

University of Alberta

**Gastropod diversity in the boreal mixedwood forest of
northern Alberta - variation among forest types and
response to partial harvesting**

by

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Abstract

Terrestrial gastropods are important decomposers, herbivores, and prey items in forest systems and constitute a poorly understood element of forest biodiversity in Canada. I studied gastropod assemblages in relation to forest cover type and in response to variable retention harvesting in the mixedwood boreal forest of northwestern Alberta. Gastropods were sampled using two methods: board traps and collection of litter samples. Gastropod assemblages were influenced by canopy composition, with most gastropods of the mixedwood showing a strong affinity for broadleaf dominated forests. Tree species mixture influenced gastropod distribution; basal tree area of either conifer or broadleaf trees was generally associated with gastropod distribution within a stand. Harvesting was clearly associated with increased abundance of many species 9 years post-harvest, however, abundance declined for other species. Harvesting with retention helps to maintain pre-harvest boreal gastropod assemblages and will likely conserve boreal gastropod assemblages if used as a tool for biodiversity management.

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Chapter 1 – Introduction

Forests are complex and dynamic ecosystems that provide many goods and services valued by humans and that support much of the world's biodiversity. Conserving biodiversity is a major focus of ecologically sustainable forestry (Canadian Council of Forest Ministers 2009, for example), and is central to most forest accreditation schemes. This thesis is focused on terrestrial gastropods, a group of dispersal-limited organisms that is poorly understood with respect to diversity and natural history in the boreal mixedwood forest. The structure of the boreal mixedwood forest has long been molded by natural disturbances such as fire, insects, disease and blowdown. Significant Canadian research effort is aimed at understanding how elements of the forest biota will be affected by imposition of large-scale industrial forestry on these landscapes. In order to achieve biodiversity conservation goals we need to understand more about species assemblages in relation to forest type, and in response to forest disturbances.

1.1 The Boreal Mixedwood Forest

Mixedwood forests, as the name implies, contain a mixture of canopy tree species. This mixture may be associated with greater productivity, more resilience, and richer biodiversity. These characteristics make mixedwood forests particularly interesting from a conservation perspective.

The boreal mixedwood forest encompasses a large proportion of the Canadian boreal landscape and is defined by a variable mixture of broadleaf and conifer trees in the canopy (Chen & Popadiouk 2002; MacDonald 1995; Rowe 1972). In Alberta, this forest type is dominated by trembling aspen (*Populus tremuloides*) as a canopy dominant in the early successional stages following disturbance. Over time it is replaced by later successional white spruce (*Picea glauca*) (Comeau et al. 2005).

Mixedwood forest composition, however, does not always reflect stand age (Macdonald et al. 2010). Successional pathways and timing can be influenced by many factors including pre-disturbance conditions, disturbance type, and landscape composition (Chen & Popadiouk 2002, Macdonald et al. 2010).

Many characteristics of mixedwood forests may be managed in support of sustainable forestry (Comeau et al. 2005). For example, mixedwood stands have attributes of both pure conifer and broadleaf stands and therefore apparently support higher species diversity relative to stands with a single species canopy (Hobson and Bayne 2000; Jacobs et al. 2007; Kernaghan et al. 2003; Macdonald and Fenniak 2007; Swallow et al. 2009). Mixedwood specialists have been observed in a temperate mixedwood, suggesting that mixedwood stands are distinct habitats with unique properties (Girard et al. 2004). Mixedwood stands are the most fertile and productive forests in the boreal region (MacDonald 1995). Aspen enhances growth of white spruce by improving nutrient cycling rates, controlling competition, reducing environmental extremes, and preventing pest attack (Man & Lieffers 1999).

Under current management regimes, the canopy composition of mixedwood forests is at risk of becoming less mixed (Hobson & Bayne 2000). This “unmixing” may pose risks for organisms that rely on habitats and food resources found only in a fine-grained canopy mixture. There are still many knowledge gaps in our understanding of how tree mixtures shape forest biodiversity. Understanding the influence of canopy composition on species assemblages will help us better manage mixedwood systems.

1.2 Landscape disturbances

Disturbance is an integral feature of boreal mixedwood forests and has shaped the landscape and the species that live there. Wildfire is a predominant natural disturbance in the boreal forest (Wein 1993). Boreal

communities are exposed to frequent severe fire disturbances, and there are many organisms that are considered to be specialists in immediate post-fire habitats (Muona & Rutanen 1994). Other organisms are able to survive fire disturbance by utilizing refuges, or through recolonization of burnt areas from nearby undisturbed patches (Kiss & Magnin 2003). In addition, fire in the boreal mixedwood promotes co-existence of multiple tree species in a single forested landscape (Bergeron et al. 2004).

The important role that disturbance plays in maintaining species composition on the landscape has been an organizing focus for modern forest management in Canada. Logging, in Alberta, has recently replaced fire as the principal boreal forest disturbance (Johnson et al. 1998; Pratt & Urquhart 1994). Under the widely used natural disturbance management model, managers attempt to “emulate natural disturbance” in the hopes that maintaining fire-like variability will conserve suitable habitats and landscape structure (Chipman & Johnson 2002; Schmiegelow et al. 2006).

Like fire, logging influences forest composition, structure, and function (Reich et al. 2001). Despite superficial similarities, fire and logging have very different ecological outcomes so that application of the natural-disturbance management model in the broad sense is not really possible (Niemelä 1999). Fortunately, there are useful tools that have come out of this management approach, like variable retention harvesting, which has shown to be useful in conserving biodiversity (Franklin 1997; Rosenvald & Löhmus 2007).

Variable retention harvesting is the process of leaving standing trees on the landscape during harvest, removing only a proportion of the available timber. This harvesting approach has several objectives, as outlined in Macdonald and Fenniak (2007), including: preserving species associated with mature forest, moving mature forests towards structure and composition of old forests, supporting particular biota, and leaving biological legacies to encourage faster post-harvest recovery of biodiversity. In effort to meet these goals, the amount of retention required

on the landscape in order to conserve biodiversity in a variety of animal and plant taxa is currently an area of much research (Caners et al. 2010; Craig & Macdonald 2009; Work et al. 2010).

1.3 Forest-dwelling gastropods

There are many organisms, like forest-dwelling gastropods, for which we know very little about responses to harvesting disturbance. Although terrestrial gastropods have been little-studied, they comprise an important part of forest faunal diversity. They are the only terrestrial representatives of the ancient phylum Mollusca and therefore contribute a unique element and poorly understood functional aspect to forests. Gastropods are crucial decomposers in many systems, and are thus important for nutrient and energy cycling (Jennings & Barkham 1979; Mason 1970). As well as being detritivores, many terrestrial gastropod species are also herbivores, influencing plant population and community dynamics mainly through seed consumption and the removal of leaves from seedlings (Ferner 1987). Gastropods are also an important food source for many other forest fauna. They are a preferred prey for many carabid beetles, spiders, and harvestmen (Digweed 1993, Nyffeler & Symondson 2001). Snails also serve as a main supply of calcium for forest passerine birds, and this resource is crucial for egg production (Graveland et al. 1994). Given the probable importance of gastropods in forest ecosystems, ecologically sustainable forest management requires an understanding of how their distribution, abundance, and composition are affected by anthropogenic disturbance.

The abundance and diversity of gastropods are influenced by a variety of environmental factors. Gastropods are particularly sensitive to their environment due to physiological limitations which have profoundly constrained the range of locations that they are able to occupy. High moisture levels are essential because gastropods are desiccation sensitive, in all life stages, and require moisture for respiration and

locomotion (Barker 2001). This restricts them to areas of higher moisture (Asami 1993) and reduced temperature extremes (Hawkins et al. 1998). Soil characteristics also are strongly correlated with gastropod distribution (Martin & Sommer 2004). The majority of terrestrial gastropods reside within the soil which is an optimum living environment, with consistent moisture, plenty of decomposing matter for food, and necessary minerals. The most important mineral for a snail is calcium as it is a “constituent of many of the animal’s structures and molecules” (Dallinger et al. 2001).

Gastropod distribution is also influenced by forest vegetation. High vegetation cover is preferred as it maintains moisture and shade, as well as providing food (Kiss and Magnin 2003). Gastropods primarily eat senescent plant material, although they are known to browse plants (Westerbergh and Nyberg 1995). Areas that differ in vegetation harbour different gastropod assemblages (Barker and Mayhill 1999).

Many factors that influence gastropod distribution are altered by forest harvesting, yet little is known about the responses of gastropods to this disturbance. The few existing studies that have investigated this relationship have found highly varied responses and have generally been conducted on small scales (Baur & Baur 1992), or have only considered one type of harvest treatment (Hylander et al. 2004) or stand type (Baur & Erhardt 1995). Gastropods are thought to be good indicators of disturbance because of their low vagility and sensitivity to microclimatic changes (Theenhaus & Scheu 1996). These characteristics give gastropods much potential as indicators of forest disturbance and recovery.

1.4 EMEND Project

Following an increasing interest in the natural disturbance paradigm of forest management, The EMEND (Ecosystem Management Emulating Natural Disturbance) project was designed and established. A central goal of EMEND was to test how much retention should be left on boreal

mixedwood landscapes in order to maintain ecosystem function (Spence & Volney 1999, Work et al. 2010). This 1000-ha experiment is located in the Clear Hills Upland, Lower Foothills Ecoregion of Alberta, approximately 90km north-west of Peace River (56°46'13"N, 118°22'28"W) in boreal mixedwood forest (Kischuk 2004; Work et al. 2004). The mean January temperature is -17.7°C and the mean July temperature is 15.9°C (Alberta Environmental Protection 1994 as cited in Kischuk 2004). Mean annual precipitation is 431 mm (Atmospheric Environment Service 1982 as cited in Kischuk 2004). The soils in this area are primarily Luvisolic with limited occurrences of Brunisolic, Gleysolic, and Solonchic soils (Kischuk 2004). The elevation ranges between 677 to 880 m above sea level (Kischuk 2004).

The forest stands used in the EMEND study area range in age from 62-124 years (Spence & Volney 1999). The dominant tree species are trembling aspen (*Populus tremuloides* Michx.), balsam poplar (*Populus balsamifera* L.), and white spruce (*Picea glauca* (Moench) Voss). The most common understory shrubs include low bush cranberry (*Viburnum edule* (Michx.) Raf), prickly rose (*Rosa acicularis* Lindl.), buffaloberry (*Shepherdia Canadensis* (L.) Nutt.), green alder (*Alnus crispa* (Ait.) Turrill), and river alder (*Alnus tenuifolia* (Du Roi) Clausen).

The EMEND experimental site consists of 100 10-hectare compartments, treated according to a two factorial design, that has been replicated 3 times. The two factors included in the experiment are cover type and harvest treatment. The first factor, cover type, consists of four forest cover types that represent a compositional gradient related to natural post-disturbance succession. The earliest successional cover type, deciduous dominated (DDOM), is represented by stands with >70% deciduous trees in the canopy. The early-mid successional cover type is deciduous dominated with spruce understory (DDOMU), consisting of stands with >70% deciduous trees in the canopy and an evident understory of spruce. This is followed in succession by the late-mid

mixedwood cover type (MX) with 40-60% spruce and aspen cover in the canopy. The latest successional cover type, conifer dominated (CDOM), consists of stands with >70% spruce trees in the canopy.

The second factor in the EMEND design is disturbance treatment. Disturbance treatments involving fire and/or harvest have been applied but this study focuses on the harvest treatments. Experimental compartments were treated with one of seven retention harvest treatments, consisting of variable levels of dispersed green tree retention as a proportion of original stand stem density: clear cut (with 1-2 % retention), 10% retention, 20% retention, 50% retention, 75% retention, and unharvested controls (100% retention). Stands were harvested in the winter of 1998/1999 in a modified uniform shelterwood pattern. All harvesting was completed using feller-bunchers that ran on 5-m wide machine corridors oriented N-S in each compartment (Fig. 1-1). Trees were harvested from the machine corridors by reaching into the 15-m wide retention strips and removing stems by prescription aimed at achieving the desired reductions in stem density.

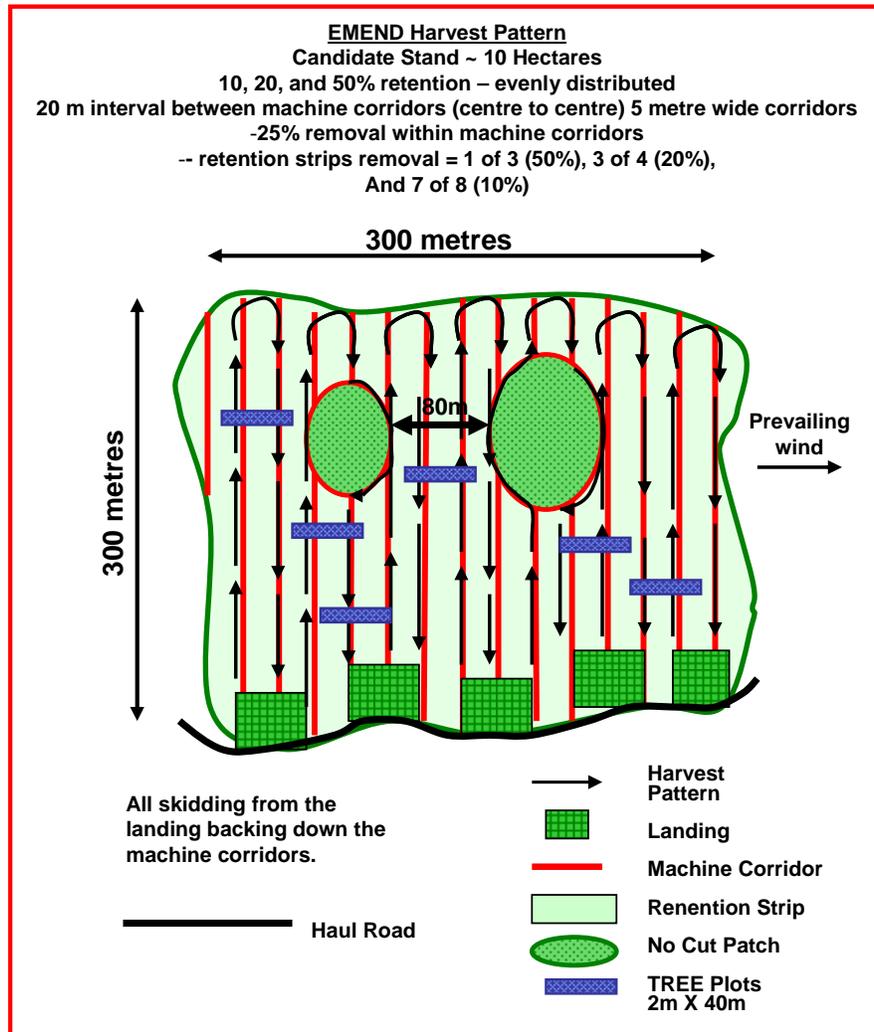


Figure 1-1: Harvest layout of variable retention harvest treatments at EMEND (after D. Sidders, from EMEND website: <http://www.emend.rr.ualberta.ca/>).

1.5 Thesis Objectives

The objectives of my thesis are to: i) conduct a survey of gastropod diversity and abundance in the four cover types of the EMEND landscape; and ii) examine the effects of partial and complete harvesting on the litter-dwelling gastropod fauna in mixedwood stands to clarify any conservation concerns.

Chapter 2 focuses on the broad influence of forest cover type on gastropod assemblages. I will show that different gastropod assemblages exist in the four forest cover types at EMEND, and that tree mixture in the

boreal mixedwood has an important role in shaping gastropod assemblages on the landscape.

Chapter 3 presents the effects of variable retention harvest on gastropod assemblages in mixedwood stands. I will show that increasing harvest intensity causes an increase in gastropod abundance, and instigates shifts in gastropod assemblage structure including notable declines in certain species. In this chapter I also investigate the significance of local heterogeneity produced by the harvest itself and will show that most gastropods actually respond favourably to machine corridors.

The gastropod fauna has not been surveyed in many areas of Alberta. In fact, no studies of this type have been published from the northern mixedwood forest of Canada. The EMEND project provided an excellent opportunity to increase our understanding of gastropod responses to forest harvesting and provide information about this interesting group of organisms for use in development of sustainable forest management strategies in Canada.

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Chapter 2 – Gastropod diversity in varying forest types of the boreal mixedwood

Introduction

The boreal mixedwood forest is an intricate patchwork of broadleaf and coniferous trees produced by disturbance events and successional development (Chen & Popadiouk 2002). These patches can be large homogenous stands dominated by either conifer or broadleaf trees or relatively small islands in stands characterized by multiple patches of both types of tree. Different forest cover types support unique ecological communities for many biotic groups, like forest arthropods (Work et al. 2004) and understory plants (Macdonald & Fenniak 2007). In Alberta, the mixedwood comprises a substantial proportion of the managed forest area, and has become a major focus for forest management research (Comeau et al. 2005, Macdonald et al. 2010). Understanding how biodiversity varies across forest cover types will help us to better manage for persistence of ecological communities.

We know little about how terrestrial gastropods are influenced by forest cover type in the boreal mixedwood. Most gastropods reside in the soil, and soil characteristics, which are strongly influenced by canopy leaf input, are strongly correlated with gastropod distribution (Martin & Sommer 2004). Most gastropods are physiologically limited to areas of higher soil calcium and pH, and these areas are generally associated with broadleaf trees (Martin & Sommer 2004). Understory vegetation (Barker & Mayhill 1999) and overstory, which mediates understory composition (Macdonald & Fenniak 2007, Chávez & Macdonald 2010), contribute to the organization of gastropod assemblages by influencing microhabitat (Kiss & Magnin 2003) and providing food. Although most forest-dwelling gastropods are considered to be generalist feeders, individuals of some species preferentially browse certain plant species (Westerbergh & Nyberg 1995). Such gastropods, in particular, tend to be found near the plants that they browse (Grime & Blythe 1969).

Past studies of gastropod assemblages in boreal mixedwood systems reveal that tree composition does influence their distribution on the landscape at both coarse and fine scales. Kralka (1986) found that most gastropod species were found in areas dominated by broadleaf tree vegetation, while others were associated with conifer dominated habitats. At a relatively smaller scale, macroinvertebrates, including gastropods, have been shown to be more abundant in small broadleaf patches that occur in black spruce dominated stands compared to the surrounding black spruce matrix (Leganière et al. 2009). Gastropods tend to show clumped distributions at a microsite scale (Heller 2001), suggesting that small patches may play an important role in gastropod distribution in mixedwood systems.

Baseline information about gastropod distribution patterns in relation to vegetation prior to harvest is rare but critical to ensure maintenance and recovery of gastropod assemblages following harvest. The aim of this chapter is to explore gastropod distribution patterns in mixedwood stands that have not been subjected to harvest. Specifically, my objectives were to describe gastropod assemblages in relation to forest cover types and to define environmental characteristics associated with to these patterns. Given that different species have different habitat requirements, I expected that species assemblages would vary among different forest cover types and that tree composition would be evident in gastropod distribution patterns. I also expected that the set of environmental parameters that are driving gastropod assemblages would differ among forest cover types.

Materials and Methods

Site selection and study design: This study was conducted in the unharvested 'control' compartments of the EMEND (Ecosystem Management Emulating Natural Disturbance), located approximately 90 km northwest of Peace River, Alberta (56°46'13"N, 118°22'28"W) (Spence

et al. 1999, Work *et al.* 2004, 2010). Each compartment was approximately 10 ha in size, and represented one of four forest cover types: deciduous dominated (DDOM), deciduous dominated with spruce understory (DDOMU), mixedwood (MX), or coniferous dominated (CDOM). Three such compartments were available for study in each cover type, for a total of 12 stands. (See Chapter 1 for a complete site description).

Sampling methods: Six random sampling points were established (statistically these are sub-samples) within each of the experimental compartments [4 forest types * 3 compartment replicates * 6 sample points = 72 sample points]. Locations for these sampling points were established 30m north of the start of each of six randomly located mensuration transects that had been established in each compartment at the beginning of the project. Each sampling point was used to establish the center of a 5m x 5m plot which was divided into four 2.5m x 2.5m subplots for study of gastropods.

I used two techniques to sample the overall gastropod diversity. Firstly, soil-dwelling species were studied in 1.5 dm² LFH layer samples (organic layer found just above mineral soil) taken from the center of each subplot, from four of the six plots in each compartment. These samples were later dried, and fractioned using a motorized sieve shaker through a series of 7 sieves with mesh sizes ranging from 4.0 – 0.5 mm. All sieved layers were sorted by hand for gastropod shells under a magnification lamp. Snails collected from each of the four subplots were pooled across each plot [i.e., 4 forest types * 3 compartment replicates * 4 sample plot = 48 pooled samples]. LFH depth was measured during sample collection, and moisture was also assessed gravimetrically as the difference between mass of the samples before and after drying. I used board traps as a second sampling method. These were 25 x 60 cm masonite hardboards embedded under a layer of upper leaf litter just outside of the six 5m² sample plots. Gastropods were collected on the upper and lower surfaces

of these boards every two weeks for a total of five collections between June and August, 2007. Specimens found during board collections were preserved in 70% ethanol.

In addition to LFH moisture and depth, other environmental parameters were measured at each sampling location. Basal area of conifer and broadleaf trees and canopy closure were measured at each plot using a wedge prism and a convex spherical densiometer respectively. Forest structure within each plot was further described by visually estimating percent cover of coarse woody debris (laying dead wood with a diameter ≥ 7 cm), shrub vegetation, herb vegetation, and moss vegetation separately.

All gastropods were identified in the laboratory to the lowest possible taxonomic level, with the aid of Forsyth (2004) and the Jim van Es Marine Invertebrate and Malacology collection (Department of Biological Sciences, University of Alberta). Most individuals were identified to species level, except for specimens of the genus *Succinea*, as this group has not been well described in Alberta. The few collected individuals of this genus were treated as a single species for analysis.

Data analysis: To look for differences in abundance of gastropods among forest cover types, I used a mixed linear model ANOVA. Compartments were treated as experimental units, so gastropod abundances of all plots in a compartment and across all collections were summed for this analysis. Post-hoc comparisons of least squares means was used to explore which cover types differed significantly from one another. Calculations were done using Proc Mixed in SAS (v. 9.2 Littell et al. 1996). To compare differences in richness between cover types, individual-based rarefaction curves were used. These curves are created by randomly sampling individuals from the total number that were collected and plotting the number of species against the number of individuals in that randomly selected subsample. This method controls for differences in species richness as result of differences in abundance by

allowing the comparison of richness at a similar abundance (Colwell 2009). Rarefaction curves were computed using the R package (v. 1.17-2 Oksanen et al. 2010).

Permutational multivariate analysis of variance (PERMANOVA) was used to determine if species composition differed statistically among forest cover types. This was calculated using absolute abundances of species from each compartment (N=72) in PC-ORD (v. 5.06 McCune & Mefford 2006). The permutation-based test-statistic is based on a distance matrix of calculated distances between each pair of sampling units (Anderson 2005). All PERMANOVA tests were calculated using summed species abundance per compartment with Bray-Curtis dissimilarity, and tests of significance were performed using 4999 unrestricted permutations.

Indicator species analysis (Dufrêne & Legendre 1997) was used to identify species that were indicative of each cover type. This method calculates an indicator value between 0 (no indication) and 100 (perfect indication) based on the relative abundance of a species and its relative frequency of occurrence (in groups of sites) (McCune & Grace 2002). Indicator values were tested for significance using a Monte Carlo randomization procedure, with 4999 permutations. Indicator species analysis was computed in PC-ORD (v. 5.06 McCune & Mefford 2006).

To visualize differences in assemblage composition among forest cover types and to investigate potential environmental associations causing these differences, a constrained ordination technique called Redundancy Analysis was used in CANOCO (v. 4.5, ter Braak & Šmilauer, 2002). This method uses multivariate environmental data to explain variance in a species data set (Legendre & Legendre 1998). This method is the multivariate analogue to regression, maximizing the proportion of the total sum of squares in the species variables that can be explained by redundancy components extracted from the environmental variables (Takane & Jung 2006). Examination of the gradient length in a detrended

correspondence analysis (ter Braak & Šmilauer 1998) suggested that the gastropod assemblage data met the assumption of linear response to the environmental variables. Forward selection was used to determine which environmental parameters influenced compositional patterns, as represented by the ordination. Cover type was included as a categorical dummy variable in the ordination. Subsequent constrained ordinations with forward selection were constructed for each cover type separately so that cover types could be compared. I used redundancy analysis when the linearity assumptions were met by the data and canonical correspondence analysis when they were not (ter Braak & Šmilauer 1998). All species data were log-transformed prior to analyses. The significance of all ordinations was tested using a Monte Carlo randomization procedure to test whether the relationship between the species and environmental data is stronger than expected by chance (McCune & Grace 2002).

To further investigate gastropod assemblage structure, dominance values (Pinzón & Spence 2010) were calculated for species in each forest cover type. Dominance values (DV) were calculated for each species as a product of proportional presence and proportional abundance relative to the other species in the assemblage. Dominance plots were constructed by plotting proportional presence (AP) against proportional abundance (w), as explained by Pinzón & Spence (2010). These plots were split into four quadrants using the midvalues of AP and w . I take the upper right quadrant to identify dominant species, the lower right quadrant subdominant species, and the upper left quadrant locally dominant species. The lower left quadrant is further split into two using the quarter w value, and is interpreted to represent common and uncommon species respectively, in the right and left subdivisions.

Results

In total, 15 species of gastropods belonging to 10 families were found across all cover types (Table 2-1; Appendix 2-A). The board traps

captured a total of 934 individuals and 9 species, with 1 species (the single slug species, *Deroceras laeve*) being collected only by this sampling method. The soil sampling method, though much more time consuming, captured 4146 individuals and 14 species, with 6 species being unique to this method.

Table 2-1: Gastropods collected from board traps and soil samples.

Family	Species	Sampling Method
Succineidae	<i>Succinea</i> sp.	Boards, Soil
Cochlicopidae	<i>Cochlicopa lubrica</i> (Müller)	Boards, Soil
Vertiginidae	<i>Vertigo cristata</i> (Sterki)	Soil
	<i>Vertigo gouldii</i> (Binney)	Soil
	<i>Vertigo modesta</i> (Say)	Soil
	<i>Columella edentula</i> (Draparnaud)	Soil
	<i>Columella columella</i> (von Martens)	Soil
Punctidae	<i>Punctum minutissimum</i> (Lea)	Soil
Discidae	<i>Discus shimekii</i> (Pilsbury)	Boards, Soil
	<i>Discus whitneyi</i> (Newcomb)	Boards, Soil
Gastrodontiidae	<i>Zonitoides arboreus</i> (Say)	Boards, Soil
Euconulidae	<i>Euconulus fulvus</i> (Müller)	Boards, Soil
Oxychiliidae	<i>Nesovitrea electrina</i> (Gould)	Boards, Soil
Agriolimacidae	<i>Deroceras laeve</i> (Müller)	Boards
Vitrinidae	<i>Vitrina pellucida</i> (Müller)	Boards, Soil

Abundance. The total abundance of gastropods differed significantly among forest cover types for board trap samples (ANOVA, $F_{3,8}=7.11$, $p=0.01$) (Fig. 2-1A) and soil samples (ANOVA, $F_{3,8}=4.76$, $p=0.03$) (Fig. 2-1B). For both sampling methods, a post-hoc comparison of least squares means indicated that the DDOM cover type had significantly more gastropods than the other cover types.

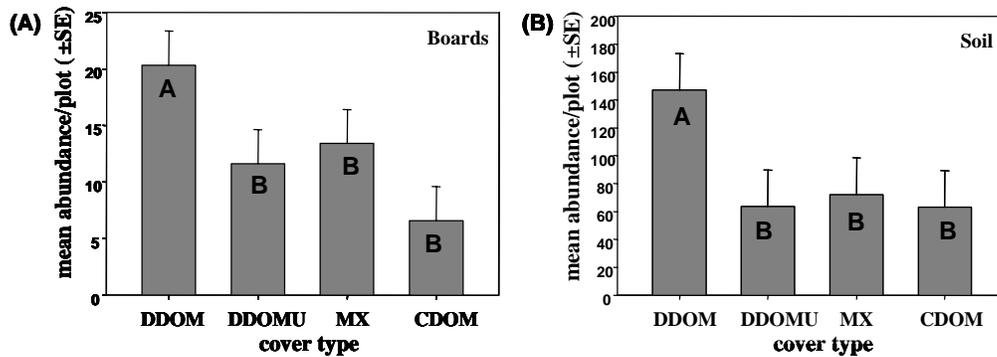


Figure 2-1: Mean abundance of gastropods per plot (subsample, N=18) in the four forest cover types using a board trap sampling method (A) and a soil sampling method (B). DDOM = deciduous dominated, DDOMU = deciduous dominated with coniferous understory, MX = mixed coniferous and deciduous, and CDOM = coniferous dominated.

Species Richness. For both sampling methods, rarefaction estimates of gastropod species indicated that samples from the DDOM cover type accumulated species faster than the other cover types, and had the greatest estimated richness (Fig. 2-2). For board trap samples, the DDOMU, MX, and CDOM cover types were all similar to one another, and different from the DDOM cover type (Fig. 2-2A). The curves for these cover types reached asymptotes at 7 species, which indicated that the sampling effort in these cover types most likely captured the full richness possible by this sampling technique. For soil samples, the DDOM and DDOMU cover types were more similar with greater estimated species richness than the MX and CDOM cover types (Fig. 2-2B). The curves of the MX and DDOM cover types approached asymptotes at 8 and 14 species respectively.

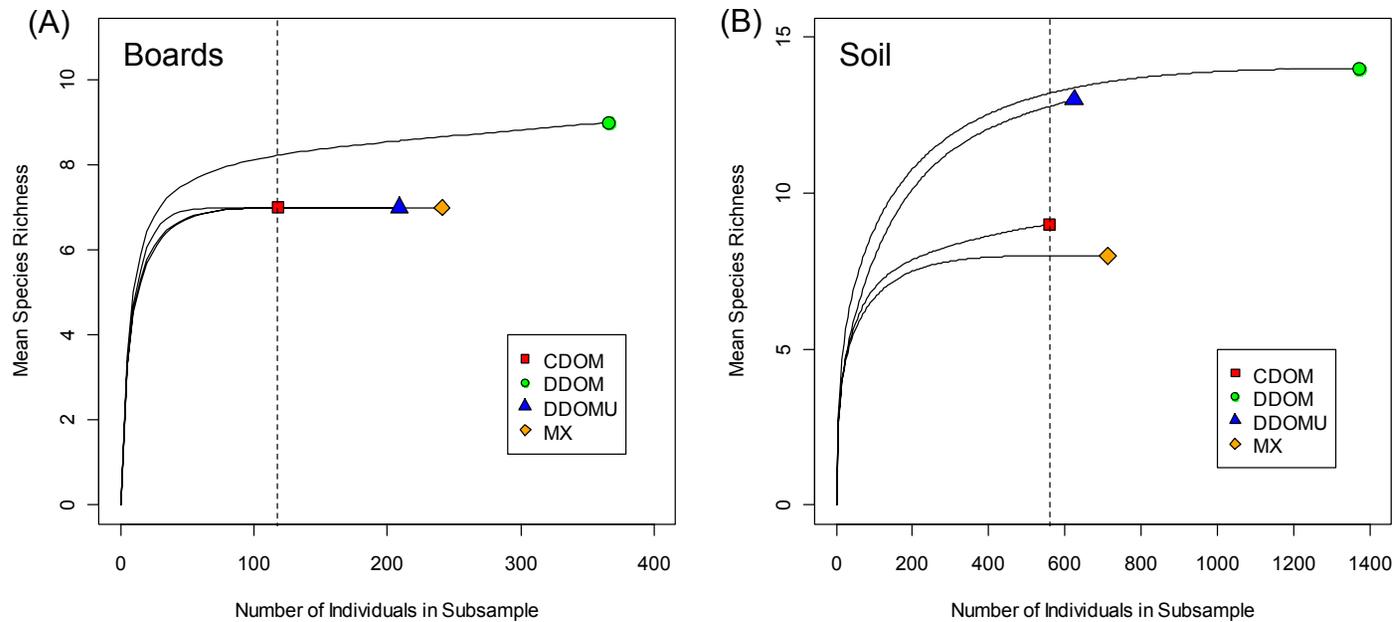


Figure 2-2: Results of individual based rarefaction estimates of gastropod species richness in varying forest cover types for board traps (A) and soil samples (B). DDOM = deciduous dominated, DDOMU = deciduous dominated with coniferous understory, MX = mixed coniferous and deciduous, and CDOM = coniferous dominated. Vertical dashed line represents the lowest number of collected individuals, and is the appropriate point of comparison between forest types.

Assemblage Composition. There were no significant differences in species composition between forest cover types, for either the board trap assemblage (PerMANOVA, $F_3=1.72$, $p=0.124$) and the soil assemblage (PerMANOVA, $F_3=1.45$, $p=0.222$).

An indicator species analysis showed that two species from the soil samples, *Euconulus fulvus* (Müller) (Indicator Value = 46.2) and *Punctum minutissimum* (Lea) (Indicator Value = 72.4), significantly indicated the DDOM forest type. The assemblage defined by board trap samples had no significant indicators.

With regard to both species richness and abundance, the DDOM cover type was distinct from the other cover types, so we subsequently performed an indicator species analysis comparing two groups – the DDOM vs the other three cover types combined (i.e. anything with a spruce component). In this analysis, *Zonitoides arboreus* (Say) was a significant indicator for the DDOM cover type in the assemblage defined by board traps (Table 2-2). For the assemblage defined by soil samples, the following three taxa significantly indicated the DDOM cover type (Table 2-3): *Euconulus fulvus* (Müller), *Punctum minutissimum* (Lea), and *Succinea* sp.

Table 2-2: Results of indicator species analysis for species from board traps comparing DDOM cover type versus all other cover types combined (DDOM, MX, and CDOM). * significant p-values

Species	Max group	Observed Indicator Value	Indicator value from randomized groups	
			mean \pm SD	p-value
<i>Succinea</i> sp.	DDOM	33.3	16.8 \pm 9.69	0.2551
<i>Cochlicopa lubrica</i> (Müller)	DDOM	33.3	16.8 \pm 9.69	0.2551
<i>Discus shimekii</i> (Pilsbury)	DDOM	77.6	60.2 \pm 14.98	0.1754
<i>Discus whitneyi</i> (Newcomb)	DDOM	63.0	56.3 \pm 4.54	0.1010
<i>Zonitoides arboreus</i> (Say)	DDOM	84.0	65.4 \pm 11.64	<u>0.0434*</u>
<i>Euconulus fulvus</i> (Müller)	DDOM	59.1	57.4 \pm 4.46	0.3325
<i>Nesovitrea electrina</i> (Gould)	DDOM	59.3	55.5 \pm 4.09	0.1890
<i>Deroceras laeve</i> (Müller)	DDOM	60.0	60.3 \pm 6.92	0.4717
<i>Vitrina pellucida</i> (Müller)	DDOM	57.8	65.1 \pm 9.94	0.7353

Table 2-3: Results of indicator species analysis for species from soil samples grouped as DDOM cover type or all other cover types combined as a single group (DDOM, MX, and CDOM).

* significant p-values

Species	Max group	Observed Indicator Value	Indicator value from randomized groups	
			mean \pm SD	p-value
<i>Succinea</i> sp.	DDOM	66.7	24.9 \pm 9.31	<u>0.0430*</u>
<i>Cochlicopa lubrica</i> (Müller)	DDOM	32.5	23.6 \pm 12.13	0.2454
<i>Vertigo cristata</i> (Sterki)	DDOM	55.6	39.8 \pm 14.37	0.3189
<i>Vertigo gouldii</i> (Binney)	DDOM	58.8	36.1 \pm 14.65	0.1296
<i>Vertigo modesta</i> (Say)	DDOM	70.7	58.4 \pm 9.02	0.1000
<i>Columella edentula</i> (Draparnaud)	DDOM	64.3	54.9 \pm 8.81	0.1608
<i>Columella columella</i> (von Martens)	DDOM	25.0	29.8 \pm 13.58	0.6749
<i>Punctum minutissimum</i> (Lea)	DDOM	88.7	49.2 \pm 15.98	<u>0.0090*</u>
<i>Discus shimekii</i> (Pilsbury)	DDOM	25.9	25.2 \pm 8.85	0.2454
<i>Discus whitneyi</i> (Newcomb)	DDOM	67.7	58.1 \pm 5.74	0.0728
<i>Zonitoides arboreus</i> (Say)	DDOM	63.4	55.0 \pm 13.63	0.2689
<i>Euconulus fulvus</i> (Müller)	DDOM	72.1	59.5 \pm 6.52	<u>0.0360*</u>
<i>Nesovitrea electrina</i> (Gould)	DDOM	50.3	54.5 \pm 3.38	0.0520
<i>Deroceras laeve</i> (Müller)	DDOM	60.0	60.3 \pm 6.92	0.4717
<i>Vitrina pellucida</i> (Müller)	Other	51.1	58.0 \pm 11.71	0.7297

Assemblage Associations. A redundancy analysis (RDA) of gastropods from board traps (Fig. 2-3A) identified three environmental variables as influencing assemblage patterns: forest cover type, basal area of broadleaf trees and shrub cover. Axes 1 and 2 explain 12.2% and 3.3%, respectively, of the variation in the gastropod assemblage. The majority of species were associated with areas dominated by broadleaf trees and high cover of shrubs. A few species were associated with mixed type forests with some conifer component, although no species were associated with conifer dominated forests.

RDA of gastropods from soil samples (Fig. 2-3B) also identified cover type and shrub cover as important environmental variables. Axes 1 and 2, respectively, explain 24.2% and 4.5% of the variation in assemblage structure. The majority of species were associated with areas with greater broadleaf tree components and high cover of shrubs.

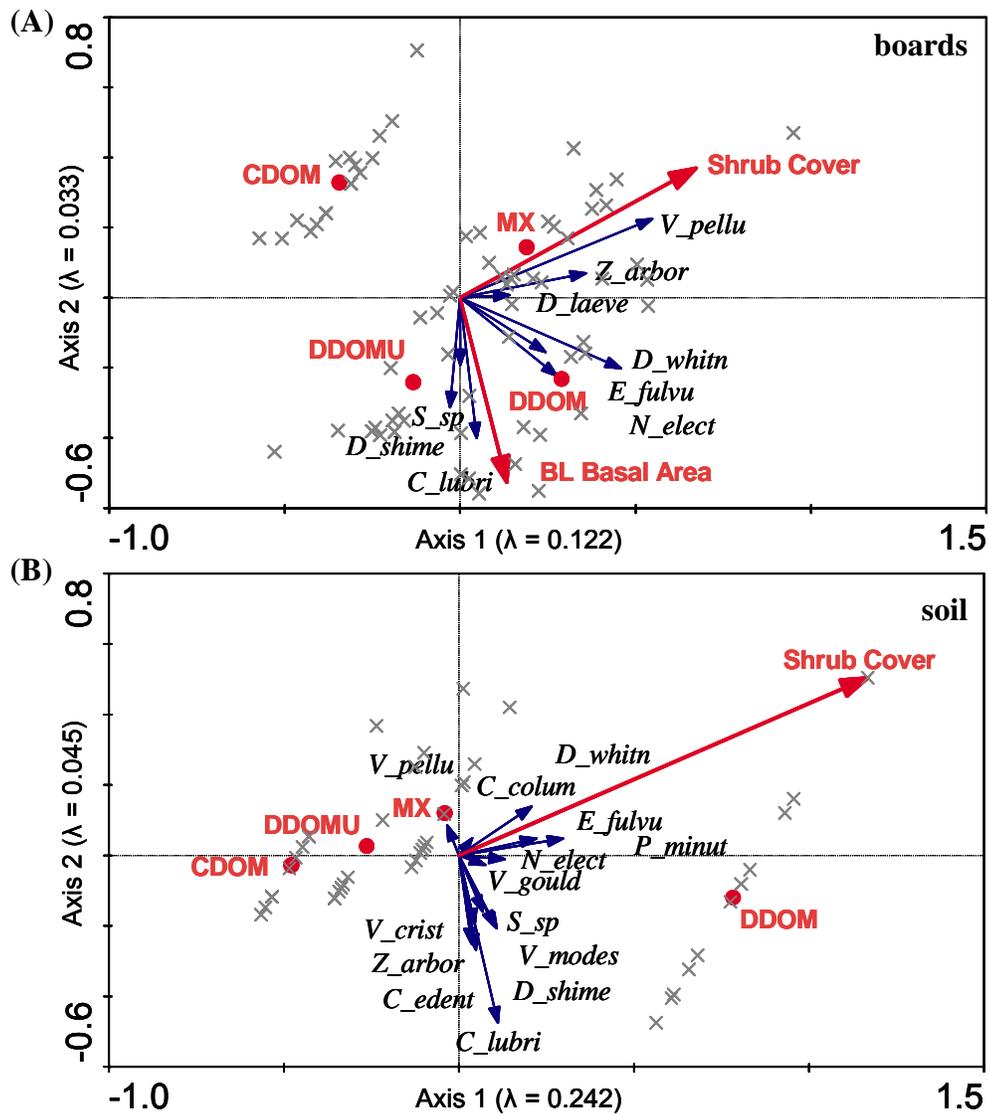


Figure 2-3: Results of constrained ordinations (RDA) of the gastropod assemblage sampled with board traps (A), and soil samples (B). Red vectors or centroids = environmental parameters, Blue vectors = species, and x-marked points = sampling locations. Environmental parameters were chosen through forward selection and those shown significantly explain variation in the assemblage. For both assemblages, the categorical variable 'Cover Type' was selected, and is represented in each ordination as four separate centroids: DDOM = deciduous dominated, DDOMU = deciduous dominated with coniferous understory, MX = mixed coniferous and deciduous, and CDOM = coniferous dominated.

When constrained ordination (RDA or CCA) of gastropods from board traps was conducted for each cover type separately, different environmental variables were selected for different cover types. In the DDOM cover type, for example, conifer basal area, and shrub cover were the strongest drivers of assemblage pattern in the RDA (Fig. 2-4A). Axes 1 and 2, respectively, explained 21.8% and 7.0% of the variation for the 9 species represented in this cover type. In the DDOMU cover type, conifer tree basal area was selected by RDA as the only significant environmental vector (Fig. 2-4B), and axes 1 and 2, respectively, explained 22.0% and 30.1% of the variation of the 7 species of this assemblage. In the MX cover type, RDA selected shrub cover as a significant contributing environmental vector (Fig. 2-4C) and axes 1 and 2, respectively, explained 16.9% and 31.9% of the variation in distribution of the 7 included species. In a CCA of gastropod associations in the CDOM cover type, basal area of deciduous trees was selected, and axes 1 and 2, respectively, explained 14.4% and 31.9% of the variation of the 7 species represented in this cover type. In situations where only one environmental variable was loaded on the first axis as a significantly contributing vector (DDOMU, MX, and CDOM cover types), the second axis was unconstrained by any environmental variables and this represents a greater amount of variation than the first axis.

For the gastropod assemblage collected in soil samples, RDA of the assemblage from the DDOM cover type identified shrub cover and LFH depth as important environmental parameters (Fig. 2-5A) and axes 1 and 2, respectively, explained 22.0% and 14.8% of the variation in distribution and abundance of the 14 included gastropod species. In the MX cover type, conifer tree basal area, coarse woody debris cover, and canopy cover were all selected as important variables in a RDA (Fig. 2-5B) and axes 1 and 2, respectively, explained 30.5% and 14.3% of the variation for 8 included species. For the DDOMU and CDOM cover type, none of the

measured environmental variables could be significantly related to composition of the gastropod assemblage defined by soil samples.

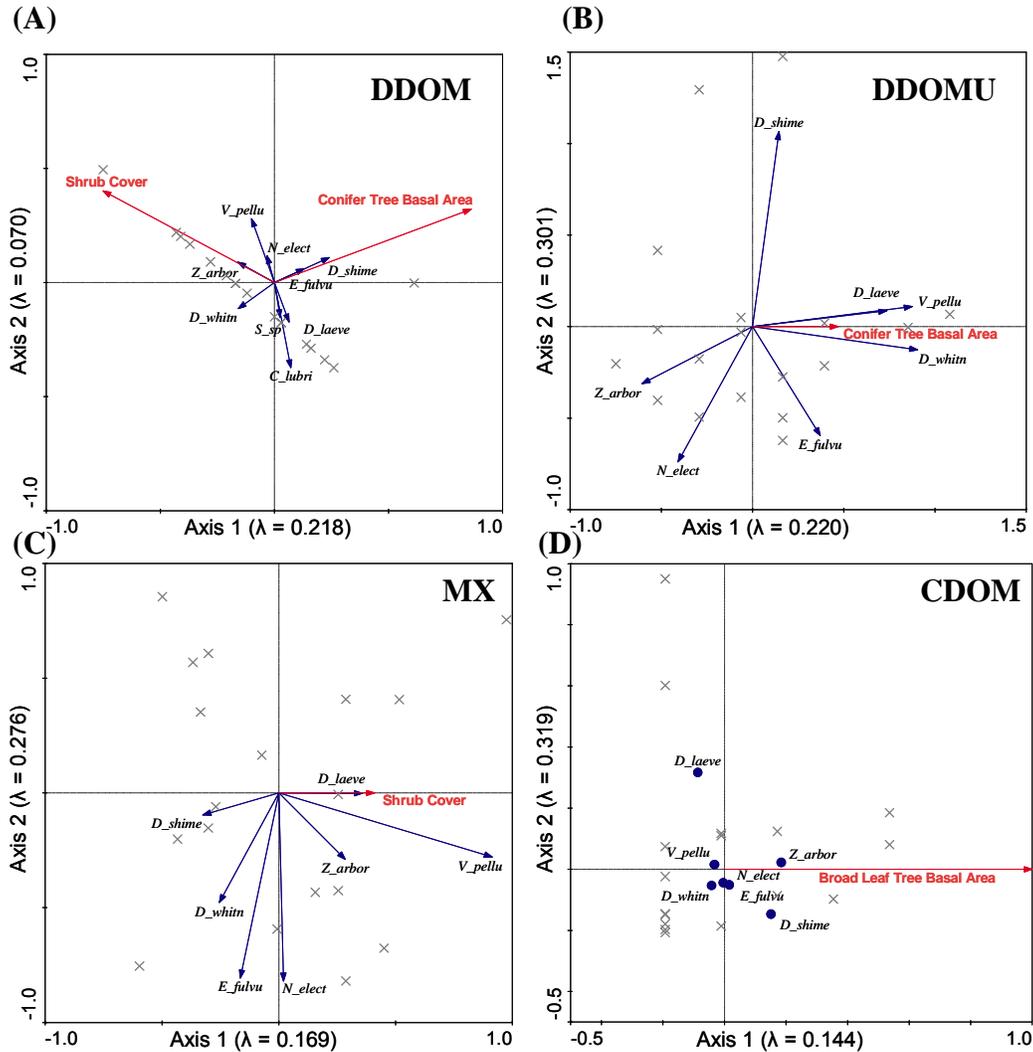


Figure 2-4: Results of constrained ordinations (RDA or CCA dependent on DCA gradient length) of the gastropod assemblage sampled with board traps conducted for each forest cover type separately; (A) DDOM = deciduous dominated (used RDA), (B) DDOMU = deciduous dominated with coniferous understory (used RDA), (C) MX = mixed coniferous and deciduous (used RDA), and CDOM = coniferous dominated (used CCA). Red vectors = environmental parameters, blue vectors = species, and x-marked points = sampling locations. Environmental vectors shown are those that significantly explain variation in the respective gastropod assemblage, as chosen through forward selection.

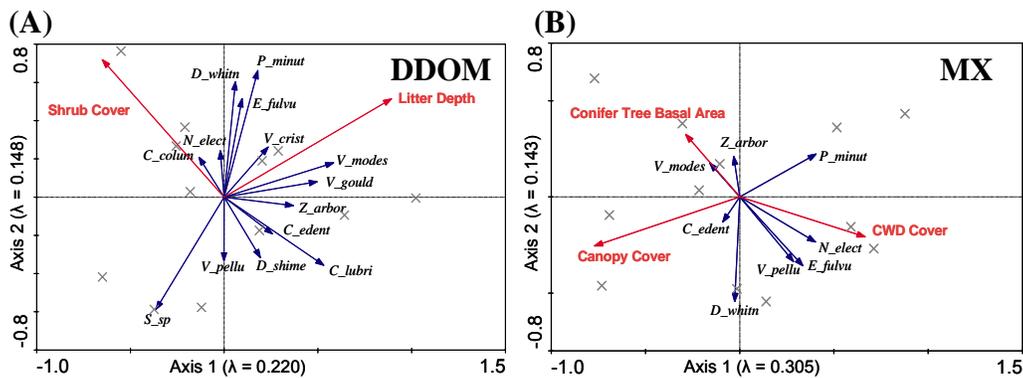


Figure 2-5: Results of constrained ordinations (RDA) of the gastropod assemblages sampled from soil in each forest cover type. (A) DDOM = deciduous dominated and (B) MX = mixed coniferous and deciduous. Red vectors = environmental parameters, blue vectors = species, and x-marked points = sampling locations. Environmental vectors shown are those that significantly explain assemblage variation as chosen through forward selection. Coarse woody debris cover has been abbreviated as CWD cover. For the DDOMU and CDOM cover types, none of the measured environmental variables were significantly related to assemblage composition.

Dominance Structure of Gastropod Assemblages. Gastropod assemblages at EMEND were composed of a few dominant species and larger number of relatively uncommon species. Assemblages in all cover types were dominated by the species *Discus whitneyi* and it had the highest dominance (DV') values for both sampling methods (Table 2-4; Table 2-5). *Nesovitrea electrina* was the second most dominant species in the majority of cover types for both sampling methods, and always fell within the dominant or subdominant categories (Table 2-4; Table 2-5).

Structure of assemblages differed among cover types. In general, forest with a higher deciduous component tended to support assemblages characterized by higher DV' values (Table 2-4; Table 2-5). For the board trap data, dominance analysis placed many species in the 'common' category in the CDOM forest type that were placed in the subdominant category in the other forest types (Fig 2-6). For data collected by soil

samples, the DDOM cover type supported the most subdominant species, and these species displayed a general shift to the left into the 'common' category in the other cover types (Fig 2-7). There were obvious differences in gastropod assemblages defined by each sampling method. In the soil assemblage *Euconulus fulvus* consistently ranked in the 3rd highest *DV'* value position (Table 2-5; Fig 2-7), but it usually ranked lower in the board trap assemblage (Table 2-4; Fig 2-6). In addition, the board trap assemblage included species like *Vitrina pellucida*, and *Discus shimekii* in much higher proportional presence and proportional abundance than the soil sampling method (Table 2-4; Table 2-5; Fig 2-6; Fig 2-7). Such results no doubt reflect differences in gastropod behaviour and suggest that board samples give a somewhat biased picture of gastropod assemblages.

Table 2-4: Relative dominance values for gastropod species in four forest cover types collected by board traps.

Species	ID	DDOM	DDOMU	MX	CDOM
<i>Succinea</i> sp.	13	0.02 U			
<i>Cochlicopa lubrica</i>	8	0.49 U			
<i>Discus shimekii</i>	11	4.59 U	7.36 U	1.39 U	0.83 U
<i>Discus whitneyi</i>	1	47.40 D	49.29 D	49.45 D	53.72 D
<i>Zonitoides arboreus</i>	7	12.57 S	1.69 U	3.90 U	5.95 S
<i>Euconulus fulvus</i>	3	6.06 S	8.56 C	8.33 S	4.96 C
<i>Nesovitrea electrina</i>	2	18.04 S	28.25 D	16.19 S	23.64 S
<i>Deroceras laeve</i>	15	2.00 C	1.49 U	2.31 U	6.36 C
<i>Vitrina pellucida</i>	10	8.82 S	3.36 U	18.42 S	4.55 C

DDOM = deciduous dominated, DDOMU = deciduous dominated with coniferous understory, MX = mixed coniferous and deciduous, and CDOM = coniferous dominated. ID values correspond to species identifier numbers in Figure 2-8. D = dominant; S = subdominant; C = common; U = uncommon species

Table 2-5: Relative dominance values for gastropod species in four forest cover types collected by soil samples.

Species	ID	DDOM	DDOMU	MX	CDOM
<i>Succinea</i> sp.	13	0.04 U			
<i>Cochlicopa lubrica</i>	8	0.69 C	0.06 U		
<i>Vertigo cristata</i>	9	0.10 U	0.01 U		0.06 U
<i>Vertigo gouldii</i>	12	0.12 U	0.11 U		
<i>Vertigo modesta</i>	5	2.62 S	1.13 C	1.04 C	1.09 C
<i>Columella edentula</i>	6	0.40 S	0.28 C	0.10 U	0.29 U
<i>Columella columella</i>	14	0.01 U	0.01 U		0.02 U
<i>Punctum minutissimum</i>	4	6.27 S	0.13 U	1.92 S	
<i>Discus shimekii</i>	11	0.09 U	0.17 U		
<i>Discus whitneyi</i>	1	57.76 D	62.27 D	63.51 D	54.83 D
<i>Zonitoides arboreus</i>	7	0.48 C	0.17 U	0.37 U	0.76 C
<i>Euconulus fulvus</i>	3	14.59 S	11.77 S	12.79 S	11.64 S
<i>Nesovitrea electrina</i>	2	16.74 S		20.08 S	30.59 D
<i>Vitrina pellucida</i>	10	0.08 U	0.49 C	0.18 U	0.710 C

DDOM = deciduous dominated, DDOMU = deciduous dominated with coniferous understory, MX = mixed coniferous and deciduous, and CDOM = coniferous dominated. ID values correspond to species identifier numbers in Figure 2-9. D = dominant; S = subdominant; C = common; U = uncommon species

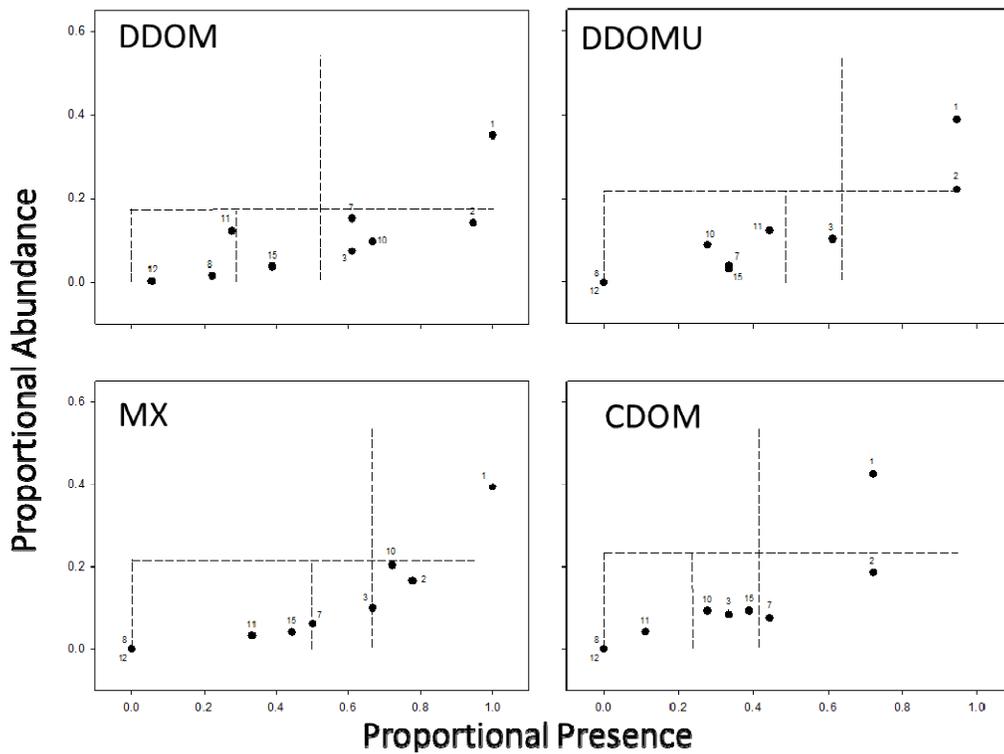


Figure 2-6: Dominance plots of gastropod assemblages in each forest cover type collected from board traps. DDOM = deciduous dominated, DDOMU = deciduous dominated with coniferous understory, MX = mixed coniferous and deciduous, and CDOM = coniferous dominated. Species are identified with numbers: 1 *Discus whitneyi*; 2 *Nesovitrea electrina*; 3 *Euconulus fulvus*; 7 *Zonitoides arboreus*; 8 *Cochlicopa lubrica*; 10 *Vitrina pellucida*; 11 *Discus shimckii*; 12 *Succinea sp.*; 15 *Derocheras laeve*. These plots were split into four quadrants using the midvalues of proportional presence and proportional abundance. The lower left quadrant is further split into two using the quarter proportional presence value.

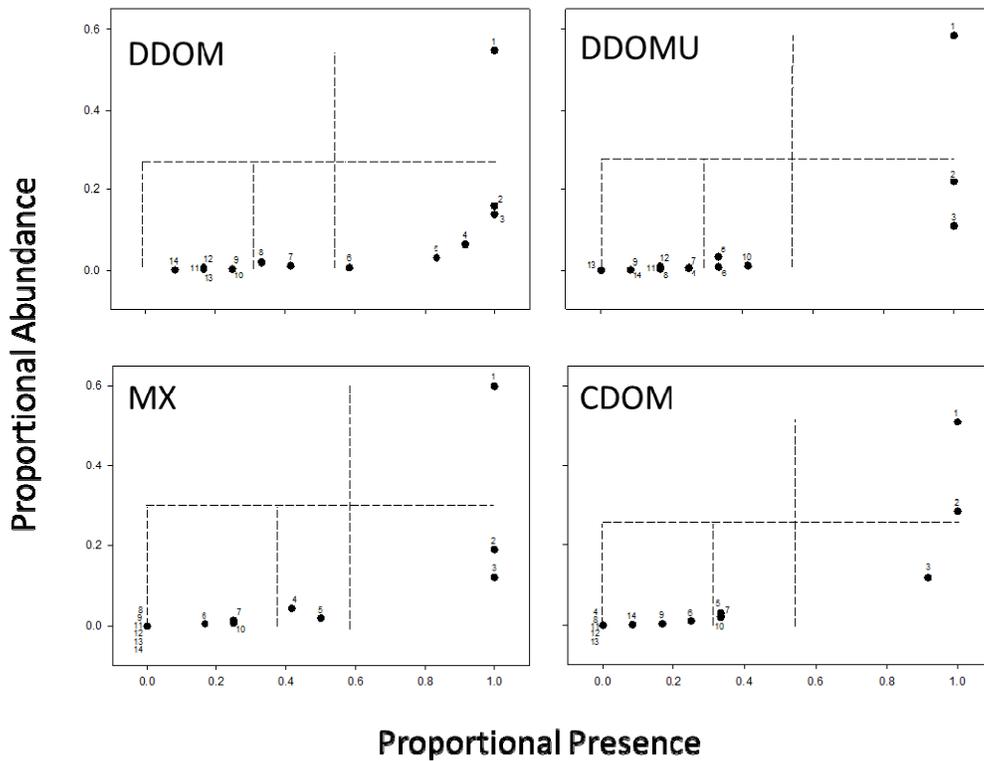


Figure 2-7: Dominance plots of gastropod assemblages in each forest cover type collected from soil samples. DDOM = deciduous dominated, DDOMU = deciduous dominated with coniferous understory, MX = mixed coniferous and deciduous, and CDOM = coniferous dominated. Species are identified with numbers: 1 *Discus whitneyi*; 2 *Nesovitrea electrina*; 3 *Euconulus fulvus*; 4 *Punctum minutissimum*; 5 *Vertigo modesta*; 6 *Columella edentula*; 7 *Zonitoides arboreus*; 8 *Cochlicopa lubrica*; 9 *Vertigo cristata*; 10 *Vitrina pellucida*; 11 *Discus shimekii*; 12 *Succinea sp.*; 13 *Columella collumella*. These plots were split into four quadrants using the midvalues of proportional presence and proportional abundance. The lower left quadrant is further split into two using the quarter proportional presence value.

Discussion

Results of my study indicate that forest cover type influences structure and composition of gastropod assemblages. Total gastropod abundance and species richness also differed among cover types. DDOM stands had the highest abundance and richness, and were distinctive from the other cover types in these regards. Although assemblage composition did not differ significantly among cover type categories, tree composition

emerged as an important driver of variation in gastropod assemblage composition on boreal mixedwood landscapes. Gastropods were also influenced by tree composition at a smaller scale, as distinctive patterns related to tree composition were evident within single cover types.

Both collection methods had advantages and disadvantages. More species were captured and likely a more complete picture of the overall snail assemblage was obtained through the soil samples, however processing these samples was much more time consuming and labor intensive. While board traps have been shown to be a more efficient way of sampling (Hawkins *et al.* 1998), they do not provide complete species collections (McCoy 1999). Although at EMEND, the slug species would have been missed without board samples.

Use of two sampling techniques provided a more complete picture of the gastropod assemblage present at EMEND. Soil sampling captured six species not found in board traps. These were minute species that were difficult to see or identify without magnification. Board traps captured one slug species that was not represented in the soil samples, perhaps because slugs would have been lost in the drying process. Thus, assemblages captured by these two sampling methods had different structures and patterns of dominance, and also appeared to be influenced by a different combinations of environmental parameters in the RDAs. Although board traps missed a substantial proportion of species, they may be more practical in dealing with large scale experiments because they are more time and resource efficient.

The North American gastropod fauna is thought to be composed of a few hardy species with wide distributions (Solem 1984). Consistent with this, all species in this study, except for *Succinea* sp., occurred in several cover types, suggesting that gastropods are mainly habitat generalists. Nonetheless, the strong positive association of both snail abundance and species richness with deciduous forests was recurrent throughout the analysis. Basal area of broad leaf trees was a good predictor of gastropod

assemblage composition (Fig 2-3). Furthermore, *Succinea* sp. was restricted to the DDOM cover type (Fig 2-4A; Fig 2-5A) and DDOM was the only cover type with significant indicator species (Table 2-3; Table 2-4). These findings agree with other studies describing strong association of gastropods with deciduous forest (Karlin 1961, Kralka 1986, Suominen *et al.* 2003). A few species were associated with stands of mixed composition (Fig 2-3), however no species was strongly associated with conifer dominated stands. It has been suggested that coniferous litter is not suitable for gastropods because of its high acidity and lack of calcium (Coney *et al.* 1982). Gastropods also seem to flourish in litter composed of items that curl (Solem 1984), such as senescent deciduous material, because such habitats provide shelter and protection from desiccation. Forest-dwelling gastropods feed primarily on dead plant material (Mason 1970), which is more abundant under a deciduous canopy (Macdonald & Fenniak 2007). In general, more species of gastropods existed at a higher level of dominance in DDOM, than in the other cover types, further suggesting that gastropod populations perform better in this habitat.

Coarse woody debris (CWD) is thought to influence soil dwelling gastropods through nutrient input into the soil (Müller *et al.* 2005), its ability to act as a sheltering habitat for soil-dwelling species (Boag 1990), and as sites for reproduction (Kappes *et al.* 2005). In this study in the MX cover type, however, some species responded positively to a higher coarse woody debris cover, and others responded negatively (Fig 2-5B), suggesting that not all species may be reliant on a high volume of CWD. Litter depth influenced gastropod composition in the DDOM cover type (Fig 2-5A), with most species associated with deeper litter. Similarly, Locasciulli & Boag (1987) showed that soil samples with greater amounts of non-compacted litter have higher densities of snails and suggested that deeper litter provides a more stable microclimate, a rich food source, and more living space (Locasciulli & Boag 1987).

Shrub cover in the understory had an influence on gastropod distributions (Fig 2-3; Fig 2-4; Fig 2-5). Boreal understory plant communities have a high turnover rate and contribute significantly to leaf litter and soil nutrients (Nilson & Wardle 2005). Plants provide food for gastropods, but they also provide microhabitats with higher moisture and reduced temperature extremes (Kiss & Magnin 2003). Higher understory plant cover is associated with a more deciduous dominated canopy at EMEND, and this is likely to significantly contribute to the value of the DDOM cover type as habitat for gastropods.

Tree composition also influences gastropod distribution, even at fine scales within stands. For example, basal tree area of either conifer or broadleaf trees was often associated with gastropod distribution in the RDAs for each cover type (Fig 2-4; Fig 2-5). Assemblages from board traps in the DDOM cover type were significantly influenced by the presence of conifer trees, despite the unlikely occurrence of a conifer tree in a plot. In the CDOM cover type, however, gastropod distribution was influenced by broadleaf basal area. These patterns suggest that single trees or small patches of deciduous trees can be significant for the distribution of gastropods on the landscape. Small scale canopy heterogeneity influences species composition in other biota, including birds, arthropods and understory plants (Niemelä et al. 1996; Hobson & Bayne 2000; Chávez & Macdonald 2010).

In comparisons of species specific responses among cover types, associations with some gastropod species changed with respect to conifer or broadleaf trees. For example, the species most positively associated with conifer tree basal area in the DDOM cover type are different from those in DDOMU cover type (Fig 2-4). This suggests that a mixed composition litter is actually better for gastropods, and thus that, different ratios of conifer:deciduous litter could be optimal for different gastropod species. In a DDOM stand, litter close to a coniferous tree may have the desired ratio for a particular species, but in a stand more dominated by

spruce the same ratio could occur further away from a conifer tree. Mixedwood stands are often said to be comprised of a combination of conifer and broadleaf specialists. However, mixedwood stands have also been considered distinct habitats that are preferred by certain species and not simply juxtapositions of deciduous and coniferous forests (Girard et al. 2004; Macdonald et al. 2010).

It is clear that tree composition influences patterns of gastropod distribution and abundance at both coarse and fine scales. For the most part, species were strongly associated with deciduous components at EMEND, a relationship that has been emphasized in previous literature (Suominen et al. 2003). In a mixedwood system, however, even deciduous dominated forests have some mixture of tree composition and this element seemed to be the main determinant of gastropod distribution patterns in this study. Boreal mixedwood forests have been managed in way that may be favor large stands of tree monocultures rather than the natural mosaic of smaller scale mixedwood patches (Hobson & Bayne 2000). If an aim of forest management is to re-establish pre-harvest forest conditions following harvest, maintaining a tree species mixture may be required to ensure broad-scale persistence of forest flora and fauna. At least this seems to be the case for forest dwelling gastropods in the boreal mixedwood.

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Chapter 3 – Gastropod response to green-tree retention harvest in the boreal mixedwood

Introduction

In recent years forest management in Canada has emphasized an “ecosystem-based” approach with major focus on issues of ecological sustainability. The goals of this approach are to maintain the economic and social aspects of timber production while preserving ecosystem functions and biodiversity (Canadian Council of Forest Ministers 2008). Variable retention harvesting systems such as “green tree retention” (GTR) have been adopted as a main way of achieving these goals (Work et al. 2003). GTR involves leaving live trees on the landscape during harvesting in the hopes that they will serve as “biological legacies” to preserve aspects of forest structure and function (Rosenvald and Löhmus 2007, Franklin et al. 1997). Such legacies can be especially important for dispersal-limited organisms that rely on habitat patches left nearby to act as sources for recolonization of second growth stands (Duffy and Meier 1992, Gandhi et al. 2007). The continuous presence of forest structures on the landscape is often referred to as ecological continuity (Rolstad et al. 2002), and this concept is widely used to describe the value of old forest components in maintaining biodiversity (Nordén and Appelqvist 2000).

Terrestrial gastropods are dispersal limited and their presence provides a suitable measure of ecological continuity (Nordén and Appelqvist 2001). Gastropod distribution is influenced by a number of factors that are altered by timber harvesting including soil calcium, plant communities, moisture, and temperature (Martin and Sommer 2004; Barker and Mayhill 1999; Asami 1993; Hawkins et al. 1998). There is some evidence that retention harvesting maintains habitat structures for sensitive snail species by providing refuges or colonization sites (Kiss and Magnin 2003). Past studies have shown that harvest disturbance does influence gastropod assemblages, although gastropod response has

varied among between studies. For example, Hylander *et al.* (2004) found that most species are negatively affected by clear-cuts in riparian areas, while Kappes (2006) suggested that gastropods are relatively resilient to harvest disturbance. Nonetheless, both studies showed that harvest sensitivity varies among species. Following hurricane disturbance, gastropod species have shown two alternative responses: 1) they increase in abundance due to an increase in resources (e.g., relocation of organic matter to the forest floor) or 2) they respond negatively due to the modification of microclimate (Bloch and Willig 2006). Similar species-specific responses may result after harvest, and species sensitive to harvest could serve as indicators of post-harvest ecological continuity.

The appropriate amount of GTR to leave on boreal landscapes is currently a topic of much research. The optimum amount of retention would achieve economically viable timber production while holding ecological cost to the system at acceptable levels. For many biological communities, including plants and arthropods, low levels of retention result in communities that resemble those in clear-cuts, while areas with higher levels of retention can more closely resemble unharvested forests (Craig and Macdonald 2009; Work *et al.* 2010).

Harvesting with GTR often involves creation of machine corridors, in which trees are completely removed to accommodate machinery used for harvest. After harvest these corridors develop understory plant communities that resemble those on clear-cuts (Craig and Macdonald 2009), with dense aspen regeneration (Lennie *et al.* 2009) that differs from nearby retention (partially harvested) strips. The soil within these corridors is compacted by machine traffic, resulting in reduced abundances of soil-dwelling organisms including ectomycorrhizae, and invertebrate mesofauna (Lazaruk *et al.* 2005; Lindo and Visser 2003). Machine corridors can encompass substantial areas of harvested landscapes, thus it is important to understand their effects on biotic communities, and if any negative effects can be mitigated by adjusting application of GTR.

Understanding how gastropods respond to harvest will help to better ensure their continued presence on managed forest landscapes, and thus contribute to overall biodiversity conservation goals. The aim of this chapter is to explore the effects of partial harvesting on gastropod assemblages in boreal mixedwood stands. Specifically, my objectives were to describe gastropod assemblages within stands with varying amounts of GTR to determine what amount of retention is required to maintain gastropod assemblages similar to those of unharvested forests. I examined structure of gastropod assemblages for possible changes with increased harvesting intensity, and to determine if any particular species were sensitive to harvest disturbance in this system and if any threshold for significant effect could be detected for such species or for the gastropod assemblage as a whole. Within high and low levels of retention, I also compared assemblages between machine corridors and retention strips.

Materials and Methods

Site selection and study design: This study was conducted at the site of the EMEND (Ecosystem Management Emulating Natural Disturbance) experiment, using retention harvest treatments in the mixedwood cover type (40-60% spruce and aspen cover in the canopy). Each harvested compartment was approximately 10 ha in size, and represented one of six harvest treatments with varying levels of dispersed GTR: clear-cut (1-2% of trees retained after harvest), 10%, 20%, 50%, 75% and control (unharvested reference compartments) (see Work et al. 2010 for details). Treatments were replicated three times for a total of 18 compartments in this study. (See Chapter 1 for a complete site description). Stands were harvested using 5-m wide parallel machine corridors alternated with 15-m wide retention strips, with harvest oriented N-S perpendicular to the direction of prevailing winds. Trees were removed by formula from retention strips to create the desired level of

post-harvest stem density for the entire stand. All retention treatments were applied in the winter of 1998/1999, and sampling for this study occurred in the summer of 2008.

Sampling methods: Six random sampling points were established within each of the experimental compartments [6 harvest treatments * 3 replicates * 6 sample points = 108]. These sampling points were located 20m south of the start of each of 6 randomly-established EMEND mensuration transects, with the single constraint that each sampling site was centered within a retention strip. Each sampling point became the center of a 10 m² circular sampling plot (r = 1.78 m).

At each sampling plot a board trap was used to sample the gastropod assemblage (Fig 3-1). These consisted of 25 x 60 cm masonite hardboards that were embedded under the upper leaf litter layer within each plot. Gastropods were collected from the upper and lower surfaces of these boards every two weeks for a total of five collections between June and August. Specimens found during board collections were preserved in 70% ethanol.

At each sampling plot a variety of environmental parameters were measured. From the center of each plot, basal area of conifer and broadleaf trees and canopy closure were measured using a wedge prism and a convex spherical densiometer, respectively. Forest structure at each plot was further described by visually estimating percent cover of coarse woody debris (laying dead wood with a diameter ≥ 7 cm), shrub vegetation, herb vegetation, and moss vegetation. Saplings within the plot were counted for broadleaf and conifer trees separately. Finally, LFH depth was measured, and moisture was assessed gravimetrically as the difference between mass before and after drying 1.5 dm² LFH layer samples.

To test for differences in gastropod assemblages between machine corridors and retention strips, 6 additional board traps were placed in the machine corridors in each experimental stand of the 20% and 75%

retention treatments. These traps were placed in a paired design, adjacent to the sample plots that were located within the retention strips (Fig. 3-1).

All gastropods were identified in the laboratory to the lowest possible taxonomic level, with the aid of Forsyth (2004) and the Jim van Es Marine Invertebrate and Malacology collection (Department of Biological Sciences, University of Alberta). Most individuals were identified to species level, except for specimens of the genus *Succinea*, as this group has not been well described in Alberta. The few collected specimens of this genus were treated as a single species for analysis.

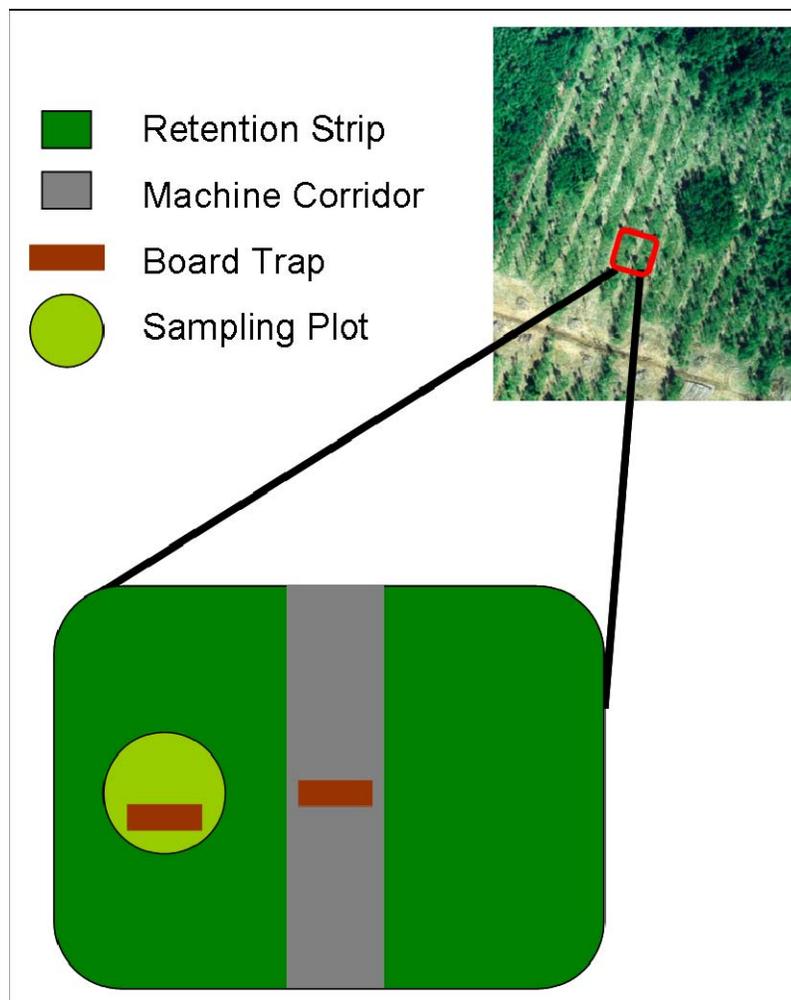


Figure 3-1: Diagram depicting paired board trap design for sampling gastropods in machine corridors and retention strips.

Data analysis: To test for differences in total gastropod abundance among retention levels, I used a mixed model ANOVA with retention percentage treated as a continuous independent variable. This was computed using Proc Mixed in SAS (v. 9.2 Littell et al., 1996). Compartments were treated as experimental units, so gastropod abundances of all plots in a compartment (retention strips only) and across all collections were summed for this analysis. Following detection of a significant retention level effect, pre-planned contrasts were used to reveal significant differences along the retention gradient that might indicate some threshold for effect (see Craig and Macdonald 2009). P values were considered significant at $\alpha = 0.05$.

To compare species richness between retention treatments, individual-based rarefaction curves were used. These curves are created by randomly sampling individuals from the total number that were collected and plotting the number of species against the number of individuals in that randomly selected subsample. This method controls for differences in species richness that arise due to differences in abundance by allowing the comparison of richness at a similar abundance (Colwell 2009). Rarefaction curves were produced using R package (v. 1.17-2 Oksanen et al. 2010).

Permutational multivariate analysis of variance (PERMANOVA) was used to compare species composition across all 6 retention levels. This method calculates a test-statistic using permutations based on a distance matrix of distances between each pair of sampling units (Anderson 2005). Following a significant F-test, retention levels were compared with pair-wise contrasts. After detecting a threshold for gastropod abundance around the 50% retention level (see results section), I also used PERMANOVA to look for difference in species composition between high retention levels (50%, 75% and 100% as a group) and low retention levels (0%, 10%, and 20% as a group). All

PERMANOVA tests were calculated using summed species abundance per compartment and the Bray-Curtis dissimilarity measure, and tests of significance were performed using 4999 unrestricted permutations in PC-ORD (v. 5.06 McCune and Mefford 2006). PERMANOVA is sensitive to differences in dispersion among groups, which could lead to rejection of the null-hypothesis despite similarity in species composition (Anderson 2004). A permutational analysis of multivariate dispersions (PERMDISP) was used to investigate any possibility of differences in sample dispersion among treatments (PERMDISP Anderson 2004), using the same options as used for PERMANOVA. This test works by calculating distances from observations to their centroids, and compares these distances using an ANOVA. PERMDISP is described by Anderson (2004) as the multivariate equivalent to the Levene's test.

Indicator species analysis (ISA, Dufrêne and Legendre 1997) was used to identify species strongly associated with any particular retention level. This was followed by an indicator species analysis using just two groups: high vs low retention (as defined above). ISA calculates an indicator value between 0 (no indication) and 100 (perfect indication), based on the relative abundance of a species and its relative frequency of occurrence (in groups of sites) (McCune & Grace 2002). Indicator values are tested for significance using a Monte Carlo randomization procedure. Indicator species analysis was computed in PC-ORD (v. 5.06 McCune and Mefford 2006).

Nonmetric Multidimensional Scaling (NMDS) ordination using PC-ORD (v. 5.06 McCune and Mefford 2006) was used to visualize possible differences in assemblage composition among retention levels. An NMDS ordination is plotted against rank order distances based on pairwise comparisons between compartments, in this instance a Bray-Curtis distance measure was used. The number of dimensions chosen and the configuration of points presented minimized 'stress', which is a measure of departure between the compartment distance measures and distance in

ordination space (McCune and Grace 2002). A 'stress' level of 5-10 is considered a good representation of the data, and depictions meeting this criterion provide a reliable basis for inference (Clarke 1993). The significance of the final ordination was tested using a Monte Carlo test that performs a randomization procedure to test whether the NMDS is extracting stronger axes than expected by chance (McCune and Grace 2002).

To explore potential environmental associations influencing the gastropod assemblage in the harvested system as a whole, a constrained ordination technique called Redundancy Analysis was used in CANOCO (v. 4.5, ter Braak and Šmilauer, 2002) to analyze board trap captures. This method uses a multivariate environmental data set to explain variance in a species data set (Legendre and Legendre 1998). This method is the multivariate analogue to regression, maximizing the proportion of the total sum of squares in the species variables that can be explained by redundancy components extracted from the environmental variables (Takane & Jung 2006). Examination of the gradient length in a detrended correspondence analysis (ter Braak and Šmilauer 1998) suggested that the gastropod assemblage data met the assumption of linear response to the environmental variables. Forward selection was used to determine which environmental parameters influenced compositional patterns, as represented by the ordination. All species data were log-transformed prior to analyses. The ordination was tested for significance using a Monte Carlo randomization procedure to test whether the relationship between the species and environmental data is stronger than expected by chance (McCune and Grace 2002).

To further investigate gastropod assemblage structure, dominance values (Pinzón and Spence 2010) were calculated for species in each retention level. Dominance values (*DV*) were calculated for each species as a product of proportional presence and proportional abundance relative to the other species in the assemblage. Dominance plots were

constructed by plotting proportional presence (*AP*) against proportional abundance (*w*), as explained by Pinzón and Spence (2010). These plots were split into four quadrants using the midvalues of *AP* and *w*. I take the upper right quadrant to identify dominant species, the lower right quadrant subdominant species, and the upper left quadrant locally dominant species. The lower left quadrant is further split into two using the quarter *w* value, and is interpreted to represent common and uncommon species respectively, in the right and left subdivisions.

To compare machine corridors and retention strips, total gastropod abundance was compared using a mixed model ANOVA as follows: $Y = \mu + R_i + C_j + RC_{ij} + S_{k(ij)} + e_{ijkl}$, where: *Y* = An observation, μ = overall mean, *R_i* = retention level, *C_j* = corridor treatment (corridor vs retention strip), *RC_{ij}* = interaction between retention level and corridor treatment, *S_{k(ij)}* = sample board nested in retention level and corridor treatment, and *e_{ijkl}* = random error. The data were log transformed prior to analysis in order to meet assumptions of normality. A post-hoc differences of least squares means test (with Bonferroni adjustment for multiple comparisons), was used to explore significant interaction between the two factors. This ANOVA was computed using Proc Mixed in SAS (v. 9.2 Littell et al., 1996).

Composition of gastropod assemblages was compared among retention levels and between machine corridors and retention strips using a two-factor permutational multivariate analysis of variance (PERMANOVA). This was coupled with a two-factor permutational analysis of multivariate dispersion (PERMDISP), as above, to investigate possible differences in sample dispersion. All tests were calculated using summed species abundance per compartment and Bray-Curtis dissimilarity, and tests of significance were performed using 4999 unrestricted permutations.

Results

In total, 1686 individual gastropods were captured, representing 9 species of 8 different families (Table 3-1).

Table 3-1: Gastropods collected from board traps.

Family	Species
Succineidae	<i>Succinea</i> sp.
Cionellidae	<i>Cochlicopa lubrica</i> (Müller)
Discidae	<i>Discus shimekii</i> (Pilsbury)
	<i>Discus whitneyi</i> (Newcomb)
Gastrodontidae	<i>Zonitoides arboreus</i> (Say)
Euconulidae	<i>Euconulus fulvus</i> (Müller)
Oxychiliidae	<i>Nesovitrea electrina</i> (Gould)
Agriolimacidae	<i>Deroceras laeve</i> (Müller)
Vitrinidae	<i>Vittrina pellucida</i> (Müller)

Abundance Gastropods were significantly more abundance in compartments with lower levels of retention than in those with greater retention (ANOVA, $F_{1,16}=8.47$, $p=0.02$; Fig. 3-2). The pre-planned, orthogonal contrasts suggest that gastropod abundance changes significantly at 50% retention (Table 3-2), and that a threshold for significant negative effect occurs somewhere between 20 and 50%.

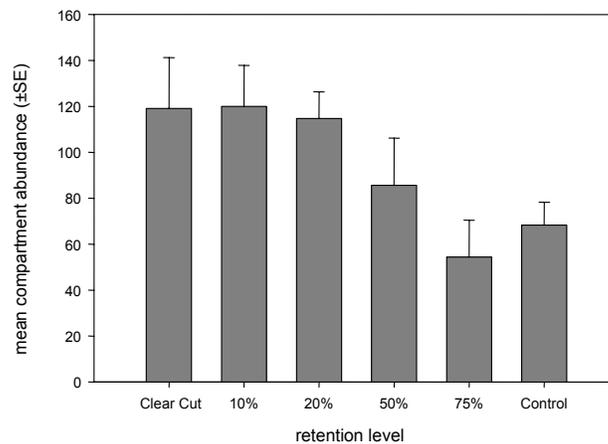


Figure 3-2: Mean abundance of gastropods in the boreal mixedwood forest at varying levels of green tree retention. Compartment level abundance reflects the sum of abundance from 6 board traps across 5 collections.

Table 3-2: Contrasts used to detect a threshold following a significant main effect of retention level on gastropod abundance from a mixed model regression. P-values are considered significant at $\alpha=0.05$.

* significant p-values

Contrast Groups	P-value
0 vs (10-100)	0.3968
(0, 10) vs (20-100)	0.1440
(0-20) vs (50-100)	<u>0.0279*</u>
(0-50) vs (75, 100)	<u>0.0206*</u>
(0-75) vs 100	0.2839

Richness Rarefaction estimates of gastropod species richness indicated no evident pattern of retention level on species richness (Fig. 3-3). All of the retention levels had a species richness ranging between 6 and 8 species. The highest species richness was found in the 75% retention treatment, followed by the clear cut treatment, the uncut and 50% treatments, the 10% treatment and finally the 20% treatment with the lowest species richness (Fig. 3-3). All of the curves approached asymptotes suggesting that the sampling effort captured the full richness possible by this sampling technique.

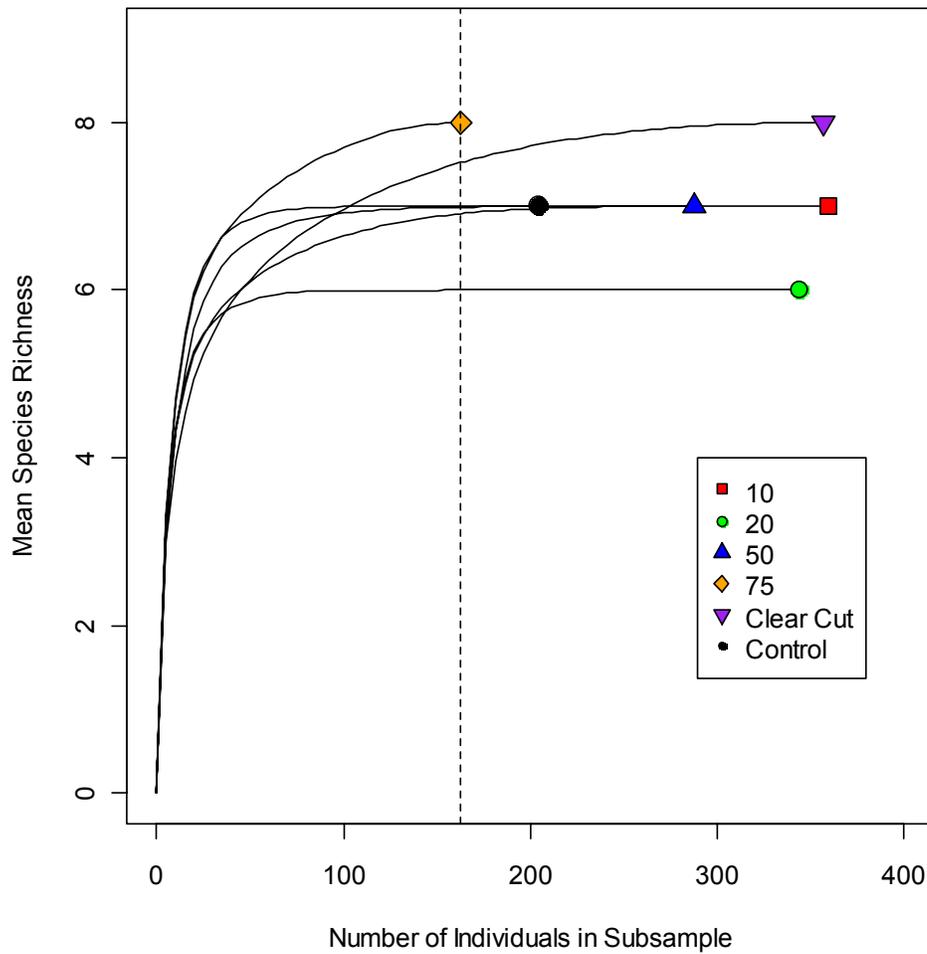


Figure 3-3: Results of individual based rarefaction estimates of gastropod species richness in varying retention harvest treatments. Vertical dashed line represents the lowest number of collected individuals, and is the appropriate point of comparison between retention harvest treatments.

Assemblage Composition. There were significant differences in species composition among the six retention levels (PERMANOVA, $F_5=2.15$, $p=0.044$), although post-hoc pairwise comparisons did not detect a significant difference between any specific pairs of retention levels (Table 3-3; $p=0.09$). The significant difference in the PERMANOVA was most likely due to differences in dispersion between groups (PERMDISP, $F_5=3.51$, $p=0.03$); however, significant difference in dispersion between any two specific retention levels could not be demonstrated by post-hoc pairwise comparisons (Table 3-4). Composition of gastropod assemblages did differ significantly between high (50-100%) and low (0-20%) retention (PERMANOVA, $F_1=5.70$, $p=0.005$), but there were no significant differences in dispersion (PERMDISP, $F_1=3.50$, $p=0.075$), suggesting that these effects represent real changes in species composition.

A species indicator analysis comparing all six retention treatments found only one significant species indicator, *Euconulus fulvus* (Müller), which was strongly associated with the 20% retention level, (Table 3-5). An indicator species analysis comparing high retention as a group vs low retention as a group found three significant species indicators for the low retention group (Table 3-6), *Discus whitneyi* (Newcomb), *Euconulus fulvus* (Müller), and *Zonitoides arboreus* (Say).

Table 3-3: Pairwise comparisons between gastropod assemblages across retention levels using a Monte Carlo randomization procedure (4999 permutations) following a significant PERMANOVA F-test ($F_5=2.15$, $p=0.044$).

Level	vs	Level	t statistic	P-value
0%		10%	0.7861	0.69
0%		20%	1.3394	0.20
0%		50%	1.6576	0.09
0%		75%	0.7300	0.80
0%		100%	1.8948	0.09
10%		20%	1.3932	0.19
10%		50%	1.7801	0.10
10%		75%	0.7849	0.61
10%		100%	2.1103	0.10
20%		50%	1.4304	0.20
20%		75%	0.7781	0.50
20%		100%	1.8264	0.10
50%		75%	1.5768	0.20
50%		100%	0.6687	0.90
75%		100%	1.8874	0.20

Table 3-4: Pairwise comparisons between retention levels using a Monte Carlo randomization procedure (4999 permutations) following a significant PERMDISP F-test (PERMDISP, $F_5=3.51$, $p=0.03$).

Level	vs	Level	t statistic	P-value
0%		10%	0.8294	0.70
0%		20%	1.9246	0.10
0%		50%	1.7515	0.20
0%		75%	0.7883	0.60
0%		100%	0.1672	1.00
10%		20%	3.8178	0.10
10%		50%	2.0761	0.20
10%		75%	1.8072	0.21
10%		100%	2.5573	0.10
20%		50%	0.0450	0.20
20%		75%	2.8247	0.10
20%		100%	9.1015	0.10
50%		75%	2.6133	0.10
50%		100%	2.7210	0.10
75%		100%	1.2163	0.40

Table 3-5: Results of indicator species analysis comparing six levels of retention harvest (0%, 10%, 20%, 50%, 75% and 100%).

* significant p-values

Species	Max group	Observed Indicator Value	Indicator value from randomized groups	
			mean \pm SD	p-value
<i>Succinea</i> sp.	75%	33.3	33.3 \pm 0.47	1.0000
<i>Cochlicopa lubrica</i> (Müller)	10%	26.7	31.4 \pm 12.98	1.0000
<i>Discus shimekii</i> (Pilsbury)	100%	40.0	27.0 \pm 13.34	0.1646
<i>Discus whitneyi</i> (Newcomb)	10%	24.7	22.2 \pm 1.91	0.1004
<i>Zonitoides arboreus</i> (Say)	0%	33.3	27.2 \pm 4.13	0.0854
<i>Euconulus fulvus</i> (Müller)	20%	30.4	23.7 \pm 2.62	<u>0.0142*</u>
<i>Nesovitrea electrina</i> (Gould)	50%	22.5	23.1 \pm 2.31	0.5993
<i>Deroceras laeve</i> (Müller)	100%	25.2	23.4 \pm 2.41	0.2869
<i>Vittrina pellucida</i> (Müller)	10%	23.5	27.6 \pm 3.79	0.9122

Table 3-6: Results of indicator species analysis comparing high levels of retention (50-100%) to low levels of retention (0-20%).

* significant p-values

Species	Max group	Observed Indicator Value	Indicator value from randomized groups	
			mean \pm SD	p-value
<i>Succinea</i> sp.	high	11.1	11.1 \pm 0.16	1.0000
<i>Cochlicopa lubrica</i> (Müller)	low	22.2	15.2 \pm 6.66	0.4717
<i>Discus shimekii</i> (Pilsbury)	high	27.8	24.8 \pm 9.26	0.1782
<i>Discus whitneyi</i> (Newcomb)	low	63.9	54.1 \pm 3.02	<u>0.0020*</u>
<i>Zonitoides arboreus</i> (Say)	low	71.8	55.7 \pm 6.44	<u>0.0176*</u>
<i>Euconulus fulvus</i> (Müller)	low	63.7	55.2 \pm 3.89	<u>0.0366*</u>
<i>Nesovitrea electrina</i> (Gould)	low	56.9	54.8 \pm 3.62	0.2697
<i>Deroceras laeve</i> (Müller)	high	56.0	55.1 \pm 3.78	0.3815
<i>Vittrina pellucida</i> (Müller)	low	54.4	57.2 \pm 5.05	0.7097

Nonmetric Multidimensional Scaling (NMDS) ordination of the data about gastropod assemblages set resulted in a significant ($p=0.008$) two-dimensional solution with a stress of 8.57 (Fig 3-4). Axes 1 and 2 explained 42.2% and 52.9% of the variance, respectively. However, the ordination does not show tight, easily interpretable groups or a clear trend in relation to retention level. Although characterized by high variation among replicates, the ordination generally places assemblages from higher retention levels (75% and 100%) in the upper right-hand side of ordination space. Those from lower retention levels (Clear Cut, 10%, and 20%) are situated in the lower left-hand side of the ordination, with points representing the 50% retention level scattered between the high and low retention groupings.

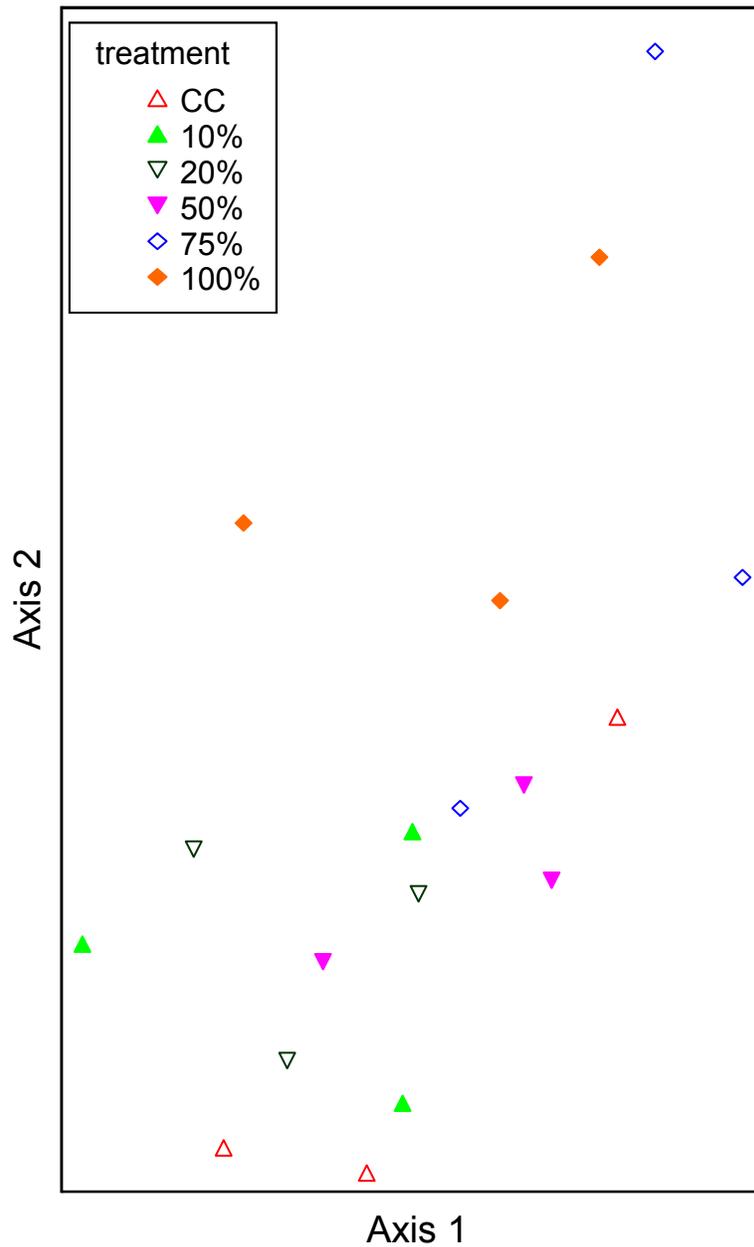


Figure 3-4: Results of NMDS ordination of 9 species collected from 18 compartments representing 6 retention harvest treatments. Each point represents one 10-ha stand belonging to one of six different retention levels (Clear Cut (CC), 10%, 20%, 50%, 75%, or 100% trees remaining).

Redundancy analysis identified two environmental variables as influencing patterns in gastropod assemblages: moss cover and canopy closure (Fig. 3-5). However the explanatory power of this ordination was low. Axis 1 and 2 explain only 6.1% and 1.1% of the variation in the species data, respectively. Interestingly, the majority of species showed an affinity for areas with low moss cover. Some species were associated with low canopy cover, like *Euconulus fulvus*, and *Zonitoides arboreus*, but others, like *Discus shimckii* were associated with high canopy cover (Fig. 3-5). The board trap captures from the unharvested stands grouped closely in comparison to the other retention levels, which were highly variable and showed no clear groupings (Fig. 3-6).

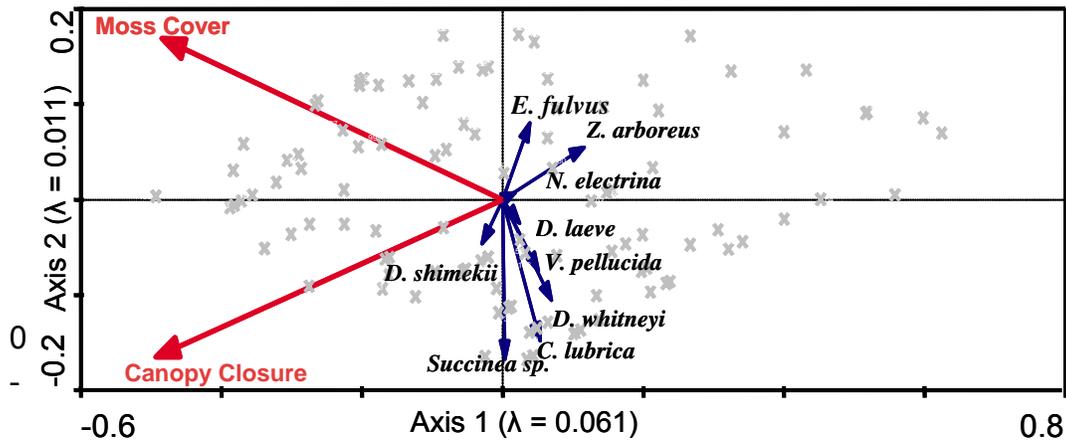


Figure 3-5: Results of constrained ordination (RDA) of the gastropod assemblage. Red vectors = environmental parameters, blue vectors = species, and x-marked points = board traps. Environmental vectors shown are those that significantly explain assemblage variation as chosen through forward selection.

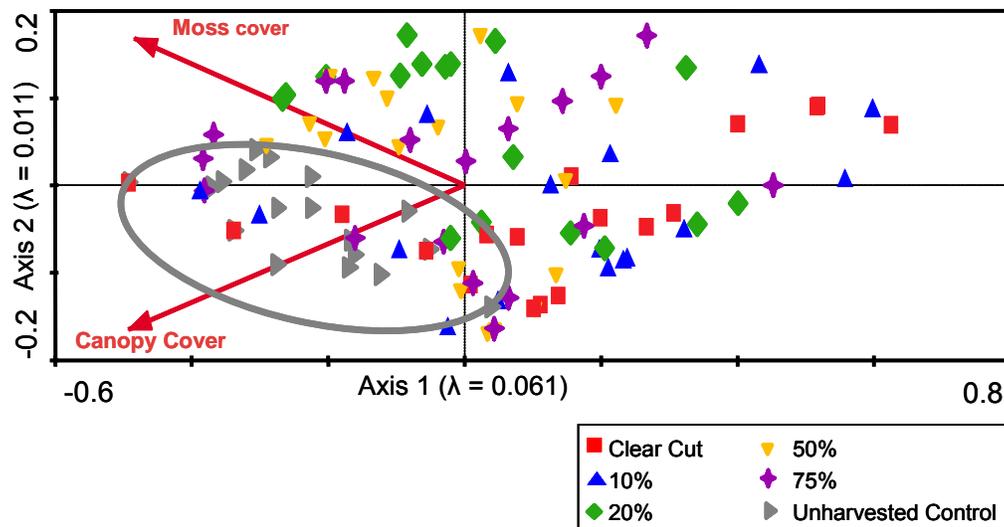


Figure 3-6: Results of constrained ordination (RDA) of the gastropod assemblage colour coded for harvest treatment. Red vectors = environmental parameters and points = board traps. Environmental vectors shown are those that significantly explain assemblage variation as chosen through forward selection. The circle indicates the board traps from the unharvested control treatment.

Dominance structure of gastropod assemblages. The gastropod assemblage at EMEND was generally composed of a few dominant species, many subdominants and a few uncommon species (Table 3-7). Assemblages at all retention levels were dominated by the species *Discus whitneyi*, which consistently had the highest *DV'* value (Table 3-7). Assemblages clearly change with harvest intensity (Table 3-7; Fig. 3-7). In unharvested compartments, *Deroceras laeve* was the second most dominant gastropod, but in response to any harvesting the *DV'* value of this slug declined and it moved to a common position. In retention levels $\leq 50\%$, *Zonitoides arboreus* became the second most dominant gastropod. *Discus shimekii* remained uncommon in all harvest treatments, and showed a decline in *DV'* value with increasing harvest intensity. The dominance results for two uncommon species, *Succinea sp.*, and *Cochlicopa lubrica*, cannot be interpreted with respect to effects of harvest intensity because they were captured too infrequently.

Table 3-7: Relative dominance values for gastropod species in six retention levels

Species	ID	100%	75%	50%	20%	10%	CC
<i>Succinea sp.</i>	9		0.22U				
<i>Cochlicopa lubrica</i>	8					0.45U	0.03U
<i>Discus shimekii</i>	5	3.17U	0.22U	0.07U			0.05U
<i>Discus whitneyi</i>	1	44.13D	53.13D	39.22D	42.36D	57.55D	42.31D
<i>Zonitoides arboreus</i>	6	2.11U	7.27C	25.89D	15.77S	16.14S	35.57D
<i>Euconulus fulvus</i>	4	9.54S	8.93S	5.42S	15.77S	6.77S	5.76S
<i>Nesovitrea electrina</i>	3	14.79S	16.07S	20.43S	18.40S	8.80S	13.36S
<i>Deroceras laeve</i>	2	22.63S	10.04S	8.44S	4.68C	7.58S	2.61C
<i>Vitrina pellucida</i>	7	3.62U	4.02S	0.54U	2.03U	2.71C	0.31U

CC indicates clear cut, and 10-100% indicates percentage of green tree retention. ID values correspond to species identifier numbers in Figure 3-7.

D = dominant; S = subdominant; C = common; U = uncommon species

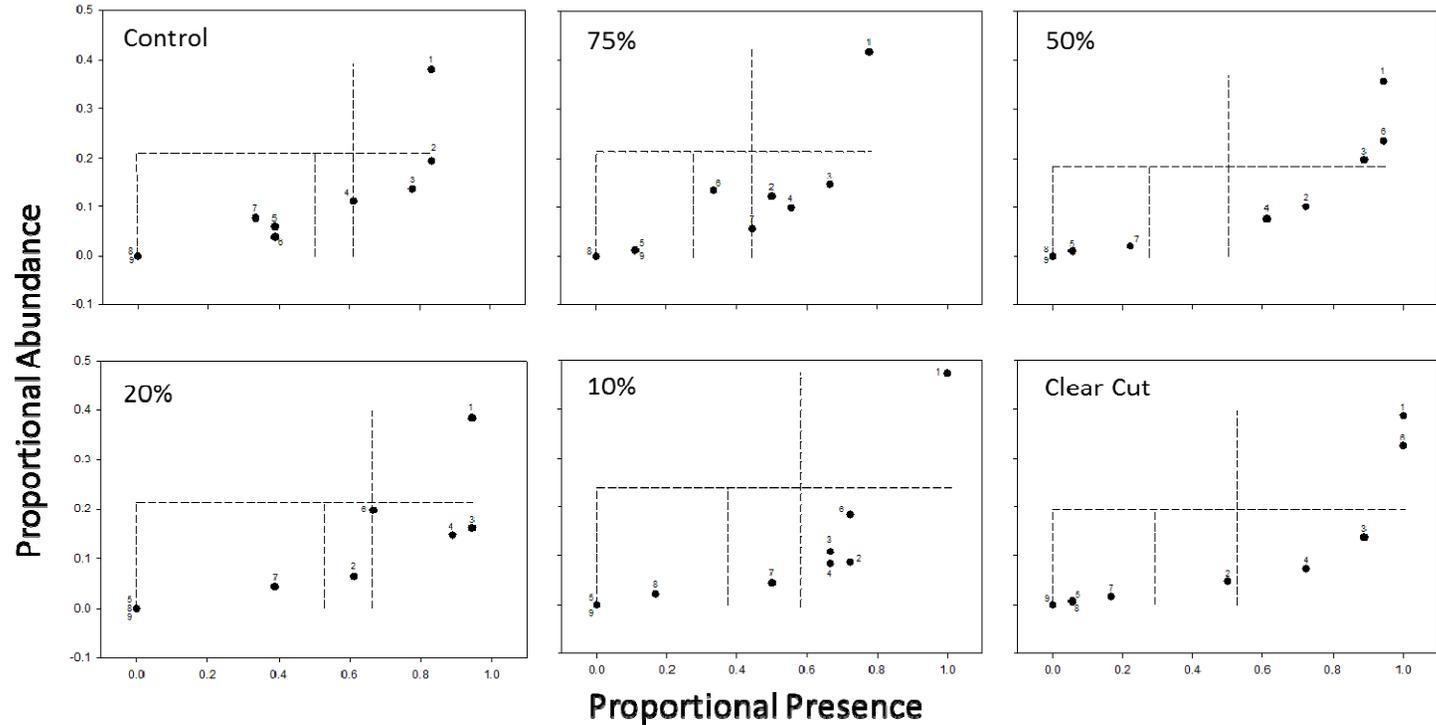


Figure 3-7: Dominance plots of gastropod assemblages in varying levels of green tree retention: clear-cut (1-2% of trees retained after harvest), 10%, 20%, 50%, 75% and control (unharvested reference compartments). Species are identified with numbers: 1 *Discus whitneyi*; 2 *Deroceras laeve*; 3 *Nesovitrea electrina*; 4 *Euconulus fulvus*; 5 *Discus shimkii*; 6 *Zonitoides arboreus*; 7 *Vitrina pellucida*; 8 *Cochlicopa lubrica*; 9 *Succinea* sp. These plots were split into four quadrants using the midvalues of proportional presence and proportional abundance. The lower left quadrant is further split into two using the quarter proportional presence value.

Machine Corridor Effects. Position relative to machine corridor and retention strips had significant interaction on total abundance of gastropods (ANOVA, $F_{1,34}=5.84$, $p=0.0212$) (Fig. 3-8). A post-hoc differences of least squares means test indicated that within 75% retention compartments, the retention strips had significantly lower snail abundance than the machine corridors (LSMEANS slice-value, $F_{1,34}=7.90$, $p=0.0081$), while in the 20% retention treatment there was no significant difference between location on or off the corridor (LSMEANS slice-value, $F_{1,34}=0.37$, $p=0.5484$). Thus, it appears that openness of the canopy has a stronger effect on gastropod abundance than does soil compaction on machine corridors.

Species composition differed significantly among retention levels (PERMANOVA, $F_1=3.69$, $p=0.0068$) and between corridor and retention strips (PERMANOVA, $F_1=3.77$, $p=0.0042$). There was no significant interaction between these two factors (PERMANOVA, $F_1=1.36$, $p=0.2567$). A significant interaction in species dispersion was detected between the two factors (PERMDISP, $F_1=7.91$, $p=0.0294$). Nonetheless, pair-wise comparisons revealed no differences in species dispersion between levels within factors, suggesting that these effects represent real changes in species composition.

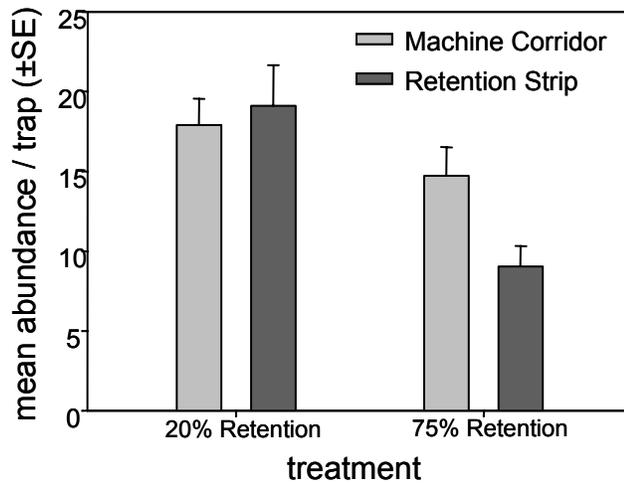


Figure 3-8: Mean abundance of gastropods per board trap over five collections in 20% and 75% retention treatments for machine corridors and retention strips separately.

Discussion

Gastropod assemblages were affected by retention level, even nine years post-harvest. Overall gastropod abundance actually increased with harvest intensity and most gastropod species seemed to thrive following harvest disturbance, similarly to observations by Ström et al. (2009). Hylander et al. (2004) observed a negative effect of clear-cutting immediately following disturbance. Strayer et al. (1986) found a rapid recovery of gastropods after clear-cutting, following an initial decline in abundance. Thus, on balance the evidence suggests little long-term deleterious effect on this dispersal limited taxon.

Variable retention harvest did, however, cause shifts in structure of gastropod assemblages, most notably changing patterns of dominance (Fig 3-7). Abundance of most gastropod species increased with harvest intensity; however, abundance declined for some species (particularly, *Deroceras laeve* and *Discus shimekii*), indicating negative response to harvest. Long-lasting response to harvest in terms of species composition was also evident within machine corridors. More tree removal from the

retention strips resulted in increased gastropod abundance similar to that observed in machine corridors.

Resources limiting for some populations may be more readily available to forest gastropods following harvest. These species primarily feed on decaying plant matter (Mason 1970) and harvest increases the amount of forest floor organic matter, through the input of logging slash (Hendrickson et al. 1989). Although harvesting can initially decrease leaf litter input from the canopy, leaf biomass in regenerating mixedwood boreal forests quickly exceeds that of mature forests, due to the high densities of regenerating aspen (Lieffers et al. 2002; Peterson and Peterson 1996). Understory vegetation cover also increases with harvest intensity (Craig and Macdonald 2009), and this would also contribute to total litter biomass. The fact that Hawkins et al. (1997) found higher gastropod density in a regenerating spruce plantation than a 70-year old mixedwood forest was attributed to there being more understory vegetation and deciduous leaf litter in the plantation.

The literature suggests that both quantity and food quality of litter increases following harvest. Early-successional plants like *Geranium* and *Rubus* more easily mobilize calcium from the mineral soil (Hamburg et al. 2003; Närhi et al. 2010). Calcium is crucial for gastropod reproduction, shell production, and nutrient metabolism (Dallinger et al. 2001), and thus, gastropod distribution is greatly influenced by the amount of available calcium in the litter layer (Juříčková et al. 2008). Following harvest, there is a net flux of calcium from the mineral soil to the forest floor and this results in a greater density of gastropods in young stands (Hamburg et al. 2003).

Hylander et al. (2004) found that within harvested systems bryophyte cover seemed to mitigate negative effects of clearcutting on gastropod assemblages. This is not consistent with my results because most gastropod species in the present study were strongly associated with areas of lower moss cover (Fig. 3-5). High moss cover, consisting

predominantly of feather mosses, is reflective of undisturbed forest floor (Mills & Macdonald 2004), and overhead tree composition (Chávez & Macdonald 2010). Gastropods were more strongly associated with broadleaf forests at EMEND (see Chapter 2 results) and broadleaf litter inhibits growth of feather mosses (Natalia et al. 2008). These relationships are most likely the cause for the negative relationship between mosses and gastropods.

A harvest threshold near 50% GTR for effects on gastropod abundance was also supported by changes in species composition. Compositional differences were evident between high and low retention groups in a PERMANOVA analysis, and this shift occurred around the 50% retention level, as indicated by groupings in the NMDS ordination (Fig. 3-4). The gastropod response accounting for this shift is apparent in dominance patterns of *Zonitoides arboreus*, a low retention species indicator (Table 3-6), that shows much higher proportional abundance and proportional presence at $\leq 50\%$ retention (Table 3-7, Fig. 3-6).

Species richness was not related to retention level (Fig 3-2), and although harvest was associated with changes in abundance, composition, and dominance, these did not result in net losses or gains of species. Some species, however, did show sensitivity to harvesting. The greatest declines were observed in the only slug species, *D. laeve*, and the snail species *D. shimemkii*. *D. laeve* dropped in dominance with even the lowest amount of canopy removal, although it did not disappear in any of the harvest treatments. Because *D. laeve* is considered a relatively mobile species (Forsyth 2004) it may be able to seek microsite refuges in these lower retention sites. On the other hand, abundance of *D. shimemkii* declined drastically with increasing harvest intensity, and this species was uncommon or simply not collected in the lowest retention levels. Higher levels of retention seemed to better conserve these harvest sensitive species.

There appears to be much small scale heterogeneity influencing gastropod assemblages on harvested landscapes. The spread of sample points in the redundancy analysis ordination, for example, was much greater for harvested than in uncut compartments (Fig. 3-5), even 9 years after harvests were applied. Although the RDA does not explain a large amount of variance in gastropod assemblages it does suggest that canopy cover and moss cover were the most important of the measured environmental factors with respect to influence on the gastropod assemblages. Both of these factors can be extremely patchy within a single stand, especially in a stand with a mixedwood canopy (Chávez and Macdonald 2010). Retention harvest simply adds to this variability. For example, random placement of sampling plots within machine corridors varied with respect to location of residual trees and harvested stumps.

Effects of canopy removal on gastropod assemblages were apparent at a small within-stand scale. Machine corridors had a higher abundance of gastropods than retention strips, but removing trees from retention strips also increased snail abundance so that snail abundance in the 20% retention strips was indistinguishable from that on machine corridors. Despite similarities in gastropod abundance, composition of the assemblages in these machine corridors differed between the 20% retention treatment and the 75% retention treatment. This suggests that retention level in the nearby retention strips influences the fauna which occupy these machine corridors (Fig 3-8). In contrast, Craig and Macdonald (2009) found that understory plant communities in machine corridors were similar, regardless of retention level, and that all resemble communities found in clear-cuts. However, my results suggest that retention level does influence the gastropod fauna which occupy these vegetatively similar strips, perhaps because even these dispersal-constrained animals are more individually mobile than plants.

Following clear-cutting in a riparian boreal forest, the initial response of gastropods was negative (Hylander et al. 2004). However,

Ström et al. (2009) found that riparian boreal forests that had been clear-cut 40-60 years prior had higher gastropod abundances than old forests that had never been clear cut. The results of the present study, conducted 9 years post-harvest, indicate that gastropod recovery may be quite rapid, even within more mesic boreal mixedwood forest. Because gastropods are generally considered to be dispersal limited organisms (Nordén and Appelqvist 2000), such a rapid recovery after harvest suggests that gastropods are surviving harvest disturbance in situ and not migrating from adjacent stands (Strayer et al. 1986). This could involve vertical migration into the soil (Hawkins *et al.* 1997) or use of moist refugia like hollows and crevices (Hylander et al. 2004).

For these gastropod species, harvesting does not seem to be overly detrimental, as most species at EMEND increased in abundance with increasing harvest intensity. In a study of gastropod response to hurricane disturbance, Bloch and Willig (2006) found that some species succeeded with the sudden abundance of resources, while others were sensitive to microclimatic changes. The present study showed similar patterns and it is challenging to evaluate their management significance. For example, increases in abundance can have negative ecological consequences when considered more broadly. Terrestrial gastropods are intermediate hosts for meningeal worm, a parasite which infects North American ungulates, and is fatal to moose. Logged areas, with increased snail abundance, show greater transmission of this parasite (Nankervis et al. 2000). Green-tree retention left on the landscape conserves sensitive gastropod species, but also prevents large increases in abundance which could pose concerns for wildlife management.

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Chapter 4 – General Discussion

Effective conservation of biodiversity requires an understanding of all taxa of concern. In this regard, understudied taxa like terrestrial gastropods in boreal forests present a significant challenge. So little is known about their natural history that there is no effective basis on which to base conservation priorities. This thesis contributes considerably to our understanding of these forest organisms and provides insight into how this important group can be managed in the face of increasing anthropogenic disturbance in the mixedwood boreal forest. At the onset of this work, I reasoned that forest-dwelling gastropods might be sensitive to harvest because of their limited dispersal ability.

In pursuing this work, I had two objectives: i) to examine the effects of forest cover type on the gastropod fauna of the mixedwood boreal forest of northern Alberta; and ii) to examine the effects of varying levels of partial harvesting on gastropod assemblages. Two major themes have emerged from my results. First, gastropod assemblages are influenced by canopy composition, with most gastropods of the mixedwood showing a strong affinity for broadleaf dominated forests. Thus, harvesting which changes canopy tree composition towards early successional broadleaf forests has implications for gastropod assemblages. Secondly, harvesting with retention helps to maintain pre-harvest gastropod assemblages and will likely conserve gastropod assemblages if used as a tool for biodiversity management. Leaving $\geq 50\%$ retention seemed to maintain gastropod abundance in stands, and in fact overall gastropod abundance increased at lower retention levels. Retention harvests retain sensitive gastropod species on forested landscapes and should sustain assemblages similar in compositions to those of intact forests.

4.1 Main Findings

The first chapter of my thesis was inspired by the increasing interest of incorporating ecological sustainability in forest management. This is more easily achieved through understanding species assemblages in relation to forest type and their responses to disturbance. In the introductory chapter, I introduced gastropods and their importance in forests as decomposers, herbivores, and prey species. I also outlined how ecological studies of gastropods before and after harvest might provide useful information to forest managers about the effectiveness of variable retention harvest for managing gastropods on the landscape as a component of broader biodiversity.

In the second chapter, I explored the influence of forest cover type on gastropod assemblages, and how a particular set of plausible environmental parameters contributes to these patterns. Deciduous dominated forests stood apart from the other forest types as having higher gastropod abundance and species richness. This forest type supported more gastropod species at higher levels of dominance (greater proportional abundance and proportional presence in collected samples) than did other cover types. Tree species mixture influenced gastropod distribution within each forest cover type; basal tree area of either conifer or broadleaf trees was generally associated with gastropod distribution within a stand. Different gastropod species showed associations with different tree species, and interestingly, these associations changed between cover types suggesting complex ecological contingency. Overall, my work suggests that maintaining a tree species mixture at a variety of scales is crucial for persistence of gastropod assemblages similar to those of unharvested stands in the mixedwood boreal forest landscape.

In chapter three I discussed the response of gastropods to variable retention harvesting. Increased gastropod abundance in stands subjected to increasing harvest intensity was apparent, even 9 years post-harvest. Abundance patterns suggested a harvest threshold of $\leq 50\%$ for

maintaining natural assemblages; with increased harvest overall gastropod abundance increases significantly. Furthermore, patterns of species dominance change, with significantly different gastropod assemblages existing under high and low retention. Most species responded positively to increasing harvest intensity; however, some species, here labeled as harvest sensitive species, showed declines. The greatest declines were in the slug species *Deroceras laeve*, and the snail *Discus shimckii*.

Gastropod assemblage composition varied greatly among samples in harvested compartments, compared to the relatively similar samples collected from unharvested compartments. Thus, harvesting increased local heterogeneity, in contrast to patterns observed in other animal taxa on the same landscape (e.g., Work et al. 2010). Machine corridors, within harvested compartments, harboured significantly more gastropods than did retention strips; however, removing trees from these strips through lower levels of retention harvest shifted gastropod assemblages toward those found on the corridors. Further, assemblage composition within machine corridors was influenced by the stem-density within the nearby retention strips in contrast to results for understory plants at EMEND (Craig and Macdonald 2009). Thus, harvesting with green-tree retention should help conserve gastropod assemblages similar to those found in intact forests.

4.2 Leaf litter, moisture and canopy removal

Throughout this thesis, there seemed to be a link between gastropods and broadleaf litter. Gastropods mainly reside in leaf litter and consume it and organisms, like fungi, associated with it (Mason 1970). In Chapter 2, I demonstrated a strong association between broadleaf dominated forests and terrestrial gastropods. Increasing harvest intensity promotes establishment of broadleaf dominated cover types

(Frey et al. 2003). In Chapter 3, I observed dense regeneration of early successional aspen-dominated plant assemblages in harvest compartments and showed that this was associated with increases in gastropod numbers. One can expect a mixedwood dominated forest to become more broadleaf dominated at higher levels of harvest intensity because of an increase in regenerating aspen sapling density. Thus, increases of gastropod abundance with increasing harvest intensity will be a consequence of gastropod affinity for broadleaf litter.

Gastropods are desiccation sensitive at all life stages, and require moisture for respiration and locomotion (Barker 2001). For this reason, snails and slugs are restricted to areas of higher moisture (Asami 1993) and reduced temperature extremes (Hawkins et al. 1998). Canopy removal generally causes decline of organisms, like bryophytes, that are sensitive to evaporative water loss (Caners et al. 2010, Fenton et al. 2003). Therefore, I expected gastropods to be sensitive to canopy removal, and was surprised by my results. It seems that the majority of gastropod species occupying the boreal mixedwood are well adapted to live in generally dry conditions.

Many species captured in this study have features believed to prevent or minimize evaporative water loss. For example, denticles like those found inside the aperture of the shell of the family Vertiginidae are speculated to serve this function (Forsyth 2004). Other species encountered in my study, like *Euconulus fulvus*, have narrow crescent-shaped apertures. Many terrestrial snails produce a mucous seal across their shell opening, called an epiphragm, which minimizes desiccation during aestivation and hibernation (Forsyth 2004). Gastropods also avoid water loss through behavioural means. For example, most snails feed during the night when the temperature is cooler and evaporative water loss is lower (Barker 2001).

When considering the initially puzzling results of the study about habitat use, it is important to remember that the leaf litter environment

differs much from the above ground environment to which organisms, like bryophytes, are exposed. Following harvest in boreal regions, soil moisture often increases, because of reduced water uptake by plants (Keenan & Kimmins 1993). As well, broadleaf litter retains more rainwater than needle-leaf litter because it can intercept a higher percentage of the throughfall precipitation (Sato et al. 2004). These characteristics of broadleaved boreal systems may add to the suitability of broadleaf litter, which is more abundant in young regenerating forests. Thus, my study suggests that moisture loss following canopy removal is not an issue for forest gastropods after all.

4.3 Gastropods and microsite variability

Gastropod assemblages displayed a high degree of variability between sampling locations within a compartment. In addition, small scale variability was evident in the machine corridor study; machine corridors supported different gastropod assemblages than the retention strips located <20 m away. Gastropods have been described as being highly dependent on microsites, reflecting dispersal limitations and desiccation sensitivity (Welsford et al. 1990). Such dependencies may explain these small scale differences observed, but the unexpected apparent ability of gastropods to colonize new areas and/or express population growth through local recruitment suggests that these dependencies are not constant constraints. Forest dwelling snails and slugs, must move more widely during rainy periods and at night (e.g., Bailey 1975, Baur 1986, Fiorentino et al. 2009), with their persistence depending on fine-grained distribution of microsites in boreal sites and, possibly, on passive dispersal mechanisms (e.g., Baur 1986, Kawakami et al. 2008).

Gastropod distribution was not well explained by the environmental parameters that I measured in this study. The redundancy analyses, presented in chapters 2 and 3 failed to explain a large amount of variation in gastropod assemblages. This suggests that none of the chosen

environmental parameters were by themselves very strongly associated with gastropod distributions. Most of the environmental parameters reflected coarse scale aspects of forest structure, and as such, may not best describe microhabitat variability important for gastropods.

An unmeasured parameter which may have contributed substantially to gastropod distribution is soil calcium. This is crucial for reproduction, shell production, and nutrient metabolism in gastropods (Dallinger et al. 2001). Calcium is among the most important factors influencing snail distribution in other forest systems (Juříčková et al. 2008; Hylander et al. 2005; Hotopp 2002). Through the input of leaf litter, calcium content of the upper soil horizons is directly related to the calcium levels of nearby plants (Vesterdal & Raulund-Rasmussen 1998), which can vary considerably in composition between sampling locales. Understory plants associated with aspen trees, like *Gallium triflorum*, have a high demand for calcium. These calcium rich plants contribute to a calcium rich litter layer (Légaré et al. 2001).

In order to better describe microsite associations, one of my original thesis goals was to describe the gastropod assemblages in relation to bryophyte diversity and cover. Bryophytes are good indicators of microenvironment including characteristics like pH, moisture, and forest floor disturbance (Mills and Macdonald 2005).

At each sampling location, bryophyte species were identified, or collected for later identification, and percent cover for each species was estimated within a 1x1 m area (Appendix 4-A). I used predictive co-correspondence analysis, an ordination method that attempts to identify patterns that are common to two assemblages (ter Braak & Schaffers 2004) (in this case, gastropods and bryophytes) to look for relationships. I found that gastropod assemblages and bryophyte assemblages at my sampling sites were completely unrelated with no patterns in common. This was indicated by negative cross-validators fit measures between the two assemblages, indicating that bryophyte species composition predicts

gastropod species composition worse than predicted by chance (Schaffers et al. 2008). This outcome was supported by the negative association between gastropod species and moss cover at my sites (see chapter 3 results and discussion).

In contrast to my results, strong gastropod-bryophyte relationships have been suggested in the literature (Davidson et al. 1990, Grime and Blythe 1969, Hylander et al. 2004, and Kimmerer and Young 1995). In order to best investigate this relationship, it may be best to target certain moss communities to directly sample gastropods from, rather than rely on their co-occurrence in a randomly located plot. Moss growth is inhibited by leaf-litter and they tend to be most abundant and most rich in the conifer-dominated forests at EMEND (Caners 2010, Natalia et al. 2008), which may be better suited habitats for exploring a moss-gastropod relationship.

4.4 Future Research

Low vagility and sensitivity to microclimatic variability make gastropods excellent indicators of disturbance as indicated in Chapter 3 (Theenhaus and Scheu 1996). The literature generally suggests that gastropods distributions reflect many factors, both biotic and abiotic, like vegetation, soil chemistry, moisture, and microsite availability. Their ability to integrate many aspects of a system could make gastropods a powerful indicator of system recovery. Exploring the intricacies of species-specific gastropod responses to microhabitat variability could clarify the potential of gastropods as such indicators. Gastropods would be easy to use as indicators in boreal forests: they are relatively easy to sample, and their lower diversity in comparison to other invertebrate groups makes local assemblages easy to identify.

Many organisms rely on gastropods for food. For example, cycrhrine and pterostichine ground beetles and harvestmen from the family Trogulidae have evolved specialized mouthparts that are able to

reach into snail shell apertures and utilize this abundant food source (Digweed 1993; Nyffeler and Symondson 2001). Snails also provide calcium for other animals; for example, forest birds eat snails and require this calcium source for egg laying (Graveland et al. 1994). It would be interesting to investigate whether or not gastropod predators are more abundant in harvested systems where gastropods are more abundant, especially those predators that are gastropod specialists.

There is still much to learn regarding the temporal responses of gastropods to forest harvesting. It has been suggested that over time, gastropod assemblages recover to resemble pre-harvest assemblages (Ström et al. 2009). Future research could investigate if assemblages in the boreal mixedwood forest show this recovery, and if harvest sensitive species are being maintained on the landscape over time. The soil samples that I used to sample gastropods for the cover type study (Chapter 2) provided six additional species that were not collected with the board traps that I used to sample the retention harvest treatments. Some of these species may also be sensitive to harvesting, and especially to soil compaction in machine corridors.

Both cover type and harvest intensity in the mixedwood boreal forest influenced gastropod assemblages. It would be interesting to further explore the interaction of these factors. Do assemblages from different cover types respond to variable retention harvest differently? As well one might ask, how quickly do gastropod assemblages in regenerating stands come to resemble assemblages in deciduous dominated cover types?

Variable retention harvesting is a management strategy derived from a natural disturbance based management model (Franklin et al. 1997). Few studies have looked at the response of gastropod assemblages to wildfire. Kiss and Magnin (2003) found that gastropod abundance is drastically reduced in the short term following fire, but recovers 5 years after disturbance. It would be interesting to investigate if gastropods respond to fire disturbance in similar way that they respond to

harvest disturbance and to examine if retention harvest can emulate natural disturbance for this group.

4.5 Management Recommendations

Most gastropod species *increased* in abundance following harvest disturbance. While we can be fairly confident that these species will remain on the landscape after harvesting, an increase in abundance could have consequences for other components of the system. For example, gastropods can influence forest succession. Gastropods prefer to eat senescent plant material, although they will also graze on live plants, enough to affect plant community dynamics. This is primarily through seed consumption and the removal of leaves from seedlings (Ferner 1987). Such grazing could have significant influences on plant distribution patterns and plant succession following disturbance, especially if grazing pressures increase as a result of increased gastropod abundance. Often, biodiversity management is focused on species richness; however, conserving relative species abundances may also be important for maintaining forest communities after disturbance. An increase in gastropod abundance could have undesirable consequences for biota that interact with gastropods. Furthermore, recovery of gastropod populations to pre-disturbance levels could provide a useful measure of forest recovery.

My thesis addresses current forest management concerns regarding biodiversity conservation by providing new information about a component of forest diversity that is not well known or understood. Leaving green tree retention on boreal landscapes appears to maintain gastropod abundance and maintain assemblages with similar composition to those found in intact forests. Harvesting can result in homogenization of the forest canopy and the associated understory, by increasing early successional species and decreasing late successional species (Frey et al. 2003, Macdonald and Fenniak 2007). Harvesting with retention

encourages persistence of canopy mixture landscapes and this, as my results have shown, is important for structuring gastropod assemblages. Harvesting was clearly associated with high abundance of many species, even 9 years post-harvest. A few harvest sensitive species like *Discus shimekii*, may require higher levels of retention in order to survive locally on northern landscapes after harvest. However, the results of this study, drawn from the first decade of recovery after harvest, suggest that green-tree retention is compatible with maintaining gastropod assemblages in mixedwood systems.

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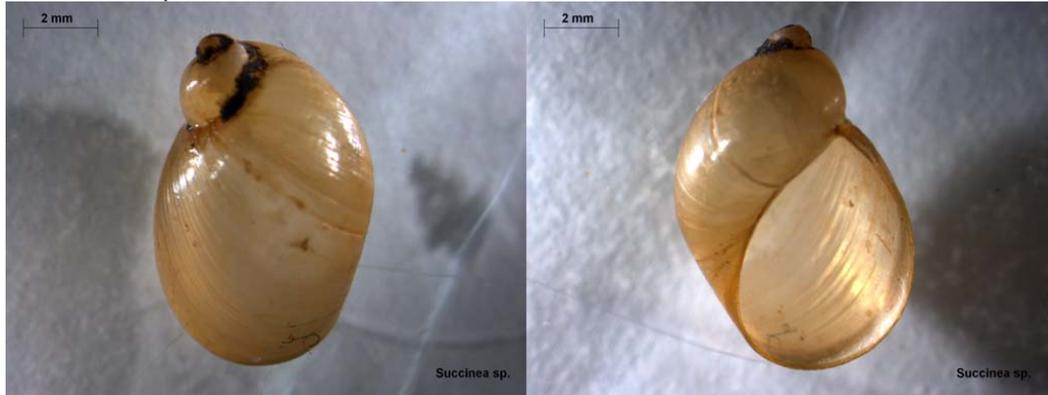
Appendices

Appendix 2-A

Representative photographs of snail species collected at EMEND.

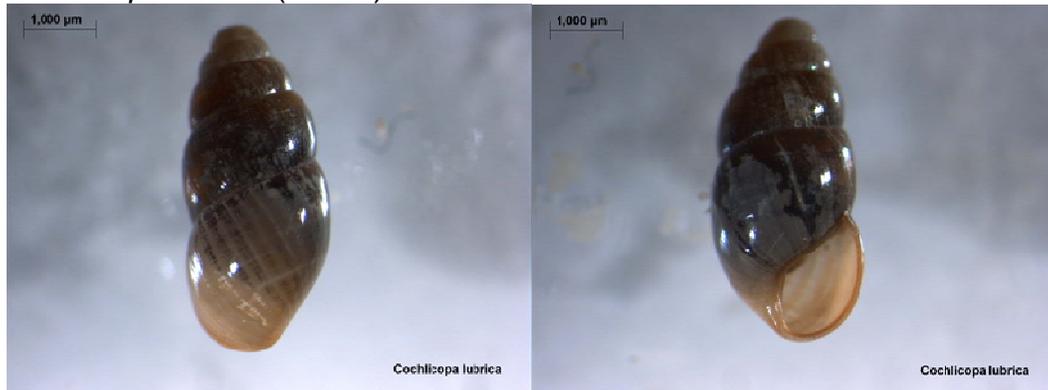
Family Succineidae

Succinea sp.



Family Cochlicopidae

Cochlicopa lubrica (Müller)



Family Vertiginidae

Vertigo cristata (Sterki)



Vertigo gouldii (Binney)



Vertigo modesta (Say)



Columella edentula (Draparnaud)



Columella columella (von Martens)



Family Punctidae

Punctum minutissimum (Lea)



Family Discidae

Discus shimekii (Pilsbury)



Discus whitneyi (Newcomb)



Family Gastrodontidae
Zonitoides arboreus (Say)



Family Euconulidae
Euconulus fulvus (Müller)



Family Oxychiliidae
Nesovitreia electrina (Gould)



Family Vitrinidae
Vitrina pellucida (Müller)



Appendix 4-A

Moss species collected from four forest cover types in 2007: DDOM = deciduous dominated, DDOMU = deciduous dominated with spruce understory, MX = mixed deciduous and coniferous, CDOM = coniferous dominated, and from six harvest treatments of varying levels of tree retention in 2008: CC = clearcut, 10 = 10% trees remaining, 20 = 20% trees remaining, 50 = 50% trees remaining, 75 = 75% trees remaining, 100 = unharvested control.

Family	Species	Forest Cover Types	Harvest Treatment
Amblystediaceae	<i>Campylium hispidulum</i> (Brid.) Mitt.	DDOM, DDOMU, MX, CDOM	CC, 20, 50, 75
	<i>Sanionia uncinata</i> (Hedw.) Loeske	DDOM, DDOMU, MX, CDOM	CC, 10, 20, 50, 75, 100
	<i>Amblystegium serpens</i> (Hedw.) Schimp.	DDOM, DDOMU, MX, CDOM	CC, 10, 50
Aneuraceae	<i>Riccardia latifrons</i> (Lindb.) Lindb.		75
Aulacomniaceae	<i>Aulacomnium palustre</i> (Hedw.) Schwägr.	DDOM, DDOMU, CDOM	CC, 10, 20, 50, 75
Brachytheciaceae	<i>Brachythecium</i> spp.	DDOM, DDOMU, MX, CDOM	CC, 10, 20, 50, 75, 100
	<i>Eurhynchium pulchellum</i> (Hedw.) Jenn.	DDOM, DDOMU, MX, CDOM	CC, 10, 20, 50, 75, 100
	<i>Tomentypnum nitens</i> (Hedw.) Loeske	DDOM, DDOMU, MX, CDOM	
Bryaceae	<i>Bryum lisae</i> De Not.		CC, 20
	<i>Pohlia nutans</i> (Hedw.) Lindb.	DDOM, DDOMU, MX	CC, 10, 20, 50, 75, 100
Climaciaceae	<i>Climacium dendroides</i> (Hedw.) F. Weber & D. Mohr	DDOM	20
Dicranaceae	<i>Dicranum fragilifolium</i> Lindb.	CDOM	
	<i>Oncophorus wahlenbergii</i> Brid.	DDOM, DDOMU	10, 75
	<i>Dicranum fuscescens</i> Turner	CDOM	
	<i>Dicranum polysetum</i> Sw.	DDOMU, MX, CDOM	
	<i>Dicranum scoparium</i> Hedw.	DDOMU	20
	<i>Dicranum undulatum</i> Brid.	DDOMU, MX	
	<i>Ceratodon purpureus</i> (Hedw.) Brid.	CDOM	CC, 10, 20, 50, 75
Geocalycaceae	<i>Chiloscyphus pallescens</i> (Ehrh. ex Hoffm.) Dumort.	DDOM	
	<i>Lophocolea heterophylla</i> (Schrad.) Dumort.	DDOMU, MX	
Hylocomiaceae	<i>Hylocomium splendens</i> (Hedw.) Schimp.	DDOM, DDOMU, MX, CDOM	CC, 10, 20, 50, 75, 100

Family	Species	Forest Cover Types	Harvest Treatment
Hylocomiaceae	<i>Pleurozium schreberi</i> (Brid.) Mitt.	DDOM, DDOMU, MX, CDOM	CC, 10, 20, 50, 75, 100
Hypnaceae	<i>Ptilium crista-castrensis</i> (Hedw.) De Not.	DDOM, DDOMU, MX, CDOM	CC, 10, 20, 50, 75, 100
Jungermanniaceae	<i>Jamesoniella autumnalis</i> (DC.) Steph.	CDOM, DDOMU	75
Leskeaceae	<i>Thuidium recognitum</i> (Hedw.) Lindb.	DDOM, DDOMU, MX, CDOM	10, 20
Mniaceae	<i>Mnium spinulosum</i> Bruch & Schimp.	DDOMU, CDOM	10, 50
	<i>Plagiomnium cuspidatum</i> (Hedw.) T. Kop.	DDOM, DDOMU, MX, CDOM	CC, 10, 20, 50, 75, 100
	<i>Plagiomnium drummondii</i> (Bruch & Schimp.) T. Kop.	DDOM, DDOMU, MX, CDOM	CC, 10, 20, 50, 75, 100
	<i>Plagiomnium ellipticum</i> (Brid.) T. Kop.	DDOM, MX, CDOM	10, 20, 100
	<i>Plagiomnium medium</i> (Bruch & Schimp.) T. Kop.	DDOM, MX, CDOM	CC, 75
	<i>Rhizomnium pseudopunctatum</i> (Bruch & Schimp.) T. Kop.	DDOM, CDOM	
Polytrichaceae	<i>Polytrichum juniperinum</i> Hedw.		CC, 10, 50, 75
Pseudolepicoleaceae	<i>Blepharostoma trichophyllum</i> (L.) Dumort.	MX	75
Ptilidiaceae	<i>Ptilidium pulcherrimum</i> (Weber) Vain.	DDOMU, MX, CDOM	
Scapaniaceae	<i>Scapania glaucocephala</i> (Taylor) Austin		10, 75
Sphagnaceae	<i>Sphagnum warnstorffii</i> Russow	CDOM	
Splachnaceae	<i>Splachnum</i> sp.	DDOM, CDOM	