THE EFFECTS OF HARVESTING AND DECAYING LOGS ON ORIBATID (ACARI: ORIBATIDA) MITE ASSEMBLAGES IN EASTERN CANADIAN MIXEDWOOD BOREAL FOREST

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PREFACE

This thesis is composed of four chapters.

Chapter 1

This chapter provides a literature review and introduction to the thesis.

Chapter 2

This chapter is a manuscript in preparation for submission to Forest Ecology and Management.

Déchêne, A.D. and C.M. Buddle. The effects of different harvesting regimes on oribatid mite assemblages in eastern Canadian boreal forest.

Chapter 3

This chapter is a manuscript in preparation for submission to Ecological Applications.

Déchêne, A.D. and C.M. Buddle. The spatial influence of decaying logs on oribatid mite assemblages in aspen-dominated mixedwood boreal forest.

Chapter 4

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

Déchêne, A.D. and C.M. Buddle. A test of Tullgren funnel extraction duration for sampling oribatid mites in boreal forest.

Chapter 5

This chapter consists of general conclusions of the thesis.

CONTRIBUTION OF AUTHORS

Both of the authors contributed to the design of the studies in chapters 2, 3 and 4. A.D. Déchêne collected the data, identified all specimens, conducted the analysis and presented the results. C.M. Buddle supervised the research and edited all chapters of this thesis.

ABSTRACT

Ecosystem-based management (e.g. partial cut harvesting) retains some components of natural forest structure such as downed woody material (DWM) and may have less impact than clear cutting on forest floor fauna. I tested how partial cut harvesting affects oribatid mite assemblages and explored the spatial influence of decomposing logs on oribatids on the forest floor at the sylviculture et aménagement forestiers écosystémique (SAFE) research station in Abitibi, Québec. The importance of determining the extraction duration of the specific apparatus used in biodiversity studies was also demonstrated. In June 2006, litter and soil were sampled in mixedwood boreal forest where the following treatments were replicated three times: clear cut harvest, 1/3 partial cut harvest, 2/3 partial cut harvest, controlled burn (after harvest) and uncut control. As well, six decayed logs were sampled at three distances each: directly on top of the log (ON), directly beside the log (ADJ) and at least one metre away from the log and any other fallen wood (AWAY). Samples ON logs consisted of a litter layer sample, an upper wood sample and an inner wood sample. Samples at the ADJ and AWAY distances consisted of litter samples and soil cores. Eight years after harvest, clear cutting appears to have had a homogenizing effect on oribatid species composition, and partial cuts had more similar species composition to the uncut control within their respective blocks. In litter, diversity decreased with increasing harvesting intensity but in soil it increased. In the burn, species richness was significantly different from the other treatments, and there was some change in species-specific abundance. The highest species richness was collected ON logs, and logs harboured a distinct oribatid species composition compared to the forest floor. There were species-specific changes in relative abundance with increasing distance away from DWM, and each layer (litter, wood and soil) exhibited a unique species composition and hosted a different diversity of oribatid mites. These results show that different harvesting regimes affect oribatid mite assemblages in various ways, and that DWM provides habitat for unique assemblages of oribatid mites and increases oribatid biodiversity in mixedwood boreal forest. This thesis supports the acceptance and implementation of a wider forest management paradigm like ecosystem-based management that includes the retention of DWM for the maintenance of biodiversity in managed forests.

RÉSUMÉ

L’aménagement écosystémique (e.g. coupe partielle) permet de conserver certains éléments structuraux tel les débris ligneux grossiers et pourrait avoir pour effet de minimiser l’impact de la récolte sur la pédofaune. J’ai évalué l’effet de la coupe partielle et l’influence spatiale du bois mort au sol sur les assemblages d’oribates (Acarina) dans le dispositif expérimental SAFE (sylviculture et aménagement forestier écosystémique) en Abitibi, Québec. L'importance de déterminer la période d'extraction appropriée selon l'équipement utilisé a aussi été démontrée. Des échantillons de sol et de litière ont été récoltés en juin 2006 en forêt boréale mixte où les traitements suivants ont été répliqués trois fois: coupe totale, rétention de 33% des tiges, rétention de 66% des tiges, brûlage dirigé après coupe et peuplement témoin. Aussi, des échantillons ont été prélevés à trois distances de six troncs en décomposition: sur le tronc (ON), immédiatement à côté (ADJ) et à une distance minimale de 1 m de tout débris ligneux (AWAY). Les échantillons ON étaient formés d’un échantillon de litière, d’un échantillon de bois superficiel et d’un échantillon de bois d’intérieur. Les échantillons ADJ et AWAY étaient formés d’échantillons de litière et de sol. Huit ans après la récolte, la coupe totale semble avoir homogénéisé la composition spécifique des assemblages d’oribates, alors que celles trouvées dans les traitements de coupe partielle restent plus semblables aux témoins. Dans la litière, la diversité diminue avec une plus haute intensité de récolte alors que l’inverse est vrai pour le sol. Suite au brûlage dirigé, la richesse spécifique est différente des autres traitements, et certains changements ont été observés au niveau de l’abondance de certaines espèces. La plus haute richesse spécifique a été observée dans les échantillons ON, et ces troncs abritaient un composition spécifique distincte de celle du sol. Des changements au niveau de l’abondance relative ont été observés à des distances plus éloignées des débris ligneux, et chacune des strates (litière, bois, sol) présente une composition spécifique unique d’oribates. Mes résultats indiquent que les assemblages d' oribates sont affectés différemment par les approches de récoltes considérées dans cette étude, et les débris ligneux au sol fournissent habitat favorisant des assemblages uniques d’oribates et augmentent la diversité de ce groupe en forêt boréale mixte. Cette thèse supporte l’acceptation et l’implémentation d’un paradigme de l’aménagement forestier

plus large comme l'aménagement écosystémiques, incluant la rétention des débris ligneux au sol pour assurer le maintien de la biodiversité en forêt aménagée.

CHAPTER 1: LITERATURE REVIEW AND INTRODUCTION

Paradigm shift: moving towards ecosystem-based management

The Canadian boreal forest, our largest biome, is a transcontinental belt covering 35% of the total land area and comprising 77% of the total forested area (Natural Resources Canada 2004). The boreal forest is dominated by coniferous species with a large deciduous component in the mixedwood zones (Danks and Foottit 1989, Natural Resources Canada 2004) and is host to a large diversity of species. As well, for centuries, the forest ecosystem has supported a number of human activities, both economic and recreational; however, in the quest to supply the ever-growing demand for timber and timber related products, the long-term health of the boreal forest, and by extension all life dependent on it, has become an area of concern and the development of ecologically sustainable forestry practices has become a priority (Franklin 1989, Burton et al. 1992, Hunter 1993, Fries et al. 1997, Work et al. 2003, Thorpe and Thomas 2007).

Forest ecosystem function is inextricably tied to its structure, but intensive forest management decreases structural complexity, which reduces species diversity and likely affects ecosystem function (Hansen et al. 1991, Bergeron et al. 1998, Hooper et al. 2005). The objective of forestry has traditionally been to maximize profit by increasing stand-level productivity through the establishment of fast growing, even-aged tree monocultures with a short rotation time (Haila 1994, Hansen et al. 1991, Bergeron and Harvey 1997, Esseen et al. 1997, Perry 1998). This has been achieved with practices such as large-scale clear cutting, prescribed burning, rapid re-planting, controlling competing non-crop vegetation, improving soil conditions (e.g. fertilizer), genetic selection and suppression of natural disturbances such as insects, fire and disease (Hansen et al. 1991, Haila 1994, Perry 1998). These types of intensive forestry practices alter forest structure and composition in ways that are very different spatially and temporally than many small and few large natural disturbance events (Franklin 1989, Hansen et al. 1991, Hunter 1993, DeLong and Tanner 1996, Bergeron et al. 1998, Perry 1998, Bergeron et al. 2002, Harvey et al. 2002) and consequently change the plant and animal communities within them. For example, the abundance and distribution of many species dependent on decaying wood are reduced in managed forests due to the loss of large snags, logs and stumps (Harmon et al. 1986, Siitonen and Martikainen 1994, Esseen et al. 1997, Kaila et al. 1997, Jonsell et al. 1998, Siitonen 2001, Hyvärinen et al. 2006), and this reduction may influence decomposition and other soil processes (Loreau et al. 2001, Hooper et al. 2005). In the last several decades however, public opinion and accumulating scientific evidence has led to the development of alternatives to traditional management practices in an attempt to mimic natural forest dynamics and to conserve forest biodiversity (Franklin 1989, Probst and Crow 1991, DeLong and Tanner 1996, Bergeron et al. 1998, Perry 1998, Bengtsson et al. 2000, Spence 2001, Bergeron et al. 2002). For example, variable retention, or partial harvest, leaves variable numbers of aggregated or dispersed trees to provide habitat continuity, uneven-aged stands and future sources of dead wood (Hunter 1993, Esseen et al. 1997, Fries et al. 1997, Lee et al. 1997, Raivio et al. 2001, Harvey et al. 2002, Ranius and Kindvall 2004) in an effort to retain elements of the original forest structure and thus maintain forest biodiversity. This approach has already been established in Sweden, Finland and Norway over the past decade (Økland 1994, Økland et al. 1996, Fries et al. 1997, Raivio et al. 2001, Siitonen 2001, Ranius and Kindvall 2004) and its integration has begun to some degree in parts of Canada (DeLong and Tanner 1996, Bergeron and Harvey 1997, Armstrong 1999, Work et al. 2003, Thorpe and Thomas 2007). This shift in the approach to forest management indicates a willingness to adapt to new ideas and recognition of the need to achieve a balance between economic demands and environmental values.

Impacts of forest management

In an unmanaged forest, naturally occurring cycles of disturbance at different spatial and temporal scales produce a patchwork of stands of variable age and composition (Haila 1994, Bergeron et al. 1998, Perry 1998, Bergeron et al. 2002, Harvey et al. 2002). This results in high habitat heterogeneity and structural complexity (Hansen et al. 1991), and greater forest structural complexity provides more habitat variation at all scales, which has the potential to support higher species diversity (Anderson 1978, Hansen et al. 1991, Kuuluvainen and Laiho 2004). Recently, the link between biodiversity and ecosystem functioning has been the focus of several discussions; high species diversity is thought to contribute to ecosystem function and the stability and resilience of ecosystems by providing essential services such as decomposition and nutrient cycling (Tilman 1996, Bengtsson et al. 2000, Loreau et al. 2001, Naeem 2002, Loreau et al. 2003, Hooper et al. 2005). For forest management, this concept has lead to the development of new management guidelines with a focus on biodiversity conservation in an attempt to maintain essential ecosystem processes in managed forests (Probst and Crow 1991, Burton et al. 1992, Fries et al. 1997, Armstrong 1999, Bengtsson et al. 2000, Spence 2001, Work et al. 2003, Thorpe and Thomas 2007). In the context of this thesis, biodiversity will refer to species diversity (i.e. richness).

Clear cut harvesting alters soil structure and forest floor habitat (Battigelli et al. 2004, Kuuluvainen and Laiho 2004), soil erosion (Worrell and Hampson 1997, Ballard 2000), contributes to substantial loss of nutrients and food resources (Perry 1998, Ballard 2000), fragments and reduces habitat (Franklin 1989, Hansen et al. 1991, Perry 1998), modifies soil temperature and moisture regimes (Ballard 2000), increases wind and light levels (Esseen et al. 1997, Bourgeois et al. 2004), reduces soil fungal biomass (Pietikainen and Fritze 1995) and simplifies ecosystem structure through a reduction of species abundance and diversity (Blair and Crossley 1988, Esseen et al. 1997, Perry 1998). Ground-based skidding displaces and mixes humus and compacts soil, reducing soil pore size, which reduces soil aeration, drainage and infiltration (Worrell and Hampson 1997, Ballard 2000, Prescott et al. 2000, Battigelli et al. 2004). Soil exposed during harvesting is also more susceptible to erosion and loss of nutrients and moisture (Worrell and Hampson 1997). Blair and Crossley (1988) reported reduced decomposition rates in a clear cut hardwood stand compared to a control eight years after harvest, and forest floor organic matter in hardwood stands decreased for up to 15 years following clear cutting (Covington 1981). The rate of humus decomposition and accumulation is also influenced by changes in the quantity and quality of litter fall after harvest (Prescott et al. 2000). These changes undoubtedly affect litter and soil fauna on the forest floor and influence their functioning as part of the decomposer community.

Several ground-dwelling arthropod taxa show variable short and long-term changes after clear cutting. Carabid beetle species richness increased and species composition changed after clear cutting (Niemelä et al. 1993) but recovered to levels found in older forest after about 15 years (Buddle et al. 2006). Staphylinid beetle diversity also increased after clear cutting but did not recover after 15 years (Buddle et al. 2006). Spider species composition, and in some cases total spider abundance, changed following clear cutting (McIver et al. 1992, Buddle et al. 2006), particularly for sedentary ground spiders and web builders (Coyle 1981); however, these changes were no longer apparent after 30 years (McIver et al. 1992, Buddle et al. 2006). In spruce forest, enchytraeid biomass and bacterial numbers were shown to increase for up to seven years after clear cutting but returned to near control levels after 13 years (Sundman et al. 1978).

Like many ground-dwelling species, oribatid mite assemblages have been shown to be affected by clear cutting in the short-term, usually due to microclimatic changes such as higher temperature, lower moisture and/or alteration of their microhabitat. In mixedwood forest two years after clear cutting, Bird and Chatarpaul (1986) demonstrated a reduction in oribatid abundance and a shift in species dominance but did not find a change in species composition. In the southern Appalachians, Abbott et al. (1980) also reported a decrease in oribatid mite abundance and a shift in dominance patterns two years after clear cutting. In the same region eight years later, oribatid density remained significantly lower and relative abundances remained changed in the clear cut site (Blair and Crossley 1988), yet 21 years after clear cutting, oribatid density and morphospecies richness exceeded that in the control (Heneghan et al. 2004). Battigelli et al. (2004) reported significantly reduced oribatid density and relative abundance one year after disturbance to the forest floor but also found decreased diversity with increasing disturbance intensity. As well, the number of rare species collected was reduced in severely disturbed sites, indicating a change in assemblage composition (Battigelli et al. 2004). Conversely, Huhta et al. (1967) found a slight increase in oribatid mean density immediately after clear cutting, which then decreased significantly eight years later (Huhta et al. 1969). Initial changes in species assemblages on the forest floor may be due in part to variation in microsite temperature and moisture from a reduction in the amount of litter and canopy cover after clear cutting (Abbott et al. 1980, Seastedt and Crossley 1981, Bird and Chatarpaul 1986, Blair and Crossley 1988, McIver et al. 1992, Donegan et al. 2001), which has the greatest impact on sedentary litter species (Coyle 1981). Oribatid populations may reflect changes in the amount and distribution of organic material (Seastedt and Crossley 1981, Abbott and Crossley 1982, Hasegawa 2001, Peck and Niwa 2005) and/or fluctuations in food resources like fungi affected by clear cutting (Huhta et al. 1967, Huhta et al. 1969). Oribatids may also be reduced immediately after clear cutting due to predation or competition from other mites or arthropods better suited to open habitat, but populations may begin to increase as the stand regenerates and microhabitat conditions again become favourable for oribatids. Changes in oribatid mite assemblages after clear cut harvesting may persist for many years (Blair and Crossley 1988, Siepel 1996), but there are very few long-term studies to verify this.

A landscape-scale, ecosystem-based approach to forest management can contribute to the long-term preservation of biodiversity, a role traditionally considered to be exclusively for preserved lands and parks (Franklin 1989, Bergeron and Harvey 1997). Ecosystem-based management is a coarse filter approach that attempts to emulate natural disturbance with the goals of maintaining ecosystem processes and preserving biodiversity under the assumption that species have evolved under natural disturbance regimes of varying intensity and frequency and therefore will be adapted to occasional habitat disruption at a landscape-scale (Hunter 1993, Haila 1994, Fries et al. 1997, Armstrong 1999, Bergeron et al. 2002, Harvey et al. 2002). Methods used in ecosystem-based management include partial cutting, retention of dead wood, prescribed or controlled burning, increased rotation times and modified spatial design of cut blocks (Hansen et al. 1991, Hunter 1993, Haila 1994, Armstrong 1999, Siitonen 2001, Spence 2001, Harvey et al. 2002). By preserving forest biodiversity, ecosystem stability and essential ecosystem processes may also be maintained, ensuring long-term ecological sustainability (Burton et al. 1992, Tilman 1996, Bengtsson et al. 2000, Loreau et al. 2001, Loreau et al. 2003, Hooper et al. 2005). Alternatives to clear cutting, such as partial cutting, spatially emulate natural disturbance, creating variably aged stands and maintaining some structural heterogeneity from the pre-harvest stand through the retention of live trees, snags and logs in clear cuts

(Franklin 1989, Hansen et al. 1991, Hunter 1993, Bergeron et al. 1998, Harvey et al. 2002). Maintaining long-term forest ecosystem health and preserving biodiversity are now integral parts of forest management in parts of Europe (Økland 1994, Økland et al. 1996, Raivio et al. 2001, Siitonen 2001, Ranius and Kindvall 2004), and most companies in western Canada have begun to integrate management plans that include biodiversity conservation as a goal (Work et al. 2003). Much more research is required to assess the efficacy of ecosystem-based management practices; in particular, success of the main goal of preserving and maintaining biodiversity in the long-term as compared to traditional methods has yet to be unequivocally confirmed (Simberloff 2001, Spence 2001).

Recent work suggests that less intense harvesting may minimize climatic and microhabitat changes compared to clear cutting. In Québec's northwestern boreal forest, Brais et al. (2004) found that canopy openness, and therefore solar radiation, increased progressively from one-third partial cuts to two-third partial cuts to clear cuts, and there was a significant increase in fresh coarse woody debris (CWD) and a significant decrease in decomposed CWD in clear cuts compared to partial cuts. In the same region of Québec, Lapointe et al. (2006) found no significant differences in various soil properties including soil pH and N availability among clear cut, partial cut and uncut sites two years after harvest. However, other studies have shown N mineralization and nitrification rates (Prescott 1997, Lindo and Visser 2003) and soil temperature and moisture (Barg and Edmonds 1999) under less intense harvesting regimes were intermediate between clear cut and uncut sites. Siira-Pietikainen et al. (2001) found that although soil pH increased and microbial biomass and total soil N and C decreased in clear cuts, none of these changes were found in partial cut treatments. However, Jerabkova et al. (2006) found no difference in N availability, soil pH, litter decomposition or microbial biomass among partial cut, clear cut and uncut forest four years after harvesting. Prescott (1997) showed the rate of needle litter decomposition under clear cutting and less intense harvesting regimes were both significantly lower than in old growth forest. Partial cutting may also reduce soil compaction and nutrient leaching (Worrell and Hampson 1997); however, the full extent of the impacts of practices like partial cutting on soil properties and microclimate on the forest floor in the boreal forest remains unresolved.

Recent studies have shown variable effects of partial cutting on several arthropod taxa. Mycetophilid flies had significantly higher diversity in partial cut spruce forest than in both new (2-3yr) and old (70-100 yr) clear cuts (Økland 1994), while another dipteran group, syrphids, had higher species richness in clear cuts and cut strips than in retention strips or unharvested spruce forest up to three years after harvesting (Deans et al. 2007). Yi and Moldenke (2005) found that seven years after logging mean abundances of several ground-dwelling arthropod taxa, including ants and spiders, increased with thinning intensity, and litter-dwelling fungivorous Collembola also showed a temporary increase in number in partial cut spruce stands compared to controls, although they decreased in clear cut sites over the same period (Siira-Pietikainen et al. 2003). In thinned forest stands (10-33% cut) in Finland, Koivula (2002) reported a more similar carabid beetle assemblage to that found in uncut stands than in clear cuts two years after harvesting. In more intensely managed forest, Cancela da Fonseca (1990) showed a loss of the dominant status of Oribatida and a decrease in their density, and Bird and Chatarpaul (1986) reported lower oribatid abundance compared to both less intensely managed and unmanaged forest. Lindo and Visser (2004) found microarthropod suborder abundance in partial cut retention patches to be more similar to uncut conifer forest than to clear cuts, but Peck and Niwa (2005) showed that thinned late successional stands had significantly lower oribatid mite abundance on the forest floor than unthinned stands. In a partially cut hardwood stand, Abbott et al. (1980) showed a moderate level of similarity in the dominance among oribatid species compared to a control, but similarity between the partial cut and clear cut was significantly different. These studies suggest that less intense harvesting may minimize the negative effects of clear cutting on litter and soil oribatid mites and thus have less impact on their richness and composition; however, work at the species-level is lacking in eastern boreal forest.

Fire is an extremely important natural disturbance in the boreal forest, but fire events are usually suppressed in managed forests to the extent that clear cutting has replaced wildfire as the dominant stand-replacing force (Hansen et al. 1991, DeLong and Tanner 1996, Bergeron et al. 1998, Armstrong 1999, Bengtsson et al. 2000). Managed forests lack variability in age-structure and stand composition due in part to fire suppression (Esseen et al. 1997, Bergeron et al. 1998). Prescribed or controlled burning is a management strategy used to reduce fuel buildup, control competing understory vegetation and prepare seedbeds for replanting (Huhta et al. 1967, Vlug and Borden 1973, Van Lear 1993, Pietikainen and Fritze 1995). Prescribed burning of clear cuts is also thought to imitate natural fire and create some of the abiotic conditions (e.g. light and temperature regimes) and structural heterogeneity associated with burned stands (Fries et al. 1997, Bergeron et al. 1998, Brand 2002). This practice has been used for many years in Australia (Abbott et al. 2003, Brennan et al. 2006), has seen a resurgence in Sweden and Finland as part of new management guidelines (Raivio et al. 2001, Martikainen et al. 2006) and has been used recently in Canada to mimic the structure of older forest (Work et al. 2003). Impacts of prescribed burning may be more severe than clear cutting alone and include changes in nutrient availability (Prescott et al. 2000, Frey et al. 2003), large nutrient loss through the volatilization of N and S and fly-ash (Ballard 2000), increased soil pH (Ahlgren and Ahlgren 1965, Pietikainen and Fritze 1995), changes in microbe populations (Ahlgren and Ahlgren 1965) and loss of vegetation, litter and slash cover, which increases soil surface temperature and moisture fluctuations (Vlug and Borden 1973, Ballard 2000).

Research has shown variable impacts of prescribed burning after clear cutting for some ground-dwelling arthropod taxa. Carabid beetle diversity and abundance were higher in burned clear cuts than in undisturbed forest (Beaudry et al. 1997, Martikainen et al. 2006), and burning after harvest changed species composition; many species found abundantly in burned sites were absent from undisturbed forest (Beaudry et al. 1997). Burned partial cuts can also benefit rare saproxylic beetle species richness and abundance due in part to an increase in the quantity of CWD (Hyvärinen et al. 2006). Abbott et al. (2003) reported higher spider diversity in sites that had been both logged and burnt than in burnt or control sites and in burned sites without prior harvest. Brennan et al. (2004) found a similar increase in spider species richness with time but also saw a change in species composition. Greenslade (1997) showed decreases in collembolan diversity and abundance immediately following a single low-intensity fire but recovery after 18 months; however, species composition changed from pre to post-fire. Dress and Boerner (2004) reported that all identified acarine suborders and Collembola also had significantly lower abundance in more frequently burned oak-hickory sites. Seastedt (1984a) showed that oribatid mite and collembolan densities in the top five cm of tallgrass prairie soil were lower in burned sites, and Vlug and Borden (1973) demonstrated that in burned-after-harvest conifer sites, oribatid densities decreased with increasing soil depth. However, five years after a single controlled burn in clear cut conifer sites, Berch et al. (2007) found no difference in oribatid density compared to unburned clear cuts, but species richness was lower in burned clear cuts. In contrast, Lussenhop (1976) found that mite (excluding Oribatida) and Collembola densities increased for several years immediately after fire in multiply-burned prairie grassland. Studies on the longer-term changes in species diversity and composition from a single burn event following a clear cut harvest should be considered fundamental in determining the impact of this increasingly common management strategy on forest floor fauna.

Downed woody material in the boreal forest

To focus efforts to maintain biodiversity, it is necessary to study the contribution of microhabitat variation to local species richness (Niemelä et al. 1996). On the boreal forest floor, substrates such as leaf litter, organic and mineral soil layers, mosses, roots, logs, stumps, cones, twigs and other fine woody debris contribute to high habitat heterogeneity. On a just single log, suitable microhabitats might include bark, accumulated leaf litter, epiphytic plants, lichens, fungi and moss as well as the wood itself, both sapwood and heartwood (Graham 1925, Aoki 1967, Fujikawa 1974, Esseen et al. 1997, Jonsell et al. 1998, Siitonen 2001). Many of these habitats are poorly understood and are likely excellent sources of biodiversity in the boreal forest.

The removal of merchantable timber during harvesting substantially reduces potential sources of carbon and nutrient input and important invertebrate habitat, most noticeably microhabitats associated with fallen trees (Hansen et al. 1991, Huston 1993, Van Lear

1993, Jonsell et al. 1998, Perry 1998, Siitonen 2001, Kuuluvainen and Laiho 2004). Coarse woody debris (CWD) (i.e. standing dead trees, fallen trees, decaying roots and other large pieces of woody material) is a critical component of natural forest structure that harbours high biodiversity (Harmon et al. 1986, Esseen et al. 1997, Siitonen 2001, Hammond et al. 2004) and is linked to many key ecosystem processes (Harmon et al. 1986, Van Lear 1993, Perry 1998). Fallen dead wood or downed woody material (DWM) accumulating on the forest floor contributes to soil fertility and stability, serves as seed germination sites, acts as long-term storage for organic matter, moisture, carbon and nutrients (Sollins et al. 1987, Harmon et al. 1986, Van Lear 1993, Perry 1998) and supports many organisms as a result of a wide range of microhabitats due to the variable size, texture and microclimate characteristics of wood (Graham 1925, Söderström 1988, Seastedt et al. 1989, Huston 1993, Bader et al. 1995, Niemelä et al. 1996, Esseen et al. 1997, Marra and Edmonds 1998, Siitonen 2001, Ehnström 2001, Grove 2002, Edman et al. 2004, Jabin et al. 2004). CWD is a dynamic habitat; in the boreal forest, there are consistent as well as sporadic inputs of CWD from natural disturbance events like wind storms, lightening, fire, disease, insects, senescence and competition, as well as losses from decomposition and fire. These disturbances can affect individual trees, entire stands or even whole landscapes, and result in a constantly changing mass, density and volume of CWD in a forest ecosystem (Harmon et al. 1986, Van Lear 1993, Siitonen 2001, Jonsson et al. 2005).

As wood decomposition progresses, carbon is lost via respiration, and nutrient (N, P, Mg) concentrations increase through leaching and N fixation (C:N ratio decreases) (Harmon et al. 1986, Sollins et al. 1987, Van Lear 1993). The primary decomposers of dead wood are bacteria, fungi and invertebrates (Seastedt and Crossley 1988, Esseen et al. 1997). Many invertebrates, insects in particular, are associated with DWM on the forest floor; they quickly colonize dead wood, fragment the log by chewing and excavating the wood, influence nutrient content through production of frass (Seastedt and Crossley 1981, Harmon et al. 1986, Evans et al. 2003) and facilitate colonization by later arriving species of insects, fungi, bryophytes and lichens (Graham 1925, Savely 1939, Söderström 1988, Harmon et al. 1986, Niemelä et al. 1995, Esseen et al. 1997, Hammond et al. 2004).

Throughout this process, vertebrates such as skunks, bears and birds searching for prey also fragment the wood. This physical fragmentation facilitates microbes (fungi and bacteria) that modify the wood chemically and structurally, decaying the log further (Harmon et al. 1986).

In forest ecosystems, arthropods are extremely species rich and dominate in number and diversity in dead wood habitat (Graham 1925, Savely 1939, Danks and Foottit 1989, Speight 1989, Esseen et al. 1997). Saproxylic organisms are those that depend, either directly or indirectly, on dead or dying wood at some life-history stage (Speight 1989), and up to 20-25% of forest-inhabiting species may be considered saproxylic (Siitonen 2001). The most commonly studied saproxylic arthropods are Coleoptera and some Diptera (Økland et al. 1996, Kaila et al. 1997, Schiegg 2000, Grove 2002, Hammond et al. 2004), although saproxylics are found in all major orders. Saproxylic insects are often associated with various dead wood characteristics such as tree species, log diameter or stage of decay (Jonsell et al. 1998, Grove 2002, Hammond et al. 2004), and different parts of a log (e.g. bark, sapwood and heartwood) are host to characteristic groups of species (Graham 1925); consequently, saproxylic taxa are sensitive to changes in the availability of their specific habitat requirements.

The spatial distribution of dead wood is also important for saproxylic insects; species richness was higher and species composition of saproxylic Coleoptera and Diptera is different in sites with high dead wood connectivity at the stand level (Schiegg 2000). Spider diversity was also higher on the surface of logs compared to the forest floor, and some web-building species benefit from DWM by using logs as habitat (Buddle 2001, Varady-Szabo and Buddle 2006). Many other forest species depend on certain DWM characteristics for their survival. For example, the succession of bryophytes and lichens on decaying DWM was linked to variables such as log diameter and decay stage (Söderström 1988). Macrofungi are a very species rich saproxylic group that has been reduced in managed forests due to the loss of woody substrate (Siitonen 2001, Edman et al. 2004), and some species of wood-rotting fungi were only found on DWM that had previously been inhabited by other specific fungal species (Niemelä et al. 1995). As well, birds (Setterington et al. 2000), bats (Campbell et al. 2005), small mammals and amphibians (Butts and McComb 2000) often use DWM as habitat and as a food resource. Many of the characteristics that saproxylic species require are present in mature forest but absent in managed forests, and this can impact the diversity and composition of saproxylic species at all scales.

With the exception of the aforementioned work, most other taxa associated with DWM are poorly understood, especially species with poor dispersal abilities like Oribatida. Oribatid mites are particularly important on the forest floor, where they are the dominant microarthropod taxon. Most species are particulate-feeding saprophages and mycophages (Norton 1985, Behan-Pelletier 1999), feeding on decaying organic material and fungi. Oribatids in DWM contribute greatly to decomposition, nutrient cycling and soil formation; they comminute organic matter, graze on microbes and disperse them on their body surface and in their fecal pellets, which stimulates microbial growth (Fager 1968, Abbott and Crossley 1982, Seastedt and Crossley 1988, Behan-Pelletier 1999). DWM likely provides a moist refuge to protect against desiccation, and although typical food resources are fungi and bacteria, a few species feed directly on the wood itself (Luxton 1972, Johnston and Crossley 1993). Oribatid mites also use calcium compounds that accumulate in decaying wood and in fungal hyphae as cuticular hardening agents (Johnston and Crossley 1993). DWM increases the habitat heterogeneity on the forest floor (Kuuluvainen and Laiho 2004), which may correlate with high oribatid species diversity (Anderson 1978). Some oribatids that occur on the forest floor also use leaf litter and woody litter, although a few may use DWM exclusively and as a result, DWM can be very species rich (Johnston and Crossley 1993). DWM and its abiotic effects such as modification of temperature, moisture, pH and nutrient input may influence the spatial distribution and composition of mite assemblages on the forest floor (Johnston and Crossley 1993, Evans et al. 2003); however, its contribution to oribatid biodiversity has not been fully explored.

The changes in abundance and distribution of DWM in managed forests create a spatial and temporal continuity gap in dead wood habitat that can lead to landscape-level extinction, or extinction debt, even for the most abundant saproxylic species (Siitonen and Martikainen 1994, Tilman et al. 1994, Siepel 1996, Grove 2002), and the survival of species with low dispersal abilities is particularly threatened (Haila 1994, Bader et al. 1995, Kaila et al. 1997, Jonsson et al. 2005). For example, in Fennoscandia, forest management has reduced CWD at the landscape level by 90-98%, which could be responsible for the loss of more than 50% of saproxylic species (Siitonen 2001). DWM as a habitat for mites is poorly understood, particularly in the Canadian boreal forest; however, it is reasonable to infer that oribatids, most of which are saprophagous, are associated with dead wood and their assemblages are likely affected by the loss of DWM in intensively managed forests. Ecosystem-based management can operate at the landscape level by leaving contiguous patches of trees (Probst and Crow 1991) and at the stand level by avoiding damage to snags and logs during harvest (Grove 2002, Ranius and Kindvall 2004, Jonsson et al. 2005). These types of approaches would eventually result in an increase of DWM at various stages of decay thus maintaining saproxylic biodiversity.

Several studies show that DWM left in managed forests may increase biodiversity of arthropods, including microarthropods, on the forest floor. A greater number of rare and threatened saproxylic species were collected in less intensely managed aspen forest than in intensely managed forest, in which DWM is less abundant (Siitonen and Martikainen 1994). Jabin et al. (2004) also found higher arthropod abundance at microsites closer to DWM, due to the sheltered microhabitats and increased moisture, nutrients and breeding sites provided by fallen wood. The species composition of ground-dwelling spiders was different (Buddle 2001, Varady-Szabo and Buddle 2006) and relative abundance and diversity was significantly higher (Varady-Szabo and Buddle 2006) on DWM compared to the forest floor. The influence of DWM on some taxa may be long-term; 18 years after the addition of logging residues, mean densities of Collembola (fungivores) and gamasid mites (predators) were significantly higher compared to sites in which residues had been removed (Bengtsson et al. 1997). Seastedt et al. (1989) showed that oribatids were the most abundant taxon in decaying wood, and that total microarthropod abundance increased as decomposition progressed, as moisture and nutrient content increased. The amount and vertical distribution of organic matter also influences microarthropod densities at different depths (Seastedt and Crossley 1981); therefore, DWM may influence vertical distribution on the forest floor. Evans et al. (2003) demonstrated that abundance of mite RTU (recognizable taxonomic units) significantly decreased with increasing distance from beech DWM, and arthropod family-level and mite RTU diversity was higher in the litter than in the fermentation layer. Similarly, Marra and Edmonds (1998) found that soil depth had a significant effect on the diversity and average density of Acari, but distance from DWM did not; however, four oribatid morphospecies showed significant differences in density with distance from DWM. DWM clearly affects forest biodiversity; however, species-level research is necessary to fully understand its influence on oribatid assemblages and the potential impacts of the loss of DWM in managed forests.

Structural heterogeneity and available energy are important determinants of biodiversity at all scales (Huston 1993), and DWM represents both of these factors and as such has a large impact on forest floor biodiversity. Traditional forest management drastically reduces the amount of DWM in an area, which affects microhabitat variation associated with fallen logs and results in decreased species diversity and impacts ecosystem function (Hansen et al. 1991, Burton et al. 1992, Haila 1994, Bengtsson et al. 2000, Siitonen 2001, Kuuluvainen and Laiho 2004). In fact, the alteration and removal of this critical habitat during harvesting likely has a greater impact on forest biodiversity than the disturbance of harvesting itself (Huston 1993). Ecosystem-based management, such as partial cutting, can retain elements of natural forest structure like DWM in managed forest thus maintaining the diversity of saproxylic species associated with this unique habitat (Esseen et al. 1997, Fries et al. 1997, Lee et al. 1997). Despite the importance of oribatid mites for the decomposition of wood and the potential implications for many forest soil processes, patterns of their abundance, species richness and composition in DWM at any stage of decay are not well known (Seastedt et al. 1989, Perry 1998).

Oribatid mites on the forest floor

Just as the forest industry has begun to shift its focus and consider a wider paradigm, soil ecology has, in the past 50 years, begun to explore one of the most diverse yet least understood components of the soil ecosystem, the decomposer community (Lee 1996, Behan-Pelletier and Newton 1999, Bardgett 2002). The decomposer community encompasses microfauna like the Protozoa and nematodes, mesofauna such as Collembola, free-living Acari, Protura and Diplura, and macrofauna including Oligochaeta and insects (Petersen and Luxton 1982, Verhoef and Brussaard 1990). Today, study of the diversity of this community and its contribution to soil ecosystem function and sustainability of management practices are among the most important areas of research in soil ecology (Lee 1996, Bardgett 2002).

Acari are the dominant arthropod taxon in the soil (Behan-Pelletier and Newton 1999), with more than 40,000 described species worldwide (Walter and Proctor 1999) and 1,915 described species and an estimated 7,567 undescribed or unrecorded species in Canada alone (Biological Survey of Canada 2003). Oribatida is the most diverse and abundant suborder of mites in litter and soil (Norton 1985, Norton 1994, Behan-Pelletier 1999) with approximately 10,000 described species worldwide (Schatz 2002) and densities that can exceed hundreds of thousands of individuals m^{-2} in forest soil (Petersen and Luxton 1982, Behan-Pelletier and Newton 1999). Oribatids are found on virtually every component of the forest: bark, moss on trees and rocks, leaf litter, twigs and cones, soils, living trees, and decaying wood, both standing and fallen (Aoki 1967, Fujikawa 1974). This diverse and ubiquitous group is sensitive to environmental changes, and their activities influence decomposition (Abbott and Crossley 1982, Seastedt 1984b, Heneghan et al. 1999), mineralization (Beare et al. 1992), nutrient cycling (Moore et al. 1988, Seastedt and Crossley 1988, Setälä and Huhta 1991), soil formation and system stability (Norton 1985, Maraun et al. 1998) on the forest floor; therefore, they are considered useful bioindicators of soil ecosystem functioning (Behan-Pelletier 1999, Loreau et al. 2001, Paoletti et al. 2007).

Oribatids are recognized as vital members of the decomposer community, that is, secondary decomposers that contribute to decomposition and nutrient cycling by mediating microbial populations through grazing activity and by facilitating further decomposition by fragmenting organic material (Luxton 1972, Seastedt 1984b, Moore et al. 1988, Beare et al. 1992, Behan-Pelletier 1999). Oribatids are primarily particulate-feeding saprophagous and mycophagous mites, feeding on living and dead organic material (Norton 1985, Moore et al. 1988, Johnston and Crossley 1993, Walter and Proctor 1999), such as moss and fungi. A few species are opportunistic predators, but there are no parasitic oribatids (Behan-Pelletier 1999). While it is possible to generalize the feeding habits of oribatids, subdivisions of their feeding modes are evident (Luxton 1972, Anderson 1975, Norton 1985, Schneider et al. 2004). Oribatids may feed on the dead parenchymal tissue of leaves (phyllophagy) or the woody structural tissue of dead plants (xylophagy), microbivores feed on fungal hyphae or spores (mycophages), on bacteria (bacteriophages) or lichens and algae (phycophages), and some species are completely non-specialized (panphytophages) (Luxton 1972, Schneider et al. 2004). Some oribatids may be obligatory xylophages, specializing on dead woody material (Luxton 1972, Behan and Hill 1978). Many oribatid species feed on more than one food source (Luxton 1972, Anderson 1975), although there is often some selectivity (Luxton 1972), and there are no species currently known to specialize on a single fungal species (Schneider and Maraun 2005). The diet of most oribatids may vary depending on habitat characteristics, season and/or microbe availability, which may be an adaptation to a variable environment (Wolf and Rockett 1984, Norton 1985). Oribatids comminute organic material, increasing the surface area available for microbial growth, stimulate respiration by grazing and microbial growth by movement of nutrients and disperse microbes on their body surface and in their fecal pellets, which comprise an essential part of soil structure (Behan and Hill 1978, Seastedt 1984b, Norton 1985, Moore et al. 1988, Maraun et al. 1998, Behan-Pelletier 1999). Their fecal pellets also increase available surface area, water absorption, N concentration and pH and aid movement of material deeper into the soil, all of which also increase microbial activity (Norton 1985). Fungivorous mites also play a role in wood decomposition by promoting further recolonization of the wood by fungi, and wood-feeding mites physically alter the substrate thus affecting its structural integrity, also enhancing microbial activity (Seastedt et al. 1989). Fragmentation of organic substrates like decaying wood and leaves also increases leaching and oxidation, which are important processes in decomposition (Seastedt 1984b).

There have been some attempts to quantify the contribution of microarthropods, including oribatids, to decomposition and nutrient cycling in forests. Some studies have found that microarthropods can be responsible for up to 69% of total foliar decomposition rate (Vossbrinck et al. 1979), although the average rate has been estimated at 23% of the total rate (Seastedt 1984b). The contribution of soil fauna to nitrogen mineralization has been calculated at approximately 30% (Verhoef and Brussaard 1990), while others estimate a 20-40% increase in nutrient mineralization rates directly and indirectly attributable to soil and litter arthropods (Seastedt and Crossley 1988). Oribatids have been shown to expedite fungal assemblage recovery after disturbance; Maraun et al. (1998) found that recolonization and restoration of total fungal biomass was more rapid in microcosms with oribatid mites than without mites. Oribatids have also been shown to increase litter mass loss and nitrogen and improve primary productivity (Seastedt 1984b, Setälä and Huhta 1991, Heneghan et al. 1999) and play an important role in the dispersal of fungal spores, hyphae and bacteria (Behan and Hill 1978).

Oribatids are considered suitable bioindicators of soil systems for a variety of reasons; they have high diversity and densities, they are sensitive to environmental changes, adults are taxonomically well known relative to other mite groups and they include varied trophic groups (Behan-Pelletier 1999, Paoletti et al. 2007). The diversity of a bioindicator taxon may reflect environmental characteristics or the diversity of other taxa (McGeoch 1998). Among the Acari, oribatids are considered to typify K-selected organisms; they are iteroparous, long-lived, have low metabolic rate, low fecundity and slow development rates (Norton 1985, Norton 1994, Behan-Pelletier 1999). For example, in temperate regions, a single female may live up to four years and lay only a few dozen eggs over her entire lifetime (Norton 1994). Consequently, many species of oribatids have little capacity for rapid population growth and few are adapted for dispersal; therefore, they are unable to easily escape environmental stress (Behan-Pelletier 1999). Ojala and Huhta (2001) extrapolated the dispersal rates of some oribatid species to 30 years and found few would be capable of dispersing more than 30 m over this time; the maximum possible distance was 120 m over 30 years for a few species, including *Oppiella nova* (Oudemans 1902), a very common oribatid on the forest floor. Severely physically disturbed environments may eradicate sensitive, slow developing species like oribatids; therefore; a change in dominance patterns and abundance can indicate environmental stress or disturbance.

Microarthropod composition on the forest floor can depend on several factors including soil pH, microclimate, organic matter composition and input and nutrient availability, (Siepel 1996, van Straalen and Verhoef 1997, Cassagne et al. 2003) and microhabitat structural diversity (Anderson 1978, Johnston and Crossley 1993, Marra and Edmonds 1998, Battigelli et al. 2004). Oribatid mites are often the most abundant microarthropod taxon collected on the forest floor, but they are also the most severely affected by disturbance. Recovery can depend on disturbance frequency, biotope quality (favourable conditions) and recolonization ability (Siepel 1996). The capacity for oribatid assemblages to recover following disturbance has not been well examined, but it is estimated that it could require anywhere from five (Battigelli et al. 2004) to 13 years (27 after fire) (Huhta 1976, Bird and Chatarpaul 1986, Blair and Crossley 1988) to return to pre-disturbance levels, depending on the severity of the perturbation. Recolonization of oribatid assemblages may be very slow once locally extinct due to their low dispersal ability (Siepel 1996, Ojala and Huhta 2001) and their low fecundity and slow development (Behan-Pelletier 1999). Additionally, oribatid species composition may remain changed for some time after disturbance; lower numbers of heat and drought intolerant species and more “avoiding” (which migrate into deeper soil) and tolerant species are found in clear cuts (Moritz 1965 in Siepel 1996) due to increased drought extremes. Long-term monitoring of the recovery of forest biodiversity following disturbance is critical to gauge the effectiveness of ecosystem management practices.

A major limitation of most previous studies on microarthropods is the coarse taxonomic resolution (Huhta et al. 1967, Seastedt and Crossley 1981, Seastedt 1984a, Evans et al. 2003, Dress and Boerner 2004, Jabin et al. 2004) or use of generalized functional groups (Lussenhop 1976, Verhoef and Brussaard 1990). Species-level identification is crucial for detailed analysis and accurate interpretation of results (Greenslade 1997). Identification to species allows extraction of relevant biological and ecological information from the literature, reveals differences that cannot be detected at higher taxonomic levels and allows better comparison with other studies (Danks and Winchester 2000). In order to link biodiversity to ecosystem function, knowledge of species-level taxonomy and ecology is essential (Behan-Pelletier and Newton 1999), but studies of litter and soil mites to the species-level in Canada are limited.

Thesis objectives and research questions

The objectives of this thesis are two-fold: to investigate the response of litter and soil oribatid assemblages under various harvesting regimes and to examine the effects of decomposing logs on the spatial distribution of oribatids on the forest floor. An additional chapter asseses the appropriate duration of extraction for the Tullgren-type funnels used in this thesis.

Chapter 2 investigates the changes in litter and soil oribatid mite assemblages in clear cut, partial cut and burned-after-harvest stands compared to uncut forest. Chapter 3 explores the influence of DWM on the spatial distribution of oribatid mite assemblages on the forest floor. For both chapters, analysis will focus on determining changes in relative abundance, species richness and composition of oribatid mites due to either harvesting treatment effects or proximity to DWM respectively. Chapter 4 examines the duration of extraction time for Tullgren-type funnels for the collection oribatid mites from leaf litter.

<u>In Chapter 2, my objective is to examine how various harvesting regimes affect oribatid mite assemblages in mixedwood boreal forest</u>

Specifically, I address the following question:

How do oribatid mite abundance, species richness and composition differ in uncut forest, partial cut (one-third and two-third) forest, clear cut and prescribed burned-after-harvest?

Litter and soil oribatid mites were collected in treatment stands (uncut control, one-third partial cut, two-third partial cut, clear cut and prescribed burn-after-harvest) at the SAFE (sylviculture et aménagement forestiers écosystémique) site in Abitibi, Québec. The null hypothesis is that there is no difference in abundance, species richness and composition of oribatids between treatment stands. An alternative prediction is that oribatid diversity and relative abundance will decrease and species composition will change with increasing disturbance intensity (Abbott et al. 1980, Bird and Chatarpaul 1986, Koivula 2002, Battigelli et al. 2004).

In Chapter 3, my objective is to examine how decomposing logs influence the vertical and horizontal distribution of oribatid mites on the forest floor.

Specifically, I address the following question:

What is the spatial influence of decaying logs on the abundance, diversity and species composition of oribatid assemblages on the forest floor?

Decayed aspen logs were sampled for oribatid mites at three horizontal distances and in four vertical layers. The null hypothesis is that there is no difference in relative abundance, species richness and composition of oribatids in any vertical layer at any distance from decayed logs. An alternative hypothesis is that oribatid diversity will decrease and species composition will change with increasing distance from the logs in all layers; however, the changes will be of a larger degree in the litter layer (Fujikawa 1974, Seastedt and Crossley 1981, Abbott and Crossley 1982, Evans et al. 2003, Jabin et al. 2004).

In Chapter 4, my objective is to test the effectiveness of a Tullgren-type funnel extractor and to record species accumulation with increasing extraction time.

Specifically, I address the following question:

What is the optimal duration of extraction for oribatid mites in mixedwood boreal forest leaf litter using Tullgren-type extractors?

Litter samples were extracted in Tullgren-type funnels for five days, and at the end of each extraction day, the collecting cup was removed and replaced, and the oribatid mites in each cup were identified and enumerated. The null hypothesis is that there is no difference in the accumulation of individuals or species each day, and an alternative hypothesis is that most individuals and species will be collected on the first day of extraction (Crossley and Blair 1991).

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CONNECTING STATEMENT

Chapter 1 provided a review of the literature regarding forest management, decaying wood and oribatid mites. There is little species-level work concerning the effects of ecosystem-based management practices on oribatid assemblages on the forest floor, particularly in eastern Canada. Chapter 2 examines the response of oribatid mite assemblages in eastern boreal forest eight years after the application of different harvesting methods including partial cutting and prescribed burning after harvest.

CHAPTER 2: EFFECTS OF DIFFERENT FOREST MANANGEMENT REGIMES ON ORIBATID MITE ASSEMBLAGES IN EASTERN CANADIAN BOREAL FOREST

Abstract

Ecosystem-based management (e.g. partial cut harvesting) attempts to mimic natural forest dynamics and recreate structural complexity. Many of the abiotic changes that occur in clear cuts have been shown to be absent or reduced in partial cuts, suggesting that less intense harvesting may minimize the impact on forest floor fauna and help maintain soil system biodiversity. I tested how different harvesting regimes affect the diversity, abundance and composition of Oribatida at the sylviculture et aménagement forestiers écosystémique (SAFE) research station located in the Abitibi region in NW Québec. Litter and soil were sampled in June 2006 in the mixedwood boreal forest at SAFE where the following treatments were applied and replicated three times: clear cut harvest, 1/3 partial cut harvest, 2/3 partial cut harvest, prescribed burn (after harvest) and uncut control. Eight years after harvest, clear cutting appears to have had a homogenizing effect on oribatid species composition, and partial cuts had species compositions more similar to the uncut control within their respective blocks; however, burned habitat harboured a relatively distinct assemblage, particularly in soil. There was a change in species richness with even the lowest intensity harvest; in litter, diversity decreased with increasing harvesting intensity but in soil it increased, and for both layers the prescribed burns were significantly different from the other treatments. These results suggest that in less intense disturbances like partial cutting changes in oribatid mite assemblages may be driven more by regional factors but in more severe disturbances such as burn-after-harvest, habitat is so greatly altered that oribatid diversity is more drastically affected.

Introduction

Forest ecosystem function is inextricably tied to its structure, but intensive forest management decreases structural complexity, which reduces species diversity and likely affects ecosystem function (Hansen et al. 1991, Bergeron et al. 1998, Hooper et al. 2005). In an unmanaged forest, naturally occurring cycles of disturbance at different spatial and temporal scales produce a patchwork of stands of variable age and composition (Haila

1994, Bergeron et al. 1998, Perry 1998, Bergeron et al. 2002, Harvey et al. 2002). This results in high habitat heterogeneity and structural complexity that support high diversity (Hansen et al. 1991). Anthropogenic disturbances such as large-scale clear cutting alter forest structure and composition in ways that are very different spatially and temporally than many small and few large natural disturbance events. Clear cut harvesting alters soil structure and forest floor habitat (Battigelli et al. 2004, Kuuluvainen and Laiho 2004), increases soil erosion (Worrell and Hampson 1997, Ballard 2000), contributes to substantial loss of nutrients and food resources (Perry 1998, Ballard 2000), fragments and reduces habitat (Franklin 1989, Hansen et al. 1991, Perry 1998), modifies soil temperature and moisture regimes (Ballard 2000), increases wind and light levels (Esseen et al. 1997, Bourgeois et al. 2004), decreases organic inputs (Covington 1981) and decomposition rates (Blair and Crossley 1988, Prescott et al. 2000), reduces soil fungal biomass (Pietikainen and Fritze 1995) and simplifies ecosystem structure through a reduction of species abundance and diversity (Blair and Crossley 1988, Esseen et al. 1997, Perry 1998). These changes undoubtedly affect litter and soil fauna and influence their functioning as part of the decomposer community.

In boreal forests, several ground-dwelling arthropod taxa show variable responses to clear cutting (e.g. Coyle 1981, Niemelä et al. 1993, Buddle et al. 2006) but effects on soil fauna are largely unknown. Oribatida is the most diverse and abundant suborder of mites in litter and soil (Norton 1985, Norton 1994) and is often considered a useful bioindicator group for soil ecosystem functioning (Behan-Pelletier 1999). Oribatid mites are recognized as vital members of the decomposer community, that is, secondary decomposers that contribute to decomposition (e.g. Seastedt 1984b, Heneghan et al. 1999) and nutrient cycling (e.g. Moore et al. 1988, Setälä and Huhta 1991) by mediating microbial populations through grazing activity and by fragmenting organic material, thus facilitating further decomposition (Behan-Pelletier 1999). Oribatid mite assemblages have been shown to be negatively impacted by clear cutting in the short-term, usually due to microclimatic changes. In mixedwood forest, Bird and Chatarpaul (1986) demonstrated a reduction in oribatid abundance and a shift in species dominance in the first two years after clear cutting but did not find a change in species composition. In the southern Appalachians, immediately after and for up to eight years after clear cutting there was a reduction in oribatid mite abundance and a shift in species dominance patterns (Abbott et al. 1980, Blair and Crossley 1988), but after 21 years, oribatid density and morphospecies richness recovered, exceeding that in the control forest (Heneghan et al. 2004). In contrast, Huhta et al. (1967) showed a slight increase in oribatid mean density immediately after clearcutting, which then significantly decreased eight years later (Huhta et al. 1969). Changes in oribatid mite assemblages after clear cut harvesting may persist for many years (Blair and Crossley 1988, Siepel 1996), but there are very few long-term studies to verify this.

Ecosystem-based management is a coarse filter approach that attempts to emulate natural disturbance with the goals of maintaining ecosystem processes and preserving biodiversity under the assumption that species have evolved under natural disturbance regimes of varying intensity and frequency and therefore will be adapted to occasional habitat disruption at a landscape scale (Hunter 1993, Haila 1994, Fries et al. 1997, Armstrong 1999, Bergeron et al. 2002, Harvey et al. 2002). By preserving forest biodiversity, ecosystem stability and essential ecosystem processes may also be maintained, ensuring long-term ecological sustainability (Bengtsson et al. 2000, Loreau et al. 2001, Loreau et al. 2003, Hooper et al. 2005). Alternatives to clear cutting, such as partial cutting, are thought to spatially emulate natural disturbance by maintaining some structural heterogeneity from the pre-harvest stand through the retention of live trees, snags and logs in clear cuts (Franklin 1989, Hansen et al. 1991, Hunter 1993, Bergeron et al. 1998, Harvey et al. 2002). Prescribed burning of clear cuts is thought to imitate natural fire and create some of the abiotic conditions (e.g. light and temperature regimes) and structural heterogeneity associated with burned stands (Fries et al. 1997, Bergeron et al. 1998).

Compared to clear cuts, partial cutting has been shown to decrease canopy openness, and therefore solar radiation (Brais et al. 2004a), decrease N mineralization and nitrification rates (Prescott 1997, Lindo and Visser 2003), increase decomposed CWD (Brais et al. 2004a), increase habitat structural complexity (Esseen et al. 1997) and maintain more similar soil pH, microbial biomass (Siira-Pietikainen et al. 2001) and soil temperature and moisture levels (Barg and Edmonds 1999) compared to uncut sites. However, other authors have found no difference in litter decomposition rates (Prescott 1997), N availability, soil pH (Lapointe et al. 2006) or microbial biomass (Jerabkova et al. 2006) among clear cut, partial cut and uncut stands. These studies suggest that less intense harvesting may often minimize some microhabitat changes potentially important to ground-dwelling arthropods.

Recent studies have shown variable effects of partial cutting, or some variation thereof, on several arthropod taxa; mycetophilid fly diversity increased (Økland 1994) while syrphid diversity decreased (Deans et al. 2007) in partial cut forest, ant and spider (Yi and Moldenke 2005) and fungivorous Collembola (Siira-Pietikainen et al. 2003) mean abundances increased with thinning intensity, and carabid beetle assemblages in thinned forest were more similar to uncut stands than to clear cuts (Koivula 2002). In more intensely managed oak-beech forest, Cancela da Fonseca (1990) showed a loss of the dominant status of Oribatida and a decrease in their density, and in a partially cut hardwood stand, Abbott et al. (1980) showed a moderate level of similarity in dominance ranks among oribatid species compared to a control, but similarity between the partial cut and clear cut was significantly different. Lindo and Visser (2004) found microarthropod suborder abundance in partial cut retention patches to be more similar to uncut conifer forest than to clearcuts, but Peck and Niwa (2005) showed that thinned late successional conifer stands had significantly lower oribatid mite abundance on the forest floor than unthinned stands. These studies suggest that less intense harvesting may have less impact on oribatid mites; however, work at the species-level is lacking in eastern boreal forest.

Managed forests lack variability in age structure and stand composition due in part to fire suppression (DeLong and Tanner 1996, Esseen et al. 1997, Bergeron et al. 1998, Armstrong 1999). Prescribed or controlled burning is a management strategy used to reduce fuel buildup, control competing understory vegetation and prepare seedbeds for replanting (Vlug and Borden 1973, Pietikainen and Fritze 1995, Brennan et al. 2006). It can also be used in an attempt to restore natural forest structure and to reintroduce fire to the ecosystem (Fries et al. 1997, Bergeron et al. 1998, Siitonen 2001, Brennan et al. 2006). Impacts of prescribed burning include changes in nutrient availability (Prescott et al. 2000, Frey et al. 2003), large nutrient loss through the volatilization of N and S and fly-ash (Ballard 2000), increased soil pH (Ahlgren and Ahlgren 1965, Pietikainen and Fritze 1995) and loss of vegetation, litter and slash cover, which increases soil surface temperature and moisture fluctuations (Vlug and Borden 1973, Ballard 2000).

The impacts of prescribed burning after clear cutting are variable for ground-dwelling arthropod taxa; carabid beetle (Beaudry et al. 1997, Martikainen et al. 2006) and spider (Abbott et al. 2003) diversity was higher in burned clear cuts, but collembolan diversity and abundance decreased initially and species composition changed (Greenslade 1997). Oribatid abundance was significantly lower in burned stands (Seastedt 1984a), particularly in more frequently burned sites (Dress and Boerner 2004) and in burned-after-harvest sites (Vlug and Borden 1973). However, five years after controlled burning in clear cuts, Berch et al. (2007) showed no difference in oribatid density compared to an unburned clear cut, but species richness was lower in the burned clear cut. In contrast, Lussenhop (1976) found that mite (excluding Oribatida) and Collembola densities increased for several years after fire in repeatedly-burned prairie grassland.

The objective of this study was to test the effects of different forest management practices on oribatid mite assemblages (abundance, species richness and composition) in mixedwood boreal forests of eastern Canada. To address this objective, I had the following research question: How do oribatid mite assemblages differ among uncut forest, partial cut (one-third and two-third) forest, clearcut and prescribed burned-after-harvest?

Methods

Study area

The study was conducted in Phase 1 of the sylviculture et aménagement forestiers écosystémique (SAFE) research site located in the Abitibi region of Québec's northwestern boreal forest (48°86'N-48°32'N, 79°19'W-79°30'W) (Fig. 2.1). Phase 1 of

SAFE consists of a cohort of aspen (*Populus tremuloides* Mchx.) dominated stands (67%) originating from a fire in 1923 (Dansereau and Bergeron 1993, Brais et al. 2004b). Other tree species in the study area include grey pine (*Pinus sabiniana* Dougl.; 16%) and eastern white cedar (*Thuja occidentalis* L.; 4%); dominant shrubs include beaked hazel (*Corylus cornuta* Marsh.) and mountain maple (*Acer spicatum* Lam.), and the dominant herbaceous plants are wild sarsaparilla (*Aralia nudicaulis* L.) and big-leaved aster (*Aster macrophyllus* L.) (Brais et al. 2004b). Mean annual temperature in the area is 0.8ºC, with a June mean temperature of 14.3ºC, and total annual precipitation is 889.8 mm (Environment Canada 2003). Soils in the area are Grey Luvisols (Canada Soil Survey Committee 1987) with a high clay content (>75%), and the forest floor is classified as a thin mor, 2-7 cm thick (Brais et al. 2004a).

In the winter of 1998-1999, the following treatments were applied and replicated three times as a randomized complete block design: clear cut harvest (CC), one-third (30% merchantable basal area removed) partial cut harvest (1/3PC), two-thirds (61% merchantable basal area removed) partial cut harvest (2/3PC) and no harvest (uncut control, CTL). A prescribed burn-after-clear cut harvest (BRN) was applied in August 1999. These treatment units ranged from 1 to 2.5 ha, and in all treatments, harvesting was done manually (Brais et al. 2004a, b).

Sampling

Over three days in mid-June 2006, I took three samples each of litter and soil in each of the five treatments in each of the three blocks, for a total of 45 samples for each layer. The three samples taken in each treatment unit were pooled for analysis to avoid pseudo-replication. Litter (i.e. freshly fallen leaves, needles, twigs, stems and bark (Hoover and Lunt 1952)) was haphazardly collected along 25 m transects (three per treatment unit), gently mixed and a one litre sub-sample was taken in order to obtain samples representative of the entire unit. At each transect, a soil core (6 cm diameter) of the H layer (i.e. well decomposed organic matter of unrecognizable origin (Hoover and Lunt 1952)) was also taken to the depth of the mineral soil horizon. All samples were taken at approximately the same time of day to minimize abiotic and vertical migratory fluctuations (Seastedt and Crossley 1981). Immediately after collection, samples were placed into individual cloth bags and kept in a cooler until extraction later the same day. All microarthropods were extracted in a nearby laboratory using Tullgren-type funnels for five days at an average temperature of 32ºC for litter and 36 ºC for soil (Marshall 1972, Crossley and Blair 1991, Edwards 1991, Chapter 4). Extraction funnels such as these use a heat source to create a temperature and humidity gradient in the substrate that forces active soil fauna to migrate downward to avoid desiccation. The animals move down through the sample, eventually falling out of the funnel into a collection vial below. Tullgren-type extractors produce 98% extraction efficiency for adult oribatid mites (Marshall 1972), and it is the preferred extraction method for organic soils, such as in forests (Crossley and Blair 1991, Edwards 1991). Oribatids were preserved in 75% ethanol. Following extraction, the dry mass of each litter and soil sample was recorded.

Species identification

All adult Oribatida were identified to species or morphospecies using a Leica DM2500 compound-light microscope, a Nikon SMZ1500 dissecting microscope and published and unpublished taxonomic material by Marshall et al. (1987), Niedbala (2002), Weigmann (2006) and Norton and Behan-Pelletier (in press). Species identifications were verified by V. Behan-Pelletier at the Canadian National Collection of Insects (CNC) with Agriculture and Agri-Food Canada in Ottawa, Ontario, Canada, and a voucher collection has been deposited at the Lyman Entomological Museum in Ste. Anne de Bellevue, Québec, Canada.

Statistical analyses

Due to the considerable difference in numbers of individuals collected in each habitat type (Table 2.1), litter and soil were analyzed separately. To compare relative abundance and raw species richness of oribatid mites among the five harvesting treatments (clear cut, one-third partial cut, two-third partial cut, burn, control), an Analysis of Variance (ANOVA) for a randomized complete block design was done using mixed model procedures in SAS software v. 9.1 (SAS Institute 2003). Tests of normality (Shapiro-Wilk test) and homogeneity of variance (likelihood ratio test) were also conducted, and data were log transformed ($x' = \log(x+1)$) if necessary. Tukey's H.S.D. *post hoc* test ($\alpha=0.05$) was used to compare means.

Rank-abundance curves were used to examine changes in dominance of the most commonly collected oribatid species among harvesting treatments. For each curve, the changes in relative abundance in each treatment of the top 25 species in litter and top 20 species in soil were ranked according to their abundance in the CTL samples, allowing an effective assessment of the patterns of species diversity for each treatment.

Indicator species analysis was conducted using the software PC-ORD v. 4.17 (McCune and Mefford 1999) to determine the strength of a species' association with a particular harvesting treatment (Dufrêne and Legendre 1997). This method uses within-species relative abundance and occurrence comparisons to measure the association between a species and a habitat type, independent of other species (Dufrêne and Legendre 1997). Singletons were removed from analysis to reduce the importance of rarely collected species (Dufrêne and Legendre 1997), and a Monte Carlo (randomization) test with 1000 permutations was used to determine the statistical significance of the maximum indicator value calculated for each species.

Individual-based rarefaction was used to compare standardized estimates of oribatid species richness among harvesting treatments using EcoSim software v. 7.72 (Gotelli and Entsminger 2006). With rarefaction analysis, species richness is standardized to the largest sample size common to all study sites by repeatedly and randomly re-sampling individuals from the total data set allowing for a reasonable comparison of diversity among treatments with unequal sampling effort (Gotelli and Colwell 2001). Rarefaction analysis provides estimates of variance allowing for meaningful statistical comparisons and shows rate of accumulation of new species with additional samples, which determines if overall sampling effort was sufficient to make such comparisons (Buddle et al. 2005). Individual-based rarefaction is most appropriate when examining overall assemblage species richness and when sampling effort is unequal among treatments or study sites (Gotelli and Colwell 2001, Buddle et al. 2005). Parameters used included number of iterations set at the maximum number of individuals and abundance levels that increased incrementally by 100 individuals for litter and by 25 individuals for soil.

Differences in oribatid species composition among the harvesting treatments were analyzed using non-metric multi-dimensional scaling (NMS) ordination using the software program PC-ORD v. 4.17 (McCune and Mefford 1999). NMS ordination is an indirect gradient analysis that ordinates samples according to co-variation and association among species and does not assume linear relationships among variables (McCune and Grace 2002). Data were log-transformed ($x' = \log(x+1)$) to decrease the weight of the more abundant species. A detrended correspondence analysis (DCA) was used as the starting configuration for subsequent NMS ordinations to reduce stress and avoid local minima (Work and McCullough 2000). A preliminary six-dimensional NMS ordination was run to determine the number of dimensions for the final analysis and to evaluate stress reduction. Parameters used included Sorensen (Bray-Curtis) distance measure, 200 iterations, 50 permutations with real data and 50 permutations with randomized data (Monte Carlo test). A final NMS analysis was then conducted with these same parameters using the recommended number of dimensions.

Multi-response randomized block permutation procedures (MRBP) were used on the log-transformed data to determine statistically significant differences in composition among harvesting treatments. MRBP is a permutation method similar to multi-response permutation procedures (MRPP) in that it is not restrained by unrealistic assumptions of normality and homogeneity of variance; however, it is more appropriate than MRPP for the analysis of a randomized complete block design (Zimmerman et al. 1985; Mielke 1991; McCune and Mefford 1999). Groups were designated by harvesting treatment, with blocks as the blocking variable, and differences in composition were assessed for all groups as well as pair-wise. Parameters used include a Euclidian distance measure, a Monte Carlo test with 1000 permutations, and blocks were medially aligned (McCune and Mefford 1999). The MRBP test statistic is given as a p-value along with the chance-corrected within-group agreement (A), which describes within-group homogeneity compared to random expectation as well as relative effect size, independent of sample size. Values for *A* equal 1 when there is perfect within-group agreement, are equal to 0 when heterogeneity is as expected by chance, and less than 0 when there is more heterogeneity than expected by chance (Mielke 1991). When a potential block effect became apparent, MRPP analysis was used to determine significant differences in species composition among the three blocks by using the blocks to define the grouping variable and a Sorensen (Bray-Curtis) distance measure (Zimmerman et al. 1985).

Results

A total of 21, 382 adult oribatid mites was collected and identified to 87 species (Table 2.1, Appendix 2.1). Of these, 18, 399 individuals in 81 species were collected from litter habitat and 2, 983 in 47 species came from soil, with 41 species occurring in both layers and eight species occurring exclusively in soil. Densities averaged approximately 408, 866 individuals m^{-3} in litter and 468, 896 individuals m^{-3} in soil. The greatest number of oribatids occurred in the clear cut (CC) treatment, and the fewest were collected in the controlled burn (BRN). In terms of raw species richness, the most species were collected in the uncut control (CTL) and the fewest were collected in the BRN. Three species, *Oppiella nova* (Oudemans 1902), *Scheloribates pallidulus* (Koch 1841) and *Tectocepheus velatus* (Michael 1880) each accounted for over 10% of the total abundance and together accounted for over 58% of all oribatid mites collected. Eleven species were represented by one individual (singletons) and three species were represented by two individuals (doubletons) collected throughout the study.

Relative abundance of oribatids in litter habitat was not affected by harvesting treatments, nor was it different among treatments in the soil layer (Table 2.2). There was a significant effect of harvesting treatment on raw species richness in litter habitat, which was primarily due to lower diversity in the BRN treatment, but there was no significant difference in the raw species richness among treatments in soil (Table 2.2). Rank-abundance curves, representing the 25 most frequently collected species in the litter (Fig. 2.2) and top 20 species in soil (Fig. 2.3) in each treatment and ranked according to abundance in the CTL sites, showed changes in the patterns of oribatid diversity with treatment. In litter, there was little change in species ranking with increasing disturbance, exception in the BRN in which there was a loss of *Carabodes polyporetes* Reeves 1991 and a decrease of *Oribatodes mirabilis* Banks 1895. As well, there was a shift in the dominant species with increasing disturbance, from *O. nova* in the CTL to *S. pallidulus* and *T. velatus* in the BRN. In soil, the four most abundant species in the CTL remained consistently so with increasing disturbance except for the disappearance of *Ceratozetes cuspidatus* Jacot 1939 in the BRN. Changes in abundance patterns in the partial cuts and clear cut were inconsistent; however, three low ranking species, *Fuscozetes fuscipes* (Koch 1844), *Oppia nr. nitens* and *Atropacarus striculus* (C.L. Koch 1835), increased considerably in number in the BRN. In the litter layer, there was one significant indicator species for the 2/3PC (*Banksinoma l. canadensis* Fujikawa 1979; denoted with (*) in Appendix 2.1), one for the CC (*F. fuscipes*), and one for the BRN (*Phthiracarus boresetosus* Jacot 1930). In soil, there were two significant indicator species for the CC (*Phthiracarus longulus* (Koch 1841) and *Quadroppia quadricarinata* (Michael 1885)), and one (*T. velatus*) for the BRN.

Rarefaction curves were done separately for litter and soil due to the large difference in numbers of mites collected in each habitat type. Rarefaction curves indicate that in litter, there was no significant difference in species richness among harvesting treatments, with the exception of the BRN treatment, in which rarefied species richness was significantly lower (Fig. 2.4). In soil, CTL treatment had significantly lower diversity then the clear cut and both partial cut treatments, while the BRN treatment had significantly higher species richness than all other treatments (Fig. 2.5). There was no significant difference in species richness among the clear cut and partial cut (1/3PC and 2/3PC) treatments in soil. All curves approach an asymptote, which indicates sampling effort was adequate, that is, accumulation of new species with more individuals would be small.

NMS ordination was used to analyze differences in oribatid species composition among the harvesting treatments for both litter and soil. For transformed litter data, a two-dimensional solution was deemed optimal and explained 91.6% of the variation in the data, with axis 1 explaining the majority (Fig. 2.6). The only treatment that tends to separate from the others is the BRN, and there appears to be some clustering of the CC treatments, although MRBP analysis does not indicate any significant effect of harvesting treatment on oribatid species composition (results not shown). There does however, appear to be a clustering of samples based on their respective blocks, and MRPP analysis using blocks as the grouping variable indicates significant differences in species composition between each possible pair of blocks as well as overall (Table 2.3). In soil habitat (Fig. 2.7), a three-dimensional solution was deemed optimal and explained 89% of the variation. Addition of the third axis does not change interpretation; therefore, it is excluded and the two axes representing the most variation are presented here. There appears to be very little separation among the CTL, CC and PC treatments; however, the BRN again appears to have a distinct assemblage, although the only significant result indicated by MRBP was that of all treatments combined (*A* statistic = 0.05, p= 0.02). As well, there is again a separation of treatments by their respective blocks, and MRPP confirms significant compositional differences between pairs of blocks and among all three blocks (Table 2.3).

Discussion

Oribatid mite assemblages were affected in various ways by different harvesting practices in eastern boreal forest, although burning clear cuts had the greatest effect on mites. There is evidence to suggest a homogenizing effect of clear cutting on oribatid litter assemblages, and that regional factors (i.e., block effects on a spatial scale of 1-10 km) are also important in structuring oribatid assemblages. Furthermore, partial cuts had more similar species composition to the uncut control within their respective blocks, suggesting factors other than harvesting treatment are shaping oribatid assemblages within a region. There was a change in rarefied species richness with even the lowest intensity harvest; in litter, diversity decreased with increasing harvesting intensity but in soil it increased, and for both layers the prescribed burns were significantly different from the other treatments. These results suggest that in less intense disturbances like partial cutting changes in oribatid mite assemblages may be driven more by regional factors, but in more severe disturbances such as burn-after-harvest, habitat is so greatly altered that oribatid diversity is more drastically affected. It is important to note that stronger overall effects of harvesting treatment may have been detected with increased sample size.

Many studies have shown that clear cutting negatively affects microarthropods like oribatids in the short-term. Most show that immediately after and for up to eight years after clear cutting, there is a reduction in oribatid mite abundance and a shift in species dominance patterns (Abbott et al. 1980, Bird and Chatarpaul 1986, Blair and Crossley 1988, Donegan et al. 2001, Lindo and Visser 2004); however, Heneghan et al. (2004) found that 21 years after clear cut harvesting, oribatid density and morphospecies richness recovered, exceeding that in the control forest. The present study showed no differences in relative abundance and some change in species richness and composition among harvesting treatments eight years after harvest; therefore, oribatid response to clear cutting is likely similar to spiders and carabid beetles in that most species can recover to near pre-disturbance levels within a relatively short period of time (McIver et al. 1992, Niemelä et al. 1993, Buddle et al. 2006).

There appeared to be a homogenizing effect of clear cutting on oribatid composition, and composition in BRN sites is somewhat distinct. As well, diversity in the BRN sites is significantly different from other treatments. More severe disturbances like burn-after-harvest, and to a lesser degree clear cutting, appear to have changed oribatid assemblages more than the other treatments possibly because some physiological tolerances for changes in abiotic factos like pH (van Straalen and Verhoef 1997) or soil moisture (Siepel 1996) has been surpassed, and eight years was not sufficient time for oribatid populations to recover completely to pre-disturbance levels. In the BRN sites, species richness was significantly lower in the litter layer but significantly higher in the soil, indicating the litter habitat may be more affected by fire than soil even eight years later, which suggests that oribatids that rely primarily on the litter layer are less able to recover. Furthermore, some oribatid species may be more severely affected than others, and this is supported by the changes in species-specific abundance among treatments.

My findings are consistent with other studies that show changes in diversity for several years after prescribed fire of various intensities and frequencies (Huhta et al. 1967, Vlug and Borden 1973, Greenslade 1997, Brand 2002, Dress and Boerner 2004). Several studies have also found microarthropod assemblages in less intensively harvested stands to be more similar to uncut forest than to clear cuts (Abbott et al. 1980, Siira-Pietikainen et al. 2003, Lindo and Visser 2004); however, until now, very little species-level work has been done for oribatids under different harvesting regimes. Similar to beetles (Niemelä et al. 1993, Martikainen et al. 2006), partial cutting may represent a balanced environment for both generalist species and those relying on more mature forest because overall there was little difference in the oribatid assemblages between the partial cuts and uncut forest.

Clear cut harvesting has been shown by many to alter forest floor habitat (Battigelli et al. 2004, Kuuluvainen and Laiho 2004), decrease organic input (Covington 1981), modify soil temperature and moisture regimes (Ballard 2000) and reduce soil fungal biomass (Pietikainen and Fritze 1995), all of which are thought to have a negative impact on microarthropods like oribatids. Some species may be differently affected by the same factors (Huhta et al. 1967), contributing to the compositional differences and species-specific responses found in the present study. Both partial cut treatments had similar species composition to each of their respective uncut controls, but the clear cuts, although not significantly different, did not, suggesting partial cutting had less effect on oribatid biodiversity after eight years than clear cutting. As well, oribatid biodiversity in partial cuts appeared to be unrelated to the amount retained (one-third or two-third), so perhaps harvesting, provided it is not a 100% harvest, may in time support an oribatid assemblage similar to that in an uncut forest. Microclimatic factors may be more similar (Prescott 1997, Brais et al. 2004a) and/or there may be greater habitat heterogeneity in partially harvested sites than in clear cuts (Marra and Edmonds 1998, Kuuluvainen and Laiho 2004). Oribatid relative abundance and species richness were not significantly different among harvesting treatments with the exception of the BRN; in the BRN, there was some change in species-specific abundance and species richness was significantly lower in the litter layer but significantly higher in the soil. In the present study, there was generally less litter on the forest floor in the BRN sites than the other harvesting treatments (pers. obs.), which may explain the significantly lower diversity in litter habitat and distinct composition in the prescribed burn-after-harvest (Donegan et al. 2001). Burning can also shift microarthropod distribution downward (Petersen and Luxton 1982), which may explain the higher richness in soil; however, in contrast to our results, Berch et al. (2007) showed lower oribatid diversity in soil in burned clear cuts compared to unburned clear cuts. Therefore, although overall abundance may not be affected, a severe disturbance such as burning-after-harvest changed oribatid diversity eight years later. It is unclear how long any post-fire changes may persist, although it has been suggested that it may take up to 27 years for assemblages to return to pre-disturbance levels (Karppinen 1957 in Huhta et al. 1967).

Although there are few species-specific changes among the harvesting treatments, there was a shift in the dominant species and the relative abundances of a small number of species was either reduced or increased in more disturbed sites compared to the control. These results suggest that although a few species are unable to persist in severely disturbed sites, such as burned-after-harvest, the majority of oribatids can maintain their populations eight years later. Many oribatid species are estimated to be capable of dispersing only 30 m in 30 years (Ojala and Huhta 2001); therefore, most species are likely able to survive the initial disturbance of harvesting and/or prescribed burning within the area. Their life history traits (e.g. long life, low metabolic rate) may in fact provide a buffer in an unpredictable environment (Norton 1994) and enable survival after disturbance.

Species composition of the harvesting treatments was more similar within blocks than among blocks, suggesting that area or region might have more of an effect on oribatid assemblage composition than harvesting regime. Large-scale habitat modification may not be as relevant to oribatid mites as smaller scale, local variation; oribatids may be able to find suitable microhabitats regardless of what happens to their macrohabitat. Oribatid species diversity has been shown to be positively correlated with microhabitat structural diversity (Anderson 1978), which is on a much smaller scale than stand-level. As well, regional factors, like topography or soil properties, could have a greater influence in structuring oribatid assemblages than harvesting by contributing to microhabitat availability, which can influence compositional structure, especially for species with limited dispersal, like oribatids. Before harvesting treatment application, analysis of soil characteristics revealed that block 2 differed from the other two blocks with respect to several measured soil parameters (Brais et al. 2004b), which might account for the distinct composition of block 2 as compared to the other blocks. The scale of study and the contribution of various environmental factors are important considerations when studying the effects of disturbance on oribatid assemblages in the boreal forest.

Conclusions

It is not yet known whether any of the new ecosystem-based management approaches will have the desired ecological impact. Studies such as this one provide species-level information regarding the effects of these practices on biodiversity using an ecologically important taxon, oribatid mites. These results can help focus management guidelines to improve their effectiveness in conserving soil ecosystem biodiversity in managed forests.

Clear cut harvesting and prescribed burning after harvest changed, but did not significantly affect, oribatid diversity and composition eight years after harvesting, but assemblages in partial cuts were more similar to uncut forest. The results of this study showed that oribatid species composition may not be as affected by partial cutting as compared to clear cutting, and for less intense harvesting practices, regional factors may have a greater influence in structuring oribatid assemblages than harvesting regime; however, in order to determine the efficacy of practices that emulate natural forest dynamics, long-term monitoring of faunal recovery is necessary.

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Table 2.1: Relative abundance and raw species richness of oribatid mites in litter and soil habitat collected from control (CTL), one-third partial cut (1/3PC), two-third partial cut (2/3PC), clear cut (CC) and controlled burn (BRN) sites.

Treatment	Layer	Relative abundance	Raw species richness
CTL	Litter	3500	61
	Soil	728	20
1/3PC	Litter	3622	58
	Soil	733	28
2/3PC	Litter	3155	59
	Soil	646	25
CC	Litter	4834	59
	Soil	525	24
BRN	Litter	3288	51
	Soil	351	27

Table 2.2: Results from ANOVA tests for the effects of harvesting treatment (control (CTL), one-third partial cut (1/3PC), two-third partial cut (2/3PC), clear cut (CC) and controlled burn (BRN) on oribatid mite relative abundance and raw species richness in litter (a) and in soil (b). Data are means ±SE (n=3), and *post hoc* comparisons (Tukey's H.S.D. test (α=0.05)) are represented by different letters.

(a)

	Treatment						
	CTL	1/3PC	2/3PC	CC	BRN	$F_{4,8}$	p-value
Mean oribatid relative abundance in litter	6.76 ±0.62	6.86 ±0.52	6.79 ±0.41	7.23 ±0.39	6.62 ±0.67	0.93	0.49
Mean oribatid raw species richness in litter	3.73 ±0.13a	3.63 ±0.15a	3.68 ±0.05a	3.77 ±0.08a	3.44 ±0.14b	4.44	**0.03**

(b)

	Treatment						
	CTL	1/3PC	2/3PC	CC	BRN	$F_{4,8}$	p-value
Mean oribatid relative abundance in soil	5.36 ±0.41	5.22 ±0.61	5.36 ±0.14	5.11 ±0.24	4.71 ±0.26	0.64	0.65
Mean oribatid raw species richness in soil	2.59 ±0.15	2.74 ±0.18	2.65 ±0.13	2.75 ±0.06	2.67 ±0.12	0.27	0.89

Table 2.3: MRPP results for block effect on oribatid species composition in litter (a) and wood/soil (b). Significant differences (p-values) are in bold.

(a)

Comparison	p-value	*A* statistic
All blocks	**0.0008**	0.137
Blocks 1 and 2	**0.029**	0.077
Blocks 1 and 3	**0.018**	0.066
Blocks 2 and 3	**0.007**	0.178

(b)

Comparison	p-value	*A* statistic
All blocks	**0.003**	0.071
Blocks 1 and 2	**0.013**	0.081
Blocks 1 and 3	**0.043**	0.044
Blocks 2 and 3	**0.041**	0.041

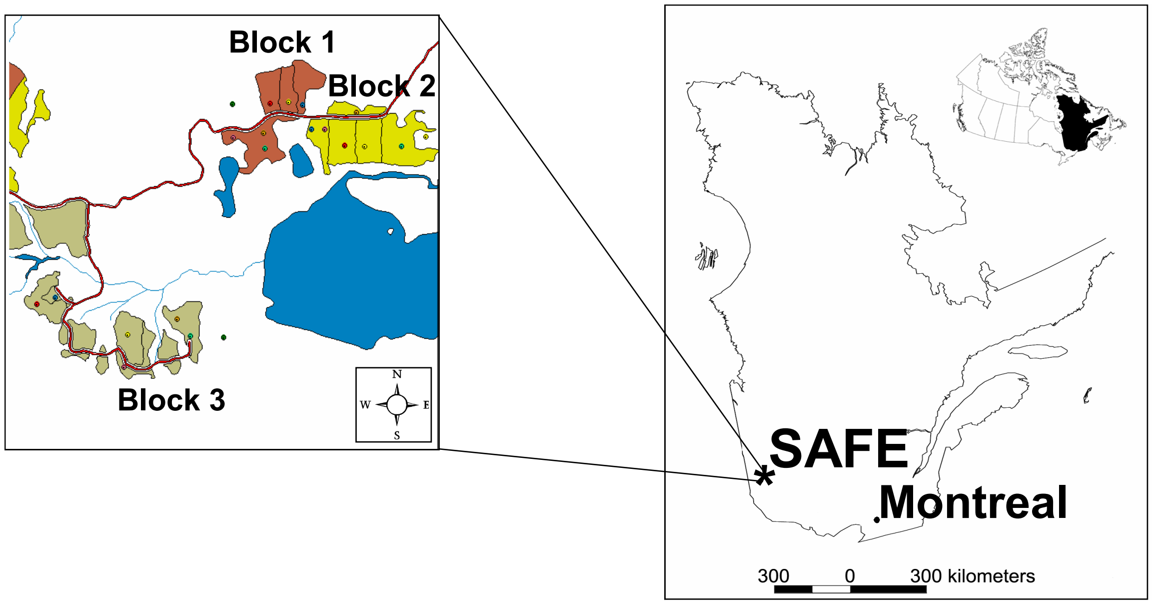

Figure 2.1: Location of study area at the sylviculture et aménagement forestiers écosystémique (SAFE) research site in Abitibi Québec. Schematic of SAFE taken from Brais et al. 2004a.

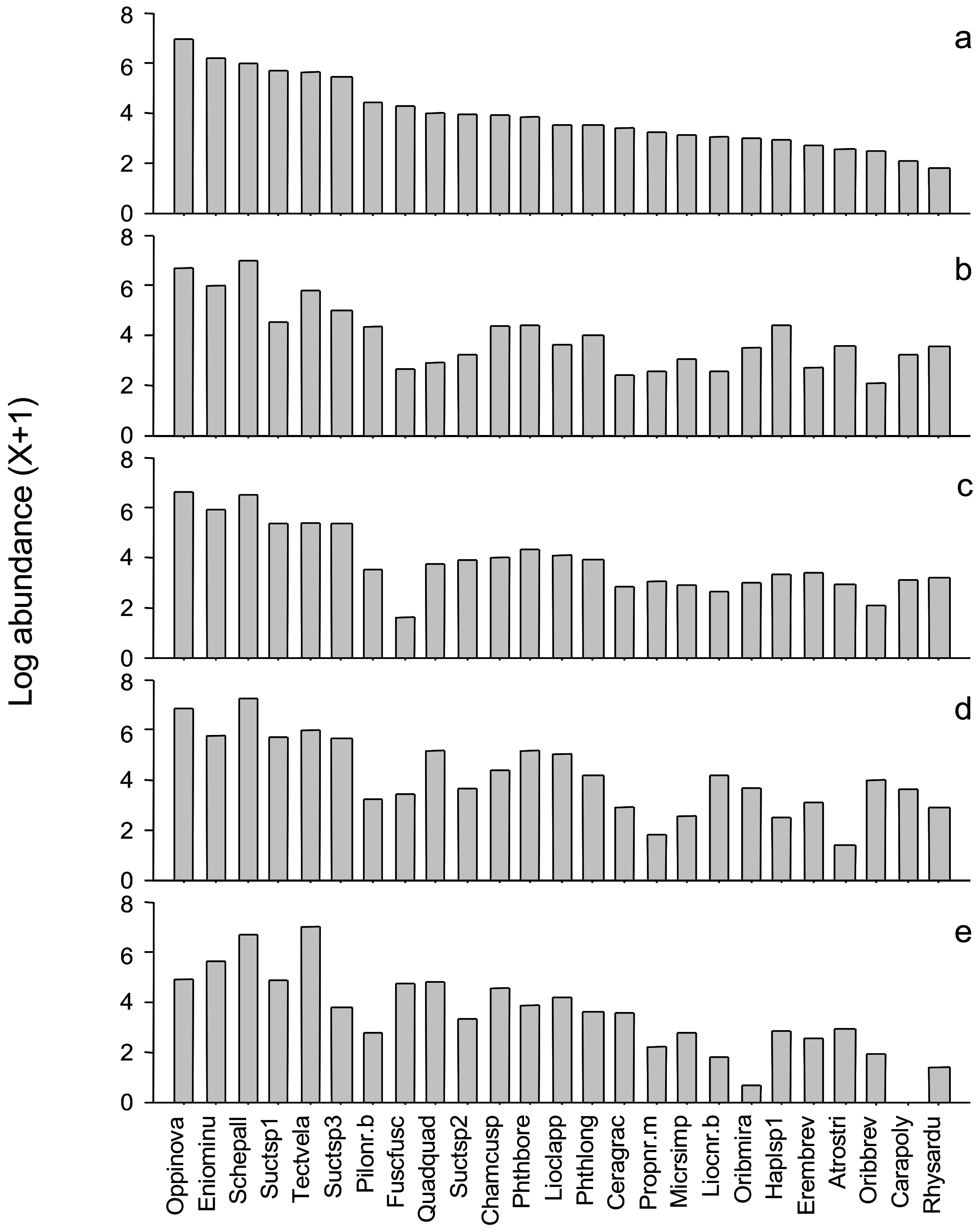

Figure 2.2: Rank abundance curves for oribatid mites collected in litter from (a) control (CTL), (b) one-third partial cut (1/3PC), (c) two-third partial cut (2/3PC), (d) clear cut (CC) and (e) controlled burn (BRN) sites. Species are ranked from most to least common collected according to their abundance in the CTL samples, and ranking is the same for all five graphs. Species codes with full names are found in Appendix 2.1.

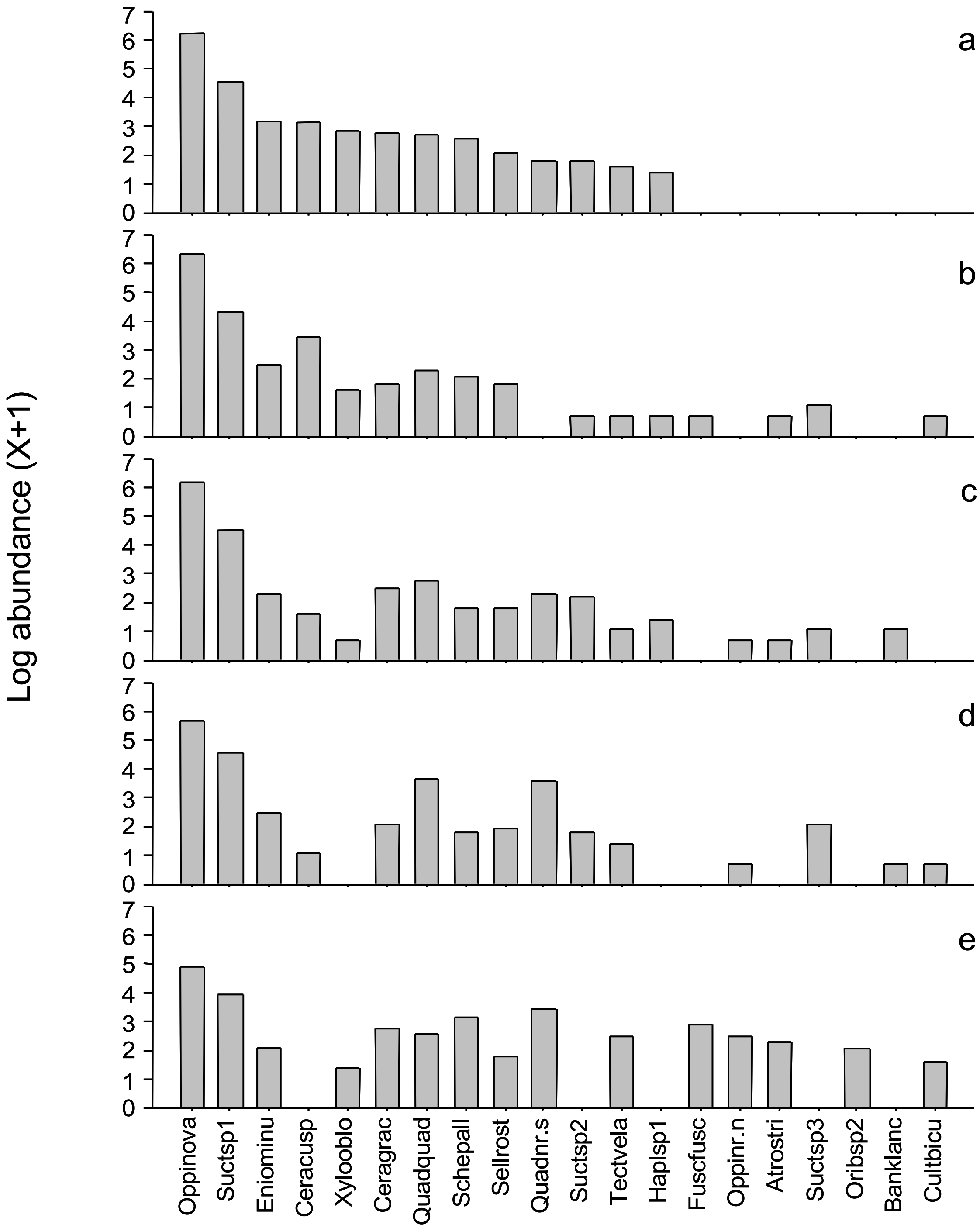

Figure 2.3: Rank abundance curves for oribatid mites collected in soil from (a) control (CTL), (b) one-third partial cut (1/3PC), (c) two-third partial cut (2/3PC), (d) clear cut (CC) and (e) controlled burn (BRN) sites. Species are ranked from most to least common collected according to their abundance in the CTL samples, and ranking is the same for all five graphs. Species codes with full names are found in Appendix 2.1.

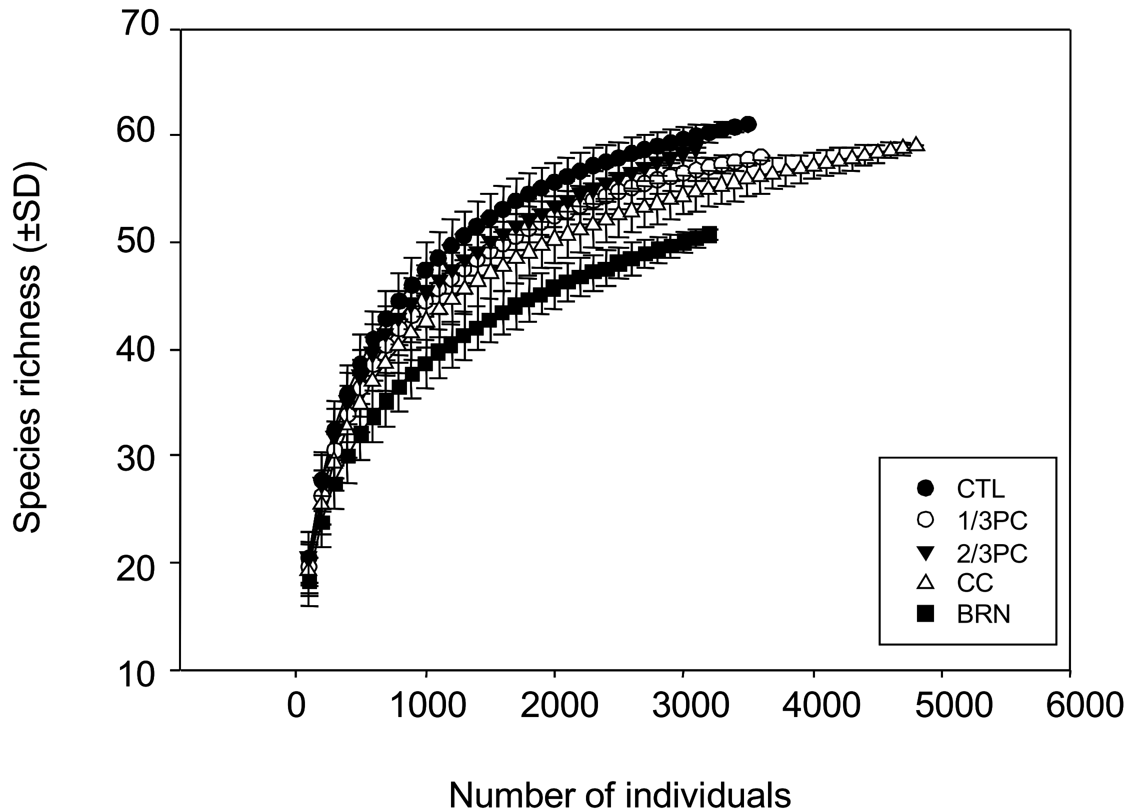

Figure 2.4: Rarefaction curves showing estimated species richness (±SD) for oribatid mites collected in litter from control (CTL), one-third partial cut (1/3PC), two-third partial cut (2/3PC), clear cut (CC) and controlled burn (BRN) sites. Analysis is based on three pooled samples (three transects each) per treatment and 81 species.

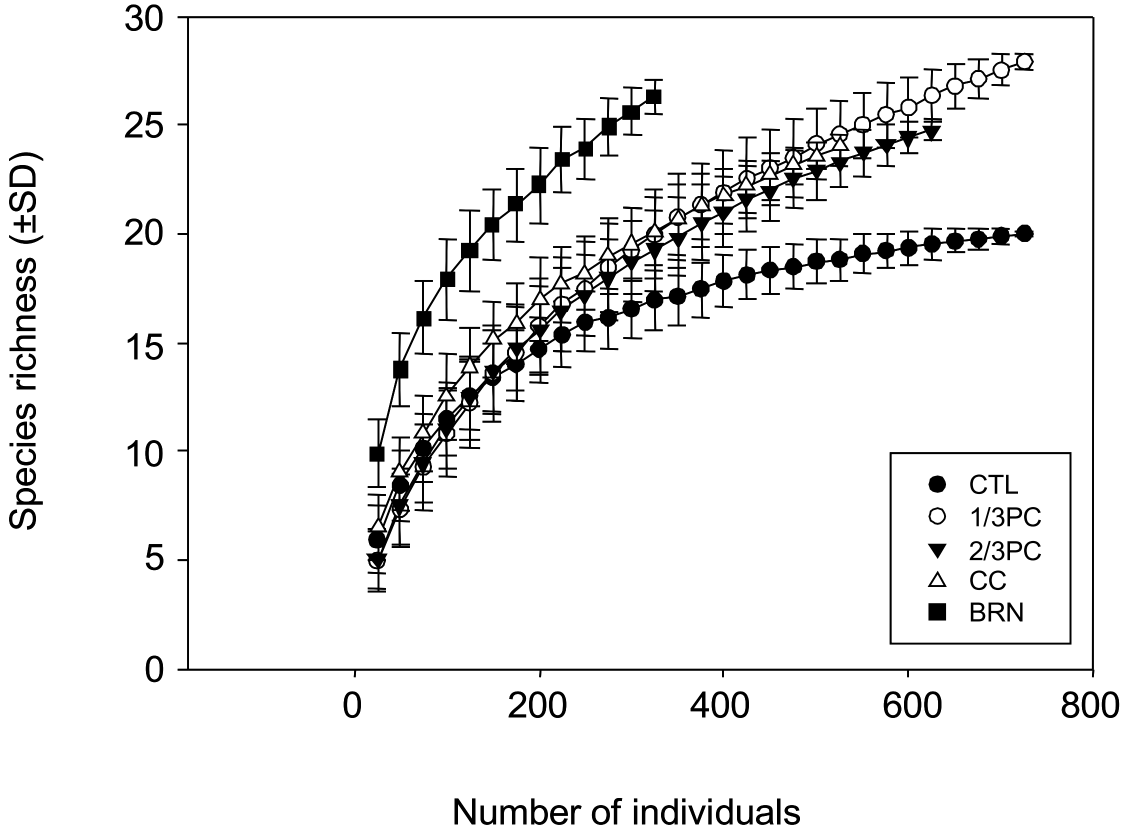

Figure 2.5: Rarefaction curves showing estimated species richness (±SD) for oribatid mites collected in soil from control (CTL), one-third partial cut (1/3PC), two-third partial cut (2/3PC), clear cut (CC) and controlled burn (BRN) sites. Analysis is based on three pooled samples (three transects each) per treatment and 47 species.

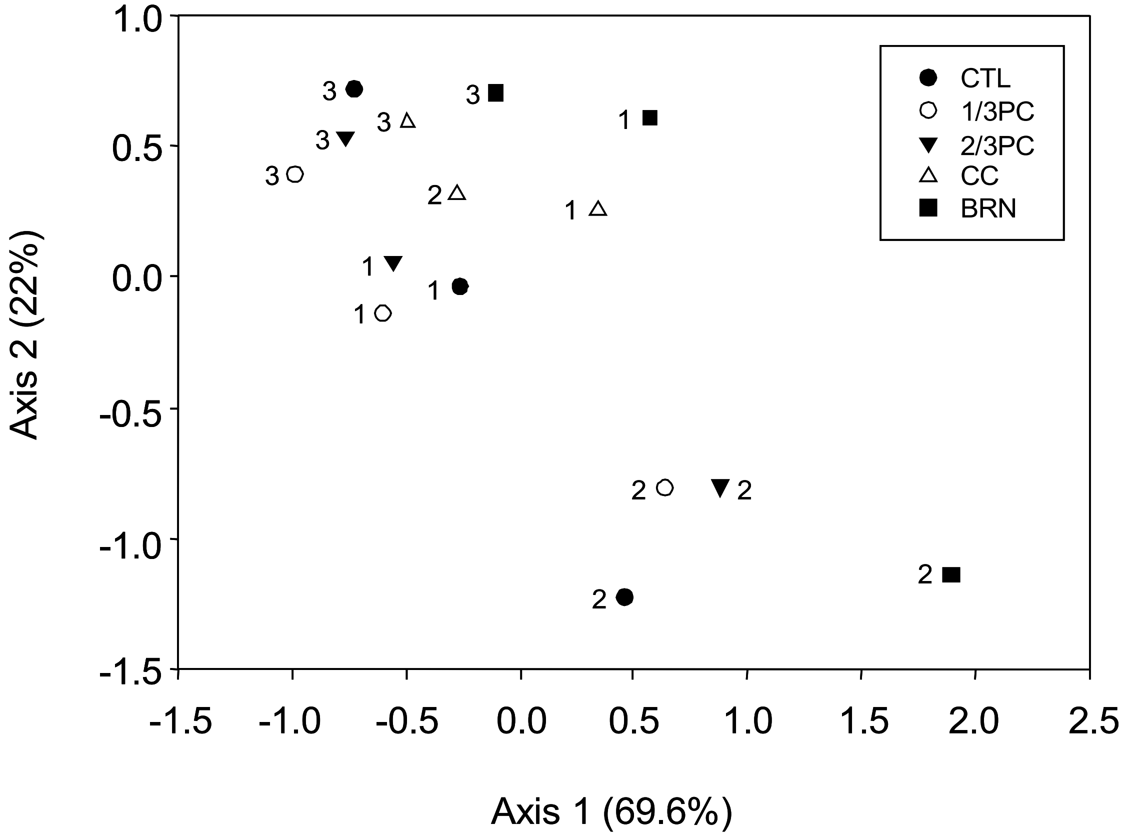

Figure 2.6: NMS ordination for oribatid mites collected in litter from control (CTL), one-third partial cut (1/3PC), two-third partial cut (2/3PC), clear cut (CC) and controlled burn (BRN) sites. Numbers beside symbols (1, 2, 3) represent the block from which the samples came. Data were log transformed ($x' = \log(x+1)$) prior to analysis, and the ordination is based on three pooled samples (three transects each) per treatment and 81 species (axis 1: $R^2 = 0.696$; axis 2: $R^2 = 0.22$; final stress = 9.8).

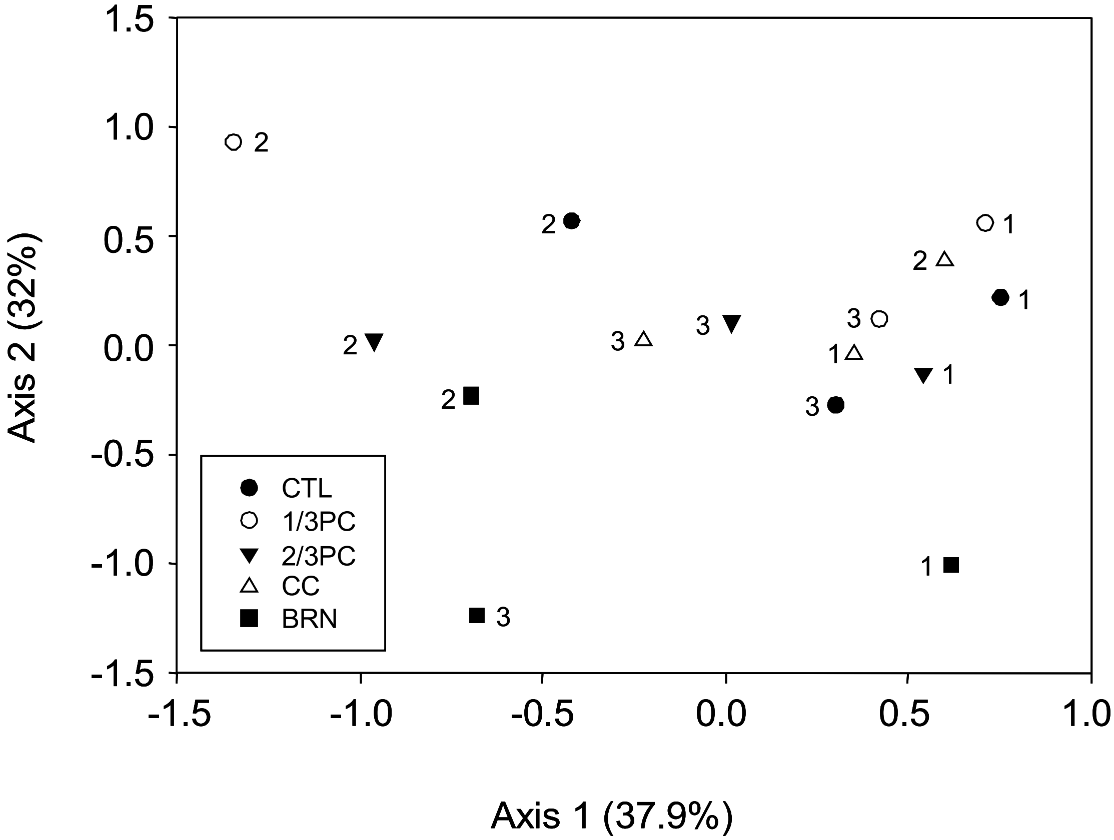

Figure 2.7: NMS ordination for oribatid mites collected in soil from control (CTL), one-third partial cut (1/3PC), two-third partial cut (2/3PC), clear cut (CC) and controlled burn (BRN) sites. Numbers beside symbols (1, 2, 3) represent the block from which the samples came. Data were log transformed (x′ = log (x+1)) prior to analysis, and the ordination is based on three pooled samples (three transects each) per treatment and 47 species (axis 1: R^2= 0.379; axis 2: R^2= 0.32; axis 3: R^2=0.19 (not shown); final stress = 9.8).

Appendix 2.1: Oribatid mite species collected from litter and soil in control (CTL), one-third partial cut (1/3PC), two-third partial cut (2/3PC), clear cut (CC) and controlled burn-after-harvest (BRN) sites. (*) indicates significant indicator species.

Spcode	Family	Genus	Species	Authority	Layer	CTL	1/3PC	2/3PC	CC	BRN	Total
Achiclar	Achipteriidae	*Achipteria*	*clarencei*	Nevin 1977	Litter	12	0	1	17	33	63
					Soil	0	0	0	0	0	0
Achisp1	Achipteriidae	*Achipteria*	sp1		Litter	0	1	0	0	0	1
					Soil	0	0	0	0	0	0
Adorammo	Liacaridae	*Adoristes*	*ammonoosuci*	Jacot 1938	Litter	1	3	0	0	0	4
					Soil	0	0	0	0	0	0
Adornr.p	Astegistidae	*Adoristes*	nr.*poppei*		Litter	0	1	0	0	0	1
					Soil	0	0	0	0	0	0
Adorsp1	Liacaridae	*Adoristes*	sp1		Litter	5	9	14	3	0	31
					Soil	0	0	0	1	0	1
Adorsp2	Liacaridae	*Adoristes*	sp2		Litter	0	1	0	5	0	6
					Soil	0	1	0	0	0	1
Adorsp3	Liacaridae	*Adoristes*	sp3		Litter	0	0	1	0	0	1
					Soil	0	0	0	0	0	0
Anacnr.h	Achipteriidae	*Anachipteria*	nr.*howardi*		Litter	0	0	4	13	4	21
					Soil	0	0	0	0	1	1
Anacsp1	Achipteriidae	*Anachipteria*	sp1		Litter	0	0	0	3	0	3
					Soil	0	0	0	0	0	0
Archluri	Phthiracaridae	*Archiphthiracarus*	*luridus*	(Ewing 1909)	Litter	0	0	0	1	0	1
					Soil	0	0	0	0	1	1
Archsp1	Phthiracaridae	*Archiphthiracarus*	sp1		Litter	5	4	2	3	2	16
					Soil	0	0	0	0	0	0
Archsp2	Phthiracaridae	*Archiphthiracarus*	sp2		Litter	4	0	1	1	0	6
					Soil	0	0	0	0	0	0
Archsp3	Phthiracaridae	*Archiphthiracarus*	sp3		Litter	0	0	1	0	0	1
					Soil	0	0	0	0	0	0
Atrostri	Phthiracaridae	*Atropacarus*	*striculus*	(Koch 1835)	Litter	12	35	18	3	18	86
					Soil	0	1	1	0	9	11
Autolong	Autognetidae	*Autogneta*	*longilamellata*	(Michael 1885)	Litter	3	15	11	7	2	38
					Soil	1	4	0	0	0	5

Spcode	Family	Genus	Species	Authority	Layer	CTL	1/3PC	2/3PC	CC	BRN	Total
Banklanc	Thyrisomidae	*Banksinoma*	*lanceolata canadensis*	Fujikawa 1979	Litter	3	3	10*	1	1	18
					Soil	0	3	2	1	0	6
Camibiur	Camisiidae	*Camisia*	*biurus*	(Koch 1839)	Litter	1	0	0	0	0	1
					Soil	0	0	0	0	0	0
Caragran	Carabodidae	*Carabodes*	*granulatus*	Banks 1895	Litter	0	4	1	8	4	17
					Soil	0	0	0	0	0	0
Caralaby	Carabodidae	*Carabodes*	*labyrinthicus*	(Michael 1879)	Litter	1	0	0	0	2	3
					Soil	0	0	0	0	0	0
Carapoly	Carabodidae	*Carabodes*	*polyporetes*	Reeves 1991	Litter	7	24	22	36	0	89
					Soil	0	1	0	0	0	1
Cerabipi	Peloppiidae	*Ceratoppia*	*bipilis*	(Hermann 1804)	Litter	16	8	5	6	0	35
					Soil	0	0	2	0	0	2
Ceracusp	Ceratozetidae	*Ceratozetes*	*cuspidatus*	Jacot 1939	Litter	6	0	0	0	0	6
					Soil	22	30	4	2	0	58
Ceragrac	Ceratozetidae	*Ceratozetes*	*gracilis*	(Michael 1884)	Litter	29	10	16	17	34	106
					Soil	15	5	11	7	15	53
Chamcusp	Chamobatidae	*Chamobates*	*cuspidatus*	(Michael 1884)	Litter	49	79	54	79	96	357
					Soil	0	0	1	0	1	2
Chamsp1	Chamobatidae	*Chamobates*	sp1		Litter	0	3	0	2	0	5
					Soil	0	0	0	0	0	0
Cultbicu	Astegistidae	*Cultroribula*	*bicultrata*	(Berlese 1905)	Litter	2	0	1	0	0	3
					Soil	0	1	0	1	4	6
Dentnr.h	Achipteriidae	*Dentachipteria*	nr.*highlandensis*		Litter	1	0	0	0	0	1
					Soil	0	0	0	0	0	0
Diaphume	Ceratozetidae	*Diapterobates*	*humeralis*	(Hermann 1804)	Litter	6	0	0	1	1	8
					Soil	0	0	0	0	0	0
Eniominu	Eniochthoniidae	*Eniochthonius*	*minutissimus*	(Berlese 1903)	Litter	485	389	366	312	274	1826
					Soil	23	11	9	11	7	61
Erembrev	Eremaeidae	*Eremaeus*	*brevitarsus*	(Ewing 1917)	Litter	14	14	29	21	12	90
					Soil	0	0	0	0	0	0
Euphnr.f	Euphthiracaridae	*Euphthiracarus*	nr.*fulvus*		Litter	1	0	1	0	0	2
					Soil	0	0	0	0	0	0
Euphnr.v	Euphthiracaridae	*Euphthiracarus*	nr.*vicinus*		Litter	7	5	9	4	1	26
					Soil	3	1	1	0	0	5

Spcode	Family	Genus	Species	Authority	Layer	CTL	1/3PC	2/3PC	CC	BRN	Total
Fuscfusc	Ceratozetidae	*Fuscozetes*	*fuscipes*	(Koch 1844)	Litter	71	13	4	30*	116	234
					Soil	0	1	0	0	17	18
Grapsp1	Oppiidae	*Graptoppia*	sp1		Litter	5	3	5	5	1	19
					Soil	0	0	0	0	0	0
Gymnnr.o	Gymnodamaeidae	*Gymnodamaeus*	nr.*ornatus*		Litter	0	0	0	0	7	7
					Soil	0	0	0	0	0	0
Gymnsp1	Gymnodamaeidae	*Gymnodamaeus*	sp1		Litter	0	0	0	0	0	0
					Soil	0	0	0	1	0	1
Hafeniti	Tenuialidae	*Hafenferrefia*	*nitidula*	(Banks 1906)	Litter	1	0	1	0	0	2
					Soil	0	0	0	0	1	1
Haplsp1	Haplozetidae	*Haplozetes*	sp1		Litter	18	80	27	11	16	152
					Soil	3	1	3	0	0	7
Hemiquad	Scheloribatidae	*Hemileius*	*quadripilis*	(Fitch 1856)	Litter	3	9	5	6	1	24
					Soil	0	0	0	0	0	0
Hemisp1	Scheloribatidae	*Hemileius*	sp1		Litter	1	0	0	0	0	1
					Soil	0	0	0	0	0	0
Hermsp1	Hermanniellidae	*Hermanniella*	sp1		Litter	3	5	5	2	0	15
					Soil	0	0	0	0	0	0
Hyporufu	Hypochthoniidae	*Hypochthonius*	*rufulus*	Koch 1835	Litter	1	0	0	1	1	3
					Soil	0	0	0	0	0	0
Liebsp1	Scheloribatidae	*Liebstadia*	sp1		Litter	2	2	2	0	0	6
					Soil	0	3	0	0	0	3
Liocbrev	Brachychthoniidae	*Liochthonius*	*brevis*	(Michael 1888)	Litter	0	1	0	0	1	2
					Soil	0	1	2	0	0	3
Lioclapp	Brachychthoniidae	*Liochthonius*	*lapponicus*	(Trägårdh 1910)	Litter	33	37	59	155	65	349
					Soil	0	0	1	0	2	3
Liocnr.b	Brachychthoniidae	*Liochthonius*	nr.*brevis*		Litter	20	12	13	65	5	115
					Soil	0	3	0	3	0	6
Micrsimp	Euphthiracaridae	*Microtritia*	*simplex*	(Jacot 1930)	Litter	22	20	17	12	15	86
					Soil	0	0	0	1	1	2
Nanheleg	Nanhermanniidae	*Nanhermannia*	*elegantula*	Berlese 1913	Litter	0	0	0	0	0	0
					Soil	0	0	0	0	2	2
Nanhsp1	Nanhermanniidae	*Nanhermannia*	sp1		Litter	3	3	2	0	2	10
					Soil	0	2	0	0	2	4

Spcode	Family	Genus	Species	Authority	Layer	CTL	1/3PC	2/3PC	CC	BRN	Total
Neoraura	Parakalummidae	*Neoribates*	*aurantiacus*	(Oudemans 1914)	Litter	3	3	0	1	3	10
					Soil	0	0	0	0	0	0
Nothsilv	Nothridae	*Nothrus*	*silvestris*	Nicolet 1855	Litter	0	1	0	0	9	10
					Soil	2	0	0	0	1	3
Oppinova	Oppiidae	*Oppiella*	*nova*	(Oudemans 1902)	Litter	1047	801	768	938	135	3689
					Soil	498	554	467	292	132	1943
Oppinr.n	Oppiidae	*Oppia*	nr.*nitens*		Litter	3	0	2	13	29	47
					Soil	0	0	1	1	11	13
Oppitran	Oppiidae	*Oppiella*	*translamellata*	Willmann 1923	Litter	0	2	1	5	1	9
					Soil	0	0	0	0	0	0
Oribbrev	Oribatellidae	*Oribatella*	*brevicornuta*	Jacot 1934	Litter	11	7	7	54	6	85
					Soil	0	0	0	2	0	2
Oribmira	Cepheidae	*Oribatodes*	*mirabilis*	Banks 1895	Litter	19	32	19	39	1	110
					Soil	0	0	0	0	0	0
Oribquad	Oribatellidae	*Oribatella*	*quadricornuta*	(Michael 1880)	Litter	2	2	0	6	0	10
					Soil	0	0	0	0	0	0
Oribsp1	Oribatellidae	*Oribatella*	sp1		Litter	4	2	1	0	0	7
					Soil	0	0	0	0	0	0
Oribsp2	Oribatellidae	*Oribatella*	sp2		Litter	0	0	0	0	0	0
					Soil	0	0	0	0	7	7
Palahyst	Palaeacaridae	*Palaeacarus*	*hystricinus*	Trägårdh 1932	Litter	0	0	0	0	0	0
					Soil	0	1	2	0	0	3
Paraleon	Scheloribatidae	*Paraleius*	*leontonycha*	(Berlese 1910)	Litter	1	2	0	0	0	3
					Soil	0	0	0	0	0	0
Pelocana	Haplozetidae	*Peloribates*	*canadensis*	Hammer 1952	Litter	0	2	7	1	0	10
					Soil	0	0	0	0	0	0
Pergsp1	Galumnidae	*Pergalumna*	sp1		Litter	0	3	2	3	3	11
					Soil	0	0	0	0	0	0
Phthbore	Phthiracaridae	*Phthiracarus*	*boresetosus*	Jacot 1930	Litter	46	81	74	171	47*	419
					Soil	2	0	0	1	0	3
Phthlong	Phthiracaridae	*Phthiracarus*	*longulus*	(Koch 1841)	Litter	33	53	51	64	37	238
					Soil	0	0	0	5*	1	6
Pilonr.b	Galumnidae	*Pilogalumna*	nr.*binadalares*		Litter	83	77	33	24	15	232
					Soil	1	0	1	1	0	3

Spcode	Family	Genus	Species	Authority	Layer	CTL	1/3PC	2/3PC	CC	BRN	Total
Platsp1	Camisiidae	*Platynothrus*	sp1		Litter	0	0	0	0	0	0
					Soil	0	0	0	0	1	1
Platthor	Camisiidae	*Platynothrus*	*thori*	(Berlese 1904)	Litter	22	14	5	15	1	57
					Soil	0	0	0	0	0	0
Podotect	Podopterotegaeidae	*Podopterotegaeus*	*tectus*	Aoki 1969	Litter	0	0	0	0	0	0
					Soil	2	3	0	1	0	6
Poecspic	Brachychthoniidae	*Poecilochthonius*	*spiciger*	(Berlese 1910)	Litter	3	3	1	1	0	8
					Soil	0	0	0	0	0	0
Propnr.m	Phenopelopidae	*Propelops*	nr.*minnesotensis*		Litter	25	12	20	5	8	70
					Soil	0	0	0	0	0	0
Protolig	Oribotritiidae	*Protoribotritia*	*oligotricha*	Maerkel 1963	Litter	2	1	2	1	4	10
					Soil	1	2	1	0	0	4
Quadnr.s	Quadroppiidae	*Quadroppia*	nr.*skookumchucki*		Litter	0	0	0	1	8	9
					Soil	5	0	9	35	30	79
Quadquad	Quadroppiidae	*Quadroppia*	*quadricarinata*	(Michael 1885)	Litter	54	17	42	171	121	405
					Soil	14	9	15	38*	12	88
Rhysardu	Euphthiracaridae	*Rhysotritia*	*ardua*	(Koch 1841)	Litter	5	34	23	17	3	82
					Soil	0	0	0	0	0	0
Schen.sp	Scheloribatidae	*Scheloribates*	n.sp.		Litter	4	1	6	2	1	14
					Soil	0	0	0	0	0	0
Schepall	Scheloribatidae	*Scheloribates*	*pallidulus*	(Koch 1841)	Litter	399	1069	680	1420	814	4382
					Soil	12	7	5	5	22	51
Schesp1	Scheloribatidae	*Scheloribates*	sp1		Litter	0	1	0	0	0	1
					Soil	0	0	0	0	0	0
Sellrost	Brachychthoniidae	*Sellnickochthonius*	*rostratus*	(Jacot 1936)	Litter	0	0	1	2	2	5
					Soil	7	5	5	6	5	28
Subisp1	Oppiidae	*Subiasella*	sp1		Litter	6	0	4	7	10	27
					Soil	0	0	0	0	0	0
Suctsp1	Suctobelbidae	*Suctobelbella*	sp1		Litter	294	91	212	297	129	1023
					Soil	92	75	90	95	51	403
Suctsp2	Suctobelbidae	*Suctobelbella*	sp2		Litter	50	24	48	38	27	187
					Soil	5	1	8	5	0	19
Suctsp3	Suctobelbidae	*Suctobelbella*	sp3		Litter	231	147	211	284	43	916
					Soil	0	2	2	7	0	11

Spcode	Family	Genus	Species	Authority	Layer	CTL	1/3PC	2/3PC	CC	BRN	Total
Tectvela	Tectocepheidae	*Tectocepheus*	*velatus*	(Michael 1880)	Litter	275	331	214	396	1107	2323
					Soil	4	1	2	3	11*	21
Trhyamer	Trhypochthoniidae	*Trhypochthonius*	*americanus*	(Ewing 1908)	Litter	19	5	5	10	1	40
					Soil	0	0	0	0	0	0
Xylooblo	Haplozetidae	*Xylobates*	*oblongus*	(Ewing 1909)	Litter	6	11	8	18	10	53
					Soil	16	4	1	0	3	24
Zygoexil	Oribatulidae	*Zygoribatula*	*exilis*	(Nicolet 1855)	Litter	0	0	1	0	0	1
					Soil	0	0	0	0	0	0

CONNECTING STATEMENT

Chapter 2 shows that partial cutting may maintain oribatid biodiversity, but prescribed burning after harvest, and to a lesser degree clear cutting, changes oribatid assemblages compared to uncut forest. In order to focus efforts to maintain biodiversity, it is necessary to study the contribution of microhabitat variation to local species richness. Chapter 3 focuses on the influence of decaying logs on oribatid mite assemblages on the forest floor.

CHAPTER 3: THE INFLUENCE OF DECAYING LOGS ON ORIBATID MITE ASSEMBLAGES IN MIXEDWOOD BOREAL FOREST

Abstract

The removal of timber during harvesting substantially reduces important invertebrate habitat, most noticeably microhabitats associated with fallen trees. I investigated the influence of decaying logs on the spatial distribution of oribatid mites on the forest floor at the sylviculture et aménagement forestiers écosystémique (SAFE) research station in the Abitibi region in NW Québec. In June 2006, six aspen logs were selected for study, and samples were taken at three distances for each log: directly on top of the log (ON), directly beside the log (ADJ) and at least one metre away from the log and any other fallen wood (AWAY). Samples ON logs consisted of a litter layer sample, an upper wood sample and an inner wood sample. Samples at the ADJ and AWAY distances consisted of litter samples and soil cores. The highest species richness was collected ON logs, and logs harboured a distinct oribatid species composition compared to the forest floor. There were species-specific changes in relative abundance with increasing distance away from DWM, which indicates an influence of DWM in structuring oribatid assemblages on the forest floor. Additionally, each layer (litter, wood and soil) exhibited a unique species composition and hosted a different diversity of oribatid mites. This study is one of the first to use species-level analyses to determine the importance of DWM to forest biodiversity by creating habitat for unique assemblages of oribatid mites.

Introduction

Coarse woody debris (CWD) (i.e. standing dead trees, fallen trees, decaying roots and other large pieces of woody material) in the boreal forest harbours high biodiversity (e.g. Harmon et al. 1986, Esseen et al. 1997, Siitonen 2001, Hammond et al. 2004) and is linked to many key ecosystem processes (Harmon et al. 1986, Van Lear 1993, Perry 1998). Fallen dead wood or downed woody material (DWM) accumulating on the forest floor contributes to soil fertility and stability, serves as seed germination sites, acts as long-term storage for organic matter, moisture, carbon and nutrients (Sollins et al. 1987, Harmon et al. 1986, Van Lear 1993, Perry 1998) and supports many organisms as a result of a wide range of microhabitats due to the variable size, texture and microclimate characteristics of wood (Graham 1925, Söderström 1988, Huston 1993, Bader et al. 1995, Esseen et al. 1997, Marra and Edmonds 1998, Siitonen 2001, Jabin et al 2004). In the boreal forest, there are consistent as well as sporadic inputs of CWD from natural disturbance events like wind storms, fire, and insects, as well as losses from decomposition and fire. These disturbances can influence forest structure at all scales and result in a constantly changing mass, density and volume of CWD in a forest ecosystem (Harmon et al. 1986, Hansen et al. 1991, Van Lear 1993, Jonsson et al. 2005).

Saproxylic organisms are those that depend, either directly or indirectly, on dead or dying wood at some life history stage (Speight 1989), and it is estimated that 20-25% of forest-inhabiting species may be considered saproxylic (Siitonen 2001). Coleoptera and Diptera (Økland et al. 1996, Kaila et al. 1997, Schiegg 2000, Grove 2002, Hammond et al. 2004), spiders (Buddle 2001, Varady-Szabo and Buddle 2006), other arthropod taxa (Bengtsson et al. 1997, Jonsell et al. 1998, Jabin 2004), wood-rotting fungi (Niemelä et al. 1995, Edman et al. 2004), bryophytes and lichens (Söderström 1988) as well as vertebrates (e.g. Butts and McComb 2000, Setterington et al. 2000, Campbell et al. 2005) benefit from DWM as habitat and/or as a food resource. In forest ecosystems, arthropods are extremely species rich and dominate in number and diversity in DWM habitat (Graham 1925, Savely 1939, Danks and Foottit 1989, Speight 1989, Esseen et al. 1997). Saproxylic insects are often associated with various dead wood characteristics such as tree species or stage of decay (Jonsell et al. 1998, Hammond et al. 2004), and different parts of a log (e.g. bark, sapwood and heartwood) are host to characteristic groups of species (Graham 1925). Changes in the availability of their specific habitat requirements can impact species diversity and composition (Siitonen and Martikainen 1994, Kaila et al. 1997, Jonsell et al. 1998, Grove 2002, Hammond et al. 2004).

Many other arthropod taxa associated with DWM, however, are not well studied. Among the most diverse of these are of the suborder Oribatida, which play an important role in wood decomposition. Seastedt et al. (1989) showed that total microarthropod abundance increased in decaying wood as decomposition progressed, and that oribatids were the most abundant taxon. Evans et al. (2003) demonstrated that the abundance of mite RTU (recognizable taxonomic units), including oribatids, significantly decreased with increasing distance from beech DWM, and mite RTU diversity was higher in the litter than in the fermentation layer. Similarly, Marra and Edmonds (1998) found that soil depth had a significant effect on the diversity and average density of Acari, but distance from coniferous DWM did not; however, four oribatid morphospecies showed significant differences in density with distance from DWM. DWM clearly influences the diversity and composition of several taxa including oribatids; however, species-level research is necessary to fully understand its effects on oribatid assemblages and the potential impacts of the loss of DWM in managed forest.

Oribatid mites are particularly important on the forest floor; most species are particulate-feeding saprophages and mycophages (Norton 1985, Behan-Pelletier 1999), feeding on decaying organic material and fungi, although a few species feed directly on wood itself (Luxton 1972, Johnston and Crossley 1993). Oribatids in DWM contribute greatly to decomposition, nutrient cycling and soil formation by fragmenting organic matter and mediating microbial growth (Fager 1968, Abbott and Crossley 1982, Seastedt and Crossley 1988, Behan-Pelletier 1999). DWM increases microhabitat heterogeneity on the forest floor (Esseen et al. 1997, Kuuluvainen and Laiho 2004), and this probably correlates with high oribatid species diversity (Anderson 1978). Some oribatids that occur on the forest floor also use leaf litter and woody litter, although a few may use DWM exclusively and as a result, fallen dead wood can be very species rich (Johnston and Crossley 1993). DWM and its effects on temperature, moisture, pH and nutrient input may influence the spatial distribution and composition of mite assemblages on the forest floor (Johnston and Crossley 1993, Evans et al. 2003); however, its contribution to oribatid biodiversity has not been fully explored.

Forest management drastically reduces the amount of CWD in an area, which affects microhabitat variation associated with DWM and results in decreased species diversity and impacts ecosystem function (Hansen et al. 1991, Burton et al. 1992, Haila 1994, Bengtsson et al. 2000, Siitonen 2001, Kuuluvainen and Laiho 2004). Ecosystem-based management, such as partial cutting, can retain elements of natural forest structure like

DWM in managed forest thus maintaining the diversity of saproxylic species associated with this unique habitat (Esseen et al. 1997, Fries et al. 1997, Lee et al. 1997). Despite the importance of oribatid mites for the decomposition of wood and the potential implications for many forest soil processes, patterns of their abundance, species richness and composition in DWM at any stage of decay are not well known (Seastedt et al. 1989, Perry 1998). The objective of this study was to determine the spatial influence of decaying logs on the abundance, diversity and species composition of oribatid assemblages on the forest floor in an aspen-dominated mixedwood boreal forest in NW Québec, Canada. Decayed aspen logs were sampled for oribatid mites at three horizontal distances and in four vertical layers. I predicted that oribatid diversity would decrease and species composition would change with increasing distance from the logs in both layers; however, the changes should be of a larger degree in the litter layer (Graham 1925, Fujikawa 1974, Seastedt and Crossley 1981, Abbott and Crossley 1982, Evans et al. 2003, Jabin et al. 2004).

Methods

Study site

The study was conducted in the uncut control treatment unit of Block 1 in Phase 1 at sylviculture et aménagement forestiers écosystémique (SAFE) research site located approximately 45 km NW of Rouyn-Noranda in the boreal mixedwood forest in Abitibi, Québec (48º 28-29', 79º 24-26'). The study site is approximately 2 ha in size and consists of aspen (*Populus tremuloides* Mchx.) dominated (67%) stands undisturbed by fire since 1923 (Brais et al. 2004b, Dansereau and Bergeron 1993). Other tree species in the site include grey pine (*Pinus sabiniana* Dougl.; 16%) and eastern white cedar (*Thuja occidentalis* L.; 4%); dominant shrubs include beaked hazel (*Corylus cornuta* Marsh.) and mountain maple (*Acer spicatum* Lam.), and dominant herbaceous plants include wild sarsaparilla (*Aralia nudicaulis* L.) and big-leaved aster (*Aster macrophyllus* L.) (Brais et al. 2004b). Mean annual temperature in the area is 0.8ºC, with a June mean temperature of 14.3ºC, and total annual precipitation is 889.8 mm (Environment Canada 2003). The forest floor is a thin mor (2-7 cm thick) with clayey Grey Luvisolic soils (Brais et al. 2004a).

Sampling

In June 2006, six aspen logs greater than five metres apart were selected for study. These were classified as decay class III-IV (decay class predominant along the length of the log) based on an ellipsoid or collapsed shape, moss coverage of 50-80% and bark retention of <50% (Stewart and Burrows 1994, Waddell 2002). Samples were taken at three distances for each log: directly on top of the log (ON), directly beside, or adjacent to, the log (ADJ) and at least one metre away from the log and any other fallen wood (AWAY). Samples ON logs consisted of a litter layer sample, i.e. freshly fallen leaves, needles, twigs, stems and bark (Hoover and Lunt 1952), an upper wood sample, i.e. upper portion of the log and an inner wood sample, i.e. loose woody material not connected to the outer wall of the log. Samples at the ADJ and AWAY distances consisted of litter samples and soil cores, i.e. well decomposed organic matter of unrecognizable origin (Hoover and Lunt 1952). Litter samples were standardized by volume (one liter) and wood and soil samples were taken with a corer (6 cm diameter) to the depth of the mineral soil horizon. One sample of each layer at each distance was taken for each log. Samples were immediately placed into individual cloth bags and kept in a cooler until extraction later the same day. All microarthropods were extracted in a nearby laboratory using Tullgren-type funnels for five days at an average temperature of 32ºC for litter and 36ºC for wood and soil (Marshall 1972, Crossley and Blair 1991, Edwards 1991, Chapter 4). During extraction, gradual drying of the sample forces active soil fauna to migrate downward through the substrate to avoid desiccation and eventually fall into a collection cup below. Tullgren-type funnels have 98% extraction efficiency for adult oribatid mites (Marshall 1972) and are the most appropriate extraction method for organic soils, such as in forests (Crossley and Blair 1991, Edwards 1991). Oribatids were collected and preserved in 75% ethanol. Following extraction, the dry mass of each sample was recorded.

At the time of sampling, soil temperature at 5 cm depth was taken at all three distances from each log as was the length, small end and large end diameter of each log. Volume (m^3/log) of the logs was calculated using Smalian's formula, $Vm^3 = (\pi/8)(D^2_s + D^2_l)$

(L)/10,000, where D_s is the small end diameter in cm, D_l is the large end diameter in cm and L is the length in metres.

Species identification

All adult Oribatida were identified to species or morphospecies using a Leica DM2500 compound-light microscope, a Nikon SMZ1500 dissecting microscope and published and unpublished taxonomic works by Marshall et al. (1987), Niedbala (2002), Weigmann (2006) and Norton and Behan-Pelletier (in press). Species identifications were confirmed by Dr. V. Behan-Pelletier at the Canadian National Collection of Insects (CNC, Agriculture and Agri-Food Canada, Ottawa, Ontario, Canada), and voucher specimens have been deposited at the Lyman Entomological Museum (Ste. Anne de Bellevue, Québec, Canada).

Statistical analyses

There was a large difference in the numbers of individuals collected in the litter and wood/soil layers; therefore, the litter layer and wood/soil layers were analyzed separately. One-way Analysis of Variance (ANOVA) was done using general linear model procedures in SAS software v. 9.1 (SAS Institute, 2003) to assess differences in the relative abundance and raw species richness of oribatid mites at the three distances (ON, ADJ and AWAY) from fallen wood. Tests of normality (Shapiro-Wilk test) and homogeneity of variance (Levene's test) determined adherence to the assumptions of parametric statistics, and data were log transformed ($x' = \log(x+1)$) if necessary. Tukey's H.S.D. test (α=0.05) was used for *post hoc* comparison of means.

Rank-abundance curves, based on the 25 most commonly collected oribatid species in the litter layer and the 20 most commonly collected species in wood/soil ranked according to their abundance in the AWAY samples, were used to demonstrate the changes in species relative abundance and diversity with proximity to DWM.

Indicator species analysis was conducted using the software PC-ORD v. 4.17 (McCune and Mefford 1999) to measure the strength of the association between a species and a habitat type (i.e. at each distance from DWM in each layer) (Dufrêne and Legendre 1997). The statistical significance of the maximum indicator value was assessed using a Monte Carlo (randomization) test with 1000 permutations. Indicator species are those found mainly in a single habitat type and are present in most of the sites of that type; species with an indicator value of more than 25% that is significant ($p<0.01$) are indicator species for that particular habitat (Dufrêne and Legendre 1997). Singletons were removed from analysis to reduce the importance of rarely collected species (Dufrêne and Legendre 1997).

Standardized estimates of oribatid species richness at each distance from DWM were compared using individual-based rarefaction estimates using the software program EcoSim v. 7.72 (Gotelli and Entsminger 2006). Individual-based rarefaction is appropriate for assessing overall assemblage species richness and when there are discrepancies in sampling effort across treatment or study sites (Gotelli and Colwell 2001, Buddle et al. 2005). Rarefaction analysis standardizes species richness to the largest sample size common to all study sites and provides estimates of variance allowing for reasonable comparisons of diversity among treatments or sites with differing sampling effort (Gotelli and Colwell 2001, Buddle et al. 2005). Rarefaction curves also depict the rate of accumulation, which helps to determine if overall sampling effort was sufficient (i.e. accumulation of new species with more individuals is very small) (Buddle et al. 2005). The number of iterations was set at the maximum number of individuals and abundance levels that increased incrementally by 115 individuals for litter and by 20 individuals for the wood/soil.

Differences in oribatid species composition among the distances from DWM were analyzed using non-metric multi-dimensional scaling (NMS) ordination using the software program PC-ORD v. 4.17 (McCune and Mefford 1999). NMS ordination is an indirect gradient analysis that ordinates samples according to co-variation and association among species and does not assume linear relationships among variables (McCune and Grace 2002). Data were log-transformed ($x' = \log(x+1)$) to decrease the weight of the more abundant species. A detrended correspondence analysis (DCA) was used as the starting configuration for subsequent NMS ordinations to reduce stress and avoid local minima (Work and McCullough 2000). A preliminary six-dimensional NMS ordination was run to determine the number of dimensions for the final analysis and to evaluate stress reduction. Parameters used included Sorensen (Bray-Curtis) distance measure, 200 iterations, 50 permutations with real data and 50 permutations with randomized data (Monte Carlo test). A final NMS analysis was then conducted with these same parameters using the recommended number of dimensions.

Multi-response permutation procedures (MRPP) were used on the log-transformed data to determine statistically significant differences in species composition among distances from DWM. MRPP is a non-parametric test that can be applied to multivariate data unrestrained by the often unrealistic assumptions of normality and homogeneity of variance (Zimmerman et al. 1985). Litter and wood/soil layers were analyzed separately, and distance was used as the grouping variable; however, an additional test with a grouping of "wood" (ON upper and inner wood samples) vs. "soil" (ADJ and AWAY soil samples) was conducted when a compositional difference between wood and soil became apparent. Parameters used included a Sorensen (Bray-Curtis) distance measure and a group weighting factor of n/sum(n). The MRPP test statistic is given as a p-value along with the chance-corrected within-group agreement (*A*), which describes within-group homogeneity compared to random expectation as well as relative effect size. Values for *A* equal 1 when there is perfect within-group agreement, are equal to 0 when heterogeneity is as expected by chance, and less than 0 when there is more heterogeneity than expected by chance (Mielke 1991).

Results

A total of 15, 867 adult oribatid mites in 80 species was collected (Table 3.1, Appendix 3.1) from litter (13, 898 individuals, 76 species), upper wood (585 individuals, 29 species), inner wood (373 individuals, 29 species) and soil (1, 011 individuals and 27 species). Densities range from approximately 772, 111 individuals m^{-3} in litter to 580, 324 individuals m^{-3} in the wood/soil layers. The greatest number of oribatids collected and the highest raw species richness occurred in the litter layer ON logs, while the lowest number of mites was collected in soil AWAY from logs, which also had the lowest diversity. Three species, *Oppiella nova* (Oudemans 1902), *Scheloribates pallidulus* (Koch 1841) and *Eniochthonius minutissimus* (Berlese 1903), each accounted for over 10% of the total abundance and together accounted for nearly 55% of all oribatid mites collected. Overall, seven species were collected only once (singletons) and three species were collected only twice (doubletons).

Volume of the logs ranged from 3.58 m^3 to 28.5 m^3 with an average of 13.66 m^3 (±3.46 SE). A simple scatter plot of number of oribatids collected against the volume (m^3) of each log (not shown) did not show any relationship between the two variables.

Relative abundance of oribatid mites was not significantly different with distance from the log for litter or wood/soil habitats (Table 3.2); however, there was a significant effect of distance on raw species richness for both layers (Table 3.2). Rank-abundance curves, representing the most commonly collected species in the litter (top 25 species; Fig. 3.1) and wood/soil (top 20 species; Fig. 3.2) layers and ranked according to abundance in the AWAY samples, show shifts in oribatid diversity and species dominance with distance from DWM. Fourteen species, including *Dentachipteria nr. highlandensis*, *Belba* sp1 and *Mycobates incurvatus* Hammer 1952, were collected only directly ON the logs, and nearly all *Podopterotegaeus tectus* Aoki 1969 were found ON logs except for one individual collected in soil AWAY (Appendix 3.1). Of these fourteen, eight species were represented by five or fewer individuals. In the litter layer, there was also an increase in species with proximity to DWM; for example *Liochthonius* sp1, *Carabodes labyrinthicus* (Michael 1879) and *Oppia nr*. *nitens*, all present ON and ADJ to DWM, were absent from the AWAY distance, and *Achipteria clarencei* Nevin 1977 was noticeably reduced at the AWAY distance. Conversely, two species, *Atropacarus striculus* (Koch 1835) and *Pilogalumna nr. binadalares*, were reduced ON DWM compared to AWAY. Dominance of the most abundant species shifted slightly as well; with proximity to DWM, *O. nova* relative abundance decreased slightly while *S. pallidulus* increased in number. In the wood and soil habitats, there was also an increase in species with proximity to DWM; for example, *Belba* sp1 and *Liochthonius* sp1 were present ON DWM but absent from ADJ and AWAY, and *Xylobates oblongus* (Ewing 1909) (now *Protoribates capucinus*) and *Suctobelbella* sp3 were absent from the AWAY distance but present at all other distances and layers. Although *O. nova* remained the dominant species, its abundance was reduced in inner wood ON DWM. In the litter layer there were ten significant indicator species for ON logs, one significant indicator species for litter ADJ to the log, two significant indicator species for inner wood and one indicator species for soil ADJ to the log (denoted with (*) in Appendix 3.1). When upper and inner wood samples were grouped as "wood" and ADJ and AWAY soil samples were grouped as "soil", there were three significant indicator species for "wood" and two species for "soil" samples.

Species richness of litter and wood/soil layers were analyzed separately due to the large difference in number of individuals collected in each layer. In the litter layer, rarefaction shows that at approximately 3100 individuals the ON samples had significantly higher diversity than either the ADJ or AWAY distances, which were not significantly different from each other (Fig. 3.3). At 280 individuals in wood and soil habitats, inner wood layer (ON distance) had significantly higher diversity than all other layers at any distance from the log (Fig. 3.4). Upper wood at the ON distance had significantly higher species richness than soil at both ADJ and AWAY distances, which were not significantly different from each other. All curves approach an asymptote (Figs 3.3 and 3.4), which indicates sampling effort was sufficient.

Non-metric multi-dimensional scaling (NMS) ordination was used to analyze the differences in oribatid species composition in the four layers at the three distances both together and separated into litter and wood/soil layers. Overall, NMS ordination explained 90.3% of the variation in the data (Fig. 3.5) and shows a clear separation of the layers, which is supported by MRPP analysis ($p< 0.00001$, A=0.191); however, litter layer samples are more tightly grouped together than are the wood and soil layers. Analysis of the litter layer alone produced a three dimensional solution, which for clarity is presented with the two axes that represent the most variation (80.4%), while the third axis explained only 11% of the variation and added little to the interpretation (Fig. 3.6). Figure 3.6 shows a separation of the ON distance from ADJ and AWAY distances along axis 1 but a definite overlap between ADJ and AWAY distances. As well, samples at ADJ and AWAY distances are more tightly grouped than are the samples from the ON distance. MRPP analysis indicates significant compositional differences in litter among all distances and between all pair-wise comparisons except between ADJ and AWAY (Table 3.3a). Analysis of the wood and soil layers (Fig. 3.7) shows a separation of upper wood (ON) and inner wood (ON) from ADJ and AWAY distances, and although there is high variation among samples within a particular distance, two axes explain 85.8% of variation in the data, while a third axis (not shown) explains 3%. MRPP analysis reveals compositional differences are significant among all distances and between all pair-wise comparisons with the exception of soil at ADJ and AWAY distances and between upper and inner wood (Table 3.3b). To assess the difference between wood and soil habitat, upper and inner wood samples were grouped as "wood" and ADJ and AWAY soil samples were grouped as "soil" and analyzed with MRPP, which showed a highly significant effect of substrate type ($p<0.0001$, $A=0.077$).

Discussion

I have shown that DWM in mixedwood boreal forest supports a more diverse and distinct oribatid assemblage compared to the forest floor. DWM provides habitat heterogeneity and structural complexity on the forest floor (Johnston and Crossley 1993, Esseen et al. 1997, Kuuluvainen and Laiho 2004), which contributes to oribatid biodiversity in the boreal forest. Oribatid relative abundance was not significantly different at any distance from logs in any layer; however, there were species-specific changes in abundance. This shows that DWM is a more important habitat to some oribatid species than to others, and suggests that some species may depend on DWM to maintain their populations in the boreal forest. There was a change in species richness in litter with distance from logs; diversity was higher ON logs compared to both ADJ and AWAY, which suggests that litter in association with DWM may posses qualities that benefit certain species of oribatid mites. As well, the inner wood layer had higher species richness than upper wood ON logs and considerably higher richness than soil at the ADJ and AWAY distances. This suggests that some oribatid species require substrates not normally found on the forest floor and may in fact specialize on fallen dead wood. These results are strongly supported by clear spatial differences in species composition; litter ON logs and upper and inner wood had species compositions not only distinct from each other, but different from litter and soil layers ADJ to and AWAY from logs. My study is one of the first to use species-level analyses to determine the importance of DWM to forest biodiversity by creating habitat and resources for unique assemblages of oribatid mites.

The results of this study complement other research regarding the effects of DWM on microarthropod biodiversity. Marra and Edmonds (1998) showed a significant effect of soil depth on the diversity and average density of Acari, but found distance from DWM had no effect. They did however find that four oribatid morphospecies representing four different genera exhibited significant differences in density with distance from DWM, suggesting that species-specific responses to DWM may influence patterns at the assemblage level. Evans et al. (2003) also found that mite RTU abundance significantly decreased with increasing distance from DWM, and mite RTU diversity and richness was higher in the litter than in the fermentation layer. Alternatively, Seastedt et al. (1989) found that microarthropod density and morphospecies diversity were lower in wood than in litter and soil combined, although Oribatida was the most abundant taxa in decaying wood. With previous work concerning the effects of DWM on microarthropod diversity, it is very possible that with greater taxonomic resolution, spatial patterns of diversity similar to those found in the present study may have been revealed; therefore, species-level identification is invaluable in biodiversity studies for detailed analysis, accurate interpretation of results and to reveal differences that cannot be detected at higher taxonomic levels.

Similar responses have been demonstrated for other taxa. Species richness and relative abundance of ground-dwelling spiders is significantly higher and spider species composition is different on the surface of DWM compared to the forest floor (Buddle 2001, Varady-Szabo and Buddle 2006). The responses of these two taxa, spiders and oribatid mites, are remarkably similar; rarefied species richness is highest on DWM, and species composition on wood differs from that adjacent to DWM and on the forest floor. This consistency suggests an importance of DWM in structuring not only particular arachnid assemblages but entire communities. Many species in other taxa, especially beetles, show a positive response to DWM; these saproxylic insects have greater diversity in DWM and exhibit a distinct compositional succession during decay (Graham 1925, Savely 1939, Danks and Foottit 1989, Speight 1989, Økland et al. 1996, Esseen et al. 1997, Schiegg 2000, Grove 2002, Jabin et al. 2004, Hammond et al. 2004). However, the specific habitat requirements of aerial saproxylic insects is likely very different than those for ground-dwelling species, especially those with low dispersal abilities. Understanding taxon-specific responses to structural elements like DWM will improve conservation efforts for a greater diversity of forest taxa.

DWM may provide oribatid mites with several resources, including food. While it is possible to generalize the feeding habits of oribatids as saprophagous or mycophagous, subdivisions of their feeding modes are evident (Luxton 1972, Anderson 1975). DWM is a structurally complex habitat that supports many organisms, including microbes, which are a major food source for most oribatids (Norton 1985, Johnston and Crossley 1993, Behan-Pelletier 1999). Many oribatid species feed on more than one food source (Luxton 1972, Anderson 1975), although there is often some selectivity (Luxton 1972). Some oribatids may even be obligatory xylophages, specializing on dead wood (Luxton 1972, Behan and Hill 1978, Johnston and Crossley 1993), and may be restricted to decaying woody substrate (Aoki 1967, Seastedt et al. 1989, Johnston and Crossley 1993).

The feeding habits of many species of oribatids are not yet known, but DWM may provide a greater range of possible food sources for more oribatids than the forest floor. DWM such as logs also accumulate litter, creating dense “pockets” of a preferred habitat for oribatids and is itself a source of food. Litter accumulating on another substrate such as DWM may also create a more favourable environment for fungal and bacterial growth, thus increasing a major food resource (Johnston and Crossley 1993, Jabin et al. 2004). Oribatid mites also use calcium compounds that accumulate in decaying wood and in fungal hyphae as cuticular hardening agents (Johnston and Crossley 1993). As well, DWM may provide more favourable microhabitat for oribatids than other forest floor habitat; DWM provides increased moisture, temperature and sheltered microhabitats, thus protecting oribatids against desiccation and predation (Johnston and Crossley 1993, Jabin et al. 2004). DWM provides increased structural complexity that creates several unique habitats, and oribatid species diversity has been shown to be positively correlated with microhabitat structural diversity (Anderson 1978). For some oribatid species, perhaps DWM fulfills some specific requirement during reproduction, development or some other life history stage; tolerance and response to different microhabitat characteristics, like soil pH (van Straalen and Verhoef 1997) can vary among species.

There were numerous species-specific changes in relative abundance with distance from DWM. Eight of the fourteen species collected only ON logs were represented by five or fewer individuals, suggesting either that DWM may be important habitat for rarely collected species or that DWM is not their primary habitat. This has been demonstrated for rare saproxylic beetles in Fennoscandia (Kaila et al. 1997, Jonsell et al. 1998), so DWM may benefit less common, potentially more specialized oribatid species as well. Other species associated with DWM may be present in low abundance in the forest floor, possibly associated with fragments of wood in the litter (Seastedt et al. 1989); therefore, an input of DWM may increase their numbers in soil and litter temporarily. For example, *C. labyrinthicus*, an indicator species for litter ON logs, is commonly found in natural and synthetic oak logs in mixedwood forest (Fager 1968). *Zygoribatula exilis* is found in low numbers but consistently on oak logs (Fager 1968) and also occurred (rarely) in litter ON logs in the present study. *Ceratozetes gracilis* and *C. cuspidatus* were indicator species for the grouping of soil samples as they are reduced or absent in samples ON logs. This is consistent with Johnston and Crossley (1993) who found that species in the genus *Ceratozetes* do not use wood as habitat. The three most frequently collected species in this study, *O. nova*, *S. pallidulus* and *E. minutissimus*, have a wide distribution, are commonly collected in forest litter and are thought to be primarily microphytophages or panphytophages (Luxton 1972), although, *S. pallidulus* has previously been more abundantly collected in decaying wood (Abbott et al. 1980, Johnston and Crossley 1993). In the present study, *S. pallidulus* was very abundant in litter ON the logs. These species likely benefit generally from the increased food availability and favourable microhabitats provided by DWM. The higher diversity found ON DWM compared to the forest floor is a result of an assemblage composed of several species that use multiple habitats in addition to DWM and other species that are more restricted in their habitat requirements (Seastedt et al. 1989, Johnston and Crossley 1993). A limitation to the interpretation of the results of this study is the lack of complete ecological data, and to a lesser extent taxonomic work, for the majority of species collected, particularly rarely collected species. Based on this research, there are probably several species of oribatids that could be considered truly saproxylic; however, much work remains in the fields of oribatid ecology and taxonomy, and species-level research is critical to improve our understanding of their patterns of occurrence in nature.

The quality, distribution and volume of DWM are altered in managed forests, which affect microhabitat variation associated with fallen dead wood and results in decreased species diversity and impacts ecosystem function (Hansen et al. 1991, Johnston and Crossley 1993, Haila 1994, Økland et al. 1996, Kuuluvainen and Laiho 2004, Hyvärinen et al. 2006). In order to focus efforts to maintain biodiversity at a landscape scale, it is necessary to study the contribution of microhabitat variation to local species richness (Niemelä et al. 1996). For saproxylic species with limited dispersal, survival depends on a balance between the input and loss of CWD at a smaller scale than those species with high dispersal abilities (Probst and Crow 1991, Haila 1994). Management plans that aim to protect vulnerable saproxylic species preserve as much large diameter CWD at various decay stages and include as many tree species as possible (Grove 2002, Jonsson et al. 2005); however, special consideration for the distance between patches of DWM and amount of substrate in each patch is necessary for taxa with low dispersal abilities (Haila 1994), like oribatid mites. Research focusing on smaller scale, single habitat features may provide greater insight into the forces structuring an assemblage or population and help to direct conservation efforts.

Conclusions

There was higher oribatid mite diversity and a distinct species composition on DWM in boreal forest. As well, there were species-specific changes in relative abundance with increasing distance away from DWM, which indicates an influence of DWM in structuring oribatid assemblages on the forest floor. DWM provides habitat heterogeneity and structural complexity for unique assemblages of oribatid mites and increases oribatid biodiversity in boreal mixedwood forest.

Forest management drastically reduces the amount of CWD in an area, which affects microhabitat variation associated with DWM and results in decreased species diversity and impacts ecosystem function (Hansen et al. 1991, Johnston and Crossley 1993, Haila 1994, Kuuluvainen and Laiho 2004, Hyvärinen et al. 2006); however, retention of live trees, snags and DWM during harvesting would provide habitat continuity in space and time (Lee et al. 1997, Grove 2002, Jonsson et al. 2005). The results of this study show that many oribatid species clearly benefit from DWM and would likely also benefit from greater retention of DWM and potential sources of dead wood in managed forests.

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Table 3.1: Relative abundance and raw species richness of oribatid mites collected from six decayed logs in a mixedwood boreal forest dominated by aspen (*Populus tremuloides*). Samples were taken four vertical layers and three horizontal distances: an upper litter layer (Litter), a soil layer (Soil), an upper wood layer (Upper wood) and an inner wood layer (Inner wood) sampled directly on top of the log (ON), directly beside the log (ADJ) and at least one metre away from the log and other DWM (AWAY).

Layer and distance	Relative abundance	Species richness
Litter ON	5623	67
Litter ADJ	5155	59
Litter AWAY	3120	50
Upper wood ON	585	29
Inner wood ON	373	29
Soil ADJ	725	21
Soil AWAY	286	19

Table 3.2: One-way ANOVA results for the effect of distance (ON, ADJ or AWAY) from DWM on oribatid mite relative abundance or raw species richness in either the litter (a) or wood/soil (b) layer. Data are means ±SE (n=6), and *post hoc* comparisons (Tukey's H.S.D. test (α=0.05)) are represented by different letters.

(a)

	Distance ON	 ADJ	 AWAY	$F_{2,15}$	p-value
Mean oribatid relative abundance in litter	6.72±0.52	6.67±0.47	6.14±0.62	2.15	0.15
Mean oribatid raw species richness in litter	3.63±0.17a	3.45±0.22ab	3.34±0.09b	4.49	**0.03**

(b)

	Distance ON (upper)	 ON (inner)	 ADJ	 AWAY	$F_{3,20}$	p-value
Mean oribatid relative abundance in wood/soil	4.09 ±1.16	3.85 ±0.86	4.48 ±0.91	3.51 ±1.06	0.98	0.42
Mean oribatid raw species richness in wood/soil	2.48 ±0.33 a	2.47 ±0.31 a	2.26 ±0.47 ab	1.79 ±0.55 bc	3.41	**0.04**

Table 3.3: MRPP results for the effect of distance (ON, ADJ and AWAY) from DWM on oribatid species composition in litter (a) and wood/soil (b). Significant differences (p-values) are in bold.

(a)

Comparison	p-value	*A* statistic
All distances	**0.0001**	0.099
ON and ADJ	**0.0016**	0.872
ON and AWAY	**0.0012**	0.122
ADJ and AWAY	0.1669	0.016

(b)

Comparison	p-value	*A* statistic
All distances	**0.001**	0.083
Upper ON and Inner ON	0.344	0.005
Upper ON and ADJ	**0.0021**	0.074
Upper ON and AWAY	**0.0059**	0.082
Inner ON and ADJ	**0.0024**	0.091
Inner ON and AWAY	**0.0025**	0.087
ADJ and AWAY	0.320	0.006

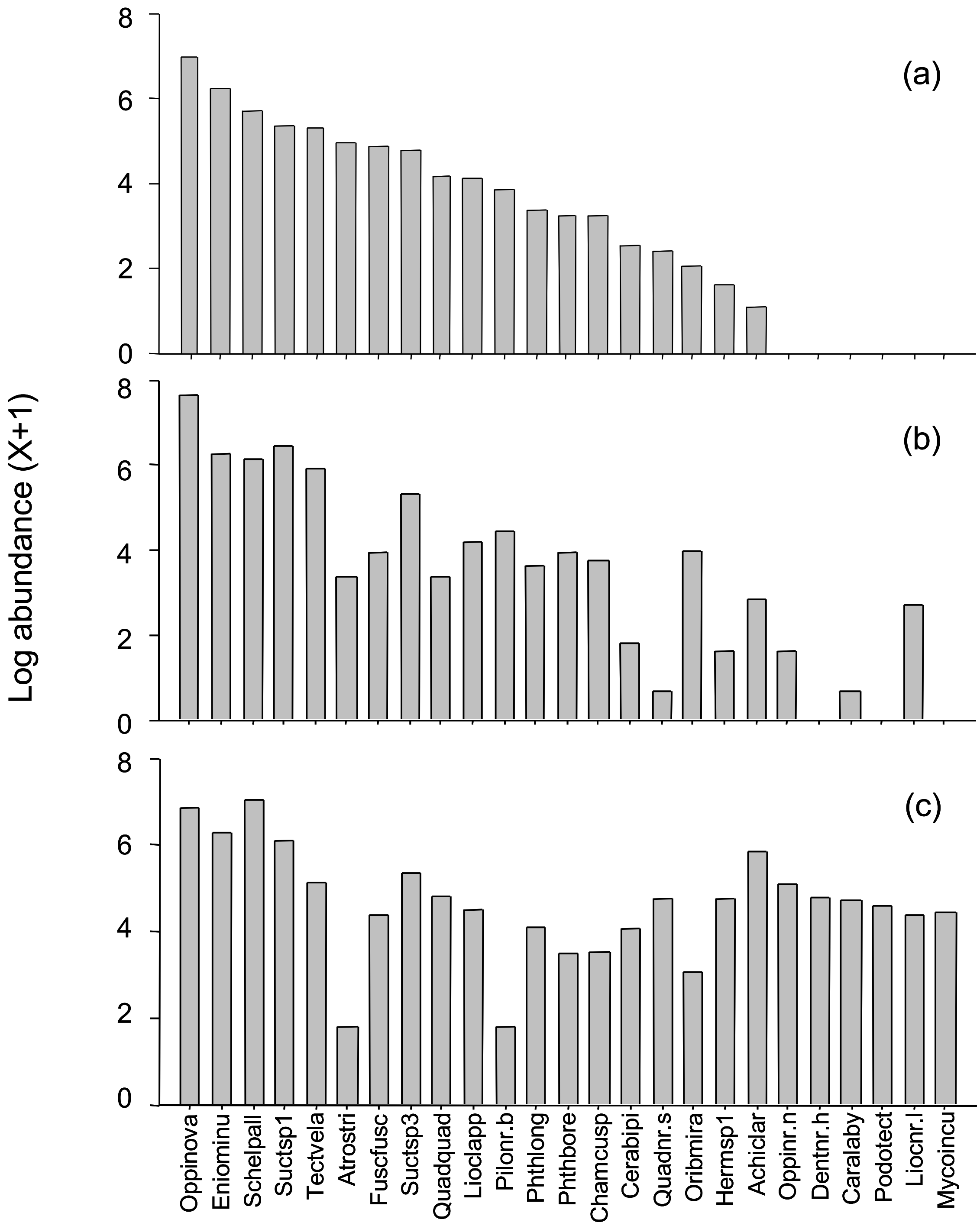

Figure 3.1: Rank abundance curves for oribatid mites collected in litter at three distances from logs: (a) at least one metre away from the log and other DWM (AWAY), (b) directly beside the log (ADJ) and (c) on top of the log (ON). Species are ranked from most to least common collected according to their abundance in the AWAY samples, and ranking is the same for all three graphs. Species codes with full names are found in Appendix 3.1.

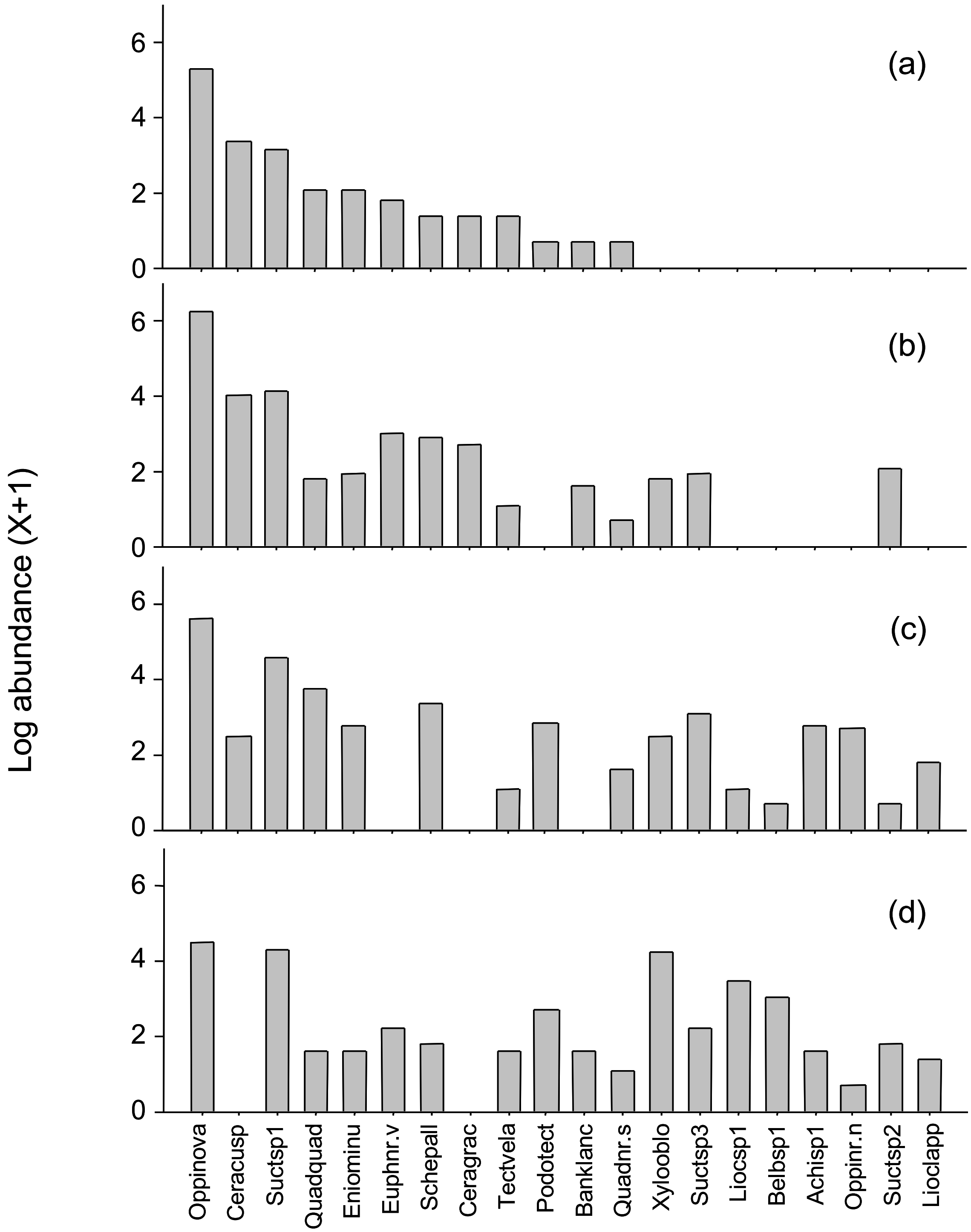

Figure 3.2: Rank abundance curves for oribatid mites collected in wood (upper and inner layers) and soil at three distances from logs: (a) at least one metre away from the log and other DWM (AWAY), (b) directly beside the log (ADJ), (c) upper wood on top of the log (ON) and (d) inner wood on top of log (ON). Species are ranked from most to least common collected according to their abundance in the AWAY samples, and ranking is the same for all three graphs. Species codes with full names are found in Appendix 3.1.

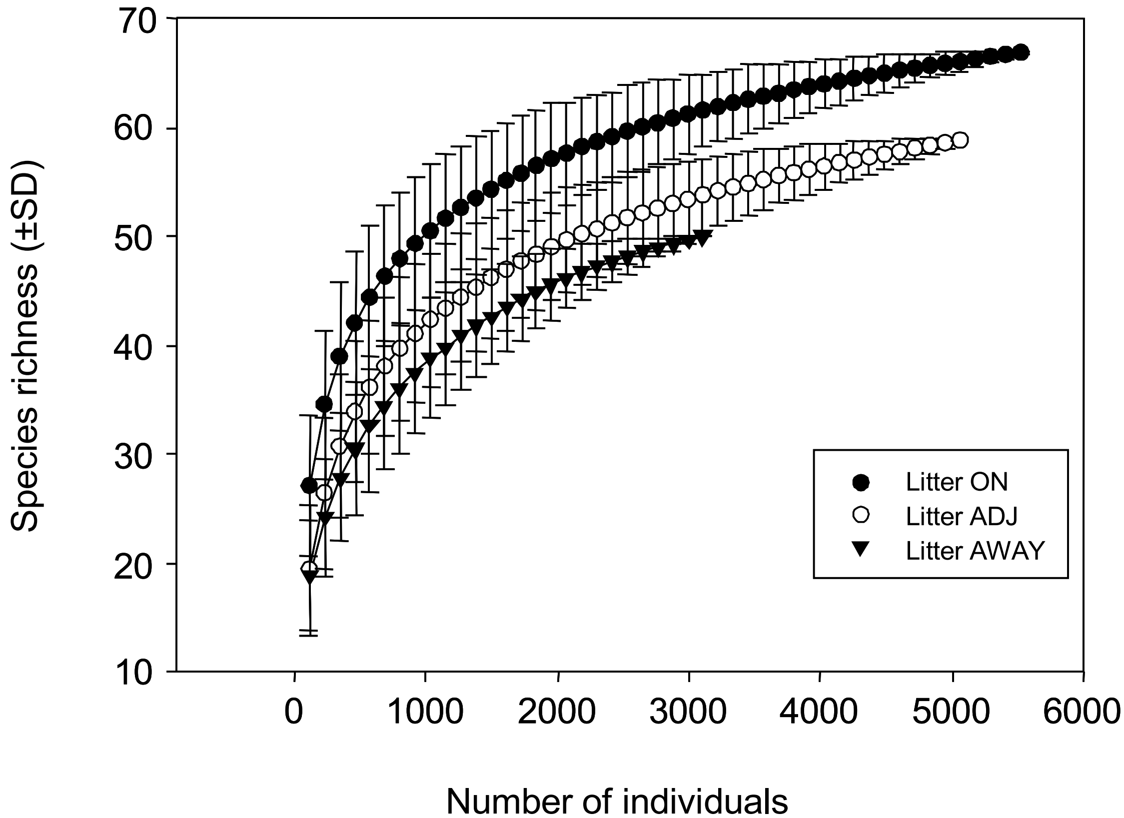

Figure 3.3: Rarefaction curves showing estimated species richness (±SD) for oribatid mites collected in litter at three distances from logs: on top of the log (ON), directly beside the log (ADJ) and at least one metre away from the log and other DWM (AWAY). Analysis is based on six samples per layer/distance combination and 76 species.

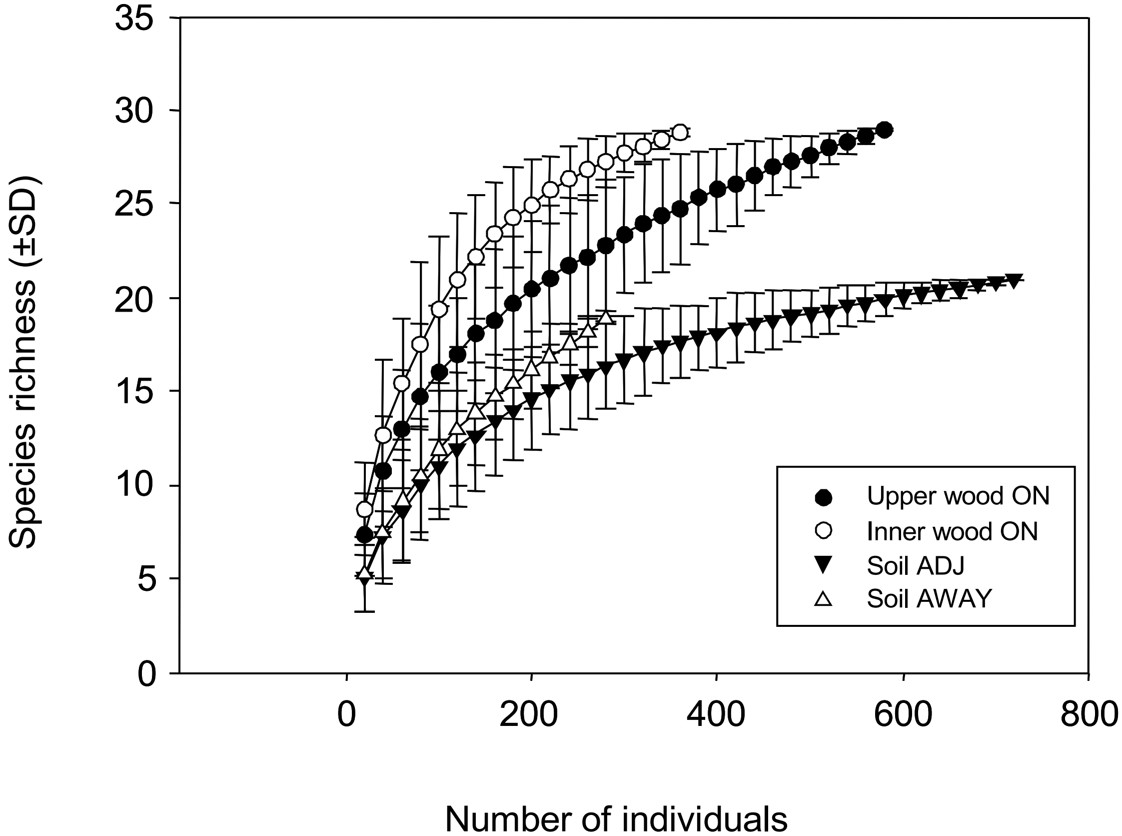

Figure 3.4: Rarefaction curves showing estimated species richness (±SD) for oribatid mites collected in wood (upper and inner layers) or soil at three distances from logs: wood on top of the log (ON), soil directly beside the log (ADJ) and soil at least one metre away from the log and other DWM (AWAY). Analysis is based on six samples per layer/ distance combination and 49 species.

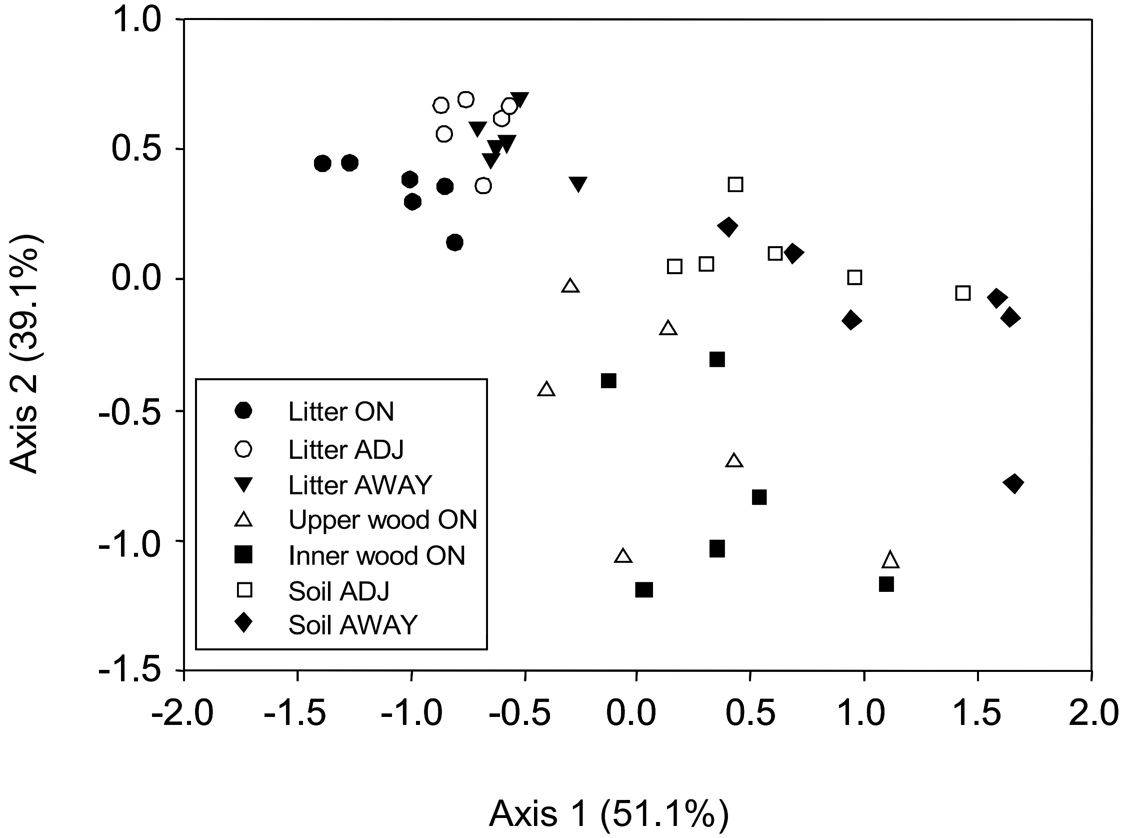

Figure 3.5: NMS ordination for oribatid mites collected in litter, wood (upper and inner layers) or soil at three distances from logs: litter and wood on top of the log (ON), litter and soil directly beside the log (ADJ) and litter and soil at least one metre away from the log and other DWM (AWAY). Data were log transformed ($x' = \log(x+1)$) prior to analysis, and the ordination is based on six samples per layer/distance combination and 80 species (axis 1: $R^2 = 0.51$; axis 2: $R^2 = 0.39$; final stress = 9.8; $p < 0.00001$; $A = 0.191$).

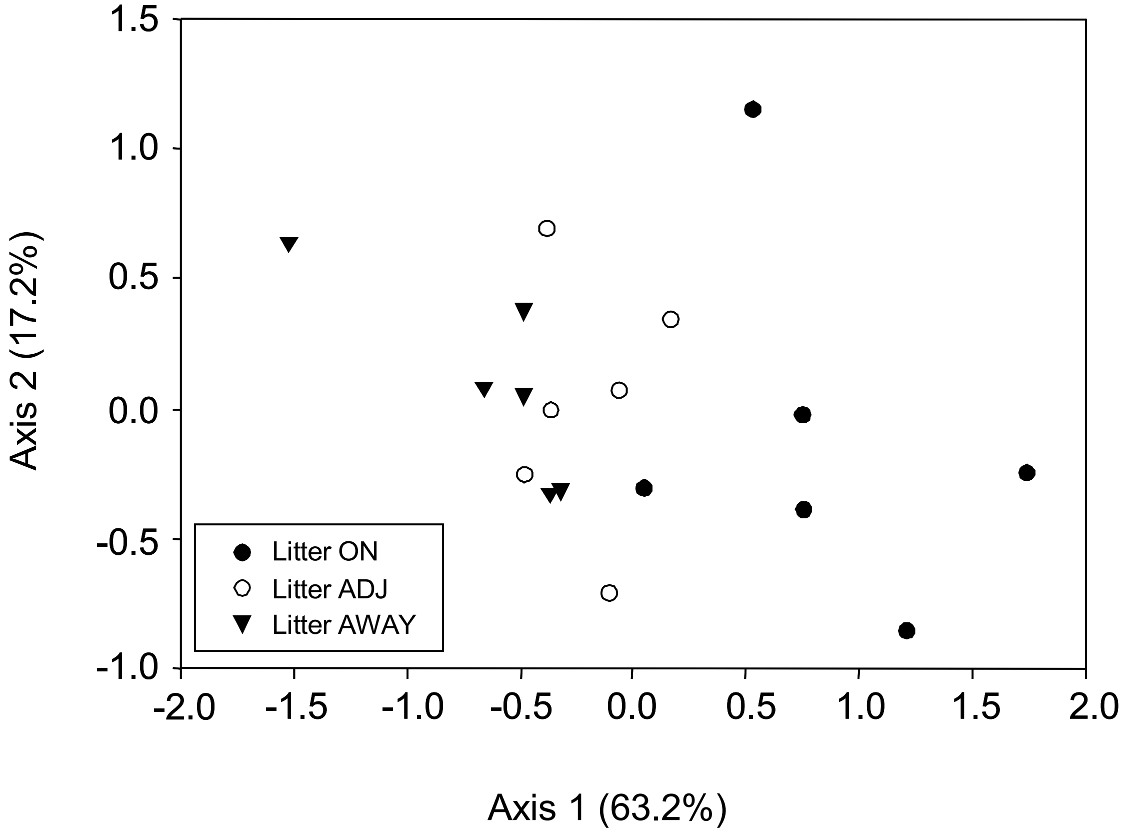

Figure 3.6: NMS ordination for oribatid mites collected in litter at three distances from logs: on top of the log (ON), directly beside the log (ADJ) and at least one metre away from the log and other DWM (AWAY). Data were log transformed (x′ = log (x+1)) prior to analysis, and the ordination is based on six samples per layer/distance combination and 76 species (axis 1: R^2=0.63; axis 2: R^2=0.17; axis 3: R^2=0.11 (not shown); final stress = 9.38).

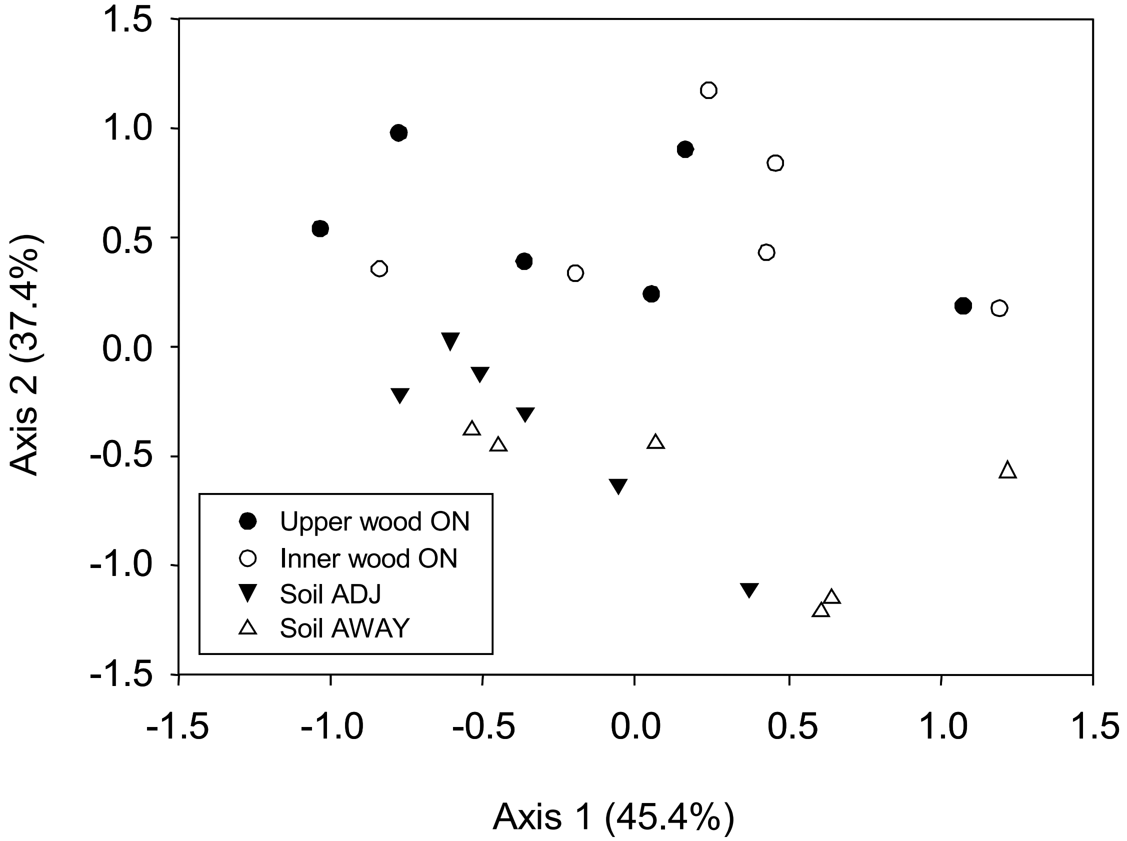

Figure 3.7: NMS ordination for oribatid mites collected in wood (upper and inner layers) or soil at three distances from logs: wood on top of the log (ON), soil directly beside the log (ADJ) and soil at least one metre away from the log and other DWM (AWAY). Data were log transformed (x′ = log (x+1)) prior to analysis, and the ordination is based on six samples per layer/distance combination and 49 species (axis 1: R^2=0.45; axis 2: R^2=0.37; axis 3: R^2=0.03 (not shown); final stress = 10.43).

Appendix 3.1: Oribatid mite species collected from six decayed logs in four vertical layers (Litter, Upper wood, Inner wood and Soil) and three horizontal distances (ON, ADJ and AWAY). (*) indicates significant indicator species.

Spcode	Family	Genus	Species	Authority	Litter ON	Litter ADJ	Litter AWAY	Upper ON	Inner ON	Soil ADJ	Soil AWAY	Total
Achiclar	Achipteriidae	*Achipteria*	*clarencei*	Nevin 1977	342*	16	2	6	0	1	0	367
Achisp1	Achipteriidae	*Achipteria*	sp1		56*	3	2	15	4	0	0	80
Adornr.p	Astegistidae	*Adoristes*	nr. *poppei*		1	0	0	0	0	0	0	1
Adorsp1	Liacaridae	*Adoristes*	sp1		0	1	0	0	0	0	0	1
Adorsp3	Liacaridae	*Adoristes*	sp3		0	1	1	0	0	0	0	2
Archluri	Phthiracaridae	*Archiphthiracarus*	*luridus*	(Ewing 1909)	7	3	0	0	1	0	0	11
Archsp2	Phthiracaridae	*Archiphthiracarus*	sp2		1	1	0	0	0	0	0	2
Atrostri	Phthiracaridae	*Atropacarus*	*striculus*	(Koch 1835)	5	28	139	0	0	0	1	173
Autolong	Autognetidae	*Autogneta*	*longilamellata*	(Michael 1885)	4	1	1	0	0	0	0	6
Banklanc	Thyrisomidae	*Banksinoma*	*l. canadensis*	Fujikawa 1979	1	5	0	0	4	4	1	15
Belbsp1	Damaeidae	*Belba*	sp1		37*	0	0	1	20	0	0	58
Caragran	Carabodidae	*Carabodes*	*granulatus*	Banks 1895	2	1	3	0	0	0	0	6
Caralaby	Carabodidae	*Carabodes*	*labyrinthicus*	(Michael 1879)	111*	1	0	0	0	0	0	112
Carapoly	Carabodidae	*Carabodes*	*polyporetes*	Reeves 1991	26	21	6	2	0	0	0	55
Cephcora	Cepheidae	*Cepheus*	*corae*	Jacot 1928	1	0	0	0	0	0	0	1
Cerabipi	Peloppiidae	*Ceratoppia*	*bipilis*	(Hermann 1804)	58	5	12	3	0	0	0	78
Ceracusp	Ceratozetidae	*Ceratozetes*	*cuspidatus*	Jacot 1939	0	23	3	11	0	55	28	120
Ceragrac	Ceratozetidae	*Ceratozetes*	*gracilis*	(Michael 1884)	1	28	22	0	0	14	3	68
Chamcusp	Chamobatidae	*Chamobates*	*cuspidatus*	(Michael 1884)	33	41	25	0	0	0	1	100
Chamsp1	Chamobatidae	*Chamobates*	sp1		32	11	0	1	0	0	0	44
Cultbicu	Astegistidae	*Cultroribula*	*bicultrata*	(Berlese 1905)	1	1	0	0	1	0	0	3
Dentnr.h	Achipteriidae	*Dentachipteria*	nr. *highlandensis*		118*	0	0	1	0	0	0	119
Eniominu	Eniochthoniidae	*Eniochthonius*	*minutissimus*	(Berlese 1903)	534	523	497	15	4	6	7	1586
Erembrev	Eremaeidae	*Eremaeus*	*brevitarsus*	(Ewing 1917)	6	2	5	0	0	0	0	13
Euphnr.f	Euphthiracaridae	*Euphthiracarus*	nr. *fulvus*		3	2	2	0	0	0	0	7
Euphnr.v	Euphthiracaridae	*Euphthiracarus*	nr. *vicinus*		5	26	24	0	8	19*	5	87
Euptorna	Cepheidae	*Eupterotegaeus*	*ornatissimus*	(Berlese 1908)	7	0	0	0	0	0	0	7
Fuscfusc	Ceratozetidae	*Fuscozetes*	*fuscipes*	(Koch 1844)	79	50	127	0	0	0	1	257
Grapsp1	Oppiidae	*Graptoppia*	sp1		8	3	3	0	0	0	0	14
Hafeniti	Tenuialidae	*Hafenferrefia*	*nitidula*	(Banks 1906)	1	0	0	0	0	0	0	1

Spcode	Family	Genus	Species	Authority	Litter ON	Litter ADJ	Litter AWAY	Upper ON	Inner ON	Soil ADJ	Soil AWAY	Total
Haplsp1	Haplozetidae	*Haplozetes*	sp1		19	25	2	3	0	0	0	49
Hemiquad	Scheloribatidae	*Hemileius*	*quadripilis*	(Fitch 1856)	2	0	1	0	0	0	0	3
Hermsp1	Hermanniellidae	*Hermanniella*	sp1		116	4	4	0	0	0	1	125
Hyporufu	Hypochthoniidae	*Hypochthonius*	*rufulus*	Koch 1835	0	0	0	0	1	0	0	1
Liebsp1	Scheloribatidae	*Liebstadia*	sp1		12*	2	1	0	0	0	0	15
Lioclapp	Brachychthoniidae	*Liochthonius*	*lapponicus*	(Trägårdh 1910)	90	65	60	5	3	0	0	223
Liocnr.b	Brachychthoniidae	*Liochthonius*	nr. *brevis*		31	11	9	0	1	0	0	52
Liocnr.l	Brachychthoniidae	*Liochthonius*	nr. *lapponicus*		79	14	0	0	0	0	0	93
Liocsp1	Brachychthoniidae	*Liochthonius*	sp1		0	0	0	2	31	0	0	33
Micrsimp	Euphthiracaridae	*Microtritia*	*simplex*	(Jacot 1930)	13	49	6	0	0	0	0	68
Mycoincu	Mycobatidae	*Mycobates*	*incurvatus*	Hammer 1952	85*	0	0	0	0	0	0	85
Nanhsp1	Nanhermanniidae	*Nanhermannia*	sp1		0	3	0	2	2	1	1	9
Neoglute	Ceratozetidae	*Neogymnobates*	*luteus*	Hammer 1955	8	0	0	0	0	0	0	8
Neoraura	Parakalummidae	*Neoribates*	*aurantiacus*	(Oudemans 1914)	1	0	1	0	0	0	0	2
Nothsilv	Nothridae	*Nothrus*	*silvestris*	Nicolet 1855	0	0	0	1	4	0	0	5
Oppinova	Oppiidae	*Oppiella*	*nova*	(Oudemans 1902)	935	2104	1080	277	89	509	196	5190
Oppinr.n	Oppiidae	*Oppia*	nr. *nitens*		162*	4	0	14	1	0	0	181
Oppitran	Oppiidae	*Oppiella*	*translamellata*	Willmann 1923	19	5	0	0	0	0	0	24
Oribbrev	Oribatellidae	*Oribatella*	*brevicornuta*	Jacot 1934	1	6	2	0	0	0	0	9
Oribheni	Oribotritiidae	*Oribotritia*	*henicos*	Niedbala 2002	3	0	0	0	2	0	0	5
Oribmira	Cepheidae	*Oribatodes*	*mirabilis*	Banks 1895	20	52	7	0	0	3	0	82
Oribquad	Oribatellidae	*Oribatella*	*quadricornuta*	(Michael 1880)	0	0	1	0	0	0	0	1
Oribsp1	Oribatellidae	*Oribatella*	sp1		2	0	2	0	0	0	1	5
Palahyst	Palaeacaridae	*Palaeacarus*	*hystricinus*	Trägårdh 1932	0	0	0	0	0	4	0	4
Paraleon	Scheloribatidae	*Paraleius*	*leontonycha*	(Berlese 1910)	4	5	10	0	0	0	0	19
Phthbore	Phthiracaridae	*Phthiracarus*	*boresetosus*	Jacot 1930	32	50	25	1	0	0	0	108
Phthlong	Phthiracaridae	*Phthiracarus*	*longulus*	(Koch 1841)	59	36	28	1	4	1	0	129
Pilonr.b	Galumnidae	*Pilogalumna*	nr. *binadalares*		5	84*	46	0	0	0	0	135
Platsp1	Camisiidae	*Platynothrus*	sp1		0	0	1	0	0	2	3	6
Platthor	Camisiidae	*Platynothrus*	*thori*	(Berlese 1904)	30	11	21	0	0	0	0	62
Podotect	Podopterotegaeidae	*Podopterotegaeus*	*tectus*	Aoki 1969	97*	0	0	16	14	0	1	128
Poecspic	Brachychthoniidae	*Poecilochthonius*	*spiciger*	(Berlese 1910)	0	6	2	1	0	0	0	9
Propnr.m	Phenopelopidae	*Propelops*	nr. *minnesotensis*		7	33	22	0	0	0	0	62

Spcode	Family	Genus	Species	Authority	Litter ON	Litter ADJ	Litter AWAY	Upper ON	Inner ON	Soil ADJ	Soil AWAY	Total
Protolig	Oribotritiidae	*Protoribotritia*	*oligotricha*	Maerkel 1963	0	4	1	0	3	1	0	9
Quadnr.s	Quadroppiidae	*Quadroppia*	nr. *skookumchucki*		114*	1	10	4	2	1	1	133
Quadquad	Quadroppiidae	*Quadroppia*	*quadricarinata*	(Michael 1885)	123	28	63	42	4	5	7	272
Rhysardu	Euphthiracaridae	*Rhysotritia*	*ardua*	(Koch 1841)	18	1	9	0	0	0	0	28
Schen.sp	Scheloribatidae	*Scheloribates*	n.sp.		6	6	2	0	1	0	0	15
Schepall	Scheloribatidae	*Scheloribates*	*pallidulus*	(Koch 1841)	1138	463	293	28	5	17	3	1947
Schesp1	Scheloribatidae	*Scheloribates*	sp1		0	1	0	0	0	0	0	1
Sellrost	Brachychthoniidae	*Sellnickochthonius*	*rostratus*	(Jacot 1936)	2	0	0	1	0	0	0	3
Subisp1	Oppiidae	*Subiasella*	sp1		12	6	0	0	0	0	0	18
Suctsp1	Suctobelbidae	*Suctobelbella*	sp1		448	633	210	97	73	62	22	1545
Suctsp2	Suctobelbidae	*Suctobelbella*	sp2		25	36	4	1	5	7	0	78
Suctsp3	Suctobelbidae	*Suctobelbella*	sp3		210	201	117	21	8	6	0	563
Suctsp4	Suctobelbidae	*Suctobelbella*	sp4		2	1	0	0	5*	0	0	8
Tectvela	Tectocepheidae	*Tectocepheus*	*velatus*	(Michael 1880)	166	371	200	2	4	2	3	748
Trhyamer	Trhypochthoniidae	*Trhypochthonius*	*americanus*	(Ewing 1908)	9	12	4	0	0	0	0	25
Xylooblo	Haplozetidae	*Xylobates*	*oblongus*	(Ewing 1909)	35	25	2	11	69*	5	0	147
Zygoexil	Oribatulidae	*Zygoribatula*	*exilis*	(Nicolet 1855)	3	0	0	0	0	0	0	3

CONNECTING STATEMENT

Chapter 3 demonstrated the importance of DWM to forest biodiversity by creating habitat for unique assemblages of oribatid mites. Both previous chapters rely on Tullgren-type funnels as an extraction method. Chapter 4 tests the extraction time for this type of passive extraction method.

CHAPTER 4: A TEST OF TULLGREN FUNNEL EXTRACTION DURATION FOR SAMPLING ORIBATID MITES IN BOREAL FOREST

Abstract

I tested the extraction duration for a Tullgren-type funnel extractor and recorded species accumulation with increasing extraction time. Litter samples were extracted in Tullgren-type funnels for five days, and at the end of each extraction day, the collecting cup was removed and replaced, and the oribatid mites in each cup were identified and enumerated. Most individuals and species were collected on the first day of extraction, and no individuals were collected on day five. This study demonstrates the importance of determining the duration of extraction appropriate for each specific apparatus used in biodiversity studies.

Introduction

Efficient extraction of microarthropods from organic material is critical to the success of soil ecosystem biodiversity studies. Tullgren-type extractors have 98% extraction efficiency for adult oribatid mites (Marshall 1972), and it is the preferred extraction method for organic soils, such as in forests (Crossley and Blair 1991, Edwards 1991). Extraction funnels such as these use a heat source to create a temperature and humidity gradient in the substrate that forces active soil fauna to migrate downward to avoid desiccation and eventually fall into a collection vial below. Although the use of Tullgren-type funnels as a method for extracting microarthropods from litter and soil has become fairly well established (Marshall 1972, Petersen and Luxton 1982, Crossley and Blair 1991, Edwards 1991), the length of extraction time varies widely in the literature, from as little as two days (Brand 2002) to ten days or more (Huhta et al. 1967, Marra and Edmonds 1998, Hasegawa 2001, Lindo and Visser 2004) or simply until samples are dry (Peck and Niwa 2005). Furthermore, there is little, if any, work on the effectiveness of a longer extraction period compared to a shorter one, nor is there documentation of the accumulation of individuals and species with increased extraction time. The objective of this chapter is to test the extraction duration for a Tullgren-type funnel extractor and to record species accumulation with increasing extraction time.

Methods

The study was conducted in Phase 1, Block 1 of the sylviculture et aménagement forestiers écosystémique (SAFE) research site located in the Abitibi region of Québec's northwestern boreal forest (48º86'N-48º32'N, 79 º19'W-79º30'W). Phase 1, Block 1 of SAFE consists of a cohort of aspen (*Populus tremuloides* Mchx.) dominated stands (67%), and contains five harvesting treatments: clear cut, one-third partial cut, two-thirds partial cut, prescribed burn-after-harvest and no harvest (uncut control). In June 2006, I collected leaf litter along 25 m transects (three replicates per harvesting treatment for a total of 15 samples), gently mixed and took a one litre sub-sample. Litter samples were extracted in Tullgren-type funnels for five days. At the end of each extraction day, the collecting cup was removed and replaced and oribatids in each cup identified to species, enumerated and preserved in 75% ethanol. Sixty-watt light bulbs were used as a heat source, and the heat in the extractors was gradually increased each day using a dimmer switch resulting in temperatures ranging from 28-30ºC on day one, 30-32ºC on day two and 32-34ºC on day three.

Results and Discussion

A total of 4, 869 adult oribatid mites in 67 species was collected. The number of individuals extracted was highest on day one (3, 530 individuals) and lowest on day five (0 individuals), the last day of extraction (Fig. 4.1), and most species (62) were extracted on day one (Fig. 4.2). Three species were extracted only on day two, and one species was extracted only on day four. As already established in the literature (Marshall 1972, Crossley and Blair 1991, Edwards 1991), it is clear that Tullgren-type extractors are effective for sampling oribatid mites from leaf litter. My work, however, was able to specifically determine the optimum length of time that the extractors should operate for aspen-dominated boreal forest in eastern Canada. These results show that after day three further accumulation of individuals or species is minimal; therefore, for these funnels, an extraction period of longer than three days does not provide any additional biological information. This information is useful for future work with mites in boreal systems. Ecological studies require replication, so reducing the time needed for extraction may enable researchers to collect additional data, and thus increase the level of confidence in inferences and increase the power of any statistical analyses. Therefore, with more information about extractor efficiency, future research can be designed differently, thus opening the door to new areas of biodiversity research with mites.

There are, however, other factors like substrate type, moisture content and maximum extraction temperature that may influence the extraction time appropriate for a particular apparatus. Future methodological studies on extractor efficiency could focus on these factors. Nevertheless, this study demonstrates the importance of determining the extraction duration of the specific apparatus used in biodiversity studies. Future research should also include assessment of extraction time appropriate for other habitats and taxa and would be a useful approach for long-term monitoring programs. The work presented here took little additional time, yet the long-term benefits could be significant; therefore, I suggest others include such methodological research along with focus on primary research objectives.

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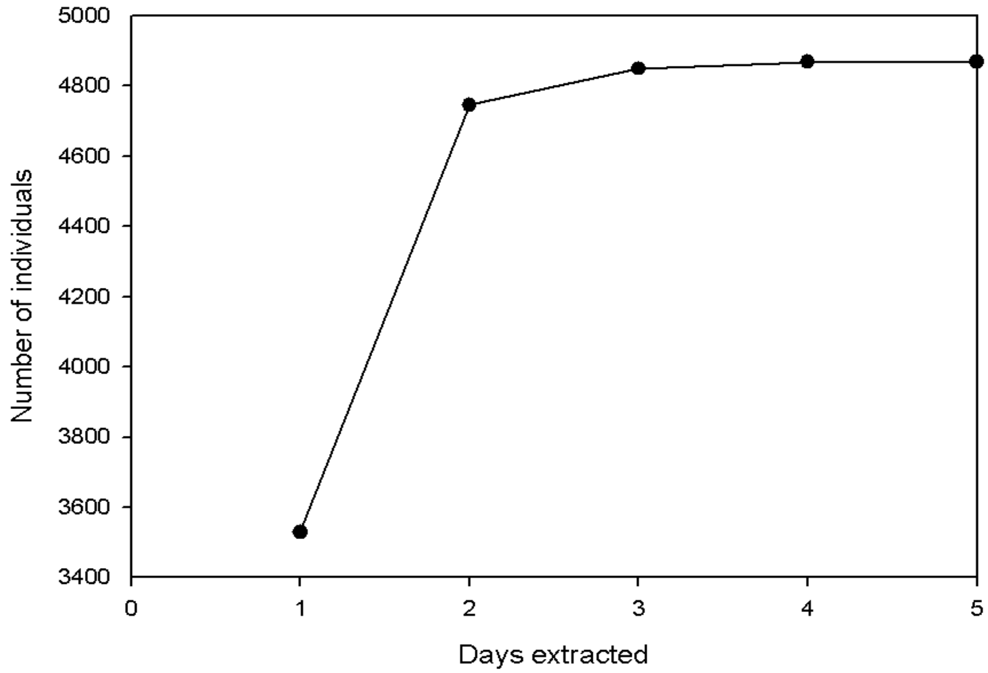

Figure 4.1: Cumulative number of adult oribatid individuals extracted from leaf litter each day using Tullgren-type extractors.

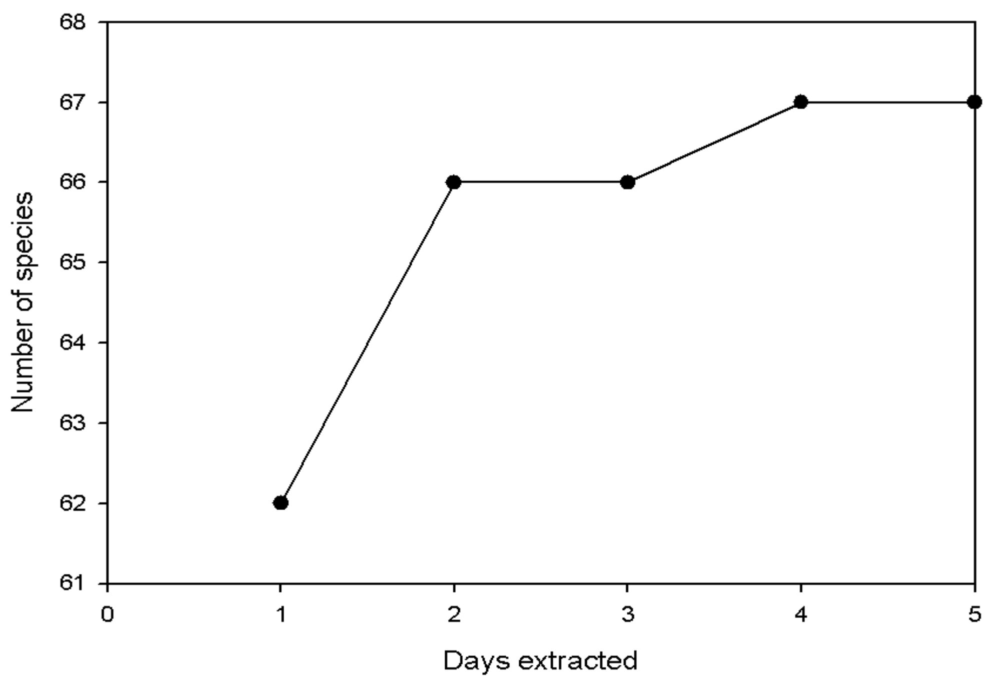

Figure 4.2: Cumulative number of oribatid species determined from adult specimens extracted from leaf litter each day using Tullgren-type extractors.

CHAPTER 5: GENERAL CONCLUSIONS

My thesis has demonstrated how different harvesting regimes influence oribatid assemblages in eastern boreal forest and revealed the importance of downed woody material (DWM) as habitat for oribatids. My research contributes to a growing body of literature about the effects of harvesting intensity on mites (Abbott et al. 1980, Bird and Chatarpaul 1986, Battigelli et al. 2004, Lindo and Visser 2004) and the association between DWM and oribatid diversity (Seastedt et al. 1989, Johnston and Crossley 1993, Marra and Edmonds 1998). My work has greatly contributed to our knowledge of species-level oribatid ecology in eastern Canadian boreal forest.

Chapter 2 investigated changes in oribatid assemblages under different harvesting regimes and found oribatid mite biodiversity was variably affected by different harvesting practices in eastern Canadian boreal forest, but regional factors may be more important in shaping oribatid assemblages. Eight years after harvest, clear cutting appears to have had a homogenizing effect on oribatid species composition, and partial cuts had more similar species composition to the uncut control within their respective blocks; however, burned habitat harboured a relatively distinct assemblage, particularly in soil. There was a change in species richness with even the lowest intensity harvest; in litter, diversity decreased with increasing harvesting intensity but in soil it increased, and for both layers the prescribed burns were significantly different from the other treatments. However, relative abundance in all harvesting treatments had returned to levels found in the control stands, suggesting a recovery in abundance after eight years.

Chapter 3 demonstrated that DWM such as logs increase oribatid mite biodiversity in boreal mixedwood forest likely by providing habitat heterogeneity and structural complexity on the forest floor (Anderson 1978, Seastedt et al. 1989, Johnston and Crossley 1993, Marra and Edmonds 1998, Kuuluvainen and Laiho 2004). The highest species richness was collected ON logs, and logs harboured a distinct oribatid species composition compared to the forest floor. There were relatively more oribatids collected ON and ADJ to logs than on the forest floor; however, there was too much variation in the data to demonstrate significant differences in abundances. As well, each layer (litter, wood and soil) exhibited a unique species composition and hosted a different diversity of oribatid mites. Furthermore, nine species not collected in Chapter 2 in any harvesting treatment were collected from logs in the study for Chapter 3, which reveals the uniqueness of DWM as a habitat for oribatids.

In Chapter 4, a test of the appropriate extraction duration for the Tullgren-type funnels used to obtain the data in both Chapters 2 and 3 revealed that three days was sufficient time to collect most individuals and species from leaf litter samples. This information is useful for future ecological work with mites in aspen-dominated boreal systems in that it will allow researchers to increase replication and thus the statistical power of analysis.

The approach of ecosystem-based management for conserving biodiversity by emulating natural disturbance is supported by both chapters. Chapter 2 suggests that eight years after harvesting, partial cutting may confer some benefit to oribatids by maintaining a more similar species composition and diversity as in uncut forest than in clear cuts. However, prescribed burning after clear cutting changed oribatid composition and species richness the most; therefore, this increasingly common practice may have detrimental effects on oribatid biodiversity if widely adopted. With the exception of the CC sites, species composition of the harvesting treatments was more similar within blocks than among blocks, suggesting that for less intense harvesting practices, regional factors (spatial scale of 1-10 km) like topography or soil properties could have a greater influence in structuring oribatid assemblages than harvesting regime. Chapter 3 clearly shows that DWM provides a critical resource for oribatids on the forest floor, and preservation of structural elements such as DWM will benefit oribatid biodiversity. Maintenance of oribatid biodiversity in managed forests may help to maintain key ecosystem processes such as decomposition and nutrient cycling (Seastedt 1984, Behan-Pelletier 1999, Heneghan et al. 1999). High species diversity is thought to contribute to ecosystem function and the stability and resilience of ecosystems by providing essential services (Tilman 1996, Naeem 2002, Loreau et al. 2001, Hooper et al. 2005). The results of this thesis support the acceptance and implementation of a wider forest management paradigm like ecosystem-based management that includes the retention of DWM;

however, while coarse-filter approaches for maintaining forest biodiversity are practical and useful, smaller scale studies are still needed to support the concept that structural complexity increases biodiversity.

Achieving habitat heterogeneity at all scales is important for preserving biodiversity (Hansen et al. 1991, Niemelä et al. 1996) but for management with a conservation focus, identification of the scale most relevant to biodiversity is fundamental. The most important scales of study from a forest management perspective are the stand level (10-100 ha) and the forest (100,000-10,000,000 ha) (Armstrong 1999), but for forest floor fauna tens of metres may be the most relevant scale (Niemelä et al. 1996). There may be doubt of the relevance of small-scale studies in determining the effects of ecosystem-level dynamics, and it has been suggested that for species with population dynamics that operate on a smaller scale, oribatids for example, responses can simply be extrapolated to a larger scale (Wiens 1989, Bengtsson et al. 2000). However, this thesis demonstrates the importance of both small-scale habitat heterogeneity and regional variation in structuring oribatid mite assemblages. Both of these factors must be taken into consideration when determining the effects of any disturbance at any scale, especially for species with low dispersal abilities. Microhabitat variation influences the distribution of forest floor species on a local scale (Niemelä et al. 1996) and thus research focusing on smaller scale single-habitat features may provide greater insight into the forces structuring an assemblage or population and help to direct conservation efforts.

The question of scale is particularly evident in the present study when examining changes in abundance and species composition with treatment (Chapter 2) or distance from DWM (Chapter 3). There were clear species-specific changes in abundance and composition with distance from DWM, but at the stand treatment level, I was unable to discern many strong patterns. In fact, treatment effects may become diluted with increasing scope. At different scales, distinct ecological patterns may be discernable and depending on the heterogeneity of the area, variation also changes with scale (Wiens 1989, Økland et al. 1996, Schiegg 2000). As well, some studies have shown that some variables are more important at a larger, landscape scale (Økland et al. 1996), while others find smaller-scale, local factors more important in shaping species assemblages (Schiegg 2000). The scale chosen for analysis often depends in part on the field of research, the objectives of study and the biology of the species in question (Wiens 1989). Oribatid mites offer a very unique perspective for ecological work and great potential to study species with low dispersal abilities, in particular when associated with specific habitats like DWM.

Future work could expand the areas explored by the current study. Larval and nymphal stages often use different resources in the same habitat; therefore, biodiversity studies that include all life-history stages will increase our general knowledge of oribatid ecology. Increasing the number of replicates to reduce variation in the data and sampling various habitat types such as logs of different species or decay stage would also be useful to understand the distribution of oribatids on the forest floor. As well, continued assessment and long-term monitoring at all scales is critical to determine the full effects of ecosystem-based management. An interesting problem to tackle would be what is termed the "peanut butter sandwich" problem by Johnston and Crossley (1993); while it is thought most oribatids feed on fungi, the question is whether they eat the entire sandwich (decaying wood) just to get at the peanut butter (fungi) or if they are after the wood itself. Even more basic to our understanding of oribatid ecology are the dynamics of single and multiple species metapopulations and how they may change at multiple scales under anthropogenic disturbance and with changing habitat availability. This is particularly relevant for species with poor dispersal abilities, like oribatid mites, for which proximity to new habitat is important.

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