species but these species are probably more associated with surrounding leaf litter than dead wood. These divisions are vague but still give general insights on how decomposition stages are important for ground-dwelling spiders.

In North America, Buddle (2001) is the only study that tested how dead wood quality affects spider assemblages. Buddle (2001) first tested if spiders use dead wood differently than the forest floor. He found lower abundance of spiders on the logs than on the forest floor but greater estimated number of species on the wood surface. This same study also tested the effect of bark and elevation of dead wood on spider assemblages. His results suggested that bark does not have any effect on the total number of spiders and even though raw species richness was higher on logs with bark, estimation of rarefied species richness showed very little difference between logs with and without bark. When hunting and web-building spiders were analyzed separately, web-building species were reduced on logs with no bark but hunting species did not show any preference for bark on logs (Buddle 2001). Therefore, complexity of the dead wood environment was an important factor for web-building species, but may be less important for hunting species. Wood elevation seemed to affect negatively spider assemblages for spider abundance (total number collected, number of hunting spiders and number of web-building spiders), spider diversity, community composition, and the common species *Bathyphantes pallidus*

(Banks), *Amaurobius borealis* Emerton and *Pardosa xerampelina* (Keyserling) were all captured less frequently on elevated wood compared to ground-level wood (Buddle 2001).

Surprisingly, little has been published on the relationship between ants and dead wood in north temperate and boreal forests. The well-known wood nesting carpenter ants have been studied to varying degrees (Sanders 1964, 1970, 1972; Bradley and Hinks 1968; Akre et al. 1994), and many studies have looked at the structure of ant populations and determined some of the wood characteristics influencing ant nesting sites (Dennis 1938; Letendre and Pilon 1973a; Chen et al. 2002). However, only Wu and Wong (1987), Lindgren and MacIsaac (2002), and Torgensen and Bull (1995) specifically studied the different characteristics of dead wood that influence ant assemblages nesting in dead wood. They found that size (diameter and length), moisture, type, decomposition stage and age of dead wood were all important, and that different species of ants showed different responses to the dead wood characteristics (Wu and Wong 1987; Torgensen and Bull 1995; Lindgren and MacIsaac 2002). For example, *Leptothorax muscorum* (Nylander) is always found in very dry and relatively firm wood and *Camponotus herculeanus* (Linnaeus) lives in wood of large sizes found mostly in shaded locations. *Myrmica incompleta* Provancher, *M. alaskensis* Wheeler and *M. fracticornis* Forel were often found under the bark of lodgepole pine stumps, which were only 12 months old and still had active bark beetle infestations, *Formica* sp. preferred dead wood of limited decay and *Lasius pallitarsis* Foerster was found in very wet, rotten wood more or less buried in the soil and those of small diameter (Lindgren and MacIsaac 2002).

Lack of study on the association of ants/spiders and dead wood is surprising for their presence in dead wood could significantly affect the dead wood environment and its ecosystem function. Effects could either be direct by changing the wood structure [e.g., tunnelling action of carpenter ants (Sanders 1964)] or chemical content [e.g., ants activity can change soil chemistry (Culver and Beattie 1983)] or indirect by feeding on organisms that directly influence the dead wood habitat [e.g., spider feeding on Collembola (Lawrence and Wise 2000)]. To understand the importance of ants/spiders in dead wood it is essential to have basic knowledge of their ecology.

Spiders in forest ecosystems

Spiders play many critical roles in forested ecosystems (Wise 1993). It is a diverse taxon, 34,000 species are known globally (Foelix 1996) with a relatively stable taxonomy (Coddington and Levi 1991). Spiders are also very abundant in ecosystems (Coddington and Levi 1991). Moulder and Reichle (1972) found that spiders inhabiting the litter zone of a *Liriodendron* forest in Tennessee had an average density of 126 individuals/m^2, and Turnbull (1973) reported spider abundance ranging from 0.64 individuals /m^2 in a meadow in Poland to 842 individuals/m^2 in pastures in England.

Spiders represent a large portion of the arthropod predator biomass in temperate forests (Van Hook 1971; Petersen and Luxton 1982). Spiders are key predators in forest-floor food-webs (Foelix 1996). They consume a high quantity of prey (Moulder and Reichle 1972; Van Hook 1971; Manley et al. 1976) and are capable of regulating populations of many species (Lawrence and Wise 2000; Wise 2004), some of which are important forest pests (e.g., Douglas-fir tussock moth, *Orgyia pseudotsugata* (McDunnough) and various budworms) (Allen et al. 1970; Jennings and Houseweart 1978; Mason and Paul 1988). Moulder and Reichle (1972) showed that spiders consumed 43.8% of the mean annual standing crop of total small animals living in the forest floor. Spiders are also consumed by other animals; they are an important food item for birds (McIntyre and Thompson 2003), salamanders (Hall 1976) and frogs (Szathmary 1997).

There are many biotic and abiotic characteristics that affect spider assemblages, and some of these could influence dead wood use by spiders. Temperature, humidity, wind, light intensity, type of vegetation, food supply, competitors and enemies all define the environment in which spiders live (Foelix 1996). However, McIver et al. (1992) found that canopy closure, litter development, and prey availability were the characteristics most affecting spider communities in Oregon.

Plant cover also influences spider assemblages (Turnbull 1973) by modifying both macro and microclimates for spiders (Turnbull 1973) and affect the structural complexity of the site (Uetz 1991). Different spiders, even among closely related species, will choose habitats of differing structural complexity (Duffey 1962; Greenquist and Rovner 1976; Robinson 1981). The structure of the habitat is very important for web-building spiders because they need to have attachment sites for web construction (Foelix 1996). When looking at spiders separated by guild (web-building and hunting spiders), Bultman and Uetz (1982) found that structural complexity seemed to affect web-building spiders more than hunting spiders. The latter guild seem to be influenced more by prey density. However, hunting spiders were also affected by structural complexity; Hurd and Fagan (1992) found a lower species richness of hunting spiders when trees and shrubs rather than grasses and forbs were dominant. Plant cover, and its layering attributes, creates a stratification of spider species. Spiders exhibit both horizontal and vertical stratification (Huhta 1971). For example, *Pardosa pullata* (Clerck) and *Pirata piraticus* (Clerck) both live in bogs with sphagnum and moss but *P. pullata* lives at the surface of the moss while *P. piraticus* is found in the stem region of the moss (Foelix 1996). Immature spiders might use the stratification of litter to escape cannibalism by adult spiders by running in the litter layer since adults stay on top of the litter layer (Edgar 1969). Immature spiders also climb vertically on to DWM and may use DWM as a platform on which to depart for ballooning (Buddle 2001). A few studies, correlative and experimental, showed that litter depth significantly affects the number of hunting spider species (Uetz 1991). The presence of plants, along with bark, mosses and branches, on DWM as well as surrounding litter could therefore affect the spider community.

Availability of prey is an important factor in determining habitat choice by spiders. Some spiders will change their web site if prey abundance is not sufficiently high (Foelix 1996). The funnel-web spider *Agelenopsis* and the orb web *Nephila* spider both build webs in locations where prey availability is high (Foelix 1996). In contrast, some orb weavers will stay at a site even if prey availability is low but they will build a larger web (Foelix 1996). Therefore, abundance and type of prey present on DWM could affect the presence and diversity of spiders.

The use of dead wood by spiders will probably change depending on the gender and development stage of the individuals. This is because males and females differ in activity level. After their last molt the male spider wanders in order to search for a mate (Foelix 1996) and dies shortly after copulation. In contrast, the female can live much longer and after copulation her main activity is to lay eggs (Foelix 1996). More female *Pardosa mackenziana* carrying egg sacs were caught on the wood than on the forest floor possibly to sun their egg sac. Immatures were also found in a higher proportion on the wood surface than on the forest floor (Buddle 2001).

Ants in forest ecosystems

Ants play critical roles in forested ecosystems (Holldobler and Wilson 1990). Ants are diverse with 9500 species known globally (Holldobler and Wilson 1990) and are also very abundant in forest ecosystems (Alonso and Agosti 2000). In a sugar maple wood in Quebec, where ant dominance is much less than in tropical areas, Francoeur (1966) estimated ants had 1.02 colonies per square meter. Ant colonies can also reach enormous size; Sanders (1970) found a colony of *C. herculeanus* that had over 12 000 workers in a coniferous forest.

Ants represent a large portion of the arthropod predator biomass in temperate forests (Alonso and Agosti 2000) and are known to feed, along with spiders, on some important forest pests including the forest tent caterpillar, *Malacosoma disstria* Hübner (Lepidoptera: Lasiocampidae) and the spruce budworm, *Choristoneura occidentalis* Freeman (Lepidoptera: Tortricidae) (Green and Sullivan 1950; Youngs and Campbell 1984; Torgensen and Bull 1995). Ants are also an important food source for other animals such as woodpeckers (Bull et al. 1992) and black bears (Raine and Kansas 1990).

Ants have an additional importance in ecosystems since they act as ecosystem engineers. Ants change habitats by transforming the structure of their nesting site, altering the vegetation present above their nests, and producing microsite enrichment (Jones et al. 1994). Moreover, their soil bioturbation is so extensive that they have been shown to turn over more soil than earthworms (Lyford 1963). Ants also interact with other organisms across various trophic levels (Alonso and Agosti 2000). Most ants are omnivores and feed on dead organic matter, as well as live plants and animals (Andersen 1995) and ants form many mutualistic associations (Alonso and Agosti 2000).

Ants are affected by many other biotic and abiotic factors and, as with spiders, their use of dead wood could be affected by these factors. Although ant populations are affected by a wide array of biotic and abiotic factors, the literature suggests that availability of sunlight (and associated changes in temperature and humidity), intra- and interspecific competition, and availability of nesting sites are key factors (Letendre and Pilon 1973b; Puntilla et al. 1991; Niemelä et al. 1996).

The effect of sunlight on ant distribution is shown by the higher density and species richness of ants in open habitats (Letendre and Pilon 1973b). Only shade tolerant species such as *Myrmica ruginodis* Nylander and *C. herculeanus* can survive in closed-canopy forests (Punttila et al. 1991). Humidity is also related to sunlight since higher heat means more evapotranspiration. Some ants prefer a maximal humidity level but many prefer habitats that are less humid (Francoeur 1973).

It has been argued that ant communities are governed by interspecific competition (Brian 1952; Brian et al. 1966; Savolainen and Vepsäläinen 1988). Some studies on competition among ants have shown that certain species of ants could live together while other species always excluded each other (Savolainen and Vepsäläinen 1988; Torgersen and Bull 1995; Lindgren and MacIsaac 2002). According to Savolainen and Vepsäläinen (1988) competition among ants is based on a hierarchy level of competition. Hierarchy level in competition is the result of the ants' foraging density. Ants become more aggressive as they become more numerous. In this competitive hierarchy, there are three levels: The *submissives* species, which are the less competitive and protect only their nests. The *encounterers* with, in addition to protecting their nest, protect also the food resources. Finally, the *territorials* species, which protect, additionally to their nest and their food sources, the area in which they forage. Competitive hierarchy probably determines the nesting habitat of ant species (Brian 1952; Savolainen and Vepsäläinen 1988). For example, the submissive *Myrmica* species may switch to underground life when present on the territory of the territorial red wood ant, *Formica rufa* Linnaeus (Marikovsky 1962). Furthermore, aggressive ant species do not usually occur together (Levins et al. 1973; Savolainen and Vepsäläinen 1988; Punttila et al. 1991). For example, wood nesting *Camponotus* are rarely associated with another ant species (Torgersen and Bull 1995). Using the competition hierarchy hypothesis, it would be possible to predict what species may co-occur in certain habitats (Vepsäläinen and Pisarski 1982) and this concept may help in understanding dead wood use by ants.

Availability of nesting sites has been considered the limiting resource for ants (Sander 1970; Herbers 1989) and many ants are known to nest in dead wood (Lindgren and MacIsaac 2002). Lindgren and MacIsaac (2002) believed that the availability of dead wood might limit populations of ants by limiting nest founding success. Also, since some ants will choose the most available type of nest (Letendre and Pilon 1973a), the amount of dead wood available could be a factor that determines nest selection by ants.

Ant communities present in the litter layer are affected by the presence of logs. Andrew et al. (2000) looked at the difference in leaf litter adjacent and away from logs and found that ant species richness was significantly higher in litter adjacent to logs than away from logs (Andrew et al. 2000). Each different position was also composed of a set of unique ant species (many of these occurring in low numbers) (Andrew et al. 2000).

GENERAL OBJECTIVES AND RESEARCH QUESTIONS

Given the importance of dead wood, the importance of ants and spiders to ecosystems, and the fact that the association of these predators with dead wood has been under-studied, the goal of my research was to better understand this relationship.

Two experiments were conducted. The first experiment is represented in chapter 2 and the second experiment in chapter three.

There were three objectives for the first experiment, describe in chapter 2:

To what degree do spiders and ants use dead wood? To answer this question my first objective was to compare the assemblage of spiders and ants found on fallen logs to those adjacent to fallen logs, and to those found foraging on the forest floor. The null hypothesis was that there was no difference in ant or spider assemblages present at the different locations; the alternative hypothesis was that the assemblage of ants and spiders were different depending on where they were found.

What are the dead wood characteristics that affect ant and spider assemblages? Wood type and **decomposition stage** are known to influence saproxylic organisms, but little was known about how these characteristics might affect generalist predators such as spiders or ants. My second objective was to determine whether the spider and ant fauna associated with dead wood was dependent on wood type (coniferous versus deciduous logs), and my third objective was to assess how log decomposition stage influenced ant and spider assemblages. The null hypothesis for the second objective was that type of wood had no effect on ant and spider assemblages using the fallen log habitat and the alternative hypothesis was that ant and spider assemblages were different depending on log type. The null hypothesis for the third objective was that different decomposition stages had no effect on ant or spider assemblages associated with fallen logs and the alternative hypothesis was that log decomposition stage significantly affected ant and spider assemblages associated with fallen logs.

There was one objective for the second experiment, describe in chapter 3:

Does use of dead wood by ants and spiders changes depending on the forest type. My fourth objective was to compare the assemblages of ants and spiders found on, adjacent to, and away from dead wood, within three forest types: maple, *Acer*: aspen, *Populus*: and fir, *Abies*. The null hypothesis was that there was no differences between ant and spider assemblages of the three forest floor positions depending on forest types and the alternative hypothesis was that the ant and spider assemblages of each position were dependant on forest type.

The two studies were conducted in Forillon National Park, Quebec, Canada. I chosed Forillon as study site because the arthropods fauna was virtually unknown except for Koponen (1990) and Francoeur (1981, 1986) and its forest should experience least change because of human disturbance due to its conservation.

REFERENCES

Akre R. D., Hansen L. D. and Myhre E. A. 1994. Colony size and polygyny in carpenter ants (Hymenoptera: Formicidae). Journal of the Kansas Entomological Society 67: 1-9

Allen D. C., Knight F. B. and Foltz J. L. 1970. Invertebrate predators of the jack-pine budworm, *Choristoneura pinus*, in Michigan. Annals of the Entomological Society of America 63: 59-64

Alonso L. E and Agosti D. 2000. Biodiversity studies, monitoring, and ants: An overview. In: Agosti D., Majer J. D., Alonso L. E. and Schulz T.R. (Eds), Ants: Standard methods for measuring and monitoring biodiversity, Smithsonian Institution, pp 1-8. Washington (DC).

Andersen A. N. 1995. A classification of Australian ant communities, based on functional groups which parallel plant life-forms in relation to stress and disturbance. Journal of Biogeography 22: 15-29

Anderson S. J. and Death R. G. 2000. The effect of forest type on forest floor invertebrate community structure. New Zealand Natural Sciences 25: 33-41

Andrew N., Rodgerson L., and York A. 2000. Frequent fuel-reduction burning: the role of logs and associated leaf litter in the conservation of ant biodiversity. Austral Ecology 5: 99-107

Bader P., Jansson S. and Jonsson B. G. 1995. Wood-inhabiting fungi and substratum decline in selectively logged boreal spruce forests. Biological Conservation 72: 355-362

Berg A., Ehnström B., Gustaffsson L., Hallingbäck T., Jonsell M. and Weslien J. 1994. Threatened plant, animal, and fungus species in Swedish forests: Distribution and habitat associations. Conservation Biology 8: 718-731

Berg A., Ehnström B., Gustafsson L., Hallingbäck T., Jonsell M. and Weslien, J. 1995. Threat levels and threats to red-listed species in Swedish forests. Conservation Biology. 9: 1629-1633

Bradley G. A. and Hinks J. D. 1968. Ants, aphids and jack pines in Manitoba. The Canadian Entomologist 100: 40-50

Brian M. V. 1952. The structure of a dense natural ant population. Journal of Animal

Ecology 21: 12-24

Brian M. V., Hibble J. and Kelly A. F. 1966. The dispersion of ant species in a Southern English heath. Journal of Animal Ecology 35: 281-290

Bryant D., Nielson D. and Tangley L. 1997. The last frontier forests: Ecosystems and economies on the edge. World Resources Institute, World Conservation Monitoring Center, World Wildlife Fund, Washington.

Buddle C. M. 2001. Spiders (Araneae) associated with downed woody material in a deciduous forest in central Alberta, Canada. Agricultural and Forest Entomology 3: 241-251

Bull E. L., Beckwith R. C. and Holthausen R. S. 1992. Arthropod diet of pileated woodpeckers in northeastern Oregon. Northwestern Naturalist 73: 42-45

Bultman T. L. and Uetz G. W. 1982. Abundance and community structure of forest floor spiders following litter manipulation. Oecologia 55: 34-41

Burton P. J., Balisky A. C., Coward L. P., Cumming S. G. and Kneeshaw D. D. 1992. The value of managing for biodiversity. The Forestry Chronicle 68: 225-237

Butts S. R. and McComb W. C. 2000. Association of forest-floor vertebrates with coarse woody debris in managed forests of western Oregon. Journal of Wildlife Management 64: 95-104

Caza C. L. 1993. Woody debris in the forests of British Columbia: a review of the literature and current research. Land Management Report 78, Ministry of Forestry, Victoria B.C.

Chen Y., Hansen L. D. and Brown J. J. 2002. Nesting sites of the carpenter ant, *Camponotus vicinus* (Mayr) (Hymenoptera: Formicidae) in Northern Idaho. Environmental Entomology 31: 1037-1042

Coddington J. A. and Levi H. W. 1991. Systematics and evolution of spiders (Araneae). Annual Review of Ecology and Systematics 22: 565-592.

Culver D.C. and Beattie A. J. 1983. Effects of ant mounds on soil chemistry and vegetation patterns in Colorado montane meadow. Ecology 64: 485-492

Danks H.V. and. Foottit R. G. 1989. Insects of the boreal zone of Canada. The Canadian Entomologist 121: 626-690

Dennis C. A. 1938. The distribution of ant species in Tennessee with reference to ecological factors. Annals of the Entomological Society of America 31: 267-308

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, Hull, Canada

Dondale C.D. and Redner J.H. 1982. The insects and arachnids of Canada. Part 9. The sac spiders of Canada and Alaska (Araneae: Clubionidae and Anyphaenidae). Agriculture Canada Publication, Hull, Canada

Duffey E. 1962. A population of spiders in limestone grassland. Journal of Animal Ecology 31: 571-599

Edgar W. D. 1969. Prey and predators of the wolf spider *Lycosa lugubris*. Journal of Zoology 159: 405-411

Ehnström B. 2001. Leaving dead wood for insects in boreal forests-suggestions for the future. Scandinavian Journal of Forest Research 3: 91-98

Elton C. S. 1966. The pattern of animal communities. Methuen, London.

Esseen P-A., Ehnström B., Ericson L. and Sjöberg K. 1992. Boreal forests – the focal habitats of Fennoscandia. In: Hansson, L. (ed.), Ecological principles of nature conservation. Elsevier, London, pp. 252-325

Esseen P-A., Ehnström B., Ericson L. and Sjöberg K. 1997. Boreal forests. Ecological Bulletins 46: 16-47

Evans A. M., Clinton P. W., Allen R. B. and Frampton C. M. 2003. The influence of logs on the spatial distribution of litter-dwelling invertebrates and forest floor processes in New Zealand forests. Forest Ecology and Management 184: 251-262

Foelix R.F. 1996. Biology of Spiders. Oxford University Press, Inc. New York, New York

Francoeur A. 1966. La faune myrmécologique de l'érablière à sucre (*Aceretum saccharophori* Dansereau) de la region de Québec. Le Naturaliste Canadien 93: 443-472

Francoeur A. 1973. Revision taxonomic des espèces néarctiques du groupe fusca, genre *Formica*. Mémoire de la Société Entomologique du Québec 3 : 1-316

Francoeur A. 1981. Les Fourmis de la Presqu' île de Forillon, Comté de Gaspé-est, Québec (Formicidae, Hymenoptera). Fabreries 4: 78-83

Francoeur A. 1986. Supplément aux fourmis de la presqu'île de Forillon, Gaspé-Est, Québec. Fabreries 12: 56-58

Gardenfors U. and Baranowski R. 1992. Beetles living in open deciduous forests prefer different tree species than those living in dense forests. Entomologisk Tidskrift 113: 1-11

Green, G. W. and Sullivan C. R. 1950. Ants attacking the larvae of the Forest Tent Caterpillar, *Malacosoma disstria*. The Canadian Entomologist 82: 194-195

Greenquist E. A. and Rovner J. S. 1976. Lycosid spiders on artificial foliage: Stratum choice, orientation preference, and prey wrapping. Psyche 83: 196-209

Hagan J.M. and Grove S. L. 1999. Coarse woody debris. Journal of Forestry 97: 6-11

Hall R. J. 1976. Summer foods of the salamender *Plethodon wehrlei* (Amphibia: Urodela: Plethodontidae). Journal of Herpetology 10: 129-131

Hamilton W. D. 1978. Evolution and diversity under bark. In Mound L. A. and Waloff N. (Eds), Diversity of insect faunas, pp. 154-175. Blackwell Scientific Publications, Oxford, UK.

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

Hammond H. E. J., Langor D.W. and Spence J. R. 2001. Early colonization of *Populus* wood by saproxylic beetles (Coleoptera). Canadian Journal of Forest Research 31: 1175-1183

Hammond H.E.J., Langor D.W. and Spence J.R. 2004. Saproxylic beetles (Coleoptera) using *Populus* in boreal aspen stands of western Canada: spatiotemporal variation and conservation of assemblages. Canadian Journal of Forest Research 34: 1-19

Hanski I. and Hammond P. 1995. Biodiversity in boreal forests. Trends in Ecology and Evolution 10:5-6

Harmon M. E., Franklin J. F., Swanson F. J., Sollins P., Gregory S. V., Lattin J. D., Anderson N. H., Cline S. P., Aumen N. G., Sedell J. R., Lienkaemper G. W., Cromack K. Jr. and Cummins K. W. 1986. Ecology of coarse woody debris in temperate ecosystems. Advances in Ecological Research 15: 133-302

Herbers J. M. 1989. Community structure in north temperate ants: Temporal and spatial variation. Oecologia 81: 201-211

Heliövaara K., and Väisänen R. 1984. Effects of modern forestry on northwestern European forest invertebrates: A synthesis. Acta Forestalia Fennica 189: 1-32

Holldobler B. and Wilson E. O. 1990. The Ants. The Belknap Press of Harvard University Press, Cambridge, Massachusetts.

Huhta V. 1971. Succession in the spider communities of the forest floor after clear-cutting and prescribed burning. Annales Zoologici Fennici 8: 483-542

Hurd L. E. and Fagan W. F. 1992. Cursorial spiders and succession: age or habitat structure? Oecologia 92: 215-221

Huston M. A. 1996. Models and management implications of coarse woody debris impacts on biodiversity. In: McMinn J. and. Crossley D.A. (eds), Biodiversity and coarse woody debris in southern forests, proceedings of the workshop on coarse woody debris in southern forests: Effects on biodiversity, Athens, GA, 18-20 October 1993, pp 139-143. Gen. Tech. Rep. SE-94. Asheville, NC.

Irmler U., Heller K. and Warning J. 1996. Age and tree species as factors influencing the populations of insects living in dead wood (Coleoptera, Diptera: Sciaridae, Mycetophilidae). Pedobiologia 40: 134-148

Jabin M., Mohr D., Kappes H and. Topp W. 2004. Influence of deadwood on density of soil macro-arthropods in a managed oak–beech forest. Forest Ecology and Management 194: 61–69

Jennings D. T. and Houseweart M. W. 1978. Spider preys on spruce budworm egg mass. Entomological News 89: 183-186

Jones C. G., Lawton J. H. and Shachak M. 1994. Organisms as ecosystem engineers. Oikos 69: 373-386

Jonsell M., Weslien J. and Ehnström B. 1998. Substrate requirements of red-listed saproxylic invertebrates in Sweden. Biodiversity and Conservation 7: 749-764

Kaila L., Martikainen P., Puntilla P. and Jakovlev E. 1994. Saproxylic beetles on dead birch trunks: effect of polypore species decaying the trunk. Annales Zoologici Fennici 31: 97-108

Kolstrom M. and Lumatjarvi J. 2000. Saproxylic beetles on aspen in commercial forests: a simulation approach to species richness. Forest Ecology and Management 126: 113-120

Komonen A. 2003. Hotspots of insect diversity in boreal forests. Conservation Biology 17: 976-981

Koponen S. 1990. Spiders Araneae on the cliffs of the Forillon National Park, Quebec. Le Naturaliste Canadien 117: 161-165

Kremen C., Colwell R. K., Erwin T. L., Murphy D. D., Noss R.F. and Sanjayan M. A. 1993. Terrestrial arthropod assemblages: Their use in conservation planning. Conservation Biology 7: 796-808

Kruys N., Fries C., Jonsson B. G., Lämås T. and Ståhl G. 1999. Wood-inhabiting cryptogams on dead Norway spruce (*Picea abies*) trees in managed Swedish boreal forest. Canadian Journal of Forest Research 29: 178-186

Kruys N and Jonsson B.G. 1999. Fine woody debris is important for species richness on logs in managed boreal spruce forests of northern Sweden. Canadian Journal of Forest Research 29: 1295-1299

Lambert R. L., Lang G. E. and Reiners W. A. 1980. Loss of mass and chemical change in decaying boles of a subalpine balsam fir forest. Ecology 61: 1460-1473

Lawrence K. L. and Wise D. H. 2000. Spider predation on forest-floor Collembola and evidence for indirect effects on decomposition. Pedobiologia 44: 33-39

Letendre M., Francoeur A., Béique R., and Pilon J-G. 1971. Inventaire des fourmis de la station de biologie de l'Université de Montréal, St-Hippolyte, Québec (Hymenoptera: Formicidae). Le Naturaliste Canadien 98: 591-606

Letendre M. and Pilon J.-G. 1973a. Nids et micromilieux de nidification utilisés par les fourmis dans les peuplements forestiers des Basses Laurentides, Québec (Hymenoptera: Formicidae). Le Naturaliste Canadien 100: 237-246

Letendre M. and Pilon J.-G. 1973b. La Faune Myrmécologique de différents peuplements forestiers caractérisant la zone des basses Laurentides, Québec (Hymenoptera: Formicidae). Le Naturaliste Canadien 100: 195-235

Levins R., Pressick M. L. and Heatwole H. 1973. Coexistence patterns in insular ants. American Scientist 61: 463-472

Lindblad I. 1998. Wood-inhabiting fungi on fallen logs of Norway spruces; relations to forest management and substrate quality. Nordic Journal of Botany 18: 243-255

Lindgren, B.S., and A.M. MacIsaac. 2002. A preliminary study of ant diversity and abundance, and their dependence on dead wood in central interior British Columbia. In : Laudenslayer W.F. Jr., Shea P. J., Valentine B., Weatherspoon C. P. and Lisle T.E. (Eds.), W. F. Laudenslayer Jr., P.J. Shea, B. E. Valentine, C.P. Weatherspoon, and T.E. Lisle. (tech. cords..). Proceedings of the symposium on the ecology and management of dead wood in western forests, November 2-4 1999, Reno, Nevada, pp 111-119. General Technical Report PSW-GTR-181, USDA Forest Service, Pacific Southwest Research Station, Albany, CA.

Lowrie D.C. 1948. The ecological succession of spiders of the Chicago area dunes. Ecology 29: 334-351

Lyford W. H. 1963. Importance of ants to brown podzolic soil genesis in New England. Harvard Forest Papers 7: 1-18

Manley G. V., Butcher J. W. and Zabik M. 1976. DDT transfer and metabolism in a forest litter macro-arthropod food chain. Pedobiologia 16: 81-98

Marikovsky P. I. 1962. On intraspecific relations of *Formica rufa* L. (Hymenoptera: Formicidae). Entomological Review 41: 47-51

Marra J. L. and Edmonds R.L. 1996. Coarse woody debris and soil respiration in a clearcut on the Olympic Peninsula, Washington, U.S.A. Canadian Journal of Forest Research 26: 1337-1345

Marra J. L. and Edmonds R. L. 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

Martikainen P. and Kouki J. 2003. Sampling the rarest: threatened beetles in boreal forest biodiversity inventories. Biodiversity and Conservation 12: 1815-1831.

Martikainen P., Siitonen J., Punttila P., Kaila L. and Rauh J. 2000. Species richness of Coleoptera in mature managed and old-growth boreal forests in southern Finland. Biological Conservation 94: 199-209

Mason R. R. and Paul H. G. 1988. Predation on larvae of Douglas-fir tussock moth, *Orgyia pseudotsugata* (Lepidoptera: Lymantriidae) by *Metaphidippus aeneolus* (Araneae: Salticidae). Pan-Pacific Entomologist 64: 258-260

McIntyre N. E. and Thompson T. R. 2003. A comparison of conservation reserve program habitat plantings with respect to arthropod prey for grassland birds. American Midland Naturalist 159: 291-301

McIver J. D., Parsons G.L. and Moldenke A. R. 1992. Litter spider succession after clear-cutting in a western coniferous forest. Canadian Journal of Forest Research 22: 984-992

Mengak M.T. and Guynn D.C. Jr. 2003. Small mammal microhabitat use on young loblolly pine regeneration areas. Forest Ecology and Management 173: 309-317

Moulder B. C. and Reichle D. E. 1972. Significance of spider predation in the energy dynamics of forest arthropod communities. Ecological Monographs 42: 473-498

Niemelä J., Haila Y. and Punttila P. 1996. The importance of small-scale heterogeneity in boreal forests: variation in diversity in forest-floor invertebrates across the succession gradient. Ecography 19: 352-368

Paquin P. and Dupérré N. 2003. Guide d'identification des araignées (Araneae) du Québec. Fabreries Supplement 11: 1-251

Petersen H. and Luxton M. 1982. A comparative analysis of soil fauna populations and their role in decomposition processes. Oikos 39: 287-388

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, Hull, Canada.

Probst J. R. and Crow T. R. 1991. Integrating biological diversity and resource management. Journal of Forestry 89: 12-17

Punttila P., Haila Y., Pajunen T. and Tukia H. 1991. Colonisation of clearcut forests by ants in the southern Finnish taiga: A quantitative survey. Oikos 61: 250-262

Raine R.M. and Kansas J. L. 1990. Black bear seasonal food habits and distribution by elevation in Banff National Park, Alberta. International Conference on Bear Research and Management 8: 297-304

Robinson J. V. 1981. The effect of architectural variation in habitat on a spider community: An experimental field study. Ecology 62: 73-80

Samuelsson J., Gustavsson L. and Ingelög T. 1994. Dying and dead trees - a review of their importance for biodiversity. Swedish Threatened Species Unit, Uppsala, Sweden.

Sanders C. J. 1964. The biology of carpenter ants in New Brunswick. The Canadian Entomologist 96: 894-909

Sanders C. J. 1970. The distribution of carpenter ant colonies in the spruce-fir forests of northwestern Ontario. Ecology 51: 865-873

Sanders C. J. 1972. Seasonal and daily activity patterns of carpenter ants *Camponotus*-spp in northwestern Ontario (Hymenoptera: Formicidae). The Canadian Entomologist 104: 1681-1687

Savely H. E. 1939. Ecological relations of certain animals in dead pine and oaks. Ecological Monographs 9: 323-385

Savolainen R. and Vepsäläinen K. A. 1988. Competition hierarchy among boreal ants: impact on resource partitioning and community structure. Oikos 51: 135-155

Siitonen J. 2001. Forest management, coarse woody debris and saproxylic organisms: Fennoscandian boreal forests as an example. Ecological Bulletins 49: 11-41

Siitonen J. and Martikainen P. 1994. Occurrence of rare and threatened insects living on decaying *Populus tremula*: A comparison between Finnish and Russian Karelia. Scandinavian Journal of Forest Research 9: 185-191

Simila M., Kouki J. and Martikainen P. 2003. Saproxylic beetles in managed and seminatural Scots pine forests: quality of dead wood matters. Forest Ecology and Management 174: 365-381

Sippola A-L., Siitonen J. and Kallio R. 1998. Amount and quality of coarse woody debris in natural and managed coniferous forests near the timberline in Finnish Lapland. Scandinavian Journal of Forest Research 13: 204-214

Söderström L. 1988. Sequence of bryophytes and lichens in relation to substrate variables of decaying coniferous wood in northern Sweden. Nordic Journal of Botany 8: 89-97

Speight M. C. D. 1989. Saproxylic invertebrates and their conservation.Council of Europe, Strasbourg

Szathmary K. 1997. Diversity of spiders (Araneae) in the diet of edible frog (*Rana esculenta* complex) in a protected wetland area in Hungary. Opuscula Zoologica Instituti Zoosystematici et Oecologici Universitatis Budapestinensis 29-30: 133-139

Torgersen T. R. and Bull E. L. 1995. Down logs as habitat for forest-dwelling ants – the primary prey of pileated woodpeckers in northeastern Oregon. Northwest Science 69: 294-303

Turnbull A. L. 1973. Ecology of the true spiders (Araneomorphae). Annual Review of Entomology 18: 305-348

Uetz G. W. 1991. Habitat structure and spider foraging. In: Bell S. S., McCoy E. D. and Mushinsky H. R. (Eds.). Habitat structure: the physical arrangement of objects in space, Chapman and Hall, pp 325-348. London.

Väisänen R., Biström O. and Heliövaara K. 1993. Sub-cordical Coleoptera in dead pines and spruces: Is primeval species composition maintained in managed forests? Biodiversity and Conservation 2: 95-113

Vallauri D., André J. and Blondel J. 2003. Le bois mort, une lacune des forêts gérées. Revue Forestière Française 55: 99-112

Van Hook R. I. 1971. Energy and nutrient dynamics of spider and orthopteran populations in a grassland ecosystem. Ecological Monographs 41: 1–26

Vepsäläinen K. and Pisarski B. 1982. Assembly of island ant communities. Annales Zoologica Fennica 19: 327-335

Waring R. H. and Running S. W. 1998. Forest ecosystems: analysis at multiple scales. Academic Press, San Diego, CA.

Wilson E. O. 1992. The diversity of life. W. W. Norton and Company. New York.

Wise D. H. 1993. Spiders in ecological webs. Cambridge University Press, Cambridge.

Wise D. H. 2004. Wandering spiders limit densities of a major microbi-detritivore in the forest-floor food web. Pedobiologia 48: 181-188

Wu J. and Wong H. R. 1987. Colonization of lodgepole pine stumps by ants (Hymenoptera: Formicidae). The Canadian Entomologist 119: 397-398

Youngs L. C. and Campbell R. W. 1984. Ants preying on pupae of the western spruce budworm, *Choristoneura occidentalis* (Lepidoptera: Tortricidae), in eastern Oregon and western Montana. The Canadian Entomologist 116: 1665-1669

Zielonka T. and Grzegorz P. 2004. The herb and dwarf shrubs colonization of decaying logs in subalpine forest in the Polish Tatra mountains. Plant Ecology 172: 63-72

CONNECTING STATEMENT

Few studies have looked at the relationships between ants/spiders and dead wood in North America. In particular, Chapter 1 emphasized that size, type and decomposition stage of dead wood are three main characteristics affecting invertebrates but these dead wood characteristics have never been experimentally tested on ants or spiders in North America.

Chapter 2 investigates the extent to which dead wood is an important habitat for generalist predators of the forest floor (i.e., ants and spiders) and provides information on the effect of wood type (coniferous or deciduous) and decomposition stage of dead wood on these predatory arthropods.

CHAPTER 2: USE OF DEAD WOOD BY GENERALIST ARTHROPOD PREDATORS AND THEIR RESPONSES TO DIFFERENT DEAD WOOD TYPES.

ABSTRACT

Downed woody material (fallen logs) offers spiders (Araneae) and ants (Hymenoptera: Formicidae) ideal sites for nesting and foraging. In a maple forest of Forillon National Park of Canada, Quebec, I compared spider and ant assemblages on, adjacent to, and away from fallen logs and tested the effects of log type and decomposition stage on these arthropods.

Spiders were affected by the presence of logs, as both species diversity and total number of individuals collected were significantly higher on the log surface compared to the forest floor. In contrast, wood type and decomposition stage of logs had few significant effects on spiders. Log type did not affect the estimated number of spider species nor the spider catch rates. Decomposition stage did not affect spider collections, but less decayed logs supported higher spider diversity than logs of advanced decay. Ants were not sufficiently abundant to perform statistical analyses. In this study, the fact that spiders used more the fallen log habitat than the forest floor provided additional support for the importance of dead wood to forest arthropod biodiversity.

INTRODUCTION

Coarse woody debris (CWD) is recognized as an essential element for the conservation of biodiversity in forests and for aspects of ecosystem function (Harmon et al. 1986; Speight 1989; Caza 1993; Samuelsson et al. 1994; Vallauri et al. 2003). CWD supports a high diversity of organisms: herbaceous plants (Zielonka and Grzegorz 2004), fungi (Lindblad 1998), bryophytes and lichens (Söderström 1988), birds (Torgersen and Bull 1995), small mammals (Mengak and Guynn 2003), amphibians (Butts and McComb 2000) and arthropods (Hamilton 1978; Hammond 1997; Siitonen 2001). Dead wood also contributes to organic matter accumulation (Lambert et al. 1980), can affect the carbon cycle by acting as a sink for atmospheric carbon (Lambert et al. 1980; Vallauri et al. 2003) and supports many species of parasitoids and predators (Ehnström 2001), some of which feed on economically important pests (Green and Sullivan 1950; Youngs and Campbell 1984; Nyffeler and Benz 1987; Mason and Paul 1988).

Arthropods contribute significantly to overall forest biodiversity (Danks and Foottit 1989; Wilson 1992) and biodiversity is linked to ecosystem integrity, as reduced biodiversity can alter ecosystem functions (Wilson 1992; Tilman et al. 2002; Hector et al. 2002). Arthropods significantly affect ecosystem function by directly or indirectly reducing primary production (Schmitz 2003), changing the physical structure of habitats (Folgarait 1998) or affecting decomposition (Lawrence and Wise 2000). Because arthropods are diverse and affect ecosystem function they should therefore be central in projects which relate to forest conservation (Agosti et al. 2000; Hammond et al. 2004).

Even though much research has been devoted to understanding the characteristics of dead wood required for dead wood dependant species (i.e., saproxylic arthropods) (e.g., Savely 1939; Speight 1989; Irmler et al. 1996; Jonsell et al. 1998; Kruys and Jonsson 1999; Siitonen 2001; Lindgren and MacIsaac 2002; Simila et al. 2003) very little information exists about the dead wood requirements of other taxa that may be associated with, but not dependent on, decaying wood.

Many predators are known to use dead wood as a habitat (Buddle 2001; Lindgren and MacIsaac 2002). Spiders (Araneae), for example, use the dead wood environment for feeding, mating, overwintering or laying eggs (Lowrie 1948; Buddle 2001), while ants (Hymenoptera: Formicidae) use dead wood for nesting (Sanders 1964; Letendre and Pilon

1973a; Torgersen and Bull 1995). Spiders and ants could have an impact on the dead wood environment and its ecosystem function either directly by changing its structure [e.g., tunnelling action of carpenter ants (Sanders 1964)] or chemical content [i.e. ant activity can change soil chemistry (Culver and Beattie 1983)] or indirectly by feeding on organisms that directly influence the dead wood habitat [e.g., spider feeding on Collembola (Lawrence and Wise 2000)]. Ants and spiders also both play critical roles in forested ecosystems (Holldobler and Wilson 1990; Wise 1993). Both taxa are diverse (Holldobler and Wilson 1990; Foelix 1996), abundant (Coddington and Levi 1991; Alonso and Agosti 2000) and represent a large portion of the arthropod predator biomass in temperate forests (Van Hook 1971; Petersen and Luxton 1982; Alonso and Agosti 2000).

Very few studies have looked at the relationship between the dead wood habitat and spiders. There have been some scattered notes in various identification guides and faunistic surveys suggesting that many ground-dwelling spider species use the dead wood habitat (Dondale and Redner 1978; 1982; Platnick and Dondale 1992; Paquin and Dupérré 2003) and some spiders (i.e. *Nuctenea umbratica* (Clerck), *Segestria florentina* (Rossi), *Coriarachne utahensis* (Gertsch), and *Coriarachne versicolor* Keyserling) have been defined as under-bark specialists (Lowrie 1948; Dondale and Redner 1978; Speight 1989). Also, Lowrie (1948) stated that there was a succession of spiders associated with the decomposition of logs. However, in North America, the only ecological study that tested various qualities of dead wood on spider assemblages (i.e., effects of bark and elevation of logs) was that of Buddle (2001). Buddle (2001) showed that spiders use dead wood differently than the forest floor with a higher estimated number of species on the wood surface compared to the forest floor. He also documented the importance of dead wood with bark as a habitat for certain species, notably the web-building guild (Buddle 2001).

Little has been published on the relationships between ant assemblages and dead wood in north temperate and boreal forests. Certain species (e.g., wood nesting carpenter ants) have been studied to varying degrees (Sanders 1964; Bradley and Hinks 1968; Sanders 1970; Sanders 1972; Akre et al. 1994), and many authors have looked at the structure of ant populations and by doing so have documented certain wood characteristics influencing ant nesting sites (Dennis 1938; Letendre and Pilon 1973a; Chen et al. 2002). In North America, only three studies (Wu and Wong 1987; Torgensen and Bull 1995; Lindgren and MacIsaac 2002) specifically studied the various characteristics of dead wood influencing ant assemblages nesting in dead wood. Size, moisture, type, decomposition stage and age of dead wood all affected the ant assemblages found in dead wood (Wu and Wong 1987; Torgensen and Bull 1995; Lindgren and MacIsaac 2002). These studies were all completed in central or western North America, and no information on the ecology of ant assemblages inhabiting dead wood in eastern forests is present in the literature.

Given the importance of dead wood to forest ecosystems, and the role of arthropods such as ants and spiders in these systems, there is clearly a need to link these two areas of study and to better understand the qualities of the dead wood habitat that make it suitable for various wood-inhabiting arthropods. Type and decomposition stage of dead wood are two of the main dead wood qualities that affect saproxylic organisms (Savely 1939; Siitonen 2001; Hammond et al. 2001). Despite their obvious significance, however, in North America these characteristics have not been tested for either spiders or ants, and should therefore be a focal point in a dead wood – ant/spider study.

My study investigated how ants and spiders use fallen logs in a maple-dominated forest in Forillon National Park of Canada(Quebec, Canada), and tested the effects of wood type and decomposition stage on spider and ant assemblages. The first objective was to confirm that spiders and ants use the surface of fallen logs. To do so I compared spider and ant assemblages found on fallen logs to those adjacent to fallen logs, and to those foraging on the forest floor. My second objective was to test the effects of wood type (coniferous and deciduous) on spider and ant assemblages, and the third objective was to determine the effect of wood decomposition stage on ant and spider assemblages.

MATERIALS AND METHODS

Site description

This work was conducted in Forillon National Park of Canada, located at the tip of the Gaspé Peninsula, Quebec, Canada (Fig. 2.1). Forillon covers 240.4 km^2 of land area, of which 95% is forest, and is surrounded by the Gulf of St. Lawrence marine region. The area was protected with creation of the park in 1970 and since then the major disturbances have been pest outbreaks and windthrow (Parks Canada 1995).

This study was completed in a ~ 4 ha sugar maple stand located at the 'La Chute' site of Forillon (Fig. 2.1). The site was situated on the north face of a small hill. The lower slope of the site was dominated by sugar maple, *Acer saccharum* Marsh, with smaller components of yellow birch *Betula alleghaniensis* Britton and balsam fir *Abies balsamea* (L.) Mill.. Understory was comprised of primarily young birches and maples. In contrast, the upper slope was dominated by balsam fir, with sugar maple and yellow birch also present. The understory here was denser than on the lower slope, and was dominated by Canada yew *Taxus canadensis* Marsh as well as young birches and maples.

Experimental design and arthropod sampling

Ants and spiders were sampled from 19 June to 19 August 2003. One experimental design was used to meet all three objectives. A series of deciduous and coniferous logs of decomposition stage II or III and of similar size were randomly chosen for study. Deciduous and coniferous logs were differentiated by visual inspection. Logs were separated by decomposition stage based on Hammond et al. (2004). Decomposition stage II logs (DSII) were classified as having 60-90% bark cover, 10-30 % mosses or lichen cover and 10-50% of the cross-sectional area showing decay. Decomposition stage III logs (DSIII) had < 60% bark cover, > 30% mosses or lichen cover and > 60% of the cross-sectional area showing decay. I was restricted to using only decomposition stage II and III logs due to the lack of other decomposition stages in the study site. Six logs were selected for each possible treatment, for a total of 24 logs. At each log ants and spiders were collected at three different locations: on logs (ON), on the forest floor directly adjacent to logs (ADJ) and on the forest floor away from logs (AWAY).

Pitfall trapping and litter sampling were used to sample spiders and ants. Twelve pitfall traps were placed on logs, four on the forest floor immediately adjacent to logs and four at 3 m from logs. The ADJ and AWAY traps were placed in the ground so that the trap surface was level with the forest floor. The ON pitfall traps were placed on the side of logs so the upper lip of the trap was close to the upper surface of the log. These were installed by nailing one third of the pitfall trap circumference to the log. Since one third of the ON pitfall trap surface was touching the logs while all the ADJ and AWAY traps surface was touching the forest floor, three pitfall traps on the log were considered equivalent to one pitfall trap on the forest floor [i.e., standardized to perimeter length, see Luff (1975)]. Six ON pitfall traps and two ADJ and AWAY pitfall traps were placed on each side of the logs, in an area less than one meter from each end of the logs.

Pitfall traps were 6.0 cm in diameter with a plastic permanent outer cup (7.0 cm height) and an inner sampling cup (5.0 cm height) containing propylene glycol as a preservative, diluted to 50% water, with a total depth of ~4 cm (113.10 cm^3). A circular plastic roof (12.0 cm in diameter) was placed ~2-3 cm over each trap using nails to protect the traps from rain. Traps were emptied about every 14 days from 19 June to 5 August. This included the period of peak activity for many northern spider assemblages (e.g., Niemelä et al. 1994; Buddle and Draney 2004). This time frame was also adequate to capture peak activity time of ants, since they have a relatively constant presence at a site and as a result a short duration collection is sufficient to have a representative sample of the ant community present at a site (Alonso and Agosti 2000).

Litter samples were taken about every 14 days from 26 June to 19 August. Two litter samples were taken adjacent and away from each study log at every collecting time. The circular area of litter collected had a diameter of 0.26 m (0.053 m^2 of litter). Litter samples were placed in a screened bucket and shaken for 5 minutes into a large plastic container. Ants and spiders falling from the litter were collected with an aspirator and placed in 70% ethanol.

Arthropod identifications and statistical analyses

Ants and spiders were identified to species using various taxonomic keys. Most spiders could be identified to species using Paquin and Dupérré (2003). However, Dondale and Redner (1978, 1982), Planick and Dondale (1992) and Dondale et al. (2003) were also used. Spider specimens were verified by Dr. C. Dondale (Canadian National Collection, Ottawa). It was not possible to positively identify immature or damaged spider specimens. Ants were identified to species using various taxonomic revisions notably Creighton (1950), Wilson (1955) and Francoeur (1973, unpublished key). Difficult species were first identified to morphospecies and then verified by Dr. Francoeur (Centre de données sur la biodiversité du Québec, Chicoutimi). Voucher specimens were deposited in the Lyman Entomological Museum (Ste Anne de Bellevue, QC) and in the Canadian National Collection (Ottawa) (spiders).

Frequency (% of sample in which ant workers were found) instead of total catches was used for ant data because the number of ant catches is dependent on the distance from the nest (Longino 2000). Spiders were divided into hunting and web-building guilds according to the following criteria: the web-building spiders are sedentary type spiders that make webs to catch prey and hunting spiders do not use webs to catch prey (Gertsch 1979). Thus, the following families were considered as web-building spiders: Therididae, Agelenidae, Linyphiidae (Erigoninae), Linyphiidae (Linyphiinae), Amaurobiidae, Hahniidae, Araneidae, Dictynidae, Cybaeidae. The following families are hunting spiders: Liocranidae, Lycosidae, Clubionidae, Mimetidae, Gnaphosidae, Salticidae, Thomosidae, Philodromidae. This classification has been used effectively in the ecological spider literature since the two guilds frequently exhibit predictable responses to various habitat types or environmental changes (e.g., Stevenson and Dindal 1982; Riechert and Lawrence 1997; Buddle et al. 2000; Buddle 2001).

Individual-based rarefaction analysis (Gotelli and Colwell 2001) was used to calculate the expected number of species, E(s), for the total number of spiders (standardized to sampling effort, number of individuals), for comparison of pitfall and litter placement, log type and log decomposition stage. Rarefaction was used as a diversity index because it considers the number of individuals collected, allows comparison of diversity between treatments at similar sample size and, by showing the rate of new species accumulation, allows for verification that enough samples were collected to make proper comparisons of diversity (Gotelli and Colwell 2001; Magurran 2004). Expected number of web-building and hunting spider species was also calculated for comparison of pitfall trap placement. The software program EcoSim700 (Acquired Intelligence Inc., Kesey-Bear) was used for rarefaction analyses (Gotelli and Entsminger 2001).

The Kolmogorov-smirnov test was used to test if the data was normally distributed, and the Levene's test was used to test if the data had homogeneity of number variance. When the data did not meet the assumptions for parametric statistics data were log-transformed (x' = log (x+1)), or data were tested using non-parametric statistics that were analogous to analysis of variance (ANOVA). The sample units for all analyses were individual logs (N=24), so individual pitfall trap or litter data were combined to represent a catch per log. Subsequent to pooling traps, the representation of catch per log was divided by the number of pitfall traps present since disturbance by mammals sometimes reduced their number.

To test effects of pitfall trap or litter placement on parametric data, I used a one-factor analysis of variance (ANOVA) with three levels of the main factor 'trap placement' (ON, ADJ, AWAY) for pitfall trap data, and with two levels of the main factor 'collection placement' (ADJ, AWAY) for litter samples. When the data did not meet the assumptions for parametric statistics I used the Kruskal Wallis test (Sokal and Rohlf 1995). Effect of pitfall trap placement, log type and log decomposition level were tested on the following variables: total number of specimens collected, total number of species, number of hunting spiders collected, number of hunting spider species collected, number of web-building spiders collected, number of web-building species collected, total number of immature specimens, and catch rates of the most common species (i.e., species that represent the bulk of the sample, with enough individuals to warrant statistical analysis). Additionally, effect of pitfall trap placement was tested on the total number of females and males collected. Effect of litter placement was tested only on total number of specimens, total number of species, number of female and male specimens and number of immature specimens for the number of collected specimens was to small to be divided by spider guild or species.

To test the effect of log type and decomposition stage on the spider data, I used a two-factor ANOVA with wood type (deciduous and coniferous) and decomposition level (Decomposition stage I or II) as main factors. When the data did not meet the assumptions for parametric statistics I used the Scheirer-Ray-Hare test (Sokal and Rohlf 1995). Tests for wood type and decomposition stage were completed only for spiders collected on the log surface. I did not test the effect of log type or decomposition level on the litter data, since the objective was to test the effect of log type on spiders using the log surface and not on spiders using the forest floor. Here, the same spider variables as for the pitfall trap and litter placement were tested.

SAS statistical package (SAS Institute Inc., Cary, NC) was used for these tests; *P*-values were not adjusted for multiple comparisons since such tests can be overly conservative, difficult to standardize, and can be considered contrary to detailed ecological work (Moran 2003).

Non-metric multidimensional scaling (NMDS) ordination analysis was conducted using the software PC-ORD (McCune and Mefford 1999), to investigate community patterns in relation to pitfall trap placement, log type and decomposition stage. NMDS ordination finds the reduced number of axes that best explain variation in species composition among samples. The program gives a stress value to all axes by comparing the distance that the samples have with the axes with dissimilarity in the community structure. When the stress value of the ordination is low, close to 0, the dissimilarity in between the samples is represented by the distances (ter Braak 1995). For this ordination, data standardized by number of pitfall trap was used and all species were included in the analysis. For all the tests, a six-dimensional ordination and an evaluation of stress factors was first performed to assess the lowest number of dimensions to be used for a final solution. To test for the effect of pitfall trap placement 72 samples, representing the three pitfall trap positions (ON, ADJ, AWAY) at each 24 logs used in the study, and 80 species were used. To test for effect of wood type and decomposition stage, only data from pitfall traps on the logs were used which resulted in an ordination with 24 samples and 69 species. The final solution was compared using Monte Carlo simulations (n=100), to test whether the final ordination differed significantly from random data matrices (McCune and Grace 2002).

RESULTS

Ants

A total of 219 ants representing four species was collected from pitfall traps: *Camponotus pennsylvanicus* (DeGeer), *Camponotus herculeanus* (Linnaeus), *Myrmica detritinodis* Emery and *Formica glacialis* Wheeler. The most commonly collected ant was *C. pennsylvanicus* with a frequency of 12.5 % (207 individuals) followed by *C. herculeanus* (5.6%, 5 individuals), *F. glacialis* (8.3%, 6 individuals) and *M. detritinodis* (1.4 %, 1 individual). Both *C. pennsylvanicus* and *M. detritinodis* are new records for Forillon National Park, increasing Francoeur's (1981, 1986) list to a total of 18 ant species known from this region of Quebec. Given the low catch rates, the ant data were not analysed further. No ants were collected using the litter sampling technique.

Spiders

A total of 5613 adult spiders was collected (5203 pitfall, 410 litter), representing 83 species (78 pitfall, 40 litter) from 16 families (Appendix 2.1). Males were represented by 3563 individuals (3497 pitfalls, 66 litter) and 2050 were females (1706 pitfall, 344 litter). A further 2573 spider specimens were immature (921 pitfall, 1652 litter). The eight most common species (representing > 2% of total catch) found in pitfall traps were the following: *Neoantistea magna* (Keyserling) (30% of all spider specimens collected), *Cryphoeca montana* Emerton (15%), *Agroeca ornata* Banks (8%), *Amaurobius borealis* Emerton (7%), *Pardosa mackenziana* (Keyserling) (5%), *Wadotes calcaratus* (Keyserling) (5%), *Callobius bennetti* (Blackwall) (4%) and *Ozyptila distans* Dondale and Redner (3%) (Appendix 2.1). The sixteen most frequently collected species (representing > 2% of the total catch) found in litter samples were the following: *A. ornata* (3%), *A. borealis* (13%), *Ceraticelus minutus* (Emerton) (3%), *Cicurina brevis* (Emerton) (3%), *Lepthyphantes alpinus* (Emerton) (2%), *Microneta viaria* (Blackwall) (3%), *Robertus riparius* (Keyserling) (2%), *Tapinocyba simplex* (Emerton) (3%), *Walckenaeria exigua* Millidge (2%), *C. montana* (7%), *N. magna* (3%), *Diplocephalus subrostratus* (O.P.-Cambridge) (6%), *Maso sundevallii* (Westring) (7%), *Neon nellii*

Peckham and Peckham (13%), *Tapinocyba minuta* (Emerton) (8%) and *Centromerus persolutus* (O.P.-Cambridge) (4%) (Appendix 2.1).

Of particular interest was the collection of *Enoplognatha intrepida* (Sørensen) and *Erigone dentipalpis* (Wider) which were expected to be present in Quebec (Paquin and Buckle 2001), and which collections in Forillon have confirmed this speculation and represent first records for these species in Quebec: *Erigone dentipalpis* was known previously from Newfoundland and the Palaearctic (Paquin and Buckle 2001) and *E. intrepida* was known to be present from Yukon to estern Ontario (Levi 1957).

Pitfall trap placement

Dead wood had a significant influence on spider assemblages. In terms of diversity, rarefaction analyses revealed significantly higher expected species richness for spiders collected in ON pitfall traps compared to ADJ or AWAY pitfall traps (Fig. 2.2a). Expected number of species of web-building spiders was also significantly higher in ON pitfalls traps followed by ADJ and AWAY pitfall traps (Fig. 2.2c); expected species richness of hunting spiders did not differ significantly by trap placement (Fig. 2.2c), but sample sizes for these collections were relatively low. Spider diversity from litter collections from ADJ pitfall traps was significantly higher than AWAY pitfall traps (Fig. 2.2b). ON pitfall traps collected the highest number of spider species even though most species were common to the three pitfall trap positions (Fig. 2.3). ADJ and AWAY traps shared more species with ON traps than with each other and ADJ traps collected more species than AWAY traps (Fig. 2.3).

There was a significant effect of pitfall trap placement (ON, ADJ, AWAY) on the number of specimens and raw species richness for the total number of spiders collected, number of hunting and web-building spiders as well as on the catch rates of immatures, females, males and of all but one common species (Table 2.1). In general, a significantly greater number of spider individuals and species were caught on the log surface compared to the forest floor (Table 2.1). However, female specimens, *A. ornata* and *N. magna* were all more commonly collected on the forest floor than on the log surface. Results of litter collections also showed an effect of position, as significantly more spiders, more female spiders, and more species were taken from samples directly adjacent to logs compared to away from logs (Table 2.1). The effects of litter placement on the number of male and immature specimens did not differ by litter sampling location (Table 2.1).

A two-dimensional solution was deemed optimal for the NMDS ordination for trap placement data. This ordination was significantly different than would be derived at random (Monte Carlo test, n = 100, both axes $P < 0.01$), and explained 86% of the overall variation in the original data matrix (first axis 25%, second axis 62%). The ordination separated the spider assemblages found in pitfalls along the y-axis, which explained most of the variation in the sample by species matrix (Fig. 2.4). Pitfall traps on the log (ON) yielded a different assemblage of spiders compared to ADJ and AWAY traps (Fig. 2.4). There was little differentiation in the overall fauna from ADJ and AWAY traps (Fig. 2.4).

Wood type and decomposition

The total expected number of species determined by rarefaction analysis revealed that traps on decomposition stage II logs contained more diverse spider assemblages compared to those from decomposition stage III logs (Fig. 2.5a). This higher diversity on DS II logs was also expressed by hunting and web-building spiders (Fig. 2.5b). Wood type did not have a significant effect on the total expected number of species (Fig. 2.5c). However, hunting spiders were more diverse on coniferous logs whereas web-building spiders were more diverse on deciduous logs (Fig. 2.5d). The total number of species and the number of species unique to each treatment (in parentheses) for coniferous, deciduous, DS II and DS III logs were the following: 53 species (16), 51 species (14), 57 species (17), 50 species (10).

Few of the variables tested were significantly affected by wood type and/or decomposition stage of logs. The exceptions included number of hunting spiders and collections of *O. distans* and *P. mackenziana*, which were all significantly more common on coniferous logs and *C. bennetti*, which was more abundant on deciduous logs (Table 2.2). Number of web-building spiders was significantly more common on DS III logs compared to DS II logs (Table 2.2). In the case of *N. magna*, there was a significant interaction effect between wood type and decomposition stage (Table 2.2). *Neoantistea magna* was more common in pitfall traps found on coniferous logs of decomposition stage III (mean number of individuals per trap (± SE), 4.6 ±0.54) then in pitfall traps placed on logs of any other treatment combination (Table 2.2).

A 3-dimensional solution was deemed optimal for the NMDS ordination separating wood type and decomposition stage. This ordination was significantly different than would be derived at random (Monte Carlo test, n = 100) for axis 1 and 3 (at $P < 0.05$), but not for axis 2. The ordination explained 80% of the overall variation in the original data matrix (first axis 28%, second axis 30% and third axis 22%). Focusing on Axis that were different than would be derived at random (axis 1 and 3), samples located on the surface of the logs of conifer decomposition stage II yielded a different assemblage of spiders compared to traps located on logs of conifer decomposition stage III (Fig. 2.6). There was little differentiation in the overall fauna from conifer and deciduous traps, decomposition stage II and III traps and deciduous II and deciduous III traps (Fig. 2.6).

DISCUSSION

Spiders of the La chute site of Forillon National Park of Canada used the dead wood habitat more than the forest floor. Along with the vast literature on the importance of dead wood to saproxylic invertebrates (e.g., Harmon et al. 1986; Speight 1989; Caza 1993; Samuelsson et al. 1994; Vallauri et al. 2003), it is becoming clear that generalist predators such as spiders are highly influenced by fallen logs. Spiders were more commonly collected, and were more diverse on the logs than on the forest floor adjacent or away from the logs, and the overall assemblage differed dramatically on the wood surface compared to the forest floor. These findings support the findings of Buddle (2001) and highlight the importance of dead wood as a key habitat for spiders. In this study, spiders collected on logs were additionally tested for effects of wood type and decomposition stage to better understand the factors driving the dead wood-spider relationship. Wood type had little effect on overall spider assemblages, but did affect guilds. Web-building and hunting spider diversity showed opposite trend in relation to wood type: Web-building spiders were more diverse on deciduous logs and hunting spiders on conifer logs. Stage of decomposition also influenced aspects of the spider assemblages at Forillon National Park. My study greatly enhanced knowledge on the spiders of Forillon National Park of Canada for 55 new species were added to the known spider species of Forillon (Koponen 1990).

Although the ant data were sparse and statistical analyses were not possible, this work has added two species records for Forillon National Park. Together with Francoeur's work, (1981, 1986), 18 ant species are now known for this region of Canada. The low diversity and number of ants collected in my sugar maple with yellow birch forest is consistent with the findings of Letendre and Pilon (1973b) and Francoeur (1966). In both cases, a dense canopy cover seems to be the responsible for low ant diversity and abundance. Furthermore, my site was north facing and Van Pelt (1963) and Letendre and Pilon (1973b) found a low number of species at northern oriented sites compared to sites oriented in other directions. Both canopy cover and orientation of sites affect the amount of solar radiation reaching the soil and high solar radiation is important for the optimal development of ant brood (Brian and Brian 1951; Pontin 1960). Collection bias may also have affected the results as ants are cryptic in nature (Letendre and Pilon 1973b) and many species associated with maple forests typically live below-ground (Francoeur 1966). This habitat was not sampled with the present work. Nonetheless, the general protocols and design used in this study could certainly be adapted to different sites or habitat to better understand the relationships between ant assemblages and the dead wood habitat.

Use of the dead wood habitat by spiders

Together with work by Buddle (2001) in Alberta's aspen-mixed wood boreal region, this work has confirmed that fallen logs represent a key habitat for spiders. Both diversity and number of spiders collected were higher on the log than on the forest floor (Fig 2.2a; Table 2.1). In addition, the ordination analysis revealed a clear distinction between spider assemblage on the wood surface compared to the forest floor (Fig. 2.4). The ordinations and rarefaction curves from this study match very closely to those of Buddle (2001), highlighting the general nature of these findings in different regions of Canada. When looking at effects of pitfall trap placement on the diversity of hunting and web-building spider separately (Fig 2.2c), only web-building spiders show a clear difference by trap position, with web-building spider diversity higher on the surface of wood compared to the forest floor. However, it is difficult to fully assess the effects of trap placement on hunting spiders due to a low number of individuals collected. Additional collections may have confirmed a similar finding to web-building spiders, especially since total collections of hunting spiders, and raw species richness of hunting spiders was significantly higher on logs (Table 2.1).

There are many reasons why the dead wood habitat could be favourable to spiders. First, logs could house invertebrates that are food for spiders. Prey abundance is an important factor in determining habitat choice by some spiders (e.g., Turnbull 1964; Olive 1982; Gillespie 1987) and since dead wood is associated with a rich insect fauna (Hamilton, 1978), it could be a key resource for spiders, especially since it is argued that most spiders are food-limited (Wise 1993). Second, the structure of dead wood could be favourable to spiders, since this feature is important for an attachment site for webs (Riechert and Gillespie 1986). Third, logs have a particular microclimate that could be favourable for spiders. Both temperature and humidity are higher in logs than in the surrounding air (Savely 1939). Finally, logs accumulate litter in their surroundings which could act as a protective area for invertebrates (Harmon et al. 1986; Andrew et al. 2000).

Spiders may not always prefer dead wood to the forest floor as Buddle (2001) found a lower collection of spiders on the wood surface than on the forest floor (except for immature spiders). The reasons for this dissimilarity could come from differences in aspen and maple forest litter and dead wood qualities, or from differences in pitfall trapping technique. In contrast to Buddle (2001), my traps were not inserted in the logs but placed on the wood surface and adjusted for pitfall trap perimeter touching the wood. However, Work et al. (2002) showed that spider abundance is dependent on pitfall trap circumference and so standardized data should be comparable. Also, I collected a higher number of females, *Agroeca ornata* and *Neoantistea magna* on the forest floor compared to on the logs, suggesting that it was also possible to collect higher numbers of spiders on the forest floor than on logs with the pitfall trapping technique used in the present study.

Even though many species (17) were collected exclusively in the pitfall traps placed on the logs, none of these were represented by more than 2 specimens; dead wood therefore likely provides an important habitat for rarely collected species in Forillon National Park, a result consistent with Buddle (2001). Five of the most common species (*Amaurobius borealis, Callobius bennetti, Cryphoeca montana, Ozyptila distans, Pardosa mackenziana*), were found more frequently on the log surface than on the forest floor. *Amaurobius borealis* is a widespread boreal species that is common in leaf litter (Freitag et al. 1982). This species was collected on dead wood by Buddle (2001), but he reported it to be more common on the forest floor than on logs. Site or collection differences may explain the difference. *Callobius bennetti* and *Cryphoeca montana* are common species in eastern North America, also typically known from leaf-litter (Freitag et al. 1982; Paquin and LeSage 2000). *Ozyptila distans* has commonly been collected in southeastern Canada, and is known from a range of habitats (Dondale and Redner 1978); dead wood is probably one of the many habitats it has adapted to. *Pardosa mackenziana* is also known from a variety of habitats (cliffs: Koponen 1990; boreal forests: Freitag et al. 1969; Buddle et al. 2000; bogs: Aitchison-Benell 1994), and Buddle (2001) collected this species more commonly on log surfaces compared to the forest floor. Although *P. mackenziana* is a general forest wolf spider, there is now mounting evidence that it selects for dead wood in northern forests, perhaps as a habitat to use selectively during certain aspects of its life-history (Buddle 2001). Future work is required to assess whether fitness of *P. mackenziana* is improved when it is able to access dead wood in a forest ecosystem.

Females, as well as specimens of *Agroeca ornata* and *Neoantistea magna,* were collected significantly more often on the forest floor compared to the log surface (Table 2.1). *Neoantistea magna* is regularly found in litter where they typically construct webs close to the ground (Opell and Beatty 1976), including in depressions made in the ground by mammals (C. Buddle, personal observation). These habitat affinities are confirmed by the present work, as this species clearly selected the forest floor against the log surface. *Agroeca ornata* is also typically a litter-dwelling spider (e.g., Hackman 1954; Buddle et al. 2000) and was rarely found on log surfaces by Buddle (2001). The reason for the lower number of females on the log surface remains unknown. However, females of some northern spider species are known to preferentially deposit egg sacs in litter (Toft 1978), and this adaptation may explain low capture rates of females on logs.

Logs seem to affect the litter habitat in a way that is favourable for spiders. Similar to Jabin et al. (2004), I found a higher diversity and collection number of spiders in litter samples adjacent from logs than away from logs. Similarly, ants are known to have higher species richness in litter close to logs compared to away from logs (Andrew et al. 2000). Many studies have shown that litter depth affects hunting spiders and that ground dwelling spider diversity increases with increasing litter depth and complexity (e.g., Uetz 1991). Also, linyphiids prefer low temperature and high moisture (Huhta 1971) and are found to aggregate non-randomly within the litter layer (Leclerc and Blandin 1990). Jabin et al. (2004) attributed the difference in the abundance of spiders at different litter positions to favourable microclimatic conditions and the aggregation of potential food items close to logs. Evans et al. (2003) suggested that the change in abundance of some invertebrate families at different distance from the logs is the result of high amount of wood accumulating under logs, which creates litter build up and changes in microsite moisture and temperature (Evans et al. 2003).

Effects of wood type and decomposition stage on spider assemblages

Buddle (2001) investigated the effects of bark and wood elevation on spider assemblages, but this study is the first to investigate the effects of wood type and decomposition stage on spider assemblages. The expected number of species, as showed by rarefaction, was higher on decomposition stage II compared to decomposition III logs. This finding confirms what is known for other organisms associated with dead wood (Esseen et al. 1992; Bader et al. 1995; Jonsell et al. 1998; Ehnström 2001). In general, medium decayed wood supports high diversity because it is more complex than less decayed wood but less uniform than highly decayed wood and still separate from the forest floor (Ehnström 2001). Thus, it likely harbours a mix of species that might be found on either more or less decayed wood. In the spider variables tested, only web-building spiders responded significantly to wood decomposition stage by being collected more frequently on decomposition III logs than on decomposition II logs. Decomposition III logs could possess higher prey availability for spiders since wood age corresponds to increases in microbial biomass (Sollins et al. 1987). Collembolans are also known to commonly inhabit highly decayed stumps in western Canada (Setälä and Marshall 1994) and are a potential spider food (Wise and Wagner 1992; Buddle 2002). Given the low number of hunting spiders collected, it is unknown whether this response may also occur for the hunting spider guild.

Wood type did not have a significant effect on spider diversity (Fig. 2.5c) or on the overall assemblage (Fig. 2.6). This confirms work of Irmler et al. (1996) who found that type of wood contributes less to the diversity of wood dwelling species than does wood decomposition stage. Usually, as dead wood ages, the wood decomposition stage becomes more important than wood type in determining invertebrate assemblages (Howden and Vogt 1951). Web-building spiders, which were the most common spider-guild collected, were more diverse on deciduous logs while hunting spiders were more diverse on conifer logs. Catches of hunting spiders were also significantly higher on conifer logs than on deciduous logs. Savely (1939) also found certain predators associated with specific log types (coniferous, deciduous), and the fact that coniferous and deciduous logs have a different associated insect fauna (Savely 1939; Jonsell et al. 1998) could explain the difference between the two spider guilds.

Some of the most commonly collected species were significantly influenced by wood type and decomposition stage. *Callobius bennetti* was found significantly more often on deciduous logs, *O. distans* was found significantly more often on coniferous logs and *N. magna* was significantly affected by the interaction of wood type and decomposition stage. *Neoantistea magna* was more common in pitfall traps found on conifer logs only when the logs were of decomposition stage III. Species-specific responses, such as these, illustrate how habitat requirements of many spiders can differ. We know little about the habitat requirements of many North American spiders and most of what we know comes from taxonomic work (e.g., Dondale and Redner 1978, 1982; Planick and Dondale 1992; Dondale et al. 2003); phenological work on boreal spiders in North America is sparse (but see Buddle and Draney 2004). There is clearly a need to study the natural history and phenology of these species in order to shed light on the current results.

Conclusions

Ant diversity and abundance was low at the La chute maple forest of Forillon National Park, making it difficult to offer concrete conclusions related to log use by ant assemblages. However, ants are important to forest ecosystem (Holldobler and Wilson 1990) and in order to better preserve our forest environment it is important to link their diversity and abundance to key features in the forest, such as fallen logs. Ants are common in other forests of Canada (e.g., Francoeur 1965; Francoeur 1966; Letendre and Pilon 1973a), and completing a project, in these or other locations, similar to the current effort would be important.

Spiders, in contrast, exhibited a strong response to the dead wood habitat, confirming findings from Alberta (Buddle 2001). In contrast to the work in western Canada, however, I found spider catch rates and raw species richness were higher in the traps placed on the logs compared to the forest floor. Additionally, litter sampling was not done by Buddle (2001), and these results illustrated the importance of the litter habitat for spiders directly adjacent to fallen logs, a finding similar to Jabin et al. (2004). The effects of wood type and decomposition stage were also compared for effects on spider assemblages, and these qualities of the dead wood habitat certainly affected aspects of the spider assemblages. In particular, high diversity was recorded on decomposition stage II logs, and wood type suggested some intriguing responses at a guild- and species-specific level. These new findings strengthen the importance of dead wood for spider assemblages in forest habitat. Spiders use the log habitat, and are highly influenced by the transformed habitat directly adjacent to dead wood. Along with saproxylic invertebrates, dead wood is also a key habitat for conservation of generalist ground-dwelling predators, such as spiders.

REFERENCES

Agosti D., Majer J. D., Alonso L. E. and Schultz T. R. 2000. Ants: Standard methods for measuring and monitoring biodiversity, Smithsonian Institution. Washington (DC).

Aitchison-Benell C. W. 1994. Bog arachnids (Aranae, Opiliones) from Manitoba taiga. Memoirs of the Entomological Society of Canada 169: 21-31

Akre R. D., Hansen L. D. and Myhre E. A. 1994. Colony size and polygyny in carpenter ants (Hymenoptera: Formicidae). Journal of the Kansas Entomological Society 67: 1-9

Alonso L. E and Agosti D. 2000. Biodiversity studies, monitoring and ants: An overview. In: Agosti D., Majer J. D., Alonso L. E. and Schulz T.R. (Eds), Ants: Standard methods for measuring and monitoring biodiversity, pp 1-8. Smithsonian Institution, Washington (DC).

Andrew N., Rodgerson L., and York A. 2000. Frequent fuel-reduction burning: the role of logs and associated leaf litter in the conservation of ant biodiversity. Austral Ecology 5: 99-107

Bader P., Jansson S. and Jonsson B. G. 1995. Wood-inhabiting fungi and substratum decline in selectively logged boreal spruce forests. Biological Conservation 72: 355-362

Bradley G. A. and Hinks J. D. 1968. Ants, aphids and jack pines in Manitoba. The Canadian Entomologist 100: 40-50

Brian M. V. and Brian A. D. 1951. Insolation and ant population in the west of Scotland. Transactions of the Royal Entomological Society of London 102: 303-330

Buddle C. M. 2001. Spiders (Araneae) associated with downed woody material in a deciduous forest in central Alberta, Canada. Agricultural and Forest Entomology 3: 241-251

Buddle C. M. 2002. Interactions among young stages of the wolf spiders *Pardosa moesta* and *P. mackenziana* (Araneae: Lycosidae). Oikos 96: 130-136

Buddle C.M. and Draney M.L. 2004. Phenology of linyphiids in an old-growth deciduous forest in central Alberta, Canada. Journal of Arachnology 32: 221-230

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

Butts S. R. and McComb W. C. 2000. Association of forest-floor vertebrates with coarse woody debris in managed forests of western Oregon. Journal of Wildlife Management 64: 95-104

Caza C. L. 1993. Woody debris in the forests of British Columbia: a review of the literature and current research. Land Management Report 78, Ministry of Forestry, Victoria B.C.

Chen Y., Hansen L. D. and Brown J. J. 2002. Nesting sites of the carpenter ant, *Camponotus vicinus* (Mayr) (Hymenoptera: Formicidae) in Northern Idaho. Environmental Entomology 31: 1037-1042

Coddington J. A. and Levi H. W. 1991. Systematics and evolution of spiders (Araneae). Annual Review of Ecology and Systematics 22: 565-592

Creighton W.S. 1950. The ants of North America. Harvard Museum of Comparative Zoology Bulletin 104: 1-585

Culver D.C. and Beattie A. J. 1983. Effects of ant mounds on soil chemistry and vegetation patterns in Colorado montane meadow. Ecology 64: 485-492

Danks H.V. and. Foottit R. G. 1989. Insects of the boreal zone of Canada. The Canadian Entomologist 121: 626-690

Dennis C. A. 1938. The distribution of ant species in Tennessee with reference to ecological factors. Annals of the Entomological Society of America 31: 267-308

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, Hull, Canada

Dondale C.D. and Redner J.H. 1982. The insects and arachnids of Canada. Part 9. The sac spiders of Canada and Alaska (Araneae: Clubionidae and Anyphaenidae). Agriculture Canada Publication, Hull, Canada

Dondale C.D., Redner J.H., Paquin P. and Levi H. W. 2003. The insects and arachnids of Canada. Part 23. The orb-Weaving spiders of Canada and Alaska (Araneae: Uloboridae, Tetragnatidae, Araneidae, Theridiosomatidae). National Research Council of Canada, Ottawa, Canada

Ehnström B. 2001. Leaving dead wood for insects in boreal forests--suggestions for the future. Scandinavian Journal of Forest Research 3: 91-98.

Esseen P-A., Ehnström B., Ericson L. and Sjöberg K. 1992. Boreal forests – the focal habitats of Fennoscandia. In: Hansson, L. (ed.), Ecological principles of nature conservation. Elsevier, London, pp. 252-325

Evans A. M., Clinton P. W., Allen R. B. and Frampton C. M. 2003. The influence of logs on the spatial distribution of litter-dwelling invertebrates and forest floor processes in New Zealand forests. Forest Ecology and Management 184: 251-262

Foelix R.F. 1996. Biology of Spiders. Oxford University Press, Inc. New York, New York.

Folgarait P. J. 1998. Ant biodiversity and its relationship to ecosystem functioning: A review. Biodiversity and Conservation 7: 1221-1244

Francoeur A 1965. Écologie des populations de fourmis dans un bois de chêne rouges et d'érables rouges. Le Naturaliste Canadien 92: 263-276

Francoeur A. 1966. La faune myrmécologique de l'érablière à sucre (*Aceretum saccharophori* Dansereau) de la region de Québec. Le Naturaliste Canadien 93: 443-472

Francoeur A. 1973. Revision taxonomic des espèces néarctiques du groupe *fusca*, genre *Formica*. Mémoire de la Société Entomologique du Québec 3 : 1-316

Francoeur A. 1981. Les Fourmis de la Presqu' île de Forillon, Comté de Gaspé-est, Québec (Formicidae, Hymenoptera). Fabreries 4: 78-83

Francoeur A. 1986. Supplément aux fourmis de la presqu'île de Forillon, Gaspé-Est, Québec. Fabreries 12: 56-58

Freitag R., Barnes B.L., Tropea R. and Leech R.E. 1982. An annotated list of spiders collected during the "Big Dig" near Wawa, Ontario, 1971. Canadian Field Naturalist 96: 383-388

Gertsch W. 1979. American spiders. Van Nostrand Reinhold Company, New York, New York.

Gillespie R. G. 1987. The mechanism of habitat selection in the long-jawed orb-weaving spider *Tetragnatha elongata* (Araneae, Tetragnathidae). Journal of Arachnology 15: 81-90

Gotelli N. J. and Colwell R. K. 2001. Quantifying biodiversity: Procedures and pitfalls in the measurement and comparison of species richness. Ecology Letters 4: 379-391

Gotelli N.J. and Entsminger G.L. 2001. Ecosim: Null Models Software for Ecology, Version 6.0. Acquired Intelligence Inc, & Kesey-Bear http://homepages.together.net/gentsmin/ecosim.htm

Green, G. W. and Sullivan C. R. 1950. Ants attacking the larvae of the Forest Tent Caterpillar, *Malacosoma disstria*. The Canadian Entomologist 82: 194-195

Hackman W. 1954. The spiders of Newfoundland. Acta Zoologica Fennica 79: 1-99

Hamilton W. D. 1978. Evolution and diversity under bark. In Mound L. A. and Waloff N. (Eds), Diversity of insect faunas, pp. 154-175. Blackwell Scientific Publications, Oxford, UK.

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

Hammond H. E. J., Langor D.W. and Spence J. R. 2001. Early colonization of *Populus* wood by saproxylic beetles (Coleoptera). Canadian Journal of Forest Research 31: 1175-1183

Hammond H. E. J., Langor D.W. and Spence J. R. 2004. Saproxylic beetles (Coleoptera) using *Populus* in boreal aspen stands of western Canada: spatiotemporal variation and conservation of assemblages. Canadian Journal of Forest Research 34: 1-19

Harmon M. E., Franklin J. F., Swanson F. J., Sollins P., Gregory S. V., Lattin J. D., Anderson N. H., Cline S. P., Aumen N. G., Sedell J. R., Lienkaemper G. W., Cromack K. Jr. and Cummins K. W. 1986. Ecology of coarse woody debris in temperate ecosystems. Advances in Ecological Research 15: 133-302

Hector A., Loreau M., Schmid B and the BIODEPTH project. 2002. Biodiversity manipulation experiments: Studies replicated at multiple sites. In: Loreau M., Naeem S. and Inchausti P. (Eds), Biodiversity and ecosystem functioning, synthesis and perspectives, pp. 36-46. Oxford University Press, New York.

Holldobler B. and Wilson E. O. 1990. The ants. The Belknap Press of Harvard University Press, Cambridge, Massachusetts.

Howden H. F. and Vogt G. B. 1951. Insect communities of standing dead pine (*Pinus virginiana* Mill). Annals of the Entomological Society of America 44: 581-595

Huhta V. 1971. Succession in the spider communities of the forest floor after clear-cutting and prescribed burning. Annales Zoologici Fennici 8: 483-542

Irmler U., Heller K. and Warning J. 1996. Age and tree species as factors influencing the populations of insects living in dead wood (Coleoptera, Diptera: Sciaridae, Mycetophilidae). Pedobiologia 40: 134-148

Jabin M., Mohr D., Kappes H and. Topp W. 2004. Influence of deadwood on density of soil macro-arthropods in a managed oak–beech forest. Forest Ecology and Management 194: 61–69

Jonsell M., Weslien J. and Ehnström B. 1998. Substrate requirements of red-listed saproxylic invertebrates in Sweden. Biodiversity and Conservation 7: 749-764

Koponen S. 1990. Spiders (Araneae) on the cliffs of the Forillon National Park of Canada,Quebec.

Le Naturaliste Canadien 117: 161-165

Kruys N and Jonsson B.G. 1999. Fine woody debris is important for species richness on logs in managed boreal spruce forests of northern Sweden. Canadian Journal of Forest Research 29: 1295-1299

Lambert R. L., Lang G. E. and Reiners W. A. 1980. Loss of mass and chemical change in decaying boles of a subalpine balsam fir forest. Ecology 61: 1460-1473

Lawrence K. L. and Wise D. H. 2000. Spider predation on forest-floor Collembola and evidence for indirect effects on decomposition. Pedobiologia 44: 33-39

Leclerc J. and Blandin P. 1990. Empirical guild analysis of forest litter linyphiids. Acta Zoologica Fennica 190: 235-238

Letendre M. and Pilon J.-G. 1973a. Nids et micromilieux de nidification utilisés par les fourmis dans les peuplements forestiers des Basses Laurentides, Québec (Hymenoptera : Formicidae). Le Naturaliste Canadien 100: 237-246

Letendre M. and Pilon J.-G. 1973b. La Faune Myrmécologique de différents peuplements forestiers caractérisant la zone des basses Laurentides, Québec (Hymenoptera : Formicidae). Le Naturaliste Canadien 100: 195-235

Levi H. W. 1957. The spider genera *Enoplognatha*, *Theridion*, and *Paidisca* in America North of Mexico (Araneae, Theridiidae). Bulletin of the American Museum of Natural History 112: 1-123

Lindblad I. 1998. Wood-inhabiting fungi on fallen logs of Norway spruces; relations to forest management and substrate quality. Nordic Journal of Botany 18: 243-255

Lindgren, B.S., and A.M. MacIsaac. 2002. A preliminary study of ant diversity and abundance, and their dependence on dead wood in central interior British Columbia. In : Laudenslayer W.F. Jr., Shea P. J., Valentine B., Weatherspoon C. P. and Lisle T.E. (Eds.), W. F. Laudenslayer Jr., P.J. Shea, B. E. Valentine, C.P. Weatherspoon, and T.E. Lisle. (tech. cords..). Proceedings of the symposium on the ecology and management of dead wood in western forests, November 2-4 1999, Reno, Nevada, pp 111-119. General Technical Report PSW-GTR-181, USDA Forest Service, Pacific Southwest Research Station, Albany, CA.

Longino J. T. 2000. What to do with the data? In: Agosti D., Majer J. D., Alonso L. E. and Schulz T. R. (Eds), Ants: Standard methods for measuring and monitoring biodiversity, pp 186-203. Smithsonian Institution, Washington (DC).

Lowrie D.C. 1948. The ecological succession of spiders of the Chicago area dunes. Ecology 29: 334-351

Luff M. L. 1975. Some features influencing the efficiency of pitfall traps. Oecologia 19: 345-357

Magurran A. 2004. Measuring biological diversity. Blackwell Publishing, Malden, Massachusetts.

Mason R. R. and Paul H. G. 1988. Predation on larvae of Douglas-fir tussock moth, *Orgyia pseudotsugata* (Lepidoptera: Lymantriidae) by *Metaphidippus aeneolus* (Araneae: Salticidae). Pan-Pacific Entomologist 64: 258-260

McCune B. and Grace J. B. 2002. Analysis of ecological communities. MjM Software Design, Gleneden Beach, Oregon.

McCune B. and Mefford M. J. 1999. PC-ORD: Multivariate analysis of ecological data (version 4.17). MjM Software Design, Gleneden Beach, Oregon.

Mengak M.T. and. Guynn D.C. Jr. 2003. Small mammal microhabitat use on young loblolly pine regeneration areas. Forest Ecology and Management 173(1-3); 309-317

Moran M. 2003. Arguments for rejecting the sequential Bonferroni in ecological studies. Oikos 100: 403-405

Niemelä J., Pajunen T., Haila Y., Punttila P., and Halme E. 1994. Seasonal activity of boreal forest-floor spiders (Araneae). The Journal of Arachnology 22: 23-31

Nyffeler M. and Benz G. 1987. Spiders in natural pest control: a review. Journal of Applied Entomology 103: 321-339

Olive C. W. 1982. Behavioral responses of a sit-and-wait predator to spatial variation in foraging gain. Ecology 63: 912-920

Opell B. D. and Beatty J. A. 1976. The Nearctic Hahniidae (Arachnida: Araneae). Bulletin of the Museum of Comparative Zoology 147: 393-433

Paquin P. and Buckle D. J. 2001. Contributions to the knowledge of spiders (Araneae) of North America. Fabreries Supplements 10: 1-191

Paquin P. and Dupérré N. 2003. Guide d'identification des araignées (Araneae) du Québec. Fabreries Supplements 11: 1-251

Paquin P. and Lesage L. 2000. Diversity and biogeography of spiders (Araneae) of the Gaspé Conservation Park, Quebec. Proceedings of the Entomological Society of Ontario 131: 67-111

Parks Canada. 1995. Forillon National Park of Canada- Management Plan. Canadian Heritage, Parks Canada. Quebec. 80 p.

Petersen H. and Luxton M. 1982. A comparative analysis of soil fauna populations and their role in decomposition processes. Oikos 39: 287-388

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, Hull, Canada

Pontin A. J. 1960. Field experiments on colony foundation by *Lasius niger* (L.) and *L. flavus* (F.). Insectes Sociaux 7: 227-230

Riechert S. E. and Gillespie R. G. 1986. Habitat choice and utilization in web-building spiders. In: Shear W. A. (ed.), Spiders: webs, behavior, and evolution, Stanford University Press, pp 23-48. Stanford, California.

Riechert S. E. and Lawrence K. 1997. Test for predation effects of single versus multiple species of generalist predators: Spiders and their insect prey. Entomologia Experimentalis et Applicata 84: 147-155

Samuelsson J., Gustavsson L. and Ingelög T. 1994. Dying and dead trees - a review of their importance for biodiversity. Swedish Threatened Species Unit, Uppsala, Sweden.

Sanders C. J. 1964. The biology of carpenter ants in New Brunswick. The Canadian Entomologist 96: 894-909

Sanders C. J. 1970. The distribution of carpenter ant colonies in the spruce-fir forests of northwestern Ontario. Ecology 51: 865-873

Sanders C. J. 1972. Seasonal and daily activity patterns of carpenter ants *Camponotus*-spp in northwestern Ontario (Hymenoptera: Formicidae). The Canadian Entomologist 104: 1681-1687

Savely H. E. 1939. Ecological relations of certain animals in dead pine and oaks. Ecological Monograph 9: 323-385

Schmitz O. J. 2003. Top predator control of plant biodiversity and productivity in an old-field ecosystem. Ecology Letters 6: 156-163

Setälä H. and Marshall V. G. 1994. Stumps as habitat for Collembola during succession from clear-cuts to old-growth Douglas-fir forests. Pedobiologia 38: 307-326

Siitonen J. 2001. Forest management, coarse woody debris and saproxylic organisms: Fennoscandian boreal forests as an example. Ecological Bulletins 49: 11-41

Simila M., Kouki J. and Martikainen P. 2003. Saproxylic beetles in managed and seminatural Scots pine forests: quality of dead wood matters. Forest Ecology and Management 174: 365-381

Söderström L. 1988. Sequence of bryophytes and lichens in relation to substrate variables of decaying coniferous wood in northern Sweden. Nordic journal of Botany 8: 89-97

Sokal R. R. and Rohlf J. F.1995. Biometry. Freeman, New York.

Sollins P., Cline S. P., Verhoeven T., Sachs D. and Spycher G. 1987. Patterns of log decay in old-growth Douglas-fir forests. Canadian Journal of Forest Research 17: 1585-1595

Speight M. C. D. 1989. Saproxylic invertebrates and their conservation. Council of Europe, Strasbourg.

Stevenson B. G. and Dindal D. L. 1982. Effect of leaf shape on forest litter spiders community organization and micro habitat selection of immature *Enoplognatha ovata* Theridiidae. Journal of Arachnology 10: 165-178.

ter Braak C. J. F. 1995. Ordination. In: Jongman R. H. G., ter Braak C. J. F. and Van Tongeren O. F. R. (Eds), Data Analysis in Community and Landscape Ecology, pp. 91-173. Cambridge University Press, Cambridge.

Tilman D., Knops J., Wedin D. and Reich P. 2002. Plant diversity and composition: Effects on productivity and nutrient dynamics of experimental grasslands. In: Loreau M., Naeem S. and Inchausti P. (Eds), Biodiversity and ecosystem functioning, synthesis and perspectives, pp.21-35. Oxford University Press, New York.

Toft S. 1978. Phenology of some Danish beech-wood spiders. Natura Jutlandica 20: 285-304

Torgersen T. R. and Bull E. L. 1995. Down logs as habitat for forest-dwelling ants - the primary prey of pileated woodpeckers in northeastern Oregon. Northwest Science 69: 294-303

Turnbull A. L. 1964. The search for prey by a web-building spider *Achaearanea tepidariorum* (C. L. Koch) (Araneae, Theridiidae). The Canadian Entomologist 96: 568-579

Uetz G. W. 1991. Habitat structure and spider foraging. In: Bell S. S., McCoy E. D. and Mushinsky H. R. (Eds.). Habitat structure: the physical arrangement of objects in space, Chapman and Hall, pp 325-348. London.

Vallauri D., André J. and Blondel J. 2003. Le bois mort, une lacune des forêts gérées. Revue Forestière Française 55: 99-112

Van Hook R. I. 1971. Energy and nutrient dynamics of spider and orthopteran populations in a grassland ecosystem. Ecological Monographs 41: 1–26

Van Pelt A. F. 1963. High altitude ants of the Southern Blue Ridge. American Midland Naturalist 69: 205-223

Wilson E. 1955. A monographic revision of the ant genus *Lasius*. Bulletin of the Museum of Comparative Zoology 113: 1-201

Wilson E. O. 1992. The diversity of life. W. W. Norton and Company. New York.

Wise D. H. 1993. Spiders in ecological webs. Cambridge University Press, Cambridge.

Wise D. H. and Wagner J. D. 1992. Evidence of exploitative competition among young stages of the wolf spider *Schizocosa ocreata*. Oecologia 91: 7-13

Work T. T., Buddle C. M., Korinus L. M. and Spence J.R. 2002. Pitfall trap size and capture of three taxa of litter-dwelling arthropods: implications for biodiversity studies. Environmental Entomology 31: 438-448

Wu J. and Wong H. R. 1987. Colonization of lodgepole pine stumps by ants (Hymenoptera: Formicidae). The Canadian Entomologist 119: 397-398

Youngs L. C. and Campbell R. W. 1984. Ants preying on pupae of the Western Spruce Budworm, *Choristoneura occidentalis* (Lepidoptera: Tortricidae), in eastern Oregon and western Montana. The Canadian Entomologist 116: 1665-1669

Zielonka T. and Grzegorz P. 2004. The herb and dwarf shrubs colonization of decaying logs in subalpine forest in the Polish Tatra Mountains. Plant Ecology 172: 63-72

Table 2.1. Results from one-way ANOVA and Kruskall-Wallis tests for the effects of pitfall trap placement (on log surface, ON; adjacent to log, ADJ; away from log, AWAY) and litter sample placement (ADJ, AWAY) on overall spider species richness and spider species which represented > 2% of the total catch. Data presented as means (n = 24) ± SE. Post-hoc comparisons of means were made using the least significant difference (LSD), with significant differences ($P < 0.05$) indicated by different letters

	Pitfall Trap Placement				Litter Placement		
	ON	ADJ	AWAY	$F_{2,69}$	ADJ	AWAY	$F_{1,46}$
Total number collected	34.29±1.30a	26.13±1.14b	23.38±1.06b	23.66**	46.83±2.39a	39.08±1.55b	7.42**
Total number of species †	21±0.6a	14.7±0.5b	14±0.5b	46.57**	7.04±0.52a	4.75±0.4b	12.42**
Number of females	13.3±0.9a	20.7±1.3b	19.8±1.2b	12.45**	8.79±0.74a	5.54±0.44b	14.15**
Number of males •	49.5±2.5a	31.4±1.6b	29.4±2.1b	27.71**	1.63±0.3	1.13±0.22	1.81
Number of hunting spiders †	4.8±0.5a	3.1±0.3b	2.8±0.3b	8.25**	———	———	———
Number of hunting species ‡	5.8±0.3a	3.4±0.3b	3.7±0.2b	24.68**	———	———	———
Number of web-building spiders	16.2±0.8a	14.3±0.7ab	13.6±0.7b	3.44*	———	———	———
Number of web-buiding species	15.1±0.5a	11.3±0.4b	10.3±0.5b	30.92**	———	———	———
Number of immature spiders	13.3±0.9a	8.8±0.8b	7±0.7b	17**	36.46±2.10	32.38±1.57	2.43
Agroeca ornata	0.9±0.1a	1.8±0.2b	1.7±0.2b	7.84**	———	———	———
Amaurobius borealis †	1.8±0.2a	0.8±0.1b	0.9±0.1b	12.85**	———	———	———
Callobius bennetti ‡	1.8±0.2a	0.2±0.1b	0.4±0.1b	37.94**	———	———	———
Cryphoeca montana †	3.7±0.4a	2.2±0.3b	2.6±0.4b	5.85**	———	———	———
Neoantistea magna	2.6±0.3a	7.2±0.5b	6.8±0.5b	33.87**	———	———	———
Ozyptila distans †	0.9±0.1a	0.4±0.1b	0.3±0.1b	11.18**	———	———	———
Pardosa mackenziana ‡	1.8±0.4a	0.3±0.1b	0.4±0.1b	9.73**	———	———	———
Wadotes calcaratus †	1.3±0.2	0.9±0.1	0.8±0.1	1.75	———	———	———

Pitfall trap data analyzed with Kruskall-Wallis test is represented by ‡ and litter data by •. Pitfall trap log transformed data is represented by †. No log transformations were performed on litter data. Significance indicated at * ($p < 0.05$) and at ** ($p < 0.01$)

Table 2.2. Results from two-way ANOVA and Scheirer-Ray-Hare two-way ANOVA testing effect of wood type (coniferous 'CON' and deciduous 'DEC') and decomposition stage of logs (decomposition stage two 'DSII', decomposition stage three 'DSIII') on overall spider species richness as well as on species which represented > 2% of the total catch. Data presented as means (n = 12) ± SE.

	Wood Type			Int.	Decomposition Stage		
	CON	DEC	$F_{1,20}$	$F_{1,20}$	II	III	$F_{1,20}$
Total number collected	35.94±1.91	32.65±1.90	1.59	1.75	32.62±1.50	35.96±2.23	1.63
Total number of species	21.17±0.79	20.75±0.91	0.13	3.15	20.83±0.94	21.03±0.76	0.05
Number of hunting spiders †	6.25±0.86	3.42±0.21	9.81**	0.11	5.23±0.83	4.44±0.65	0.76
Number of hunting spider species	6.17±0.42	5.5±0.34	1.51	0.38	6.17±0.44	5.5±0.31	1.51
Number of web-building spiders	16.31±1.22	15.98±1.13	0.06	2.43	14.04±0.77	18.25±1.17	9.2**
Number of web-building spider species	15±0.67	15.25±0.74	0.07	3.38	14.67±0.76	15.58±0.62	0.93
Number of immature	13.38±1.31	13.24±1.16	0.01	0.78	13.35±1.34	13.26±1.12	0
Agroeca ornata	0.96±0.21	0.85±0.18	0.13	0.01	0.77±0.17	1.04±0.21	0.93
Amaurobius borealis	2.1±0.31	1.48±0.15	3.09	0.12	1.75±0.23	1.83±0.28	0.05
Callobius bennetti	1.31±0.21	2.25±0.34	5.57*	0.77	2.02±0.3	1.55±0.32	1.42
Cryphoeca montana	3.31±0.48	4.09±0.54	1.14	0.04	3.25±0.34	4.16±0.63	1.54
Neoantistea magna	2.98±0.57	2.13±0.32	4.05	5.33*	1.44±0.26	3.67±0.41	28.26**
Ozyptila distans	1.15±0.19	0.65±0.14	4.67*	1.58	0.77±0.13	1.02±0.21	1.2
Pardosa mackenziana †	2.92±0.72	0.62±0.12	10.28**	1.07	2.19±0.71	1.35±0.48	1.37
Wadotes calcaratus	1.48±0.28	1.02±0.25	1.38	0.58	1.25±0.25	1.25±0.29	0

Pitfall trap data analyzed with Scheirer-Ray-Hare two-way ANOVA test is represented by †. No log transformations were performed on the data. Significance indicated at * ($p < 0.05$) and at ** ($p < 0.01$)

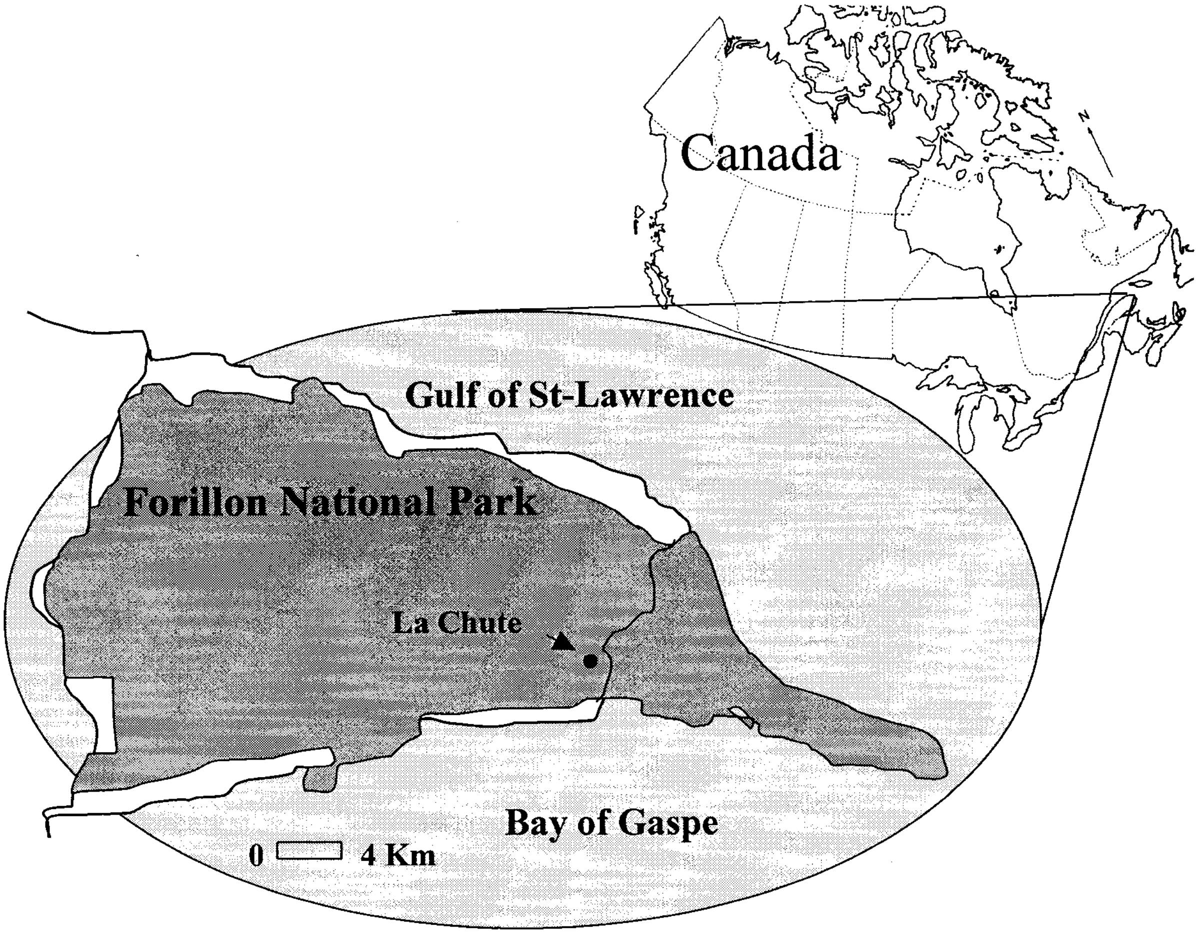

Fig. 2.1. Location of Forillon National Park of Canada, and location of sugar maple (*Acer saccharum* Marsh.) study site ('La Chute' 48°50'44.0'' N, 64°16'02.6'' W).

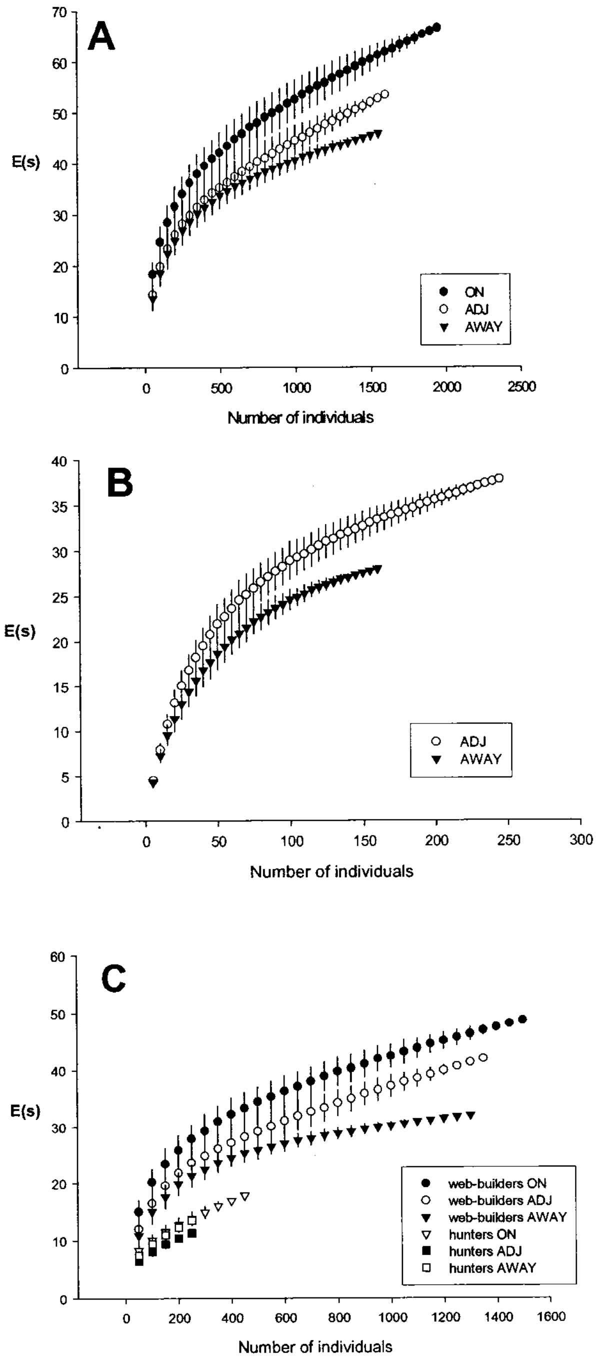

Fig. 2.2. Rarefaction estimates of expected number of spider species, E (s) by sub-sample size (number of individuals) for total number of spiders collected by different placements of (A) pitfall trap locations (on surface of log, ON; adjacent to log, ADJ; away from log, AWAY); (B) litter collections (ADJ, AWAY) and for; (C) web-building and hunting species of different pitfall trap locations. Error bars are ± 1 SD.

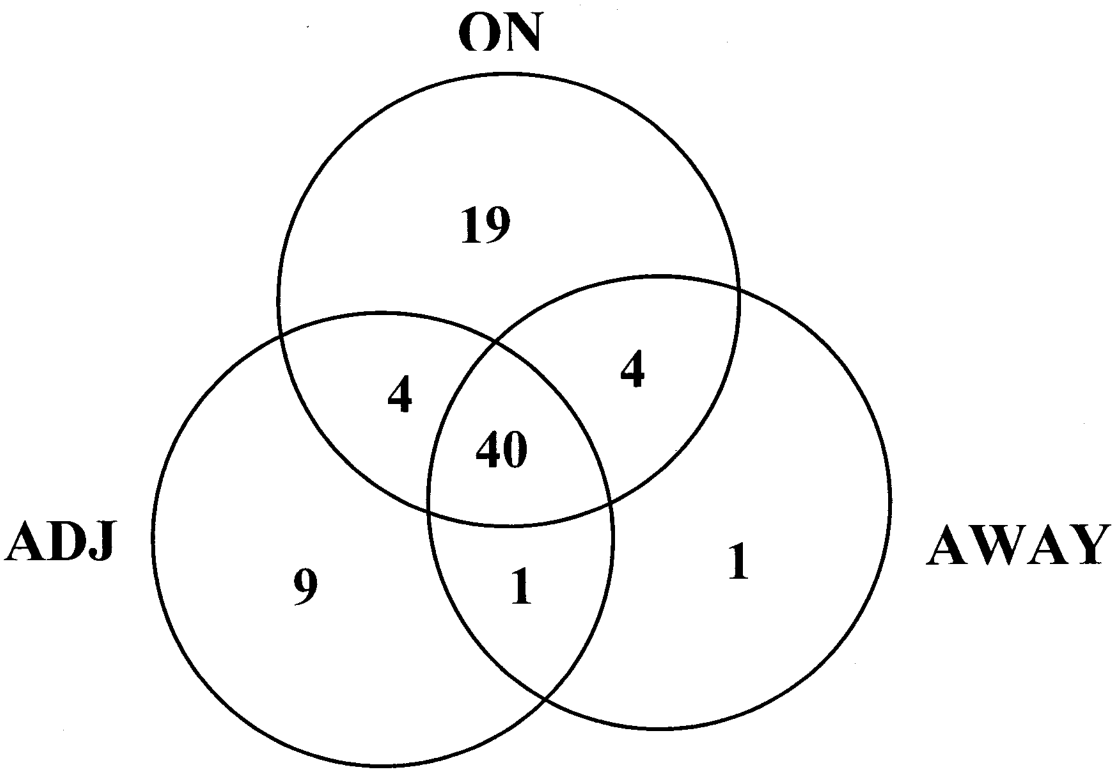

Fig. 2.3. Venn diagram representing the number of spider species collected at different pitfall trap placements (on surface of log, ON; adjacent to log, ADJ; away from log, AWAY).

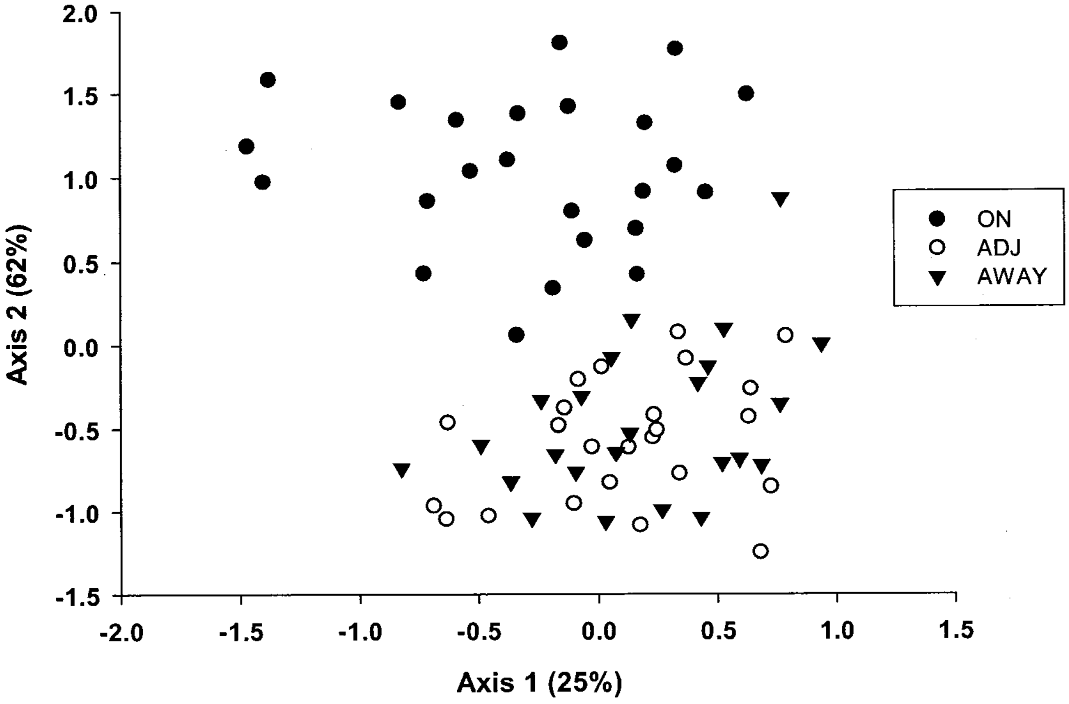

Fig. 2.4. Nonmetric multidimensional scaling (NMDS) ordination (axis 1 and 2) plot of 80 species of spiders collected in 24 pitfall traps placed on log surface (ON), adjacent from logs (ADJ) and away from log (AWAY).

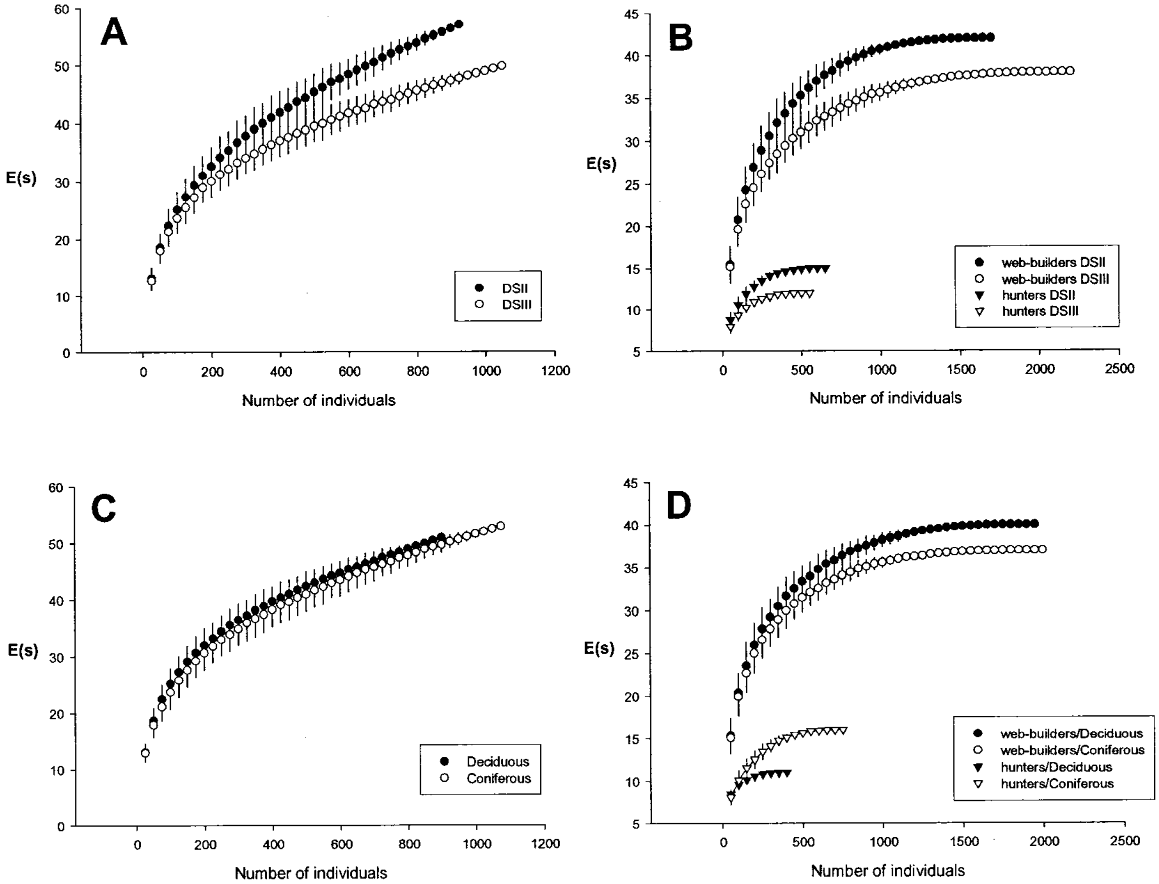

Fig. 2.5. Rarefaction estimates of expected number of spider species, E (s) by sub-sample size (number of individuals) for different decomposition level (DSII, DSIII) on (A) total number of spiders and (B) hunting and web-building spiders, as well as for different log type (coniferous, deciduous) on (C) total number of spiders and (D) hunting and web-building spiders. Error bars are ±1 SD.

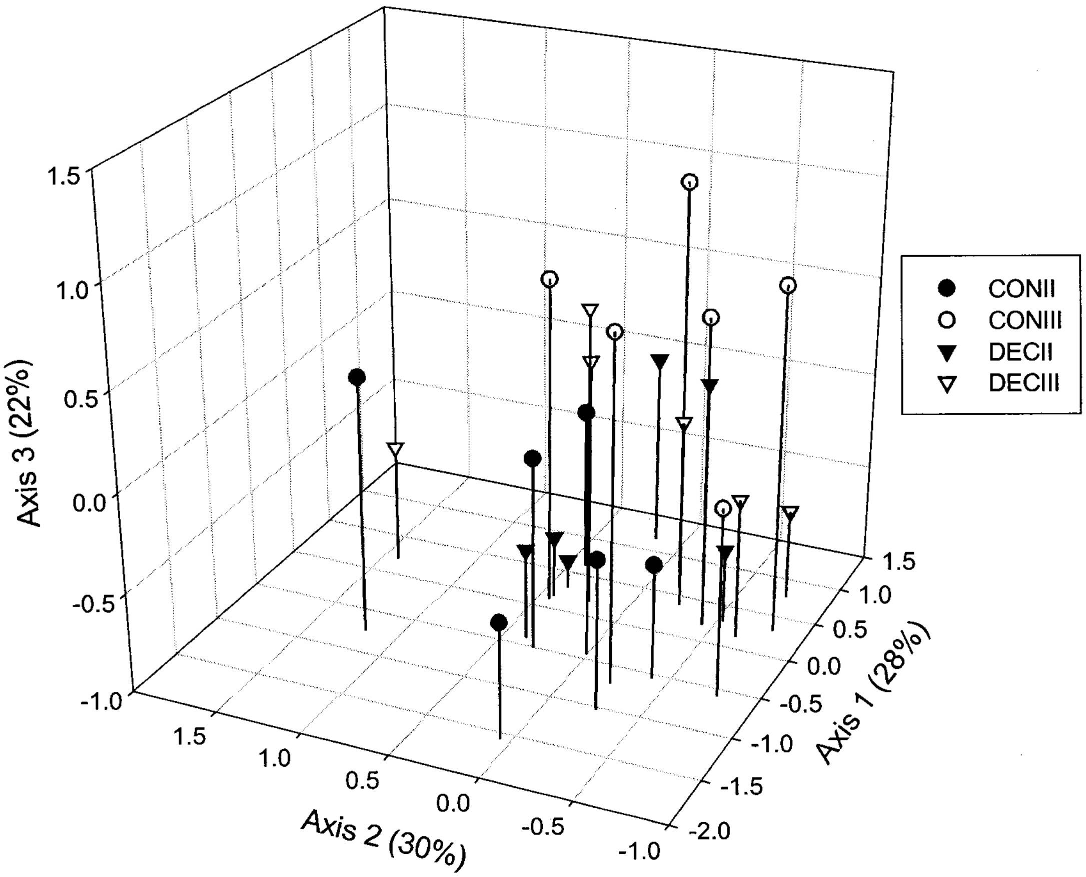

Fig. 2.6. Nonmetric multidimensional scaling (NMDS) ordination (axis 1, 2 and 3) plots of 69 species of spiders collected by pitfall trapping on 6 logs of coniferous logs of decomposition stage II (CONII), coniferous logs of decomposition stage III (CONIII), deciduous logs of decomposition stage II (DECII) and deciduous logs of decomposition stage III (DECIII).

Appendix 2.1. Spider (Araneae) families and species collected at the La chute sugar maple site of Forillon National Park of Canada, Quebec. The number of specimens is divided by collection type (litter or pitfall trap samples). Litter samples are further divided by position (adjacent to log, ADJ; away from log, AWAY). Pitfall samples are divided by position (on log surface, ON; adjacent to log, ADJ; away from log, AWAY). Ninety-six pitfalls were associated with each position. Pitfall trap samples on log are further divided by either wood type (coniferous or deciduous) or decomposition stage (decomposition stage II or III). Each wood type and decomposition level category represents 48 pitfall traps.

Family	Species	Litter			Pitfall							
		ADJ	AWAY	Total	ON	(DEC	CON	DSII	DSIII)	ADJ	AWAY	Total
Agelenidae	*Agelenopsis utahana* (Chamberlin and Ivie)	0	0	0	67	34	33	36	31	8	18	93
Amaurobiidae	*Amaurobius borealis* Emerton	3	25	55	170	69	101	84	86	79	87	336
	Callobius bennetti (Blackwall)	1	0	1	168	105	63	97	71	19	42	229
	Coras montanus (Emerton)	0	0	0	1	1	0	1	0	1	1	3
	Cybaeopsis tibialis (Emerton)	0	0	0	2	1	1	1	1	6	3	11
	Wadotes calcaratus (Keyserling)	0	2	2	119	48	71	60	59	84	78	281
Araneidae	*Araneus iviei* (Archer)	0	0	0	1	0	1	1	0	0	0	1
	Zygiella nearctica Gertsh	0	0	0	1	0	1	1	0	0	0	1
Clubionidae	*Clubiona bishopi* Edwards	3	1	4	25	10	15	17	8	4	16	45
	Clubiona canadensis Emerton	0	0	0	32	22	10	23	9	1	4	37
Cybaeidae	*Cybaeota calcarata* (Emerton)	4	1	5	0	0	0	0	0	1	0	1
Dictynidae	*Cicurina brevis* (Emerton)	8	4	12	19	5	14	6	13	29	18	66
	Cryphoeca montana Emerton	17	1	27	349	190	159	156	193	206	246	801
Gnaphosidae	*Haplodrassus hiemalis* (Emerton)	0	0	0	1	0	1	1	0	1	1	3
	Micaria pulicaria (Sundevall)	0	0	0	1	0	1	1	0	0	0	1
	Zelotes fratris Chamberlin	0	0	0	2	0	2	1	1	3	3	8
Hahniidae	*Neoantistea magna* (Keyserling)	1	4	14	242	99	143	69	173	675	654	1571
Linyphiidae	*Aphileta misera* (O.P.-Cambridge)	0	0	0	1	1	0	1	0	0	0	1
(Erigoninae)	*Ceraticelus fissiceps* (O.P.-Cambridge)	1	2	3	0	0	0	0	0	0	0	0

Family	Species	Litter			Pitfall							
		ADJ	AWAY	Total	ON	(DEC	CON	DSII	DSIII)	ADJ	AWAY	Total
	Ceraticelus laetabilis (O.P.-Cambridge)	2	0	2	7	5	2	6	1	1	0	8
Linyphiidae	*Ceraticelus minutus* (Emerton)	8	5	13	6	4	2	5	1	0	1	7
(Erigoninae)	*Ceraticelus silus* Dondale	0	0	0	1	1	0	0	1	0	0	1
	Ceratinella buna Chamberlin	3	5	8	20	13	7	8	12	10	7	37
	Diplocephalus subrostratus (O.P.-Cambridge)	11	13	24	64	27	37	15	49	17	17	98
	Eperigone maculata (Banks)	4	2	6	3	3	0	2	1	1	1	5
	Erigone dentipalpis (Wider)	0	0	0	1	0	1	1	0	0	0	1
	Gnathonaroides pedalis (Emerton)	0	0	0	0	0	0	0	0	1	0	1
	Islandiana flaveola (Banks)	0	0	0	1	0	1	1	0	0	0	1
	Maso sundevallii (Westring)	21	7	28	46	25	21	20	26	3	3	52
	Oedothorax montifer (Emerton)	0	0	0	1	1	0	1	0	0	0	1
	Pocadicnemis americana Millidge	3	2	5	10	1	9	8	2	11	7	28
	Sciastes truncatus (Emerton)	0	0	0	2	0	2	1	1	0	0	2
	Sisicottus montanus (Emerton)	0	0	0	9	8	1	2	7	1	2	12
	Tapinocyba minuta (Emerton)	9	24	33	1	1	0	0	1	1	2	4
	Tapinocyba simplex (Emerton)	11	0	11	0	0	0	0	0	1	0	1
	Tunagyna debilis (Banks)	0	0	0	2	0	2	0	2	0	0	2
	Walckenaeria arctica Millidge	0	0	0	0	0	0	0	0	1	0	1
	Walckenaeria atrotibialis (O.P.-Cambridge)	1	0	1	2	2	0	1	1	2	7	11
	Walckenaeria auranticeps (Emerton)	0	0	0	0	0	0	0	0	1	0	1
	Walckenaeria castanea (Emerton)	5	1	6	3	1	2	1	2	9	12	24
	Walckenaeria directa (O.P.-Cambridge)	3	1	4	11	5	6	5	6	30	20	61
	Walckenaeria exigua Millidge	7	3	1	45	14	31	18	27	10	7	62
	Zornella cultrigera (L.Koch)	0	0	0	0	0	0	0	0	3	0	3
Linyphiidae	*Agyneta* sp.A	1	0	1	1	0	1	0	1	1	0	2
(Linyphiinae)	*Bathyphantes pallidus* (Banks)	1	0	1	16	8	8	2	14	52	15	83
	Centromerus persolutus (O.P.-Cambridge)	13	5	18	5	4	1	1	4	14	7	26
	Lepthyphantes alpinus (Emerton)	6	4	1	26	13	13	10	16	7	6	39
	Lepthyphantes intricatus (Emerton)	0	0	0	1	1	0	0	1	15	4	20

Family	Species	Litter			Pitfall							
		ADJ	AWAY	Total	ON	(DEC	CON	DSII	DSIII)	ADJ	AWAY	Total
Linyphiidae	*Lepthyphantes turbatrix* (O.P.-Cambridge)	0	0	0	16	7	9	8	8	2	0	18
(Linyphiinae)	*Macrargus multesimus* (O.P.-Cambridge)	1	2	3	1	0	1	0	1	1	1	3
	Microneta viaria (Blackwall)	9	4	13	12	6	6	5	7	13	6	31
	Neriene clathrata (Sundevall)	1	0	1	3	1	2	2	1	1	1	5
	Neriene radiata (Walckenear)	4	1	5	8	4	4	3	5	0	1	9
	Neriene variabilis (Banks)	1	0	1	0	0	0	0	0	0	0	0
	Oreonetides rotundus (Emerton)	0	0	0	15	5	10	8	7	1	4	20
	Oreonetides vaginatus (Thorell)	0	0	0	1	1	0	0	1	0	0	1
	Oreophantes recurvatus (Emerton)	0	0	0	0	0	0	0	0	1	0	1
	Porrhomma terrestre (Emerton)	1	0	1	1	1	0	1	0	0	0	1
	Sisicus penifuser Bishop and Crosby	0	2	2	0	0	0	0	0	0	0	0
	Tenuiphantes zebra (Emerton)	0	0	0	0	0	0	0	0	1	0	1
	Wubana pacifica (Banks)	0	0	0	1	0	1	1	0	0	0	1
Liocranidae	*Agroeca ornata* Banks	6	5	11	86	40	46	37	49	174	161	421
Lycosidae	*Alopecosa aculeata* (Clerck)	0	0	0	2	1	1	2	0	1	1	4
	Pardosa mackenziana (Keyserling)	0	0	0	169	29	140	105	64	32	39	240
	Pardosa moesta Banks	0	0	0	6	5	1	4	2	0	1	7
	Pardosa uintana Gertsch	0	0	0	1	0	1	1	0	0	0	1
	Pardosa xerampelina (Keyserling)	0	0	0	0	0	0	0	0	1	1	2
	Trochosa terricola Thorell	0	0	0	7	3	4	4	3	5	2	14
Mimetidae	*Ero canionis* Chamberlin and Ivie	0	0	0	1	0	1	1	0	0	0	1
Philodromidae	*Philodromus exilis* Banks	0	0	0	1	1	0	0	1	0	1	2
Salticidae	*Neon nellii* Peckham and Peckham	3	23	53	38	18	20	16	22	27	17	82
	Pelegrina flavipes (Peckham and Peckham)	0	0	0	1	1	0	1	0	0	0	1
Theridiidae	*Achaearanea ohlertii* (Thorell)	1	0	1	0	0	0	0	0	0	0	0
	Enoplognatha intrepida (Sorensen)	0	0	0	0	0	0	0	0	1	0	1
	Robertus fuscus (Emerton)	0	0	0	1	1	0	1	0	0	0	1
	Robertus riparius (Keyserling)	7	2	9	36	26	10	21	15	28	24	88
	Rugathodes sexpunctatus (Emerton)	1	0	1	7	1	6	2	5	1	1	9

Family	Species	Litter			Pitfall							
		ADJ	AWAY	Total	ON	(DEC	CON	DSII	DSIII)	ADJ	AWAY	Total
Theridiidae	*Steatoda borealis* (Hentz)	0	0	0	1	1	0	1	0	0	0	1
	Theridion frondeum Hentz	1	0	1	0	0	0	0	0	0	0	0
Thomisidae	*Ozyptila distans* Dondale and Redner	3	1	4	85	30	55	37	48	41	24	150
	Ozyptila sincera canadensis Dondale and Redner	0	0	0	0	0	0	0	0	0	1	1
	Xysticus emertoni Keyserling	0	0	0	1	0	1	0	1	0	0	1
	Xysticus luctuosus (Blackwall)	0	0	0	1	0	1	0	1	1	0	2

CONNECTING STATEMENT

Chapter 2 of this thesis has shown that dead wood is an important habitat for spiders. However, comparison with a similar previous study, which also investigated spiders' use of dead wood (Buddle 2001), showed some different findings. Both studies were conducted in different forest types and as mentioned in Chapter 1, forest type could affect invertebrate use of dead wood. Therefore, Chapter 3 investigated the effect of forest type (maple, *Acer*; aspen, *Populus*; fir, *Abies*) on dead wood use by ants and spiders to clarify this difference and to enhanced the amount of information available on use of dead wood by generalist predators of the forest floor.

CHAPTER 3: EFFECT OF FOREST TYPE ON USE OF DEAD WOOD BY GENERALIST ARTHROPOD PREDATORS

ABSTRACT

Spiders (Araneae) and ants (Hymenoptera: Formicidae) are known to use dead wood habitat (i.e., fallen logs) and this use could change depending on forest type. In Forillon National Park, spider and ant assemblages were compared on, adjacent to, and away from fallen logs in different forest types (aspen, fir, maple). Spider use of dead wood was dependent on forest type. Spider diversity was highest on logs in maple and aspen forest but highest away from logs in fir forest. Spider assemblages on and away from logs were clearly separated in NMSD ordination in the maple and aspen forest but not in the fir forest. Ants were not affected by the interaction between pitfall trap placement and forest type but were shown to use the log surface differently than the forest floor. This study shows an effect of forest type on uses of dead wood by forest floor arthropods.

INTRODUCTION

Coarse woody debris, CWD, is an important element of forest ecosystems because it creates organic matter accumulation (Lambert et al. 1980), promotes the natural regeneration of trees (Harmon et al. 1986) and can affect the carbon cycle by acting as a sink for atmospheric carbon (Lambert et al. 1980; Vallauri et al. 2003). Dead wood also supports high plant and animal biodiversity (Torgersen and Bull 1995; Hammond 1997; Lindblad 1998; Siitonen 2001; Zielonka and Grzegorz 2004).

Many organisms, some of which are directly dependent on dead wood for survival, contribute significantly to dead wood decomposition and nutrient recycling (Samuelsson et al. 1994). Some generalist predators of the forest floor are also known to use the dead wood habitat (e.g., ants and spiders) (Wu and Wong 1987; Torgersen and Bull 1995; Buddle 2001; Ehnström 2001; Lindgren and MacIsaac 2002; Chapter 2), and could also affect the dead wood environment and its ecosystem function. This impact could either be direct by changing dead wood structure [e.g., tunnelling action of carpenter ants (Sanders 1964)] or chemical content [e.g., ants activity can change soil chemistry [Culver and Beattie 1983)] or indirect by feeding on organisms that have themselves an impact on the dead wood environment [e.g., spider feeding on collembolans (Lawrence and Wise 2000)]. Many ant species are known to nest in dead wood (Sanders 1964; Letendre and Pilon 1973a; Torgensen and Bull 1995) and many spiders use the surface of dead wood or are associated with dead wood (Lowrie 1948; Speight 1989; Buddle 2001; Chapter 2).

Ants and spiders play critical roles in forest ecosystems (Holldobler and Wilson 1990; Wise 1993). Both taxa are diverse, abundant (Coddington and Levi 1991; Alonso and Agosti 2000), and represent a large portion of the arthropod predator biomass in temperate forests (Van Hook 1971; Petersen and Luxton 1982; Alonso and Agosti 2000). Spiders and ants are also known to feed on some important forest pest (Green and Sullivan 1950; Allen et al. 1970; Jennings and Houseweart 1978; Youngs and Campbell 1984; Mason and Paul 1988; Torgensen and Bull 1995), and themselves are an important food source for other animals (Hall 1976; Raine and Kansas 1990; Bull et al. 1992; Szathmary 1997; McIntyre and Thompson 2003). Even though many studies have looked at dead wood characteristics affecting organisms dependent directly on dead wood (i.e., saproxylic invertebrates (Savely 1939; Irmler et al. 1996; Jonsell et al. 1998; Siitonen 2001; Simila et al. 2003) very few studies have occurred in Canada (exceptions include Hammond 1997; Hammond et al. 2001; Hammond et al. 2004; Saint-Germain et al. 2004) and few have investigated taxa that may not be directly dependent on dead wood for survival, such as ants and spiders.

The use of dead wood by spiders and ants could change depending on the forest type in which they are found. Different forest types harbour distinct invertebrate assemblages (Letendre and Pilon 1973b), which themselves have diverse ecological needs (Anderson and Death 2000). Furthermore, dead wood of different tree species harbours insects that have dissimilar environmental preferences (Ehnström 2001).

Interspecific competition plays a significant role in assembling ant communities (Brian 1952; Brian et al. 1966; Savolainen and Vepsäläinen 1988) and often creates a disparity in spatial distribution of ant species, which have similar ecological requirement (e.g., species living in dead wood) (Punttila et al. 1991). Therefore, if a very competitive ant species is associated with a certain forest type, it could negatively affect the dead wood nesting ant species present in this forest. Distinction in ant species among different habitats could result in a change in dead wood use due to competition.

Use of dead wood by spiders could also be dependent on forest type. Buddle (2001) and Chapter 2 of this thesis studied the relationship between spiders and dead wood by comparing assemblages of spiders in pitfall traps placed on the logs to those located on the forest floor. Although the general conclusions from these two studies were similar, both studies yielded different results about spider abundance. Buddle (2001) found a higher number of spiders on the forest floor than on the logs and in Chapter 2 it was found that more spiders occurred on the logs than on the forest floor. Even though both studies were very similar, there could be a few reasons that could explain this difference. One difference that might have affected the use of dead wood by spider is the difference of forest type in which the studies were conducted: Buddle's (2001) work was completed in Alberta's boreal mixwood region of Canada, and Chapter 2 focused on a maple forest in Forillon National Park, Quebec.

There are good reasons to believe the relationships between dead wood and invertebrate assemblages will differ by forest type, but this has not been adequately studied in North American north-temperate forests. To address this, my study investigated how ants and spiders use fallen logs in different forest types in Forillon National Park (Quebec, Canada). My objective was to compare the assemblage of ants and spiders found on, adjacent to, and away from dead wood, within three forest types: maple (*Acer*), aspen (*Populus*) and fir (*Abies*) forests.

MATERIALS AND METHODS

Site description

This work was conducted in Forillon National Park of Canada, which is situated at the tip of the Gaspé Peninsula, Quebec, Canada (Fig. 3.1). Forillon covers 240.4 km^2 of land area, of which 95% is forest, and is surrounded by the Gulf of St. Lawrence marine region. The forest area was protected with the creation of the park in 1970 and since then the major disturbances have been pest outbreaks and windthrow (Parks Canada 1995).

Four replicates of three different forest types were chosen for this study: sugar maple *Acer saccharum* Marsh (Aceraceae), trembling aspen *Populus tremuloides* Michx. (Salicaceae) and balsam fir *Abies balsamea* (L.) Mill. (Pinaceae), for a total of 12 sites (Fig. 3.1, Table 3.1). The sites were chosen for their dominance of sugar maple, trembling aspen or balsam fir trees, and for their general homogeneity of other qualitative site characteristics.

Experimental design and sampling

An area of 10 x 10 m was delimited within each of the twelve forests, ensuring that each contained three fallen logs, for a total of 36 study logs. Ants and spiders were collected at three different locations for every log: on the logs (ON), on the forest floor directly adjacent to the logs (ADJ) and on the forest floor away from the logs (AWAY).

Two collecting methods were used to collect both ants and spiders (litter and pitfall trap sampling) and one method to further collect ant specimens (wood cutting). Three pitfall traps were place on every log (ON) and one was placed on the forest floor immediately adjacent to every log (ADJ). Therefore, in every forest a total of nine pitfall traps was placed on logs (ON) and three on the forest floor next to the logs (ADJ). Additionally, in each forest, three pitfall traps were placed on the forest floor away from any logs in the plot (AWAY). The ADJ and AWAY traps were placed in the forest soil so that the trap surface was level with the forest floor. The ON pitfall traps were placed on the side of logs so the upper lip of the trap was close to the upper surface of the log. These were installed by nailing one third of the pitfall trap circumference to the log. Since one third of the ON pitfall trap circuference was touching the logs while all the ADJ and AWAY traps surface was touching the forest floor, three pitfall traps on the log were considered equivalent to one pitfall trap on the forest floor [(i.e., standardized to perimeter length, see Luff (1975)]. Pitfall traps were placed randomly on the log and on the forest floor adjacent to the log in an area of less than one meter from each end of the logs. Pitfall traps were 6.0 cm in diameter with a plastic permanent outer cup (7.0 cm height) and an inner sampling cup (5.0 cm height). The inner cup contained a total depth of ~4 cm (113.10 cm^3) of propylene glycol (preservative), which was diluted to 50% water. A circular plastic roof (12.0 cm in diameter) was placed ~2-3 cm over each trap using nails to protect the traps from rain. Traps were opened for 14 days from 30 July to 13 August 2003. Although this short sampling window may not overlap with the phenology of all spiders located within these forests (e.g., Niemelä et al. 1994; Buddle and Draney 2004), this experiment provided a snap-shot picture of the effects of forest type on these assemblages, and comparisons within this design are still possible with a short sampling window. However, ants have a relatively constant presence at a site over the course of a season (Alonso and Agosti 2000), and thus the short sampling window should be sufficient to collect the ant species present.

Litter samples were taken adjacent and away from each study log. Litter sampling was performed once at every site, from 15-21 August. Two litter samples were taken adjacent and away from each study log at every collecting time. The circular area of litter collected had a diameter of 0.26 m (0.053 m^2 of litter). Litter samples were placed in a screened bucket and shaken for 5 minutes into a large plastic container. Ants and spiders falling from the litter were collected with an aspirator and placed in 70% ethanol.

Woodcutting was used to collect ants that nest in dead wood. Using a small axe, all logs were cut in three lengthwise and all other dead wood present in the studied area investigated for the presence of ants. Ants present in dead wood were collected with an aspirator and placed in 70% ethanol. Sampling of ants in dead wood was performed from 15-20 August, once at each site. Data from this collecting technique were not used in analysis but served to improve the faunal survey of ants present in dead wood at Forillon National Park.

Environmental variables that affect the microhabitat of the forest (i.e., climate and structural complexity) were measured to help explain variation in the ant and spider data. Percentage of canopy cover, percent cover of small trees, plants and mosses on forest floor, soil moisture and amount of litter and surrounding dead wood all affect either structure or climate of forest and were chosen as environmental variables. Litter depth was placed in one of three categories: thick, little, scattered. Sites were considered having thick litter if the litter was within 4-6 cm, little litter (1-3 cm) and scattered litter when litter was present but not constant. Percent cover of small trees, plant and mosses on the forest floor and percentage of canopy cover were evaluated by looking at the forest floor or canopy surface included in the study area.

Arthropod identifications and statistical analyses

Most spiders could be identified to species using Paquin and Dupérré (2003). However, Dondale and Redner (1978, 1982), Planick and Dondale (1992) and Dondale et al. (2003) were also used and specimens were verified by Dr. C. Dondale (Canadian National Collection, Ottawa). It was not possible to positively identify immature or damaged spider specimens. Ants were identified to species using various taxonomic revision notably Creighton (1950), Wilson (1955) and Francoeur (1973, unpublished key). Difficult species were first identified to morphospecies and then verified by Dr. A. Francoeur (Centre de données sur la biodiversité du Québec, Chicoutimi). Voucher specimens were deposited in the Lyman Entomological Museum (Ste Anne de Bellevue, QC) and in the Canadian National Collection (Ottawa) (spiders).

Rarefaction analysis was used to calculate the expected number of species, E(s), for the total number of spiders and ants (standardized to sampling effort, number of individuals or number of samples), for comparison of pitfall trap placement and forest type and of pitfall trap placement in every forest type (i.e., only in maple, aspen or fir forest). I used individual-based rarefaction for the spider data and a sample-based rarefaction for ant data (Gotelli and Colwell 2001). For the comparison of pitfall trap placement by ants, AWAY pitfall traps were not used since they were pooled together when collected. Rarefaction was used as a diversity index because it allows comparison of diversity between treatments at similar sample size, it considers the number of individuals collected and, by showing the rate of new species accumulation, allows for verifying that enough samples were collected to make proper comparisons of diversity (Gotelli and Colwell 2001; Magurran 2004). The software program EcoSim700

(Acquired Intelligence Inc., Kesey-Bear) was used for rarefaction analyses (Gotelli and Entsminger 2001).

When the data did not meet the assumptions for parametric statistics, data were log-transformed ($x' = \log(x+1)$), or tested using non-parametric statistics that were analogous to analysis of variance (ANOVA). The sample units for all analyses were the pitfall trap placement or litter sampling position in each different forest ($n = 12$), so individual pitfall traps or litter samples were combined to represent a catch per position in a forest type. Subsequent to pooling traps, the representation of catch per log was divided by the number of pitfall trap present since disturbance by mammals sometimes reduced their number. One of the maple sites (Maple 2) experienced a large amount of disturbance and as a result was excluded from all statistical tests. Frequency (% of samples in which ant workers were found) instead of total catches was used for ant data because the number of ant catches is dependent on the distance from the nest (Longino 2000).

To test effects of forest type and pitfall trap placement or forest type and litter sample placement on spider and ant data I used a two-factor ANOVA with nested stands. I used either forest type (fir, aspen, maple) and pitfall trap placement (ON, ADJ, AWAY) or forest type (fir, aspen, maple) and litter placement (ADJ, AWAY) as main factors. Effect of pitfall trap placement (ON, ADJ, AWAY) and forest type was tested on the following variables: total number of ant (as frequency) and spider specimens collected and total number of ant and spider species. Effect of litter placement (ADJ, AWAY) and forest type (fir, aspen, maple) was tested on the following variables: total number of spiders specimens collected and total number of spider species. When the data did not meet the assumptions for parametric statistics I used the Scheirer-Ray-Hare test (Sokal and Rohlf 1995). SAS statistical package (SAS Institute Inc., Cary, NC) was used for these tests; *P*-values were not adjusted for multiple comparisons since such tests can be overly conservative, difficult to standardize, and can be considered contrary to detailed ecological work (Moran 2003).

Non-metric multidimensional scaling (NMDS) ordination analysis was conducted, using the software PC-ORD (McCune and Mefford 1999), to investigate spider community patterns in relation to pitfall trap placement and forest type. NMDS ordination finds the reduce number of axes that best explain variation in species composition among samples. The program gives a stress value to all axes by comparing the distance that the samples have with the axes with dissimilarity in the community structure. When the stress value of the ordination is low, close to 0, the dissimilarity in between the samples is represented by the distances (ter Braak 1995). Data standardized by number of pitfall traps was used. A six-dimensional ordination and an evaluation of stress factors was first performed to assess the optimal number of dimensions for a final solution. For this ordination 35 samples and 38 species were used. The final solution was compared to randomly generated data matrices using Monte Carlo simulations (n = 100), to test whether the final ordination differed significantly from what could have occurred by chance (McCune and Grace 2002).

I performed a canonical correspondence analysis (CCA), using the software PC-ORD (McCune and Mefford 1999), to look at the effect of environmental variables of forest type on spider assemblages. CCA selects the linear combination of environmental variables that explains the most of the dispersion of the species score and then clusters the sites, according to this selection, in a *n*-dimensional space (Jongman et al. 1995). The CCA was evaluated by the strength of the eigenvalues, and by the percent variation explained by the ordination. Each axis, representing an environmental variable, has an associated Eigenvalue. This Eigenvalue is a measure of the proportion or variation in a sample or species dispersion that is explained by that axis (Gauch 1982). Eigenvalues closer to one represent an axis that is representative of the species composition differences in sites presents along that axis. With the Monte Carlo simulations it was possible to test significance of the axis eigenvalue and then known how the environmental factors affected the samples or species along that axis (ter Braak and Prentice 1988). Standardized pitfall trap data were used, including all species in the analysis. Litter depth (cm), percentage of canopy cover, percent cover of mosses on forest floor, percent cover of small trees and plants on the forest floor were used as single environmental variables representing the forest type.

Additional correlations between forest environmental variables and forest type and ant or spider variables were tested to discern general associations. The following environmental variables were tested for their relation with ant and spider variables and forest type: percentage of canopy cover, percent moss cover, percent cover by small trees, percent cover of plant and litter depth. Amount of litter was a categorical variable (categories mentioned above) and was tested using a one-way ANOVA. Mosses, canopy cover, plant on soil and small trees were tested for their correlation with forest type or spider and ant variables using the Spearman rank correlation test (Sokal and Rohlf 1995).

RESULTS

Ants

A total of 116 ants representing eight species was collected from pitfall traps and a further 20 specimens and two species was collected from wood cutting (Appendix 3.1). No specimens were collected from litter samples. In general, ants were scarce in pitfall trap collections, as only 45% of these samples contained ants. The most commonly collected ants in pitfall traps were *Camponotus herculeanus* (Linnaeus) with a frequency of 18.18% (25 individuals), followed by *Myrmica alaskensis* Wheeler (16.88 %, 63 individuals), *Formica glacialis* Wheeler (15.58%, 16 individuals), *Formica neorufibarbis* Emery (3.90%, 3 individuals), *Myrmica detritinodis* Emery (3.90%%, 3 individuals), *Formica fusca* Linnaeus (2.60%, 2 individuals) and *Lasius pallitarsis* Foerster (2.60%, 2 individuals). *Camponotus nearcticus* Emery is a new record for Forillon National Park, increasing the number of ant species known from this park to 19 (Francoeur 1981, 1986; Chapter 2).

Spiders

A total of 361 adult spiders was collected (297 pitfall, 67 litter), representing 49 species (38 pitfall, 24 litter) from 14 families (Appendix 3.2 & 3.3). A further 313 spider specimens were immature (149 pitfall, 164 litter). Most species were rarely collected: Species with five or fewer specimens represented 80% of the total number of species collected, and others were represented by less than 26 specimens. The only exception was *Neoantistea magna* (Keyserling), which was represented by 155 specimens in pitfall trap collections (52% of the total collection).

Pitfall trap placement by forest type

Pitfall trap placement by forest type had an effect on spider diversity. Results from rarefaction analyses by pitfall trap placement, separated by forest type, revealed maple and aspen forests to harbour more diverse assemblages on the log surface compared to the forest floor (Fig. 3.2a,b). Spider assemblages in fir forests, in contrast, were more diverse in AWAY pitfall traps compared to other trap locations (Fig. 3.2c). In all cases, however, sample sizes were low, and future collections are required to verify these conclusions.

Comparison of diversity between pitfall positions of different forests could not be performed with the ant data because too few individuals were collected.

No variables were affected by the interaction of pitfall trap position and forest type (Table 3.2a) but two variables were affected by the interaction of litter sample position and forest type (Table 3.2b). In the litter sample, the total number of spiders collected was higher in ADJ traps only in the fir and maple forest (Fig. 3.3a,b).

A three-dimensional solution was deemed optimal for NMDS ordination showing spider assemblages in pitfalls of all position and in all the forest types (Fig. 3.4). This ordination was significantly different than would be derived at random (Monte Carlo test, n = 100, axis 1 $P = 0.01$, axis 2 $P = 0.02$, axis 3 $P = 0.05$), and explained 82% of the overall variation in the original data matrix (first axis 34%, second axis 28% and third axis 20 %). Only when labeled by pitfall trap position in forest type (not by pitfall trap or forest type alone) did this ordination show any discernable patterns. Therefore, the ordination is here presented in three different graphs, one for each forest (Fig. 3.4). Aspen and maple forest were similar in that spider assemblages of ON and AWAY pitfall traps were somewhat separated by axis 3 and ADJ traps were somewhat between the other placements, with some overlap (Fig. 3.4a,b). Fir forest showed no clear separation in the spider assemblage of ON, ADJ or AWAY pitfall traps (Fig 3.4c).

Pitfall trap and litter placement

In terms of diversity, expected number of spider species at a collecting sample of 60 individuals was not significantly different between ON, ADJ, and AWAY pitfall traps (Fig. 3.5a). In contrast, ants had a higher expected number of species in ON pitfall traps compared to in ADJ pitfall traps (Fig. 3.5c). The expected number of spider species was higher in ADJ than AWAY litter samples (Fig. 3.5b). However, more spider individuals of the ON pitfall traps and of AWAY litter sample placement would have been required to draw more satisfactory comparisons.

Spiders or ants never used the surface of logs more than the forest floor. The total number of spiders was significantly higher in ADJ or AWAY pitfall traps than in ON pitfall traps (Table 3.2a). None of the data from litter collection were significant for litter placement alone (Table 3.2b).

Forest type

Ants and spiders showed different responses to forest type. Expected number of spider species was higher in the fir forests followed by the aspen forest (Fig. 3.6a). Ants were more diverse in the aspen forest followed by the fir forest (Fig. 3.6c), and very few individuals of species of ants were collected in the maple forest. The litter data offered a different pattern, as spiders collected from sifting litter were more diverse in maple forests followed by fir forests, and very few individuals were collected in the aspen forest (Fig. 3.6b).

Raw spider species richness and number of specimens collected in litter samples was highest in maple forest, followed by fir forest and aspen forest (Table 3.2b). For raw spider species richness, only maple and aspen forest were significantly different while for the number of spider specimens collected all forests were significantly different. Raw ant species richness was significantly higher in fir forest than either maple or aspen forest and ant frequency was also higher in the fir forest but only significantly more than the maple forest (Table 3.2a).

Environmental variables

The CCA ordination explained a small portion of the variation in the spider data (i.e., 37%), and only one axis differed from what could have been derived randomly (Monte Carlo, n = 1000, axis 1 = $P < 0.01$, axis 2 = $P > 0.05$, axis 3 = $P > 0.05$); therefore, this ordination is not presented here. When testing environmental data on spider and ant variables, using one-way ANOVAs or correlations, only litter depth and percentage of moss cover significantly affected some of the data. Litter depth significantly affected litter sampling spider variables. Total number of spiders collected ($P = 0.007$) was significantly higher in thick litter (Mean ± SE; 32.75 ± 6.33) and less abundant in both little (15.8 ± 2.75) and scattered litter (6.00 ± 1.16). Similar results were found for the number of spider species ($P = 0.002$): thick litter, 6.00 ± 0.82; little litter, 3.4 ± 0.51; scatered litter, 1.00 ± 0.58. Litter type was also significantly associated with forest type ($P < 0.001$). Maple forests had thick litter, fir forest had little litter and aspen forest had scattered litter. Percentage of mosses significantly affected both ant variables. Both number of ant species ($P = 0.008$) and ant frequency ($P = 0.042$) were higher in places with a high percentage of mosses. Percentage cover of moss was also associated with forest type ($P = 0.009$): fir forest had a significantly higher percentage of moss cover (60.00 ± 20.41) than aspen (1.25 ± 1.25) or maple forest (no moss).

DISCUSSION

This study provided additional support that spiders use the dead wood environment and showed that this use is sometimes dependant on forest type. Ants did not respond to interactions between pitfall trap placement and forest type but were shown to use the log surface differently than the forest floor. In contrast to what was expected based on previous research, spider abundance of different pitfall trap positions did not significantly differ by forest type. These patterns would have to be verified with an extended sampling period, as collections were relatively low for both taxa.

Effects of forest type on dead wood use by ants

Due to the low number of ants collected, it was not possible to compare diversity by pitfall trap placement within each forest type and no ordinations of the overall data were possible. None of the ant variables responded significantly to the interaction between pitfall trap placement and forest type which suggests that ants' use of dead wood was not dependent on forest type. This is different than expected based on known ant biology. Ants are known to be influenced by dead wood type (i.e., size, moisture, type, decomposition stage and age) (Wu and Wong 1987; Torgersen and Bull 1995; Lindgren and MacIsaac 2002) and dead wood type changes depending on forest type. Also, ant communities may be governed by interspecific competition (Brian 1952; Brian et al. 1966; Savolainen and Vepsäläinen 1988). For example, Torgersen and Bull (1995) looking at ant nesting in dead wood found that wood nesting *Camponotus* were rarely associated with other ant groups. Even thought ants have stable nest sites and a short collecting survey can inform about what ants are present in a particular site (Alonso and Agosti 2000), collecting over the entire summer season summer would have increased the overall sample size and allowed for more concrete conclusions.

My study suggested that ants use log surface differently than the forest floor. Expected number of ant species was significantly higher in the ON pitfall traps than in the ADJ traps. Ant frequency and number of species were not significantly different between pitfall trap position (ON, ADJ, AWAY) (Table 3.2ab). Andrew et al. (2000) found that ant abundance was not significantly different in litter adjacent and away from logs but that ant species richness was higher in litter adjacent to logs than away from logs and that each position had a unique set of ant species. Here, it was not possible to test effect of litter collection position on ant assemblages since no ants were collected with the litter collecting technique.

Ants were affected by forest type, confirming findings of other literature on ants (Letendre and Pilon 1973b; Francoeur 1966; Francoeur 2001). The fir forests had the highest ant frequency and number of ant species and maple forests had the lowest ant diversity and frequency (Table 3.2a). However, aspen forests contained the highest number of expected ant species based on rarefaction analyses (Fig. 3.6c). Ant density and diversity have been shown to be low in certain sugar maple forests of Quebec (Francoeur 1966; Letendre and Pilon 1973b) and Letendre and Pilon (1973b) found ant species richness to be higher in aspen forests than in conifer forests. Additionally, Chapter 2 of this thesis showed low ant abundance in a different maple forests in Forillon.

There could be many reasons for the difference in frequency and species richness between the different forest types. Leaf litter on the ground is known to reduce the efficiency with which resources can be located, retrieved, and defended by ants (Anderson and Death 2000) and litter depth was associated with forest type. Maple forests had a much thicker litter layer than either fir or aspen forests and a thick litter layer could have resulted in low ant productivity in maple forests (Anderson and Death 2000). Ant number of species and frequency was also correlated with percentage of moss cover, which was significantly higher in fir forests than aspen or maple forests. Aspen forests contains more herbaceous plants (not estimated here) than the fir forests that has a sparse understory of shade tolerant species (Hughes et al. 2000). Also, bias due to collecting technique could result in apparent low ant abundance in the maple forests. Ants are cryptic in nature (Letendre and Pilon 1973b) and many of the ants associated with maple forests are species that live underground (Francoeur 1966), which would not have been represented using the pitfall trap or litter sampling technique.

Effects of forest type on dead wood use by spiders

Together with work by Buddle (2001) in Alberta's aspen-mixed wood boreal region, and with Chapter 2 of this thesis, this work has confirmed that fallen logs represent a key habitat for spiders in aspen and maple forests. Both aspen and maple forests had the highest expected number of spider species in the following order of pitfall trap placement: ON > ADJ > AWAY (Fig. 3.2ab). However, it is difficult to fully assess the effects of trap placement on spiders in aspen forests due to a low number of individuals collected (Fig. 3.2b). The ordination also separated spider assemblages in the ON pitfall traps from the AWAY pitfall traps in the aspen and maple forests (Fig. 3.4ab). A new finding, however, was that spider assemblages of different pitfall trap positions vary depending on forest type. Fir forests had highest diversity away from logs (Fig. 3.2c) and the ordination did not clearly separate any of the pitfall positions of the fir forests. A major difference between maple and fir forests was the diameter of the logs. Excluding aspen forests, the difference between the maple and the fir forests could come from variations in log dimension. Maple forests had larger diameter logs (0.3 ± 0.04m) than fir forests (0.12 ± 0.01m). In general, wood of larger diameter relates to higher species richness and abundance of various invertebrate groups (e.g., Bader et al. 1995; Kruys et al. 1999; Kolstrom and Lumatjarvi 2000; Simila et al. 2003; Hammond et al. 2004). This is because trees of larger diameter contain more microhabitats, take longer to decompose and house more species of fungi on which some invertebrates are dependent (Väisänen et al. 1993; Marra and Edmonds 1996; Kruys and Jonsson 1999; Kolstrom and Lumatjarvi 2000; Komonen 2003).

Total collection of spiders did not respond significantly to interactions between pitfall trap placement and forest type. This is different from what was expected based on Buddle (2001), who found a higher spider abundance in ADJ and AWAY pitfall traps in aspen dominated forest and Chapter 2 of this thesis found higher collections of spiders in ON pitfall traps in a sugar maple forests. These two studies collected data over the entire summer season and contained a much larger sample than the present work. It is therefore possible that use of the forest floor (including dead wood) changes over the summer season.

Forest type affected the use of litter by spiders. In aspen forests there was no real differentiation between spider abundance in ADJ or AWAY litter placement but in maple and fir forests the number of collected spiders was highest in ADJ than AWAY litter collection (Fig. 3.3). Chapter 2 of this thesis and Jabin et al. (2004) also found higher abundance of spiders in litter collected adjacent to logs than away from logs. The distinction between ADJ and AWAY litter position within different forest types could again be due to smaller log diameter. Fir (0.12 ± 0.01m) and aspen logs (0.1 ± 0.01m) were much smaller in diameter than maple logs (0.3 ± 0.04m). Logs accumulate litter in their surrounding (Evans et al. 2003) and larger logs would probably favor a thicker litter buildup. Litter depth and structure affects spider assemblages (Uetz 1991) and the litter habitat houses many microarthropods, primarily mites and Collembola, which serve as the main source of food for immature and small-bodied adult litter spiders (Hallander 1970; Wise and Wagner 1992). It is probably for the same reason that the number of spider species in litter, independent of litter collection placement, was higher in maple forest followed by fir and finally aspen forest. Litter type significantly affected both the number of collected specimens and species of spiders. Both spider variables were higher in thicker litter compared to little or scattered. Furthermore, as mentioned above, litter depth was associated with forest type: all the maple forest sites had thick litter, all the fir sites had little litter and all except one of the aspen sites had scattered litter. Comparing two forest types, Anderson and Death (2000) also found that the highest spider diversity was found at the site having the most ground cover (including litter).

Conclusion

Even though conclusions were limited by the lack of seasonal sampling, a definite effect of the interaction between forest type and pitfall trap placement (ON, ADJ, AWAY) or litter placement (ADJ, AWAY) was found for spider assemblages of Forillon National Park. Log size and litter depth could be some of the factors responsible for this interaction. However, the interaction did not explain the difference in spider abundance of different pitfall trap placement in two distinct forest types as found by Buddle (2001) and Chapter 2 of this thesis.

Ants were not affected by the interaction between pitfall trap placement and forest type but the low number of ants collected could be the reason. However, for the first time ants were shown to use the log surface differently than the forest floor as diversity of ants was higher in ON than ADJ pitfall traps. This study also confirmed that ant assemblages in Quebec are dependent on the forest type in which they are found.

REFERENCES

Allen D. C., Knight F. B. and Foltz J. L. 1970. Invertebrate predators of the jack-pine budworm, Choristoneura pinus, in Michigan. Annals of the Entomological Society of America 63: 59-64

Alonso L. E and Agosti D. 2000. Biodiversity studies, monitoring and ants: An overview. In: Agosti D., Majer J. D., Alonso L. E. and Schulz T.R. (Eds), Ants: standard methods for measuring and monitoring biodiversity, pp 1-8. Smithsonian Institution, Washington (DC).

Anderson S. J. and Death R. G. 2000. The effect of forest type on forest floor invertebrate community structure. New Zealand Natural Sciences 25: 33-41

Andrew N., Rodgerson L., and York A. 2000. Frequent fuel-reduction burning: the role of logs and associated leaf litter in the conservation of ant biodiversity. Austral Ecology 5: 99-107

Bader P., Jansson S. and Jonsson B. G. 1995. Wood-inhabiting fungi and substratum decline in selectively logged boreal spruce forests. Biological Conservation 72: 355-362

Brian M. V. 1952. The structure of a dense natural ant population. Journal of Animal Ecology 21: 12-24

Brian M. V., Hibble J. and Kelly A. F. 1966. The dispersion of ant species in a southern English heath. Journal of animal Ecology 35: 281-290

Buddle C. M. 2001. Spiders (Araneae) associated with downed woody material in a deciduous forest in central Alberta, Canada. Agricultural and Forest Entomology 3: 241-251

Buddle C.M. and Draney M.L. 2004. Phenology of linyphiids in an old-growth deciduous forest in central Alberta, Canada. Journal of Arachnology 32: 221-230

Bull E. L., Beckwith R. C. and Holthausen R. S. 1992. Arthropod diet of pileated woodpeckers in northeastern Oregon. Northwestern Naturaliste 73: 42-45

Coddington J. A. and Levi H. W. 1991. Systematics and evolution of spiders (Araneae). Annual Review of Ecology and Systematics 22: 565-592

Creighton W.S. 1950. The ants of North America. Harvard Museum of Comparative Zoology Bulletin 104: 1-585

Culver D.C. and Beattie A. J. 1983. Effects of ant mounds on soil chemistry and vegetation patterns in Colorado montane meadow. Ecology 64: 485-492

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, Hull, Canada

Dondale C.D. and Redner J.H. 1982. The insects and arachnids of Canada. Part 9. The sac spiders of Canada and Alaska (Araneae: Clubionidae and Anyphaenidae). Agriculture Canada Publication, Hull, Canada

Dondale C.D., Redner J.H., Paquin P. and Levi H. W. 2003. The insects and arachnids of Canada. Part 23. The orb-Weaving spiders of Canada and Alaska (Araneae: Uloboridae, Tetragnatidae, Araneidae, Theridiosomatidae). National Research Council of Canada, Ottawa, Canada

Ehnström B. 2001. Leaving dead wood for insects in boreal forests--suggestions for the future. Scandinavian Journal of Forest Research 3: 91-98

Evans A. M., Clinton P. W., Allen R. B. and Frampton C. M. 2003. The influence of logs on the spatial distribution of litter-dwelling invertebrates and forest floor processes in New Zealand forests. Forest Ecology and Management 184: 251-262

Francoeur A. 1966. La faune myrmécologique de l'érablière à sucre (*Aceretum saccharophori* Dansereau) de la region de Québec. Le Naturaliste Canadien 93: 443-472

Francoeur A. 1973. Revision taxonomique des espèces néarctiques du groupe fusca, genre *Formica*. Mémoire de la Société Entomologique du Québec 3 : 1-316

Francoeur A. 1981. Les Fourmis de la Presqu' île de Forillon, Comté de Gaspé-est, Québec (Formicidae, Hymenoptera). Fabreries 4: 78-83

Francoeur A. 1986. Supplément aux fourmis de la presqu'île de Forillon, Gaspé-Est, Québec. Fabreries 12: 56-58

Francoeur A. 2001. Les fourmis de la forêt boréale (Formicidae, Hymenoptera). Le Naturaliste Canadien 125: 108-114

Gauch H. G. 1982. Multivariate analysis in community ecology. Cambridge University Press, Cambridge, Massachusetts, USA.

Gotelli N. J. and Colwell R. K. 2001. Quantifying biodiversity: Procedures and pitfalls in the measurement and comparison of species richness. Ecology Letters 4: 379-391

Gotelli N.J. and Entsminger G.L. 2001. Ecosim: Null Models Software for Ecology, Version 6.0. Acquired Intelligence Inc, & Kesey-Bear http://homepages.together.net/gentsmin/ecosim.htm

Green, G. W. and Sullivan C. R. 1950. Ants attacking the larvae of the Forest Tent Caterpillar, *Malacosoma disstria*. The Canadian Entomologist 82: 194-195

Hall R. J. 1976. Summer foods of the salamender *Plethodon wehrlei* Amphibia Urodela Plethodontidae. Journal of Herpetology 10: 129-131

Hallander H. 1970. Prey, cannibalism and microhabitat selection in the wolf spiders *Pardosa chelata* O.F. Muller and *P. pullata* Clerck. Oikos 21: 337-340.

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

Hammond H. E. J., Langor D.W. and Spence J. R. 2001. Early colonization of Populus wood by saproxylic beetles (Coleoptera). Canadian Journal of Forest Research 31: 1175-1183

Hammond H. E. J., Langor D.W. and Spence J. R. 2004. Saproxylic beetles (Coleoptera) using *Populus* in boreal aspen stands of western Canada: spatiotemporal variation and conservation of assemblages. Canadian Journal of Forest Research 34: 1-19

Harmon M. E., Franklin J. F., Swanson F. J., Sollins P., Gregory S. V., Lattin J. D., Anderson N. H., Cline S. P., Aumen N. G., Sedell J. R., Lienkaemper G. W., Cromack K. Jr. and Cummins K. W. 1986. Ecology of coarse woody debris in temperate ecosystems. Advances in Ecological Research 15: 133-302

Holldobler B. and Wilson E. O. 1990. The Ants. The Belknap Press of Harvard University Press, Cambridge, Massachusetts.

Hughes J. B., Daily G. C. and Ehrlich P. R. 2000. Conservation of insect diversity: a habitat approach. Conservation Biology 14: 1788-1797

Irmler U., Heller K. and Warning J. 1996. Age and tree species as factors influencing the populations of insects living in dead wood (Coleoptera, Diptera: Sciaridae, Mycetophilidae). Pedobiologia 40: 134-148

Jabin M., Mohr D., Kappes H and. Topp W. 2004. Influence of deadwood on density of soil macro-arthropods in a managed oak–beech forest. Forest Ecology and Management 194: 61–69

Jennings D. T. and Houseweart M. W. 1978. Spider preys on spruce budworm egg mass. Entomological News 89: 183-186

Jongman R. H. G., Ter Braak C. J. F. and Van Tongeren O. F. R. 1995. Data analysis in community and landscape ecology. Cambridge university press, Cambridge, USA

Jonsell M., Weslien J. and Ehnström B. 1998. Substrate requirements of red-listed saproxylic invertebrates in Sweden. Biodiversity and Conservation 7: 749-764

Kolstrom M. and Lumatjarvi J. 2000. Saproxylic beetles on aspen in commercial forests: a simulation approach to species richness. Forest Ecology and Management 126: 113-120

Komonen A. 2003. Hotspots of insect diversity in boreal forests. Conservation Biology 17: 976-981

Kruys N and Jonsson B.G. 1999. Fine woody debris is important for species richness on logs in managed boreal spruce forests of northern Sweden. Canadian Journal of Forest Research 29: 1295-1299

Kruys N., Fries C., Jonsson B. G., Lämås T. and Ståhl G. 1999. Wood-inhabiting cryptogams on dead Norway spruce (*Picea abies*) trees in managed Swedish boreal forest. Canadian Journal of Forest Research 29: 178-186

Lambert R. L., Lang G. E. and Reiners W. A. 1980. Loss of mass and chemical change in decaying boles of a subalpine balsam fir forest. Ecology 61: 1460-1473

Lawrence K. L. and Wise D. H. 2000. Spider predation on forest-floor Collembola and evidence for indirect effects on decomposition. Pedobiologia 44: 33-39

Letendre M. and Pilon J.-G. 1973a. Nids et micromilieux de nidification utilisés par les fourmis dans les peuplements forestiers des Basses Laurentides, Québec (Hymenoptera : Formicidae). Le Naturaliste Canadien 100: 237-246

Letendre M. and Pilon J.-G. 1973b. La Faune Myrmécologique de différents peuplements forestiers caractérisant la zone des basses Laurentides, Québec (Hymenoptera : Formicidae). Le Naturaliste Canadien 100: 195-235

Lindgren, B.S., and A.M. MacIsaac. 2002. A preliminary study of ant diversity and abundance, and their dependence on dead wood in central interior British Columbia. In : Laudenslayer W.F. Jr., Shea P. J., Valentine B., Weatherspoon C. P. and Lisle T.E. (Eds.), W. F. Laudenslayer Jr., P.J. Shea, B. E. Valentine, C.P. Weatherspoon, and T.E. Lisle. (tech. cords..). Proceedings of the symposium on the ecology and management of dead wood in western forests, November 2-4 1999, Reno, Nevada, pp 111-119. General Technical Report PSW-GTR-181, USDA Forest Service, Pacific Southwest Research Station, Albany, CA.

Lindblad I. 1998. Wood-inhabiting fungi on fallen logs of Norway spruces; relations to forest management and substrate quality. Nordic Journal of Botany 18: 243-255

Longino J. T. 2000. What to do with the data? In: Agosti D., Majer J. D., Alonso L. E. and Schulz T. R. (Eds), Ants: Standard methods for measuring and monitoring biodiversity, pp 186-203. Smithsonian Institution, Washington (DC).

Lowrie D.C. 1948. The ecological succession of spiders of the Chicago area dunes. Ecology 29: 334-351

Luff M. L. 1975. Some features influencing the efficiency of pitfall traps. Oecologia 19: 345-357

Magurran A. 2004. Measuring biological diversity. Blackwell Publishing, Malden, Massachusetts.

Marra J. L. and Edmonds R.L. 1996. Coarse woody debris and soil respiration in a clearcut on the Olympic Peninsula, Washington, U.S.A. Canadian Journal of Forest Research 26: 1337-1345

Mason R. R. and Paul H. G. 1988. Predation on larvae of Douglas-fir tussock moth, *Orgyia pseudotsugata* (Lepidoptera: Lymantriidae) by *Metaphidippus aeneolus* (Araneae: Salticidae). Pan-Pacific Entomologist 64: 258-260

McCune B., Grace J. B. 2002. Analysis of ecological communities. MjM Software Design, Gleneden Beach, Oregon.

McCune B. and Mefford M. J. 1999. PC-ORD: Multivariate analysis of ecological data (version 4.17). MjM Software Design, Gleneden Beach, Oregon.

McIntyre N. E. and Thompson T. R. 2003. A comparison of conservation reserve program habitat plantings with respect to arthropod prey for grassland birds. American Midland Naturalist 159: 291-301

Moran M. 2003. Arguments for rejecting the sequential Bonferroni in ecological studies. Oikos 100: 403-405

Niemelä J., Pajunen, T., Haila, Y., Punttila, P., and E. Halme. 1994. Seasonal activity of boreal forest-floor spiders (Araneae). The Journal of Arachnology 22: 23-31

Paquin P. and Dupérré N. 2003. Guide d'identification des araignées (Araneae) du Québec. Fabreries Supplement11: 1-251

Parks Canada. 1995. Forillon National Park of Canada- Management Plan. Canadian Heritage, Parks Canada. Quebec. 80 p.

Petersen H. and Luxton M. 1982. A comparative analysis of soil fauna populations and their role in decomposition processes. Oikos 39: 287-388

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, Hull, Canada.

Punttila P., Haila Y., Pajunen T. and Tukia H. 1991. Colonisation of clearcut forests by ants in the southern Finnish taiga: a Quantitative Survey. Oikos 61: 250-262

Raine R.M. and Kansas J. L. 1990. Black bear seasonal food habits and distribution by elevation in Banff National Park, Alberta. International Conference Bear Research and Management 8: 297-304

Saint-Germain M., Drapeau P. and Hébert C. 2004. Xylophagous insect species composition and patterns of substratum use on fire-killed black spruce in central Quebec. Canadian Journal of Forestry 34: 677-685

Sanders C. J. 1964. The biology of carpenter ants in New Brunswick. The Canadian Entomologist 96: 894-909

Samuelsson J., Gustavsson L. and Ingelög T. 1994. Dying and dead trees - a review of their importance for biodiversity. Swedish Threatened Species Unit, Uppsala, Sweden.

Savely H. E. 1939. Ecological relations of certain animals in dead pine and oaks. Ecological Monograph 9: 323-385

Savolainen R. and Vepsäläinen K. A. 1988. Competition hierarchy among boreal ants: impact on resource partitioning and community structure. Oikos 51: 135-155

Siitonen J. 2001. Forest management, coarse woody debris and saproxylic organisms:

Fennoscandian boreal forests as an example. Ecological Bulletins 49: 11-41

Simila M., Kouki J. and Martikainen P. 2003. Saproxylic beetles in managed and seminatural Scots pine forests: quality of dead wood matters. Forest Ecology and Management 174: 365-381

Sokal R. R. and Rohlf F. 1995. Biometry. Freeman, New York.

Speight M. C. D. 1989. Saproxylic invertebrates and their conservation. Council of Europe, Strasbourg.

Szathmary K. 1997. Diversity of spiders (Araneae) in the diet of edible frog (*Rana esculenta* complex) in a protected wetland area in Hungary. Opuscula Zoologica Instituti Zoosystematici et Oecologici Universitatis Budapestinensis 29-30: 133-139

ter Braak C. J. F and Prentice I. C. 1988. A theory of gradient analysis. Advances in Ecological Research 18: 271-317

Torgersen T. R. and Bull E. L. 1995. Down logs as habitat for forest-dwelling ants - the primary prey of pileated woodpeckers in northeastern Oregon. Northwest Science 69: 294-303

Uetz G. W. 1991. Habitat structure and spider foraging. In: Bell S. S., McCoy E. D. and Mushinsky H. R. (Eds.). Habitat structure: the physical arrangement of objects in space, Chapman and Hall, pp 325-348. London.

Väisänen R., Biström O. and Heliövaara K. 1993. Sub-cordical coleoptera in dead pines and spruces: Is primeval species composition maintained in managed forests? Biodiversity and Conservation 2: 95-113

Vallauri D., André J. and Blondel J. 2003. Le bois mort, une lacune des forêts gérées. Revue Forestière Française 55: 99-112

Van Hook R. I. 1971. Energy and nutrient dynamics of spider and orthopteran populations in a grassland ecosystem. Ecological Monographs 41: 1–26

Wilson E. 1955. A monographic revision of the ant genus *Lasius*. Bulletin of the Museum of Comparative Zoology 113: 1-201

Wise D. H. 1993. Spiders in ecological webs. Cambridge University Press, Cambrige.

Wise D. H. and J. D. Wagner. 1992. Evidence of exploitative competition among young stages of the wolf spider Schizocosa ocreata. Oecologia 91: 7-13.

Wu J. and Wong H. R. 1987. Colonization of lodgepole pine stumps by ants (Hymenoptera: Formicidae). The Canadian Entomologist 119: 397-398

Youngs L. C. and Campbell R. W. 1984. Ants preying on pupae of the Western Spruce Budworm, *Choristoneura occidentalis* (Lepidoptera: Tortricidae), in eastern Oregon and western Montana. The Canadian Entomologist 116: 1665-1669

Zielonka T. and Grzegorz P. 2004. The herb and dwarf shrubs colonization of decaying logs in subalpine forest in the Polish Tatra Mountains. Plant Ecology 172: 63-72

Table 3.1. Site positions for each forest site within Forillon National Park of Canada, Quebec, Canada.

	Maple				Aspen				Fir			
	1	2	3	4	1	2	3	4	1	2	3	4
Position												
Latitude (N)	48.87843	48.89725	48.87656	48.85878	48.89153	48.87910	48.83938	48.89971	48.89151	48.84384	48.83118	48.81429
Longitude (W)	64.37736	64.33942	64.38244	64.37046	64.51780	64.37974	64.24113	64.34864	64.51920	64.23925	64.28470	64.26169

Table 3.2. Two-way ANOVA and Scheirer-Ray-Hare two-way ANOVA testing the effect of different forest type and (A) pitfall trap placement (on log surface, ON; adjacent to log, ADJ; away from log, AWAY) on total number of spider specimens and species richness as well as on number of ant species and frequency, and testing the effect of different forest type and (B) litter sample placement (ADJ, AWAY) on number of spider specimens and species. Means for placement of pitfall trap or litter samples (n = 12), for forest type (aspen and fir n = 4, maple n = 3) presented with ±SE. Post-hoc comparison of means was made using the least significant difference (LSD), with significant differences ($P < 0.05$) indicated by different letters.

A)

	Forest type				Int.	Pitfall trap placement			
	Aspen	Fir	Maple	F 2,16	F 4,16	ON	ADJ	AWAY	F 2,16
Total number of spiders collected ‡	0.74±0.07	0.65±0.09	0.64±0.07	0.83	0.74	0.58±0.08	0.73±0.09	0.73±0.06	1.7
Number of spider species †	4.17±0.35	4.08±0.51	2.89±0.54	2.54	2.94	3.36±0.39	3.90±0.25	4.09±0.71	0.6
Number of ant species †	1.00±0.28a	1.75±0.33b	0.44±0.24a	6.14**	1.97	1±0.30	1.27±0.38	1.09±0.32	0.23
				F 2,8	F 2,8				F 1,8
Ant frequency †	37.5±9.84ab	62.5±13.27b	16.67±11.39 a	4.35*	1.5	33.33±8.99	48.48±12.20	---------	1.4

B)

	Forest type				Int.	Sample placement		
	Aspen	Fir	Maple	F 2,9	F 2,9	ADJ	AWAY	F 1,9
Total number of spiders collected ‡	0.65±0.06a	0.87±0.12b	1.21±0.07c	50.39**	13.12**	1.02±0.09a	0.8±0.09b	22.32**
Number of spider species †	0.75±0.37a	1.75±0.62ab	3.5±0.66b	5.81*	2.44	2.5±0.58	1.5±0.50	2.25

Data analyzed with Scheirer-Ray-Hare two-way ANOVA test represented by † and log transformed data represented by ‡.
Significance indicated at * ($p < 0.05$) and at ** ($p < 0.01$)

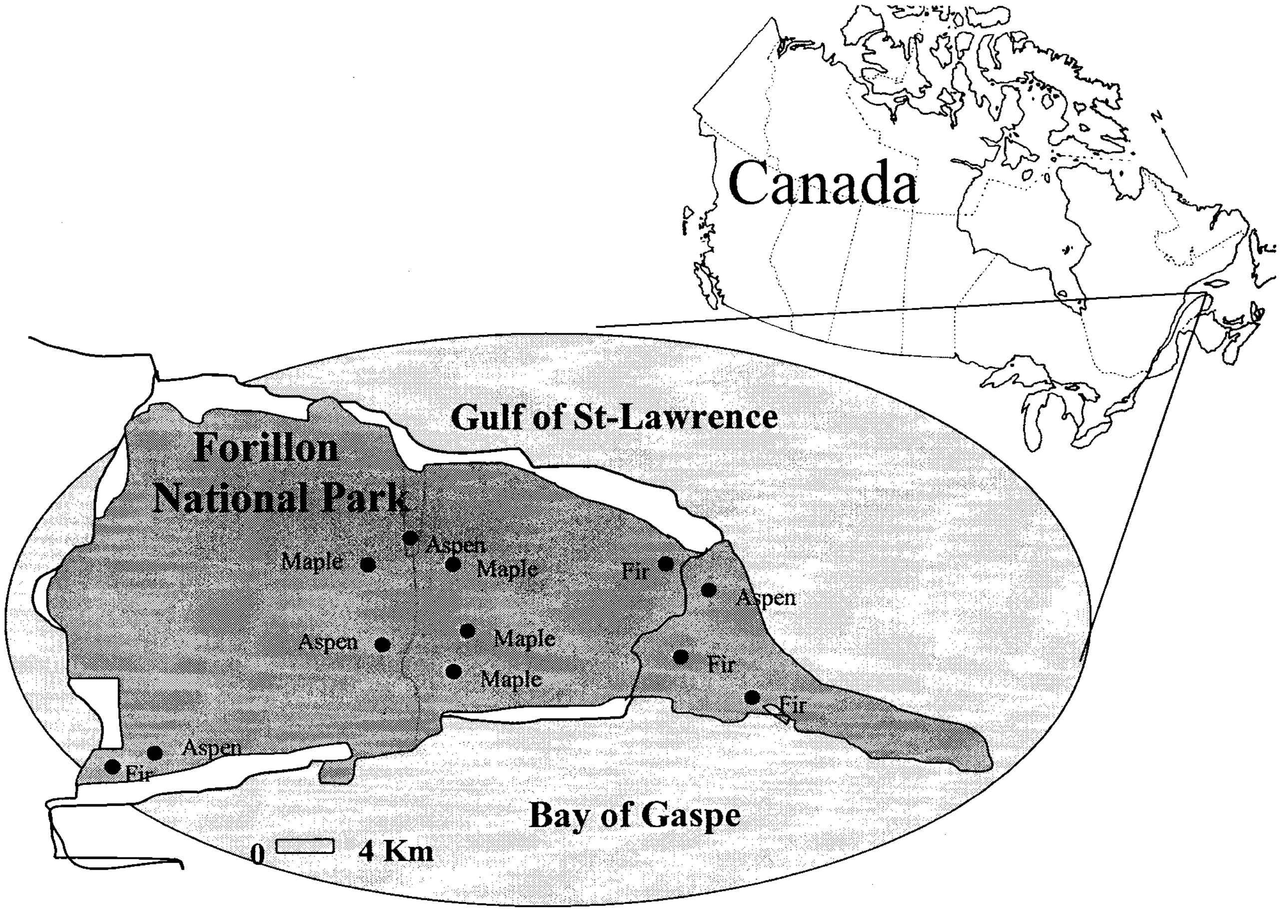

Fig. 3.1. Location of the Forillon National Park of Canada and the location of study forest sites (maple, *Acer*; aspen, *Populus*; fir, *Abies*).

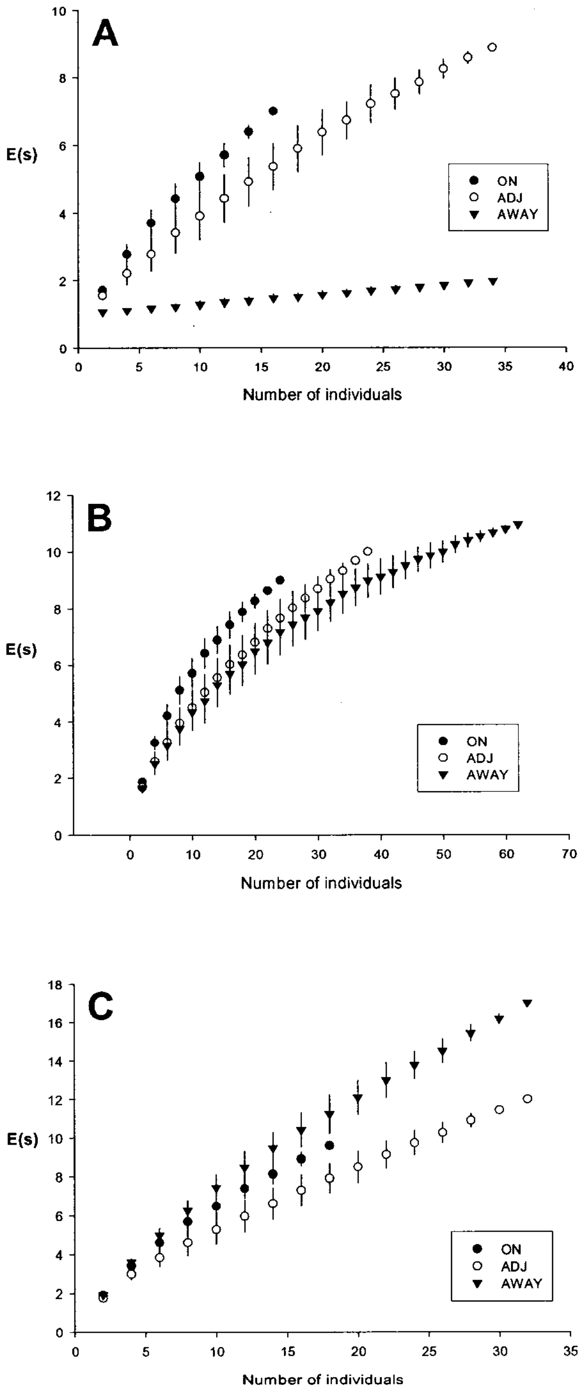

Fig. 3.2. Rarefaction estimates of the expected number of spider species, E (s) by sub-sample size (number of individuals) for different placement of pitfall (on surface of log, ON; adjacent to log, ADJ; away from log, AWAY) in (A) maple forest, (B) aspen forest, and (C) fir forest. Error bars are ± 1 SD.

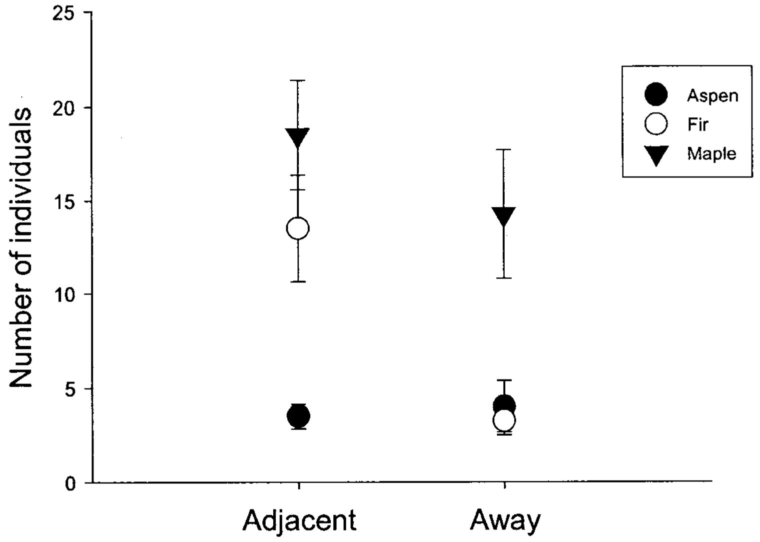

Fig. 3.3. Mean (± SE) number of spiders collected in litter samples adjacent and away from logs in aspen (*Populus*), fir (*Abies*) and maple (*Acer*) forest.

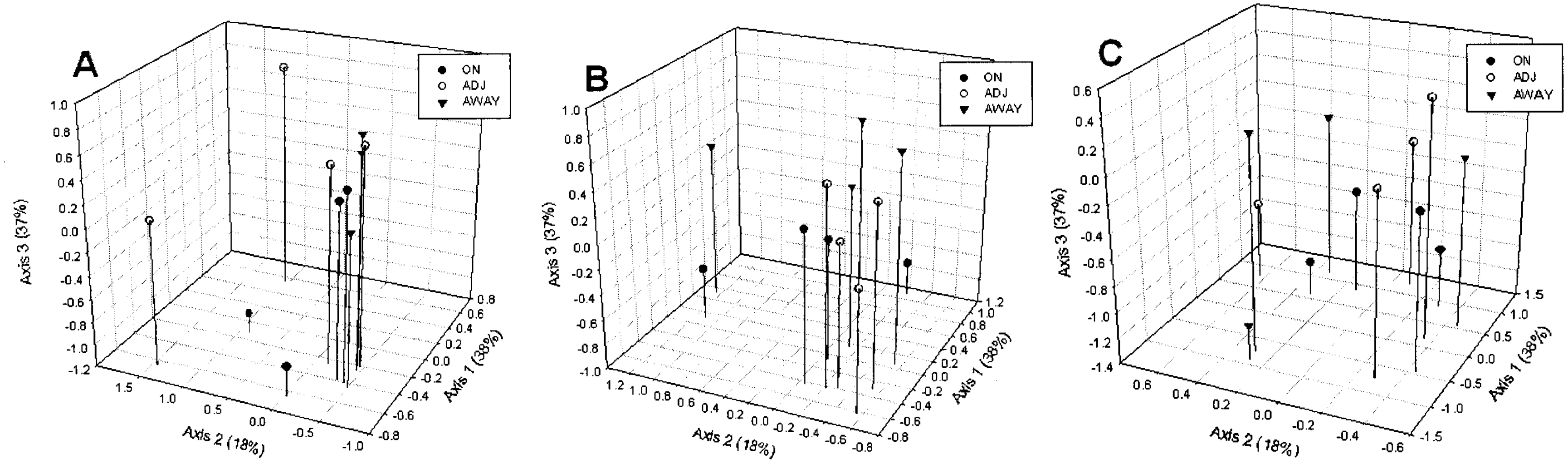

Fig. 3.4. Nonmetric multidimensional scaling (NMDS) ordination (axis 1, 2 and 3) plots of 38 species of spiders collected by pitfall trapping in 3 pitfall trap positions, on log (ON), adjacent to log (ADJ) and away from log (AWAY) in (A) maple forest, (B) aspen forest and (C) fir forest.

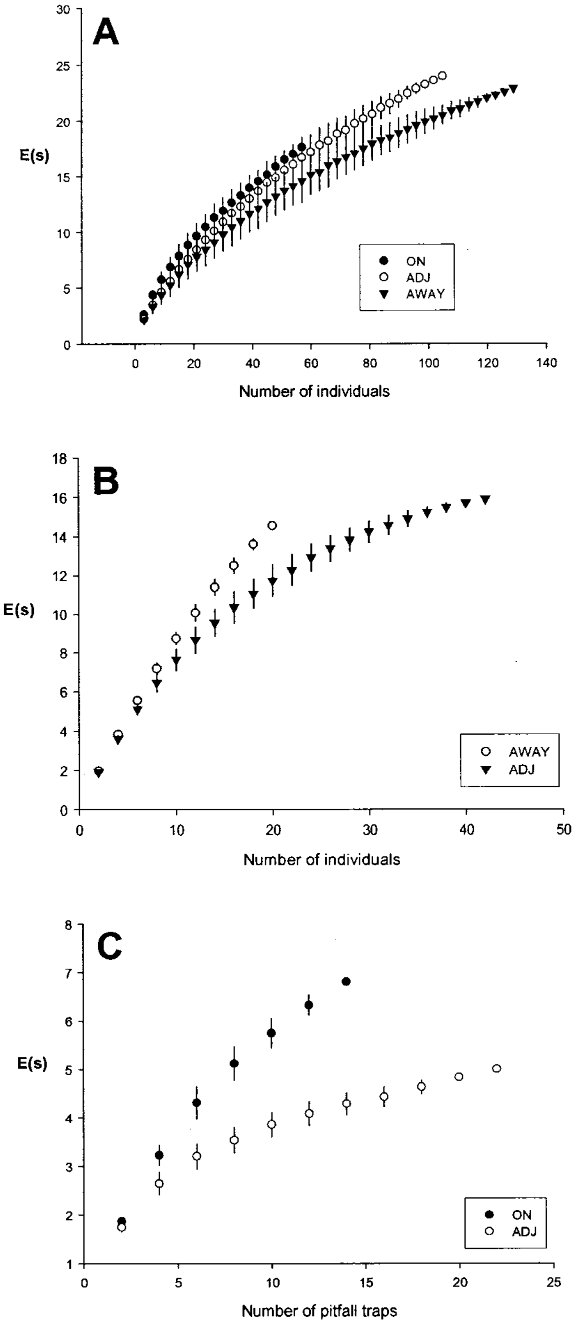

Fig. 3.5. Rarefaction estimates of the expected number of spider species, E(s) by sub-sample size (number of individuals) for different placement of (A) pitfall trap collections (on surface of log, ON; adjacent to log, ADJ; away from log, AWAY), (B) litter collections (ADJ, AWAY) and (C) rarefaction estimates of the expected number of ant species, E(s) by sample size (number of pitfall traps) for different placement of pitfall traps (ON, ADJ, AWAY). Error bars are ± 1 SD.

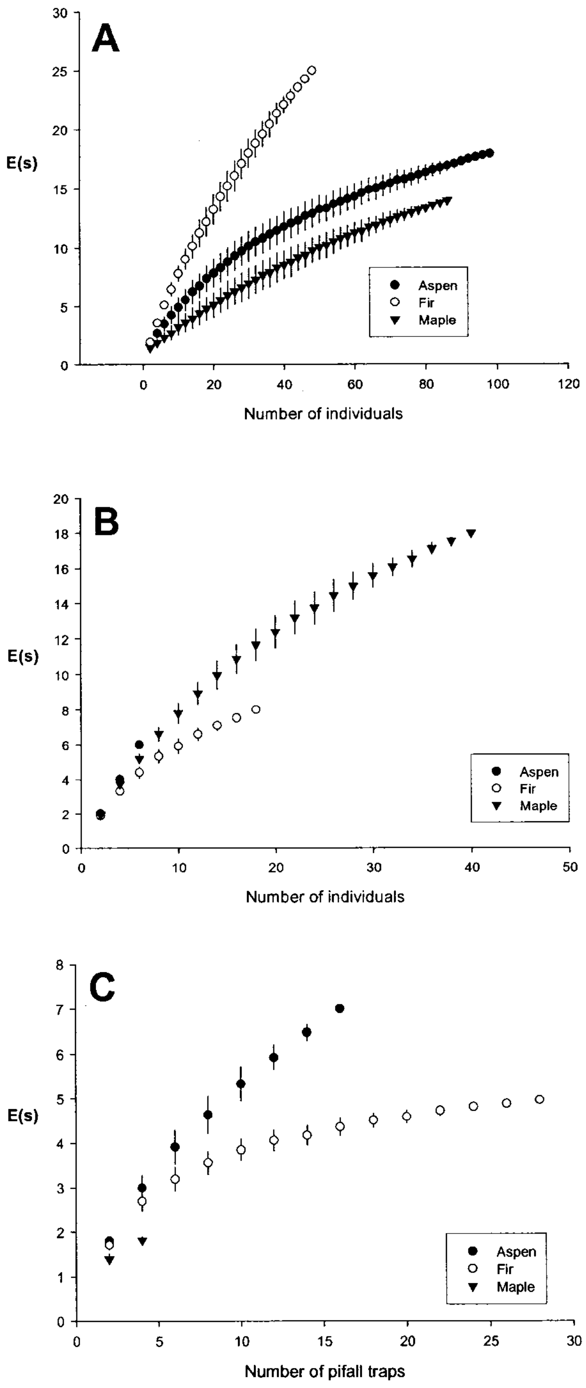

Fig. 3.6. Rarefaction estimates of the expected number of spider species, E(s) by sub-sample size (number of individuals) for different forest type (maple, fir, aspen) of (A) pitfall trap collections, (B) litter collections and (C) rarefaction estimates of the expected number of ant species, E(s) by sample size (number of pitfall traps) for different forest type (maple, fir, aspen). Error bars are ± 1 SD.

Appendix 3.1. Ant (Hymenoptera: Formicidae) sub-families and species collected at Forillon National Park of Canada, Quebec. The number of specimens is divided by pitfall trap position (on log surface, ON; adjacent to log, ADJ; away from log, AWAY), collections of ants by pitfall trap (maple, MAP; aspen, ASP; fir, FIR) or collections of ants by wood cutting (MAP, ASP, FIR) in forest type. Thirty-six pitfall traps were associated with each pitfall trap position and each forest type.

Sub-Family	Species	Pitfall trap placement				Forest type (Pitfall trap)				Forest type (Cut wood)			
		ON	ADJ	AWAY	Total	MAP	ASP	FIR	Total	MAP	ASP	FIR	Total
Formicinae	*Camponotus pennsylvanicus* (De Geer)	1	0	0	1	0	1	0	1	0	0	0	0
	Camponotus herculeanus (Linnaeus)	3	19	3	25	4	0	21	25	1	0	2	3
	Camponotus nearcticus (Emery)	0	0	0	0	0	0	0	0	0	1	0	1
	Formica glacialis Wheeler	6	6	4	16	0	9	7	16	0	0	0	0
	Formica neorufibarbis Emery	2	0	2	4	0	1	3	4	0	1	0	1
	Formica fusca Linnaeus	0	0	2	2	1	1	0	2	0	0	0	0
	Lasius pallitarsis (Provencher)	1	1	0	2	0	1	1	2	0	0	0	0
Myrmicinae	*Leptothorax canadensis* Provancher	0	0	0	0	0	0	0	0	0	1	0	1
	Myrmica alaskensis Wheeler	7	14	42	63	0	6	57	63	0	7	7	14
	Myrmica detritinodis Emery	1	1	1	3	0	3	0	3	0	0	0	0

Appendix 3.2. Spider families and species collected at Forillon National Park of Canada, Quebec. The number of specimens is divided by collection type (litter or pitfall trap samples). Litter samples are further divided by position (adjacent to log, ADJ; away from log, AWAY). Pitfall samples are divided by position (on log surface, ON; adjacent to log, ADJ; away from log, AWAY). Thirty-six pitfall traps were associated with each pitfall trap position.

Family	Species	Pitfall				Litter		
		ON	ADJ	AWAY	Total	ADJ	AWAY	Total
Agelenidae	*Agelenopsis utahana* (Chamberlin and Ivie)	13	2	1	16	0	0	0
Amaurobiidae	*Amaurobius borealis* Emerton	0	0	0	0	7	1	8
	Callobius bennetti (Blackwall)	2	1	0	3	0	0	0
	Cybaeopsis euopla (Bishop and Crosby)	0	1	0	1	0	0	0
	Wadotes calcaratus (Keyserling)	1	2	3	6	1	0	1
Clubionidae	*Clubiona bishopi* Edwards	5	0	0	5	0	0	0
	Clubiona canadensis Emerton	1	0	0	1	0	0	0
Cybaeidae	*Cybaeota calcarata* (Emerton)	0	0	0	0	1	0	1
Dictynidae	*Cicurina brevis* (Emerton)	0	1	1	2	1	0	1
	Cryphoeca montana Emerton	0	0	0	0	0	2	2
Gnaphosidae	*Zelotes fratris* Chamberlin	1	0	2	3	0	0	0
Hahniidae	*Antistea brunnea* (Emerton)	0	1	4	5	0	0	0
	Hahnia cinerea Emerton	1	0	0	1	2	2	4
	Neoantistea magna (Keyserling)	20	59	76	155	0	0	0
Linyphiidae (Erigoninae)	*Ceratinella buna* Chamberlin	1	1	0	2	2	1	3
	Diplocephalus subrostratus (O.P.-Cambridge)	0	2	2	4	0	1	1
	Eperigone maculata (Banks)	0	0	0	0	0	2	2
	Maso sundevallii (Westring)	0	0	0	0	3	0	3
	Pocadicnemis americana Millidge	0	0	1	1	0	0	0
	Sciastes truncatus (Emerton)	1	1	0	2	0	0	0
	Sisicottus montanus (Emerton)	1	0	4	5	4	0	4
	Tapinocyba minuta (Emerton)	0	0	0	0	2	2	4

Family	Species	Pitfall				Litter		
		ON	ADJ	AWAY	Total	ADJ	AWAY	Total
Linyphiidae	*Tapinocyba simplex* (Emerton)	0	0	0	0	2	1	3
(Erigoninae)	*Tunagyna debilis* (Banks)	0	2	0	2	0	1	1
	Walckenaeria directa (O.P.-Cambridge)	0	2	5	7	0	1	1
	Walckenaeria exigua Millidge	0	1	1	2	5	0	5
Linyphiidae	*Bathyphantes concolor* (Wider)	0	6	5	11	0	0	0
(Linyphiinae)	*Bathyphantes pallidus* (Banks)	2	5	3	10	0	0	0
	Centromerus persolutus (O.P.-Cambridge)	0	0	0	0	2	0	2
	Centromerus sylvaticus (Blackwall)	0	0	1	1	0	0	0
	Lepthyphantes alpinus (Emerton)	6	7	12	25	0	1	1
	Lepthyphantes intricatus (Emerton)	1	0	0	1	0	0	0
	Lepthyphantes turbatrix (O.P.-Cambridge)	0	0	1	1	0	0	0
	Microneta viaria (Blackwall)	0	1	1	2	5	1	6
	Oreophantes recurvatus (Emerton)	0	1	1	2	0	0	0
	Pityohyphantes subarcticus Chamberlin and Ivie	1	0	0	1	0	0	0
	Porrhomma terrestre (Emerton)	0	1	0	1	0	0	0
	Sisicus penifuser Bishop and Crosby	0	0	0	0	1	0	1
	Tenuiphantes zebra (Emerton)	0	1	0	1	0	0	0
Liocranidae	*Agroeca ornata* Banks	1	0	1	2	0	2	2
Lycosidae	*Alopecosa aculeata* (Clerck)	0	0	1	1	0	0	0
	Pardosa mackenziana (Keyserling)	0	1	1	2	0	0	0
	Pirata montanus Emerton	0	0	1	1	0	0	0
	Trochosa terricola Thorell	3	2	2	7	2	0	2
Philodromidae	*Philodromus placidus* Banks	0	3	0	3	0	0	0
Salticidae	*Neon nellii* Peckham and Peckham	0	0	0	0	3	2	5
Theridiidae	*Robertus riparius* (Keyserling)	0	0	0	0	0	1	1
Thomisidae	*Xysticus britcheri* Gertsch	0	1	0	1	0	0	0
	Xysticus canadensis Gertsch	1	0	0	1	0	0	0

Appendix 3.3. Spider families and species collected at Forillon National Park of Canada, Quebec. The number of specimens is divided by collection type (litter or pitfall trap samples). Litter and pitfall trap samples are further divided by forest type (aspen, maple, fir). Aspen and fir forest were represented by four forests and maple by three forests. Thirty-six pitfall traps were associated with each forest type.

Family	Species	Forest type (litter)				Forest type (pitfall traps)			
		Maple	Aspen	Fir	Total	Maple	Aspen	Fir	Total
Agelenidae	*Agelenopsis utahana* (Chamberlin and Ivie)	0	0	0	0	3	6	6	15
Amaurobiidae	*Amaurobius borealis* Emerton	4	0	2	6	0	0	0	0
	Callobius bennetti (Blackwall)	0	0	0	0	1	1	1	3
	Cybaeopsis euopla (Bishop and Crosby)	0	0	0	0	0	0	1	1
	Wadotes calcaratus (Keyserling)	1	0	0	1	2	3	1	6
Clubionidae	*Clubiona bishopi* Edwards	0	0	0	0	3	1	1	5
	Clubiona canadensis Emerton	0	0	0	0	1	0	0	1
Cybaeidae	*Cybaeota calcarata* (Emerton)	1	0	0	1	0	0	0	0
Dictynidae	*Cicurina brevis* (Emerton)	1	0	0	1	0	1	1	2
	Cryphoeca montana Emerton	1	0	1	2	0	0	0	0
Gnaphosidae	*Zelotes fratris* Chamberlin	0	0	0	0	1	0	2	3
Hahniidae	*Antistea brunnea* (Emerton)	0	0	0	0	0	0	5	5
	Hahnia cinerea Emerton	4	0	0	4	1	0	0	1
	Neoantistea magna (Keyserling)	0	0	0	0	66	66	21	153
Linyphiidae	*Ceratinella buna* Chamberlin	3	0	0	3	0	0	2	2
(Erigoninae)	*Diplocephalus subrostratus* (O.P.-Cambridge)	0	1	0	1	0	3	1	4
	Eperigone maculata (Banks)	2	0	0	2	0	0	0	0
	Maso sundevallii (Westring)	2	0	1	3	0	0	0	0
	Pocadicnemis americana Millidge	0	0	0	0	0	0	1	1
	Sciastes truncatus (Emerton)	0	0	0	0	0	0	2	2
	Sisicottus montanus (Emerton)	0	0	4	4	0	0	5	5
	Tapinocyba minuta (Emerton)	4	0	0	4	0	0	0	0
	Tapinocyba simplex (Emerton)	1	0	2	3	0	0	0	0

Family	Species	Forest type (litter)				Forest type (pitfall traps)			
		Maple	Aspen	Fir	Total	Maple	Aspen	Fir	Total
Linyphiidae (Erigoninae)	*Tunagyna debilis* (Banks)	0	1	0	1	0	2	0	2
	Walckenaeria directa (O.P.-Cambridge)	0	1	0	1	2	5	0	7
	Walckenaeria exigua Millidge	1	0	2	3	1	0	1	2
Linyphiidae (Linyphiinae)	*Bathyphantes concolor* (Wider)	0	0	0	0	0	11	0	11
	Bathyphantes pallidus (Banks)	0	0	0	0	2	7	1	10
	Centromerus persolutus (O.P.-Cambridge)	2	0	0	2	0	0	0	0
	Centromerus sylvaticus (Blackwall)	0	0	0	0	0	0	1	1
	Lepthyphantes alpinus (Emerton)	0	0	1	1	0	7	18	25
	Lepthyphantes intricatus (Emerton)	0	0	0	0	0	0	1	1
	Lepthyphantes turbatrix (O.P.-Cambridge)	0	0	0	0	0	1	0	1
	Microneta viaria (Blackwall)	5	1	0	6	1	1	0	2
	Oreophantes recurvatus (Emerton)	0	0	0	0	0	1	1	2
	Pityohyphantes subarcticus Chamberlin and Ivie	0	0	0	0	0	1	0	1
	Porrhomma terrestre (Emerton)	0	0	0	0	0	0	1	1
	Sisicus penifuser Bishop and Crosby	0	0	1	1	0	0	0	0
	Tenuiphantes zebra (Emerton)	0	0	0	0	0	1	0	1
Liocranidae	*Agroeca ornata* Banks	1	1	0	2	0	2	0	2
Lycosidae	*Alopecosa aculeata* (Clerck)	0	0	0	0	0	0	1	1
	Pardosa mackenziana (Keyserling)	0	0	0	0	1	0	1	2
	Pirata montanus Emerton	0	0	0	0	0	0	1	1
	Trochosa terricola Thorell	1	1	0	2	1	4	2	7
Philodromidae	*Philodromus placidus* Banks	0	0	0	0	0	1	2	3
Salticidae	*Neon nellii* Peckham and Peckham	5	0	0	5	0	0	0	0
Theridiidae	*Robertus riparius* (Keyserling)	1	0	0	1	0	0	0	0
Thomisidae	*Xysticus britcheri* Gertsch	0	0	0	0	0	0	1	1
	Xysticus canadensis Gertsch	0	0	0	0	0	0	1	1

CHAPTER 4: GENERAL CONCLUSION

In two separate experiments completed in Forillon National Park, Quebec, I looked at the use of dead wood by generalist arthropods predators [i.e., spiders (Araneae); ants (Hymenoptera: Formicidae)]. In the first experiment (Chapter 2), I compared spider and ant assemblages on, adjacent to, and away from fallen logs, and tested the effects of log type and decay stage on the ant and spider assemblages found on logs. In a different study (Chapter 3), spider and ant assemblages were compared on, adjacent to, and away from fallen logs in different forest types. These studies have greatly enhanced knowledge about the use of dead wood by generalist arthropod predators on the forest floor.

Logs were shown to be an important habitat for forest floor spiders, confirming another study completed in Alberta (Buddle 2001). In the La chute maple site of Forillon (Chapter 2), collections of spiders were significantly higher in pitfall traps located on the wood surface compared to traps on the forest floor and spider assemblages from the log surface were clearly separated from assemblages of the forest floor, as determined by ordination analysis. Spider diversity on the surface of logs at La chute maple site (Chapter 2) and in maple and aspen forests of Forillon (chapter 3) was higher than on the forest floor. My research did not depend solely on pitfall trap collections, as litter sampling was done as an additional sampling technique. In Chapter 2, this sampling revealed that more spiders, and a higher diversity of spiders, occurred in litter adjacent to logs compared to collections further away on the forest floor, a finding similar to Jabin et al. (2004).

Type of dead wood (coniferous or deciduous) and decomposition stage also affected spider assemblages (Chapter 2). In particular, high diversity was recorded on decomposition stage II logs, and wood type suggested some intriguing responses at a guild- and species-specific level. For example, the number of hunting spiders and *Pardosa mackenziana* (Keyserling) specimens were significantly higher on coniferous than deciduous logs. In contrast, catch rates of *Callobius bennetti* (Blackwall) were higher on deciduous compared to coniferous logs.

Even though conclusions were limited by the lack of seasonal sampling in Chapter 3, I nevertheless found that the use of dead wood by spiders depended on forest type. Spider diversity was highest on the surface of logs in maple and aspen forest but highest on the forest floor away from logs in fir forest. Spider assemblages on and away from logs were somewhat separated in NMSD ordination in the maple and aspen forest but not in the fir forest. Only in the maple and fir forest did I see a clear difference between litter spider collections adjacent and away from logs. The fact that log size and litter depth depend on forest type could explain part of the interaction between spider collection placement and forest type. More investigation on this subject (i.e., with a longer collection period) should be done to clarify dead wood use by spiders in different forest types.

Unfortunately, in Chapter 2 of this thesis, ants' use of dead wood was not evaluated due to low sample sizes. In chapter 3 of this thesis, ant diversity was higher on the surface of logs compared to adjacent to logs. Ants were not affected by the interaction between pitfall trap placement and forest type but again the low sample size made it difficult to offer concrete conclusions related to log use by ant assemblages. This study did, however, confirm that ant assemblages in Quebec are dependent on the forest type in which they are found. Ants are more common in other forest regions of Canada (e.g., Francoeur 1965; Francoeur 1966; Letendre and Pilon 1973), and projects, in these or other locations, similar to the current effort (Chapters 2 and 3) are recommended.

The new findings of Chapter 2 and 3 strengthen the role of dead wood as critical habitat for arthropods. Together with the vast literature on arthropods that are directly dependent on dead wood for survival (saproxylic invertebrates) (Savely 1939; Irmler et al. 1996; Jonsell et al. 1998; Kruys and Jonsson 1999; Siitonen 2001; Simila et al. 2003), and with the studies of Buddle (2001) and Lindgren and MacIsaac (2002), my research has further illustrated that dead wood is a key habitat for generalist predators such as spiders and ants.

Dead wood is known to be a critical element of forest ecosystems and ants and spiders are certainly major predators of the forest floor and can therefore influence many ecological processes (i.e., decomposition, insect-plant interaction, plant growth). Understanding the interactions occurring within the ecosystem is essential to properly manage our forests (Kimmins 1997). Given the importance of dead wood and ants and spiders, the information provided by this study will therefore be useful for forest conservation plans.

The preservation of forest biodiversity is important to consider in resource management (Probst and Crow 1991; Burton et al. 1992). My study confirmed that dead wood is a critical element for the conservation of forest biodiversity. Even though many studies had found that dead wood was critical for the retention of saproxylic biodiversity (Heliövaara and Väisänen 1984; Siitonen and Martikainen 1994; Kaila et al. 1994; Väisänen et al. 1993; Vallauri et al. 2003), this study along with Buddle (2001) showed that dead wood is also a critical habitat for the retention of forest floor generalist arthropod predator biodiversity. If consideration of biodiversity is to be at the forefront of conservation plans in northern forests, such plans should take dead wood into consideration.

REFERENCES

Buddle C. M. 2001. Spiders (Araneae) associated with downed woody material in a deciduous forest in central Alberta, Canada. Agricultural and Forest Entomology 3: 241-251

Burton P. J., Balisky A. C., Coward L. P., Cumming S. G. and Kneeshaw D. D. 1992. The value of managing for biodiversity. The Forestry Chronicle 68: 225-237

Francoeur A 1965. Écologie des populations de fourmis dans un bois de chêne rouges et d'érables rouges. Le Naturaliste Canadien 92: 263-276

Francoeur A. 1966. La faune myrmécologique de l'érablière à sucre (*Aceretum saccharophori* Dansereau) de la region de Québec. Le Naturaliste Canadien 93: 443-472

Heliövaara K., and Väisänen R. 1984. Effects of modern forestry on northwestern European forest invertebrates: A synthesis. Acta Forestalia Fennica 189: 1-32

Irmler U., Heller K. and Warning J. 1996. Age and tree species as factors influencing the populations of insects living in dead wood (Coleoptera, Diptera: Sciaridae, Mycetophilidae). Pedobiologia 40: 134-148

Jabin M., Mohr D., Kappes H and. Topp W. 2004. Influence of deadwood on density of soil macro-arthropods in a managed oak–beech forest. Forest Ecology and Management 194: 61–69

Jonsell M., Weslien J. and Ehnström B. 1998. Substrate requirements of red-listed saproxylic invertebrates in Sweden. Biodiversity and Conservation 7: 749-764

Kaila L., Martikainen P., Puntilla P. and Jakovlev E. 1994. Saproxylic beetles on dead birch trunks: effect of polypore species decaying the trunk. Annales Zoologici Fennici 31: 97-108

Kimmins J. P. 1997. Forest ecology: A foundation for sustainable management, second edition. Prentice-Hall inc, New Jersey.

Kruys N. and Jonsson B.G. 1999. Fine woody debris is important for species richness on logs in managed boreal spruce forests of northern Sweden. Canadian Journal of Forest Research 29: 1295-1299

Letendre M. and Pilon J.-G. 1973. Nids et micromilieux de nidification utilisés par les fourmis dans les peuplements forestiers des Basses Laurentides, Québec (Hymenoptera : Formicidae). Le Naturaliste Canadien 100: 237-246

Lindgren, B.S., and A.M. MacIsaac. 2002. A preliminary study of ant diversity and abundance, and their dependence on dead wood in central interior British Columbia. In : Shea P. J., Laudenslayer W.F. Jr., Valentine B., Weatherspoon C. P. and Lisle T.E. (Eds.), Symp. Proc.: Ecology and management of dead wood in western forests, pp 111-119. USDA For. Serv. Gen. Tech. Rep. PSW-181, Pac. SW. Res. Stn., Albany, CA

Probst J. R. and Crow T. R. 1991. Integrating biological diversity and resource management. Journal of Forestry 89: 12-17

Savely H. E. 1939. Ecological relations of certain animals in dead pine and oaks. Ecological Monograph 9: 323-385

Siitonen J. 2001. Forest management, coarse woody debris and saproxylic organisms: Fennoscandian boreal forests as an example. Ecological Bulletins 49: 11-41

Siitonen J. and Martikainen P. 1994. Occurrence of rare and threatened insects living on decaying *Populus tremula*: A comparison between Finnish and Russian Karelia. Scandinavian Journal of Forest Research 9: 185-191

Simila M., Kouki J. and Martikainen P. 2003. Saproxylic beetles in managed and seminatural Scots pine forests: quality of dead wood matters. Forest Ecology and Management 174: 365-381

Väisänen R., Biström O. and Heliövaara K. 1993. Sub-cordical coleoptera in dead pines and spruces: Is primeval species composition maintained in managed forests? Biodiversity and Conservation 2: 95-113

Vallauri D., André J. and Blondel J. 2003. Le bois mort, une lacune des forêts gérées. Revue Forestière Française 55: 99-112