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Patterns and causes of variation in understory plant diversity and composition in mature boreal mixedwood forest stands of western Canada

by

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Dedication

To my Abba, I love you.

Abstract

Boreal mixedwood forest stands are comprised of a mixture of small canopy patches of varying dominance by conifer (mostly white spruce (*Picea glauca* (Moench) Voss)) and broadleaf (mostly trembling aspen (*Populus tremuloides* Michx.) trees. The purpose of this work was to extend our understanding of the patterns and causes of variation in understory vascular plant communities in unmanaged, mature boreal mixedwood forests. First, I assessed variation in understory community composition in relation to canopy patch type (conifer, mixed conifer-broadleaf, broadleaf, gaps) within mixedwood stands. The mosaic of canopy patches leads to different micro-habitat conditions for understory species, allowing for communities that include both early and late successional species and contributing to greater understory diversity. This study suggests that the mosaic of small canopy patches within mixed forest stands resembles a microcosm of the boreal mixedwood landscape, across which understory community composition varies with canopy composition at the stand scale. Second, I investigated the hierarchical organization of understory diversity in relation to the heterogeneous mosaic of canopy patch types through additive partitioning of diversity. The largest proportion of species richness was due to turnover among patches within patch type while individual patches had higher evenness. The mosaic of canopy patch types within mixedwood forests likely plays a crucial role in maintaining the hierarchical levels at which understory diversity is maximized. Third, I examined interactions among understory plant species by investigating the effect of shrub removal on biomass, composition and diversity of herbs using a 3-yr removal study in a natural understory community. There is asymmetric competition for light between erect shrub and herb species but herb response to erect shrub removal was species-specific. Plant interactions play an important role in structuring boreal understory communities. Finally, I explored the relative influence of space, environmental variables, and their joint effects, on understory composition and richness. The environmental variation caused by small canopy patches and biotic processes, such as species interactions, converge at the fine scale to create a spatially patchy structure in understory communities in boreal mixedwood forests. Modifications in the natural mixture of small canopy patches could disrupt the spatial and environmental structures that shape understory composition and diversity patterns.

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Contents

List of Tables

List of Figures

List of Appendices

Chapter 1

Introduction

Mature, unmanaged forest ecosystems exhibit natural patterns of plant diversity, abundance and composition that are frequently absent from managed forests; these patterns provide a point of comparison for the effects of natural and anthropogenic disturbance (UNEP 2002; Frelich and Reich 2003). Most of the remaining mature, unmanaged natural forests of the world are within boreal, or taiga, regions (UNEP 2002). On a global basis, boreal forests fulfill crucial ecological roles including maintenance of biodiversity and storage of carbon, as well as providing economic services such as provision of wood fibre for pulp and wood products (Nilsson and Wardle 2005; Mayer et al. 2005). Despite the global importance of boreal forests, very little is understood about their ecological processes in comparison to those of tropical and temperate forests (Nilsson and Wardle 2005).

Boreal mixedwood forests are considered the most productive and diverse systems forests of the North American boreal landscape (Chen and Popadiouk 2002; Lieffers et al., 2008). Mixedwood forests dominate mesic sites across the southern portion of the western Canadian boreal forest. At the landscape level, boreal mixedwood forests comprise a mosaic of stands with varying dominance by trembling aspen (*Populus tremuloides* Michx.), balsam poplar (*Populus* *basamifera* L.) and white spruce (*Picea glauca* (Moench) Voss) with lesser amounts of black spruce (*Picea mariana* (Mill.) B.S.P.), balsam fir (*Abies balsamea* (L.) Mill.), lodgepole pine (*Pinus contorta* Dougl.) and paper birch (*Betula papyerifera* Marsh.) (Chen and Popadiouk 2002; Lieffers et al., 2008). At a finer scale, this mosaic includes 'mixed' forest stands which are comprised of a mixture of small canopy patches of varying conifer and broadleaf composition. These mixed stands have been associated with higher diversity of several biotic groups, including songbirds (Hobson and Bayne, 2000) arthropods (Work et al., 2004; Buddle et al., 2006) and understory vascular plants (Macdonald and Fenniak, 2007).

Understory plant communities are a critical component of boreal ecosystems (Nilsson and Wardle 2005). They are the most important contributors to overall boreal vegetation diversity (Hart and Chen 2006) and provide habitat for faunal communities (Hobson and Bayne, 2000; Work et al., 2004; Buddle et al., 2006). Also, understory plants directly and indirectly regulate forest structure by influencing nutrient cycling, competing with tree seedlings at the establishment stage and by modifying micro-climate conditions where tree seedlings grow and are often considered as indicators of soil moisture and nutritional status (Hart and Chen 2006). Despite the great importance of boreal understory plant communities, the vast majority of published ecological work from the boreal zone has focused on the tree layer overlooking the understory layer and, there is limited understanding of how understory communities are structured within boreal mixedwood forest stands.

In the past two decades, mixedwood forests have become highly desirable for commercial harvesting, which has dramatically increased (Chen and Popadiouk 2002). As such, a deeper understanding of the natural patterns of understory diversity, abundance, and composition in boreal mixedwoods, as well as the processes underlying these patterns, is of great importance for sustainable management of boreal forests, in which biodiversity conservation is of particular concern with respect to sustainable forest management. From theory, it is known that micro-habitat heterogeneity (Kotliar and Wiens 1990; Oborny et al. 2000; Frelich et al., 2003), species interactions (Díaz et al. 2003; Brooker 2006; Tilman 2007) and plant spatial patterns (Dale 1999) have important influences on plant community structure. However, the influence of these factors on understory communities found within mixedwood boreal stands have not been investigated until now. The overall purpose of this work was to extend understanding of the patterns of understory diversity, abundance and composition in unmanaged and mature boreal mixedwood forests, in order to use this knowledge as a benchmark for sustainable forest management. I purposely focused on the local (stand) level which is where some key ecological processes that structure plant communities operate (Keddy 2005), where management decisions are made (Colwell and Coddington 1994; Roberts and Gilliam 1995) and where measures towards management, conservation and restoration may be undertaken. Through the following four chapters, I address the influence of small canopy patch types, species interactions and spatial structure on understory communities.

Chapter 2: The influence of canopy patch mosaics on understory plant community composition in boreal mixedwood forest: Forested landscapes are comprised of a mosaic of canopy patches differing in size and biotic and abiotic characteristics that critically influence the composition of plant communities (Halpern and Spies 1995). In boreal forests, the effect of large canopy patches (i.e., 'stands') on understory communities has received considerable attention in the literature (Frelich et al. 2003; Macdonald and Fenniak 2007). Nevertheless, little is known about the ecological importance of small canopy patches for structuring understory community composition. Natural plant compositional patterns are often used as a framework to assess ecosystem resistance and resilience to natural and anthropogenic disturbances their understanding is, therefore, a key element for sustainable forest management (De Grandpré and Bergeron 1997; Tilman et al. 1997; Chapin et al. 2000). In this study, I assess the composition of understory vascular plant communities in relation to the mosaic of conifer, mixed conifer-broadleaf and broadleaf canopy patch types as well as canopy gaps and their associated structure and environment within natural, mature boreal mixedwood forest stands.

Chapter 3: Partitioning vascular understory diversity in mixedwood boreal forests: the importance of mixed canopies for diversity conservation: Mixedwood forests host the greatest diversity of understory vascular plants of the boreal landscape (Macdonald and Fenniak 2007). Thus, in order to assess the potential biodiversity impacts of forest management practices, we need to understand the hierarchical organization of understory diversity within these mixed forests. Progress in understanding how understory diversity is organized across different levels of observation, and the level at which it is maximized, requires a conceptualization and quantification of the hierarchy of plant patch configuration that exists across mature boreal mixedwood stands. Additive partitioning of species diversity provides a framework by which total diversity can be assessed at hierarchical levels of organization (Crist et al. 2003). This study presents an additive partition of understory diversity in relation to the heterogeneous mosaic of conifer, mixed conifer-broadleaf and broadleaf tree patches as well as canopy gaps found in mixedwood forest stands. The patterns of species abundance among canopy patch types are also addressed in order to infer the ecological processes shaping understory diversity. This and the previous study support the importance of maintaining a 'mixed' boreal mixedwood in order to conserve natural patterns of understory diversity as well as their underlying ecological processes.

Chapter 4: Understory species interactions in mature boreal mixedwood forests: Interactions among plant species play an important role in regulating composition and diversity of plant communities (Brooker 2006). It is well acknowledged that trees and understory plant species interact with one another throughout the different stages of boreal forest succession, but very little is known about the effect of interactions between shrub and herb species on understory community structure. I examined plant interactions in mature and unmanaged boreal mixedwood forests by investigating the effect of shrub removal on biomass, composition and diversity of herbs. For this, I carried out a 3-yr removal study in a naturally assembled community. This study was performed in a naturally assembled community to capture the local set of species as well as the natural abundance patterns occurring in mature mixedwood boreal forest stands. The results suggest that there is asymmetric competition for light between erect shrubs and herb species and that interactions among plant species have a significant effect on understory community structure in mature boreal mixedwood forests.

Chapter 5: Spatial patterns of understory plant communities in mature boreal mixedwood forests: the influence of environmental and spatial factors: The spatial arrangement of plant species is a fundamental aspect that needs to be considered to understand the ecology of plant communities (Dale 1999). At the community level, plants can be spatially autocorrelated as the product of dynamic processes originated by the species assemblage itself such as dispersal strategies and species interactions. At larger scales, plants tend to be spatially structured as they depend upon environmental factors that are spatially structured themselves (Legendre and Legendre 1998; Legendre et al. 2002). There is a recent and increasing interest in measuring and understanding patterns of spatial variation, in relation to environmental factors, in plant community composition and diversity (Karst et al. 2005; Jones et al. 2008; Legendre et al. 2009; Gazol and Ibáñez 2010). Nonetheless, there is currently a very limited understanding of the spatial structure of boreal understory communities (Kembel and Dale 2006). The last study explored the relative influence of space and environmental variables, as well as their joint effects, on understory composition and diversity within boreal mixedwood stands. This study illustrates the important role that space plays as an explanatory variable and the necessity to include spatial variables when studying boreal understory plant communities.

The concluding chapter summarizes the results and presents brief management and conservation implications and suggestion for further research.

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Chapter 2

The influence of canopy patch mosaics on understory plant community composition in boreal mixedwood forest

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2.1. Introduction

Forested landscapes are comprised of a mosaic of canopy patches differing in size and biotic and abiotic characteristics that critically influence the composition of plant communities (Halpern and Spies, 1995). While the effect of large patches on biotic communities has received considerable attention in the literature, the ecological importance of small patches for community structure has also been recognized (Lindenmayer et al., 2008). The boreal mixedwood landscape consists of a mosaic of forest stands with varying dominance by conifers (mostly white spruce (*Picea glauca* (Moench) Voss)) or broadleaf trees (mostly trembling aspen (*Populus tremuloides* Michx.)). This pattern of stand composition is the product of complex interactions involving terrain factors, regeneration processes and succession following disturbance events such as fire and insect outbreaks (Andison and Kimmins, 1999; Chen and Popadiouk, 2002; Park et al., 2005). Within this mosaic, forests defined as ‘mixed’ at the stand scale are themselves comprised of a mixture of small canopy patches of varying conifer/broadleaf composition (Haeussler et al., 2004; Macdonald and Fenniak, 2007) as well as canopy gaps (Chen and Popadiouk, 2002). The proportion and spatial distribution of white spruce in the canopy is a function of seed source availability, seedbed conditions and timing of recruitment after disturbance (Peters et al., 2006).

Issues in management of boreal mixedwood forests are currently receiving considerable attention in North America and northern Europe (Andison and Kimmins, 1999). One of the main management concerns is that forestry practices may be favoring the establishment of relatively pure, spatially separated stands of conifer or broadleaf trees (i.e., ‘unmixing’ the mixedwoods: Hobson and Bayne, 2000; Haeussler et al., 2004; Lieffers et al., 2008). It has been suggested that mixed forest stands may have greater timber productivity and resistance to pathogen and insect attacks as compared to either ‘pure’ broadleaf or conifer (Andison and Kimmins, 1999; Man and Lieffers, 1999). Likewise, the unique vegetation and structural attributes found within boreal mixed forest stands have been associated with higher diversity of birds (Hobson and Bayne, 2000), arthropods (Work et al., 2004; Buddle et al., 2006) and understory plants (Macdonald and Fenniak, 2007).

Understory plant communities exert a strong influence on the functioning of forest ecosystems (Halpern and Spies, 1995; Nilsson and Wardle, 2005;

Gilliam, 2007). In boreal forests, understory communities are the most important contributors to vascular plant biodiversity, provide habitat for faunal communities and have economic values for provision of non-timber forest products (Nilsson and Wardle, 2005; Hart and Chen, 2006). Further, boreal understory communities can directly and indirectly regulate forest structure by competing with tree seedlings at the establishment stage, by modifying microclimate conditions where tree seedlings grow and by influencing nutrient cycling (Macdonald and Fenniak, 2007; Hart and Chen, 2008; and as reviewed by Hart and Chen, 2006). Studies that looked at the relationship between the composition of the forest canopy and that of understory communities across the boreal landscape concluded that: (i) many understory plant species have a wide habitat tolerance (Rowe 1956; Frelich et al., 2003); (ii) there is a strong association between canopy type at the scale of forest stands and understory composition; and (iii) conifer and broadleaf trees have different effects on the understory environment because of the way each affects light, soil nutrients and the physical environment of the forest floor (Frelich et al., 2003; Qian et al., 2003; Hart and Chen, 2006 (review paper); Macdonald and Fenniak, 2007; Hart and Chen, 2008). Nevertheless, we currently have a very poor understanding of how understory composition is linked to the mosaic of small canopy patches that comprise boreal mixed forest stands. There is an urgent need to improve our understanding of the ecological structure and processes in mixedwood forest stands as a point of reference for informing future forest management and conservation practices.

Our objective was to assess the composition of understory vascular plant communities in relation to the mosaic of canopy patch types (i.e. a patch of conifer, broadleaf, mixed conifer-broadleaf trees as well as canopy gaps), and their associated structure and environment within unmanaged, mature boreal mixedwood forest stands. We purposely selected a ‘patch-level’ approach in order to detect the non-random variation of environmental heterogeneity that occurs at a fine scale as a product of the mosaic of canopy patches (Niemela et al., 1996; Frelich et al., 2003). Based on the well-documented association between canopy composition and the understory environment and plant communities (see review paper by Hart and Chen, 2006 and also Macdonald and Fenniak, 2007), we hypothesized that each patch type would be associated with different microhabitat conditions and plant communities. Thus, the existence of these small patches would be important for explaining the overall plant diversity in boreal mixedwood forest stands.

2.2. Methods

2.2.1. Study site, field and lab procedures

The study was conducted in the Boreal Mixedwood Ecoregion in forest stands near Lac La Biche, Alberta, Canada (55º N, 112º E ~610 meters above sea level) (Strong, 1992). The mesic sites of this region host boreal mixedwood forests with varying canopy co-dominance of broadleaf trees (mainly trembling aspen) and conifers (mainly white spruce). The region has a boreal climate with short summers with a mean temperature of 13.5° C (May through August) and long winters with a mean temperature of -13.2° C (November through February); the mean annual precipitation of the area is 397mm and occurs mostly during the summer (Strong, 1992). The soils of the area are typical of the boreal plains of northeastern Alberta with Gray Luvisols predominating on moderately well-drained, medium-textured moraine, and lacustrine material. Parent material is mostly sedimentary rocks weathered in situ or translocated by glacial activity (Kocaoglu, 1975; Kocaoglu and Bennett, 1983).

Within a ~ 30 km^2 area, we sampled within the portion of the forest land base that had been classified as ‘mixed’ (having between 40% and 60% canopy cover of both coniferous and broadleaf trees) at the stand (polygon) scale by the most recent forest vegetation inventory. The region was dominated by more or less contiguous cover of mixedwood stands of similar age. Thus on-the-ground distinction of ‘stand’ boundaries was usually not obvious. Therefore, we did not include “stand” as a factor in any of the analyses. However, sampling was concentrated in either the northern or southern portion of the total study area and these two were treated as blocks in subsequent analyses. We used a stratified random approach to establish a total of 98 circular sampling plots of 50 m^2 (4-m radius) that represented four canopy patch types as follows: (1) Conifer patches (26 plots): Having at least 70% (canopy cover) of conifer trees (mainly *Picea glauca)*; (2) Broadleaf patches (25 plots): at least 70% broadleaf canopy cover (mainly *Populus tremuloides*); (3) Mixedwood patches (23 plots): At least 40% and no more than 60 % conifer cover; (4) Gap patches (24 plots): canopy openings where a 50 m^2 circular plot could be located without any canopy cover above the understory strata. Each plot was at least 50 meters away from forest edges, cut lines or trails and plots were at least 30 meters apart from each other. Based on forest and vegetation inventory maps, all sampled forests were approximately 100 years of age and similar in canopy cover and general understory vegetation.

Within each circular plot, we estimated the percentage of ground cover of (i) fine woody debris (FWD) (debris pieces <8cm diameter), (ii) coarse woody debris (CWD) (>8 cm diameter), (iii) bryophytes (all species combined), and (iv) litter. We also identified all canopy trees and measured their diameter at 1.3 m (breast) height (DBH). We then calculated basal area (BA) for conifer (BAC) and broadleaf (BAD) trees separately and for the two together (BAT). At the centre of each circular plot, we set up a 2 m x 2 m quadrat in which we estimated percentage cover for all vascular plants. The 2 x 2 m quadrat was subdivided into four (1 x 1 m sub-plots) to improve accuracy in cover estimates and these were averaged to result in a single cover estimate per species per patch. Nomenclature followed Moss (1983); three species were indentified at the genus level only (one *Salix* and two *Carex* spp.). At the four corners of the subplot, we also measured the depth of the litter (L) and organic layers (FH) and calculated an average value for each plot.

To quantify nutrient availability we buried nylon bags with 45mL of IONAC® NM-60, H+/OH- Form mixed bed exchange resin (J.T. Baker) within the mineral soil layer at the east corner of each subplot, for a period of two months. After this time, the nylon bags were brought back to the lab, extracted as described by Thiffault et al. (2000) and analyzed using a Technicon Autoanalyser to obtain the concentrations of available PO_4^-, NO_3^- and NH_4^+ and an Atomic Absorption Spectrophotometer to obtain the concentration of Ca^{2+}, Mg^{2+} and K^+. Also, at the east corner, we measured soil moisture and temperature at a depth of 30 cm in August of 2003 by means of Time Domain Reflectometry and a thermocouple respectively; the measures were taken at least 24 hours after a major precipitation event.

Finally, at the centre of each plot we took hemispherical canopy photographs at 1 m above the ground during the leaf-on (August) and leaf-off (November) periods. The timing of photography was designed to ensure uniform sky condition and to avoid direct insolation, as recommended by Comeau et al. (1998) and Gendron et al. (1998). Thus, photographs were taken either: approximately 1 h after dawn, 1 h before dusk, or on overcast days. Photographs were analyzed using SLIM (Spot Light Intercept Model) v. 2.2e (Comeau et al., 2003) software which incorporates seasonal sun angle and data on cloud cover and opacity for the specific geographic location and calculates the percentage of direct, diffuse and total (average of diffuse and direct) solar radiation during the leaf-on and leaf-off periods.

2.2.2. Data analysis

We tested for differences in understory species composition among the four canopy patch types by means of pair-wise multi-response permutation procedures (MRPP) using the rank-transformed Sørensen (Bray-Curtis) distance measure. MRPP is a multivariate nonparametric technique for testing group differences (i.e. species composition). It calculates the mean within-group distance of the observed pattern and then uses permutation procedures to determine whether this distance is greater than expected by chance. MRPP provides a T-statistic that describes the separation among groups (the more negative T is, the stronger the separation is) and its associated significance. It also gives an A (Agreement)-statistic which describes within-group similarity; A ranges from <0 to 1 where 1 indicates that all items are identical within groups. Even with significant separation of groups, A-statistic values less than 0.1 are common with community data (McCune and Grace, 2002). In order to detect which species, if any, were indicators of a particular canopy patch type we performed an indicator species analysis (ISA) (Dufrêne and Legendre, 1997; McCune and Grace, 2002). The MRPP and ISA analyses were performed using PC-Ord for Windows (v. 4.5) (McCune and Mefford, 1999).

To assess differences in species relative abundances among patch types, we selected the ten most abundant species from each canopy patch type and then compared their covers among patch types. Because the distributions of individual species cover values were highly non-normal, we used a non-parametric Kruskal-Wallis test and when there were significant differences among patch types we followed up with a series of pair-wise Wilcoxon-Mann-Whitney tests (Proc Univariate in SAS v.9.1; SAS Institute, 2003). Winsorized means for the relative abundance of each of these species were also calculated (Proc Univariate in SAS v.9.1; SAS Institute, 2003).

We tested for differences in environmental characteristics (as listed in Table 2.1.) among canopy patch types using an randomized block design analysis of variance (ANOVA; incomplete block because one of the patch types was only present in one of the areas). The analysis was carried out by means of PROC MIXED (SAS v.9.1; SAS Institute, 2003) using the following model:

$$Y_{ijk} = \mu + P_i + A_j + \varepsilon_{ijk} \qquad \text{[eqn. 1]}$$

where Y_{ij} = value for the given environmental characteristic in the j^{th} area for the i^{th} canopy patch type; μ = overall mean; P_i = canopy patch type (i = 1 to 4; fixed); A_j = Area (block: northern or southern portion of the study area) (j= 1 to 2; random); ε = experimental error.

We tested the residuals for normality (Kolmogorov-Smirnov statistic) and homogeneity of variance (Levene's test) and transformed variables as necessary to meet these assumptions. Following a significant main effect of patch type, significant differences were further explored using least square means with a

Bonferroni correction of α = 0.0083. For variables that could not be transformed to meet the assumptions of ANOVA (cover of litter and bryophytes, broadleaf basal area) we used a non-parametric Kruskal-Wallis test (using Proc npar1way in SAS v.9.1). When this showed a significant difference among patch types, we followed up with a series of pair-wise Wilcoxon-Mann-Whitney tests with a Bonferroni correction of α = 0.0083 (SAS v. 9.1). For these variables we present Winsorized means (Proc Univariate in SAS v.9.1; SAS Institute, 2003).

Lastly, we used constrained ordinations to evaluate the relationship between the environmental characteristics and understory composition of each plot. These were done first for all canopy patch types combined and then for each canopy patch type separately. We chose distance-based Redundancy Analyses (db-RDA), a recently-developed approach to constrained ordination in which sample scores from a Principal Coordinate Analysis (PcoA) are used as the species data into a redundancy analysis. One advantage of db-RDA is that it allows for the use of ecologically meaningful measures of community similarity or distance rather than a straight-line Euclidean distance. Further, it uses Monte-Carlo simulations to test the significance of the environmental variables, and thus does not require the assumption of normality (Legendre and Anderson, 1999; McArdle and Anderson, 2001). In his way, dbRDA ‘bridges the gap’ between statistical linear models and the need for realistic non-Euclidean measures of association of ecological data (Legendre and Anderson, 1999). We conducted the PCoA using a Bray–Curtis (Sørensen) distance and followed this with the redundancy analysis (RDA). We tested environmental variables (listed in Table

2.1.) for inclusion in the RDA by means of forward step-wise selection. Once we identified the significant variables (P-value <0.05), we ran a final RDA including only those. Finally, for interpretation purposes, we used the original matrix of species covers by sample plot as a supplemental dataset so that species could be projected in ordination space. For this, we selected the species which had Pearson correlation coefficients of ≥ 0.25 with the significant ordination axes. We performed these analyses in CANOCO (v. 4.5) (ter Braak and Šmilauer, 2002).

2.3. Results

2.3.1. Understory species composition in relation to canopy patch type

The MRPP indicated that all canopy patch types were significantly different from one another ($P<0.01$) (Table 2.2.). The greatest difference was between conifer and broadleaf patches ($A = 0.17$; $T=-14.20$) followed by mixedwood vs. broadleaf ($A = 0.12$; $T=-10.52$) and conifer vs. gap ($A = 0.11$; $T=-8.89$). Overall, conifer vs. mixedwood patches and broadleaf vs. gap patches were more similar to one another than were other pairwise comparisons among patch types (Table 2.2.). The Indicator Species Analysis (ISA) identified 21 species out of a total of 78 (see Appendix 1) as significant indicators of a specific canopy patch type (Table 2.3). Conifer, mixed and gap patches had only two indicator species each. The orchid *Goodyera repens* and ericaceous dwarf shrub *Vaccinium vitis-idaea* were indicators of conifer patches while the perennial herb *Trientalis borealis* and seedlings or saplings of *Abies balsamea* were indicators of mixedwood patches. Indicators of gap patches were the early-successional herb *Epilobium angustifolium* and the shrub *Rosa woodsii* (Table 2.3.). Broadleaf patches had 15 indicator species including several common early-successional species of the boreal mixedwood and of which the grass *Calamagrostis canadensis* and the shrub *Rosa acicularis* had the highest indicator values.

2.3.2. Changes in species relative abundances

The 10 most abundant (highest cover values) species in each of the four different canopy patch types were drawn from a common pool of 16 species (Table 2.4.). Although there was overlap in the most abundant species among patch types, their relative abundances differed. As compared to conifer patches, gap and broadleaf patches had higher cover values for *Fragaria virginiana, Lathyrus venosus, Mertensia paniculata,* and *Petasites palmatus* and the shade intolerant, 'early successional' species *Calamagrostis canadensis* and *Epilobium angustifolium.* The perennial herb *Aralia nudicaulis* was the most abundant species under conifer patches, which also had relatively higher cover of the evergreen trailing shrub *Linnaea borealis* (Table 2.4.). Mixedwood, broadleaf, and gap patches also tended to have higher shrub cover (*Rosa acicularis* and *Viburnum edule*) than did conifer patches. Under mixedwood patches, the most abundant species was the shrub *Viburnum edule* closely followed by the herb *Aralia nudicaulis* while *Rosa acicularis* was the most abundant species under broadleaf patches. Under canopy gaps, the graminoid *Calamagrostis canadensis* was the most abundant species followed by the shrub *Rosa acicularis* (Table 2.4.).

2.3.3. Environmental characteristics of canopy patch types

There were substantial differences among the four canopy patch types for several of the measured environmental characteristics (Table 2.1.). Conifer and mixedwood patches had similar conifer basal area, which was greater than in broadleaf or gap patches. Total basal area did not differ among patch types except for gap patches where it was, not surprisingly, lower (Table 2.1.). Gap patches had lower available PO_4^- than any other patch type while mixedwood patches had lower available Mg^{2+}. There were no significant differences among patch types in terms of available NO_3^- , NH_4^+ Ca^{2+} or K^+ nor did patch types differ in litter or organic layer depth. Broadleaf patches had warmer soils while conifer patches had lower soil moisture than the other patch types. Mixedwood and broadleaf patches had higher litter cover while conifer patches had higher moss cover than other patch types. There were no significant differences in cover of dead wood (fine or coarse) among patch types. Gaps had greater estimated direct, diffuse and total incoming light during both the leaf-on period and diffuse light during the leaf-off period than any other patch type. For direct and total light during the leaf-off period, gaps and broadleaf patches had similar light conditions (Table 2.1.). Conifer patches had the lowest estimated light (leaf-on and leaf-off, direct, diffuse and total light) compared to the other patch types except mixed patches had similarly low values for direct light during the leaf-off period.

2.3.4. Relating environmental characteristics to understory composition

Seven environmental variables were significantly related to understory community composition in the analysis including all four patch types. Together these explained only 16.5 % of the variation in understory community composition (Table 2.5., Figure 2.1.a). Total light at leaf-off, cover of coarse woody debris, soil moisture and temperature were positively correlated to the first axis; higher values of these variables were associated with Gap and Broadleaf patch types. Soil NH_4^+ and cover of fine woody debris were correlated with the second axis and were not clearly associated with a particular patch type. Soil Ca^{2+} was correlated to the third axis. The species associations with the different canopy patch types in ordination space followed the previously mentioned patterns of changes in relative abundance, i.e., species like *Calamagrostis canadensis, Epilobium angustifolium, Fragaria virginiana,* and *Rosa acicularis* had high scores on axis 1 of the ordination, showing an association with broadleaf and gap patches. In contrast, the evergreen trailing shrub *Vaccinium vitis-idaea* and the orchid *Goodyera repens* had negative scores on axis 1, showing an association with conifer patches (Figure 2.1.b).

Even when each patch type was analyzed by separate ordinations there was significant environmental variation that was related to variation in understory community composition. For conifer patches, diffuse light during the leaf-off time period was the only significant environmental variable and it explained 7% of the total variation in the understory species data (Table 2.5., Figure 2.2.). The orchid *Habenaria orbiculata* was associated with lower light levels. Under mixedwood patches, soil temperature was the only significant variable, explaining 10.5% of the variation in the species data (Table 2.5.). The orchid *Habenaria obtusata*, the grass *Elymus innovatus* and the herbs *Fragaria virginiana* and *Galium boreale* were associated with higher soil temperature while *Abies balsamea* (regeneration) was associated with lower soil temperatures (Figure 2.2.). Broadleaf patches had three significant variables explaining 22% of the variation: direct light during the leaf-off period, Ca^{2+} availability and litter cover (associated with the third axis).

Some shrubs (i.e. *Amelanchier alnifolia*) were associated with high light while others (i.e. *Ribes oxyacanthoides* and *Rosa woodsii*) as well as *Populus tremuloides* (regeneration) were related to higher calcium availability (Figure 2.2.). Gap patches had two significant environmental variables: coarse woody debris cover and soil temperature which together explained 21% of the variation (Table 2.5.). The graminoid *C. canadensis* was related to higher CWD while *Rosa acicularis* was associated with higher soil temperature (Figure 2.2.).

2.4. Discussion

Our results suggest that the mosaic of small canopy patches within mixed forest stands resembles a microcosm of the boreal mixedwood landscape, across which understory community composition varies with canopy composition at the stand scale (Macdonald and Fenniak, 2007). The mosaic of small canopy patches in mixed boreal forest stands allows for understory plant communities that include both shade intolerant (early-successional) and shade tolerant (late-successional) species. Our study corroborates previous work highlighting the ecological importance that mosaics of small patches have, through creation of environmental and habitat heterogeneity, on plant species composition (Bennett et al., 2006; Lindenmayer et al., 2008). Structural heterogeneity and niche diversity have been implicated in the relatively high biotic diversity of birds (Hobson and Bayne, 2000), arthropods (Work et al., 2004; Buddle et al., 2006), and understory plant communities (Macdonald and Fenniak, 2007) in boreal mixed forest stands. The fine-scale relationships between canopy patches and biotic communities that I demonstrate here, however, have not been previously documented.

North American boreal forests hold a low number of tree species, yet there are substantial differences in the way broadleaf and coniferous trees influence environmental conditions for understory communities (Hart and Chen, 2006; Macdonald and Fenniak, 2007). Conifer trees create harsh understory conditions as their dense canopy decreases light transmission and their recalcitrant, acidic litter lowers soil pH and nutrient availability (our results and also: Constabel and

Lieffers, 1996; Lieffers et al., 1999; Berger and Puettmann, 2000; Macdonald and Fenniak, 2007). Plant assemblages under conifer patches were characterized by low-nutrient demanding and shade-tolerant species that have previously been identified as having an association with either white spruce or balsam fir forest stands (Rowe, 1956; La Roi, 1967). Their most common species (*Aralia nudicaulis* and *Maianthemum canadense*) are generalists that, once established, can persist for several years in these communities (Edwards, 1984; Worthen and Stiles, 1986). Also, several uncommon species such as *Moneses uniflora* and late successional orchid species (*Goodyera repens*, *Habenaria obtusata* and *H. orbiculata*) were only present when conifer trees were dominant or co-dominant.

The co-dominance of conifer and broadleaf trees in mixed patches resulted in understory communities that included shade tolerant species alongside nutrient-demanding, shade intolerant species (see Figure 2.1.b). Species that tend to be more abundant in boreal conifer stands (e.g., *Trientalis borealis*, *Pyrola secunda*) co-existed with species that are commonly found in broadleaf stands (e.g., *Rubus spp.*, *Galium spp.*) (Rowe, 1956; La Roi, 1967). Our finding that conifer and mixed patches were more similar to one another in understory composition than either was to broadleaf patches mirrors patterns among mixedwood stands of different composition (Macdonald and Fenniak, 2007). It also supports the idea that, in this largely aspen-dominated landscape, the presence of conifers is particularly influential for environmental conditions and plant communities in the understory (Macdonald and Fenniak, 2007).

In comparison to conifer trees, broadleaf trees give rise to more benign micro-environmental conditions. Light availability under broadleaf tress is higher, particularly during the leaf-off period (Messier et al., 1998; Constabel and Lieffers, 1996) and with their nutrient-rich litter they facilitate nutrient cycling (Paré and Bergeron, 1996; Légaré et al., 2001; Qian et al., 2003). Thus, it was not surprising that broadleaf patches had a higher abundance of shade-intolerant herbs and the highest abundance of shrub species. Tall shrubs have important effects on canopy succession through competition with tree regeneration (Lieffers et al., 1999) and also contribute to the natural vertical structure of forests, provide food and shelter for wildlife species, and play a potentially important role in nutrient cycling (Hart and Chen, 2006). For example, *Alnus crispa*, which was an indicator of broadleaf patches, has a strong effect on nutrient availability in forests because of its ability to fix soil nitrogen (Rhoades et al., 2001). Overall, the compositional patterns and the indicator species of broadleaf patches were very similar to those of broadleaf stands within a mixedwood landscape (i.e. Ringius and Sims, 1997; Légaré et al., 2001; Macdonald and Fenniak, 2007).

The presence, and spatial arrangement, of canopy gaps is fundamental for the maintenance of the natural structural heterogeneity and successional pathways of boreal forests (De Grandpré et al., 1993; De Grandpré and Bergeron, 1997). Canopy gaps act as transient patches in which increased light availability and changed forest floor characteristics (e.g., warmer soils, regeneration microsites, coarse woody debris) facilitate establishment of certain understory plant species (Chen and Popadiouk, 2002; Fahey and Puettmann, 2007). We found a high abundance of two early-successional species, the graminoid *Calamagrostis canadensis* (the most common species) and the forb *Epilobioum angustifolium* (the strongest indicator species). Both species have potentially important effects on future successional development within patches. On one hand, the grass *C. canadensis* is a very aggressive species that can seriously limit white spruce regeneration. On the other hand, *E. angustifolium* represents less of a problem for white spruce regeneration as it has lower shoot density and does not form a persistent litter layer (Lieffers et al., 1993; Landhäuser et al., 1996). Thus, dominance of canopy gaps by *E. angustifolium* and other forbs can decrease the invasiveness of *C. canadensis* and its competition with white spruce saplings (Landhäuser et al., 1996). These two species represent an example of the critical effect that dominant species (Grime, 1998) and interactions among functional groups (herbs and trees) have on ecosystem processes (Tilman et al., 1997) in boreal mixedwood forests.

Given the mature successional stage of these forests, more canopy gaps are expected to appear and this will lead to a release of advance tree regeneration and to changes in overstory structure and composition. The actual pathway of succession in these forests, however, is difficult to predict as it will depend on canopy gap size (and implicitly, the type of disturbance that originated the canopy gaps), and the availability of reproductive propagules and favorable microsites for tree regeneration (Chen and Popadiouk 2002). The mixed canopy structure of these forests could be maintained though a cyclic pathway of gap-canopy replacements; could converge over time into a conifer-domination or; a stand-replacing fire could revert it back to an aspen-dominated forest (Chen and Popadiouk 2002). Changes in understory composition in these forests will, in turn, follow the pattern of canopy succession.

Understory composition can also change if canopy cover is altered due to forest management practices (Macdonald and Fenniak 2007). Changes in understory community in response to manipulation of canopy composition in boreal mixedwood stands would likely most be due to shifts in relative abundance of understory species. This is because many boreal understory species are present across a wide range of habitat types but with differing relative abundances (Rowe 1956). This may be partly explained by the clonal nature of many species, which allows them to access resources from favorable patches (Økland 1995).

In natural communities, species abundance patterns change faster in response to anthropogenic activities than does species richness (Hooper and Vitousek, 1997; Chapin et al., 2000; Hooper et al., 2005). It is changes in relative abundance of dominant species that are expected to have the greatest influence on ecosystem function and productivity (Tilman et al., 1997; Smith and Knapp, 2003; Mokany et al., 2008). For example, changes in abundance of some ericaceous shrubs can inhibit tree seedling establishment, ultimately altering stand dynamics and succession (Tellier et al., 1995; Landhäuser et al., 1996; Hart and Chen, 2006). Changes in patterns of uncommon species could also have indirect effects through species interactions on niche partitioning and ecosystem functioning (Lyons et al., 2005) but this topic remains largely unexplored in the boreal forests. Some of the less abundant species such as orchids (i.e. *Goodyera* *repens, Habenaria obtusata* and *H .orbiculata*), *Pyrola spp*. and *Moneses uniflora* depend on sexual, rather than clonal, reproduction and on pollinating insects for dispersal of pollen (Kevan et al., 1993). Little is known about the impacts of a potential canopy homogenization due to management practices on the ability of understory species to maintain themselves on the landscape. It is possible, however, that poorly dispersed species with particular canopy-type affinities would have difficulty maintaining themselves in a landscape that consisted of larger stands of homogeneous (conifer- or broadleaf- dominated) composition.

The observed differences in understory composition across canopy patch types were associated with micro-environmental conditions such as light, soil moisture, temperature and nutrients. Environmental variation associated with canopy composition explained only a small portion of the variation in understory composition, however. A wide variety of unaccounted for factors, such as plant establishment and dispersion strategies, small-scale disturbance, interactions with other plants and fauna, no doubt exert an important influence on understory plant composition (Frelich et al., 2003).

Overall, our results point to the importance of the mosaic of patch types in maintaining landscape-scale understory composition and diversity as well as habitat heterogeneity in these mixed forests. This mosaic may allow for niche partitioning translating into more complete resource use (Petchey, 2000) at the stand scale. In turn, this supports the greater diversity in these mixed forests as compared to ‘pure’ broadleaf or conifer stands (Macdonald and Fenniak, 2007). The mosaic of small canopy patches within these mixed forests seems to be an essential element for the natural configuration of understory communities and, potentially, for other taxa that depend on understory vegetation for food and habitat (Hobson and Bayne, 2000; Work et al., 2004; Buddle et al., 2006). If forest practices and policies tend to result in control of foest composition to favor mono-dominant stands (Chen and Popadiouk, 2002; Lieffers et al., 2008) the potential loss of heterogeneity in internal stand structure could have undesirable consequences for the diverse biotic communities found in mature boreal mixedwood forests.

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Tables

Table 2.1. Mean values (Least Square) of environmental characteristics for each canopy patch type

	Conifer Patches	Mixedwood Patches	Broadleaf Patches	Gap Patches	P-value ^{a,b}
SOIL NUTRIENTS					
NO_3^- (ppm)	0.80 (0.23)	1.03 (0.52)	1.06 (0.44)	0.89 (0.32)	N. S
NH_4^+ (ppm)	1.10 (0.33)	1.35 (0.63)	1.47 (0.37)	1.13 (0.38)	N. S.
PO_4^- (ppm)	15.93 ^{A} (3.33)	14.67 ^{AB} (2.96)	15.59 ^{AB} (3.87)	8.18^{B} (1.82)	0.0010
Ca^{2+} (meq/L)	8.98 ^{A} (1.72)	6.45 ^{A} (0.98)	9.19 ^{A} (1.63)	6.90 ^{A} (1.24)	0.0116
Mg^{2+} (meq/L)	3.50 ^{AB} (0.82)	2.36 ^{B} (0.63)	4.81 ^{A} (0.98)	3.35 ^{AB} (0.63)	0.0003
K^+ (meq/L)	5.12 ^{A} (0.84)	2.85 ^{A} (0.40)	3.89 ^{A} (0.66)	3.94 ^{A} (0.59)	0.0268
EDAPHIC FACTORS					
Litter layer depth (cm)	3.80 (0.59)	3.07 (0.45)	3.21 (0.40)	3.47 (0.45)	N. S.
Organic layer depth (cm)	12.23 (1.35)	11.6 (3.80)	9.93 (1.33)	9.60 (1.24)	N. S.
Moisture (%)	11.58 ^{B} (1.95)	14.75 ^{A} (1.66)	20.56 ^{A} (4.36)	21.36 ^{A} (3.60)	<0.0001
Temperature (°C)	12.02 ^{B} (0.21)	12.59 ^{B} (0.31)	13.67 ^{A} (0.58)	12.49 ^{B} (0.25)	<0.0001
GROUND COVER (%)					
Fine woody debris	10.62 ^{A} (3.20)	16.93 ^{A} (2.84)	12.17 ^{A} (2.74)	8.93 ^{A} (3.33)	0.0126
Coarse woody debris	8.93 ^{A} (2.99)	7.29 ^{A} (3.28)	11.91 ^{A} (3.11)	14.09 ^{A} (4.90)	0.0400

Litter[c]	41.29^{B} (31-51)	69.23^{A} (65-79)	73.0^{A} (67-79)	7.40^{B} (32-60)	<0.0001
Moss[c]	27.14^{A} (16 -38)	2.17^{C} (0.36-4)	0.09^{D} (0.08-0.26)	7.40^{B} (0.32-15)	<0.0001
BASAL AREA (m^{2} ha^{-1})					
Conifer[d]	74.63^{A} (14.02)	61.03^{A} (15.03)	4.28^{B} (0.24)	10.42^{B} (9.71)	<0.0001
Broadleaf [c]	12.26^{C} (3-21)	36.0^{B} (20-52)	62.97^{A} (53-72)	7.15^{D} (27-48)	<0.0001
Total (Conifer + Broadleaf)	74.63^{A} (14.01)	61.03^{A} (15.30)	58.68^{A} (9.36)	10.42^{B} (9.71)	<0.0001
LIGHT (PPFD – µmol s^{-1} m^{2})					
Diffuse Leaf-on	29.38^{B} (2.65)	37.84^{B} (3.21)	37.20^{B} (2.59)	65.45^{A} (3.12)	<0.0001
Direct Leaf-on[d]	29.99^{B} (2.99)	29.83^{B} (3.52)	37.58^{B} (3.71)	53.73^{A} (5.65)	<0.0001
Total Leaf-on	29.75^{B} (2.38)	33.86^{B} (3.08)	37.32^{B} (2.79)	59.90^{A} (3.97)	<0.0001
Diffuse Leaf-off	31.27^{D} (2.02)	50.37^{C} (4.36)	64.74^{B} (1.97)	75.34^{A} (3.83)	<0.0001
Direct Leaf-off	35.82^{B} (3.33)	25.68^{B} (5.13)	57.85^{A} (3.60)	51.39^{A} (6.33)	<0.0001
Total Leaf-off	33.17^{B} (1.79)	39.96^{B} (3.23)	61.84^{A} (2.08)	65.24^{A} (4.43)	<0.0001

---

a. The value within brackets is the 95% confidence interval. Given also is the significance (P-value) from analysis of variance testing for differences among canopy patch types

b. For a given environmental factor, means with different superscript letters were significantly different based on comparison of least square means using a Bonferroni correction of $\alpha = 0.0083$

c. Variables analyzed by a non-parametric Kruskal-Wallis test. Given are their Windsorized means.Values with different superscript letters were significantly different based on pairwise Wilcoxon-Mann-Whitney comparisons using a Bonferroni correction of $\alpha = 0.0083$. The values within brackets are the lower and upper 95% confidence limits

d. Variable was log-transformed prior to analysis; untransformed means are present here

Table 2.2. Results of multi-response permutation procedure tests (MRPP) among canopy patch types

Canopy patches pair-wise comparison	T-statistic	*P*-value	A-value
Conifer vs. Mixedwood	- 3.12	0.007	0.03
Conifer vs. Broadleaf	-14.20	< 0.001	0.17
Conifer vs. Gaps	- 8.89	< 0.001	0.11
Mixedwood vs. Broadleaf	-10.52	< 0.001	0.12
Mixedwood vs. Gaps	- 4.80	< 0.001	0.06
Broadleaf vs. Gaps	- 2.83	0.010	0.04

Table 2.3. Species Indicator Values (IV) per canopy patch type

Canopy Type/Species	Observed Indicator Value (IV)	*P*-value[a,b]
CONIFER		
Vaccinium vitis-idaea	25.4	0.011
Goodyera repens	19.2	0.003
MIXEDWOOD		
Abies balsamea (regeneration)	23.9	0.002
Trientalis borealis	19.6	0.027
BROADLEAF		
Calamagrostis canadensis	46.2	0.001
Rosa acicularis	45.3	0.001
Lathyrus venosus	41.1	0.002
Galium boreale	36.4	0.001
Fragaria virginiana	34.7	0.006
Mertensia paniculata	34.6	0.002
Petasites palmatus	33.4	0.023
Lonicera involucrata	30.0	0.002
Amelanchier alnifolia	29.1	0.001
Vicia americana	28.8	0.003
Ribes oxyacanthoides	21.9	0.021
Achillea millefolium	21.8	0.005
Fragaria vesca	21.4	0.009
Alnus crispa	20.6	0.018
Galium triflorum	17	0.049
GAP		
Epilobium angustifolium	33.7	0.005
Rosa woodsii	26.1	0.001

a. Only species with *P*-values <0.05 are shown

b. *P*-values are based on the proportion of randomized trials with expected IV>observed IV

Table 2.4. Mean cover values for the most abundant species among the four patch types

	Conifer Patches	Mixedwood Patches	Broadleaf Patches	Gap Patches	*P*-value [a,b]
Abies balsamea (regeneration)	0.0^{BC} 0.0[d]	2.05^{A} 0.13	0.0^{B} 0.0	0.18^{B} 0.0	0.0009
Aralia nudicaulis	14.80 8.84	11.43 5.23	8.36 6.76	9.75 7.25	N.S.
Calamagrostis canadensis	0.11^{C} 0.0	1.4^{B} 0.56	7.88^{AB} 3.28	15.16^{A} 8.91	<0.0001
Cornus canadensis	3.75 3.32	6.30 3.91	10.36 9.16	10.95 9.70	N.S.
Elymus innovatus	3.50^{A} 1.11	2.08^{AB} 0.73	2.36^{B} 0.0	5.91^{AB} 2.41	0.04
Epilobium angustifolium	1.15^{C} 0.0	0.17^{C} 0.0	3.64^{AB} 2.76	6.68^{A} 3.18	0.0001
Fragaria virginiana	2.38^{B} 1.96	1.04^{B} 0.82	6.92^{A} 6.92	4.08^{A} 3.16	0.003
Lathyrus venosus	1.38^{B} 0.61	0.82^{B} 0.0	5.70^{A} 3.58	2.12^{B} 2.12	0.001
Linnaea borealis	3.50^{A} 3.07	1.04^{B} 0.82	1.76^{B} 0.72	3.95^{AB} 2.58	0.03
Maianthemum canadense	7.25 5.26	7.06 3.80	10.92 7.52	10.83 7.29	N.S.
Mertensia paniculata	2.65^{B} 0.84	1.91^{B} 0.56	7.48^{A} 6.68	3.54^{AB} 2.62	0.01
Mitella nuda	3.23 3.32	5.43 4.0	2.12 1.12	5.79 4.16	N.S.
Petasites palmatus	2.88^{B} 0.88	1.97^{B} 1.10	6.54^{A} 6.62	5.08^{AB} 2.87	0.04
Rosa acicularis	3.76^{C} 2.58	9.07^{B} 7.22	24.61^{A} 23.01	14.7^{B} 11.20	<0.0001
Rosa woodsii	0.88^{B} 0.0	0.80^{B} 0.0	1.17^{B} 0.0	6.55^{A} 4.12	0.01
Rubus pubescens	5.50 3.80	3.30 2.82	5.40 4.08	7.58 6.75	N.S.

Viburnum edule	5.20 2.77	12.64 9.50	10.13 6.64	11.73 10.36	N.S.

a. The top 10 species are based on mean cover for each patch type, some species were in the top 10 for more than one patch type

b. Results of the comparison among patch types based on a non-parametric Kruskal-Wallis test. For each species, patch types with different superscript letters were significantly different based on pair-wise Wilcoxon-Mann-Whitney comparisons ($\alpha = 0.05$)

c. First row: arithmetic mean

d. Second row: Winsorized mean

Table 2.5. Results of redundancy analysis showing the environmental variables significantly ($P<0.05$) associated with understory composition

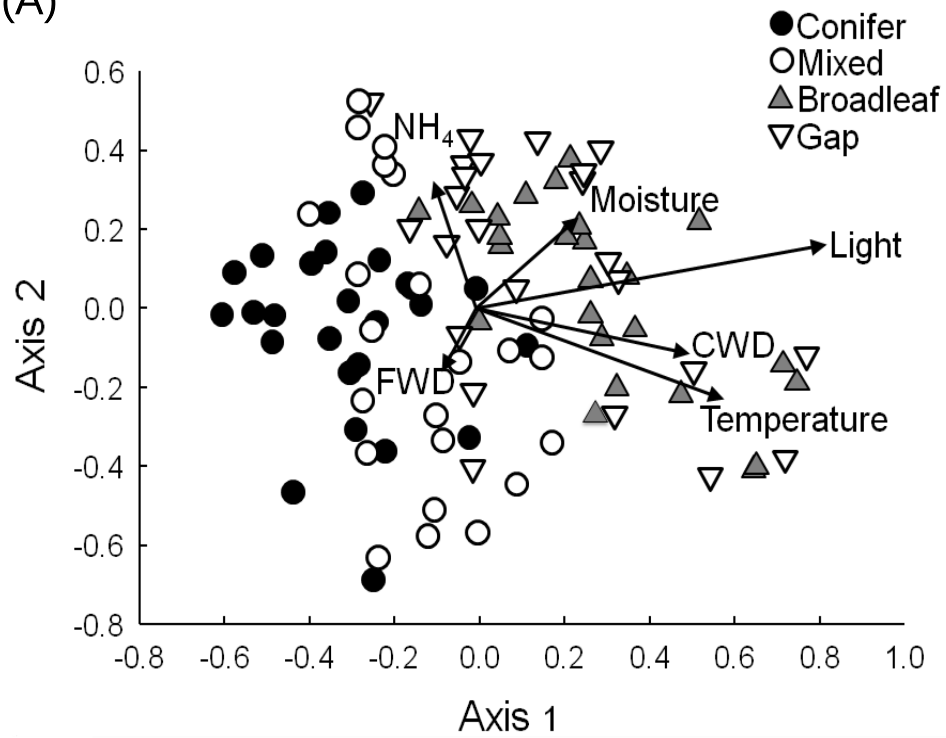
Variable/ Patch type [a,b]	Axis 1	Axis 2	Axis 3
ALL PATCHES TOGETHER			
Trace: 16.5			
Total light leaf-off	0.752	- 0.189	0.010
Ammonium	- 0.068	- 0.310	0.087
Fine woody debris	- 0.061	0.259	0.216
Coarse woody debris	0.454	0.152	0.192
Soil moisture	0.216	- 0.285	- 0.123
Soil temperature	0.513	0.148	- 0.347
Calcium	- 0.055	- 0.134	- 0.290
CONIFER PATCHES			
Trace:6.7			
Diffuse light leaf-off	0.834	-----	-----
MIXED PATCHES			
Trace:10.5			
Soil temperature	-0.735	-----	-----
BROADLEAF PATCHES			
Trace:22.3			
Direct light leaf-off	- 0.418	- 0.655	0.031
Litter cover	0.188	0.133	0.698
Calcium	0.645	- 0.378	- 0.176
CANOPY GAPS			
Trace:21.4			
Coarse woody debris	0.680	0.509	-----
Soil temperature	0.646	-0.543	-----

a. As determined by means of stepwise forward selection of variables in a distance-based Redundancy Analysis. Presented are the inter-set correlations (Pearson) of significant variables, in the order of the forward selection, with the three first axes.

b. Trace values (sum of the canonical eigenvalues) are also presented

Figures

(A)


Conifer
Mixed
Broadleaf
Gap
NH4
Moisture
Light
CWD
FWD
Temperature
Axis 2
Axis 1
0.6
0.4
0.2
0.0
-0.2
-0.4
-0.6
-0.8
-0.8
-0.6
-0.4
-0.2
0.0
0.2
0.4
0.6
0.8
1.0

(B)

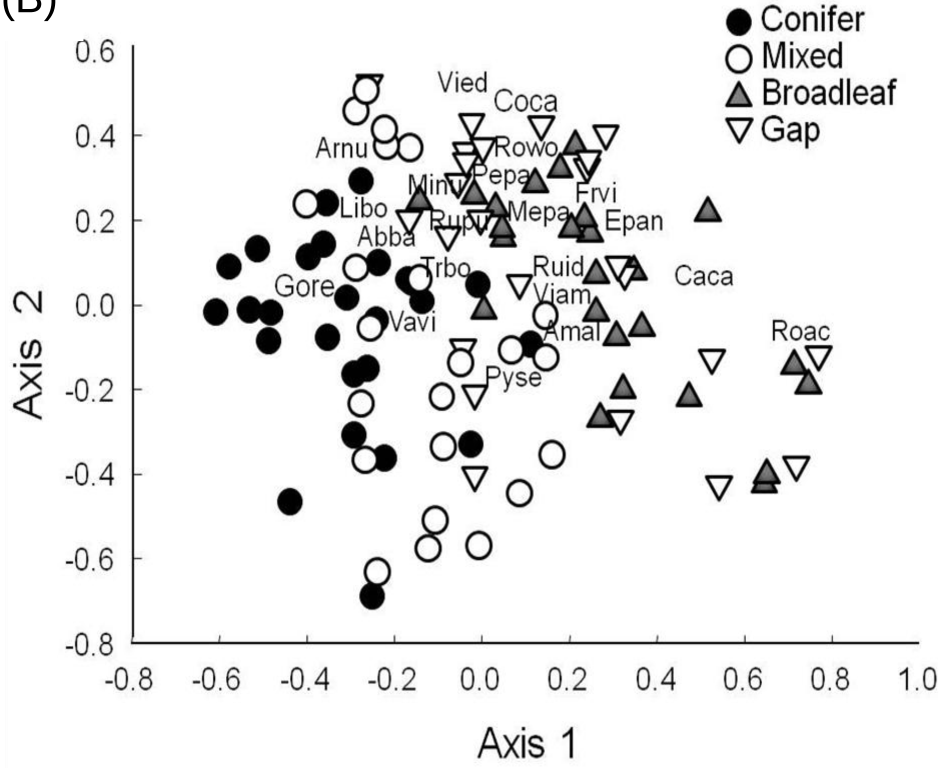

Conifer
Mixed
Broadleaf
Gap
Vied
Coca
Arnu
Rowo
Pepa
Minu
Frvi
Libo
Rupu
Mepa
Epan
Abba
Trbo
Ruid
Caca
Gore
Viam
Vavi
Amal
Roac
Pyse
Axis 2
Axis 1
0.6
0.4
0.2
0.0
-0.2
-0.4
-0.6
-0.8
-0.8
-0.6
-0.4
-0.2
0.0
0.2
0.4
0.6
0.8
1.0

Figure 2.1. (A) Relationship of understory plant composition to environmental variables.

These were determined by means of a stepwise forward selection of variables in a distance-based Redundancy Analysis (see Table 2.5. for details). Arrows indicate the direction of increasing values of the significant environmental variables (FWD: fine woody debris CWD: coarse woody debris; Moisture: soil moisture; Temperature: soil temperature) while the points indicate individual patches, coded by patch type. Calcium is not shown as it was more strongly associated to the third axis. The environmental scores were scaled down two times to those of the sample scores and some patch points were slightly moved from their original position to improve readability. **(B)** The four letter codes indicate the locations of plant species with a correlation of ≥ 0.25 to the ordination axes (see Appendix 1 for species codes). Some species points were slightly moved from their original position to improve readability.

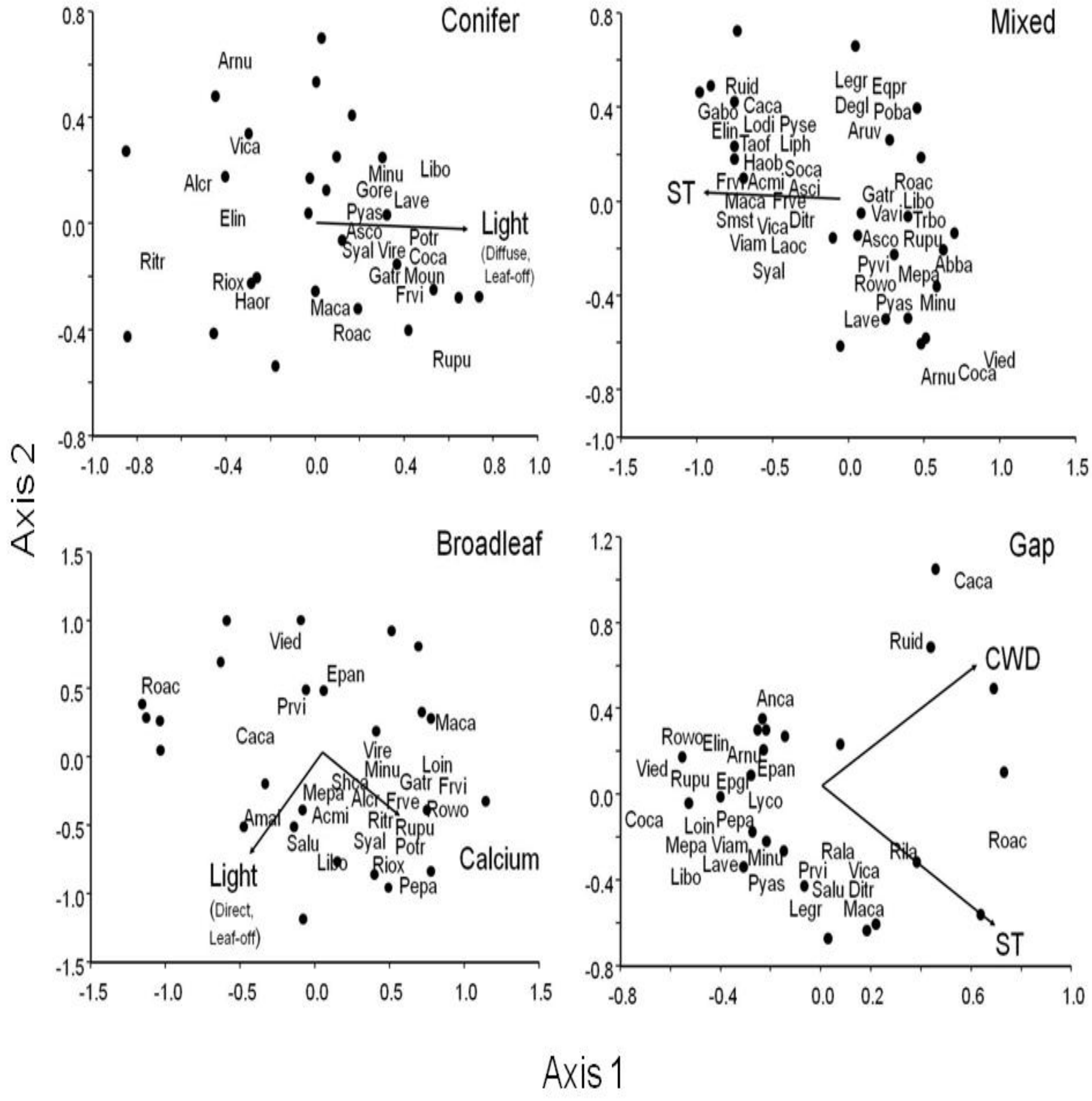


Figure 2.2. Results of Distance-based redundancy analyses (db-RDA) for each canopy patch type.

The arrow shows the direction of increasing value of significant environmental variables (CWD: coarse woody debris; ST: soil temperature; Moisture: soil moisture; Temperature: soil temperature. See Table 2.5. for details). The four letter codes indicate the locations of species with a correlation of ≥ 0.25 in ordination space; species codes are listed in Appendix 1 (in Supplementary Content). The environmental scores were scaled down two to three times to those of the sample scores and some patch points were slightly moved from their original position to improve readability.

Chapter 3

Partitioning vascular understory diversity in mixedwood boreal forests: the importance of mixed canopies for diversity conservation

3.1. Introduction

The patterns of plant species richness and evenness - the two components of diversity - vary across different scales of observation but not necessarily in the same way nor are these two affected by the same ecological processes (Wagner et al. 2000; Chandy et al. 2006). Unraveling the patterning of richness and evenness across different scales of observation can provide insight into the ecological processes structuring plant communities, an aspect that is critical for management and conservation measures (Wagner et al. 2000; Chandy et al. 2006).

Understory plant communities hold a large proportion of plant diversity in forest ecosystems and fulfill important ecological roles such as providing habitat and food for faunal communities and playing key roles in nutrient cycling, forest succession, and long-term stand productivity (Gentry and Emmons 1987; Halpern and Spies 1995; Nilsson and Wardle 2005; Hart and Chen 2006; Gilliam 2007; Hart and Chen 2008). The boreal mixedwood forest, which exists as a landscape mosaic of stands with varying dominance by broadleaf or coniferous trees, hosts the most diverse understory communities of the North American boreal forests (Hart and Chen 2006; 2008). Within this mosaic, stands with a mixed canopy host the greatest diversity for understory plants (Hart and Chen 2006; Macdonald and Fenniak 2007) and other biotic groups such as birds (Hobson and Bayne 2000) and arthropods (Hammond et al. 2001; Work et al. 2004; Buddle et al. 2006). Understory plant community composition and diversity are strongly influenced by canopy composition (Hart and Chen 2006; Macdonald and Fenniak 2007) and while it is widely accepted that plant diversity is higher when resource heterogeneity is high (Huston 1979), the patterns and processes underlying biotic diversity within forest stands of mixed canopy composition remain largely unexplored.

An understanding of the hierarchical organization of understory species richness and evenness in relation to canopy patches and the associated micro-environmental heterogeneity is necessary for managing vascular plant diversity in mixedwood forests, which in recent decades have become highly desirable for commercial harvesting. Current silvicultural and regeneration regulations in some regions of Canada favor the establishment and growth of relatively pure stands of conifers, separate from stands of broadleaf trees (Man and Lieffers 1999; Chen and Popadiouk 2002; Haeussler et al. 2004). Such modifications of canopy structure can potentially change the natural processes that govern mixedwood forests, in turn modifying the patterning of understory plant diversity at both local and regional scales. Additive partitioning of species diversity provides a framework within which to assess diversity patterns at different levels of organization, providing an estimation of the relative contribution of within (α) and between (β) community diversity to total diversity (γ) (Allan 1975; Lande 1996; Loreau 2000; Crist et al. 2003; Gering et al. 2003). From a management and conservation perspective, additive partitioning allows the characterization of the heterogeneity of a region at different levels of observation and the identification of the scale at which maximum diversity occurs (Allan 1975; Lande 1996; Loreau 2000; Crist et al. 2003; Gering et al. 2003).

We investigated the hierarchical organization of understory vascular plant diversity in relation to the heterogeneous mosaic of canopy patch types within mature, unmanaged mixed canopy stands in the boreal mixedwood forest through additive partitioning of diversity. In addition, we explored the patterns of species abundance among canopy patch types in order to infer the ecological processes shaping understory diversity. Given that understory species dominance is high in mature boreal forests (Hart and Chen 2006) we anticipated that dominant species may strongly influence understory diversity patterns through effects on species evenness. Indeed, the functional relevance of dominant species has received considerable attention recently (Tilman et al. 1997; Smith and Knapp 2003; Emery and Gross 2007; Mokany et al. 2008 but see Lyons et al. 2005). As such, we paid special attention to the identity of common and dominant understory species. We hypothesized that (i) the additive partition of understory richness and diversity (expressed as an index that incorporates species abundance and evenness) follow different trends which are strongly affected by the patterns of dominant and common species and, (ii) the natural intermix of canopy patch types within mixedwood forest stands is crucial for the maintenance of understory diversity by giving rise to different ecological mechanisms that shape diversity patterns uniquely.

3.2. Methods

3.2.1. Study Site and Field Procedures

The study was conducted in the Boreal Mixedwood Ecoregion in forest stands near Lac La Biche, Alberta, Canada (55º N, 112º E ~610 meters above sea level) (Strong 1992) in the summer of 2003. Mesic sites in this region host boreal mixedwood forests with canopy co-dominance by broadleaf trees (primarily *Populus tremuloides* Michx. (trembling aspen)) and conifers (mainly *Picea glauca* (Moench) Voss (white spruce)). The region has a boreal climate with a mean summer temperature of 13.5° C (May through August) and a mean winter temperature of -13.2° C (November through February). The mean annual precipitation is 397mm which occurs mostly during the summer (Strong 1992).

Within a ~ 30 km^2 landscape, we sampled within the portion of the forest land base that had been classified as 'mixed' (having between 40% and 60% canopy cover of both coniferous and broadleaf trees) at the stand (polygon) scale by the most recent forest vegetation inventory in the region. All sampled forests were of fire origin, approximately 100 years old and previously unmanaged. Sampling was concentrated in either the northern or southern portion of the total study area; the two areas were approximately 30 km from one another. Within these two areas, we used a stratified random approach to select a total of 98 sample points in four different canopy patch types: (1) Conifer patches (26 plots): Composed of at least 70% (by canopy cover and tree density) conifer (mainly *P. glauca*). (2) Broadleaf patches (25 plots): at least 70% broadleaf trees (mainly *P.*

tremuloides). (3) Mixed patches (23 plots): At least 40% and no more than 60 % conifer (mainly *P. glauca*). (4) Gap patches (24 plots): Canopy openings where a 50 m^2 circular plot could be located without any canopy cover above the understory strata. Each sample point was at least 50 meters away from forest edges, cut lines or trails, and points were at least 30 meters apart from each other to avoid autocorrelation. One of the patch types was only present in one of the two areas.

Because the patchiness of canopy composition in mixedwood forests likely gives rise to high micro-site heterogeneity, it was necessary to define the appropriate ‘observation window’ (Niemela et al. 1996) that ensured the detection of such heterogeneity and avoided the obscuring of habitat heterogeneity behind averages. Based on tree size and density and crown structure in these forests, we chose to sample within 50 m^2 circular (4-m radius) plots at each sample point in order to detect non-random micro-habitat variation within mixedwood stands caused by the spatial variation of canopy patches. At each sample point, visual estimates of plant cover were made for each vascular plant species within a 2 m x 2 m sub-plot centered within the larger plot; this was divided into four 1 m x 1 m sub-plots to increase accuracy of visual cover estimates. Three genera were indentified at the genus level only (one *Salix* and two *Carex* spp.). Nomenclature followed Moss (1983). Prior to calculation of the diversity index, cover estimates were averaged over the four 1 x 1 m sub-plots to give a single cover value per species for each patch.

3.2.2. Data Analysis

Observed and estimated richness

In each plot, we calculated species richness. In order to assess whether our sample size captured variation in species richness, we estimated total species richness for each canopy patch type using several non-parametric richness estimators (Jackknife 1, Jackknife 2, Chao 1, Chao 2, Incident-based Coverage Estimator (ICE), and Abundance Coverage Estimator (ACE)) by means of the EstimateS program with 1,000 randomizations for each data set (Colwell 2005).

Additive partitioning

The additive partitioning of diversity ($\gamma = \beta + \overline{\alpha}$) was originally suggested by Allan (1975) and re-considered by Lande (1996). It differs from Whittaker's (1960; 1972) multiplicative model ($\gamma = \beta\overline{\alpha}$) in that alpha and beta diversity have the same units which makes possible the calculation of their relative contribution to gamma diversity over a range of scales (Lande 1996; Loreau 2000; Crist et al. 2003; Gering et al. 2003). We partitioned understory plant richness and diversity (quantified as Shannon's index (H')) across the four canopy patch types in mature mixedwood forests based on the following model: $\gamma_{\text{-mixedwood landscape}} = \alpha_{\text{-individual patch}} + \beta_{\text{1-within canopy patch type}} + \beta_{\text{2-among canopy patch type within area}} + \beta_{\text{3-between areas}}$ (Fig. 3.1.). For each canopy patch type separately, understory plant diversity was partitioned using the following model: $\gamma_{\text{-canopy patch type}} = \alpha_{\text{-individual patch}} + \beta_{\text{1-within canopy patch type}}$. We used the software program PARTITION (Veech and Crist 2009) to test whether the observed diversity partition was significantly different from what would have been obtained by chance alone. For the partition with all the patches together, we used a restricted-individual based randomization for the $\alpha_{\text{-individual patch}}$ and $\beta_{\text{1-within canopy patch type}}$ levels and a sample-based randomization for the $\beta_{\text{2-among canopy patch type within area}}$ and $\beta_{\text{3-between areas}}$ levels. We chose these randomization procedures because most boreal understory plants have clonal growth and differentiating plant individuals would have been arbitrary and erroneous. For the partition for each patch type, we used an unrestricted individual based randomization as this is the only possible randomization procedure in PARTITION when the lowest level of analysis equals the highest level of data (Veech and Crist 2009). Each randomization process was repeated 1000 times in order to obtain null distributions for each of the diversity measures (S & H') at all levels of the two partitions. The observed values were then compared against expected values generated by the randomization procedure and the proportion of null values that were greater or lower than the observed values was used as the statistical significance (*P*-value) (Crist et al. 2003; Veech and Crist 2009).

Species relative abundance & Dominant and most abundant species

We examined relative abundance distributions for the understory assemblages for each canopy patch type by means of rank abundance plots. To enhance our understanding of the additive partitioning and species relative abundance distributions, we compared mean cover of the five most abundant (dominant) species from each canopy patch type. We also calculated their Winsorized mean as their abundance distributions were non-normal. We defined dominant species as those that had the greatest percentage cover per canopy patch type. The measures were calculated in SAS (v.9.1; SAS Institute 2003) using Proc Univariate.

3.3. Results

3.3.1. Species diversity indices & observed and estimated richness

Observed and estimated total richness was greatest for mixed patch types, followed by gaps and then conifer and broadleaf patch types (Table 3.1.). We chose the Jackknife 2, Chao 2 and ICE estimators because they reached the observed number of species sooner that the other estimators and stopped increasing earlier or increased less with increasing number of plots (Magurran 2004). Average estimated total richness based on these three estimators, was 64.6 species for conifer patches, 83 for mixed, 62 for broadleaf, and 71 for gaps (Table 3.1.). The observed total richness represented ~ 76 – 89 % of the estimated value, suggesting that our sample size was adequate to characterize the understory species assemblage in these forests (Table 3.1.). Observed richness for all plots combined was 78 species (see Appendix 1).

3.3.2. Additive Partitioning of Diversity

For the partition at the landscape level, diversity at the $\alpha_{\text{-individual patch}}$ was significantly lower ($P<0.001$) while $\beta_{\text{1-within canopy patch type}}$ levels was significantly higher ($P<0.001$) than expected if species had been distributed at random (Table 3.2). At the $\beta_{\text{2-among canopy patch type within area}}$ level, richness was significantly higher ($P=0.05$) while Shannon's index was not significantly different than expected by random (Table 3.2). Conversely, for the $\beta_{\text{3-between areas}}$ level, richness was not significantly different while Shannon's index was significantly lower than the null distribution ($P<0.001$). When each patch type was analyzed separately observed values of richness and Shannon's diversity were lower at the $\alpha_{\text{-individual patch}}$ level and higher than expected at the $\beta_{\text{1-within canopy patch type}}$ level. The greatest proportion of richness for each of the four canopy patch types, and for mixedwood stands overall, was at the $\beta_{\text{1-within canopy patch type}}$ level (Table 3.2). In contrast, for Shannon's H' the greatest proportion was at the $\alpha_{\text{-individual patch}}$ level (64 – 69 %) (Table 3.2).

3.3.3. Species Relative Abundance

Conifer and gap patches had a steep rank-abundance slope (Fig. 3.2). Mixed patches had a shallower slope of species abundance distribution while broadleaf patches had the shallowest slope (Fig. 3.2).

The 5 most abundant (highest cover values) species in each of the four different canopy patch types were drawn from a common pool of 7 species (Table 3.3). There was overlap in the most abundant species among patch types however, their mean abundances differed.

The perennial herb *Aralia nudicaulis* was the dominant species under conifer patches followed by the herbs *Maianthemum canadense* and *Rubus pubescens* (Table 3.3.). Under mixed patches, the dominant species was the shrub *Viburnum edule* closely followed by the herb *Aralia nudicaulis* and the shrub *Rosa acicularis.* The shrub *Rosa acicularis* was the dominant species under broadleaf patches followed by the herbs *Maianthemum canadense* and *Cornus canadensis*. Finally, under canopy gaps, the graminoid *Calamagrostis canadensis* was the dominant species followed by the shrubs *Rosa acicularis* and *Viburnum edule* (Table 3.3.).

3.4. Discussion

This study was the first to undertake a hierarchical partitioning of understory diversity in boreal forests. The results suggest that the mosaic of canopy patch types within mixedwood forests plays a crucial role in maintaining the hierarchical levels at which understory richness and evenness are maximized. The additive partition indicated that the maximum levels of species richness and Shannon's (H') diversity occurred at different scales of observation. These findings support the argument that different processes determine diversity at different spatial scales (Loreau 2000; Crawley and Harral 2001).

In comparison to temperate and tropical forests, plant species richness in boreal forests is relatively low, holding only 291 vascular species that are usually found in mixtures composed of 39 to 77 species (La Roi 1967; Chen and Popadiouk 2002; Hart and Chen 2006). We found a total of 78 vascular plant species (listed on Appendix 1 in Supporting Information) in these mixedwood stands and understory assemblages for the different canopy patch types were composed of 54 to 63 understory species. The additive partitioning showed that the largest proportion of richness was at the $\beta_{1\text{-within canopy patch type}}$ level. The high species richness at the β_1 level was likely a result of the micro-environmental heterogeneity (Wagner et al. 2000; Chandy et al. 2006) and stochastic factors leading to the inclusion of infrequent and specialist species as more patches were sampled (Summerville et al. 2003). The lower richness at the $\beta_{2\text{-among canopy patch type}}$

$_{\text{within area}}$ level and the lack of significance at the $\beta_{\text{3-between areas}}$ level suggests that it is at the intermediate hierarchical levels, rather than the largest, where understory richness is maximized in boreal mixedwood forest stands. In the separate analyses of each canopy patch type, the $\beta_{\text{1-within canopy patch type}}$ level also had the largest proportion of richness. The importance of intermediate hierarchical levels for plant species richness has also been observed in studies in other bio-geographic regions (i.e. Chandy et al. 2006; Chiarucci et al. 2008).

In contrast to the pattern for species richness, the greatest proportion of diversity for Shannon's diversity index was at the $\alpha_{\text{-individual patch}}$ level. Because Shannon index is based on the proportional abundance of each species, this suggests that species dominance is lower at the plot level but increases as we move up the hierarchy due to the accumulated influence of the abundance of common species. The occurrence of uncommon species, which underlie the observed results for richness, would have relatively little influence on the diversity indices. Overall, these results could be interpreted as evidence that uncommon species are distributed at larger spatial scales (Gering et al. 2003), and in boreal mixedwood forest stands, among canopy patch types.

Patterns of species relative abundance canprovide some insight into processes underlying differences in diversity patterns among assemblages (Roberts and Gilliam 1995; Magurran 2004); in our case, among canopy patch types. Steep relative abundance curves usually indicate a pronounced species dominance attributable to competitive exclusion or dominance by a few tolerant species to local environmental conditions (Magurran 2004). Conifer and gap patches represented the two ‘extremes’ in terms of canopy cover and we suggest that different processes underlie their similar steep species abundance curves. Under a conifer-dominated canopy availability of light and soil nutrients is low (Messier et al. 1998; Légaré et al. 2001; Hart and Chen 2006; Macdonald and Fenniak 2007). Thus, it seems that diversity patterns under conifer patches are not strongly affected by inter-specific competition. Rather, these harsh conditions act as a filter inhibiting the establishment of light and nutrient demanding species while favoring the dominance of those species that can tolerate and thrive under such conditions (Messier et al. 1998; Hart and Chen 2006; Bartemucci et al. 2006; Macdonald and Fenniak 2007; Hart and Chen 2008). This concurs with the predictions of Tilman’s resource-ratio hypothesis that late-successional communities will have high dominance of a few well-adapted species and thus lower species richness (Tilman 1985). Indeed, the most abundant species in conifer patches, *Aralia nudicaulis* and *Maianthemum canadense,* are shade-tolerant species that, once established, can persist for several years (Edwards 1984; Worthen and Stiles 1986). This dominance by a few tolerant species likely explains why conifer patches had lower overall richness and $\alpha_{\text{-individual patch}}$ richness and diversity than the other patch types.

In canopy gaps resource availability to the understory is high because of reduced competition with trees for below-ground resources and increased solar radiation, which in turn can warm the soil and increase nutrient mineralization (De Grandpré and Bergeron 1997; Hart and Chen 2006; Fahey and Puettmann 2007). These conditions likely allow for the continued existence of late successional species that occupied the space prior to gap formation along with new establishment of early-successional species (DeGrandpré and Bergeron 1997) leading to relatively high richness at the $\alpha_{\text{-individual patch}}$ and $\beta_{\text{1-within canopy patch type}}$ levels. However, those species that have the ability to grow rapidly in response to the abundance of available resources and to out-compete slow-growing species were dominant in these patches suggesting that in this case competitive exclusion led to species dominance underlying the observed relative abundance curve. Indeed, *Calamagrostis canadensis,* the dominant species of these patches, is an aggressive colonizer of recently disturbed areas that uses an "opportunistic guerrilla" strategy (Macdonald and Lieffers 1993) to efficiently exploit favorable (warmer soils and higher incoming light) and less crowded micro-sites (Macdonald and Lieffers 1993; Landhäuser et al. 1996).

The shallow relative abundance distribution for mixed patches is likely a reflection of the micro-environmental heterogeneity among mixed patches along with stochastic processes of regeneration. This could result in occurrence of infrequent species, the identity of which differs among plots, such that mixed patches had the highest $\beta_{\text{1-within canopy patch type}}$ level of all canopy patch types. At the same time, this micro-environmental variability may allow for the co-existence of shade tolerant species along with resource-demanding, shade-intolerant species and generalist species (Chávez and Macdonald 2010). These results support the environmental heterogeneity hypothesis (Huston 1979) suggesting that environmental differences among mixed patches lead to conditions of resource availability and competitive influence suitable for a variety of understory species such that mixed patches have higher total species richness (Huston 1979; Hart and Chen 2008).

Lastly, the shallowest rank abundance distribution under broadleaf patches could be the product of the relatively benign environmental conditions, in terms of light and nutrient availability under a broadleaf canopy (Lieffers et al. 1999; Berger and Puettman 2000; Légaré et al. 2001; Hart and Chen 2006) which likely favor the establishment of a number of different fast growing shrubs and herbs (Chávez and Macdonald 2010). The high species richness and diversity at the $\alpha_{\text{-individual patch}}$ level and the relatively even abundance distribution of these assemblages implies low interspecific competition and high niche complementarity and thus, a better utilization of available resources (Mwangi et al. 2007). This observation concurs with the findings of Chen et al. (2004) and Macdonald and Fenniak (2007) who reported that resource availability was a key factor influencing understory assemblages under aspen-dominated canopies at the stand level.

Our results agree with those of Wagner et al. (2000), Summerville et al. (2003) and Chandy et al. (2006) in that species evenness and abundance are likely determined by local-level processes such as species interactions, dominance, and gap dynamics while species richness is more influenced by processes occurring at larger scales such as environmental heterogeneity and regional species pool, although we did not explore the latter idea. Likely species interactions, climatic and topographic factors and local disturbances (Veech and Crist 2007) are important in shaping understory diversity patterns in mixedwood landscapes. We purposely focused on the local and intermediate scales, where some key ecological processes that structure diversity patterns operate (Niemela et al. 1996; Keddy 2005), as these are the scales at which management decisions are made (Colwell and Coddington 1994; Roberts and Gilliam 1995) and at which measures towards management, conservation and restoration may be undertaken.

The results of this study could be applied to development of regeneration standards that would allow for development of more natural mixtures following harvest of mixedwood forests (Lieffers et al. 2008). Further, in planning for patch retention partial harvesting systems, large retention patches (e.g. > 2 ha; DMI 2008) that include small patches (~4 m-radius) of both conifer and broadleaf trees could help to preserve natural patterns of understory diversity, in turn supporting conservation of associated faunal communities. In conclusion, our study points to the importance of maintaining micro-environmental heterogeneity within boreal mixedwood stands, in the form of an intermix of small patches of varying canopy composition, to conserve and restore understory plant species richness and diversity.

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Tables

Table 3.1. Observed and estimated total understory richness for each canopy patch type

	Observed Total Richness[a]	ICE	Chao2	Jack2	Estimated Total Richness[b]	Representation of Observed Richness (%)[c]
Conifer	54	62 (0.0)	62 (5.6)	70 (2.4)	64.6	83.6
Mixed	63	82 (0.0)	79 (8.1)	88 (0.0)	83.0	75.9
Broadleaf	55	59 (0.01)	60 (4.8)	67 (0.0)	62.0	88.7
Gap	60	70 (0.0)	67 (5.6)	76 (2.6)	71.0	84.5

a. The total number of species found in all sample plots for a given canopy type. Observed richness for all study plots combined = 78

b. Arithmetic mean of the three best non-parametric richness estimators: ICE = Incidence-based coverage estimator, Chao2 = Chao2; Jack2 = Jackknife 2. The value within brackets is the standard deviation.

c. Observed Total Richness as a percentage of Estimated Total Richness.

Table 3.2. Additive partitioning of understory diversity across mixedwood stands and for each canopy patch type

		Richness				**Shannon's H'**			
	Level of Partition	**Observed**	**%**	**Expected**[a]	***P-value***	**Observed**	**%**	**Expected***	***P-value***
Mixedwood Forests[b]									
α_1	Within an individual patch	15.80	20.00	30.55	<0.0001	2.224	88.40	30.55	<0.0001
β_1	Within each canopy patch type	32.40	41.28	17.62	<0.0001	0.968	10.01	0.182	<0.0001
β_2	Among canopy patch types per area	18.80	24.62	17.15	0.05	0.248	1.30	0.223	N.S.
β_3	Between areas	11.00	14.10	13.47	N.S.	0.058	0.29	0.086	<0.0001
γ	Total	78		78.79		3.498		3.503	
Conifer Canopy Patches									
α_1	Within an individual patch	13.50	25.0	28.30	<0.0001	2.12	64.29	3.00	<0.0001
β_1	Within canopy patch type	40.50	75.0	25.70	<0.0001	1.18	35.71	0.31	<0.0001
γ	Total	54		54		3.30		3.30	
Mixed Canopy Patches									
α_1	Within an individual patch	14.30	22.70	27.60	<0.0001	2.17	66.24	2.86	<0.0001
β_1	Within canopy patch type	48.70	77.30	35.40	<0.0001	1.11	33.76	0.34	<0.0001
γ	Total	63		63		3.28		3.20	
Broadleaf Canopy Patches									
α_1	Within an individual patch	18.60	33.82	36.30	<0.0001	2.36	71.73	3.20	<0.0001
β_1	Within canopy patch type	36.40	66.18	18.70	<0.0001	0.93	28.27	0.17	<0.0001
γ	Total	55		55		3.30		3.37	
Canopy Gap Patches									
α_1	Within an individual patch	16.70	27.83	35.80	<0.0001	2.28	67.98	3.20	<0.0001
β_1	Within canopy patch type	43.30	72.17	24.20	<0.0001	1.08	32.02	0.17	<0.0001
γ	Total	60		60		3.36		3.38	

a. Expected values were based on the mean of 1000 randomizations of the data (for more details, see Methods section)

b. The partition of 'Mixedwood Forests' includes the four canopy patches together (Also see Figure 3.1.)

Table 3.3. Mean and Winsorized mean values for the five most abundant species for each patch type [a]

Conifer Patches	Mean/ Winsorized Mean	Mixed Patches	Mean/ Winsorized Mean	Broadleaf Patches	Mean/ Winsorized Mean	Gap Patches	Mean/ Winsorized Mean
Aralia nudicaulis	14.80 8.84	*Viburnum edule*	12.64 9.50	*Rosa acicularis*	24.61 23.01	*Calamagrostis canadensis*	15.16 8.91
Maianthemum canadense	7.25 5.26	*Aralia nudicaulis*	11.43 5.23	*Maianthemum canadense*	10.92 7.52	*Rosa acicularis*	14.7 11.20
Rubus pubescens	5.50 3.80	*Rosa acicularis*	9.07 7.22	*Cornus canadensis*	10.36 9.16	*Viburnum edule*	11.73 10.36
Viburnum edule	5.20 2.77	*Maianthemum canadense*	7.06 3.8	*Viburnum edule*	10.13 6.64	*Cornus canadensis*	10.95 9.70
Rosa acicularis	3.76 2.58	*Cornus canadensis*	6.30 3.91	*Aralia nudicaulis*	8.36 6.76	*Maianthemum canadense*	10.83 7.29

a. The Winsorized mean was calculated by replacing each observation below the first quartile with the value of the first quartile and the observations of the third quartile with the value of the third quartile

Figures

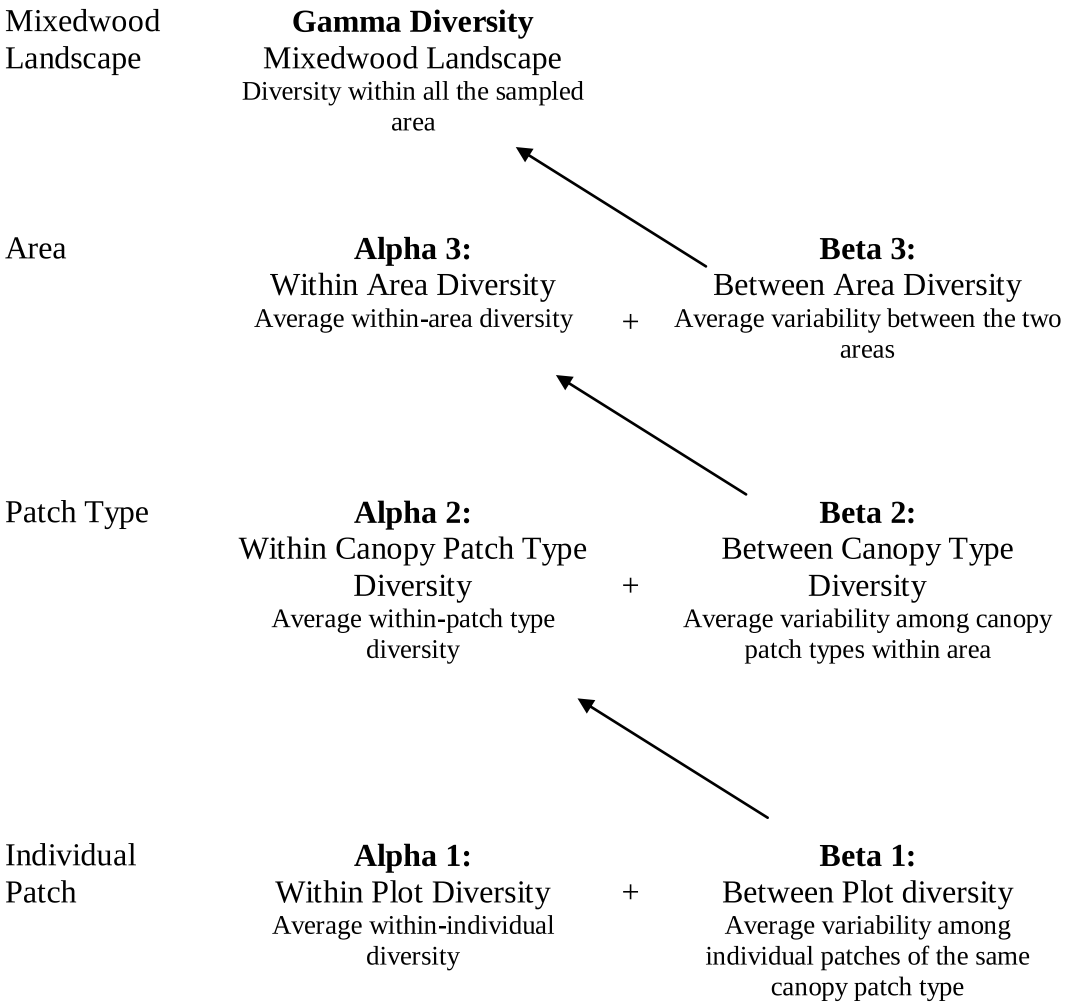

Figure 3.1. Hierarchical levels in the additive partitioning of diversity: the diversity of each scale is additively linked to form the diversity of the next higher level (adapted from Gering et al. 2003).

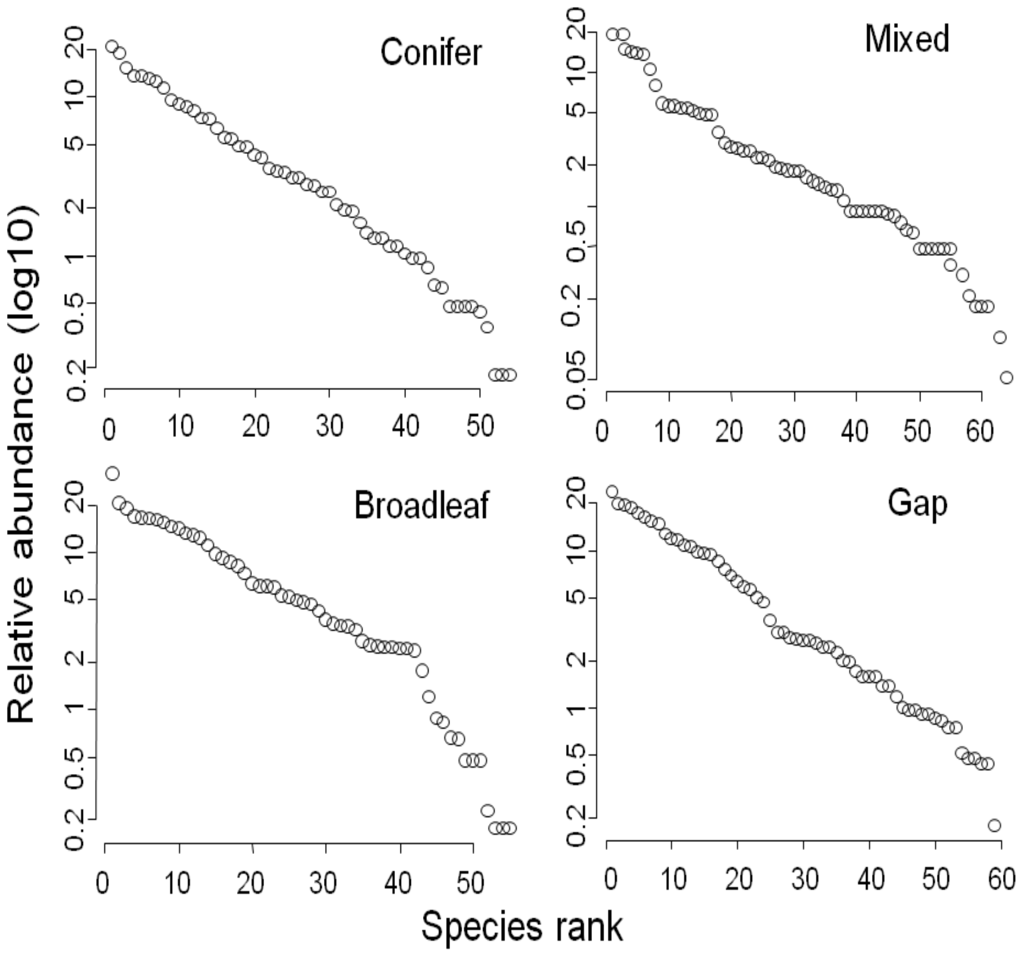

Figure 3.2. Plots of rank relative abundance of species in the understory assemblages for the four different canopy patch types.

The X-axis gives the rank of relative abundance of a given species while the Y-axis shows the actual relative abundance of a species using a $\log_{10}$ scale.

Chapter 4

Understory species interactions in mature boreal mixedwood forests

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4.1. Introduction

Interactions among plant species play an important role in regulating composition of local communities and ecosystems (Brooker 2006) and in mediating ecosystem functioning when a given species or functional group is lost (Díaz et al. 2003). Plant interactions entail complex combinations of competition and facilitation among species but the precise effect of species interactions on community structure and ecosystem productivity is closely tied to local availability of resources, such as light, water and nutrients (Tilman 2007). Much of the experimental work on plant interactions has been performed in synthetically assembled communities with a relatively low number of species with responses monitored for a few growing seasons (Díaz et al. 2003; Jiang et al. 2009). These studies provide limited insight into the natural dynamics of late-sucessional plant communities where realistic diversity and abundance patterns are present (Thompson et al. 2005; Jiang et al. 2009).

Understory plant communities fulfill important ecological roles in forested landscapes (Maguire and Forman 1983; Gilliam 2007). In the boreal forest, understory shrubs and herbs represent the largest proportion of boreal plant diversity and provide food and habitat for wildlife species (De Grandpré et al. 2003; Nilsson and Wardle 2005). Also, understory communities indirectly control forest successional trends by altering the microclimatic conditions in the forest floor and influencing recruitment of tree species (Hart and Chen 2006). In turn, boreal trees exert important effects on the microenvironment below the canopy and are a key driver of understory plant community composition and diversity (Macdonald and Fenniak 2007; Chávez and Macdonald 2010). In this way, trees and understory plant species constantly interact throughout the different stages of boreal forest succession either by competing at the seedling stage (Lieffers et al. 1993; Constabel and Lieffers 1996) or by trees affecting microclimate conditions for the growth of understory species (Macdonald and Fenniak 2007; Chávez and Macdonald 2010). Thus, knowledge of the natural dynamics of understory plant interactions is important for a better understanding of forest ecosystem functioning (Gilliam and Roberts 2003). Nevertheless, very little is known about interactions among understory functional groups in mature boreal mixedwood forests and in boreal forest in general (but see Arii and Turkington 2002; Wardle and Zackrisson 2005; Hautala et al. 2008).

Boreal herbaceous communities are constantly exposed and responding to local natural disturbances, such as trampling by vertebrates, single tree mortality and windthrows, which modify the composition and distribution of herb species (Roberts and Gilliam 2003; De Grandpré et al. 2003). The degree of change in the herbaceous layer after disturbance can be importantly influenced by the presence and density of the shrub layer as this modifies the quantity and quality of light reaching the forest floor (De Grandpré et al. 2003; Roberts 2004). Light is the primary limiting resource for the establishment and growth of understory vascular plants across forest ecosystems, including boreal forests (Rowe 1956; George and Bazzaz 2003; Neufeld and Young 2003). Under closed-canopy boreal forest stands light is transmitted through the overstory, shrub (above 50 cm) and herbaceous (forest floor up) layers with such a vertical stratification of vegetation only 2–5.9% of light reaches the forest floor (Constabel and Lieffers 1996; Messier et al. 1998; Hart and Chen 2006). In size-structured communities, such as forest understory communities, there is asymmetric competition for light between taller and shorter plants because taller individuals intercept incoming light (Schwinning and Weiner 1998; Kohyama and Takada 2009). The shrub layer is, therefore, expected to limit the biomass production, composition and diversity patterns of the herbaceous layer. Assessing the response of the herbaceous layer to the presence or absence of erect shrubs is important for understanding effects of small-scale disturbance in boreal forests.

In this study, we removed erect shrubs in mature boreal mixedwood stands to investigate: whether the absence of a given plant growth form (erect shrubs) influences biomass, diversity and composition of another plant growth form (the herbaceous layer). Herein ‘herbaceous layer’ and ‘herb’ refer to all vascular species of the forest floor including graminoids, forbs, trailing shrubs (e.g., *Linnaea borealis*) and species which have a woody base but herbaceous stem (e.g., *Cornus canadensis*) (see Crane 1989; Howard 1993). We carried out the study in a naturally assembled community because we wanted to capture the local set of species as well as the natural abundance patterns occurring in mature mixedwood boreal forest stands. We hypothesized that increases in light to the herbaceous layer due to erect shrub removal, could lead to changes in biomass and abundance patterns of herbs. We did not expect significant changes in species richness because plant interactions tend to have a higher impact on species abundance (Beatty 1984; Callaway and Walker 1997) and changes in composition of boreal understory plant communities tend to be more influenced by changes in species relative abundance than in species richness (Hart and Chen 2006; Chávez and Macdonald 2010).

4.2. Methods

4.2.1. Study Site and Field Procedures

The study was conducted at the Ecosystem Management Emulating Natural Disturbance (EMEND) research site (see http://www.emend.rr.ualberta.ca/index.asp), located in northwest Alberta, Canada (approximate site center: 56° 46' 13" N, 118° 22' 28" W) in the Clear Hills Upland Ecoregion within the Boreal plains Ecozone (Strong and Leggat 1992; Kishchuk 2004). Forests in the area are co-dominated by trembling aspen (*Populus tremuloides* Michx.), balsam poplar (*Populus basamifera* L.) and white spruce (*Picea glauca* (Moench) Voss) with lesser amounts of black spruce (*Picea mariana* (Mill.) B.S.P.), balsam fir (*Abies balsamea* (L.) Mill.), lodgepole pine (*Pinus contorta* Dougl.) and paper birch (*Betula papyrifera* Marsh.). Soils have developed on fine-textured glacial till or glaciolacustrine deposits and soil types include (generally) well drained Luvisols (Dark Grey Luvisol, Orthic Grey Luvisol) with limited occurrences of Brunisolic, Gleysolic and Solonetzic soils (Kishchuk 2004). Site elevation ranges from 677 to 880 m above sea level. The region has a boreal climate with cold winters (mean January temperature: -16.6° C), warm summers (mean July temperature: 16° C) and has a mean annual precipitation of 402 mm, most of which is received during the summer (Environment Canada 2008).

We performed this study in two forest stands classified as “mixed” at the stand (polygon) scale by forest inventories i.e., they had between 40-60% of canopy cover of conifer (mostly white spruce) and broadleaf trees (mostly trembling aspen). The two stands were approximately 10 ha in size, 100 years of age, of fire origin and previously unmanaged. In June 2004, we established 20 (10 pairs) 5-m diameter circular plots. Plot selection was based upon the following criteria: (i) all pairs were under mixedwood canopies having at least 40% and no more than 60% of conifer trees in the plot (based on both density and canopy cover); (ii) each pair had the same dominant shrubs - mainly *Viburnum edule (*low bush cranberry) *and Rosa acicularis* (prickly rose) – with similar percentage cover and height (approx. 1.50 m tall); (iii) the plots of each pair were approximately 2 m apart from one another and, (iv) pairs were at least 30 m apart from one another and at least 50 m away from forest edges or cut lines. One plot of each pair was randomly selected to be the treatment or "removal" plot where all the erect shrub species were clipped and removed (average 907 g dry biomass per plot) from the plots in June of 2004. The other plot was used as a "control" where erect shrubs were left intact. We manipulated growth forms or functional groups rather than species richness because manipulation of functional groups often provides better insight into the effects that non-random species loss have on community structure than does manipulation of species richness (Díaz et al. 2003; Balvanera et al. 2006), although opinions are divided for this issue (Balvanera et al. 2006).

At each plot, we made visual estimates of percent cover (1-100%) for each vascular plant species in the understory (shrubs + herbs) within a 3-m diameter circular sub-plot which was further divided into four quarters to increase accuracy of cover estimates. Nomenclature followed Moss (1983). In 2004, visual cover estimates were made prior to shrub removal and in 2006 prior to the harvest of herb biomass. In 2006, we harvested all the above-ground parts of the herbaceous layer from the 10 pairs. We did not collect any of the orchid species (*Habenaria* spp., *Goodyera repens* and *Calypso bulbosa*) due to concerns for their conservation. Moreover, orchids were quite infrequent contributing little to overall biomass. The harvested plants were classified by species, dried with electrical fans in a research trailer while in the field and then oven-dried at 64 °C for 24h (in the Natural Resources Analytical Laboratory (NRAL) of the University of Alberta) and weighed to estimate their biomass. We measured the following environmental characteristics within the 5-m circular plots: *(A) Canopy composition*: All canopy trees (trees with DBH>5cm) were counted and their diameters at breast height (DBH, 1.3 m) measured in order to calculate basal area (BA) for conifer (BAC) and broadleaf (BAD) trees separately and for the two together (BAT). (*B) Ground Cover:* We estimated the percentage of ground cover of (i) downed fine woody debris (pieces <8 cm diameter), (ii) downed coarse woody debris (CWD) (pieces >8 cm diameter), (iii) mosses and, (iv) litter. *(C) Edaphic factors:* At the center of each plot, we buried nylon bags with 45 ml of Amberlite IR-150 anion-cation exchange resin (J.T. Baker) within the mineral soil layer in June of 2005. Bags were retrieved after a period of two months and extracted as described by Thiffault et al. (2000). We then analyzed them using a Technicon Autoanalyzer to obtain the concentrations of available PO_4^{3-}, NO_3^- and NH_4^+ and an Atomic Absorption Spectrophotometer to obtain the concentrations of Ca^{2+}, Mg^{2+} and K^{+} (in the NRAL). In August of 2005, we measured the depth of the litter (L) and organic layers (FH) at the plot centre and collected samples of organic (FH) and mineral layers (~20 cm depth). We measured pH in a paste of a 1:2 soil:water mixture for mineral soil and 1:4 soil:water for organic using a Fisher AR20 pH meter with glass. Lastly, we measured soil moisture and temperature at a depth of 30 cm. once over the growing season in August of 2005 at the plot center by means of Time Domain Reflectometry and a thermocouple respectively; the measures were taken at least 24 hours after a major precipitation event. (*D) Incoming Light:* At the centre of each plot we took two hemispherical canopy photographs at two different heights during both the leaf-on (August) and leaf-off (November) periods in 2005. To fully capture the influence of shrub canopy one photo was taken at 50 cm (below shrub layer) and the other at 1 m above the ground (at the shrub layer). Photographs were taken either: approximately 1 h after dawn, 1 h before dusk, or on overcast days in order to ensure uniform sky condition and to avoid direct insolation (Comeau et al. 1998; Gendron et al. 1998). Images were analyzed using SLIM (Spot Light Intercept Model) v. 2.2e (Comeau et al.1998; Comeau et al. 2003) software, which takes into account seasonal sun angle and data on cloud cover and opacity for the specific geographic location to calculate the percentage of direct, diffuse and total (average of diffuse and direct) solar radiation.

4.2.2. Data Analysis

Species Diversity & Abundance

Species diversity per plot for herbs was assessed using the Shannon's (H') and Simpson's (1-D), diversity indices, and species richness (S). The Shannon's index was calculated from the equation $H' = -\sum_{i=1}^{S} p_i In(p_i)$ where p_i is the proportional abundance of the *ith* species and the Simpson index from the equation $D = \sum_{i=1}^{S} p_i^2$ where n_i is the abundance (cover) of the *i*th species per plot and N is the total abundance per plot (sum of cover values). For both, S is the number of species per plot (Magurran 2004). We calculated these using biomass data as measures of species abundance. All the wintergreens (*Pyrola* spp.) were grouped together as were violets (*Viola* spp.), horsetails (*Equisetum* spp.) and grasses (*Calamagrostis canadensis* and *Elymus innovatus*).

To test for differences in diversity between control and removal plots, we used a Randomized Complete Block Analysis of Variance (ANOVA) by means of PROC MIXED (SAS v.9.1) with the following model: $Y_{ijk} = \mu + T_i + S_j + (TS)_{ij} + P(S)_{jk} + \varepsilon_{ijk}$

Where Y_{ijk} = Diversity measure for the i^{th} treatment on the j^{th} pair at the k^{th} stand; μ = overall mean; T_i = treatment (i = 1 to 2; fixed); S_j = Stand (block) (j= 1 to 2; random); $(TS)_{ij}$ = Interaction between stand and treatment; $P(S)_{jk}$ = Pair nested within stand (k = 1 to 10) and; ε = experimental error. Residuals were tested to ensure they met the assumptions of normality (Kolmogorov-Smirnov statistic) and homogeneity of variance (Levene's test) (PROC GLM; SAS v. 9.1; SAS Institute 2003).

We sampled a total of 42 species in the herbaceous layer (listed in Appendix 2) of which seven taxa (six species and the three *Pyrola* spp. that were grouped during the harvesting of biomass) were present in all 10 pairs of plots. These were designated as "common" species (listed in Table 4.1.). Three of these (*Cornus canadensis, Mertensia paniculata* and *Rubus pubescens*) were considered to also be dominant based on their high biomass. We assessed the effect of treatment (erect shrub removal) on the biomass of each of these seven taxa separately and on biomass of the seven together. To test whether the abundance of these seven taxa was significantly different between control and removal plots prior to shrub removal, we compared pre-treatment (2004) cover values for each of the seven and for all seven combined. There were no significant differences in species cover in 2004, before implementation of the removal treatment. We used the Randomized Complete Block Analysis of Variance (ANOVA) described above to perform these analyses.

Using the same Randomized Complete Block Analysis of Variance (ANOVA) model, we tested whether there was a difference in environmental conditions between the paired control and removal plots. We compared mean values for the 25 measured environmental characteristics: soil nutrients (PO_4^{3-}, NO_3^-, NH_4^+, Ca^{2+}, Mg^{2+} and K^+), edaphic factors (litter and organic layer depth, moisture and temperature), ground cover percentage (litter, moss coarse and fine woody debris), basal area (conifer, broadleaf and total), direct, diffuse and total light during leaf on and off periods and total annual light.

Plant Competition Intensity

We used the logarithm of response ratio (lnRR) competition intensity index to measure competitive interaction between shrub and herb species using the herb biomass data (collected in 2006; two years after shrub removal) in control and removal plots. The index was calculated using the following equation: $\ln([X_{\text{removal}}]/[X_{\text{control}}])$ where "X" represents the aboveground herb biomass in the removal and control plots (Goldberg et al. 1999). We selected this index because it is symmetrical for competitive and facilitative interactions and does not set a ceiling value on the maximum possible competition intensity (Goldberg et al. 1999). Positive lnRR values indicated that there was greater herb biomass after the shrub removal treatment suggesting a competitive influence of erect shrubs on herbs. Conversely, negative lnRR values should occur when there was lower herb biomass after treatment, indicating a facilitative relation between erect shrubs and herbs (Goldberg et al. 1999). For mathematical properties of lnRR see Goldberg et al. (1999) and Oksanen et al. (2006).

For each pair (control-removal) of plots, we calculated the following lnRR indices: A) an overall index including all herb species; B) an index including the seven most common herbs and; C) a separate index for each of the seven common herbs. Then, to assess the potential influence of the removal of erect shrubs on the competition intensity among herb species, we regressed the lnRR of each of the seven common herbs as a function of the following variables: A) Total herb biomass (all herb species combined); B) Total biomass of each of the seven common herbs (excluding the biomass of the "response" taxa); C) Biomass of each of the seven common taxa regressed on each of the others separately (e.g., the InRR value of species "Y" in a removal plot as a function of the biomass of species "X" in that plot). All the regressions were performed in SAS v. 9.1 (SAS Institute 2003) using PROC REG.

Species Composition

To assess the influence of the removal treatment on herb species composition, we compared the removal and control plots by means of a permutation-based nonparametric MANOVA (PerMANOVA; Anderson 2001). We used a Randomized Complete Block design with pairs as blocks and Bray-Curtis as a distance measure. To identify herbs that could be used as indicators of either removal or control plots, we performed an indicator species analysis (ISA) (Dufrêne and Legendre 1997; McCune and Grace 2002). These analyses were performed using PC-Ord for Windows (v. 4.5) (McCune and Mefford 1999). To assess whether the intensity of competition from which the community was released by the shrub removal treatment affected the extent of change in community composition, we calculated Bray-Curtis ecological distances between the paired control and removal plots with the biomass data for the 42 species using the function vegdist in the vegan package of R (v. 2.3.1.) (Oksanen et al. 2009). Then, we regressed the Bray-Curtis values versus the InRR values of the

42 species together as well as the seven common herbs (PROC REC SAS v. 9.1; SAS).

To relate environmental characteristics to understory species composition, we used a constrained ordination. We chose a distance-based Redundancy Analysis (dbRDA) (Legendre and Anderson 1999; McArdle and Anderson 2001) because it can be used with non-Euclidean distances. Also, significance testing is done using non-parametric permutations and thus there is no assumption of normality. The dbRDA was performed by first calculating a Bray–Curtis (Sørensen) ecological distance on the (untransformed) herb biomass per plot to data. A Principal Coordinate Analysis (PCoA) was then used to extract the principal coordinates of the distance matrix correcting for negative eigenvalues. We used this resulting matrix as the species data in a Redundancy Analysis (RDA), wherein the environmental matrix contained continuous environmental variables and orthogonal dummy variables coding for the two treatments (removal and control).

A total of 25 environmental variables (mentioned above) were tested for inclusion as explanatory variables in this analysis. Because the number of environmental and forest structure variables exceeded the number of plots, it was not possible to test all the variables together. Thus, we made subsets of environmental variables and conducted separate dbRDAs on these subsets using using stepwise-forward selection with Monte-Carlo permutations to test each variable for significance. For our final analysis we included only the variables that were constantly significant ($P < 0.05$). In order to consider the paired design of the study, we used each pair as a block (coded as a co-variable). Finally, for interpretation purposes, we used the original species data (not the distance-based) matrix as a supplemental dataset. Also, to investigate the effect of shrub removal on community composition, we ran a dbRDA including a dummy variable coding for treatment as a single environmental variable. We performed these analyses in CANOCO (v. 4.5) (ter Braak and Šmilauer 2002).

4.3. Results

4.3.1. Species Diversity & Abundance

None of the assessed diversity measures (1-D, H' and S) were significantly different between the control and removal plots before or after the imposed treatment (results not shown).

Total herb biomass and the biomass of the seven common herbs combined was significantly higher ($p < 0.032$ and $p < 0.008$ respectively) in removal plots than in control plots (Table 4.1.). The seven common taxa in the herbaceous layer together had higher biomass than the all rest of the herbaceous layer species combined for both the removal ($p<0.0001$) and control ($p<0.028$) plots. Collectively, these seven taxa accounted for more than 60% of total herbaceous layer biomass in control plots and over 70% in removal plots (Table 4.1.). Mean biomass of *Linnaea borealis* was significantly higher in the removal plots than in control plots; this was also the case for *Cornus canadensis*. The abundance of the other five common taxa was not significantly different between treatments.

Diffuse, direct and total incoming light at 50 cm above the ground during the leaf-on period were significantly lower in control plots than in the removal plots as was total annual light at 50 cm above the ground (Table 4.2.). Indeed, light at the 50 cm in the removal plots increased to the levels recorded in the control plots at 100 cm. The rest of the measured environmental variables (basal area, ground cover, edaphic factors) were not significantly different between control and removal plots (results not shown).

4.3.2. Plant Competition

The average of the InRR value for all the herbs combined was positive (0.30), indicating a slight release from competition due to shrub removal (Table 4.1.). The average lnRR value for the seven dominant species together was also positive (0.38) and so were the average lnRR values for *Linnaea borealis* and *Cornus canadensis* (1.24 and 0.53 respectively) indicating a release from competition (Table 4.1.). The lnRR values for the rest of the herb species were close to zero indicating that the removal treatment did not have a detectable effect on them over the period of two years following clipping. The lnRR values of *Linnaea borealis* ($p=0.02$; Adjusted $R^2=0.46$) and of *Pyrola* spp. ($p=0.004$; Adjusted $R^2=0.65$) were negatively related to the biomass of *Mitella nuda* (Table 4.3.). This suggests that when the biomass of co-occurring *M. nuda* was higher, *L. borealis* and *Pyrola* spp. showed less release due to shrub removal. Conversely, the lnRR values for *Linnaea borealis* were positively related to the biomass of co-occurring *Pyrola* spp. ($p=0.03$; Adjusted $R^2=0.41$) (Table 4.3.). The latter suggests that *L. borealis* showed more release from competition following shrub removal in plots which also had higher biomass of *Pyrola* spp. The rest of the regressions between lnRR values and biomass of individual herbs were non-significant (results not shown).

4.3.2. Species Composition

Based on the PerMANOVA, understory community composition was significantly different between removal and control plots ($p=0.03$). The Indicator Species Analysis identified that *Cornus canadensis* (IV = 63.9) and *Linnaea borealis* (IV = 74.8) were significantly ($p < 0.02$) more abundant and frequent in removal plots. Competition intensity (lnRR) calculated with all the herbs and the seven dominant herb species combined were positively related to the Bray-Curtis ecological distance between paired control-removal plots ($p=0.003$; Adjusted $R^2=0.68$ and $p=0.002$; Adjusted $R^2=0.67$ respectively) (Table 4.4.). This indicated that the plots wherein competition was strongest showed the greatest difference in community composition after shrub removal.

The following seven environmental variables were significantly related to understory community composition (presented in the order of forward selection): Total light during the leaf-on period at 1 m which was positively correlated to the first axis; treatment (control vs. removal plots) being negatively correlated to the second axis; soil temperature and total basal area which were positively correlated to the forth axis and; total annual light at 1 m, total light during the leaf-on period at 50 cm and soil Mg^{2+} which were positively correlated to the first axis (Table 4.5.). Together, these variables explained 40% of the variation in understory composition. Treatment by itself explained only 6.3% of the variation in herb composition.

4.4. Discussion

We assessed interactions among forest understory vascular plants of in mature and unmanaged boreal mixedwood forests by investigating whether the removal of erect shrubs would influence the biomass, composition and diversity of the herbaceous layer. We observed significant effects of erect shrub removal on herb biomass and community composition and these were mainly due to the increases in abundance of dominant and common herbs. In general, our results suggest that there is asymmetric competition for light between erect shrubs and herb species. As such, interactions among these two growth forms or functional groups likely have a significant effect on understory community composition in mature boreal mixedwood forests. Our study also confirms the significant contribution that dominant and common plant species make to plant community structure and to biomass recovery after a functional group is removed (Smith and Knapp 2003; Bret-Harte et al. 2008).

There are important discrepancies between plant interactions observed in natural communities and those observed in synthetic plant assemblages (Díaz et al. 2003; Balvanera et al. 2006). Plant interactions in natural communities are influenced by assembly processes such as resource heterogeneity, variation in dispersal strategies and phenological stages across the present species as well as realistic species abundance distributions (Díaz et al. 2003; Balvanera et al. 2006; Jiang et al. 2009). As such, the influence that environmental heterogeneity and dominance patterns exert on plant species interactions in the field is becoming a focus of research, particularly in heterogeneous ecosystems, rather than an unwanted source of variance (Díaz et al. 2003; Jiang et al. 2009). Apart from our study, only a few others have examined the dynamics of understory plant interactions in boreal forests through removal experiments in natural communities (e.g., Arii and Turkington 2002; Wardle and Zackrisson 2005; Hautala et al. 2008). Through these removal studies, understanding has been gained regarding the rapid response of dominant species to the removal of co-occurring species and about the important role that dominant and common species play for boreal ecosystem recovery after an entire functional group or growth form is removed (Wardle and Zackrisson 2005; Hautala et al. 2008.

Our study also points to the importance of common and dominant species for biomass recovery in boreal forests. The significant difference in herbaceous species composition between removal and control plots was largely attributable to rapid changes in abundance of the most common taxa, particularly of *Linnaea borealis* and *Cornus canadensis* the two species that were significant indicators of removal plots. This further confirms the importance of considering abundance patterns, not just richness, for the assessment of boreal understory communities (Chávez and Macdonald 2010). Responses of less common or subordinate herb species to shrub removal may have been limited by their lower ability to acclimatize to the changes in micro-environmental conditions (i.e., increases in soil temperatures and evapo-transpiration rates), by their morphological and phenological differences or by competitive suppression by the dominant herb species (Symstad and Tilman 2001). These findings support the idea that dominant species tend to confer short-term resistance to reduction in ecosystem functions when other community members are lost (Smith and Knapp 2003). These results are further supported by other removal studies carried out in ecosystems where seed recruitment is less important for community assemblage, such as the tundra (Bret-Harte et al. 2008) and seasonally dry forests (D’Antonio et al. 1998) which have also reported that empty spaces left by the removal of co-occurring species tend to be occupied by common species that are already dominant and that expand though vegetative growth (Díaz et al. 2003).

Flowering frequency is low and suitable microsites for seed germination are scarce in boreal forests; thus, seed recruitment is not as important as vegetative growth for site occupancy in the understory (Økland 1995). Clonal growth importantly influences interactions among plants (Oborny et al. 2000; Oborny and Kun 2002; Kun and Oborny 2003). Through physiological integration, interconnected ramets share their surplus resources (i.e., water, soil nutrients and photoassimilates), increasing the probability of survival and reproduction among ramets of the same genet (Oborny et al. 2000; Oborny and Kun 2002; Kun and Oborny 2003). A higher degree of ramet integration tends to confer higher competitive advantage to herb species inhabiting spatially heterogeneous systems, where resources are patchily distributed (Stuefer et al. 1996; Oborny et al. 2000) as they typically are in boreal forests (Carleton and Maycock 1980; Chávez and Macdonald 2010). In this study, the significant biomass increase of the stoloniferous forb *Linnaea borealis* after shrub removal was likely influenced by its ability to share resources among its clonal fragments.

In patches with higher light availability in the forest floor, the ramets of *L. borealis* increase their branching frequency to enhance carbon assimilation, provided that light availability remains favourable for 2-3 years (Niva et al. 2006) which was the elapsed time after treatment in our study.

The results of this study suggest that species interactions play an important role in influencing plant community structure, in terms of herb abundance and composition, in boreal mixedwood forests. However, stand density, incoming light, soil moisture and nutrients all together explained a larger proportion of the variation in herbaceous composition than did the shrub removal treatment; this emphasizes the strong influence that environmental heterogeneity exerts on boreal plant communities (Carleton and Maycock 1980; Macdonald and Fenniak 2007). The significant effect of light at the shrub level (1 m from the forest floor) and below it (50 cm from the forest floor) highlights the importance that both canopy trees and shrubs have in mediating the amount of incoming light that reaches the herbaceous layer (20 cm from the forest floor) (Constabel and Lieffers 1996; Hart and Chen 2006) and the effect of this on understory plant community composition.

Competition for water and nutrients can potentially limit the growth of forest herbs (Hicks and Turkington 2000; Anderson 2003; Neufeld and Young 2003). Because shrubs immobilize large quantities of nutrients in the summer, the removal of erect shrubs could have increase nutrient availability for herbs (Anderson 2003). We did not assess belowground interactions and did not detect a significant difference in moisture or nutrients after shrub removal.

Herb response to erect shrub removal was species-specific and increases in herb cover occurred mostly by vegetative growth of existing individuals. This response coincides with that seen after micro-scale disturbance events in which the soil layer is not severely affected (e.g., trampling and browsing by vertebrates, small wind storms) (Roberts 2004). Changes in plant communities due to neighbor removal are thought to be slow in boreal forests (Bryant et al. 1983). The significant changes in herb biomass and species composition that we detected only two years after shrub removal, however, support the idea that responses to the removal of a growth form or functional group can be rapid in northern forests (Lenière and Houle 2009), at least for dominant and common species. Also, it supports the idea that understory herbs have the capacity to quickly respond to changes in their environment following disturbance (Lenière and Houle 2009). In comparison to other forest ecosystems, boreal forests have harsher climatic conditions and lower resource availability (Hicks and Turkington 2000; Arii and Turkington 2002). Thus, the results of this study do not support the traditional idea that herbaceous communities in the forest floor of harsh environments are stress tolerators and lack the ability to rapidly or positively react to increases in resource availability (Grime 1977; 2001). Our results, agree with Arii and Turkington (2002) that, in boreal forests, not all understory herbs can be classified as stress-tolerators.

In accordance with theory regarding the influence of habitat heterogeneity and patch dynamics on clonal plants (Kotliar and Wiens 1990; Oborny et al. 2000) and results from this and other field studies (Niva et al. 2006; Chávez and

Macdonald 2010), we suggest that the matrix of contrasting light patches is important for mediating plant-plant interactions in boreal mixedwood forests. Overall, this study indicates that interactions among understory plant species play an important role in structuring boreal understory communities. Changes in the natural dynamics of these interactions may indirectly modify the natural structure of boreal understory communities.

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Tables

Table 4.1. Results of mean biomass (g of dry biomass) for the control and removal treatments of the dominant (D) and common (C) species at the time of harvest of herb biomass in 2006 [a]

Species	Control	Removal	P-value	InRR[b]
Cornus canadensis (D&C)	43.269 (±13.93)[c]	76.642 (±33.66)	0.03	0.53 (±0.40)[c]
Epilobium angustifolium (C)	19.902 (±14.22)	23.677 (±17.15)	N.S.	0.14 (±0.88)
Linnaea borealis (C)	9.963 (±4.56)	29.524 (±12.11)	0.02	1.24 (±1.30)
Mertensia paniculata (D&C)	30.283 (±11.72)	17.622 (±17.62)	N.S.	-0.15 (±0.42)
Mitella nuda (C)	9.332 (±4.47)	12.706 (±5.09)	N.S.	0.08 (±0.31)
Pyrola spp. combined (C)	6.261 (±3.37)	8.868 (±4.17)	N.S.	0.12 (±0.99)
Rubus pubescens (D&C)	34.507 (±15.38)	41.123 (±17.76)	N.S.	0.17 (±0.52)
All common & dominant species	151.93 (±36.26)	221.93 (±40.77)	0.008	0.38 (±0.24)
All 42 species	237.747 (±13.93)	310.891 (±69.65)	0.032	0.30 (±0.29)

[a] These herbs were found in all of the pairs of sampling plots

[b] lnRR values representing competition intensity between shrub and herb species

[c] The value within brackets is the ±95% confidence limit

Table 4.2. Mean values (95% confidence interval) for incoming light measured at 50cm and 1m above the ground for control and clipped plots

Light (PPDF – μmol s^{-1} m^{2})	Control 50 cm	Control 1 m	Clipped 50 cm	Clipped 1 m	P-value
Diffuse Leaf-on [a]	28.14^{B} (1.59)	33.84^{A} (1.34)	32.99^{A} (1.63)	32.69^{A} (1.65)	<0.0001
Direct Leaf-on	19.94^{B} (2.94)	25.38^{A} (2.9)	26.93^{A} (2.88)	26.41^{A} (2.58)	0.0016
Total Leaf-on	24.3^{B} (1.92)	29.91^{A} (1.7)	30.16^{A} (1.75)	29.82^{A} (1.65)	<0.0001
Diffuse Leaf-off	42.51 (2.07)	43.65 (2.11)	43.31 (2.3)	43.04 (2.57)	N.S.
Direct Leaf-off	23.52 (4.32)	22.42 (3.55)	25.4 (3.74)	26.05 (4.27)	N.S.
Total Leaf-off	34.98 (2.29)	35.23 (1.92)	36.2 (2.38)	36.29 (2.51)	N.S.
Total Annual (Diffuse & Direct with Leaf-on & Leaf-off)	29.64^{B} (1.34)	32.57^{A} (1.24)	33.18^{A} (1.78)	33.05^{A} (1.74)	0.0031

[a] Values for a given variable that have different superscript letters were significantly different based on least squared means comparisons (at $\alpha < 0.05$)

Table 4.3. Results of the analysis of the log response ratio (lnRR) of individual target plants as a function of the biomass of co-occurring species by means of linear regressions

Target species (InRR) [a]	Co-occurring Species Biomass	R^2	Adjusted R^2	SS	B[b]	F value	P value
Linnaea borealis	*Mitella nuda*	0.52	0.46	6.62	-0.12	8.75	0.018
Linnaea borealis	*Pyrola* spp.	0.47	0.41	6.06	0.14	7.26	0.027
Pyrola spp.	*Mitella nuda*	0.69	0.65	9.29	-0.14	16.32	0.004

a. Only the significant regressions are shown

b. Slope of regression

Table 4.4. Results of the analysis of the effect of competition intensity (lnRR) for all species and for the seven most common taxa of the herbaceous layer on the Bray-Curtis distance of species composition between the paired control-clipped plots

Dependent Variable	Independent Variable	R^2	Adjusted R^2	SS	b [a]	F value	P value
Bray-Curtis	All herbs (lnRR value)	0.70	0.65	0.06	0.19	17.60	0.003
Bray-Curtis	Seven Dominant taxa (lnRR value)	0.71	0.67	0.06	0.24	19.66	0.002

[a] Slope of regression.

Table 4.5. Results of redundancy analysis showing the environmental variables that were significantly ($P<0.05$) associated with herb species composition

Variable [a]	Axis 1	Axis 2	Axis 3	Axis 4
Trace: 0.408				
Eigenvalues [b]	0.118	0.091	0.067	0.053
Total light Leaf-on at 1m	0.724	-0.455	0.145	-0.267
Treatment	-0.149	-0.605	-0.117	0.124
Soil temperature	0.412	-0.179	0.537	0.554
Total basal area	-0.196	0.087	0.275	0.511
Total annual light at 1 m	0.814	-0.229	-0.026	-0.210
Total light Leaf-on at 50cm	0.475	-0.125	0.154	-0.337
Mg^{2+}	0.337	0.153	-0.140	0.306

a. As determined by using stepwise forward selection of variables in a distance-based Redundancy Analysis. Presented are the inter-set correlations (Pearson) of significant variables, in the order of the forward selection. The trace value (sum of all the canonical eigenvalues) and the eigenvalues of the first four axes are also presented

b. Axis 1 and all combined axes are significant at $P = 0.002$

Chapter 5

Spatial patterns of understory plant communities in mature boreal mixedwood forests: the influence of environmental and spatial factors

5.1. Introduction

The spatial arrangement of plant species is a basic aspect that needs to be explored in ecological studies (Dale 1999). Plant spatial patterns mainly originate from the synchronous action of two mechanisms (Legendre and Legendre 1998; Legendre et al. 2002). First, at the community level, plants can be spatially autocorrelated as the result of dynamic processes caused by the species assemblage itself such as dispersal strategies and species interactions (Legendre and Legendre 1998). Second, at larger scales, plants can be spatially structured because they depend upon environmental factors that are spatially structured themselves. This environmental structure is reflected in species through habitat-species relations, that induces spatial dependence (Legendre and Legendre 1998; Dray et al. 2006). Traditionally, ecologists sought to remove the effects of space on plant community structure. However, there is a recent and increasing interest in measuring and understanding patterns of spatial variation, in relation to environmental factors, in plant community composition and diversity (Karst et al. 2005; Jones et al. 2008; Legendre et al. 2009; Gazol and Ibáñez 2010).

Incorporating spatial variation in plant community studies can be achieved by partitioning the amount of variation in plant composition and diversity that is explained by the environmental and spatial components (Bocard et al. 2004; Jones et al. 2008; Legendre et al. 2009). A detailed assessment of spatial variation requires the inclusion of all the scales perceived in a given dataset and this can be achieved through the use of principal coordinates of neighbour matrices analysis (PCNMs, Borcard and Legendre 2002; Borcard et al. 2004; Dray et al. 2006). PCNMs allow for the extraction of all the patterns of spatial structure found in a given sampling protocol and their use has been successfully applied in plant communities of temperate (Gazol and Ibáñez 2010) and tropical forests (Jones et al. 2008; Legendre et al. 2009) but not in boreal forests.

The boreal mixedwood forests consists of a mosaic of canopy patches of varying size and differing levels of dominance by conifers (mostly white spruce (*Picea glauca* (Moench) Voss)) and broadleaf trees (mostly trembling aspen (*Populus tremuloides* Michx.)). Understory plant communities are an essential component of boreal forest because they represent most of the boreal vegetation diversity and they perform crucial ecological roles for the functioning of these ecosystems (Hart and Chen 2006 (review paper)). For instance, boreal understory plants regulate stand structure by competing with tree seedlings, contribute to nutrient cycling and provide food and habitat for wildlife species (Hart and Chen 2006). Understory plant composition and diversity are importantly influenced by canopy tree composition and density as these modify the micro-habitat of the understory layer in terms of light and nutrient availability and the physical environment of the forest floor (Frelich et al. 2003; Qian et al. 2003; Macdonald and Fenniak, 2007; Chávez and Macdonald 2010). In this way canopy tree patches lead to a heterogeneous and patchy spatial distribution of understory plants (Kembel and Dale 2006) both at the landscape (Macdonald and Fenniak, 2007) and at the stand level (Chávez and Macdonald 2010). Although the influence of environment on understory communities has been widely studied (Frelich et al., 2003; Qian et al., 2003; Hart and Chen, 2006; Macdonald and Fenniak, 2007; Chávez and Macdonald 2010), their spatial structure has received much less attention in the literature (but see Kembel and Dale 2006). The aim of this study was to assess the relative influence of space and environmental variables, as well as their joint effects, on understory composition and diversity. For this, we identified the scales at which understory (herbs + shrubs) composition and diversity are structured using PCNMs. Then, though variation partitioning, we analyzed the relative importance of space and environment in explaining variation in composition of these communities.

5.2. Methods

5.2.1. Study Site and Field Procedures

The study was conducted at the Ecosystem Management Emulating Natural Disturbance (EMEND) research site (see http://www.emend.rr.ualberta.ca/index.asp), which is located in northwest Alberta, Canada (approximate site center: 56° 46' 13" N, 118° 22' 28" W) in the Clear Hills Upland Ecoregion within the Boreal plains Ecozone (Strong and Leggat 1992; Kishchuk 2004). Forests in the area are co-dominated by trembling aspen (*Populus tremuloides* Michx.), balsam poplar (*Populus basamifera* L.) and white spruce (*Picea glauca* (Moench) Voss) with lesser amounts of black spruce (*Picea mariana* (Mill.) B.S.P.), balsam fir (*Abies balsamea* (L.) Mill.), lodgepole pine (*Pinus contorta* Dougl.) and paper birch (*Betula papyerifera* Marsh.). Soils have developed on fine-textured glacial till or glaciolacustrine deposits and soil types include (generally) well drained Luvisols (Dark Grey Luvisol, Orthic Grey Luvisol) with limited occurrences of Brunisolic, Gleysolic and Solonetzic soils (Kishchuk 2004). Site elevation ranges from 677 to 880 m above sea level. The region has a boreal climate with cold winters (mean January temperature -16.6° C), warm summers (mean July temperature of 16° C) and has a mean annual precipitation of 402 mm, which falls mostly during the summer (Environment Canada 2008).

The study was performed in three stands classified as “mixed” at the polygon scale by forest inventories i.e., they had between 40-60% of canopy cover of conifer (mostly white spruce) and broadleaf trees (mostly trembling aspen). The three stands were approximately 100 years of age, of fire origin, and previously unmanaged. At each stand, we established one transect of 2x2 m contiguous plots subdivided into four 1x1 m quadrats. Two of these transects (transects 1 &2) were 150 m in length and one was 200 m long (transect 3). The transects were semi-randomly placed being at least 50 meters away from forest edges or cutlines.

We made visual estimates of percent cover (1-100%) for each understory vascular plant species in the four 1 x 1 m quadrats (to improve accuracy) and averaged their cover values to the plot level. Nomenclature followed Moss (1983). Transects 2 & 3 were assessed at two times during the season: in early June (early season) and early August (late season) in order to examine seasonal temporal variability in species composition.

The following environmental characteristics were measured at each sampling plot: *(A) Canopy composition*: All canopy trees were counted and their diameters at breast height (DBH, 1.3 m) were measured in order to calculate basal area (BA) for conifer (BAC) and broadleaf (BAD) trees separately and for the two together (BAT). *(B) Ground Cover:* We made visual estimates of the percentage of ground cover of (i) downed fine woody debris (pieces <8 cm diameter), (ii) downed coarse woody debris (CWD) (pieces >8 cm diameter), (iii) mosses and, (iv) litter. *(C) Edaphic factors:* At the centre of each plot, we measured soil moisture and temperature once over the growing season by means of Time Domain Reflectometry and a thermocouple respectively; the measures were taken at least 24 hours after a major precipitation event. We also measured the depth of the litter (L) and organic layers (FH) and collected samples of organic (FH) and mineral layers (~20 cm depth). In the lab, we measured pH in a paste of a 1:2 soil:water mixture for mineral soil and 1:4 soil:water for organic using a Fisher AR20 pH meter with glass. Lastly, at the center of each plot of the 200 m transect, we assessed nutrient availability by means of ion exchange resin bags. For this we buried nylon bags with 45 ml of Amberlite IR-150 anion-cation exchange resin (J.T. Baker) within the mineral soil layer. Bags were retrieved after a period of two months and extracted as described by Thiffault et al. (2000). We then analyzed them using a Technicon Autoanalyzer to obtain the concentrations of available PO_4^{3-}, NO_3^- and NH_4^+ (in the Natural Resources Analytical Lab, Dept. of Renewable Resources, University of Alberta). *(D) Incoming Light:* At the centre of each plot we took two hemispherical canopy photographs during both the leaf-on (August) and leaf-off (November) periods. Photographs were taken either: approximately 1 h after dawn, 1 h before dusk, or on overcast days in order to ensure uniform sky condition and to avoid direct insolation (as per Comeau et al. 1998; Gendron et al. 1998). Images were analyzed using SLIM (Spot Light Intercept Model) v. 2.2e (Comeau et al.1998; Comeau et al. 2003) software, which takes into account seasonal sun angle and data on cloud cover and opacity for the specific geographic location to calculate the percentage of direct, diffuse and total (average of diffuse and direct) solar radiation.

5.2.2. Data Analysis

Principal Coordinates of Neighbor Matrices (PCNMs)

Principal coordinates of neighbor matrices (PCNM, Borcard and Legendre 2002, Borcard et al. 2004) is an eigen-based spatial filtering method (Griffith and Peres-Neto 2006) that decomposes sites' spatial coordinates into spatial variables. In this way, PCNMs are a set of variables that represent spatial structures at all the possible scales comprised by the sampling design creating a spatial 'spectral decomposition' among all the sampling sites (Bocard et al. 2004). PCNM are uncorrelated variables and can, therefore, be used as predictors in multiple regressions or canonical ordinations to quantify the influence of spatial patterns on the response variable without multicollinearity concerns. The PCNM method yields the best results when using a uniform sampling design with equidistant x and y coordinates, such us our sampling protocol (Bocard et al. 2004).

Generation of PCNM base functions

The PCNM base functions were generated for the 100-plot (200 m) transect and for the two 75-plot (150 m) transects separately using the package spacemakeR in R (Dray 2006, R version 0.0-4/r78) in the R statistical language (R Development Core Team 2009). First, we constructed a matrix of pair-wise Euclidean distances for all the possible distances between the sampling plots of each transect. Second, we defined a threshold value to construct a truncated distance matrix. The truncation distance used to construct spatial eigenfunctions was 2 m, the distance between the center of each sampling plot. In this way, we retained only the closest plots as neighbors (Bocard and Legendre 2002). Third, we computed a principal coordinate (PCoA) analysis of the truncated distance matrix; this step allows the spatial information to be represented in a form that is compatible with multiple regressions or canonical ordinations. The number of significant generated PCNM variables is the rounded upper integer corresponding to two-thirds (2n/3) of the number of plots (Bocard and Legendre 2002). Thus, we obtained 67 PCNM variables for the 100-plot transect (44 positive) and 50 for the two 75-plot transect (32 positive). Dray et al. (2006) demonstrated that the PCNM approach is closely related to Moran's index of spatial autocorrelation and that PCNM based functions are particular cases of Moran's eigenvector maps. Thus, the fourth step was to test the Moran's I index for each PCNM eigenfunction with permutation procedures and keep only those that represent significant ($P \leq 0.05$) spatial autocorrelation – either positive or negative- for subsequent analyses (Dray et al. 2006).

Variation Partitioning

The dependent variables for the variation partitioning were species composition (percent cover by species) and richness. We assessed herbs and shrubs separately. Composition data was detrended prior to the analyses. The composition data were transformed using a Hellinger distance (Legendre and Gallagher 2001).

To identify the environmental and spatial (PCNMs) variables that were significantly ($P \leq 0.05$ after 999 permutations) contributing to the variation of each dependent variable we first used forward selection procedures following the method described by Blanchet et al. (2008). We ran separate forward selections for the environmental, positive and, negative spatial (PCNMs) variables. The negative spatial variables were not related to any of the dependent variables thus they were excluded from subsequent analysis. Only the significant environmental and positive spatial variables were used in subsequent analyses. The forward selections were performed using the function “forward.sel” in the Packfor package (Dray 2007) of the R statistical language (R Development Core Team 2009).

We used variation partitioning to estimate the fraction of variation explained by the environmental and spatial variables and their combined effects. The partition of herb and shrub composition (multivariate response variable) was based on a canonical redundancy analysis (RDA) while the partition of species richness (univariate response variables) was based on linear regressions. Because PCNMs are sinusoidals of decreasing periods, these can be grouped into sub-groups of different scales based on the similarity among their periods (Bocard and Legendre 2002). Based on the PCNM sinusoid patterns, we grouped the significant PCNM eigenfunctions into the following spatial subgroups: broad (sinusoid periods of ~41-101m for the 200m transect; ~30-76m for 150m transects); medium (sinusoid periods of ~29-40m for 200m transect; ~16-29m for 150m); and fine (sinusoid periods of ~3-39m for 200m transect; ~3-15m for 150m transects). We first performed a variation partitioning with the significant environment and spatial variables and another variation partitioning with each of the PCNMs subgroups (broad, medium and fine PCNMs) and the significant environmental factors. Results of variation partitioning were based on the adjusted coefficient of multiple determination (R_a^2, Ezekiel 1930) following

Peres-Neto et al. (2006). This adjusted form is corrected for the explanation that would be provided by the same number of explanatory variables measured over the same number of points. These analyses were performed with the “varpart” function in the vegan package (Oksanen et al. 2007). Finally, we tested the significance of each fraction of the variation partitioning using the functions “anova.cca” and “rda” in the vegan library of R (Oksanen et al. 2007). We did a separate variation partitioning analysis for each transect and for the early and late seasons (transects 2 & 3).

5.3. Results

5.3.1. Herb composition & richness

The forward selection procedures retained 28-34 PCNMs and 5-7 environmental variables ($P \leq 0.05$) as being significant in explaining variation in herb community composition. Total explained variation was explained by three components: [a] environmental factors that were not spatially structured; [b] environmental variables that were spatially structured and; [c] spatial variables. The variation (R_a^2) in herb composition explained by these variables was 47-66% (Table 5.1.). The significant environmental variables that were not explained by spatial variation represented only about 2% of the total variation (Table 5.1., fraction [a]). Of the overall explained variation, 45-65% was due to spatial structure as it was explained by the PCNM eigenfunctions (Table 5.1., fractions [b] + [c]); 4.8-21% of this was due to environmental variables that were spatially structured (Table 5.1., fraction [b]). The most important environmental variables in explaining herb composition were diffuse light during the leaf-off period and soil temperature (Table 5.2.).

Regarding herb richness, 4-11 PCNM and 1-4 environmental variables were retained by the forward selections ($P \leq 0.05$) explaining 36-66% of overall variation. The non-spatially structured environmental variables explained 2-8% of the variation (Table 5.1.; fraction [a]). In contrast, 30-65% of the overall variation was spatially structured; 0-21% of this amount was due to the join influence of the significant environmental variables and spatial structuring [Table 5.1.; fractions [b] +[c] & [b]). Of the significant environmental variables, soil temperature and diffuse light during the leaf-on period explained most of the variation in herb richness (Table 5.3.).

The separate partition examining the PCNM sub-groups (representing different spatial scales) indicated that most of the variation in herb composition and richness was explained by spatial structuring at the broad/medium scales (results not shown).

5.3.2 Shrubs composition & richness

Variation in shrub composition was explained by 13-17 PCNMs and 4-6 environmental variables (as per the forward selection; $P \leq 0.05$) which represented 40-50% of total variation (Table 5.1.). Only 0.07-14% was explained by the significant environmental variables that were not spatially structured (Table 5.1.; [a]). However, 25-47% of the overall variation was explained by the PCNM eigenfunctions; 9-16% of this variation was also explained by the significant environmental variables (Table 5.1.; [b] +[c] & [b]). Soil temperature and diffuse light during both the leaf-on and leaf-off periods were the environmental variables that contributed the most to variation in shrub composition (Table 5.4.).

There were 3-16 PCNMs and 1-3 environmental variables retained by forward selection ($P \leq 0.05$) explaining 19-63% of the total variation in shrub richness. The environmental variables that were not spatially structured explained <3% of the variation. Of the total explained variation, 16-63% was spatially structured of which, 4-28% was also explained by the significant environmental variables (Table 5.1.; [b] +[c] & [b]). Litter cover and diffuse light during the leaf-on and leaf-off periods explained most of the variation in shrub composition

(Table 5.1.). Most of the variation in shrub composition and richness was explained by PCNMs representing the broad/medium spatial scales (results not shown).

5.4. Discussion

The identification of the spatial structures of species composition and diversity is a fundamental issue in ecology and an indispensable component for ecosystem management and conservation plans (Bocard et al. 2004; Pearman and Weber 2007). We assessed the influence of spatial structures relative to environmental variation, as well as their joint effects, on understory composition and diversity within boreal mixedwood stands. Our results indicate that spatial structuring explained substantially more of the variation in the dependent variables than did environmental variation that was not spatially structured. There was a substantial fraction of the variation in the dependent variables that was explained by the joint influence of environment and space (i.e., explained by environmental variables that were spatially structured). However, this component was most often still less than the variation explained by space alone. These results suggest that biotic processes traditionally related to spatial autocorrelation could explain a large proportion of the variation of understory composition and diversity at the fine scale considered in this study. On the other hand, environmental factors are also important in shaping these understory communities through induced spatial dependence. Overall, our study highlights the importance of considering environmental and spatial variables, as well as their joint effect, in the assessment of plant communities (Legendre et al. 2009).

With the considered spatial and environmental variables, we were able to explain a substantial proportion of the variation in understory composition and richness. In both cases, the spatial component contributed the most to the explained understory variation. However, its contribution varied among transects and growing seasons (early vs. late). These results are consistent with previous findings that within-stand distribution of boreal understory vegetation is very heterogeneous and patchy and variation in spatial patterns among plots and transect is common (Kembel and Dale 2006). The influence of space was more evident on herbs than on shrubs suggesting that other variables than those considered here structured the spatial distribution of this functional group. For the most part, the magnitudes of spatial variation of herb richness and composition were similar; most of their dominant spatial structure was broad-scaled suggesting that herbs are patterned in patches of ~40-100 m. We found more, and stronger, relationships with spatial variables when community composition was the dependent variable than for species richness. This is probably because composition provides a less synthetic description of community structure than just the number of species (Legendre et al. 2009). Indeed, as reported by Legendre et al. (2009), most of the richness-related PCNMs were largely a subset of the composition-related PCNMs.

The influence of space on plant communities has frequently been attributed to dispersal effects (Cottenie 2005; Karst et al. 2005; Jones et al. 2008; Legendre et al. 2009). In boreal forests, seed dispersal distances are very short and opportunities for establishment of new seedlings are limited thus, we attribute the large effect of the purely spatial fraction on understory communities to propagule dispersion. Almost all boreal herbs are clonal perennials that rely heavily on vegetative reproduction to maintain themselves in old stands (Tappeiner and Alaback 1989). Boreal herbs are well adapted to heterogeneous environments having the potential to search for patches of high resource availability through a “spatial division of labor” among potentially independent ramets (Stuefer et al. 1996). This ramet co-operation allows them to increase their biomass, through reciprocal translocation of water and nutrients, and to gain access to resources over considerable distances (Stuefer et al. 1996; Niva et al. 2006). For example, in mature boreal stands, the connected ramets of common species such as *Cornus canadensis* and *Rubus spp*. have been reported to reach a length of 436 and 503 cm respectively (Tappeiner and Alaback 1988). In this context, changes in understory community structure can be importantly driven by the spatial arrangement of existing understory species patches (Fortin et al. 1999; Frelich et al. 2003; Kembel and Dale 2006). Clonal spread can also influence other biotic processes such as species interactions that shape understory composition and diversity patterns (Oborny et al. 2000) in boreal mixedwood forests. Because clonal propagation is an important driver of the spatial distribution of boreal plants (Stuefer et al. 1996; Niva et al. 2006), the actual measurement of the contribution of ramet distribution at various scales would enhance our understanding of the spatial structure of understory communities in mature boreal mixedwood forests.

The purely environmental fraction of explained variation was quite modest. Diffuse light and soil temperature explained most of the environmental variation; the influence of these factors on understory community structure was recognized in an earlier study of understory composition at the fine scale (Chávez and Macdonald 2010). The influence of the environmental component, however, had an important joint effect with the spatial variable component. This finding suggests that the influence of environment on understory communities occurs mainly through induced spatial dependence (Legendre and Legendre 1998) although this process is more commonly considered to function at larger scales. Following hierarchy theory (Allen and Starr 1982) induced spatial dependence on understory communities may originate from the following mechanism. At the landscape level, boreal mixedwood forests are primarily structured by large-scale geomorphologic processes and disturbance events (mainly fire); the interaction of these processes gives rise to mosaic forest stands of varying canopy dominance (Andison and Kimmins, 1999; Chen and Popadiouk, 2002). Within this mosaic, there are mixedwood stands that are comprised of smaller contagious canopy patches with different levels of dominance by conifer and broadleaf trees (Haeussler et al., 2004; Macdonald and Fenniak, 2007). These tree patches dramatically modify the micro-environmental characteristics underneath their canopies inducing the formation of similar patchy spatial patterns in understory plants (Kembel and Dale 2006; Chávez and Macdonald 2010).

Measuring all the environmental variables that affect understory communities in these mixedwood stands is not possible but with the PCNM approach, it was possible to include all the spatial patterns encompassed in our transects. Thus, it is possible that the spatial component captured part of the unmeasured environmental variables (Cottenie 2005). The unexplained variation

(~40%) in understory plant community composition could be due to a variety of other factors, including topography, climate, landscape-scale and fine-scale disturbance, species interactions, clonal propagation, as well as stochastic process and ecological drift (Legendre et al. 2009). All these factors have been related to broader scales but their effect is still important at fine scales (Cottenie 2005; Karst et al. 2005) such as the considered in here.

In general, our results suggest that the effects of dispersal, clonal spread and environment converge at the fine scale to create a spatially patchy structure in understory communities in boreal mixedwood forests. This illustrates the important role that space plays as an explanatory variable and the necessity to include spatial variables when studying boreal understory plant communities. From theory, we know that the mixture of tree patches found in these forests support the environmental heterogeneity found in the understory layer (Macdonald and Fenniak 2007; Chávez and Macdonald 2010) and though our results, we detected that this maintains the observed spatial structures in the understory. It follows then, that modifications in the spatial continuity of these forests could disrupt the spatial and environmental structures that shape understory composition and diversity patterns.

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Tables

Table 5.1. Variation partitioning results for species composition and richness showing the variation explained by environment, the joint influence of environment and space, space and the unexplained variation (Residuals)

Dependent Variable[a]	**Number of PCNMs ($P \leq 0.05$)**	**Environment not spatially structured [a]**	**Environment spatially structured [b]**	**Space [c]**	**Residuals [d]**
Herb Composition					
Transect 1	28	0.014	0.195	0.450	0.339
Transect 2 Early Season	31	0.000	0.175	0.432	0.394
Transect 2 Late Season	31	0.006	0.210	0.395	0.387
Transect 3 Early Season	32	0.000	0.078	0.425	0.496
Transect 3 Late Season	34	0.020	0.048	0.406	0.524
Herb Richness					
Transect 1	6	0.079	0.000	0.393	0.547
Transect 2 Early Season	4	0.058	0.179	0.128	0.633
Transect 2 Late Season	11	0.015	0.211	0.439	0.334
Transect 3 Early Season	10	0.023	0.170	0.306	0.500
Transect 3 Late Season	10	0.049	0.154	0.305	0.490
Shrub Composition					
Transect 1	16	0.144	0.154	0.101	0.599
Transect 2 Early Season	13	0.041	0.138	0.262	0.557
Transect 2 Late Season	13	0.065	0.155	0.240	0.538
Transect 3 Early Season	16	0.007	0.098	0.326	0.567
Transect 3 Late Season	17	0.020	0.107	0.369	0.503
Shrub Richness					
Transect 1	3	0.029	0.042	0.119	0.808
Transect 2 Early Season	10	0.008	0.281	0.320	0.389
Transect 2 Late Season	8	0.000	0.205	0.338	0.469
Transect 3 Early Season	11	0.009	0.273	0.237	0.479
Transect 3 Late Season	16	0.000	0.240	0.395	0.367

a. Given is the number of PCNMs included in the analysis; i.e., those that were found to be significantly related to the given dependent variable (by forward selection). Also given are the values of adjusted R_a^2 (adjusted for the number of variables included) for each of the variation fractions. See Tables 5.2-5 for the environmental variables that were included in a given analysis.

Table 5.2. Environmental variables significantly related to herb composition (selected by forward selection P≤0.05)

Herb Composition[a]	**R^2**	**R^2 cumulative**	**Adjusted R^2 cumulative**
Transect 1:			
Light (Diffuse, leaf-off period)	0.130	0.130	0.118
Litter cover	0.035	0.166	0.143
Fine woody debris cover	0.031	0.197	0.163
Soil pH (organic layer)	0.026	0.223	0.179
Soil litter depth	0.027	0.250	0.197
Exposed mineral soil cover	0.022	0.273	0.209
Transect 2 Early Season:			
Soil temperature	0.105	0.105	0.093
Litter cover	0.054	0.160	0.136
Coarse woody debris cover	0.038	0.199	0.165
Light (Diffuse, leaf-off period)	0.023	0.222	0.178
Total basal area	0.022	0.244	0.189
Light (Direct, leaf-off period)	0.022	0.266	0.202
Soil litter depth	0.019	0.286	0.211
Transect 2 Late Season:			
Soil temperature	0.106	0.106	0.093
Litter cover	0.059	0.166	0.142
Coarse woody debris cover	0.040	0.206	0.172
Light (Total, leaf-on period)	0.031	0.237	0.193
Soil organic layer depth	0.024	0.261	0.208
Soil litter depth	0.018	0.280	0.217
Transect 3 Early Season:			
Light (Diffuse, leaf-off period)	0.042	0.042	0.032
Litter cover	0.023	0.066	0.046
Light (Total, leaf-off period)	0.021	0.088	0.059
Light (Total, leaf-on period)	0.019	0.107	0.069
Fine woody debris cover	0.016	0.124	0.077
Transect 3 Late Season:			
Light (Diffuse, leaf-off period)	0.037	0.037	0.027
Broadleaf basal area	0.021	0.059	0.039
Soil organic layer depth	0.019	0.078	0.049
Soil litter depth	0.021	0.100	0.062
Litter cover	0.015	0.115	0.068

a. Given are the individual R^2 values for each environmental variable and the cumulative non-adjusted R^2 and adjusted R_a^2 values for all the variables

Table 5.3. Environmental variables significantly related to herb richness (selected by forward selection P≤0.05)

Herb Richness[a]	**R^2**	**R^2 cumulative**	**Adjusted R^2 cumulative**
Transect 1:			
Light (Diffuse, leaf-on period)	0.072	0.072	0.060
Transect 2 Early Season:			
N.S			
Transect 2 Late Season:			
Soil temperature	0.159	0.159	0.148
Soil litter depth	0.089	0.248	0.227
Transect 3 Early Season:			
Litter depth	0.112	0.112	0.103
Light (Diffuse, leaf-on period)	0.038	0.149	0.131
Fine woody debris cover	0.037	0.186	0.160
Soil temperature	0.041	0.227	0.194
Transect 3 Late Season:			
Light (Diffuse, leaf-on period)	0.096	0.096	0.087
Soil PO_4	0.059	0.155	0.137
Light (Direct, leaf-off period)	0.046	0.201	0.176
Soil litter depth	0.036	0.237	0.204

a. Given are the individual R^2 values for each environmental variable and the cumulative non-adjusted R^2 and adjusted R_a^2 values for all the variables

Table 5.4. Environmental variables significantly related to shrub composition (selected by forward selection $P \leq 0.05$)

Shrub Composition[a]	$\mathbf{R^2}$	$\mathbf{R^2}$ **cumulative**	**Adjusted** $\mathbf{R^2}$ **cumulative**
Transect 1:			
Light (Direct, leaf-on period)	0.082	0.082	0.069
Light (Diffuse, leaf-off period)	0.179	0.260	0.240
Soil pH (organic layer)	0.053	0.312	0.284
Exposed mineral soil cover	0.025	0.337	0.299
Transect 2 Early Season:			
Conifer basal area	0.031	0.209	0.164
Soil temperature	0.057	0.142	0.119
Soil organic layer depth	0.036	0.178	0.144
Fine woody debris cover	0.027	0.236	0.18
Litter cover	0.086	0.086	0.074
Transect 2 Late Season:			
Soil temperature	0.079	0.079	0.066
Litter cover	0.077	0.156	0.133
Fine woody debris cover	0.034	0.19	0.155
Soil organic layer depth	0.034	0.223	0.179
Conifer basal area	0.034	0.256	0.202
Coarse woody debris cover	0.029	0.284	0.221
Transect 3 Early Season:			
Light (Diffuse, leaf-on period)	0.049	0.049	0.039
Light (Direct, leaf-on period)	0.046	0.095	0.076
Light (Diffuse, leaf-off period)	0.025	0.119	0.091
Light (Direct, leaf-off period)	0.024	0.142	0.106
Transect 3 Late Season:			
Light (Diffuse, leaf-off period)	0.048	0.048	0.038
Light (Direct, leaf-on period)	0.056	0.103	0.084
Soil organic layer depth	0.036	0.138	0.111
Soil litter depth	0.025	0.163	0.128

a. Given are the individual R^2 values for each environmental variable and the cumulative non-adjusted R^2 and adjusted R_a^2 values for all the variables

Table 5.5. Environmental variables significantly related to shrub richness (selected by forward selection P≤0.05)

Shrub richness[a]	**R^2**	**R^2 cumulative**	**Adjusted R^2 cumulative**
Transect 1:			
Light (Diffuse, leaf-off period)	0.084	0.071	0.071
Transect 2 Early Season:			
Litter cover	0.134	0.134	0.123
Soil temperature	0.176	0.310	0.290
Transect 2 Late Season:			
Litter cover	0.112	0.112	0.100
Soil temperature	0.103	0.214	0.192
Transect 3 Early Season:			
Light (Diffuse, leaf-on period)	0.196	0.196	0.187
Light (Direct, leaf-off period)	0.073	0.268	0.253
Soil pH (organic layer)	0.037	0.305	0.283
Transect 3 Late Season:			
Light (Diffuse, leaf-on period)	0.167	0.167	0.159
Light (Total, leaf-off period)	0.086	0.253	0.238

a. Given are the individual R^2 values for each environmental variable and the cumulative non-adjusted R^2 and adjusted R_a^2 values for all the variables

Chapter 6

Conclusion

Understory plant communities are an essential component of boreal forests and there is growing interest among researchers and forest managers to understand their natural structure and to incorporate this knowledge into sustainable forest management practices. This thesis contributes to the understanding of the patterns of diversity, abundance and composition of vascular understory plants within unmanaged, mature mixedwood boreal forest stands and provides key information for their management and conservation.

The first study (chapter 2; a version published as Chávez and Macdonald 2010) addressed composition of understory vascular plant communities in relation to the mosaic of canopy patch types, and their associated structure and environment, within unmanaged and mature boreal mixedwood forests. The fine-scale relationships between canopy patches and understory communities assessed in this study had not been previously documented. The results suggest that mixedwood stands, composed of various canopy patch types, resemble a microcosm of the larger boreal mixedwood landscape in terms of the patterns of diversity and composition of understory vascular plant communities. Differences in understory composition among patch types were driven mostly by changes in the relative abundance of species. This implies that natural or anthropogenic disturbances that affect canopy composition may result largely in changes in species relative abundance patterns in understory plant communities. Composition variation among patch types mirrored patterns that had previously been observed at the landscape scale among different mixedwood forest stands. That is, fine scale differences between patch types were similar to large scale differences in stand types. The latter indicates that the mosaic of small canopy patches within mixed forest stands leads to different micro-habitat conditions for understory species, allowing for communities that include both early and late successional species, thus contributing to greater understory diversity.

Considering understory diversity within a hierarchical framework is useful to identify the observation levels at which maximum levels of plant richness and evenness occur across mixedwood forest stands. Chapter 3 of this thesis presents the first hierarchical partitioning of understory diversity carried out in boreal forests. The additive partitioning allowed for the characterization of the heterogeneity of boreal mixedwood forests at different levels of observation. The diversity partition indicated that maximum levels of understory richness were attributable to species turnover among patches within canopy patch type while species evenness was maximized at the patch level. The assessment of rank abundance patterns suggested that the canopy patch types differed in terms of the ecological mechanisms influencing diversity patterns. Overall, this study indicates that the mosaic of canopy patch types within mixedwood forests plays a crucial role in maintaining the hierarchical levels at which understory richness and evenness are maximized. The results of chapters 2 & 3 could be applied to the development of regeneration standards that would allow for development of more natural mixtures following the harvesting of mixedwood forests. Further, in planning for patch retention partial harvesting systems, large retention patches that include small patches (~4 m-radius) of both conifer and broadleaf trees could help to preserve natural patterns of understory diversity and composition.

In addition to the influence of canopy composition on understory communities, interactions among plant species play an important role in regulating composition and diversity of understory communities. Chapter 4 (a version accepted for publication in Botany) focused on understory species interactions among plant growth forms in the understory of mature boreal mixedwood forests, by investigating the effect of shrub removal on biomass, composition and diversity of herbs. There were significant effects of shrub removal on herb biomass and community composition, but not on the number of herb species. Changes in species composition were mainly explained by increases in biomass of dominant herbs in the removal plots, most of which was explained by the rapid growth of *Linnaea borealis* and *Cornus canadensis.* It was inferred that clonal growth played an important role in mediating increases in abundance of, as well as species interactions among, boreal herbs after shrub removal. These results demonstrated that while canopy tree species have an important influence on understory plant communities, interactions among understory plant species can also play an important role in structuring boreal understory communities. Thus, changes in the natural dynamics of interactions between shrub and herb species may indirectly modify the natural structure of boreal understory communities. In addition, the fact that we saw substantial changes in species composition only two years after shrub removal indicates that understory herbs can have the capacity to quickly respond to changes in their environment following disturbance. These findings are important because they enable us to begin to understand the processes influencing understory vegetation, and assist us to better understand how to manage understory biodiversity in managed forests.

The fifth and final data chapter explored the influence of spatial structures relative to environmental variation, as well as their joint effects, on understory composition and diversity within boreal mixedwood stands. This study illustrated the important role that space plays as an explanatory variable and the necessity to include it when studying boreal understory plant communities. A substantial fraction of the variation in understory diversity and composition was explained by the joint influence of space and environmental variables that were spatially structured. It was inferred that certain biotic process were important in explaining the spatial structure of understory communities. In this way, the environmental variation caused by small canopy patches and biotic processes, such as species interactions and clonal distributions, converged at the fine scale to create a spatially patchy structure in understory communities in boreal mixedwood forests. It follows then, that modifications in the spatial continuity of these forests could disrupt the spatial and environmental structures that shape understory composition and diversity patterns.

Overall, the findings of this thesis deepen the understanding of the natural patterns of understory diversity and composition and their driving factors. This knowledge can be used as a point of reference to assess the impacts of forest management practices on understory community structure found within mature and natural boreal mixedwood forests. Finally, the measurement of plant ramet distribution would enhance our understanding of the influence of micro-habitat heterogeneity, species interactions and the spatial patterns of understory communities in mature boreal mixedwood forests. Clonal propagation is key structuring factors of boreal understory communities (Stuefer et al. 1996; Niva et al. 2006) and should be incorporated in further research.

References

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Appendix 1

List of the 78 vascular plants (and sample codes) found in the sample plots of Chapters 2 & 3. Nomenclature follows Moss (1983).

Species	**Species code**
Abies balsamea (L.) Mill.	Abba
Achillea millefolium L.	Acmi
Actaea rubra (Ait.) Willd.	Acru
Alnus crispa (Ait.) Pursh	Alcr
Alnus rugosa Nutt.	Alru
Amelanchier alnifolia Nutt.	Amal
Anemone canadensis L.	Anca
Aralia nudicaulis L.	Arnu
Arctostaphylos uva-ursi (L.) Spreng.	Aruv
Aster ciliolatus Lindl.	Asci
Aster conspicuus Lindl.	Asco
Betula papyrifera Marsh.	Bepa
Calamagrostis canadensis (Michx.) Beauv.	Caca
Carex spp. 1	Care
Carex spp. 2	Carr
Cornus canadensis L.	Coca
Cornus stolonifera Michx.	Cost
Delphinium glaucum S. Wats.	Detr
Disporum trachycarpum (S. Wats.) B. & H.	Ditr
Elymus innovatus Beal	Elin
Epilobium angustifolium L.	Epan
Epilobium glandulosum Raf.	Epgl
Equisetum pratense Ehrh.	Eqpr
*Equisetum sylvaticum*L.	Eqsy
Fragaria vesca L.	Frve
Fragaria virginiana Duchesne	Frvi
Galium boreale L.	Gabo
Galium triflorum Michx.	Gatr
Geocaulon lividum (Richards.) Fern.	Geli
Goodyera repens (L.) R.Br.	Gore
Habenaria obtusata (Pursh) Richards.	Haob
Habenaria orbiculata (Pursh) Torr.	Haor
Lathyrus ochroleucus Hook.	Laoc
Lathyrus venosus Muhl.	Lave
Ledum groenlandicum Oeder	Legr
Lilium philadelphicum L.	Liph
Linnaea borealis L.	Libo
Lonicera dioica L.	Lodi

Lonicera involucrata (Richards.) Banks	Loin
Lycopodium complanatum L.	Lyco
Maianthemum canadense Desf.	Maca
Mertensia paniculata (Ait.) G. Don.	Mepa
Mitella nuda L.	Minu
Moneses uniflora (L.) A.Gray	Moun
Petasites palmatus (Ait.) A. Gray.	Pepa
Picea glauca (Moench) Voss	Pigl
Poa pratensis L.	Popr
Populus balsamifera L.	Poba
Populus tremuloides Michx.	Potr
Prunus pensylvanica L.f.	Prpe
Prunus virginiana L.	Prvi
Pyrola asarifolia Michx.	Pyas
Pyrola secunda (L.) House	Pyse
Pyrola virens Sw.	Pyvi
Ranunculus lapponicus L.	Rala
Ribes hudsonianum Richards.	Rihu
Ribes lacustre (Pers.) Poir.	Rila
Ribes oxyacanthoides L.	Riox
Ribes triste Pall.	Ritr
Rosa acicularis Lindl.	Roac
Rosa woodsii Lindl.	Rowo
Rubus idaeus L.	Ruid
Rubus pubescens Raf.	Rupu
Salix lutea Nutt.	Salu
Salix spp.	Sali
Shepherdia canadensis (L.) Nutt.	Shca
Smilacina stellata (L.) Desf.	Smst
Solidago canadensis L.	Soca
Symphoricarpos albus (L.) Blake	Syal
Symphoricarpos occidentalis Hook.	Syoc
Taraxacum officinale Weber	Taof
Trientalis borealis Raf.	Trbo
Vaccinium myrtilloides Michx.	Vamy
Vaccinium vitis-idaea L.	Vavi
Viburnum edule (Michx.) Raf.	Vied
Vicia americana Muhl.	Viam
Viola canadensis L.	Vica
Viola renifolia A. Gray	Vire

Appendix 2

List of vascular plants found in the sample plots of Chapter 3. Nomenclature follows Moss (1983).

Tree species

Abies balsamea (L.) Mill.
Betula papyrifera Marsh.
Picea glauca (Moench) Voss
Populus balsamifera
Populus tremuloides

Shrub species

Alnus crispa (Ait.) Pursh
Amelanchier alnifolia Nutt.
Cornus stolonifera Michx.
Ledum groenlandicum Oeder
Lonicera dioica L.
Ribes lacustre (Pers.) Poir.
Ribes oxyacanthoides L.
Rosa acicularis Lindl.
Rubus idaeus L.
Salix spp.
Shepherdia canadensis (L.) Nutt.
Vaccinium caespitosum
Vaccinium myrtilloides Michx.
Vaccinium vitis-idaea L.
Viburnum edule (Michx.) Raf.

Herb species

Graminoids

Calamagrostis canadensis (Michx.) Beauv.
Elymus innovatus Beal

Forbs

Achillea millefolium L.
Actaea rubra (Ait.) Willd.
Anemone canadensis L.
Arnica cordifolia Hook.
Aralia nudicaulis L.
Astragalus americanus (Hook.) M.E. Jones
Aster ciliolatus Lindl.
Aster conspicuus Lindl.
Calypso bulbosa (L.) Oakes
Circaea alpina L.
Cornus canadensis L.
Delphinium glaucum S. Wats.
Epilobium angustifolium L.
Equisetum arvense L.
Equisetum pratense Ehrh.
Equisetum scirpoides Michx.
Geocaulon lividum (Richards.) Fern.
Goodyera repens (L.) R.Br.
Habenaria obtusata (Pursh) Richards.
Habenaria orbiculata (Pursh) Torr.
Lathyrus ochroleucus Hook.
Linnaea borealis L.

Lycopodium annotinum L.
Lycopodium complanatum L.
Maianthemum canadense Desf.
Mertensia paniculata (Ait.) G. Don.
Mitella nuda L.
Moneses uniflora (L.) A.Gray
Osmorhiza depauperata Philippi
Petasites palmatus (Ait.) A. Gray.
Pyrola asarifolia Michx.
Pyrola secunda (L.) House

*Equisetum sylvaticum*L.
Fragaria virginiana Duchesne
Galium boreale L.
Galium triflorum Michx.
Pyrola virens Sw.
Rubus pubescens Raf.
Viola canadensis L.
Viola renifolia A. Gray