PATTERNS AND MECHANISMS OF UNDERSTOREY VEGETATION ASSOCIATED WITH STAND DEVELOPMENT IN BOREAL FORESTS

By

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ABSTRACT

The understorey vegetation comprises the greatest plant diversity and contributes substantially to ecosystem functioning and services in boreal forests. Although many studies have examined patterns of understorey species diversity in relation to stand development following stand replacing disturbances and overstorey characteristics, the mechanisms driving these patterns remain largely speculative. Furthermore, despite their ecological importance, the dynamics of understorey biomass, production and turnover rates following stand-replacing disturbance and overstorey succession remain poorly understood. The objective of this dissertation is to improve the understanding of patterns and mechanisms of understorey vegetation, and their ecological functions with stand development in central boreal forests of Canada. To achieve this goal, I first studied the effects of coarse woody debris (CWD) decay class and substrate species on the patterns of epixylic vegetation abundance, diversity and composition in the boreal forest. Second, I examined the mechanisms underlying patterns of understorey vegetation by linking resource availability and heterogeneity to understorey species diversity. Finally, I investigated the dynamics of understorey biomass, production and turnover rates in the central boreal forests of Canada.

In chapter 2 and 3, the pattern of epixylic vegetation abundance, diversity and composition on coarse woody debris decay class and substrate species were examined in stands of varying ages and overstorey compositions types. The percent cover, species richness and evenness of epixylic vegetation differed significantly with both CWD decay class and substrate species. Multivariate analysis showed that understorey species composition differed significantly with decay classes and substrate species and their interactions. My findings suggest that conservation of epixylic diversity would require forest managers to maintain a diverse range of CWD decay classes and substrate species. Since stand development and overstorey compositions influence CWD decay classes and substrate species as well as colonization time and environmental conditions, our results further suggested that managed boreal landscapes should consist of a mosaic of different successional stages and a broad suite of overstorey types to support diverse understorey plant communities.

In chapter 4, the mechanisms for understorey species diversity and cover were studied using structural equation modeling (SEM) to link time since fire (stand age), light availability and heterogeneity, substrate heterogeneity and soil nitrogen to understorey vegetation cover and species diversity in boreal mixedwood stands. The best model for total understorey cover showed a positive direct effect of stand age, and an indirect effect via mean light level and shrub cover, with a positive total effect; percent broadleaf canopy had a direct negative effect and an indirect effect via shrub cover. The model for total understorey species richness showed an indirect effect of stand age via mean light, light heterogeneity, and substrate heterogeneity, with a positive total effect; percent broadleaf canopy had an indirect effect via light heterogeneity, and substrate heterogeneity. The models for vascular plants followed similar trends to those for total understorey cover and species richness; however, there was an opposite indirect effect of light heterogeneity for both cover and species richness of non-vascular plants. The overall results highlight the importance of time since colonization, light availability and heterogeneity, substrate specialization and growth dynamics in determining successional patterns of boreal forest understorey vegetation.

In chapter 5, the dynamics of understorey biomass, production and turnover rates following stand-replacing disturbance and throughout forest succession were examined. I found that herbaceous biomass and production peaked in early stages of stand development, whereas total, woody and bryophytes biomass and production peaked at intermediate stages of succession. Herbaceous and woody turnover rates were higher is early stages, and bryophytes turnover rates were higher at intermediate stages. Understorey total, woody and herbaceous biomass, production and turnover rates were higher under deciduous broadleaf overstorey, and those of bryophytes were higher under conifer stands. However, mixedwood stands favoured the growth of both woody and non-woody plants, and were intermediate between broadleaf and conifer stands in supporting understorey biomass and production. This study highlights the role of overstorey succession in long-term forest understorey biomass, production and turnover dynamics and its importance for modeling total forest ecosystem contribution to the global carbon cycle.

In summary, this study demonstrated that multiple processes determine changes in understorey vegetation with stand development in boreal forests and highlight that understorey vegetation species diversity, and its biomass, production and turnover dynamics are driven by time since colonization following stand replacing fire, coupled with associated changes in resource availability and heterogeneity mediated via overstorey succession. This study highlight that the shifts in forest age structure and composition have strong impact on the dynamics of understorey vegetation and its ecological functions. Therefore management interventions should aim at maintaining diverse range of stand ages and overstorey types for conserving biodiversity and their ecological functions in the boreal forest of Canada.

Key-words: Boreal forest; bryophytes; coarse woody debris; decay class; epixylic plants, , lichens; mechanisms, non-vascular plants, overstorey composition, resource availability, resource heterogeneity, stand development, substrate species; understorey vegetation, vascular plants.

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NOTE TO THE READER

This is a manuscript-based thesis. All chapters were written individually according to varying publication requirements of selected peer-reviewed journals. Efforts have been made to integrate those chapters into one coherent thesis with caution. However, the styles for writing, references, and organizations of figures and tables may slightly differ between chapters.

Chapters:

2. Kumar P, Chen HYH, Thomas SC, and Shahi C. 2017. Effects of coarse woody debris on plant and lichen species composition in boreal forests. *Journal of Vegetation Science* 28(2): 389-400.

3. Kumar P, Chen HYH, Thomas SC, and Shahi C. 2017. Epixylic vegetation abundance, diversity and composition vary with coarse woody debris decay class and substrate species in boreal forest. *Canadian Journal of Forest Research*. DOI: 10.1139/cjfr-2017-0283.

4. Kumar P, Chen HYH, Thomas SC, and Shahi C. 2017. Linking resource availability and heterogeneity to understorey species diversity through succession in boreal forest of Canada. *Journal of Ecology.* DOI:10.1111/1365-2745.12861.

5. Kumar P, Chen HYH and Thomas SC, 2017. Dynamics of understorey biomass, production and turnover associated with long long-term overstorey succession in boreal forests of Canada--(In preparation).

CHAPTER 1: GENERAL INTRODUCTION

Understorey vegetation comprises the majority of species diversity in temperate and boreal forest ecosystems (Whigham 2004, Gilliam and Roberts 2014), and contributes substantially to ecosystem functioning and services (Halpern and Spies 1995, Nilsson and Wardle 2005, Hart and Chen 2006, Gilliam 2007, Zhang et al. 2017). The understorey vegetation plays a major role in regulating forest vegetation succession (Royo and Carson 2006), nutrient cycling, energy flow and long-term stand output (George and Bazzaz 1999, Wardle et al. 2004, Nilsson and Wardle 2005, Kolari et al. 2006). Forest management in boreal forests has tended to focus on the overstorey composition and diversity, while little attention has been paid to understorey vegetation, such as woody ericaceous shrubs, herbaceous plants and bryophytes. Despite the ecological importance of understorey vegetation, the mechanisms that determine the patterns of understorey species diversity with stand development following stand-replacing disturbance and overstorey characteristics are not fully known, as the present literature is largely speculative and descriptive rather than analytical. In addition, understorey vegetation with high turnover rates are a major contributor to carbon and nutrient cycling, however, the dynamics of understorey biomass, production and turnover rates associated with long-term overstorey succession remain poorly understood. Therefore, mechanistic understanding of the dynamics of understorey vegetation following stand-replacing disturbance is essential to clarify the long-term implication of forest management on biodiversity and ecosystem function and services.

Theoretically, two general conceptual models have been developed to explain patterns of species diversity in the natural ecosystems. The resource heterogeneity hypothesis predicts that species diversity in resource limited understorey environments are regulated by the heterogeneity in resources as plants are specialized on particular resource regimes or combinations of abiotic factors (Huston 1979, Stein et al. 2014). The resource quantity hypothesis on the other hand, suggest that light is the most limiting resource for species in forest understorey, and understorey species diversity is mainly determined by average light levels (Stevens and Carson 2002, Bartels and Chen 2010).

In the boreal forests, natural disturbances shapes the structure and composition of the species and have important implications on the resulting forest mosaic age-class distribution and species compositions (Bergeron et al. 2001, Chen and Popadiouk 2002, Taylor and Chen 2011, Bergeron et al. 2014). Understorey vegetation cover and species diversity are expected to change with stand age as vegetation requires time to colonize the available resources after fire, and the associated changes in the resource availability (such as light and soil nutrients availability) and resource heterogeneity (light variability and substrate diversity in the form of coarse woody debris, leaf litter, exposed mineral soil and tip-up mounds) that track the stand development. Furthermore, an important influence that complicates patterns of understorey vegetation is the existence of multiple successional pathways in canopy tree composition (Chen and Popadiouk 2002, Peters et al. 2006, Taylor and Chen 2011). Differences in canopy species composition - particularly the relative abundance of broadleaved versus coniferous trees - may strongly affect resource quantity and heterogeneity and result in distinct environmental conditions and understorey vegetation (Barbier et al. 2008, Bartels and Chen 2010, Chávez and Macdonald 2012, Bartels and Chen 2013). The distinct resource conditions (such as light and soil nutrients availability, light variability and substrate diversity) that may exist under several tree species mixtures and stand ages, and their subsequent effects on understorey vegetation warrant further studies.

There is a suite of direct and indirect factors that simultaneously influence understorey cover and species diversity through stand development, but their relative importance is little understood. The purpose of this dissertation is to improve the understanding of patterns and mechanisms of understorey vegetation processes associated with stand development in boreal forests. The specific objectives addressed by this thesis include: (1) to examine the effects of coarse woody debris decay class and substrate species on plant and lichen species composition in boreal forests; (2) to examine how pattern of epixylic vegetation abundance, diversity and composition vary with coarse woody debris decay class and substrate species in boreal forest stands of different ages and compositions; (3) to identify the mechanisms for understorey vegetation by linking resource availability and heterogeneity to understorey species diversity through succession; and (4) to examine the dynamics of understorey biomass, production and turnover associated with long-term overstorey succession in boreal forests of Canada.

Chapter two and three of this thesis presents empirical studies of the effects of CWD decay class and substrate species on understorey species abundance, diversity, and composition in the central boreal forests of Canada. These studies specifically examined the patterns of epixylic vegetation on CWD decay classes and substrate species and test the independent and interactive effects of CWD decay and substrate species on epixylic abundance, species diversity and composition in stands of varying age and overstorey type. Chapter four of this study presents an empirical study of the mechanisms underlying patterns of understorey plant diversity by linking time since fire (stand age), light availability and heterogeneity, substrate heterogeneity and soil nitrogen to understorey vegetation cover and species diversity. Chapter five presents an empirical study of the dynamics of understorey biomass, production and turnover patterns in boreal forests of Canada. This study explicitly examined how biomass, production and turnover rates of understorey herbaceous, woody plants and bryophytes change following stand replacing fire, and whether age-related dynamics in understorey herbaceous, woody plants and bryophytes biomass, production and turnover rates differ among overstorey types. In the conclusion chapter, I present the summary of my findings and highlight multiple mechanisms underlying the pattern of understorey vegetation in the boreal forest of Canada, and its importance for modeling total forest ecosystem contribution to the global carbon. I also make recommendations for future research and suggest management implications.

CHAPTER 2: EFFECTS OF COARSE WOODY DEBRIS ON PLANT AND LICHEN SPECIES COMPOSITION IN BOREAL FORESTS

2.1 Abstract

Although the importance of coarse woody debris (CWD) for understorey species diversity has been recognized, the relative effects of coarse woody debris decay class and substrate species on understorey species composition have received little attention. We examined how the species composition of understorey vegetation change with CWD decay class and substrate species in boreal mixedwood forests of Canada. To cover a wide range of CWD decay classes and substrate species, we sampled fire-origin boreal forest stands that varied in stand age and canopy tree species composition. Vegetation on CWD was sampled by visually estimating percent cover of each species within a 0.1 m × 0.5 m quadrat, randomly laid lengthwise on top of the each sampled CWD log. We also recorded the forest floor vegetation by establishing an adjacent plot of the same size at a distance of 1.0 m in a random direction from the CWD vegetation sample. Multivariate analysis showed that understorey species composition differed among decay classes and substrate species. A nonmetric multidimensional scaling (NMDS) ordination of understorey species composition revealed a clear separation of decay classes 1 and 2 from higher decay classes, and that decay classes 4 and 5 shared several species with the forest floor. The species composition on the forest floor was found to be completely different from the species composition on CWD decay classes 1, 2 and 3. Two distinct groupings of substrates according to CWD species composition were found: conifer species (*Pinus banksiana* and *Picea* spp.) and broadleaf species (*Betula papyrifera* and *Populus* spp.), with *Abies balsamea* taking an

intermediate position. Indicator species analysis showed distinct understorey species affiliations to substrate species at advanced decay classes. Understorey species composition on the CWD of *Pinus banksiana* showed particularly pronounced changes from the dominance of lichens on decay classes 2 and 3 to dominance by mosses and vascular species on decay classes 4 and 5. Understorey species composition on CWD not only differed with decay class, but also with CWD substrate species. Conservation strategies should aim at retaining diversity of CWD in terms of both decay classes and species composition in boreal forests.

2.2 Introduction

Coarse woody debris (CWD) is an important structural and functional component of forest ecosystems (Harmon et al. 1986, Spies et al. 1988) that plays crucial roles in providing habitats for plants, animals and fungal species, for forest productivity and in biogeochemical cycles (Franklin et al. 1981, Harmon et al. 1986, Spies et al. 1988, Franklin and Spies 1991, Samuelsson et al. 1994, Jonsson et al. 2005, Bunnell and Houde 2010, Stokland et al. 2012, Dittrich et al. 2014, Ohtsuka et al. 2014, Koster et al. 2015). High importance of decaying wood for understorey species richness and compositional turnover, particularly of bryophytes and lichens, has been demonstrated in many studies (Söderström 1988, Soderstrom 1989, Andersson and Hytteborn 1991, Crites and Dale 1998, Rambo and Muir 1998, Kruys and Jonsson 1999, Siitonen 2001, Turner and Pharo 2005, Bunnell et al. 2008, Spribille et al. 2008, Botting and DeLong 2009, Jüriado et al. 2009, Dittrich et al. 2014), while the effects of CWD substrate species and decay classes on understorey species composition as a whole, as well the comparison of species composition on CWD and forest floor substrates, have received little attention.

CWD and the forest floor are the two primary rooting substrates for understorey plant species in forest ecosystems. The understorey vegetation communities found on CWD are typically dominated by bryophyte and lichen species, whereas the forest floor is mostly, in addition, dominated by vascular plants species. Understorey vegetation communities established on CWD vary through the course of decay dynamics. Freshly fallen logs, classified as early decayed logs, are commonly dominated by lichen communities, whereas more highly decayed logs provide a substrate for unique moss and liverwort communities (Crites and Dale 1998, Rambo and Muir 1998, Bunnell et al. 2008, Botting and DeLong 2009). Structural and chemical properties of CWD vary with decomposition state (Alban and Pastor 1993, Laiho and Prescott 2004). The degree of decay also reflects the relative time available for species colonization (Bartels and Chen 2015), thus influencing species composition as a result of dispersal limitation and successional processes. Understorey species on individual decay class can also vary between forests of different stand ages, suggesting that both time and structural properties along with different stand ages are important in determining species composition (Hyvarinen et al. 1992, Uliczka and Angelstam 1999, Mills and Macdonald 2005).

In addition to the effects of decay processes, understorey vegetation communities may differ among CWD substrate species as a result of species-specific physical and chemical properties such as wood texture and bark pH (Barkman 1958, Jüriado et al. 2009, Fritz and Heilmann-Clausen 2010, Mežaka et al. 2012, Pereira et al. 2014, Putna and Mežaka 2014). Conifer bark is generally more acidic (Hauck and Javkhlan 2009, Hauck 2011, Putna and Mežaka 2014), while bark from broadleaf tree species is generally higher in pH and moisture content (Culberson 1955, Jüriado et al. 2009). There is evidence that vegetation communities found on broadleaf CWD differ from those found on coniferous CWD species (McAlister 1997, Rambo 2001, Mills and Macdonald 2005). Vascular plants generally establish on substrates that are nutrient-rich and less acidic, whereas many bryophytes and lichen species can tolerate higher acidity (Hauck and Jurgens 2008, Pereira et al. 2014). Although species-specificity of bryophyte and lichen communities associated with CWD species has been recognized (Culberson 1955, Gustafsson and Hallingbäck 1988, McAlister 1997, Rambo and Muir 1998, Rambo 2001, Spribille et al. 2008, Caruso and Rudolphi 2009), the combined effects of substrate species and decay class on understorey vegetation communities seem so far not to have been considered.

Here we examine the influence of CWD substrates on understorey vegetation communities in the central boreal forest of Canada. Specifically, we assess how composition of understorey vegetation changes with CWD decay class and substrate species in stands of varying ages and tree species composition. We hypothesized that understorey species composition differs among CWD decay classes, and between CWD and the forest floor, because of the time available for colonization and substrate suitability increases with CWD decay stage (Crites and Dale 1998, Caruso and Rudolphi 2009). We also hypothesized that coniferous and broadleaf substrate species host different community compositions, because differences in their physical and chemical properties (Kuusinen 1996, McAlister 1997, Hauck and Javkhlan 2009) result in differences in the opportunities for establishment of bryophyte and lichen species on the CWD. Interactive effects of CWD decay class and substrate species were also predicted as a result of differences in decay dynamics among woody species. To cover a wide range of CWD decay classes and substrate species, we sampled fire-origin boreal forest stands that varied in terms of canopy composition and stand age.

2.3 Material and methods

2.3.1 Study area and stand selection

The study was conducted in the mixed-wood boreal forests north of Lake Superior and west of Lake Nipigon in the Black Spruce Forest, located approximately 100 km north of Thunder Bay, Ontario, Canada (49°23'N to 49°36'N, 89°31'W to 89°44'W). The area falls within the Moist Mid-Boreal (MBX) ecoclimatic region (Ecoregions Working Group 1989) and is characterized by warm summers and cold, snow-rich winters. Mean annual temperature is 2.5°C and mean annual precipitation is 712 mm at the closest meteorological station located in Thunder Bay, Ontario (Environment Canada 2015). The overstory is typically dominated by *Pinus banksiana* Lamb., *Populus tremuloides* Michx., *Betula papyrifera* Marsh., *Picea mariana* [Mill.] B.S.P., *Picea glauca* [Moench] Voss and *Abies balsamea* [L]. Mill. Common understorey shrubs and herbs are *Acer spicatum* Lam., *Rubus pubescens* Raf., *Alnus incana* [L]. Moench, *Corylus cornuta* Marsh., *Calamagrostis canadensis* Michx., *Maianthemum canadense* Desf., *Viola renifolia* A. Gray, and *Aster macrophyllus* L. (Hart and Chen 2008). Wildfire is the most common natural disturbance agent in the study area, with site-specific fire-return intervals ranging from 40 to 820 years (Senici et al. 2013), and an average fire return interval of approximately 100 years for the past century (Senici et al. 2010).

2.3.2 Sampling and measurements

To cover a wide range of CWD decay classes and substrate species, fire-origin boreal forest stands were sampled, representing chronosequences 34, 98, 146 and 210 years since last stand - replacing fire of diverse overstorey composition (Brassard and Chen 2008). At any given stand development stage on mesic sites in the region, stands originating from fire can be dominated either by conifer, broadleaf, or mixed-wood in the overstorey (Taylor and Chen 2011). We thus made an effort to sample all three overstorey stand types for each age class, with three replicates for each age class and overstorey type. All combinations were sampled, except for a 146 year-old mixedwood stand, for which no accessible site was found. The total number of sampled stands therefore was 35.

To minimize between-site variability, all selected stands were located on mesic sites on flat or mid-slope positions, with no slope exceeding 5%. All stands were located on well-drained (sandy or silty loam) glacial moraines, >50 cm in thickness, which is the prevailing soil type in the study area. To ensure that each sample stand met the selection criteria, soil pits were dug in each candidate stand to verify that the site was mesic, following procedures and criteria described in Taylor et al. (2000).

2.3.3 Coarse woody debris

In each stand, a 400-m^2 circular plot with a radius of 11.28 m was established, within which all sampling was done. CWD logs $\geq$ 10 cm in diameter were located within each plot and the decay class and species of CWD were identified and recorded in the field. Following the field manual of BC Ministry of Forests and Range and BC Ministry of Environment (2010), we assigned each selected CWD piece to one of the five categories with 1 being the least decayed and 5 being the most decayed, based on its portion on the ground, hardness of wood texture, presence or absence of branches (if originally present), bark intactness, wood appearance, and presence and depth of invading roots (Table 2.1). Morphological characteristics as defined by Brassard and Chen (2008) were used to identify CWD species. These included: branching pattern oriented up for *Pinus banksiana*; parallel or downward for *Picea* spp. and *Abies balsamea;* (2) presence of papery longer-lived bark (indicating *Betula papyrifera* or *Abies balsamea)*; (3) wood color and texture (broadleaf species had whitish and conifer reddish wood color; *Pinus banksiana* wood texture is 'blockier' than other conifers); (4) bark and foliage features; and (5) larger CWD size potential of *Pinus banksiana* and *Populus* spp.

Table 2.1. Decay classes of coarse woody debris (CWD) modified from British Columbia (BC) Ministry of Forests and Range and BC Ministry of Environment (2010: table 7.1).

	Class 1	Class 2	Class 3	Class 4	Class 5
Texture	Hard	Sap rot (but still hard, thumbnail penetrates)	Spongy, large pieces	Extensive decay	Small pieces, soft portions
Portion on ground	Elevated on support points	Elevated but sagging slightly	Sagging or broken	Fully settled on ground	Partly sunken
Branches	Hard with twigs	Branches soft	Branches/stubs absent	Absent	Absent
Bark	Firm	Loose	Trace	Absent	Absent
Wood appearance	Fresh/recent	Colour fading	Fading colour	Light or brown	Reddish brown
Invading roots	None	None	In sapwood	In heartwood	In heartwood

2.3.4 Recording of vegetation

Understorey vegetation surveys were conducted during the period of peak vegetation cover in July and August 2014. Vegetation on CWD was sampled by visually estimating the percent cover of each species following the method of Mueller-Dombois and Ellenberg (1974a) within a

0.10 × 0.50 m (0.05 m^2) quadrat, randomly laid lengthwise on top of the each sampled CWD log. For each CWD plot, a forest floor vegetation sample of the same size was established at a distance of 1.0 m in a random direction from the CWD vegetation plot, conditioned on CWD not being encountered. Efforts were made to identify all species in the sampled quadrats. However, some small and rare species, especially of lichens and liverworts, are difficult to detect and identify in the field (Kuusinen 1996). We did, however, not detect any thread-like liverworts of the genera *Cephalozia* spp. and *Lophozia* spp. and omission of minute liverwort species in this study is likely not to represent a major loss species. Several species of hepatics with rounded leaves may have been combined in the aggregate *Jamesoniella autumnalis*. *Cladonia coniocraea* (Flörke) and *Cladonia ochrochlora* (Flörke) were recorded as *Cladonia* agg. due to difficulty in distinguishing these species when podetia were absent (Botting and DeLong 2009). The quantitatively important bryophyte families Brachytheciaceae and Mniaceae were recorded collectively due to problems with identification. However, identification problems were limited to a small fraction of the total understorey vegetation.

2.3.5 Data analysis

Permutation multivariate analysis of variance (perMANOVA) was used to examine the effect of decay class and substrate species on understorey species composition. PerMANOVA is a nonparametric, multivariate method that uses permutation techniques to test for compositional differences between more than one factor (Anderson 2005). PerMANOVA was performed by use of the *adonis* function of the “vegan” package in R (Oksanen et al. 2015, R Development Core Team 2015) with Bray-Curtis dissimilarity measure and 1000 permutations of the composition data. To summarise variation in understorey species composition, we used nonmetric multidimensional scaling (NMDS) (Kruskal 1964a, b, Minchin 1987) as implemented in the “vegan” package in R. NMDS is a robust ordination technique (Kenkel and Orloci 1986, Minchin 1987, McCune and Grace 2002); well suited for community data, because it preserves the rank order of dissimilarities among samples and avoids assumptions of normality and homogeneity of variance which are not commonly met in ecological community data. We performed analyses (a) to examine differences in the species composition between CWD decay classes and forest floor and (b) to examine the differences in species composition between CWD substrate species and forest floor. NMDS ordinations were obtained by use of *metaMDS* function in the “vegan” package in R and was run on species compositional data with the following options and settings: Bray-Curtis dissimilarity index, two dimensions (axes); up to 100 runs from different random seeds to search for two similar solutions, with all other options set to default arguments. The “ordiellipse” function was used to show concentrations of quadrats with similar properties (e.g., from the same substrate) in the ordination diagram. We also performed parallel detrended correspondence analysis (DCA) (Hill 1979, Hill and Gauch 1980) to confirm that the main gradient structure of the data had been found by the NMDS ordination (Økland 1996). We checked for correlations of corresponding axis of the NMDS and the DCAs using Procrustes test (Minchin 1987, Peres-Neto and Jackson 2001) (see Fig. S2.1.)

We performed indicator species analysis (ISA) using the “multipatt” function in R package “indicspecies”(De Caceres and Legendre 2009), using “IndVal.g” as the statistical value to identify understorey species affiliations to a particular decay class and substrate species. ISA calculates indicator values for each understorey species based on species abundance scores and the proportional frequency of all species in a particular group (McCune and Grace 2002). Species occurring in only one site were omitted before this analysis. The P-value generated represents the probability that the calculated indicator value is greater than that found by chance. Only species with P-values less than 0.1 were considered an indicator species for a particular substrate and decay class (McCune and Grace 2002, Hart and Chen 2008). All statistical analyses were conducted in R, version 3.2.2 (R Development Core Team 2015).

2.4 Results

A total of 314 CWD logs were found in the 35 plots; 74, 89, 73, and 78 CWD logs in each of the stand age classes of 34, 98, 146, and 210 years, respectively. The majority of CWD logs in lower stand-age classes (34 and 98 years) were from decay classes 3, 4 and 5, whereas in higher stand-age classes (146 and 210 years) CWD logs ranging from decay class 2 to 5 were uniformly represented (Fig. 2.1). In general, the frequency of occurrence of understorey species increased with stand age class, with the exception of a few species, such as *Cladonia* lichen and *Dicranum* moss species (Table 2.2). A total of 68 operational taxonomic units (OTUs) were recorded on CWD and forest floor, including 16 OTUs of lichens, 17 OTUs of bryophytes, and 35 OTUs of vascular plants. The vascular plant OTUs included herbs, shrubs, trees and clubmosses.

The results from perMANOVA showed that the species composition of understorey vegetation differed significantly among decay classes and substrate species (Table 2.3). Moreover, the effect of decay class differed with substrate species as indicated by a significant interaction effect of decay class and substrate species.

The NMDS ordination (Fig. 2.2) shows clear differentiation of the species composition according to decay classes. Most notably, decay class 1and 2 were separated from higher decay classes (Fig. 2.2a). The logs of decay class 1 were characterized by lichen species, which were

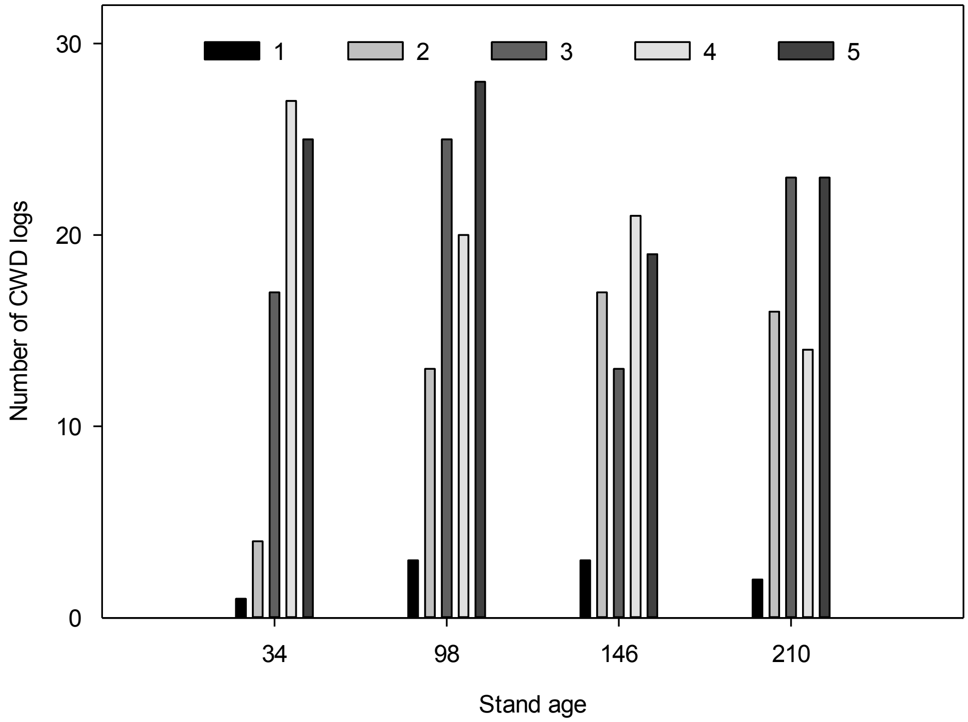

Figure 2.1. Frequency distribution of coarse woody debris (CWD) logs on decay classes for different stand ages.

found in substantial quantity on living trees (Table 2.2). On decay class 2 logs, the first appearance of early epixylic species of *Cladonia*, *Ptilidium pulcherrimum* and Brachytheciaceae were observed, in addition to the epiphytic species (Table 2.2). *Cladonia* spp., *Ptilidium pulcherrimum*, and Brachytheciaceae dominated decay class 3, and substantial quantities of *Dicranum* and Mniaceae mosses and *Pleurozium schreberi*, *Ptilium crista-castrensis* feathermosses appeared on this decay class, (Table 2.2). Mosses (*Dicranum,* Brachytheciaceae*,* Mniaceae) and feathermosses (*Pleurozium schreberi*, *Ptilium crista-castrensis*) became dominant over lichens and liverworts in decay class 4 (Table 2.2). Finally decay class 5 was dominated by *Dicranum polysetum*, feathermosses (*Pleurozium schreberi*, *Ptilium crista-*

castrensis and *Hylocomium splendens*) and vascular plant species. Some species on decay classes 4 and 5 were shared with the forest floor, which mainly comprised vascular plants, whereas majority of vegetation on CWD substrates were dominated by lichens and bryophytes (Table 2.2).

A complete change of the species composition took place from CWD decay class 1 via higher decay classes to the forest floor (see table 2.2 and the fact that the difference among end-point quadrats along NMDS axis 1 exceeded 3 H.C. units), in accordance with typical successional pattern.

The substrates fell into two distinct groups in the NMDS ordination (Fig. 2.2): *Pinus banksiana* and *Picea* spp. made up one group and *Betula papyrifera* and *Populus* spp. another group, while *Abies balsamea* occupied an intermediate position (Fig. 2.2b). On freshly fallen conifer substrates (decay class one and two), epiphytic species (*Hypogymnia physodes, Usnea subfloridana*, *Parmelia sulcata*, *Vulpicida pinastri*, *Evernia mesomorpha*) along with primary thalli of *Cladonia* lichens were prevalent, whereas on freshly fallen broadleaf tree species other epiphytic species (*Xanthoria fallax*, *Peltigera canina*) in addition to those present on the conifer species substrates, were present, along with Brachytheciaceae mosses (Table 2.2). With further decomposition of CWD from decay class 2 to 3, a complex of typical epixylic lichens of the genus *Cladonia* (*Cladonia coniocraea*, *C. ochrochlora*, *C. cenotea*, and *C. cervicornis*) and the liverworts *Ptilidium pulcherrimum* and *Jamesoniella autumnalis* increased in dominance on conifer CWD, on which also *Dicranum* spp. occurred in small quantities. In contrast, on broadleaf CWD of decay class 2 and 3 the mosses Brachytheciaceae*,* Mniaceae and *Callicladium haldanianum* were most common, along with the liverwort *Ptilidium pulcherrimum* and trace amounts of *Cladonia* lichens (Table 2.2). Decay class 3 and 4 conifer CWD were dominated by

Cladonia lichens, liverworts, *Dicranum* spp., whereas decay class 3 and 4 broadleaf CWD were completely dominated by Mniaceae and Brachytheciaceae mosses along with the liverwort *Ptilidium pulcherrimum* (Table 2.2). Finally, on decay class 4 and 5, *Dicranum* species along with feathermosses (for example *Ptilium crista-castrensis* on *Picea* spp., *Pleurozium schreberi* on *Pinus banksiana* and *Hylocomium splendens* on *Abies balsamea*) and vascular plant species established on conifer CWD, whereas Brachytheciaceae and Mniaceae mosses along with feathermosses (mostly *Ptilium crista-castrensis and Pleurozium schreberi)* and vascular plant species established on broadleaf CWD (Table 2.2). The species composition on *Abies balsamea* was similar to other coniferous substrate species in the early decay classes, but showed a mixture of species common to both conifer and broadleaf substrates in later stages of decay.

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Table 2.2. Frequency of understorey plant species on the forest floor (FF) and combinations of CWD substrates and decay class in stands of four age classes. Substrates: Bw – *Betula papyrifera*, Po – *Populus* spp., Pj – *Pinus banksiana*, Sx – *Picea* spp., Bf – *Abies balsamea*; FF – forest floor. Total frequency (tot. freq.) is a total count of all quadrates in which the species is present.

		Stand ages				Substrate species					Decay classes					tot. freq.
	34	98	146	210	BW	Po	Pj	Sx	Bf	1	2	3	4	5	FF	
Number of logs	74	89	73	78	21	97	73	32	91	9	50	78	82	95		
Lichens species																
Hypogymnia physodes	0.16	0.22	0.22	0.27	0.43	0.12	0.26	0.28	0.22	0.56	0.82	0.23				69
Usnea subfloridana	0.06	0.11	0.15	0.19	0.33		0.11	0.16	0.20		0.62	0.07				41
Xanthoria fallax	0.18					0.12										16
Parmelia sulcata		0.10				0.06	0.07				0.10	0.09				12
Peltigera canina		0.08				0.09						0.06				12
Phaeophyscia pusilloides		0.10				0.08					0.10	0.09				14
Evernia mesomorpha	0.18						0.14					0.07				14
Vulpicida pinastri							0.07									06
Cladonia coniocraea	0.43	0.25	0.23	0.08		0.12	0.41	0.41	0.24			0.46	0.39	0.07		77
Cladonia cenotea		0.06					0.07									08
Cladonia ochrochlora							0.07									05
Cladonia agg.	0.51	0.22	0.42	0.27		0.22	0.51	0.25	0.47		0.22	0.63	0.51	0.08		110
Cladonia chlorophaea		0.06	0.10						0.07			0.06	0.11			15
Cladonia cervicornis	0.31					0.05	0.29					0.14	0.17			30
Cladonia rangiferina	0.20						0.16						0.08	0.07	0.02	22
Bryophytes species																
Brachytheciaceae	0.31	0.38	0.55	0.69	0.76	0.89			0.48		0.46	0.60	0.47	0.43		153
Mniaceae		0.31	0.33	0.42	0.33	0.45			0.33			0.32	0.36	0.32		88
Dicranum ontariense	0.43	0.12	0.16	0.14			0.53	0.16	0.21			0.32	0.39	0.09		68
Dicranum fuscescens	0.09					0.06							0.09			09
Dicranum polysetum	0.49	0.29	0.30	0.19		0.11	0.49	0.50	0.38			0.13	0.49	0.51	0.09	127
Polytrichum commune															0.03	11
Callicladium haldanianum			0.07			0.05										05
Hylocomium splendens		0.06	0.11	0.27		0.05			0.30				0.15	0.22	0.07	56
Ptilium crista-castrensis	0.42	0.36	0.33	0.27	0.24	0.25	0.41	0.56	0.35			0.24	0.46	0.53	0.26	191
Pleurozium schreberi	0.76	0.52	0.51	0.26		0.33	0.73	0.81	0.51			0.32	0.74	0.76	0.26	142
Rhytidiadelphus triquetrus				0.15					0.14					0.09	0.15	63

Ptilidium pulcherrimum	0.47	0.25	0.27			0.19	0.42	0.22	0.24		0.16	0.42	0.41	0.05		81
Jamesoniella autumnalis			0.08						0.07			0.05	0.06			12
Vascular plants species																
Maianthemum canadense	0.19	0.12	0.19	0.15		0.14	0.19	0.22	0.16				0.07	0.47	0.55	225
Coptis trifolia									0.05					0.08	0.11	43
Cornus canadensis	0.21	0.07	0.23	0.14		0.11	0.21	0.16	0.16				0.12	0.42	0.57	226
Clintonia borealis															0.49	159
Aralia nudicaulis															0.29	92
Epilobium angustifolium															0.02	05
Viola renifolia															0.07	22
Streptopus roseus															0.30	99
Trientalis borealis		0.06	0.07	0.17		0.10			0.11				0.09	0.21	0.15	75
Mitella nuda		0.08		0.19		0.10			0.15				0.08	0.20	0.22	94
Viola blanda															0.07	26
Aster macrophyllus															0.11	35
Equisetum sylvaticum															0.05	17
Lycopodium annotinum				0.06					0.05					0.09	0.12	49
Lycopodium obscurum															0.09	34
Lycopodium lucidulum															0.03	12
Linnea borealis	0.22	0.12	0.19	0.08		0.06	0.23	0.16	0.20				0.24	0.27	0.13	88
Gaultheria hispidula	0.09	0.20	0.12				0.15	0.53					0.09	0.26	0.05	50
Acer spicatum															0.16	52
Diervilla lonicera															0.09	27
Lonicera canadensis															0.10	32
Vaccinium angustifolium															0.13	41
Ledum groenlandicum															0.07	21
Rosa acicularis															0.06	20
Vaccinium myrtilloides															0.06	20
Rubus pubescens		0.06				0.05								0.09	0.27	94
Abies balsamea															0.04	18

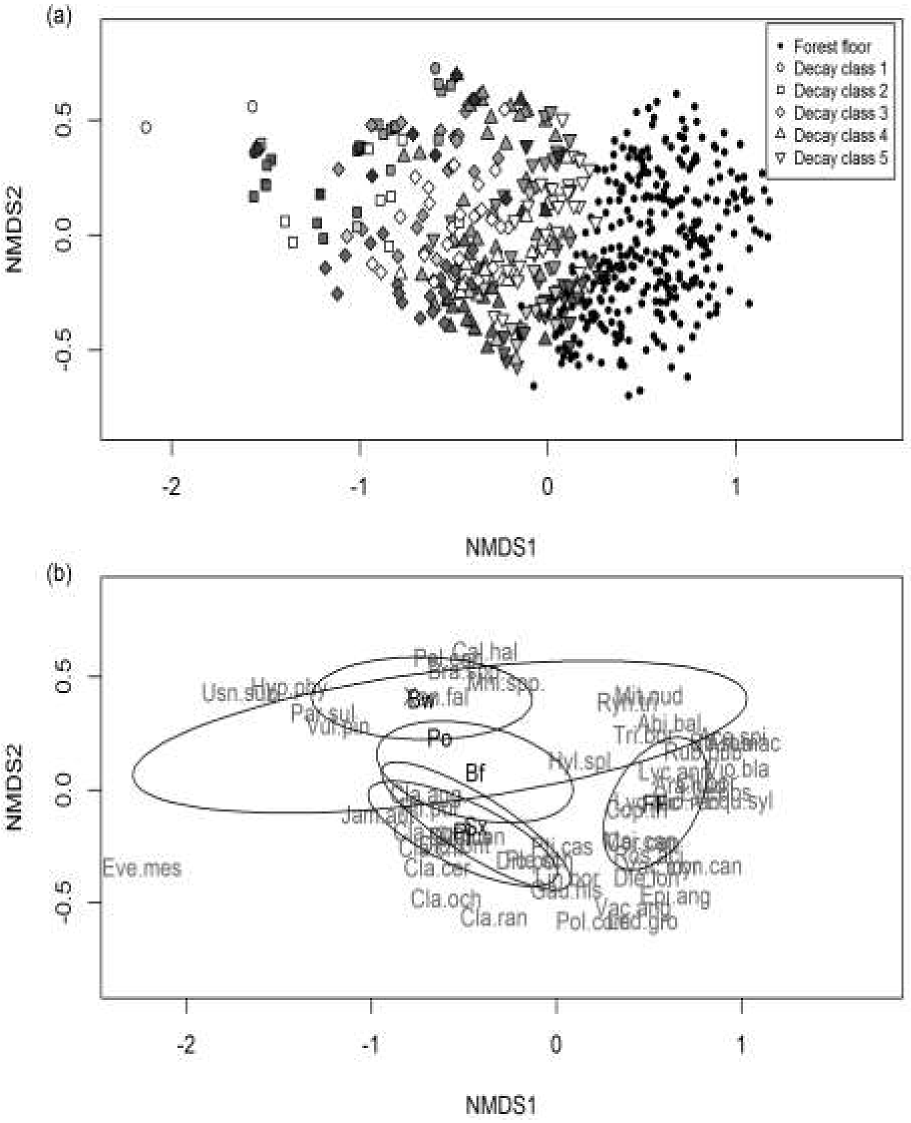

Figure 2.2. Two-dimensional nonmetric multidimensional scaling ordination of understorey species composition of 314 CWD logs and adjacent forest-floor quadrats. (a) Substrates are FF (forest floor) and CWD taxa Po (*Populus* spp.), Bw (*Betula papyrifera*), Pj (*Pinus banksiana*), Sx (*Picea* spp.), Bf (*Abies balsamea*). Decay classes 1 to 5 are indicated by symbol shapes on legends. Only species present in at least five sites were used for the ordination. Points nearest each other in ordination space have similar floristic assemblages, whereas those located farther apart are less similar. (b) Species optima (obtained by weighted averaging of quadrat scores) plotted onto the NMDS ordination. OTU codes consist of the first three letters of the genus and the species names (see Table 2.2). Ordination axes are scaled in half-change (H.C.) units.

Table 2.3. Results of permutation multivariate analysis of variance test (perMANOVA) testing the effects of decay class (D), substrate species (S) and interactions on understorey species composition.

Source	d.f.	MS	F	P	Partial R^2
D	4	6.0	39.9	<0.001	0.22
S	4	0.9	5.7	<0.001	0.03
D × S	16	0.7	4.3	<0.001	0.10
Plot	34	1.0	6.5	<0.001	0.30
Residual	255	0.2			

Notes: the columns give the degrees of freedom (d.f.), mean squares (MS) and F, P and Partial R^2 values.

Indicator species analysis showed understorey species affiliation to different substrate species at advanced decay classes (Table 2.4). Logs of early decay classes (decay class 1 and 2) in all substrate species except *Pinus banksiana* showed no unique understorey species association. As CWD decomposition increased from decay class 2 to 5, the dominance of understorey species on *Pinus banksiana* changed from lichens, *Usnea subfloridana* on decay class 2 and *Cladonia* spp. on decay class 3, to a moss, *Dicranum ontariense*, on decay class 4, to feathermoss, *Pleurozium schreberi*, and finally to the herb *Cornus canadensis* on decay class 5 (Table 2.4). The dominance of understorey species on logs of decay class 5 also varied with substrate species. For example, decay class 5 logs of *Betula papyrifera* were dominated by Brachytheciaceae and Mniaceae mosses and *Mitella nuda*, logs of *Picea* spp. were characterized by *Dicranum polysetum*, *Ptilium crista-castrensis* and *Gaultheria hispidula*, and logs of *Abies balsamea* were dominated by *Hylocomium splendens.*

Table 2.4. Indicator values for understorey species associated with decay class and substrate species. Only indicator species with $P < 0.10$ are reported. P-values are derived from permutation tests. Substrates: Pj – *Pinus banksiana*, Sx – *Picea* spp., Bf – *Abies balsamea*, Bw – *Betula papyrifera*. Taxonomic group: L – lichens, B –bryophytes, V – vascular plants.

Decay class	Substrate	Species	P-value	Taxonomic group
2	Pj	*Usnea subfloridana*	0.085	L
3	Pj	*Cladonia coniocraea*	0.045	L
3	Pj	*Cladonia* agg.	0.040	L
3	Pj	*Cladonia cervicornis*	0.065	L
4	Pj	*Dicranum ontariense*	0.020	B
5	Pj	*Pleurozium schreberi*	0.005	B
5	Pj	*Cornus canadensis*	0.090	V
5	Sx	*Dicranum polysetum*	0.096	B
5	Sx	*Ptilium crista-castrensis*	0.085	B
5	Sx	*Gaultheria hispidula*	0.025	V
5	Bf	*Hylocomium splendens*	0.010	B
5	Bw	Brachytheciaceae	0.030	B
5	Bw	Mniaceae	0.065	B
5	Bw	*Mitella nuda*	0.005	V

2.5 Discussion

We find that understorey species composition established on CWD differ with CWD decay class and substrate species and, consistently, between CWD and the forest floor. With advancing CWD decay from decay class 1 to class 5, community composition of understorey plants shifts from the dominance of facultative epiphytes to early and late epixylic to epigeic species. The structure, chemistry and moisture content of the CWD substrate changes with decay (Alban and Pastor 1993, Laiho and Prescott 2004), as does the time available for colonization (Bartels and Chen 2015). Both of these processes certainly contribute to the observed species compositional shift, to dominance of bryophytes and vascular plants at later stages of decay.

Understorey species succession on CWD begins with the transition of CWD between decay stages 1 and 2. The epiphytic species, associated with the bark of living trees, are preserved on CWD for some time after the tree dies. Also some species that belong to the normally distinct epiphytic communities of the bases of living trees (Kenkel and Bradfield 1986, Thomas et al. 2001) persist for some time on decaying bark of freshly fallen logs. During the transition of CWD to the second stage of succession, the first stage of epixylic succession is replaced by scattered lichen thalli along with some liverworts and moss species. With further bark sloughing and decomposition, by which wood partially loses its hardness, early epixylic communities (mostly of the genus *Cladonia*) become prominent. When, humus development takes place during the final decay stages, these taxa are replaced by late epixylic species (McCullough 1948, Barkman 1958, Söderström 1988, Laaka 1995, Rambo and Muir 1998, Rambo 2001, Jansová and Soldán 2006, Botting and DeLong 2009). The final stage of succession is characterized by epigeic species, mostly feathermosses and vascular plants that normally grow on the forest floor. Substrate of woody origin gradually become part of the forest floor and epixylic vegetation is completely replaced by epigeic species. The results of the present study thus support our hypothesis that species composition of understorey plants differ among CWD decay classes, and between CWD decay classes and the forest floor.

Understorey species composition is also affected by CWD substrate species, in accordance with results of previous studies of differences in understorey species composition between conifer and broadleaf CWD substrates (Barkman 1958, Palmer 1986, McAlister 1997). These differences may be attributed to the specific physical and chemical properties of the wood of tree species (Makinen et al. 2006, Jüriado et al. 2009, Fritz and Heilmann-Clausen 2010, Mežaka et al. 2012, Pereira et al. 2014, Putna and Mežaka 2014). In particular, differences in moisture-holding capability, texture and bark pH among substrate species are likely to be responsible for differences in community composition (Culberson 1955, Hale 1955, McAlister 1997, Mills and Macdonald 2005, Rambo 2010, Mežaka et al. 2012, Pereira et al. 2014). Conifer bark is generally more acidic, with pH ranging from 3.0 to 4.5 (Hauck and Javkhlan 2009, Hauck 2011, Putna and Mežaka 2014), as compared to broadleaf species having pH generally above 5 (Culberson 1955, Kuusinen 1996, McAlister 1997, Mežaka et al. 2008). In addition, the duration of CWD decomposition plays an important role in determining species composition on CWD substrate species, with higher abundance and species richness associated with slower decomposition. The bark of conifers generally decays slowly, as compared to that of broadleaf species, and remains stable for many years, which may provide better opportunities and time for colonisation of both lichens and bryophytes (Harmon et al. 1986, Harmon 1989, Makinen et al. 2006). Therefore, conifer CWD substrates likely provide a more favourable habitat for lichens and bryophytes that are able to tolerate more acidic conditions. The majority of species growing on broadleaf CWD substrates are pleurocarpous mosses, which are likely to be favoured by the higher bark moisture and/or bark pH of broadleaf species (Culberson 1955, Jüriado et al. 2009). The presence of species common to both broadleaf and coniferous substrates on *Abies balsamea* CWD may be due to the higher pH of fir bark (Hauck and Spribille 2005, Hauck and Javkhlan 2009), and perhaps slower bark fragmentation (Harmon 1989) compared to other conifer species.

Indicator species analysis reveal particularly strong differences in community composition among CWD decay classes. No unique species was associated with a specific combination of early decay class and substrate species, suggesting that early successional species persist for some time into CWD development. This pattern is similar to that of epiphytic macrolichens in boreal forests (Bartels and Chen 2015). Particularly for the CWD of *Pinus banksiana*, lichen species were dominant at decay class 2 and 3, followed by mosses and vascular plants at decay classes 4 and 5. These findings are consistent with the patterns of succession on CWD reported previously (McCullough 1948, Muhle and LeBlanc 1975, Botting and DeLong 2009): early dominance by lichens, followed by mosses and liverworts at intermediate decay classes, and finally by herbs and dwarf shrub species in the final stages of decay. Among substrate species, conifer substrates are generally dominated by feathermosses and dwarf shrub species at decay class 5, whereas broadleaf species are dominated by Brachytheciaceae and Mniaceae mosses and herbaceous species. Pronounced differences in community composition for *Pinus banksiana* substrate species may be due to low bark pH and very thick bark (Hauck and Javkhlan 2009).

In conclusion, our analyses highlight that the composition of understorey vegetation differs with both CWD decay class and substrate species and between CWD and forest floor. We find a complete shift of the species composition during understorey species succession on CWD, which is completed when the last stages of wood decomposition and fragmentation is reached. Epiphytic communities, associated with the bark of living trees, are preserved on freshly fallen CWD. Then with decomposition and bark sloughing, epiphytic species are replaced by epixylic species, which have highest frequencies in intermediate to late stages of decay. Finally, with humus development and further decay of CWD, the final stage of succession is characterized by the epigeic species. Therefore, the course of succession can be described as a gradual increase first in the number of epixylic species and then in the number of ground species up to complete disappearance of the substrate upon incorporation, in the forest floor. Understorey species composition not only differs with decay class, but also with CWD substrate species, suggesting that substrate species is also important for understorey vegetation. Therefore, to conserve the species richness of understorey vegetation in boreal forests, management should aim at conserving the diversity of CWD in terms of both decay classes and tree species.

CHAPTER 3: EPIXYLIC VEGETATION ABUNDANCE, DIVERSITY AND COMPOSITION VARY WITH COARSE WOODY DEBRIS DECAY CLASS AND SUBSTRATE SPECIES IN BOREAL FOREST

3.1 Abstract

Although the importance of coarse woody debris (CWD) to understorey species diversity has been recognized, the combined effects of CWD decay and substrate species on abundance and species diversity of epixylic vegetation have received little attention. We sampled a wide range of CWD substrate species and decay classes as well as forest floor in fire-origin boreal forest stands. Percent cover, species richness and evenness of epixylic vegetation differed significantly with both CWD decay class and substrate species. Trends in cover, species richness and evenness differed significantly between non-vascular and vascular taxa. Cover, species richness and species evenness of non-vascular species were higher on CWD, whereas those of vascular plants were higher on the forest floor. Epixylic species composition also varied significantly with stand ages, overstorey compositions, decay classes, substrate species and their interactions. Our findings highlight strong interactive influences of decay class and substrate species on epixylic plant communities, and suggest that conservation of epixylic diversity would require forest managers to maintain a diverse range of CWD decay classes and substrate species. Since stand development and overstorey compositions influence CWD decay classes and substrate species as well as colonization time and environmental conditions in the understorey, our results indicate that managed boreal landscapes should consist of a

mosaic of different successional stages and a broad suite of overstorey types to support diverse understorey plant communities.

3.2 Introduction

Coarse woody debris (CWD) plays a key role in biodiversity and ecosystem functioning as it provides habitat for many plants and animals (Bunnell and Houde 2010, Stokland et al. 2012), and contributes to carbon and nutrient cycles (Harmon et al. 1986, Laiho and Prescott 1999, Ohtsuka et al. 2014). The importance of CWD to maintaining understorey species diversity has been emphasized by numerous authors (Andersson and Hytteborn 1991, Crites and Dale 1998, Rambo and Muir 1998, Kruys and Jonsson 1999, Humphrey et al. 2002, Mills and Macdonald 2004, Bunnell et al. 2008, Botting and DeLong 2009, Caruso and Rudolphi 2009, Dittrich et al. 2014, Checko et al. 2015). It is widely recognized that numerous plant species are specialized to a greater or lesser extent on CWD substrates, and such species are termed “epixylic”. The focus of most prior studies of epixylic plants has either been on non-vascular (lichens and bryophytes) or vascular groups occurring on different CWD decay classes. These studies have generally found that species richness and abundance of non-vascular species (lichens and bryophytes) peak in intermediate to later stages of decay, while those of vascular plants continue to increase at advance stages of decay. A few studies have also examined the effect of substrate species of deadwood on patterns of epixylic plant abundance and diversity (McAlister 1997, Rambo 2001, Mills and Macdonald 2004, Nowinska et al. 2009). The simultaneous effects of CWD decay classes and substrate species have recently been examined in terms of understorey vegetation species composition (Kumar et al. 2017a), but not abundance and species diversity. Species richness and evenness may respond differently to different ecological processes (Stirling and Wilsey 2001, Wilsey and Stirling 2007);

however, no studies to our knowledge have explicitly assessed patterns of species evenness in relation to CWD decay. In addition, very few studies have made a comparison of species abundance and diversity on deadwood substrates to corresponding forest floor substrates (Dittrich et al. 2014, Checko et al. 2015).

Decaying CWD provides a variable substrate at different stages of decomposition and is colonised by a different subset of species as compared with the adjacent forest floor substrates (Lee and Sturgess 2001, 2002, Dittrich et al. 2014). Decaying CWD logs are typically colonised by lichens and bryophytes species, which take advantage of lower competition than on the forest floor (Humphrey et al. 2002, Dittrich et al. 2014), whereas the forest floor is mostly dominated by vascular plant species. The structural and chemical properties of CWD change with the decomposition process (Ganjegunte et al. 2004, Butler et al. 2007, Petrillo et al. 2015, Shorohova et al. 2016), until CWD becomes an integral part of the forest floor. These progressive changes in CWD properties over time are likely to be a main driver of the colonization and growth of different non-vascular and vascular species. The early stages of CWD decomposition are dominated by non-vascular (mostly lichen) species, some of which normally grow on living trees as epiphytes, whereas the later stages of decay are characterized by bryophytes and vascular plant species (McCullough 1948, Barkman 1958, Söderström 1988, Jansová and Soldán 2006, Botting and DeLong 2009, Kumar et al. 2017a). Eventually, the CWD merges with the forest floor in the final stages of decay; in boreal systems the substrate is occupied by feathermosses and vascular plants that normally grow on the forest floor (Söderström 1988, Andersson and Hytteborn 1991, Kumar et al. 2017a). In addition to changes in physical and chemical properties of the CWD with decay (Laiho and Prescott 2004, Butler et al. 2007, Petrillo et al. 2015), the time available for colonization increases (Bartels and Chen 2015). Both the decay process and time elapsed will likely influence abundance and diversity because of dispersal limitation and successional processes.

Patterns in epixylic plant communities may also differ among CWD substrate species because of species-specific differences in physical and chemical traits (pH and texture) of barks (Barkman 1958, Weedon et al. 2009, Mežaka et al. 2012, Pereira et al. 2014, Putna and Mežaka 2014, Shorohova and Kapitsa 2014, Shorohova et al. 2016). For example, the barks of coniferous species are generally drier and more acidic than those of broadleaved tree species (Culberson 1955, Barkman 1958, Hauck and Javkhlan 2009, Jüriado et al. 2009, Mežaka et al. 2012). Furthermore, broadleaved tree species, particularly fast-growing species such as *Populus* spp. and *Betula* spp. common in boreal forests, generally have higher decomposition rates than coniferous species (Barkman 1958, Weedon et al. 2009, Russell et al. 2014, Shorohova and Kapitsa 2014). As a result**,** different epixylic plant communities have been observed on broadleaved and coniferous CWD substratum (Palmer 1986, McAlister 1997, Rambo 2001, Mills and Macdonald 2005). Non-vascular species (bryophytes and lichens) can generally tolerate substrates with higher acidity (Hauck and Jurgens 2008, Pereira et al. 2014), whereas most vascular plants establish on substrates that are nutrient-rich and less acidic. Although the species-specificity of non-vascular species associated with CWD species has been recognized (Culberson 1955, McAlister 1997, Rambo 2001, Spribille et al. 2008, Caruso and Rudolphi 2009, Kumar et al. 2017a), the combined effects of CWD decomposition and CWD substrate species on understorey vegetation abundance, species richness and evenness remain unclear.

In boreal forests, fire is the major natural disturbance responsible for creation and elimination of dead wood on the forest floor (Arseneault 2001, Karjalainen and Kuuluvainen 2002, Brassard and Chen 2006). However, the importance of other disturbances such as insect outbreak and windthrow in altering stand structure has been also recognized (Chen and Popadiouk 2002, Brassard and Chen 2006, Bergeron et al. 2014). Post-disturbance CWD dynamics usually results in a U-shaped pattern, where the volume of CWD of pre-fire origin decreases logarithmically and the CWD of post-fire origin increases exponentially from increased tree mortality associated with competition, ageing and disturbances such as windthrow and insect outbreaks (Sturtevant et al. 1997, Brassard and Chen 2006, Luo and Chen 2011). In addition to stand development, structure and composition of the overstorey also affect the volume and compositional diversity of CWD (Brassard and Chen 2008), because overstorey structure and composition influences stand productivity (Zhang et al. 2012), tree mortality (Chen and Luo 2015), and CWD decomposition rates (Makinen et al. 2006). The structure and composition of the overstorey varies through forest succession in boreal forests: multiple successional pathways can result in either broadleaf, conifer or mixedwood-dominated stands (Chen and Popadiouk 2002, Taylor and Chen 2011). CWD in broadleaf stands may influence the epixylic plant communities differently than the CWD in conifer-dominated stands as a result of distinct environmental conditions in different stand types (Barbier et al. 2008, Chávez and Macdonald 2012, Bartels and Chen 2013, Huo et al. 2014). Broadleaf stands have higher resource availability in the understorey than conifers (Messier et al. 1998, Hart and Chen 2006, Chávez and Macdonald 2010), and are preferred by species that require resource-rich environments as compared to species that are able to tolerate nutrient-poor conditions in conifer stands. Mixedwood stands on the other hand provide heterogeneous conditions and exhibit greater spatial and temporal variability in understorey resources (Bartemucci et al. 2006, Macdonald and Fenniak 2007). Therefore, stand age along with overstorey species composition may influence CWD volume and diversity as well as the extent of post-disturbance recovery of epixylic plant communities on individual CWD substrata.

The purpose of this study was to examine the combined effect of CWD decay classes and substrate species on abundance, species diversity and composition of understorey vegetation in the central boreal forest of Canada. To cover a wide range of CWD decay classes and substrate species, we sampled fire-origin boreal forest stands that varied in canopy species composition and stand age. We expected that total vegetation cover would be higher on the later decay classes of the broadleaved substrate species because of higher moisture content at later stages of decay, which would particularly enhance recruitment and growth of feather mosses and vascular plant species at later stages of decay. We hypothesized that both species richness and evenness would be higher on intermediate decay classes of coniferous substrates, because the acidic bark and slower rate of fragmentation in conifers may provide favorable opportunities for establishment and colonization of both non-vascular and vascular species and because some species would out-compete others at late decay stages. By contrast, CWD of broadleaved species might not show such a pattern due to greater bark sloughing and fragmentation. We also expected that epixylic plant community composition would differ with stand age and overstorey composition due to colonization time associated with stand age and environmental conditions as well as physical and chemical properties of CWD substrate species associated with overstorey composition. Finally, we predicted that epixylic plant communities would differ among CWD decay classes and the forest floor, because of increased time available for colonization, and changes in substrate suitability with CWD decay and forest floor development.

3.3 Materials and methods

3.3.1 Study area

Data analyzed are identical to that of a companion study examining species composition on coarse woody debris, with a focus on indicator species of decay class and CWD substrate species (Kumar et al. 2017a): additional details on study sites and sampling design are provided in that paper. Sampling was conducted at boreal mixed-wood sites approximately 100 km north of Thunder Bay, Ontario, Canada (49°23'N to 49°36'N, 89°31'W to 89°44'W). Mean annual temperature is 2.5°C and annual precipitation is 712 mm at the closest meteorological station (Thunder Bay, Ontario: (Environment Canada 2015). Canopy trees include jack pine (*Pinus banksiana* Lamb.), trembling aspen (*Populus tremuloides* Michx.), white birch (*Betula papyrifera* Marsh.), black spruce (*Picea mariana* Mill. B.S.P.), white spruce (*Picea glauca* [Moench] Voss) and balsam fir (*Abies balsamea* L. Mill.). Fire is the main disturbance agent in the region, with an average fire return interval of approximately 100 years (Senici et al. 2010).

3.3.2 Sampling design

We sampled a set of stands representing a replicated chronosequence (with stands of age 34, 98, 146, and 210 years since last stand replacing fire) and of diverse overstorey composition (Brassard and Chen 2008). Fire-origin stands in the region can be dominated by conifer, broadleaved trees, or a mixture (Taylor and Chen 2011): in so far as possible we sampled all three overstorey stand types for each age class, with three replicates for each. All combinations of age class and overstorey type were sampled, with the exception of a 146-year-old stand that did not have road access, resulting in a total of 35 sampled stands. All selected stands were located on mesic sites at flat or mid-slope positions, with no slope exceeding 5%. Soil parent material consisted of well-drained (sandy or silty loam) glacial moraines, >50 cm in thickness.

3.3.3 Data collection

Sampling was conducted in a 400-m^2 circular plot randomly selected in each stand. Logs $\geq$ 10 cm in diameter at midpoint within each plot were randomly selected and decay class recorded. We assigned each selected CWD piece (downed woody debris on forest floor only) to one of five decay class categories, following the field manual of BC Ministry of Forests and Range and BC Ministry of Environment (2010). Categorization was based on CWD contact with the ground, wood texture, presence or absence of branches, wood strength, bark intactness, and presence and depth of invading roots. The characteristics of decay class 1 were logs elevated from ground, bark or branches hard and intact, and no invading roots present; those of decay class 2 included logs elevated but slightly sagging, presence of sap rot so that a thumbnail can penetrate, loose bark and soft branches with no invading roots; those of decay class 3 included logs sagging or broken, advanced decay (spongy/large pieces) with trace bark, no branches, and invading roots present in sapwood; those of decay class 4 included logs fully settled on ground, extensive decay (crumbly-mushy), bark and branches absent, and invading roots present in heartwood; and those in decay class 5 included small pieces and soft portions, bark and branches absent, and invading roots present in heartwood. Morphological characteristics as defined by Brassard and Chen (2008) were used to identify CWD to species (as detailed in (Kumar et al. 2017a)).

Vegetation surveys were conducted in July and August 2014. We visually estimated the percent cover of each species following the method of Mueller-Dombois and Ellenberg (1974a) within a 0.10 x 0.50 m (0.05 m^2) quadrat, randomly laid lengthwise on top of the each sampled CWD log. We also sampled forest floor vegetation by establishing an adjacent plot of the same size at a distance of 1.0 m in a random direction from the CWD vegetation sample. With a few exceptions, all plants were identified to species; we omitted minute liverwort species; *Cladonia coniocraea* (Flörke) and *Cladonia ochrochlora* (Flörke) were recorded as *Cladonia* agg.; and the moss genera *Brachythecium* and *Mnium* were not separated to species. The omission of some minor species could lead to potential bias in our results. However, pooled species constituted only 11.8 % of the total understorey vegetation sampled by cover.

3.3.4 Data analysis

Species abundance was evaluated as sum of individual species percent cover on each quadrat, species richness was treated as the total number of species recorded on each quadrat, and species evenness was expressed as how evenly the species in the community are distributed. Species evenness was calculated following Pielou (1969) as $Evenness = \frac{-\sum p_i \log p_i}{\ln(Richness)}$, where p_i is the proportion of species i percent cover to total vegetation cover. Total vegetation cover was treated as the sum of species-specific cover values on an individual CWD piece. In addition to total understorey cover, richness and evenness, we separately analyzed species cover, richness and evenness for non-vascular and vascular groups. The non-vascular species included lichens and bryophytes, whereas vascular plants included herbs, shrubs, trees, ferns, and clubmosses. To test for substrate species and CWD decay class effects on understorey cover, species richness and evenness, we used the following general linear mixed effect model:

$$Y_{ijkl} = \mu + D_i + S_j + D \times S_{ij} + \pi_k + \varepsilon_{l(ijk)} \quad (1)$$

where Y_{ijkl} is understorey plant species cover, richness or evenness (separately analyzed by total, non-vascular and vascular groups), μ is the overall mean, D_i (i = 1, 2…5) is decay class, S_j (j = 1, 2…5) is substrate species, π_k is plot random effect that accounts for spatial autocorrelation among logs within each sample plot as well as the variation in stand age and overstorey type related to plot, and $\varepsilon_{l(ijk)}$ (l =1, 2…n) is random sampling error within decay class, substrate species and plot. We conducted the mixed effect analysis using restricted maximum likelihood estimation in R with the *lme4* package (Bates et al. 2016, R Development Core Team 2017). However, vascular plant data did not conform to the assumption of normality based on Shapiro–Wilk's test and skewed to left. To mitigate the violation to the normality assumption and to improve coefficient estimates, we bootstrapped the fitted coefficients of linear models by using "ggplot2" (Wickham 2009). We bootstrapped the 95% confidence intervals and considered estimates to be significantly different if their confidence intervals did not overlap other's mean. For species richness, we specified the residual distribution as Poisson. The significance of the predictors was tested using F-tests by means of analysis of variance or deviance, and the variance or deviance explained by each variable in the model was calculated as a percentage of variance or deviance explained by the variable to that of null model. To explicitly test the effect of stand age and overstorey composition on understorey cover, species richness or evenness, we added these variables and their two-way interactions (removing insignificant higher order interactions) in a revised general linear mixed effect model. The results of the revised model are presented in supplementary information (Table S3.1).

We used permutation multivariate analysis of variance (perMANOVA) to examine the effect of stand age, overstorey composition, decay class, substrate species, and their interactions on understorey species composition. PerMANOVA is a nonparametric, multivariate analysis that uses permutation techniques to test for compositional differences between more than one factor (Anderson 2005). We used perMANOVA with Bray-Curtis dissimilarity and 1000 permutations for the composition data. To examine trends in the composition data, we used nonmetric multidimensional scaling (NMDS) (Kruskal 1964a), a robust ordination technique for community data that are non-normal or evaluated on discontinuous or ordinal scales (McCune and Grace 2002). The analysis was performed: (a) to examine differences in the species composition on CWD between stand ages and overstorey compositional types, and (b) to examine the differences in species composition between CWD decay classes, CWD substrate species, and forest floor. All statistical analyses were conducted in R3.4.2 (R Development Core Team 2017).

3.4 Results

We recorded a total of 68 understorey species on CWD and forest floor, including 33 non-vascular species and 35 vascular species (Table S3.2). Total epixylic cover differed with decay class ($P < 0.001$; Table 3.1), and the effect of substrate species was dependent on decay class, indicated by a significant interaction of decay class and substrate species (Table 3.1). Decay class was the main contributing factor, explaining 47.2% of the variance, while the interaction explained 4.2% of variance. Within decay classes 1 and 2, epixylic vegetation cover did not differ among the five substrate species, while at decay class 3, *Pinus banksiana* and *Populus* substrate species had a higher percent cover than other species (Fig. 3.1). At decay classes 4 and 5, percent cover was higher on *Populus* spp., *Picea* spp. and *Pinus banksiana* than that on *Betula papyrifera* and *Abies balsamea*. Compared with forest floor, *Populus* spp., *Picea* spp. and *Pinus banksiana* at decay classes 4 and 5 had higher percent cover, while all substrate species had lower percent cover on decay classes 1 and 2.

Table 3.1. Results of general or generalized linear mixed effects model showing the effects of decay class (*D*) and substrate species (*S*) on understorey cover, species richness and species evenness, separately analysed by total, non-vascular and vascular vegetation. Bold fonts indicates statistical significance (α = 0.05).

Attribute	Source	df	Total		Non-vascular		Vascular	
			Deviance or variance explained (%)	*P*	Deviance or variance explained (%)	*P*	Deviance or variance explained (%)	*P*
Cover	*D*	4	47.2	**<0.001**	34.6	**<0.001**	48.2	**<0.001**
	S	4	0.5	0.339	0.5	0.524	0.3	0.918
	D × *S*	16	4.2	**0.003**	4.3	**0.031**	4.5	0.654
Richness	*D*	4	42.8	**<0.001**	29.0	**<0.001**	68.2	**<0.001**
	S	4	12.6	**<0.001**	13.0	**<0.001**	0.5	0.577
	D × *S*	16	7.1	0.21	7.5	0.137	0.9	0.995
Evenness	*D*	4	10.2	**<0.001**	11.4	**<0.001**	65.3	**<0.001**
	S	4	3.9	**0.009**	4.1	**0.011**	1.0	0.447
	D × *S*	16	13.6	**<0.001**	15.8	**<0.001**	5.1	0.274

Notes: the columns give the degrees of freedom (df), variance or deviance explained and P values.

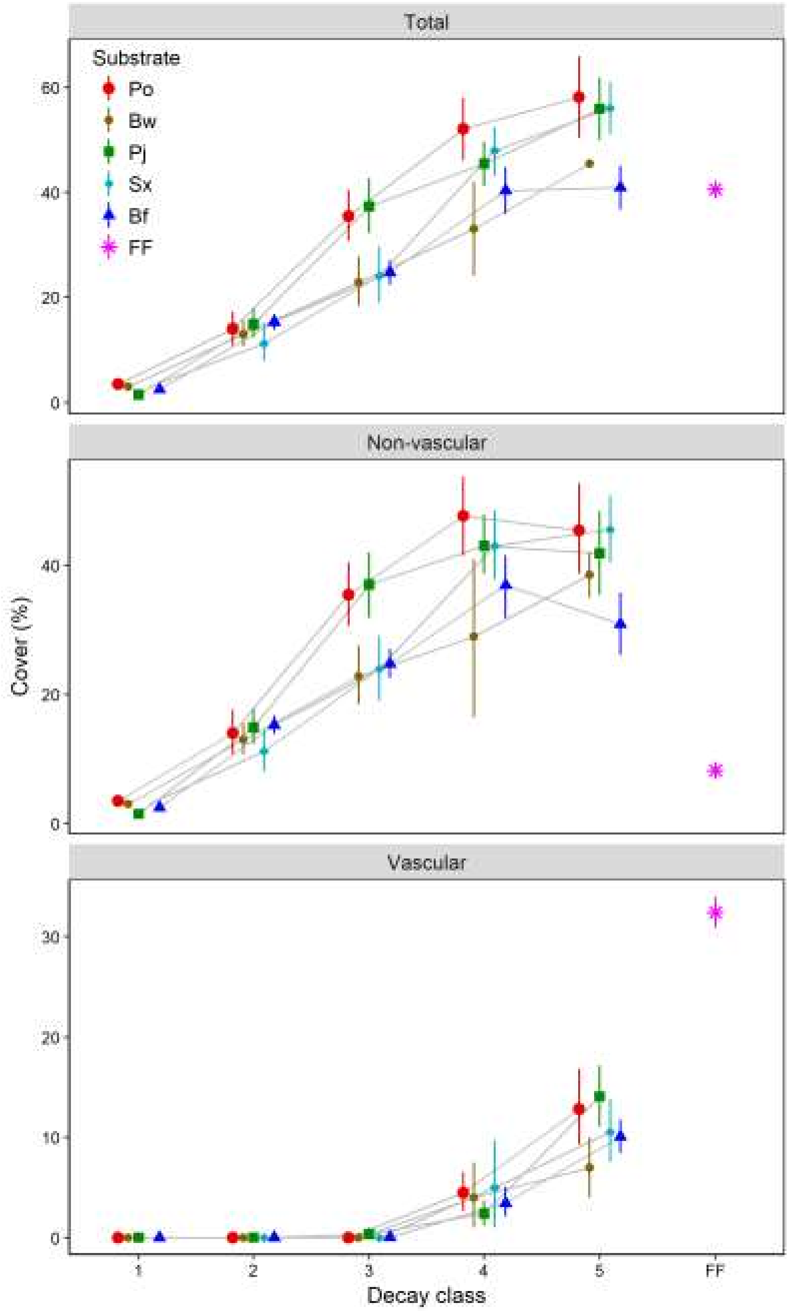

Figure 3.1. Total, non-vascular and vascular understorey vegetation cover (means and bootstrapped 95% confident intervals) in relation to decay class and substrate species. Substrate species are Po- *Populus* spp., Bw- *Betula papyrifera*, Pj- *Pinus banksiana*, Sx- *Picea* spp., Bf- *Abies balsamea* and FF- forest floor.

Across all sampling units, percent cover for non-vascular species was on average 33.2% and 4.6% for vascular species. The effects of decay class and substrate species on non-vascular percent cover were similar to those for total percent cover (Table 3.1, Fig. 3.1). The percent cover of non-vascular species increased with decay classes, peaked on decay class 4, and decreased thereafter on *Populus* spp., *Pinus banksiana* and *Abies balsamea* substrates, whereas the percent cover on *Betula papyrifera* and *Picea* spp. increased throughout the decay classes. On average, the percent cover was highest on *Populus* spp. The percent cover of vascular plant species varied significantly with decay class but not with substrate species (Table 3.1). The percent cover of non-vascular species on the forest floor was similar to substrates of decay class 2. Vascular plant species cover was much higher on the forest floor than that on CWD of all decay classes. No vascular plant species were found on decay classes 1 and 2, with the percent cover of vascular plant species increasing from decay class 3 to decay class 5 on all substrate species.

The linear mixed effect model indicated that total species richness differed strongly with decay class and substrate species without a significant interaction (Table 3.1), but the model violated the normality assumption ($P = 0.005$). Bootstrap analysis showed that total species richness increased continuously with decay class on broadleaved substrates, but peaked at decay class 4 on coniferous substrates (Fig. 3.2). Non-vascular species richness peaked on decay class 3 or 4 for all substrate species. Vascular plant species richness varied significantly only with decay class ($P < 0.001$; Table 3.1), and increased from decay class 3 to decay class 5 (Fig. 3.2). Compared with the forest floor, total species richness on decay classes 1 and 2 was lower, and species richness of non-vascular species was higher in all decay classes except class 1, while species richness of vascular plants was lower on all decay

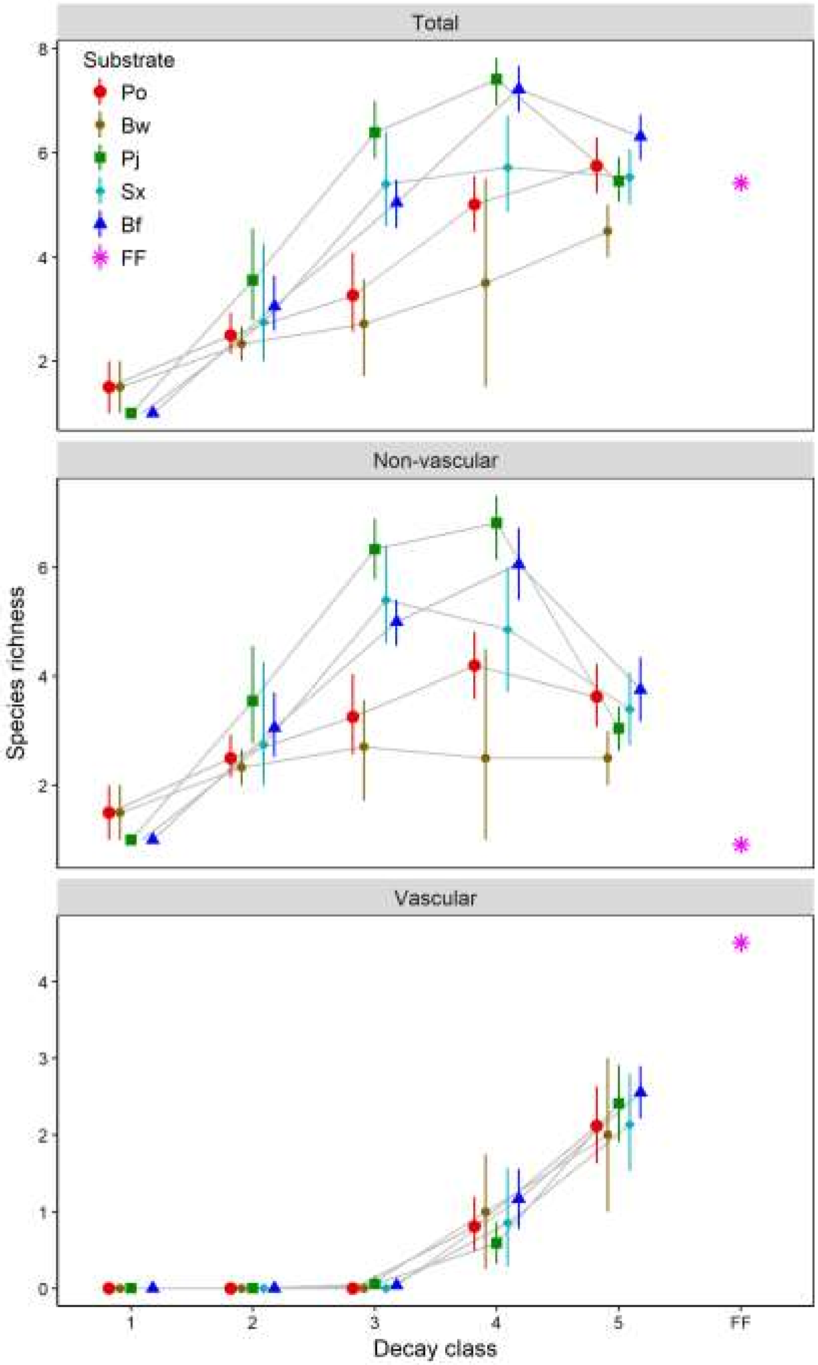

Figure 3.2. Total, non-vascular and vascular understorey species richness (means and bootstrapped 95% confident intervals) per 0.05m^2 quadrat in relation to decay class and substrate species. Substrate species are Po- *Populus* spp., Bw- *Betula papyrifera*, Pj- *Pinus banksiana*, Sx- *Picea* spp., Bf- *Abies balsamea* and FF- forest floor.

classes. Total species richness on coniferous substrates was higher than that on broadleaved substrates at decay classes 3 and 4, but there was little difference between two substrate groups in other decay classes (Fig. 3.2). This pattern was similar for non-vascular species richness (Fig. 3.2).

Total species evenness differed significantly with decay class and substrate species with a significant interaction between the two factors (Table 3.1). Decay class was the main contributing factor, explaining 10.2% of the variance, while the interaction explained 13.6% of the variance in species evenness. Due to sparseness of species occurrence, species evenness could not be evaluated on decay class 1. At decay classes 2 and 4, *Pinus banksiana* CWD substrate species, at decay class 3, *Picea* spp., and at decay class 5, *Abies balsamea* CWD substrate species had higher total species evenness than that on other CWD substrate species (Fig. 3.3). The effect of decay class and substrate species on non-vascular species evenness was similar to that for total species evenness (Table 3.1, Fig. 3.3). Vascular plant species evenness increased significantly from decay class 4 to 5. Compared with forest floor, decay classes 2 and 3 had on average similar total species evenness, but decay classes 4 and 5 had lower total species evenness; CWD at decay class 4 had lower, and at class 5 had similar vascular species evenness.

The species composition of epixylic plant communities differed significantly among stand ages, overstorey composition, decay classes and substrate species, with significant interactions among these predictors (Table 3.2). While main effects of these predictors accounted for majority of the variations in the species composition of epixylic plant communities (as indicated by partial R^2 values), significant interaction terms showed that the compositional responses to one predictor were significantly dependent on the levels of other

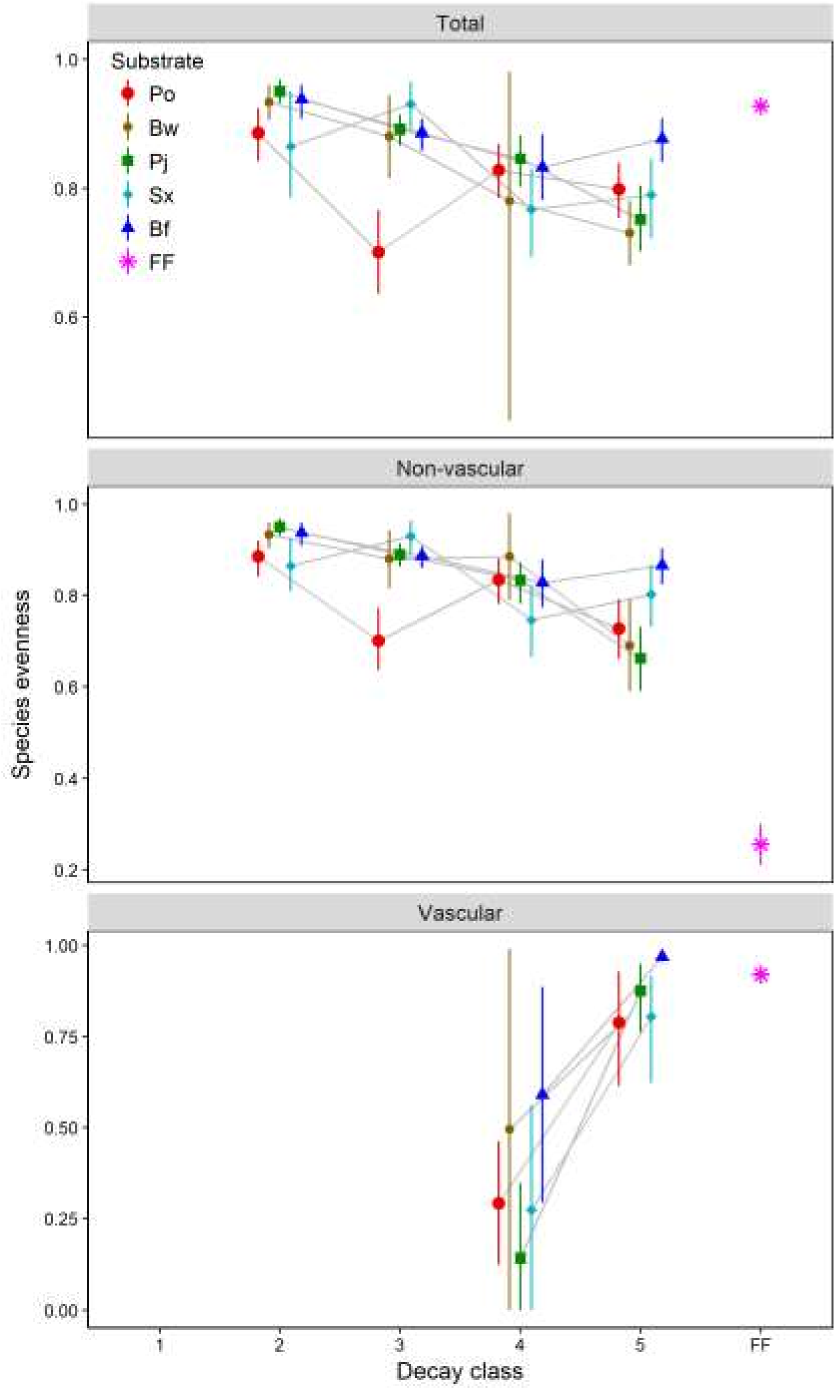

Figure 3.3. Total, non-vascular and vascular understorey species richness (means and bootstrapped 95% confident intervals) per 0.05m^2 quadrat in relation to decay class and substrate species. Substrate species are Po- *Populus* spp., Bw- *Betula papyrifera*, Pj- *Pinus banksiana*, Sx- *Picea* spp., Bf- *Abies balsamea* and FF- forest floor.

predictor (s). When patterns of epixylic species composition were visualized using nonmetric multidimensional scaling ordination (Fig. 3.4a), epixylic communities on CWD in stands of different ages separated well in ordination space, with young stand (34 years old) showing afair separation from older stands (210 years old) while intermediate aged stands (98 and 146 years old) were positioned in between. Epixylic species composition on CWD differed between broadleaf and conifers stands, but there was overlap between conifers and mixedwood stands (Fig. 3.4a). The NMDS ordination also showed clear differentiation of the

Table 3.2. Results of permutation multivariate analysis of variance (perMANOVA) testing the effects of stand ages (A), overstorey compositions (C), decay classes (D), substrate species (S) and their interactions on epixylic species composition. Bold fonts indicates statistical significance (α = 0.05).

Source	df	SS	F	P	Partial R^2
A	3	8.4	22.4	**0.001**	0.08
C	2	11.8	47.6	**0.001**	0.11
D	4	25.4	51.1	**0.001**	0.23
S	4	5.5	10.9	**0.001**	0.05
A × D	12	5.8	3.9	**0.001**	0.05
C × D	8	5.2	5.3	**0.001**	0.05
A × S	9	2.1	1.9	**0.001**	0.02
C × S	7	1.3	1.5	**0.013**	0.01
D × S	14	4.9	2.8	**0.001**	0.04
A × C× D	18	3.4	1.5	**0.002**	0.03
A × D× S	11	2.6	1.9	**0.001**	0.02
C × D× S	6	0.6	0.8	0.855	0.01
Plot	29	10.1	2.8	**0.001**	0.09
Residual	186	23.1			

Notes: the columns give the degrees of freedom (df), sums of squares (SS), Partial R^2, F and P values.

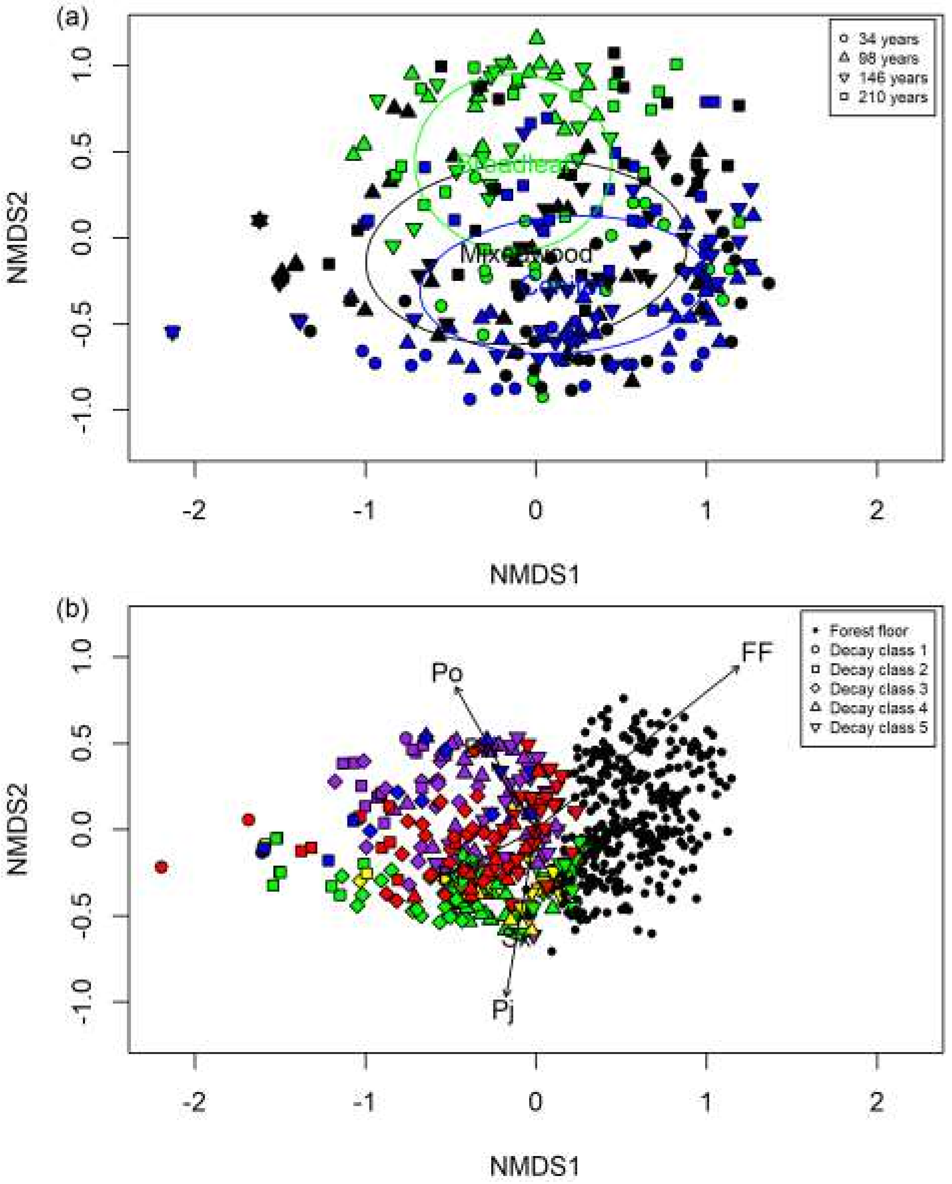

Figure 3.4. Two-dimensional nonmetric multidimensional scaling ordination showing: (a) the differences in the epixylic species composition on CWD between stand ages and overstorey compositional types. Overstorey types are broadleaf (green), conifer (blue) and mixedwood (black) and symbol shapes on legends differentiate stand ages. (b) the differences in epixylic species composition between CWD decay classes, CWD substrate species, and adjacent forest-floor substrates. Substrate species are Po- *Populus* spp. (purple), Bw- *Betula papyrifera* (blue), Pj- *Pinus banksiana* (green), Sx- *Picea* spp. (yellow), Bf- *Abies balsamea* (red) and FF- forest floor (black) and symbol shapes on legends differentiate decay classes. Points nearest each other in ordination space have similar floristic assemblages, whereas those located farther apart are less similar. Vectors (arrows) indicate the significant ($P < 0.05$) joint axis correlation with decay class and substrate species, and length of the vector represents the strength of the correlation.

species composition among CWD decay classes, substrate species and the forest floor (Fig. 3.4b). Most notably, there is a distinction in species composition according to decay classes: decay class 1 and 2 are grouped apart from later decay classes and there are two distinct groupings of substrates: Conifers species (*Pinus banksiana* and *Picea* spp.) and broadleaf species (*Betula papyrifera* and *Populus* spp.), but with *Abies balsamea* showing species composition common to conifers and broadleaf species. On the other hand, species composition on the adjacent forest floor substrates differed strongly from the CWD substrates, particularly those not well decayed (Fig. 3.4b).

3.5 Discussion

We found that abundance, species richness, and species evenness of epixylic vegetation differed with both decay class and CWD substrate species. Epixylic vegetation abundance, measured as percent cover, increased with decay class from 1 to 5. This finding is consistent with previous studies (Andersson and Hytteborn 1991, Mills and Macdonald 2004, Botting and DeLong 2009, Checko et al. 2015). Likewise, species richness generally increased through the decay process, though a decrease in richness of non-vascular plant species was seen in the later stages of decay. In addition, we found that substrate species strongly influenced understorey vegetation patterns, in terms of abundance, species richness and species evenness of total, non-vascular, and vascular species. Moreover, there were significant decay class and substrate species interactions in the analyses, consistent with the conclusion that successional dynamics of epixylic plant communities varies with substrate species. Finally, patterns of epixylic species composition were also influenced by stand age and overstorey composition as well as their interaction, highlighting the importance of colonization and understorey environments associated with stand age and overstorey composition, respectively.

Non-vascular and vascular plants responded differently to decay class and substrate species. In general, all CWD substrate species show a trend of increased vegetation abundance as CWD decay advances; in particular, feathermosses and vascular plants increase in abundance with the process of CWD decay. The time available for colonization increases (Bartels and Chen 2015), along with changing structure, chemistry and moisture content of the CWD substrate along the decay continuum (Alban and Pastor 1993, Laiho and Prescott 2004, Butler et al. 2007, Petrillo et al. 2015). Thus, the combination of substrate receptivity and an increasing probability of recruitment contribute to increasing abundance of bryophytes, particularly feathermosses and vascular plants in later stages of decay. Although data do not permit an evaluation of the relative importance of these factors, the importance of increasing CWD moisture content and pH is also suggested by the high abundance of understorey vegetation found on later decay classes of *Populus* spp., which tends to have higher wood moisture content and pH than other taxa (Culberson 1955, Alban and Pastor 1993, Putna and Mežaka 2014).

Our findings highlight the importance of both decay class and substrate species as determinants of epixylic plant community richness and evenness. The observed increase in species richness of understorey vegetation in higher decay classes is in agreement with the results from previous studies, which have also noted higher species richness in advanced stages of decay (Crites and Dale 1998, Rambo and Muir 1998, Laiho and Prescott 2004, Mills and Macdonald 2004, Bunnell et al. 2008, Botting and DeLong 2009, Caruso and Rudolphi 2009, Dittrich et al. 2014, Checko et al. 2015). However, most of these studies analyzed species richness of individual groups (either lichens, bryophytes or vascular plants), whereas our study includes overall species diversity for all groups (non-vascular and vascular plants). The increase in species richness with decay reflects continuous colonisation of different species; in addition, heterogeneity in the decay process may also contribute to accumulation of species, as some "holdover" species from prior decay classes persist later in the decay process. High abundance of a few species early in the decay process was associated with low species richness. Early epixylic communities start to dominate with bark sloughing and further decomposition, and finally they are replaced by late epixylic species with humus development in the later stages of decay (McCullough 1948, Barkman 1958, Söderström 1988, Laaka 1995, Rambo and Muir 1998, Rambo 2001, Botting and DeLong 2009, Kumar et al. 2017a). The final stage of succession was characterized by epigeic species, mostly feathermosses and vascular plants that characteristically grow on the forest floor (Söderström 1988, Andersson and Hytteborn 1991, Kumar et al. 2017a). The observed decrease in the species evenness at late CWD decay stages is attributable to increasing dominance of specific non-vascular species that varied among substrate species. For example, in a companion study that utilized indicator species analysis on the same data set, we found that decay class 5 logs of *Betula papyrifera* were dominated by Brachytheciaceae and Mniaceae mosses and *Mitella nuda*, logs of *Pinus banksiana* were characterised by *Pleurozium schreberi* and *Cornus canadensis,* logs of *Picea* spp. were characterised by *Dicranum polysetum*, *Ptilium crista-castrensis* and *Gaultheria hispidula*, and logs of *Abies balsamea* were dominated by *Hylocomium splendens* (Kumar et al. 2017a).

In addition to effects of decay class, CWD substrate species also affected understorey species richness and evenness. Previous studies have noted higher species diversity on broadleaved substrate species than on conifers (McAlister 1997, Rambo 2001, Mills and Macdonald 2004, Nowinska et al. 2009, Putna and Mežaka 2014, Checko et al. 2015). In contrast, we found on average higher epixylic species richness and evenness on coniferous substrates than broadleaved substrates. More importantly, we found that the effects of substrate species on epixylic species diversity are dependent on decay class and evaluated understorey species groups. Species-specific changes in CWD physical and chemical properties may contribute to these differences (Jüriado et al. 2009, Fritz and Heilmann-Clausen 2010, Pereira et al. 2014, Putna and Mežaka 2014, Shorohova and Kapitsa 2014). The coniferous log generally decays slowly and remains stable for many years (Harmon et al. 1986, Harmon 1989, Makinen et al. 2006, Shorohova and Kapitsa 2014), which may provide better opportunities and time for colonisation of lichens and bryophytes, thereby increasing their species diversity. In addition, coniferous bark is generally more acidic (Hauck and Javkhlan 2009, Hauck 2011, Putna and Mežaka 2014) as compared to broadleaved species (Culberson 1955, Kuusinen 1996, McAlister 1997, Mežaka et al. 2008). Among substrate species in the present study, the highest species diversity of epixylic plants was found on *Pinus banksiana;* this may be attributable to its low bark pH and thicker bark (Hauck and Javkhlan 2009). Differences in trends of species richness and evenness between conifers and broadleaf substrates also include a decline in species richness of non-vascular plants from decay class 4 to 5 that is associated with a large increase in the cover of vascular plants (correlation coefficient = -0.55, $P < 0.001$) and a decrease in evenness (correlation coefficient = 0.23, $P = 0.002$), particularly of non-vascular plants. We suggest that this pattern is attributable to the growth of feathermosses and competitive effects of vascular plants at later stages of decay (Kumar et al. 2017a).

Sampling in the present study utilized a replicated chronosequence that allowed for the representation of multiple canopy successional pathways in boreal forest (Chen and Popadiouk 2002, Taylor and Chen 2011), allowing analyses that demonstrate distinct epixylic plant communities on CWD decay class and substrate species that depend on stand age and overstorey composition type. Variation in epixylic plant communities with stand age and overstory composition suggest different successional trajectories for different stands (Fig. 4a). For instance, many lichen species such as *Xanthoria fallax, Evernia mesomorpha, Cladonia* spp. and mosses such as *Dicranum* spp., *Pleurozium schreberi* were predominant in young stands, whereas the lichen *Usnea subfloridana*, and the moss species *Hylocomium splendens* and *Rhytidiadelphus triquetrus* were found exclusively in older stands. Furthermore, the lichen species *Xanthoria fallax*, *Peltigera canina*, and the mosses *Brachythecium* spp*., Mnium* spp., *Callicladium haldanianum* were found exclusively in broadleaf stands, while *Hypogymnia physodes*, *Cladonia* lichens and *Dicranum* spp., *Pleurozium schreberi* mosses were found predominantly in conifer stands. Moreover, epixylic species composition differed with CWD decay class and substrate species as well as between CWD and forest floor substrates, as found in a companion study (Kumar et al. 2017a). Previous studies have also revealed the differences in lichens and bryophytes species composition along the CWD decomposition gradient (Muhle and LeBlanc 1975, Mills and Macdonald 2005, Nascimbene et al. 2008, Botting and DeLong 2009). Differences in understorey plant species composition between conifer and broadleaf substrates have likewise been documented (Barkman 1958, Palmer 1986, McAlister 1997). Differences in moisture, texture and pH levels of the bark of substrate species have been suggested as likely determinants (Culberson 1955, Hale 1955, McAlister 1997, Mills and Macdonald 2005, Mežaka et al. 2012, Pereira et al. 2014). The beneficial effect of CWD substrates on lichens and bryophytes is in part attributable to reduced competition on deadwood surface relative to the forest floor (Humphrey et al. 2002, Dittrich et al. 2014).

Our results indicate that CWD decay class and substrate species have strong influences on epixylic vegetation abundance, diversity and composition. Furthermore, stands of different ages and overstorey composition types support different epixylic species composition, indicating that shifts in forest age structure and composition can strongly influence the successional dynamics of epixylic plant communities. Management activities strongly affect both forest age structure and composition (Chen et al. 2017b), CWD decay class and substrate species (Brassard and Chen 2008), and in turn epixylic vegetation abundance, diversity and composition. For example, short rotation harvesting regimes could result in the loss of epixylic species with affinity for suitable habitat conditions in older stands. On the other hand, epixylic species associated with specific CWD substrate species would go extinct without sufficient presence of the tree species in the overstorey to generate species-specific CWD. Therefore, to minimize impacts to sensitive lichens and bryophytes associated with CWD, it is important to maintain a diverse range of CWD decay classes and substrate species by a diverse range of forest age structure and overstorey composition. These results concur with the previous suggestions that managed boreal landscapes should consist of a mosaic of different successional stages and a broad suite of dominant overstorey species (Boudreault et al. 2002, Brassard and Chen 2008, Bartels and Chen 2015), thereby supplying appropriate amounts of CWD across the full range of decay classes and substrate species, to maintain bryophyte and lichen species habitat in forests.

3.6 Conclusion

Our results show that abundance and species richness and evenness of understorey vegetation differed with both CWD decay classes and substrate species, and between CWD and the forest floor. The trends in abundance, richness and evenness also differed for non-vascular and vascular plant groups. Abundance of understorey vegetation on CWD increased along the decompositional gradient in all CWD substrate species. These findings indicate that understorey species require suitable substrates and an extended period of time to colonize CWD. Epixylic species composition also differed with stand age, overstorey composition, decay class and substrate species, as well as with their interactions. These results highlight that conservation of epixylic diversity and restoration of their ecological functions would require forest managers to maintain a diverse range of CWD decay classes and substrate species in boreal forests. Moreover, distinct epixylic plant communities found in young and older stands and among overstorey composition types further suggest that managed boreal landscapes should consist of a mosaic of different stand ages and a broad suite of dominant overstorey species to support diverse understorey plant communities. Future research in this area should focus on further elucidation of species-specific relations between CWD substrate and understorey vegetation communities, and on better understanding the underlying mechanisms that determine community patterns.

CHAPTER 4: LINKING RESOURCE AVAILABILITY AND HETEROGENEITY TO UNDERSTOREY SPECIES DIVERSITY THROUGH SUCCESSION IN BOREAL FOREST OF CANADA

4.1 Abstract

Understorey vegetation comprises the majority of species diversity and contributes greatly to ecosystem functioning in boreal forests. Although patterns of understorey abundance, species diversity and composition associated with forest stand development are well researched, mechanisms driving these patterns remain largely speculative. We sampled fire origin stands of varying stand ages and overstorey compositions on mesic sites of the boreal forest of Canada and used structural equation modeling (SEM) to link time since fire (stand age), light availability and heterogeneity, substrate heterogeneity and soil nitrogen to understorey vegetation cover and species diversity. The most parsimonious model for total understorey cover showed a positive direct effect of stand age (r = 0.43) and an indirect effect via mean light level (0.18) and shrub cover (-0.11), with a positive total effect (0.50); the percent broadleaf canopy had a direct negative effect (-0.22) and an indirect effect via shrub cover (-0.11). The model for total understorey species richness showed an indirect effect of stand age via mean light (0.24), light heterogeneity (0.10), and substrate heterogeneity (0.07), with a positive total effect (0.52); percent broadleaf canopy had an indirect effect via light heterogeneity (0.09), and substrate heterogeneity (-0.10). Soil nitrogen did not significantly influence either understorey cover or species richness. The models for vascular plants followed similar trends to those for total understorey cover and species richness; however,

there was an opposite indirect effect of light heterogeneity for both cover and species richness of non-vascular plants. Shrub cover had positive direct and negative direct and indirect effects on both vascular and non-vascular cover and species richness. Our findings indicate that understorey cover and species diversity are driven by time since disturbance, light availability as influenced by overstorey and shrub layers, but with important additional effects mediated by light and substrate heterogeneity. Non-vascular understorey vegetation is more strongly determined by time since disturbance than vascular vegetation, and negatively affected by broadleaf tree abundance. The overall results highlight the importance of colonization, light availability and heterogeneity, substrate specialization and growth dynamics in determining successional patterns of boreal forest understorey vegetation.

4.2 Introduction

The herbaceous layer contains the greatest plant diversity in boreal and temperate forest ecosystems and contributes substantially to ecosystem functioning and services (Halpern and Spies 1995, Nilsson and Wardle 2005, Hart and Chen 2006, Gilliam 2007, Zhang et al. 2017). Although many studies have examined patterns of understorey species diversity in relation to stand development following stand replacing disturbances and overstorey characteristics (Halpern and Spies 1995, Hart and Chen 2006, 2008, Gilliam and Roberts 2014), the possible mechanisms driving these patterns remain largely speculative (Barbier et al. 2008). Two general conceptual models have been developed to explain patterns of species diversity in natural environments. The resource heterogeneity hypothesis predicts that species diversity is a function of heterogeneity in resources because plants are specialized on particular resource regimes or combinations of abiotic factors (Huston 1979, Stein et al. 2014). In contrast, the resource quantity hypothesis suggests that light is the most limiting resource for nearly all understorey species, and understorey species diversity is mainly determined by average light levels (Stevens and Carson 2002, Bartels and Chen 2010).

In disturbance-driven boreal forests, understorey vegetation cover and species diversity are expected to be strongly influenced by stand age as a consequence of dispersal limitation (vegetation requiring time to colonize available resources following the disturbance), and due to changes in resource availability that track stand development (Hart and Chen 2006) (Fig. 4.1). Early in stand development, high resource availability (light and soil nutrients) and abundant growing space generally result in rapid colonization and increases in the cover and species diversity of shade-intolerant and nutrient-demanding species (De Grandpré et al. 1993, Hart and Chen 2006). However, with further increase in age, closed overstorey canopy generally reduces the resources available to understorey plants (Bartels and Chen 2010, Reich et al. 2012, Zhang et al. 2017), thereby decreasing the cover and species richness of species that established during the stand initiation stage. For example, light is generally considered to be the most limiting resource in forest understorey (Neufeld and Young 2014). The decrease in light availability is most rapid after closure of the initial post-fire cohort of shade-intolerant hardwoods and pines, but commonly continues as shade-tolerant conifers become increasingly dominant in the overstorey at late successional stages. On the other hand, as stands further mature, substrate heterogeneity, in the form of micro-topographic tip-up mounds and coarse woody debris (CWD) of different decay stages increases (Beatty 1984, Chen and Popadiouk 2002, Bartels and Chen 2010, Kumar et al. 2017a), which might result in higher cover and species diversity of non-vascular plants. Similarly, soil nitrogen, a key limiting nutrient in fire-driven boreal forests, may also increase with stand development ages due to increased nitrogen fixation (Akaike 1974, Zackrisson et al. 2004, Hume et al. 2016), and litter production (Chen et al. 2017a), with the predominant form of nitrogen changing from NO_3^- to NH_4^+ (DeLuca et al. 2002a).

There is thus a suite of direct and indirect factors that simultaneously influence understorey cover and species diversity through stand development, but their relative importance is little understood. The pattern most commonly emphasized in prior work is that stand age is positively associated with substrate diversity and light variability, which in turn increase understorey cover and species richness (Fig. 4.1). We hypothesize that stand age will also directly influence understorey vegetation cover and species richness, because stand age reflects time for colonization for understorey plants (Vellend et al. 2006) (Fig. 4.1). In addition, stand age may indirectly increase shrub cover, which in turn decreases overall understorey cover and species richness, following reduced resource availability (Fig. 4.1). Because shade-intolerant “pioneer” plant species in boreal systems are predominantly vascular plants, we further hypothesize that understorey vascular cover and species richness will decrease, whereas non-vascular cover and species richness will increase with stand age (Fig. 4.1).

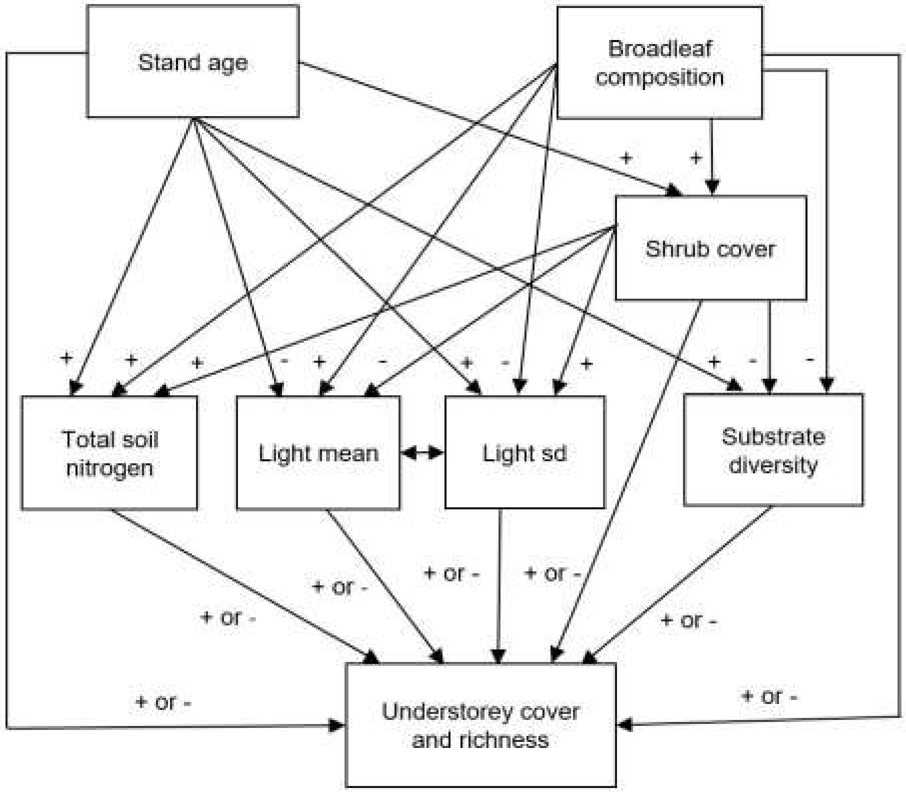

Figure 4.1. Conceptual model of hypothesized relationships showing the direct and indirect effects of exogenous and endogenous variables on understorey species richness and cover. The diagram should be interpreted as cascade of effects. The hypothesized cascade is that first exogenous variables (stand age and overstorey broadleaf composition) affect shrub cover, and then these three variable (stand age, overstorey broadleaf composition, and shrub cover) further impact resource availability and heterogeneity, understorey light availability, variability, total soil nitrogen and substrate diversity), which in turn affect understorey cover and species richness of vascular and non-vascular species. Signs ('+' or '− ') indicate direction of relationships that expected to vary with understorey plant group under study.

An important influence that complicates patterns of understorey vegetation succession in boreal forests is the existence of multiple successional pathways in canopy tree composition, (Chen and Popadiouk 2002, Peters et al. 2006, Taylor and Chen 2011). Differences in canopy species composition - particularly the relative abundance of broadleaved versus coniferous trees - may strongly affect resource quantity and heterogeneity and result in distinct environmental conditions and understorey vegetation (Barbier et al.

2008, Chávez and Macdonald 2012, Bartels and Chen 2013, Huo et al. 2014) (Fig. 4.1). Broadleaved trees generally produce conditions of higher understorey resource availability (light and soil nutrients), which increases the abundance and diversity of vascular plants, whereas late successional coniferous trees provide favourable conditions for establishment of non-vascular species because of low light availability and a recalcitrant litter layer (Messier et al. 1998, Légaré et al. 2002, Hart and Chen 2006, Chávez and Macdonald 2010). Furthermore, broadleaves and conifers also differ in terms of the quality and quantity of understorey light (Messier et al. 1998, Reich et al. 2012), as well as leaf litter quality, soil pH, and nutrient cycling (Légaré et al. 2005, Hart and Chen 2006, Chávez and Macdonald 2010, Augusto et al. 2015). Therefore, understorey vegetation is expected to be influenced by complex interactions between overstorey composition, which influences both shrub layers and resource availability and heterogeneity (Fig. 4.1). Given that a higher proportion of broadleaved trees in the overstorey leads to greater resource availability for the understorey vegetation (Messier et al. 1998, Bartels and Chen 2013), we hypothesize that increasing broadleaf proportion would increase shrub cover which will further increase the understorey vascular plant cover and species richness, but decrease non-vascular cover and species richness because coarse woody debris and thick humus layer under coniferous stands may favour bryophytes and lichens, but inhibit shrub and vascular species (Botting and DeLong 2009, Kumar et al. 2017a) (Fig. 4.1). Secondly, increasing shrub cover will indirectly decrease understorey light avaibility, which in turn may reduce overall understorey cover and species richness (Fig. 4.1). However, increasing shrub cover may also increase soil nutrient availability and light heterogeneity, which could potentially increase understorey non-vascular cover and species richness (Fig. 4.1).

The present study sought to understand multiple mechanisms for the dynamics of understorey cover and species diversity by linking post-fire stand development, overstorey composition, resource availability and heterogeneity. We sampled understorey herbaceous vegetation, stand age, basal area, overstory composition, shrub cover, understorey light conditions, percent cover of litter, exposed mineral soil, tip-up mounds, exposed rocks, fallen woody debris and total soil nitrogen, These data are integrated to assess the hypotheses elaborated above using structural equation models (SEMs).

4.3 Material and methods

4.3.1 Study area and forest inventory data

The study was conducted in the mixed-wood boreal forests north of Lake Superior and west of Lake Nipigon in the Black Spruce Forest, located approximately 100 km north of Thunder Bay, Ontario, Canada (49°23'N to 49°36'N, 89°31'W to 89°44'W). The area falls within the Moist Mid-Boreal (MBX) ecoclimatic region (Ecoregions Working Group 1989) and is characterized by warm summers and cold, snow-rich winters. Mean annual temperature and mean annual precipitation from 1981 to 2010 were 1.9ºC and 824 mm, respectively, at the closest climatic station of Cameron Falls (Environment Canada 2016). The overstorey on mesic sites is typically dominated by *Pinus banksiana* Lamb., *Populus tremuloides* Michx., *Betula papyrifera* Marsh., *Picea mariana* [Mill.] B.S.P., *Picea glauca* [Moench] Voss and *Abies balsamea* [L]. Mill. Common understorey shrubs and herbaceous species in the study area are *Acer spicatum* Lam., *Rubus pubescens* Raf., *Alnus incana* [L]. Moench, *Corylus cornuta* Marsh*., Calamagrostis canadensis* Michx., *Maianthemum canadense* Desf., *Viola renifolia* A. Gray, and *Aster macrophyllus* L. (Hart and Chen 2008). Wildfire is the most common natural disturbance agent in the study area, with site-specific fire-return intervals ranging from 40 to 820 years (Senici et al. 2013), and an average fire return interval of approximately 100 years for the past century (Senici et al. 2010).

4.3.2 Field data collection

Fire-origin stands on mesic sites were selected using stand development stages (Chen and Popadiouk 2002) to ensure a wide range of stand ages classes were sampled. Based on available fires in the study area, we were able to sample six time since stand replacing fire (TSF) classes, representing early stand initiation, late stand initiation, stem exclusion, early canopy transition, late canopy transition, and gap dynamics stages, respectively (Chen and Popadiouk 2002). At any given stand development stage on mesic sites in the region; stands originated from fire can be dominated by conifer, broadleaf or mixed-wood in the overstorey (Chen and Popadiouk 2002, Ilisson and Chen 2009, Taylor and Chen 2011). Therefore, we sampled overstorey composition from relatively pure conifer stands, broadleaf and conifer mixtures, and pure broadleaf stands on similar sites. We used stratified random sampling to select stands with a range of stand ages and overstorey composition, including pure trembling aspen, mixed conifers to various levels of broadleaf and conifer mixtures. We targeted three replicates for each stand age and overstorey type combination; however, due to the infrequency of fire and the preference of local forestry companies for harvesting mature stands, we were only able to find two replicates for 146-years-old mixedwood stands with road or boat access, resulting in a total of 53 stands sampled (Table 4.1)

Table 4.1. Characteristics of the 53 sampled stands of fire origin in the boreal forests of Ontario, Canada.

Age	Overstorey*	n	Stand density (stems ha^{-1}) or basal area (m^2 ha^{-1})*,†	Stand composition (%) †					
				Trembling aspen	White birch	Jack pine	Spruce spp.	Balsam fir	Others‡
7	B	3	11533 (4173)	92 (3)	3 (3)	3 (3)			2 (1)
	C	3	5933 (1790)	1 (1)	1 (1)	98 (1)			1 (0)
	M	3	9200 (1301)	28 (3)	15 (4)	48 (7)			4 (1)
15	B	3	10242 (60)	89 (7)	6 (4)				5 (3)
	C	3	4433 (405)	8 (5)		92 (5)			
	M	3	5400 (693)	49 (6)	3 (2)	40 (5)	5 (4)		2 (1)
33	B	3	26 (1)	93 (4)	4 (4)	1 (1)	1 (0)		1 (1)
	C	3	22 (1)	3 (2)	1 (1)	96 (3)			
	M	3	13 (2)	52 (7)		41 (9)	7 (6)		
98	B	3	49 (7)	94 (1)	2 (2)		2 (2)	1 (1)	1 (1)
	C	3	52 (2)	3 (2)		43 (12)	50 (17)	4 (3)	
	M	3	41 (5)	42 (12)	15 (12)	10 (6)	15 (8)	17 (3)	
146	B	3	57 (7)	87 (3)	7 (4)		5 (1)	2 (1)	
	C	3	52 (9)	1 (1)	2 (2)	52 (26)	37 (27)	4 (1)	4 (4)
	M	2	36 (3)	38 (2)	30 (1)		12 (5)	19 (4)	1 (1)
210	B	3	39 (3)	56 (23)	24 (18)		10 (6)	10 (5)	
	C	3	39 (8)	6 (6)	7 (4)		37 (19)	50 (12)	
	M	3	46 (3)	10 (5)	38 (5)	4 (3)	39 (7)	9 (5)	

*Overstorey types: B = broadleaf, C = conifer, M = mixed-wood.

[†]Values are means with 1 SE in parentheses. Stand density (stems ha^{-1}) was determined for the younger (7- and 15-year-old) stands and basal area (m^2 ha^{-1}) for mature stands.

[‡]The ‘Others’ category includes *Salix* spp., *Acer spicatum*, *Corylus cornuta, Sorbus decora,* and *Prunus pensylvanica.*

The selected stands were spatially interspersed across large areas in order to minimize spatial autocorrelation. All selected stands were >1 ha in area, and visually homogeneous in structure and composition. To minimize effects of edaphic variability, all selected stands were located on mesic sites on flat or mid-slope positions, with no slope exceeding 5%. All stands were located on well-drained (sandy or silty loam) glacial moraines, >50 cm in thickness, which is the prevailing soil type in the study area. To ensure that each sample stand met the selection criteria, soil pits were dug in each candidate stand to verify that the site was mesic, following procedures and criteria described in Taylor et al. (2000).

In each stand, a 400-m^2 circular plot (radius = 11.28 m), located at least 50 m from forest edges, was established, within which all sampling was done. Within the plot, all live trees were tallied by species and their corresponding diameters at breast height (DBH ≥ 9 cm, 1.3 m above the root collar) were measured and recorded. Small trees (height ≥ 1.3 m and DBH ≤ 9 cm) were measured within a 50-m^2 circular subplot (3.99 m radius; shared plot center with the 400-m^2 plot). DBH measurements were used to estimate basal area of tree species sampled. The overstorey was characterized using the proportion of broadleaf tree species (i.e. trembling aspen and white birch) in each stand, expressed as percentage basal area.

Stand age (SA, years) for each plot was determined according to records of the last stand-replacing fire and/or by coring three dominant/co-dominant trees of each tree species inside or near the plot. For stands younger than 70 years old, detailed fire records were available. For stands older than 70 years, tree ages were used to estimate TSF, described in Senici et al. (2010). Stand ages were previously determined for our study sites (Hart and Chen 2008). For stands older than 70 years, we were able to select either post-fire *Pinus banksiana* or *Populus tremuloides* trees and snags to determine TSF. No fewer than three canopy stems were sampled for each stand. For each selected tree, a core or disk at breast-height (1.3 m above root collar) was taken and brought to the laboratory. Cores were mounted on constructed core strips and disks were transversely cut and sanded to make rings visible. Rings were then counted using a hand-held magnifier until the same count was obtained three successive times. Tree ages were corrected to time since fire by adding eight years to the ring counts made at breast height using the model developed by Vasiliauskas and Chen (2002). For the oldest burned area (i.e., 209-yr-old stands), one live tree and seven snags of *Pinus banksiana* were sampled and disks were cut at the base of stems in 2005. The ring count of the live tree was 201 and that of snags ranged from 140 to 180 years in 2005. We added 8 years to the live tree age determined in 2005 as time since fire for the oldest area, corresponding to our sampling of the overstorey layer in 2013.

Understorey vegetation surveys were conducted during the period of peak vegetation cover in July-August 2016. Both shrub and ground layer were sampled by visually estimating the percent cover within a circular 400 m^2 plot (radius of 11.28 m) (Mueller-Dombois and Ellenberg 1974b). All plants were identified to the species level. The shrub layer was defined as any species of height between 1.3 and 4.0 m (Hart and Chen 2008); as such, species found in the shrub layer could also be present in the ground layer. All plant species (i.e. all of vascular and non-vascular plants) <1.3 m in height were sampled as a part of understorey vegetation. The understorey vegetation consisted of vascular plants (including tree seedlings, or saplings and shrubs), bryophytes (including all mosses, hornworts and liverworts), and lichens (consisting of all ground-growing individuals). As consistent with the “singular hypothesis” (Naeem 2002, Zhang et al. 2016) that each species contributes uniquely to ecosystem functions, we chose species richness as a measure of understorey species diversity. Species richness was calculated separately for total, vascular and non-vascular species. We also calculated species cover separately for total, vascular and non-vascular species. Since different ecological processes may regulate cover and species richness (Grace 1999), we analyzed separate models for understorey cover and species richness.

We used percentage canopy openness as a proxy for understorey light availability of all sampled stands, with measurements conducted using a spherical densiometer. Spherical densiometer measurements approximate the fraction of the sky not covered by foliage, hereafter referred as canopy openness, which is strongly positively correlated with a diverse range of understorey light availability measures (Comeau et al. 1998). All measurements were taken when the sky was uniformly overcast. Within each 400-m^2 circular plot, ten random stations were chosen to take percentage canopy openness measurements with densiometer at 1.3 m height from the ground, one reading in each direction (N, S, E, and W) and averaged for the station. The mean value of canopy openness measurements for each plot was used to represent the average light availability (quantity) and the standard deviation of these measurements was used as a measure of light heterogeneity.

Substrate heterogeneity was assessed by visually estimating the percent cover of litter, exposed mineral soil, tip up mounds, exposed rocks and fallen woody debris (CWD) on the forest floor within each 400-m^2 circular plot. We used Shannon diversity index to calculate the substrate diversity/heterogeneity. Within each selected plot, forest floor (LFH horizons) and mineral soil (0–15 cm) were sampled to determine total nitrogen content (total N, mg g^{-1}) (Hume et al. 2016). There is substantial evidence that many boreal forest plants have some capacity for uptake of organic N forms in addition to nitrate and ammonium (Lipson and Näsholm 2001), supporting the use of total N or C:N ratio as an integrated measure of N availability (Kranabetter et al. 2007). Forest floor and mineral samples taken from ten random locations were composited into one sample of each. Total N was determined by dry combustion using a LECO CNS 2000 analyzer (LECO Corporation, St. Joseph, MI, USA).

4.3.3 Data analysis

We used structural equation modeling (SEMs) to analyze the connections between empirical data and theoretical ideas. To validate the specification of SEM and aid in interpretation of the SEM results (Grace et al. 2012, 2016), we examined the bivariate relationships representing each directional causal path according to the hypotheses in Fig. 4.1, using partial regression analysis. Normality was tested for all variables based on a Shapiro-Wilk goodness-of-fit test. The complementary partial relationships to the SEM models of overstorey tree, stand ages, shrub cover, and light availability (light mean), variability (standard deviation of light) and substrate diversity to understorey cover and species richness are shown in Table S4.1 and Figs S4.1–S4.3, respectively.

The goodness-of-fit for the model was determined from the maximum likelihood chi-square tests, and the model was judged as a good fit if P value > 0.05, which indicates that the model fits produce covariance matrices not statistically different from observed covariance matrices (Grace et al. 2010). The chi-square test may be influenced by sample size, therefore, we also reported the comparative fit index (CFI) which is least affected by sample size (Rosseel 2012). Goodness-of-fit was validated using goodness-of-fit index (GFI). The GFI and CFI values > 0.95, respectively, suggest a good model fit (Rosseel 2012). Models with significant fits were compared using Akaike’s information criterion (Akaike 1974), which determines the model closest to the unknown process that generates the patterns represented by the data (Burnham and Anderson 2003).

As an alternative to the model in Fig. 4.1, we developed a prior model with stand basal area linking the effect of stand development on stand basal area and its influences on soil nitrogen, light mean, light standard deviation, and substrate diversity, while allowing stand age isolated to represent the effect of time since colonization on shrub cover and understorey cover or richness (Fig. S4.4). Initially, we considered all plausible interaction paths among the variables obtained from the study system (Fig. 4.1, S4.4). When the overall model did not produce an adequate fit, modified models were developed by removing direct and indirect pathways with low path coefficients (Grace et al. 2010). Path coefficients are standardized regression coefficients, and measure the magnitude of effect of a predictor variable on the response variable, while holding other variables constant. The significant path coefficient for directional paths (single-headed arrows) indicates that the causal relationship is statistically significant. The total effects, combining the direct and indirect standardized effects (Grace and Bollen 2005, Grace et al. 2016), of a given exogenous variable on understorey cover and species richness were also calculated to enhance the interpretation of our SEM results. The SEM was implemented using the *lavaan* package (Rosseel 2012), version 3.4.0 (R Development Core Team 2017).

4.4 Results

A total of 142 understorey species were recorded in the 53 sampled plots, which included 24 species in the shrub layer, 102 in the herb layer, 25 bryophytes and 15 lichen species. All species present in the shrub layer were also present in the herb layer.

We removed predictors that had no significant effect from subsequent models as follows. Total soil N had no significant direct effect on understorey cover nor species richness; we thus removed total soil N. Substrate diversity and light variability had no significant direct effect on total understorey cover. The direct effect paths of overstorey broadleaf composition and stand age on total understorey species richness were also insignificant. These non-significant paths were consequently removed. Similarly, for vascular species richness, direct links of stand age to vascular species richness, and to non-vascular species richness, and the direct effect paths of stand age to non-vascular species richness and substrate diversity were removed. The resultant SEM models (Fig. 4.2, Table S4.1) yielded adequate fits for total understorey cover ($\chi^2 = 0.545$, df = 1, $P = 0.460$, CFI = 1.000; GFI = 0.996), vascular cover ($\chi^2 = 0.567$, df = 2, $P = 0.753$, CFI = 1.000; GFI = 0.996) and non-vascular cover ($\chi^2 = 0.567$, df = 2, $P = 0.753$, CFI = 1.000; GFI = 0.996). The SEMs for species richness (Fig. 4.3, Table S4.1) also conformed well for total understorey species richness ($\chi^2 = 4.986$, df = 7, $P = 0.662$, CFI = 1.00; GFI = 0.975), vascular species richness ($\chi^2 = 4.540$, df = 4, $P = 0.338$, CFI = 0.994; GFI = 0.974) and non-vascular species richness ($\chi^2 = 0.702$, df =3, $P = 0.873$, CFI = 1.000; GFI = 0.996).

In the final SEM (Fig. 4.2), stand age had both positive direct (standardized coefficient, r = 0.43) and indirect effects via light mean (r = 0.18) and a negative indirect effect via shrub cover (r = -0.11), while overstorey percent broadleaf had negative a direct (r = -0.22) and indirect effect via shrub cover (r = -0.11) on total understorey cover (Fig. 4.2a). Increased shrub cover with stand age and overstorey percent broadleaf further had a negative direct effects (r = -0.25) and positive indirect effect via light mean (r = 0.10) on total understorey cover (Fig. 4.2a). Stand age also had positive indirect effect via light mean (r = 0.24), light standard deviation (r = 0.10), and substrate diversity (r = 0.07), with a positive total effect (r = 0.52) on total understorey species richness (Fig. 4.3a, Table S4.1). In contrast, overstorey percent broadleaf had a positive indirect effect via light standard deviation (r = 0.09), and a negative indirect effect via substrate diversity (r = -0.10) on total species richness (Fig. 4.3a). Shrub cover had a positive indirect

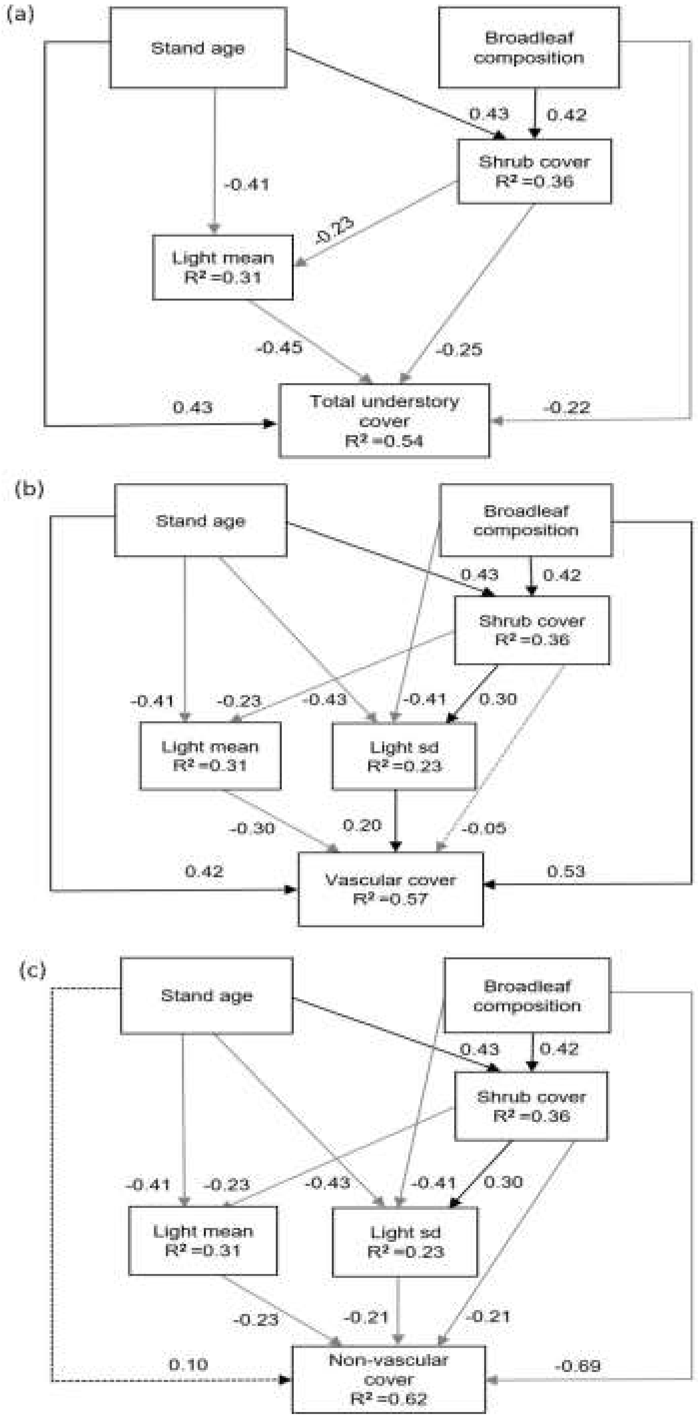

Figure 4.2. Structural equation models (SEM) linking stand age, overstorey broadleaf composition to shrub cover and all of three variables to light availability, light variability and substrate diversity to total, non-vascular and vascular understorey species cover. Solid lines represent statistically significant positive paths and grey lines show the significant negative paths at ($P \leq 0.05$), except for the path between shrub cover and light availability ($P = 0.06$). Dashed

arrows indicate non-significant paths (P > 0.05) that were necessary to include in order to obtain the most parsimonious model. The coefficients are standardized for each causal path.

effects via light mean (r = 0.13) and a negative indirect effect via light standard deviation (r = -0.07) on total species richness (Fig. 4.3a).

Stand age had similar direct (r = 0.42) and indirect effects via light mean (r = 0.12) on vascular cover as total understorey cover. However, stand age also had negative indirect effect via light standard deviation (r = -0.09) (Fig. 4.2b). Overstorey percent broadleaf had a positive direct effects (r = 0.53) and a negative indirect effect via light standard deviation (r = -0.08) on vascular cover. Increased shrub cover had further positive indirect effect via light mean (r = 0.07) and light standard deviation (r = 0.06) on vascular cover (Fig. 4.2b). Stand age also had positive indirect effect via shrub cover (r = 0.12), light mean (r = 0.17) and substrate diversity (r = 0.07), while overstorey percent broadleaf had positive a direct (r =0.30) and indirect effect via shrub cover (r = 0.12) and a negative indirect effect via substrate diversity (r = -0.11) on vascular species richness (Fig. 4.3b). Shrub cover further had positive a direct (r = 0.29) and indirect effect via light mean (r = 0.09) on vascular species richness (Fig. 4.3b).

In contrast to results for vascular plants, stand age had a positive indirect effect via light mean (r = 0.09) and light standard deviation (r = 0.09), and a negative indirect effects via shrub cover (r = -0.09) on non-vascular plant cover (Fig. 4.2c). Overstorey percent broadleaf had negative a direct (r = -0.69), and indirect effect via shrub cover (r = -0.09), and a positive indirect effects via light standard deviation (r = 0.09) on non-vascular cover (Fig. 4.2c). Shrub cover further had negative a direct (r = -0.21) and indirect effect via light standard deviation (r = -0.06) and a positive indirect effects via light mean (r = 0.05) on non-vascular cover (Fig. 4.2c). Stand age also had positive indirect effect via light mean (r = 0.21), and light standard deviation (r =

0.14) and a negative indirect effects via shrub cover (r = -0.11) on non-vascular species richness (Fig. 4.3c). Overstorey percent broadleaf had negative a direct (r = -0.31) and indirect effect via shrub cover (r = -0.11) and a positive indirect effect via light standard deviation (r = 0.14). Shrub cover further had a negative direct (r = -0.25) and indirect effect via light standard deviation (r = -0.10) and positive indirect effects via light mean (r = 0.12), on non-vascular species richness (Fig. 4.3c).

The resultant alternate models with basal area as a path between stand age and resource availability and heterogeneity (Fig. S4.5, S4.6) had a good fit to the data for total understorey cover (χ^2 = 3.690, df = 5, P = 0.595, CFI = 1.000; GFI = 0.978), and species richness (χ^2 = 12.212, df = 13, P = 0.510, CFI = 1.000; GFI = 0.954). Similarly, alternate models for vascular cover and richness (χ^2 =2.974, df = 7, P = 0.887, CFI = 1.000; GFI = 0.985; and χ^2 = 7.515, df = 9, P = 0.584, CFI = 1.000; GFI = 0.963, respectively), and non-vascular cover and richness (χ^2 = 0.669, df = 2, P = 0.716, CFI = 1.000; GFI = 0.995; and χ^2 = 5.124, df = 8, P = 0.744, CFI = 1.000; GFI = 0.974, respectively) also conformed well to the data.

In the alternate models, stand age had a positive direct effect on total understorey cover (r = 0.43) and stand basal area (r = 0.78). Basal area also had a positive indirect effect via light mean (r = 0.24) on total understorey cover (Fig. S4.5a), and a positive indirect effect via light mean (r = 0.31), light standard deviation (r = 0.12) and substrate diversity (r = 0.07) on total understorey species richness (Fig. S4.6a). Similarly, stand age had a positive direct effect on vascular cover (r = 0.42) and stand basal area (r = 0.78). Increased basal area additionally had a positive indirect effect via light mean (r = 0.17) and a negative indirect effect via light standard deviation (r = -0.10) on vascular cover (Fig. S4.5b), and a positive indirect effect via light mean (r = 0.23) and substrate diversity (r = 0.07) on vascular species richness (Fig. S4.6b). Finally,

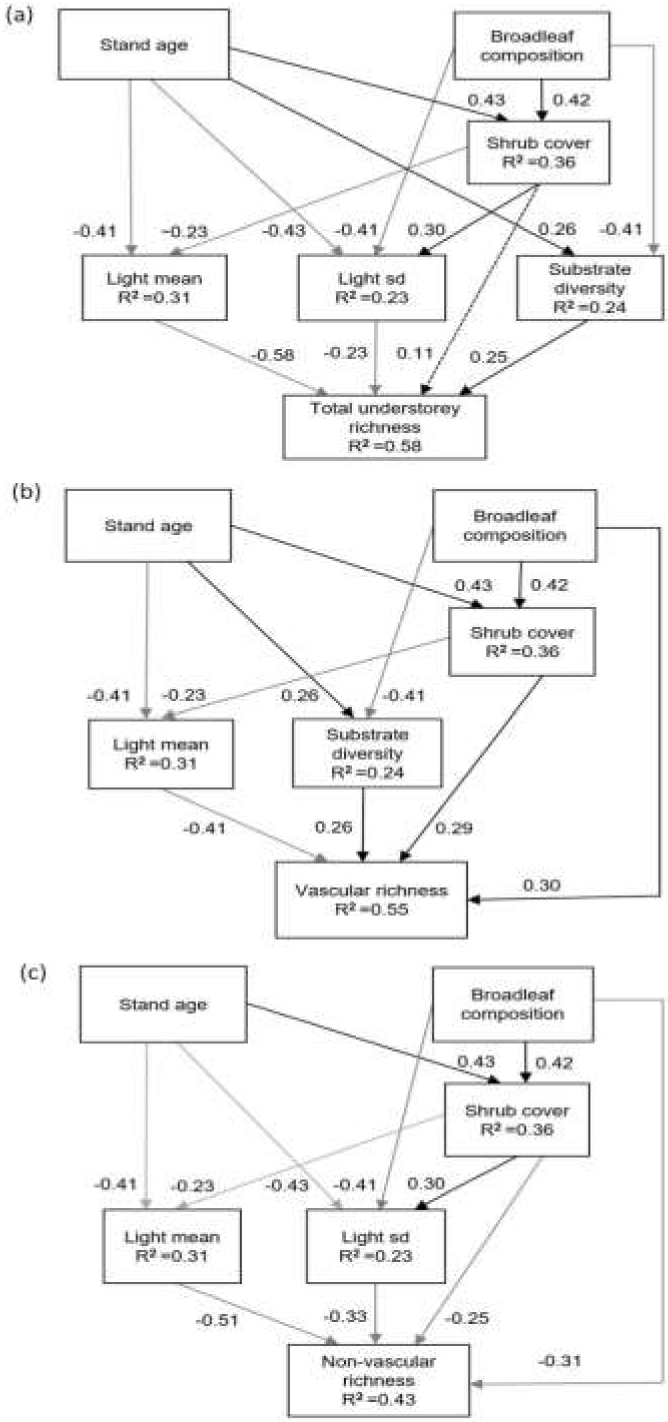

Figure 4.3. Structural equation models (SEM) linking stand age, overstorey broadleaf composition to shrub cover and all of three variables to light availability, light variability and substrate diversity to total, non-vascular and vascular understorey species richness. Solid lines represent statistically significant positive paths and grey lines show the significant negative paths at ($P \leq 0.05$), except for the path between shrub cover and light availability ($P = 0.06$). Dashed

arrows indicate non-significant paths ($P > 0.05$) that were necessary to include in order to obtain the most parsimonious model. The coefficients are standardized for each causal path.

stand age had a positive indirect effect via basal area ($r = 0.41$) on non-vascular cover (Fig. S4.5c), and increased basal area with stand age further had a positive indirect effect via light mean ($r = 0.27$) and light standard deviation ($r = 0.17$) on non-vascular species richness (Fig. S4.6c).

4.5 Discussion

The analysis presented is, to our knowledge, the first to empirically evaluate alternative mechanisms that drive patterns of understorey cover and species richness through forest stand development in boreal forests – specifically addressing the multiple and complex interactions between stand age, overstorey composition, shrub layer development, and the influences of each of these on understorey resource availability and heterogeneity. Results indicate that several direct and indirect processes drive cover and species richness of understorey vegetation. Perhaps the most obvious pattern is that of a positive relationship between stand age and understorey vegetation cover, which is expected due to time-dependent colonization and plant growth following a disturbance event. The SEM models presented distinguish this process from correlated changes in environmental variables, such as light availability and competitive interactions with shrub-layer vegetation. Previous studies have also emphasized that presence of different microsites, such as diverse coarse woody debris in mature stands, can increase vegetation cover and species richness, particularly of bryophytes and lichens (Mills and Macdonald 2004, Marialigeti et al. 2009, Kumar et al. 2017a). Here, SEM models detected a positive effect of variation in light levels for vascular and non-vascular plant cover, but microsite variability was excluded as a predictor. Coarse woody debris is the most abundant source of substrate heterogeneity in this system; in related work, we found that early decay-class woody debris showed much lower total vegetation cover than did the forest floor (Kumar et al. 2017a).

Overstorey canopy composition and shrub cover were also influential factors affecting cover, with particularly strong differential impacts on vascular vs. non-vascular plants. Increased abundance of broadleaf species in the canopy had a negative direct effect on total cover driven by large negative effects on non-vascular plants; in contrast, broadleaf abundance had a positive direct effect on vascular plant cover. The negative effects are broadly consistent with resource pre-emption by the overstorey reducing resources available to understorey plants (Grime 1973, Reich et al. 2012, Neufeld and Young 2014, Zhang et al. 2016, 2017). The pronounced negative effects of broadleaf trees on non-vascular plant cover and species richness may also be related to physical inhibitory and allelopathic effects of broadleaf litter on bryophyte and lichen species (Légaré et al. 2005, Hart and Chen 2006, Startsev et al. 2008, Marialigeti et al. 2009). The strong positive relationship between overstorey broadleaf proportional abundance and vascular understorey plant cover is probably best viewed as a negative effect of acidic, recalcitrant conifer litter on vascular plants (Beatty 1984, Barbier et al. 2008). Shrub cover was positively associated with stand age and overstorey broadleaf composition, and in turn negatively influenced total understorey cover. The positive association between shrub cover and stand age is most likely due to time required for relatively large shrub species, such as *Acer spicatum* and *Corylus cornuta*, to become dominant in the understorey. Similar to broadleaf composition, shrub cover positively influenced the vascular richness and negatively influenced the non-vascular cover and species richness. The soil nutrient feedback and microclimatic conditions under shrub layers particularly benefitted the vascular species. This is evident through a positive correlation between shrub cover and total soil nitrogen (Table S4.2). In contrast, the negative effects of the shrub cover on non-vascular species is likely related to inhibitory effects of the shrub litter on bryophyte and lichen species (Frego and Carleton 1995, Thompson et al. 2005, Bartels and Chen 2013).

Light availability was negatively correlated with stand age and shrub cover, but did not differ with overstorey broadleaf composition. Boreal forest understories are often characterized by dense shrub thickets that reduce light levels at the forest floor (Messier et al. 1998, Aubin et al. 2000, Bartels and Chen 2013). This is evident in our study as a negative correlation between shrub cover and light availability (Fig. S4.1 and Table S4.2). We found no association between overstorey composition and understorey light levels. This result is similar to previous studies in the boreal forest that have not found differences in the light environment in the understorey across a canopy compositional gradient from trembling aspen stands to mixed to conifers stands (Messier et al. 1998, Légaré et al. 2001).

Light variability was negatively associated with stand age and with the proportion of broadleaf canopy, which indirectly had an overall negative impact on understorey cover and species richness of total and non-vascular plants. In many forest types, stands at the "stem exclusion stage" show predictably low understorey light levels, with an increase in canopy openness and light penetration later in stand development (Oliver and Larson 1996, Jules et al. 2008, Halpern and Lutz 2013). However, this pattern is less pronounced in boreal forests, with light penetration to the forest floor generally decreasing monotonically with stand age (Ross et al. 1986). Most boreal understorey species are shade-tolerant, and light availability in the understorey is high relative to other forest types (Messier 1996).

We found that substrate diversity was positively associated with stand age, which indirectly increased the overall understorey species richness but not cover. This result is consistent with increases in microsite heterogeneity in the form of tip-up mounds and coarse woody debris with increasing stand age (Mills and Macdonald 2004, Brassard and Chen 2006, Bartels and Chen 2010, Kumar et al. 2017a), facilitating coexistence by edaphic niche specialization. However, substrate diversity was negatively associated with overstorey broadleaf composition, and this indirectly reduced the vascular and total species richness of understorey plants. Environmental and resource conditions are more homogenous over space and time in pure stands as compared to the mixedwood stands, which are characterized by greater heterogeneity in understorey resources (Bartemucci et al. 2006, Macdonald and Fenniak 2007, Bartels and Chen 2010), and are generally more productive than conifer or broadleaf stands (Zhang et al. 2012, Zhang et al. 2017). Enhanced productivity is expected to result in accelerated stand-development and self-thinning; this is expected to enhanced substrate diversity in the form of coarse woody debris and exposed mineral soil in productive or mixed wood stands (e.g., Sturtevant et al. 1997).

We found no effect of total nitrogen, used as a measure of soil nutrient availability, on understorey vegetation cover nor on species richness with stand development on mesic sites of boreal forests. We also used total carbon to total nitrogen ratio or total phosphorus concentration, collected from the same sites (Hume et al. 2016), in addition to total soil nitrogen, and we found no effect of these nutrient variables on understorey vegetation cover and species richness. Our study sites, unlike others used for examining the effects of the changes of soil nutrients due to topography and soil parent material on understorey vegetation (Chipman and Johnson 2002, Chen et al. 2004), are inherently similar in topography and soil texture (Hume et al. 2016). Therefore, our results indicate that the changes of soil nutrient availability through stand development on inherently similar sites (Hume et al. 2016) have substantially less influence on understorey vegetation than time since colonization, light availability and heterogeneity, and substrate heterogeneity mediated via overstorey development.

4.6 Conclusion

Our study demonstrated that multiple processes determine changes in understorey vegetation with stand development in boreal forests. Our results indicate that indirect effects of stand age and overstorey composition could either amplify or dampen effects of resource availability and heterogeneity on understorey vegetation, in terms of both total cover and species richness. The forest overstorey-understorey relationship is complex and is context dependent, and our results demonstrate that multiple interactions occur simultaneously. For example, we found that shrub cover has both facilitative and inhibitory effects on boreal understorey plant communities: shrub cover enhanced heterogeneity in the light environment, promoting species richness of vascular plants, but reducing that of non-vascular plants. This indicates the importance of both biotic and abiotic factors in determining variability in understorey vegetation. We did not find that soil resource availability was the main driver of either understorey cover or species richness. Rather, there are large, independent effects of light resource variability and substrate diversity, both of which are affected by stand age and overstorey composition, that are essential to understanding patterns of understorey vegetation abundance and diversity with stand development in boreal forests. Our findings highlight the conclusion that multiple mechanisms, including time since colonization, light availability and heterogeneity, and substrate heterogeneity, determine patterns of understorey vegetation abundance and diversity through forest stand development following stand-replacing disturbances.

CHAPTER 5: DYNAMICS OF UNDERSTOREY BIOMASS, PRODUCTION AND TURNOVER ASSOCIATED WITH LONG-TERM OVERSTOREY SUCCESSION IN BOREAL FORESTS OF CANADA

5.1 Abstract

Understorey vegetation hosts the most diversity in temperate and boreal forest ecosystems and contributes substantially to ecosystem processes and functions. Despite its ecological importance, the dynamics of understorey biomass, production and turnover rates following stand-replacing disturbance and throughout forest succession remain poorly understood. Using a replicated chronosequence spanning 210 years following fire, we examined the dynamics of understorey biomass, production and turnover associated with stand development and overstorey types (broadleaf, mixedwood, and conifer) in the central boreal forest of Canada. We found that understorey herbaceous biomass and production were related as both increased with stand age following fire, peaked in early stages of stand development, and then remained relatively stable thereafter with slight increase in canopy transition stage, whereas woody and bryophytes biomass and production were found to be related as they increased with stand age, peaked at intermediate stages and decreased thereafter. Herbaceous and woody turnover rates were higher is early stages, and those of bryophytes were higher at intermediate to later stages of succession. Understorey total, woody and herbaceous biomass, production and turnover rates were higher in deciduous broadleaf overstorey and those of bryophytes were higher in conifer stands, with mixedwood being intermediate between broadleaf and coniferous stands in supporting understorey biomass and production. Our findings suggest that understorey biomass, production

and turnover rates in the boreal forest are driven by time since colonization following stand replacing fire, coupled with changes in resource availability and heterogeneity mediated via overstorey succession. This study highlights the role of overstorey succession in long-term forest understorey biomass, production and turnover dynamics and its importance for modeling total forest ecosystem contribution to the global carbon cycle.

5.2 Introduction

In boreal and temperate forest ecosystems most of the diversity is in the understorey (Whigham 2004, Gilliam and Roberts 2014), however the ecological functions of understorey plants are studied less frequently as compared to overstorey trees because of their small stature and biomass (Nilsson and Wardle 2005, Gilliam 2007). Despite a small proportion in biomass from understorey plants, the understorey can contribute substantially to total ecosystem production because of their high turnover rates that contribute to carbon and nutrient cycles (Chapin 1983, Gilliam 2007, Cavard et al. 2011). This contribution is even more important in evergreen forests where the turnover rate of overstorey trees is low (Chapin 1983). In addition, in disturbed ecosystems, understorey plants are the most important component of senesced material returned to soil at early stages, as they take up the available nutrients after disturbance and return them rapidly back to soil through decomposition and thus contribute to soil nutrient pools or slow down the nutrient loss after disturbance (Zavitkovski 1976, Chapin 1983, Palviainen 2005). This results in an increase in the cycling and accumulation of carbon and nutrients, which in turn results in higher productivity of both overstorey as well as understorey plants. Therefore, understanding understorey biomass, production and turnover rate is essential to estimate the processes of growth and survival, and total forest ecosystem contributions to carbon and nutrient cycles.

In the forest ecosystem, overstorey biomass and production generally shows a rapid increase in young stands, peaks at intermediate stages, and gradually declines in later stages (Gower et al. 1996, Ryan et al. 1997, Taylor et al. 2014, Chen and Luo 2015). Understorey biomass, production and turnover rates are also expected to change with stand development, as a result of associated changes in resource avaialiblity that track stand development and time avaliable for understorey species to colonize (Kumar et al. 2017b). For example, at early stages of stand development, higher light and nutrients availability coupled with abundant growing space result in rapid colonization rates, and increase the cover or biomass of herbaceous species in the understorey (Hart and Chen 2006, 2008, Kumar et al. 2017b). With further development of the stand, resource pre-emption by the overstorey canopy reduces the resources available to understorey vegetation (Bartels and Chen 2010, Reich et al. 2012, Kumar et al. 2017b), thereby decreasing the cover and biomass of previously established shade-intolerant and nutrient-demanding herbaceous species. However, species tolerant of low resource conditions, such as woody plants and bryophytes, increase in abundance and biomass under shade-tolerant trees in late-successional conditions (DeLuca et al. 2002b, Zackrisson et al. 2004, Hart and Chen 2006, 2008). As the stand further matures, the understorey environment becomes more heterogeneous as a result of canopy breakup (Chen and Popadiouk 2002, Bartels and Chen 2010, Kumar et al. 2017a), which might increase the overall (woody and non-woody) cover or biomass of understorey vegetation. Although, previous studies have estimated understorey production (Zavitkovski 1976, Hanley and Brady 1997, Gonzalez-Hernandez et al. 1998, Kolari et al. 2006, Sakai et al. 2006), long-term development of understorey production in relation to stand age remain poorly understood (Bond-Lamberty et al. 2004, Mack et al. 2008). The existing data on understorey biomass, production and turnover rates are scanty and inadequate to allow for a comprehensive evaluation of long-term dynamics of understorey biomass, production and turnover rates. Furthermore, despite the characteristic ddiversity of understorey plant life forms, few studies have simultaneously examined all species groups and life forms.

Through succession in boreal forests, structure and composition of the overstorey generally tend to vary, because of differences in pre-disturbance forest species composition and post-disturbance availability of tree species propagules, results in either broadleaf, conifers or mixedwood dominance at given stage of stand development (Chen and Popadiouk 2002, Peters et al. 2006, Taylor and Chen 2011). Although understorey biomass and production are expected to change with stand age (as hypothesized above), how changes in overstorey species composition, resulting from divergent successional pathways, interact and influence temporal dynamics in understorey biomass, production and turnover rates remains unclear. Overstorey species composition influences understorey environment through modification of resources, particularly availability and variability of light, water and soil nutrient resources and other effects such as physical characteristics of litter layer (Barbier et al. 2008, Augusto et al. 2015), which in turn can affect the understorey biomass, production and turnover rates. Deciduous broadleaf overstorey transmits more light to the understorey and deciduous litter is much higher in nutrient content than conifer litter, increasing base cations and pH, thus favouring herbaceous and woody plants, while inhibiting most bryophytes (Paré and Bergeron 1996, Légaré et al. 2005, Hart and Chen 2006, Chytrý et al. 2010, Augusto et al. 2015). In contrast, coniferous litter is high in lignin content, C/N ratio and reduces soil pH and nutrient content, favouring bryophytes (Prescott 2002, Augusto et al. 2015). Mixedwood stands thus provide a heterogeneous environment in the understorey and exhibit greater variability in understorey resources (Bartemucci et al. 2006, Macdonald and Fenniak 2007), which might result in the higher understorey biomass, production and turnover rates. However, empirical evidence for overstorey effects on understorey biomass, production and turnover rates is limited (Gonzalez-Hernandez et al. 1998, Cavard et al. 2011, Zhang et al. 2017).

This study examines the effect of stand development following stand-replacing fire with diverse overstory composition types on understorey biomass, production and turnover rates in the central boreal forests of Canada. We specifically address the following questions: i) how biomass, production and turnover rates of understorey total, herb, woody and bryophytes change following stand replacing fire, and ii) whether age-related dynamics in understorey biomass, production and turnover rates differ among forest compositional type? Given that understorey dynamics vary with life forms, we hypothesized that following fire, understorey herbaceous biomass, production and turnover rates would be higher in the early stages of stand development because of rapid colonization rates of fast growing herbaceous species; whereas, bryophytes, biomass, production and turnover rate would be higher in the intermediate stages of stand development because of increased time for colonization for bryophytes to become dominant. In addition, woody as well as total understorey biomass, production and turnover rates would also be higher in intermediate stages because woody plants will have long time to maximize their biomass and production, and do not turn over until maturation. Furthermore, given the known effects of overstorey composition on understorey, we hypothesize that independent of stand age, deciduous broadleaf overstorey would support higher understorey total, herb and woody biomass, production and turnover rates relative to those formed by coniferous overstorey, with mixed overstorey supporting intermediate understorey biomass, production and turnover rate.

5.3 Materials and methods

5.3.1 Study area

The study was conducted in the mixed-wood boreal forests north of Lake Superior and west of Lake Nipigon in the Black Spruce Forest, located approximately 100 km north of Thunder Bay, Ontario, Canada (49°23'N to 49°36'N, 89°31'W to 89°44'W). The area falls within the Moist Mid-Boreal (MBX) ecoclimatic region (Ecoregions Working Group 1989) and is characterized by warm summers and cold, snow-rich winters. Mean annual temperature and mean annual precipitation from 1981 to 2010 were 1.9ºC and 824 mm, respectively, at the closest climatic station of Cameron Falls (Environment Canada 2016). The overstorey on mesic sites is typically dominated by *Pinus banksiana* Lamb., *Populus tremuloides* Michx., *Betula papyrifera* Marsh., *Picea mariana* [Mill.] B.S.P., *Picea glauca* [Moench] Voss and *Abies balsamea* [L]. Mill. Common understorey shrubs and herbaceous species in the study area are *Acer spicatum* Lam., *Rubus pubescens* Raf., *Alnus incana* [L]. Moench, *Corylus cornuta* Marsh*., Calamagrostis canadensis* Michx., *Maianthemum canadense* Desf., *Viola renifolia* A. Gray, and *Aster macrophyllus* L. (Hart and Chen 2008). Wildfire is the most common natural disturbance agent in the study area, with site-specific fire-return intervals ranging from 40 to 820 years (Senici et al. 2013), and an average fire return interval of approximately 100 years for the past century (Senici et al. 2010).

5.3.2 Sampling design

To determine the effect of time since fire, we selected stands on mesic sites covering a wide range of stand age classes. As a result of available fires in the study area, we were able to sample six time since stand replacing fire (TSF) classes, representing early stand initiation, late stand initiation, stem exclusion, early canopy transition, late canopy transition, and gap dynamics stages, respectively (Chen and Popadiouk 2002). At any given stand development stage on mesic sites in the region; stands originated from fire can be dominated by conifer, broadleaf or mixed-species in the overstorey (Chen and Popadiouk 2002, Ilisson and Chen 2009, Taylor and Chen 2011): in so far as possible we sampled all three overstorey stand types (i.e. broadleaf, conifer, and mixedwood) for each stand age class. We targeted three replicates for each age and overstorey compositional type, however due to the infrequency of fire and the preference of local forestry companies for harvesting mature stands, we were only able to find two replicate for 146-years-old mixedwood and broadleaf stands with road or boat access, resulting in a total of 52 stands sampled.

The selected stands were spatially interspersed across large areas in order to minimize spatial autocorrelation. All selected stands were >1 ha in area, and visually homogeneous in structure and composition. To minimize effects of edaphic variability, all selected stands were located on mesic sites on flat or mid-slope positions, with no slope exceeding 5%. All stands were located on well-drained (sandy or silty loam) glacial moraines, >50 cm in thickness, which is the prevailing soil type in the study area. To ensure that each sample stand met the selection criteria, soil pits were dug in each candidate stand to verify that the site was mesic, following procedures and criteria described in Taylor et al. (2000).

Time since stand replacing disturbance (SA, years) for each plot was determined according to records of the last stand-replacing fire and/or by coring three dominant/co-dominant trees of each tree species inside or near the plot. For stands younger than 70 years old, detailed fire records were available. For stands older than 70 years, tree ages were used to estimate TSF, described in Senici et al. (2010). Stand ages were previously determined for our study sites (Hart and Chen 2008). For stands older than 70 years, we were able to select either post-fire *Pinus banksiana* or *Populus tremuloides* trees and snags to determine TSF. No fewer than three canopy stems were sampled for each stand. For each selected tree, a core or disk at breast-height (1.3 m above root collar) was taken and brought to the laboratory. Cores were mounted on constructed core strips and disks were transversely cut and sanded to make rings visible. Rings were then counted using a hand-held magnifier until the same count was obtained three successive times. Tree ages were corrected to time since fire by adding eight years to the ring counts made at breast height using the model developed by Vasiliauskas and Chen (2002). For the oldest burned area (i.e., 209-yr-old stands), one live tree and seven snags of *Pinus banksiana* were sampled and disks were cut at the base of stems in 2005. The ring count of the live tree was 201 and that of snags ranged from 140 to 180 years in 2005. We added 8 years to the live tree age determined in 2005 as time since fire for the oldest area, corresponding to our sampling of the overstorey layer in 2013.

5.3.3 Field data collection

In each stand, a 400-m^2 circular plot (radius = 11.28 m), located at least 50 m from forest edges, was established, within which all sampling was done. Within each plot, overstorey and understorey were classified based on the crown positions in a stand (Avery and Burkhart 2002). In the 8-16 yr-old stands, all trees with ≥ 1.3 m in height were part of canopy. For stands ≥ 34 years of age, overstorey trees coincided with trees with diameter at breast height (d.b.h., 1.3 m above root collar) ≥ 9.0 cm. Overstorey trees were tallied for the entire plot, with each tree being identified to the species level, and measured for height and diameters at breast height (DBH ≥ 9 cm, 1.3 m above the root collar). Small trees (height ≥ 1.3 m) were measured within a 50-m^2

circular subplot (3.99 m radius; shared plot center with the 400-m^2 plot). Stem density and basal area by species were summed to plot level and overstorey type was assigned based on the percentage of stem density and basal area for 8-16-yr-old and older stands, respectively. Broadleaf and conifer stands were defined as having >65% broadleaf or conifer tree species composition by stem density or stand basal area. Mixedwood stands were defined as those where neither broadleaf nor conifer tree species comprised more than 65% of composition by stem density or stand basal area.

Understorey vegetation was classified according to their life form, because different life forms or species have inherent capability to allow varying amounts of light reaching to understorey according to their stature (Klinka et al. 1996, Chen et al. 2004, Kumar et al. 2017b). Life forms were grouped into woody plants (shrubs and trees), herbaceous plants (forbs, graminoids, clubmosses, and ferns), and terrestrial bryophytes and lichens. Understorey sampling was conducted following Canada's National Forest Inventory Ground Sampling Guidelines. In this protocol, woody and non-woody (i.e. herbaceous plants and bryophytes) life forms were sampled differently, as woody plants require larger spatial sampling efforts. To sample the biomass and production of the woody plants, three 2×2 m subplots were randomly established within each 400 m^2 main plots. The height and stem diameter of individual species (with basal diameter or 15 cm above root collar $\leq$ 5 cm) were numbered, tagged and measured for two consecutive years. Height of the saplings was measured as the vertical distance between the stem base and the base of the highest live meristem and in case of large shrubs, height was measured to the highest live leaf or highest live twig if the species was deciduous (Clark and Clark 2001). Stem diameter was measured with the help of caliper to the nearest 0.1 mm at the marked point of measurements at 15 cm above ground level for some species and at basal diameter for other species because of their sizes. The woody biomass was estimated using allometric equations (Smith and Brand 1983, Bond-Lamberty et al. 2002) (scaled up to (Mg $ha^{-1}year^{-1}$), over two consecutive years, where annual production was the difference between two years. The biomass production was calculated as the net change in biomass between two years plus biomass loss due to mortality.

For herbaceous plants and terrestrial bryophytes, one 2 × 2 m subplot was randomly established in each plot, where the percentage of cover and height for all herbaceous plants and bryophytes were recorded for two consecutive years. To determine the allometric relationship, i.e. biomass estimated from cover and height, we also established and harvested a total of 21 2 × 2 m subplots outside the main plots including all stand ages and overstorey types. All harvested samples were sorted by species and brought to the laboratory for biomass determination. In the laboratory, all harvested samples were oven dried at 70°C for 48-72 h to constant weight and weighed. Understorey species were grouped into the following growth forms: short forb (<40 cm), tall forb (>40 cm), clubmosses, horsetails, graminoids, bryoids (mosses and lichens) (see Fig. S5.1). These relationships were then used to estimate biomass from cover and height for each species in each plot. Therefore, changes in the percent cover and height in two consecutive years, using allometric equations (biomass ~ cover and height) helped us to estimate the biomass difference between two years. Because above ground parts of the herbaceous plants die annually, annual production was considered equal to their peak biomass (August) in 2016. For bryophytes, change in the heights and cover values between two years were used to estimate annual growth rates. Turnover rate (per year) for total, shrub, herb and bryophytes were calculated as the ratio of the total amount of live biomass produced in one year (Mg $ha^{-1}year^{-1}$) over their respective mean standing biomass (Mg ha^{-1}) expressed as a percentage.

5.3.4 Data analysis

To determine the effects of time since fire (stand age) and overstory composition type on total, woody, herbaceous and bryophytes biomass, production and turnover rates, following general linear model was used:

$$Y_{ijk} = \mu + A_i + C_j + A \times C_{ij} + \varepsilon_{k(ij)} \qquad (2)$$

where: Y_{ijk} is understorey biomass (standing biomass, Mg ha^{-1}), production (Mg ha^{-1} year^{-1}) and turnover rate (% yr^{-1}) of a given constituent, μ = overall mean, A_i = stand age class (i= 1, 2, 3…6), C_j = overstory composition (j=1, 2, 3), $\varepsilon_{k(ij)}$ (k= 1,2,3) is sampling error among replicates within stand age and overstory combination type. We separately analyzed biomass, production and turnover rate for total (woody, herb and bryophyte combined), woody, herbaceous and bryophytes. We used Shapiro–Wilk test to check assumptions of normality, and Bartlett's test for homogeneity of variance. When necessary, we used natural log-transformation to better meet these assumptions. We also performed multiple comparisons of means (a = 0.05) using Tukey's honest significant differences (HSD) test. All statistical analyses were performed in R, version 3.4.2 (R Development Core Team 2017).

5.4 Results

5.4.1 Understorey biomass

Biomass of all understorey components differed significantly with stand age and overstorey type, without significant interaction effects of stand age and overstorey type, except for bryophyte biomass (Table 5.1). Total understorey biomass increased continuously with stand age, reached a maximum in 146-year-old stands, and decreased thereafter (Fig. 5.1A). Total understorey biomass was significantly higher among broadleaf stands than conifer stands, while total understorey biomass values in mixedwood stands were intermediate to those of broadleaf and conifer stands (Fig. 5.1A). The effects of stand age and overstorey type on woody biomass were similar to those for total understorey biomass and followed similar dynamics (Table 5.1, Fig. 5.1B). Herbaceous biomass also differed significantly with stand age and overstorey type (Table 5.1); it increased from 8 to 16-year-old stands, peaked at 16-year-old stands in broadleaf and mixedwood stands, but peaked at 34-year-old in conifer stands (Fig. 5.1C). Among broadleaf stands, herbaceous biomass decreased up to 98-year-old stands, increased in 146-year-old stands, and then decreased in 210-year-old stands (Fig. 5.1C). Among mixedwood stands, herbaceous biomass decreased to 34-year-old stands, increased in 98-year-old stands, and remained unchanged thereafter in 146 and 210-year-old stands (Fig. 5.1C). For conifer stands, herbaceous biomass decreased from 34-year-old stands to 98-year-old stands, and remained unchanged thereafter (Fig. 5.1C). Herbaceous biomass was significantly higher among broadleaf stands than conifer stands, while herbaceous biomass in mixedwood stands were intermediate to those of broadleaf and conifer stands (Fig. 5.1C). Bryophyte biomass differed significantly with stand age and overstorey type with a significant interaction effect of stand age and overstorey type (Table 5.1). Bryophyte biomass at 8 and 16-year-old stands did not differ among overstorey type, while in 34, 98, 146 and 210-year-old stands, bryophyte biomass was higher among conifers than mixedwood or broadleaf stands (Fig. 5.1D). Overall, bryophyte biomass was highest in 98-year-old conifer stands (Fig. 5.1D).

Table 5.1. Effects of time since disturbance (A, stand age in years) and overstorey composition type (C) and their interactions on understorey total, woody, herb and bryophyte biomass (Mg ha^{-1}), production (Mg ha^{-1} year^{-1}) and turnover rate (percent yr^{-1}). Bold fonts indicates statistical significance (α = 0.05).

Attribute	Source	df	SS	F	P
Total biomass	A	5	111.18	8.54	**<0.001**
	C	2	17.27	3.32	**0.048**
	A × C	10	29.47	1.13	0.369
Woody biomass	A	5	99.72	7.63	**<0.001**
	C	2	21.76	4.16	**0.024**
	A × C	10	36.30	1.39	0.227
Herb biomass	A	5	0.02	3.02	**0.023**
	C	2	0.04	13.95	**<0.001**
	A × C	10	0.02	1.43	0.208
Bryophyte biomass	A	5	11.25	7.62	**<0.001**
	C	2	25.24	42.73	**<0.001**
	A × C	10	10.15	3.44	**0.003**
Total production	A	5	11.67	10.11	**<0.001**
	C	2	1.05	2.28	0.118
	A × C	10	1.75	0.76	0.665
Woody production	A	5	27.56	6.80	**<0.001**
	C	2	6.51	4.02	**0.027**
	A × C	10	7.22	0.89	0.551
Herb production	A	5	0.03	2.76	**0.034**
	C	2	0.08	16.84	**<0.001**
	A × C	10	0.03	1.38	0.229
Bryophyte production	A	5	14.10	9.27	**<0.001**
	C	2	32.30	53.11	**<0.001**
	A × C	10	7.93	2.61	**0.018**
Total turnover	A	5	4.23	4.95	**0.002**
	C	2	1.02	2.99	0.063
	A × C	10	4.46	2.61	**0.018**
Woody turnover	A	5	3.09	3.09	**0.021**
	C	2	0.99	2.47	0.100
	A × C	10	5.20	2.60	**0.018**

Herb turnover	A	5	0.07	4.43	**0.003**
	C	2	0.03	5.19	**0.011**
	A × C	10	0.08	2.54	**0.021**
Bryophyte turnover	A	5	0.67	4.97	**0.002**
	C	2	0.50	9.28	**0.001**
	A × C	10	1.06	3.92	**0.001**

Notes: the columns give the degrees of freedom (df), sum of squares, F and the P-values.

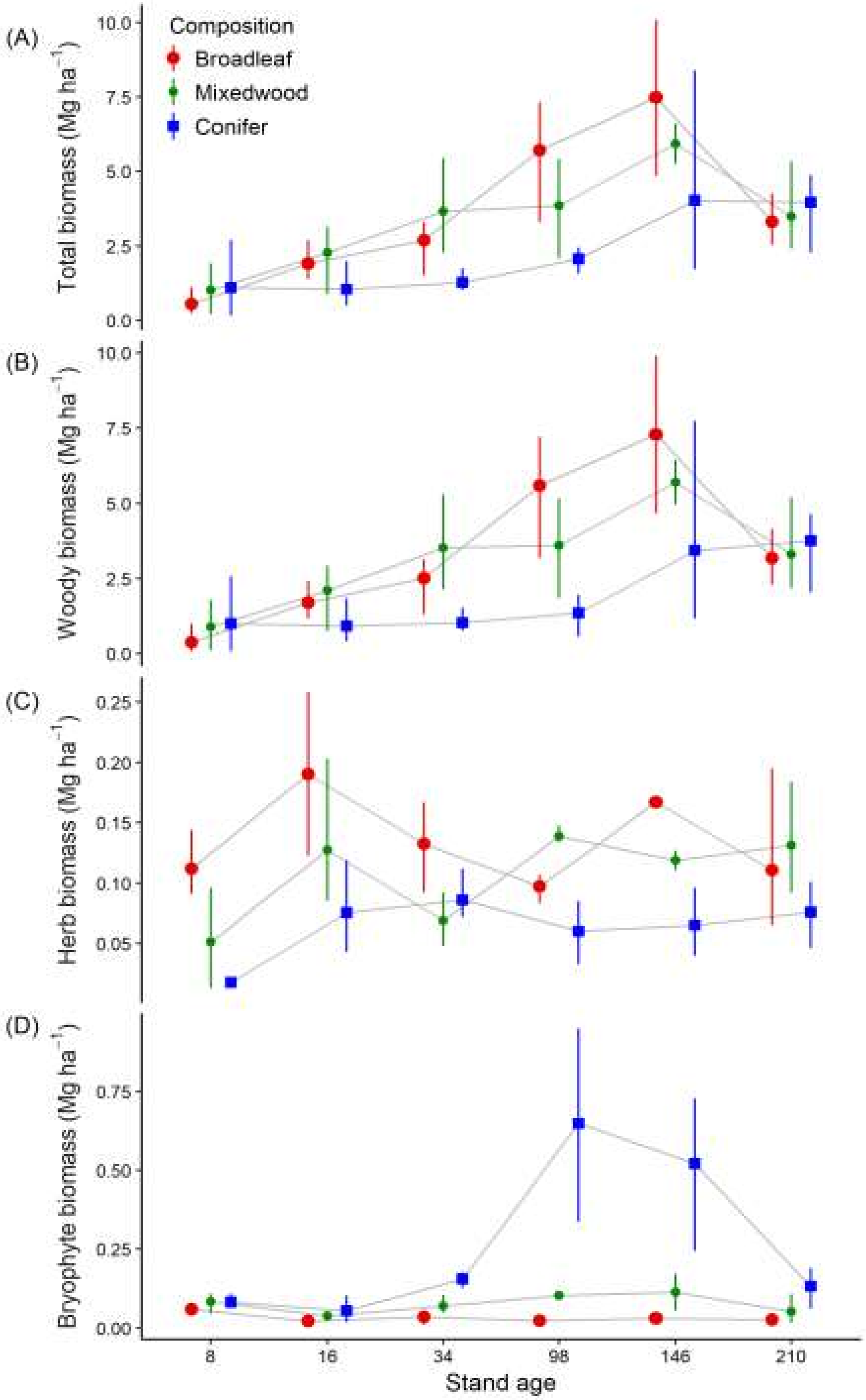

Figure 5.1. Understorey total, woody, herbaceous and bryophytes biomass (mean and bootstrapped 95% confident intervals) in relation to time since stand replacing disturbance (stand age) and overstorey types.

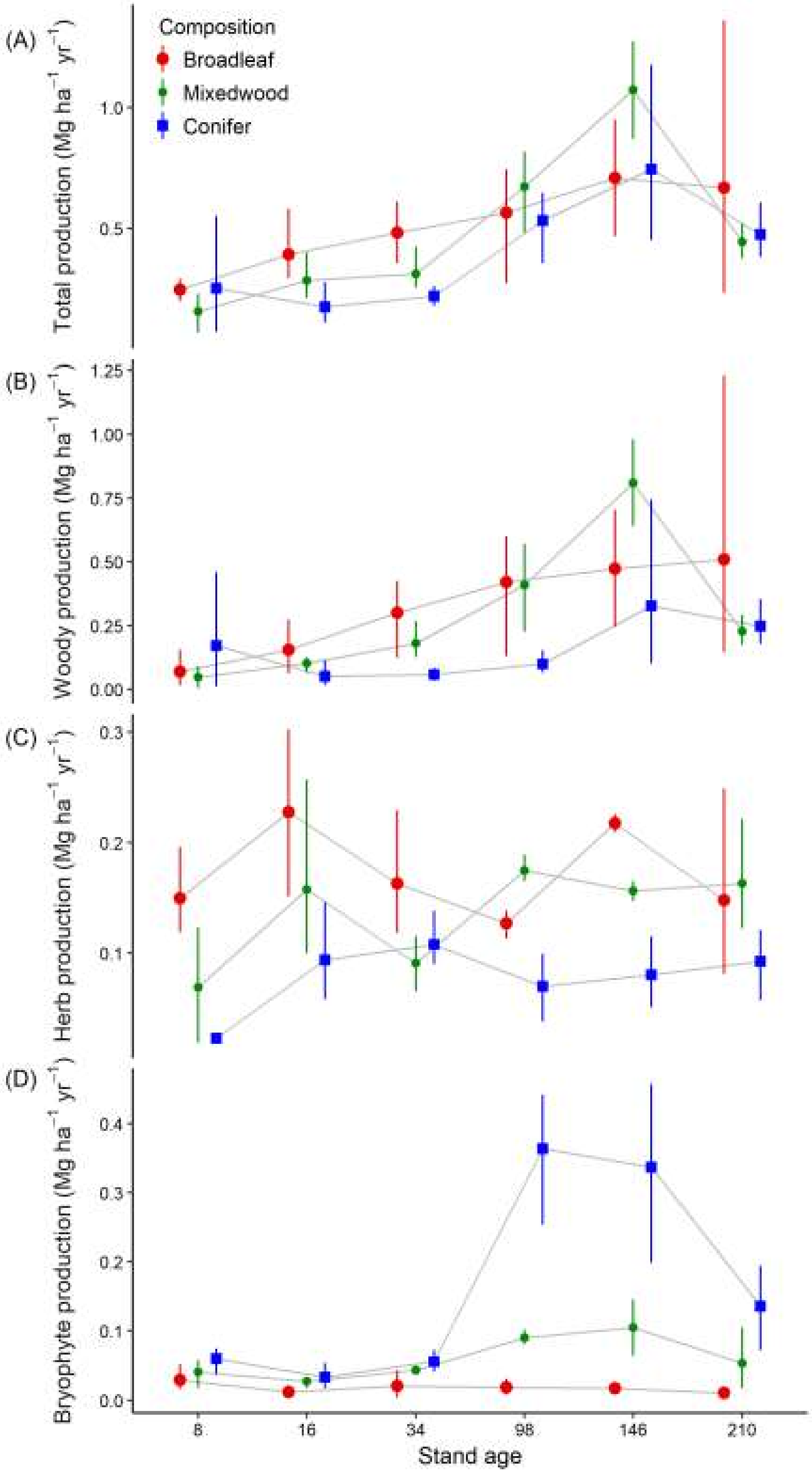

Figure 5.2. Understorey total, woody, herbaceous and bryophytes annual growth rates, hereafter referred as production (mean and bootstrapped 95% confident intervals) in relation to time since stand replacing disturbance (stand age) and overstorey types.

5.4.2 Understorey production

Annual production for understorey total, woody, herbaceous and bryophytes generally followed similar dynamics as those for biomass but with greater variability. Total understorey production differed significantly with stand age but did not differ among overstorey types (Table 5.1). Total understorey production increased continuously with stand age, except for a slight decrease in conifer stands at 16-year-old stands, reached to maximum in all 146-year-old stands, and decreased thereafter (Fig. 5.2A). The effects of stand age and overstorey type on woody production were similar to those for woody biomass (Table 5.1): it increased continuously with stand age in broadleaf stands, peaked at 146-year-old in mixedwood stands and decreased thereafter in 210-year-old-stands (Fig. 5.2B). Among conifer stands, woody production decreased from 8 to 16-year-old stands, increased thereafter to 146-year-old stands, peaked and then remained unchanged (Fig. 5.2B). Woody biomass production on an average was higher for broadleaf stands followed by mixedwood and conifer stands (Fig. 5.2B). The effects of stand age and overstorey type on herbaceous plant and bryophyte production were similar to those for herbaceous and bryophyte biomass (Table 5.1) and followed similar dynamics (Fig. 5.2C and Fig. 5.2D).

5.4.3 Understorey turnover rates

Total understorey turnover rates differed significantly with stand age, and the effect of overstorey type was dependent on stand age as indicated by a significance of the stand age and by overstorey type interaction term (Table 5.1). Within 8-year-old, broadleaf stands had significantly higher total understorey turnover rates than mixedwood and conifers stands, while in 16 and 34-year-old stands, there was no significant difference among overstorey types (Fig.

5.3A). However, in 98 and 146-year-old stands, conifer stands had a higher turnover rate than mixedwood or broadleaf stands, while in 210-year-old stands, total understorey turnover rates were higher for mixedwood stands (Fig. 5.3A). Total understorey turnover rates were highest in 8-year-old broadleaf stands (Fig. 5.3A). The effects of stand age and overstorey type on woody turnover rates were similar to those for total understorey turnover rates (Table 5.1). Within 8, 16 and 34-year-old stands, broadleaf stands had higher woody turnover rates than mixedwood and conifer stands, while at 98 and 146-year-old stands, woody turnover rates were higher among mixedwood stands, and at 210-year-old stands, broadleaf stands had higher woody turnover rates than mixedwood and conifer stands. Woody biomass turnover rates on an average were higher under broadleaf stands than mixedwood or conifer stands (Fig. 5.3B). Herbaceous turnover rates differed significantly with stand age and overstorey type with significant interactions between the two factors (Table 5.1). Within 8 and 34-year-old stands, herbaceous turnover rates were higher among mixedwood stands than broadleaf and conifer stands, and in 16-year-old stands, herbaceous turnover rates were higher in conifer stands, while in 98, 146 and 210-year-old age categories, broadleaf stands had higher herbaceous turnover rates than the other two overstorey types. Herbaceous biomass turnover rates in young stands on average were higher among mixedwood stands, whereas in older stands, herbaceous turnover rates were higher among broadleaf stands (Fig. 5.3C). Bryophytes turnover rates varied significantly with stand age and overstorey type with a significant interaction (Table 5.1). In 8 and 16-year-old stands, bryophytes turnover rates were higher among conifer stands; in 34, 98, 146-year-old stands, bryophytes turnover rates were higher in mixedwood stands; and in 210-year-old-stands, mixedwood and conifers showed higher turnover rates than broadleaf stands. Bryophytes turnover rates on average were higher among mixedwood stands than conifer and broadleaf stands (Fig. 5.3D).

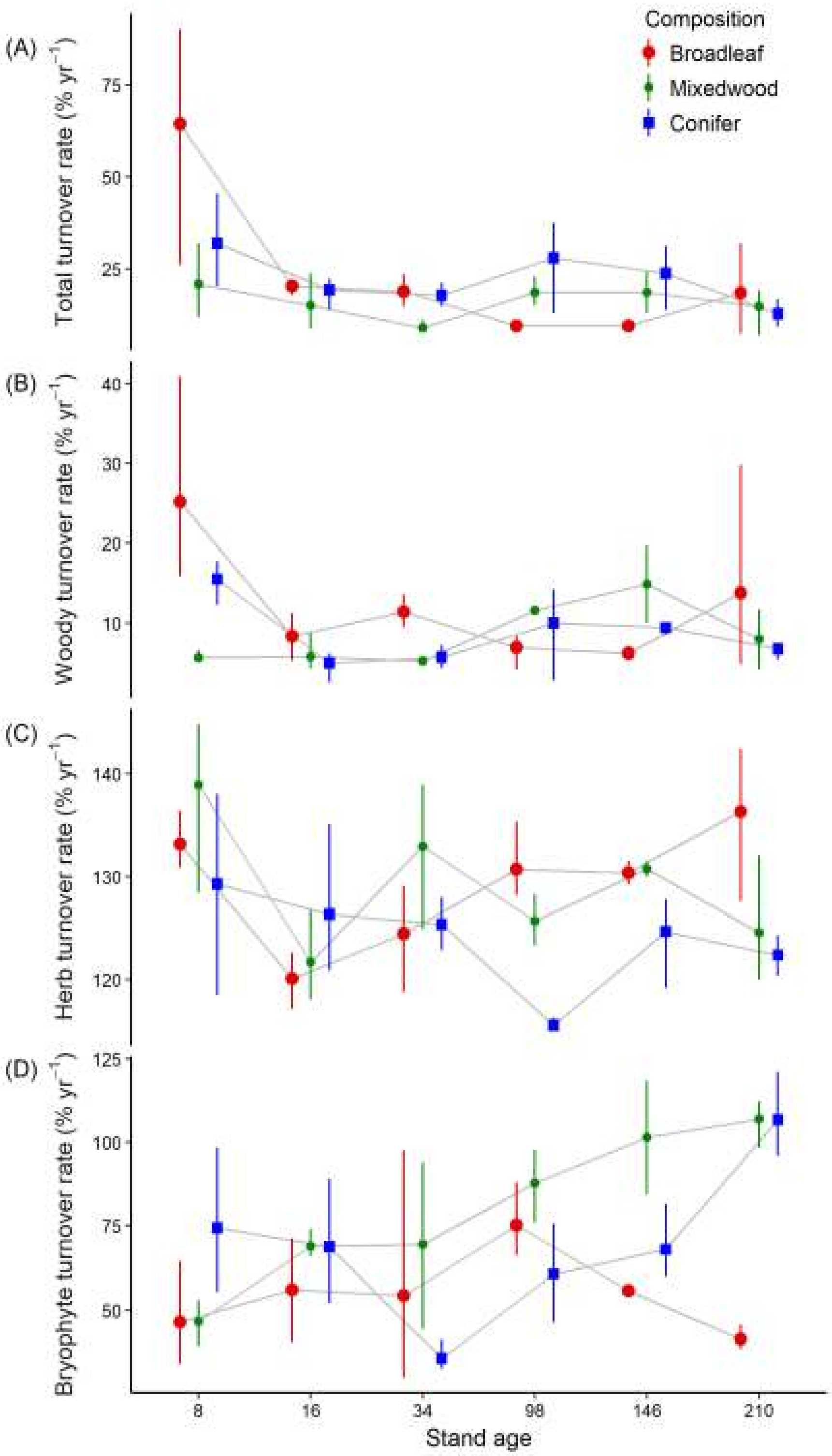

Figure 5.3. Understorey total, woody, herbaceous and bryophytes turnover rates (mean and bootstrapped 95% confident intervals) in relation to time since stand replacing disturbance (stand age) and overstorey types.

5.5 Discussion

Our analysis represents the first comprehensive investigation of understorey biomass, production and turnover rate dynamics associated with forest stand development and succession in the boreal forest of Canada. We found that understorey total, woody, herbaceous and bryophyte biomass, production and turnover rates differed with stand development stage and among overstorey types. As expected, understorey herbaceous biomass, production and turnover rates were higher in the early stages of stand development, whereas, total, woody and bryophytes biomass and production were higher in intermediate to later stages of succession. These findings are consistent with the generally recognized pattern of boreal forest succession after fire (DeLuca et al. 2002b, Hart and Chen 2006, 2008), whereby herbaceous cover and biomass increase rapidly in stand initiation stages, decrease in the stem exclusion stage, and then increase in the canopy transition and gap dynamic stage; whereas the cover and biomass of shrub and bryophytes increases continuously with time since fire. In our previous research related to the underlying mechanisms for understorey plant diversity, we attributed this to time-dependent colonization and plant growth following a disturbance event and associated changes in light availability and variability, and in addition to substrate heterogeneity effects mediated via overstorey development (Kumar et al. 2017b).

The decrease in understorey herbaceous biomass, production and turnover rates in the stem exclusion stage is related to the substantial increase in the proportion of abundance of overstorey tree biomass and increased competition for available resources between individual trees as plants grow in the overstorey. Resource pre-emption by the overstorey tree layer, which leads to higher biomass accumulation through greater occupation of available resources, reduces light and potentially other resources available to understorey vegetation, thereby decreasing the cover and biomass of herbaceous species (Bartels and Chen 2010, Reich et al. 2012, Kumar et al. 2017b, Zhang et al. 2017). Indeed, in our recent chronosequence study in the boreal forest, we observed low levels of understorey light at the stem exclusion stage, with an increase in canopy openness and light penetration later in stand development (Kumar et al. 2017b). Increases in total and woody biomass and production in intermediate stages of succession are likely the result of increased resource conditions following canopy breakup, as stands undergo varying levels of age-related mortality, and structural heterogeneity in the overstorey and understorey is high (Chen and Popadiouk 2002, Bartels and Chen 2010, Taylor and Chen 2011). Increase in woody understorey biomass and production at intermediate to later stages of succession is also attributed to long time required for shade-tolerant shrub species, such as *Acer spicatum* Lamb., *Corylus cornuta* to maximize their biomass, as these tall shrubs were the major component of the understorey biomass and production in this study.

Bryophyte biomass, production and turnover rates also increased with time since fire, peaking in the intermediate stages and declining thereafter in later stages. This corroborates the associated changes in the overstorey structure and composition following stand development and increase in microsite heterogeneity, in the form of diverse coarse woody debris and tip-up-mounds at later stages of stand development (Beatty 1984, Mills and Macdonald 2004, Kumar et al. 2017a, Kumar et al. 2017b). Our results are consistent with previous studies, that found an increase in bryophytes cover and biomass with time since fire (DeLuca et al. 2002b, Zackrisson et al. 2004, Hart and Chen 2006, 2008). However, the biomass, production and turnover rates of bryophytes at intermediate stages (98 and 146-year-old) of succession in this study greatly exceed the values for herbaceous species.

We found higher understorey total, woody and herbaceous biomass, production and turnover rates in deciduous broadleaf-dominated stands compared with conifer stands, confirming the evidence in previous studies of boreal forests (Gower et al. 1997, Reich et al. 2001, Cavard et al. 2011). Understorey total, woody and herbaceous biomass and production were higher under broadleaf stands, while conifer stands had higher bryophytes biomass and production rate, with mixedwood stands occupying intermediate position for biomass but had higher total and woody understorey production and bryophyte turnover rates. Higher herb and woody biomass in the deciduous broadleaf stands are primarily driven by higher light availability and the positive effect of broadleaf litter on soil quality, as broadleaf litter decomposes quickly and is high in nutrient content and pH (Paré and Bergeron 1996, Légaré et al. 2005, Hart and Chen 2006, Chytrý et al. 2010, Augusto et al. 2015). Broadleaf stands in our study area generally support higher diversity and cover of understorey herbs and shrubs (particularly a dense cover of tall shrubs such as *Acer spicatum* Lamb., *Alnus* spp.,*Corylus cornuta*) (Hart and Chen 2008, Kumar et al. 2017b), and have higher litterfall production (Chen et al. 2017a) compared to mixedwood and conifer stands.

The low bryophyte biomass and production under deciduous broadleaf stands, as bryophytes were favoured in the low resource environments associated with conifer stands, is best explained by the slow growth of most bryophyte species and their inability to grow above leaf litter layer because of physical inhibitory and allelopathic effects of broadleaf litter on bryophytes (Légaré et al. 2005, Hart and Chen 2006, Startsev et al. 2008, Marialigeti et al. 2009). Previous studies have also reported positive relationships between bryophyte abundance and conifer dominance (Légaré et al. 2002, Cavard et al. 2011, Kumar et al. 2017b). The tolerance of bryophytes to low resource environment in conifer stands, can also be explained partly by their ability to fix atmospheric nitrogen as bryophyte contains high densities of cyanobacteria that fix atmospheric nitrogen into forms available to plants (DeLuca et al. 2002b, Zackrisson et al. 2004, Houle et al. 2006, DeLuca et al. 2007).

Mixedwood stands in our study appeared to be intermediate between conifer and broadleaf overstorey types in terms of total, woody, herb and bryophytes biomass and production. However, mixedwood stands had higher understorey total and woody production in intermediate stages, higher herb turnover rates in young stands, higher woody turnover rates in intermediate stands and higher bryophytes layer turnover rate in later stand development stages. This is because mixedwood stands are characterized by greater heterogeneity in understorey resources (Bartemucci et al. 2006, Macdonald and Fenniak 2007, Bartels and Chen 2010), which allows for growth, development and facilitation of both woody and non-woody vegetation (Bartels and Chen 2010). Higher turnover rates in mixedwood stands can also be explained by the fact that fast-growing herbaceous and shrub species are particularly benefitted in the mixedwood stands, which might results in higher understorey biomass and production rates in these stands.

5.6 Conclusion

In summary, our study provides a comprehensive evaluation for understorey biomass, production and turnover dynamics over a long temporal gradient of succession in boreal forests. Using a replicated long chronosequence, we found that understorey herbaceous biomass, production and turnover rates increased in young stands immediately after fire, and then remained relatively stable thereafter with a slight increase at the canopy transition stage, whereas shrub and bryophytes biomass and production increased with stand age, peaked at intermediate stages and decreased thereafter at later stages. Our findings suggest that in the disturbance-driven boreal forest, understorey biomass, production and turnover rates are driven by time since colonization following stand-replacing fire, coupled with associated changes in resource availability and heterogeneity mediated by overstorey succession. Understorey woody and herbaceous biomass, production and turnover rates may be positively associated with higher resource availability under deciduous broadleaf overstorey types, whereas the opposite was observed for bryophytes, which might be inhibited by deciduous broadleaf litter, and favoured by limited resource conditions in conifer stands. However, resource heterogeneity induced by mixedwood stands might have favoured the growth of both woody and non-woody plants, and were intermediate between broadleaf and coniferous stands, but had higher herb turnover rates in early stages of succession, and high woody and bryophytes turnover rates in intermediate stages of succession. This study highlights the role of overstorey succession in long-term forest understorey biomass, production and turnover dynamics and its importance for modeling total forest ecosystem contribution to the global carbon.

CHAPTER 6: GENERAL CONCLUSION

In summary, this study demonstrated that multiple processes determine changes in understorey vegetation with stand development in boreal forests and highlights that understorey vegetation abundance and species diversity, and its biomass, production and turnover rate dynamics are driven by time since colonization following stand replacing fire, coupled with associated changes in resource availability and heterogeneity, mediated via overstorey succession. Individual mechanisms involved are highly interrelated, and any efforts to disentangle the mechanisms of understorey vegetation need to rely on multi-scale approaches. Indirect effects of time since disturbance and overstorey composition could either increase or decrease the effect of resource availability and heterogeneity on understorey vegetation, in terms of both total cover and species richness. Furthermore, overstorey composition effects on understorey resource environments and understorey vegetation patterns again lead to the conclusion that forest overstorey-understorey relationship is complex and is context-dependent. For example, high shrub cover has both facilitative and inhibitory effects on boreal understorey plant communities: shrub cover enhanced heterogeneity in the light environment, promoting species richness of vascular plants, but reducing that of non-vascular plants. The overall results highlight the importance of colonization, light availability and heterogeneity, substrate specialization and growth dynamics in determining successional patterns of boreal forest understorey vegetation.

We did not find soil resource availability was a major driver of either understorey cover or species richness, as this study was conducted in sites that were inherently similar in topography and soil texture. The changes of soil nutrient availability through stand development on inherently similar sites in our study have substantially less influence on understorey vegetation. Rather, there are large independent effects of light resource variability and substrate diversity, both of which are affected by stand age and overstorey composition that are essential to understanding patterns of understorey vegetation abundance and diversity with stand development on mesic sites of boreal forests.

The patterns of epixylic vegetation abundance, species diversity and composition are strongly influenced by CWD decay class and substrate species, and between CWD and forest floor. We find a shift of the species composition during understorey species succession on CWD, which is completed when the last stages of wood decomposition and fragmentation is reached. Understorey species composition not only differs with decay class, but also with CWD substrate species. Furthermore, stands of different ages and overstorey composition types support different epixylic species composition, indicating that shifts in forest age structure and tree species composition can strongly influence the successional dynamics of epixylic plant communities.

Finally, we found higher biomass and production in the early stage of succession, and those of woody and bryophytes at intermediate to later stages of succession. These results highlight the importance of time since colonization coupled with the associated changes in resource availability and heterogeneity mediated via overstorey succession in the boreal forest to understorey biomass and production. High resource conditions induced by deciduous broadleaf overstorey favoured higher woody and herbaceous biomass, production and turnover rates, and those of bryophytes were favoured by resource-limited conifer stands, with heterogeneous conditions induced by the mixedwood favoured both woody and non-woody biomass and production. This study highlights the role of overstorey succession in long-term forest understorey biomass, production and turnover dynamics and importance of understorey for modeling total forest ecosystem contribution to the global carbon cycle. Although the mechanisms inferred in this study adequately explain the dynamics of understorey biomass, production and turnover rates, an understanding of the hypothesized mechanisms including time since colonization, resource availability and heterogeneity in regulating understorey biomass, production and turnover rates needs further verification. Therefore, future research could focus on testing these hypothesized mechanisms in regulating understorey biomass, production and turnover rates.

6.1 Management Implications

Forest biomass harvesting is a predominant form of anthropogenic disturbance in the boreal forest and has a potential to influence species abundance, diversity and composition. Management activities strongly affect both forest age structure and composition (Chen et al. 2017b), CWD decay class and substrate species (Brassard and Chen 2008), and in turn epixylic vegetation abundance, diversity and composition. For example, short rotation harvesting regimes could result in the loss of epixylic species with affinity for suitable habitat conditions in older stands. On the other hand, epixylic species associated with specific CWD substrate species would go extinct without sufficient presence of the tree species in the overstorey to generate species-specific CWD. Therefore, to minimize the impacts to sensitive lichens and bryophytes associated with CWD, management intervention should aim at conserving the diversity of CWD in terms of both decay classes and tree species. Since stand development and overstorey compositions influence CWD decay classes and substrate species as well as colonization time and environmental conditions in the understorey, our results concur with the previous suggestions that managed boreal landscapes should consist of a mosaic of different successional stages and a broad suite of dominant overstorey species (Boudreault et al. 2002, Brassard and Chen 2008, Bartels and Chen 2015), thereby supplying appropriate amounts of CWD across the full range of decay classes and substrate species, to maintain bryophyte and lichen species habitat in forests.

Furthermore, this study also provides the evidence that shifts in forest age structure and composition have strong impact on the dynamics of understorey vegetation and its ecological functions in terms of biomass, production and turnover rates. In particular, old growth stands in this study had diverse understorey vegetation communities and higher substrate diversity in terms of CWD diversity, which is a major driver of substrate heterogeneity and understorey diversity in the boreal forests. Therefore, management interventions should aim at maintaining diverse range of stand ages, particularly old stands, and overstorey types for conserving biodiversity and their ecological functions at the boreal landscape. Moreover, mixedwood stands were found to be more diverse than coniferous and broadleaved stands, and had understorey vegetation communities that comprise a combination of coniferous and broadleaved specialists, we also recommend that mixedwood stands should be maintained to conserve the biodiversity in the boreal forests of Canada.

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APPENDIX I. SUPPLEMENTAL INFORMATION FOR CHAPTER 2

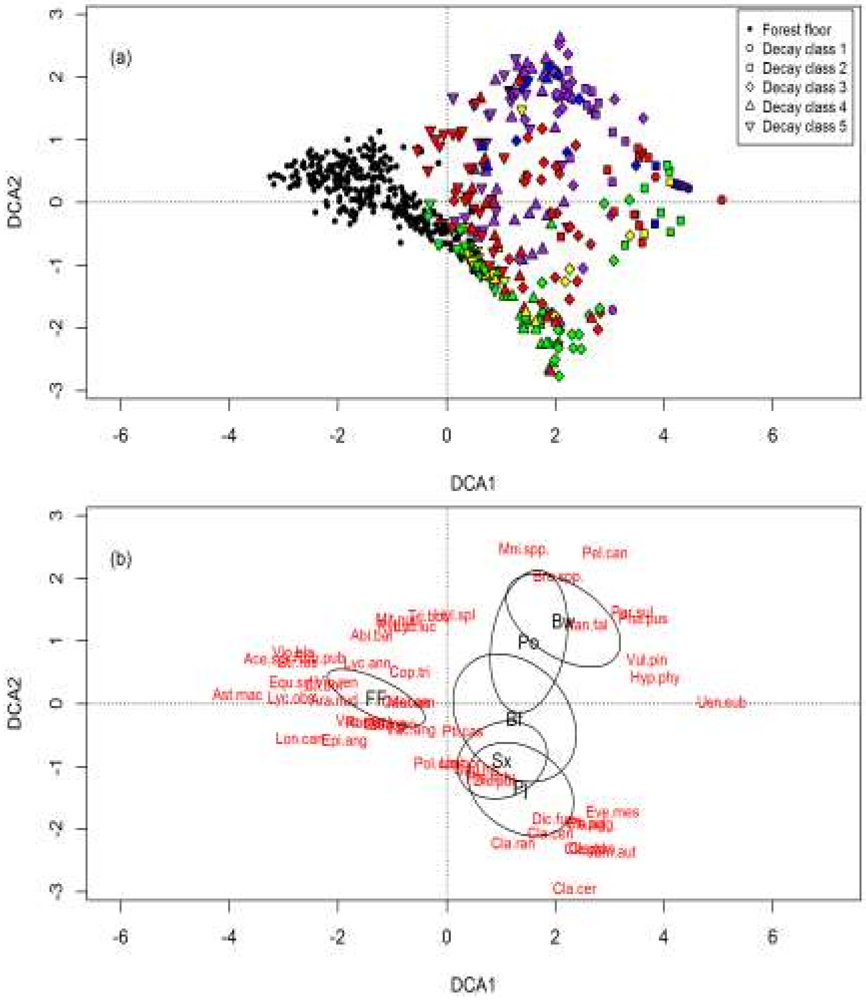

Figure S2.1. Detrended correspondence analysis (DCA) ordination of understorey species composition of 314 CWD logs and adjacent forest-floor quadrats (a) Substrates are FF (forest floor; black) and CWD taxa Po (*Populus* spp.; purple), Bw (*Betula papyrifera*; blue), Pj (*Pinus banksiana*; green), Sx (*Picea* spp.; yellow), Bf (*Abies balsamea*; red) and decay classes (1 to 5) are differentiated by symbol shapes on legends. Only species present in at least five sites were incorporated into the ordination. The first two DCA axes are shown (eigenvalues 0.79 and 0.62, respectively). (b) DCA graph showing difference in understorey species composition between different CWD substrate species and forest floor. OTU codes consist of the first three letters of the genus and the species names (see Table 2). Ordination axes are scaled in half-change (H.C.) units.

Symmetric Procrustes analysis comparing NMDS and DCA ordinations

Procrustes Sum of Squares (m12 squared): 0.4829

Correlation in a symmetric Procrustes rotation: 0.7191

Significance: 0.001 (significance is assessed by permutation tests)

Permutation: free

Number of permutations: 999

APPENDIX II. SUPPLEMENTAL INFORMATION FOR CHAPTER 3

Table S3.1. Results of general or generalized linear mixed effects model showing the effects of stand age (A), overstorey composition (C), decay class (D) and substrate species (S) and their interactions on understorey cover, species richness and species evenness, separately analysed by total, non-vascular and vascular vegetation. Bold fonts indicates statistical significance (α = 0.05).

Attribute	Source	df	Total		Non-vascular		Vascular	
			Deviance or variance explained (%)	*P*	Deviance or variance explained (%)	*P*	Deviance or variance explained (%)	*P*
Cover	A	3	1.60	**0.004**	2.25	**0.008**	0.11	0.997
	C	2	1.03	**0.003**	1.2	**0.014**	0.36	0.613
	D	4	74.48	**<0.001**	63.28	**<0.001**	38.12	**<0.001**
	S	4	0.98	**0.023**	0.80	0.212	1.57	0.376
	A × C	6	0.42	0.557	0.49	0.728	0.55	0.958
	A × D	12	1.77	**0.026**	3.29	**0.009**	1.08	0.982
	A × S	9	0.63	0.488	1.05	0.460	2.31	0.617
	C × D	8	1.16	0.097	1.29	0.308	6.48	**0.029**
	C × S	7	0.40	0.700	0.52	0.798	3.77	0.185
	D × S	14	3.82	**0.000**	4.74	**0.002**	4.06	0.683
Richness	A	3	11.98	**0.001**	14.76	**<0.001**	0.31	0.965
	C	2	7.92	0.146	6.43	**0.047**	0.07	0.889
	D	4	35.70	**<0.001**	24.83	**<0.001**	44.29	**<0.001**
	S	4	8.05	**0.015**	8.10	**0.023**	0.86	0.609
	A × C	6	2.56	0.867	2.93	0.779	1.67	0.513
	A × D	12	3.56	0.758	1.55	0.991	2.50	0.644
	A × S	9	1.63	0.896	2.46	0.507	3.08	0.294
	C × D	8	3.38	0.930	2.50	0.937	2.57	0.431
	C × S	7	0.45	0.994	1.75	0.417	5.09	**0.029**
	D × S	14	2.97	0.861	4.95	0.409	3.01	0.798
Evenness	A	3	1.94	0.457	1.35	0.635	0.79	0.772
	C	2	1.87	0.107	0.99	0.290	0.02	0.967
	D	4	4.01	**0.049**	6.20	**0.004**	51.72	**<0.001**
	S	4	2.09	0.285	1.82	0.332	0.62	0.742

A × C	6	1.16	0.833	0.77	0.921	3.07	0.139
A × D	10	8.58	**0.017**	11.04	**0.001**	2.26	0.704
A × S	9	3.00	0.512	1.90	0.775	5.08	**0.045**
C × D	6	3.08	0.287	2.40	0.417	2.44	0.456
C × S	7	3.31	0.337	2.34	0.548	4.54	**0.048**
D × S	12	11.30	**0.001**	11.69	**0.005**	3.71	0.618

Notes: the columns give the degrees of freedom (df), variance or deviance explained and P values. Natural logarithmic transformation was applied to understorey cover and species evenness data to meet the requirement of normality and homogenous variances for general linear models. For species richness, we used a generalised linear model (GLM) with a Poisson error distribution and a logarithmic link function.

Table S3.2. Average percent cover values of non-vascular and vascular understorey vegetation found on each stand age, overstorey composition, CWD substrate species and decay class in the central boreal forest of Canada. Overstorey compositions are Bro. - broadleaf, Mix. - Mixedwood, Con. – Conifer, and substrate species are Po- *Populus* spp., Bw- *Betula papyrifera*, Pj- *Pinus banksiana*, Sx- *Picea* spp., Bf- *Abies balsamea* and FF – forest floor.

	Stand ages				**Overstorey**			**Substrate species**					**Decay classes**						
	34	98	146	210	Bro	mix	Con	Po	Bw	Pj	Sx	Bf	1	2	3	4	5	FF	tot. abun
Number of logs	74	89	73	78	92	109	113	97	21	73	32	91	9	50	78	82	95		
Non-vascular species																			
Hypogymnia physodes	0.80	1.20	1.21	1.82	0.90	1.30	1.52	0.57	2.98	1.18	1.75	1.48	1.06	5.36	1.19	0.23	0.05		395
Usnea subfloridana	0.20	0.34	0.45	0.86	0.27	0.56	0.62	0.10	1.21	0.47	0.38	0.81	0.83	2.62	0.22				156
Xanthoria fallax	0.32	0.09	0.05	0.03	0.27	0.05	0.04	0.31		0.11			0.22	0.14	0.13	0.11	0.11		38
Parmelia sulcata	0.14	0.35	0.21		0.15	0.11	0.16	0.22		0.26	0.06	0.02		0.3	0.37				44
Peltigera canina	0.07	0.27	0.19	0.10	0.28	0.04	0.12	0.32		0.07		0.08		0.14	0.22	0.21	0.02		43
Phaeophyscia pusilloides	0.19	0.82	0.48		0.14	0.60	0.12	0.70		0.12		0.15		0.36	0.78	0.12	0.02		91
Evernia mesomorpha	0.43	0.03	0.02		0.11	0.09	0.13	0.10	0.14	0.30			0.33	0.16	0.19	0.11			35
Vulpicida pinastri	0.15	0.11	0.06			0.11	0.08	0.10		0.15				0.34	0.05				21
Leptogium milligranum	0.11	0.06	0.03		0.05	0.03	0.04	0.08		0.07					0.06	0.06	0.03		13
Cladonia coniocraea	1.09	0.55	0.46	0.08	0.33	0.46	0.73	0.31		0.96	0.81	0.42		0.04	1.13	0.74	0.14		164
Cladonia cenotea	0.03	0.06	0.03			0.04	0.03			0.10	0.06				0.04	0.06	0.01		10
Cladonia ochrochlora	0.09					0.06				0.10					0.03	0.06			7
Cladonia agg.	2.62	1.33	1.62	1.06	1.07	1.67	2.30	0.91	0.10	2.86	1.06	2.27		0.62	3.71	2.26	0.37		540
Cladonia chlorophaea	0.07	0.10	0.10		0.04	0.05	0.11	0.04		0.03	0.19	0.10			0.13	0.13			21
Cladonia cervicornis	0.95	0.04	0.03	0.04	0.18	0.19	0.35	0.13		0.81	0.09	0.03			0.50	0.43	0.04	0.01	80
Cladonia rangiferina	0.70	0.09	0.05		0.13	0.11	0.32	0.13		0.55	0.16	0.03			0.22	0.23	0.26	0.04	74
Brachythecium spp.	5.16	9.21	8.02	8.88	18.8	3.94	1.88	17.9	12.2	0.41	0.78	3.40	0.22	2.98	9.82	9.39	7.06	0.02	2365
Mnium spp.	0.12	4.62	3.84	2.49	6.14	1.17	1.18	6.19	1.95	0.07	0.88	1.63		0.10	1.54	4.21	3.71	0.01	825
Dicranum ontariense	4.03	1.02	1.47	0.49	0.60	1.25	3.4	0.10		5.64	1.00	1.33			2.54	4.2	0.35		587
Dicranum fuscescens	0.73	0.07	0.04		0.59		0.05	0.49		0.08		0.07			0.10	0.54	0.08	0.04	60
Dicranum polysetum	2.69	1.88	1.70	0.96	0.89	1.42	2.77	0.65	0.10	2.34	4.03	2.00		0.02	0.31	2.60	3.25	0.38	666
Dicranum flagellare	0.11	0.02	0.01			0.07	0.02	0.08		0.03						0.12			10
Polytrichum commune	0.20	0.07	0.04			0.19				0.21		0.07			0.08		0.16	0.11	54
Polytrichum juniperinum			0.02		0.01			0.05				0.02				0.02	0.05		7
Callicladium haldanianum			0.17		0.29			0.28							0.19	0.09	0.05		27
Orthotrichum speciosum		0.06	0.06		0.11			0.10						0.20					10
Hylocomium splendens		0.26	0.38	1.74	0.45	0.81	0.61	0.19		0.03		1.96				0.54	1.62	0.48	350
Ptilium crista-castrensis	3.15	3.08	2.86	1.27	1.35	1.83	4.17	1.76	0.86	2.78	6.44	1.97			1.06	2.65	5.02	3.31	1815
Pleurozium schreberi	14.0	9.15	8.26	2.62	3.51	7.83	12.4	4.57	0.43	13.5	17.0	6.27		0.06	2.08	9.99	16.5	2.43	3317
Rhytidiadelphus triquetrus		0.17	0.20	1.06	0.22	0.59	0.27	0.18	0.19			1.01		0.08	0.50	0.20	0.57	1.32	526

Sphagnum wulfianum	0.05	0.03	0.02				0.06			0.05		0.03					0.07	0.05	22
Ptilidium pulcherrimum	4.26	1.73	1.53	0.19	1.79	1.91	1.81	1.79	0.62	3.15	0.94	1.42		0.6	3.10	3.22	0.42	0.01	579
Jamesoniella autumnalis	0.07	0.19	0.25	0.05		0.10	0.35			0.16	0.38	0.29		0.14	0.22	0.27	0.04		50
Vascular species																			
Maianthemum canadense	1.07	0.48	0.59	0.63	1.01	0.34	0.82	0.80	0.14	0.81	0.66	0.64				0.3	2.04	3.00	1162
Coptis trifolia		0.08	0.14	0.04	0.01	0.09	0.13	0.02		0.16	0.03	0.12				0.02	0.25	0.31	123
Cornus canadensis	1.88	0.34	0.72	0.76	0.96	0.97	1.07	1.06	0.24	1.45	0.75	0.78				0.56	2.77	5.05	1894
Clintonia borealis		0.20	0.22		0.28		0.08	0.26		0.14						0.10	0.28	4.00	1291
Aralia nudicaulis				0.06			0.05					0.05				0.06		2.72	859
Chamerion angustifolium																		0.08	26
Viola renifolia	0.04					0.03		0.03								0.04		0.32	103
Streptopus roseus			0.07	0.05	0.16			0.11				0.04					0.16	1.41	458
Trientalis borealis	0.26	0.55	0.39	0.59	0.87	0.30	0.13	0.66	0.52	0.14	0.16	0.37				0.51	0.86	0.61	316
Mitella nuda		0.35	0.27	0.72	0.55	0.18	0.26	0.43	0.33			0.56				0.37	0.74	0.94	395
Viola blanda	0.05	0.07	0.07		0.12	0.04		0.11		0.05							0.16	0.68	227
Galium triflorum																		0.07	21
Aster macrophyllus																		1.15	360
Equisetum sylvaticum																		0.18	57
Lycopodium annotinum	0.04	0.10	0.14	0.26		0.13	0.27	0.09		0.10	0.13	0.27				0.05	0.43	0.75	282
Lycopodium obscurum	0.07			0.14	0.17			0.05				0.12					0.17	0.89	295
Lycopodium lucidulum		0.06	0.12		0.15		0.04	0.14			0.16					0.07	0.14	0.22	89
Lycopodium complanatum																		0.07	22
Linnea borealis	1.18	0.40	0.38	0.21	0.13	0.48	0.89	0.26	0.19	1.14	0.47	0.46			0.01	0.73	1.14	0.57	348
Gaultheria hispidula	0.51	1.62	1.23		0.37	0.18	1.62	0.32		1.07	3.69	0.14			0.08	0.57	1.97	0.26	323
Acer spicatum			0.05		0.09			0.08									0.08	1.32	422
Calamagrostis canadensis																		0.04	12
Diervilla lonicera																		1.03	324
Lonicera canadensis																		1.40	441
Vaccinium angustifolium																		0.94	295
Ledum groenlandicum																		0.58	182
Rosa acicularis																		0.48	150
Vaccinium myrtilloides					0.05			0.05									0.05	0.62	199
Rubus pubescens	0.07	0.38	0.21	0.14	0.29	0.21		0.29				0.20					0.48	2.12	712
Ribes triste	0.24				0.20			0.19								0.22		0.06	36
Petasites palmatus																		0.07	21
Salix spp.																		0.11	36
Picea spp.																		0.08	26
Abies balsamea				0.15		0.02	0.09					0.13				0.07	0.06	0.19	72
Danthonia spicata		0.03	0.02					0.03								0.04		0.08	29

Notes: tot. abun.: total percent cover values of each species on the present sites

APPENDIX III. SUPPLEMENTAL INFORMATION FOR CHAPTER 4

Table S4.1. Direct, indirect and total standardized effects of stand age, overstorey percent broadleaf composition, shrub cover, and light mean, light sd and substrate diversity on cover and species richness of total, non-vascular and vascular understorey species presented in Fig. 2a, Fig. 2b, Fig. 2c and Fig. 3a., Fig. 3b., Fig. 3c respectively.

SEM model	Explanatory variable	Paths to understorey vegetation	Effect
Model in Fig. 2a. for total understorey species cover	Stand age	Direct effect	0.431
		Indirect effect	-0.066
		Total effect	0.365
	Broadleaf composition	Direct effect	-0.221
		Indirect effect	-0.247
		Total effect	-0.468
	Shrub cover	Direct	-0.249
		Indirect effect	0.104
		Total effect	-0.145
	Light mean	Direct effect	-0.447
		Total effect	-0.447
Model in Fig. 2b. for vascular species cover	Stand age	Direct effect	0.416
		Indirect effect	0.144
		Total effect	0.560
	Broadleaf composition	Direct effect	0.534
		Indirect effect	0.025
		Total effect	0.559
	Shrub cover	Direct effect	
		Indirect effect	0.130
		Total effect	0.130
	Light mean	Direct effect	-0.299
		Total effect	-0.299
	Light sd	Direct effect	0.202
		Direct effect	0.202
Model in Fig. 2c. for non-vascular species cover	Stand age	Direct effect	
		Indirect effect	-0.126
		Total effect	-0.126
	Broadleaf composition	Direct effect	-0.692
		Indirect effect	-0.222
		Total effect	-0.914
	Shrub cover	Direct effect	-0.212
		Indirect effect	0.054
		Total effect	-0.219
	Light mean	Direct effect	-0.231
		Total effect	-0.231
	Light sd	Direct effect	-0.206
		Total effect	-0.206
Model in Fig. 3a. for total understorey species richness	Stand age	Direct effect	
		Indirect effect	0.517
		Total effect	0.517
	Broadleaf composition	Direct effect	
		Indirect effect	0.106
		Total effect	0.106

	Shrub cover	Direct effect	
		Indirect effect	0.067
		Total effect	0.067
	Light mean	Direct effect	-0.581
		Total effect	-0.581
	Light sd	Direct effect	-0.229
		Total effect	-0.229
	Substrate diversity	Direct effect	0.246
		Total effect	0.246
Model in Fig. 3b. for vascular species richness	Stand age	Direct effect	
		Indirect effect	0.742
		Total effect	0.742
	Broadleaf composition	Direct effect	0.299
		Indirect effect	0.394
		Total effect	0.693
	Shrub cover	Direct effect	0.286
		Indirect effect	0.096
		Total effect	0.382
	Light mean	Direct effect	-0.414
		Total effect	-0.414
	Substrate diversity	Direct effect	0.259
		Total effect	0.259
Model in Fig. 3c. for non-vascular species richness	Stand age	Direct effect	
		Indirect effect	0.016
		Total effect	0.016
	Broadleaf composition	Direct effect	-0.312
		Indirect effect	-0.197
		Total effect	-0.509
	Shrub cover	Direct effect	-0.249
		Indirect effect	0.021
		Total effect	-0.228
	Light mean	Direct effect	-0.508
		Total effect	-0.508
	Light sd	Direct effect	-0.327
		Total effect	-0.327

Abbreviations: Light sd- Standard deviation of light

Table S4.2. Pearson's correlation coefficients between variables for each SEM model.

	SA	PBC	SC	LM	LSD	N	SD
PBC	0.00		0.42**	-0.17	-0.29*	0.07	-0.41**
SA			0.43**	-0.51**	-0.30*	0.50**	$0.26^{\dagger}$
SC				-0.41**	-0.06	$0.25^{\dagger}$	-0.11
VC	0.48**	0.50**	0.46**	-0.54**	-0.13	$0.26^{\dagger}$	-0.15
NVC	0.19	-0.69**	-0.35**	-0.12	-0.07	0.21	0.34**
TUC	0.56**	$-0.25^{\dagger}$	0.03	-0.53**	-0.17	0.40**	0.21
VR	0.49**	0.39**	0.56**	-0.57**	-0.18	0.39**	0.07
NVR	0.22	$-0.23^{\dagger}$	-0.15	-0.41**	-0.32*	0.34**	0.18
TUR	0.50**	0.17	0.35**	-0.66**	-0.32*	0.48**	0.15
LM					0.18	-0.52**	0.09
LSD						-0.31*	0.14
N							0.07

Abbreviations are: SA, stand age (years); PBC, percent broadleaf composition; SC, shrub cover; VC, vascular cover; NVC, non-vascular cover; TUC, total understorey cover, VR, vascular species richness; NVR, non-vascular species richness; TUR, total understorey species richness; LM, light mean, LSD, standard deviation of light; N, total soil nitrogen and SD, substrate diversity. Significances are at $P < 0.01$ (**), < 0.05 (*) and marginally significant at $0.05 < P < 0.1$ (†).

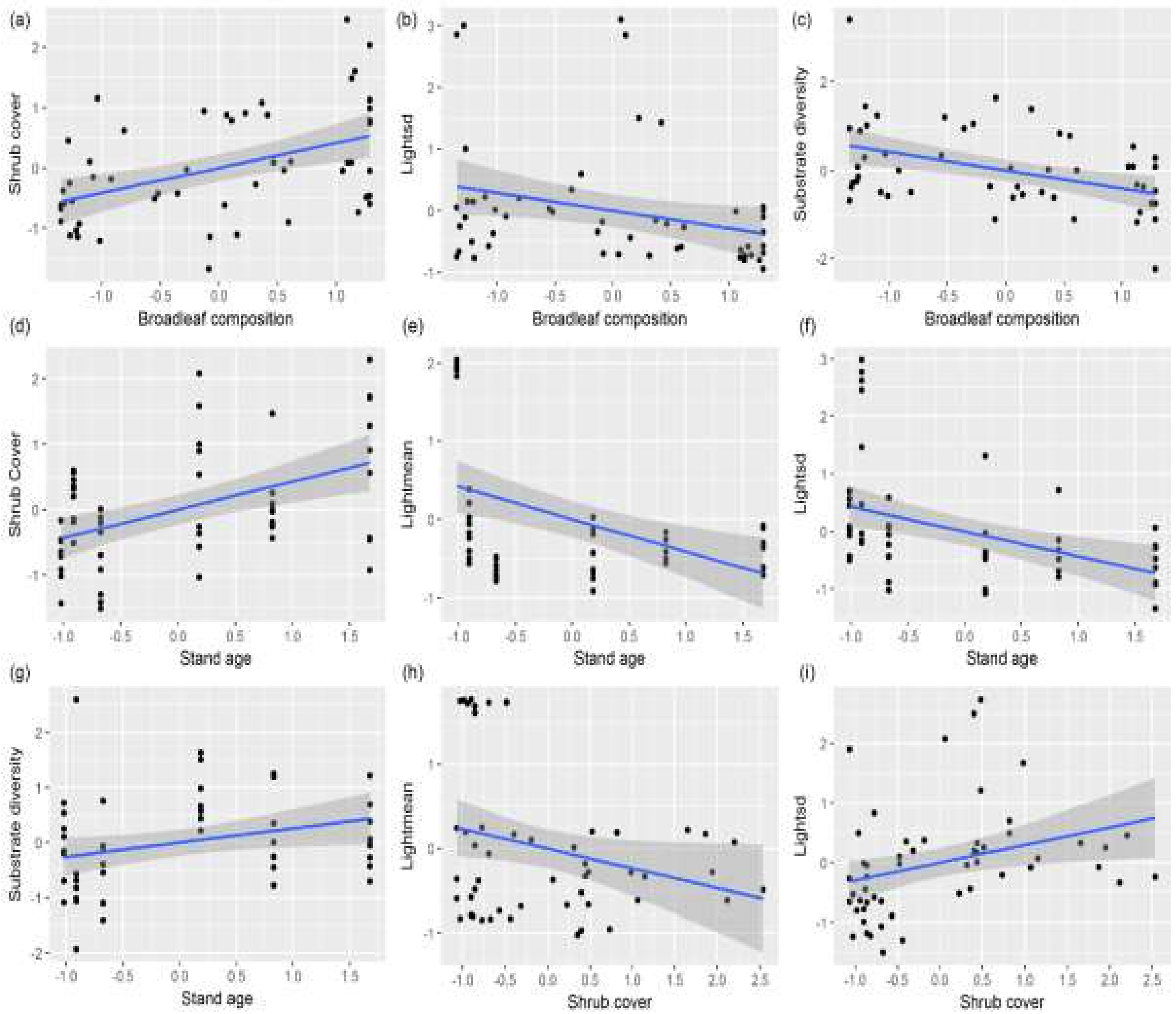

Figure S4.1. The plot level partial relationships for all predictors in the structural equation model for understorey species. The units are standardized residual deviations from predicted partial scores.

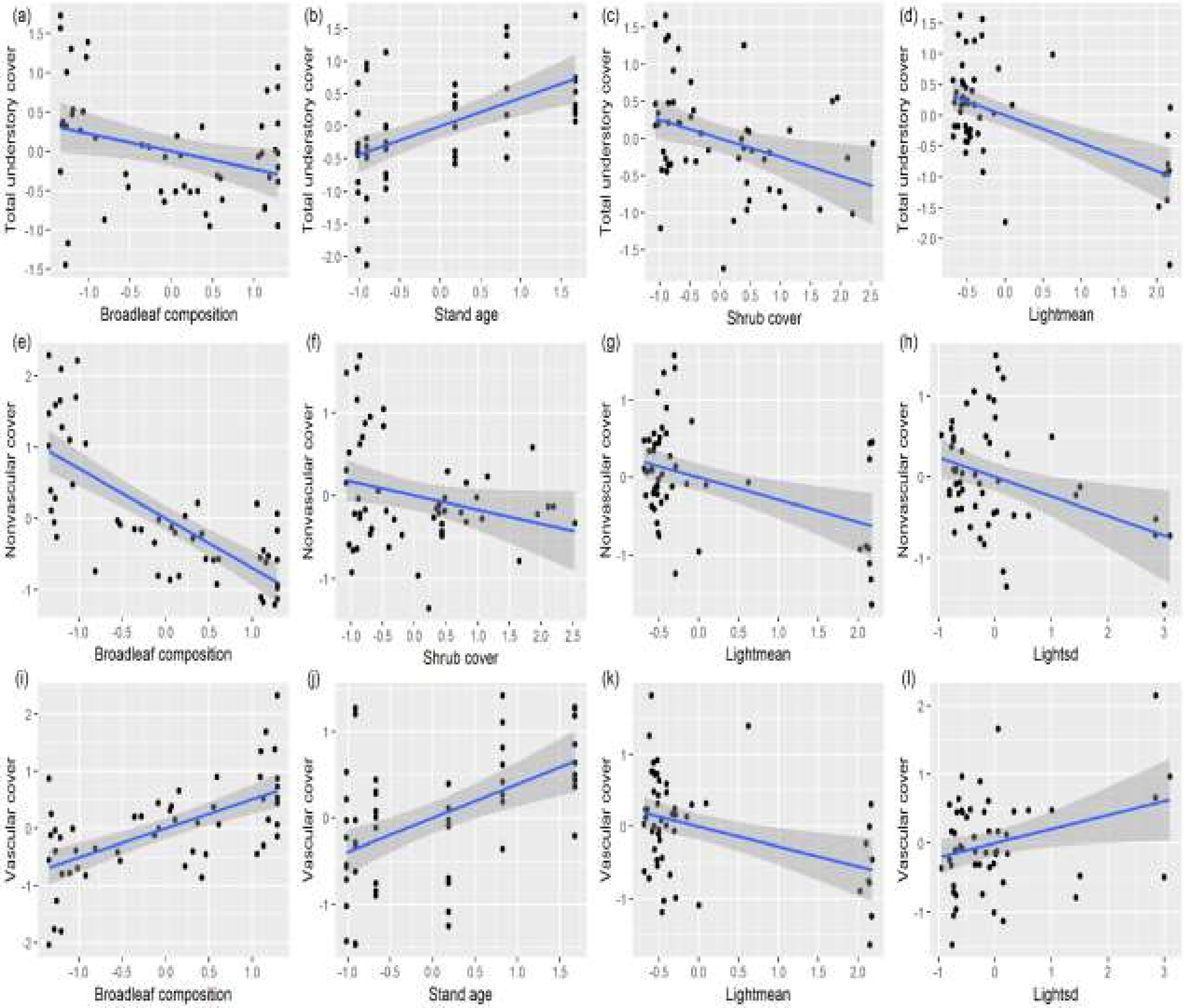

Figure S4.2. The plot level partial relationships for all hypothesized causal paths in the structural equation model for total, non-vascular and vascular species cover of understorey plants. The units are standardized residual deviations from predicted partial scores.

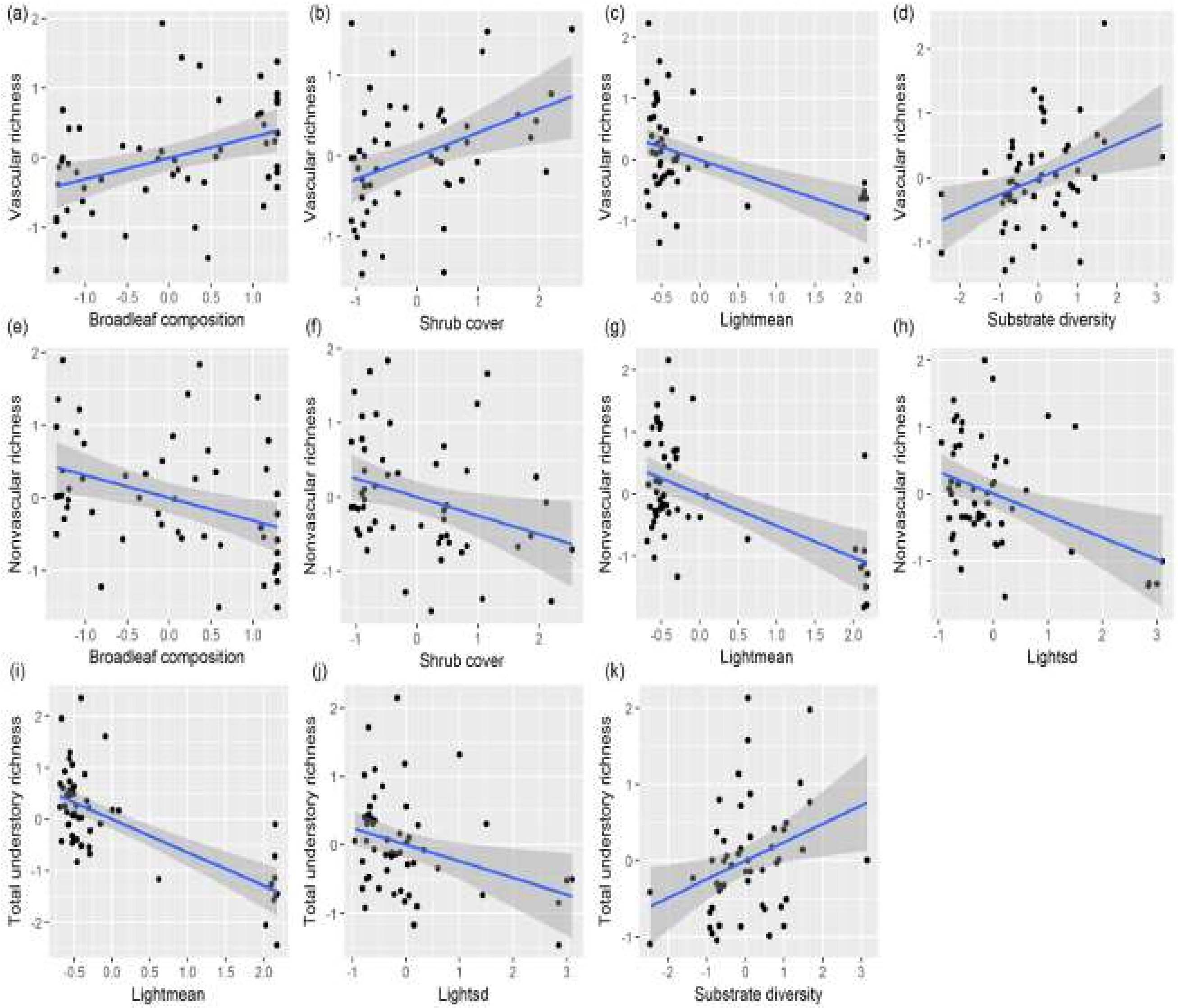

Figure S4.3. The plot level partial relationships for all hypothesized causal paths in the structural equation model for total, non-vascular and vascular richness of understorey plants. The units are standardized residual deviations from predicted partial scores.

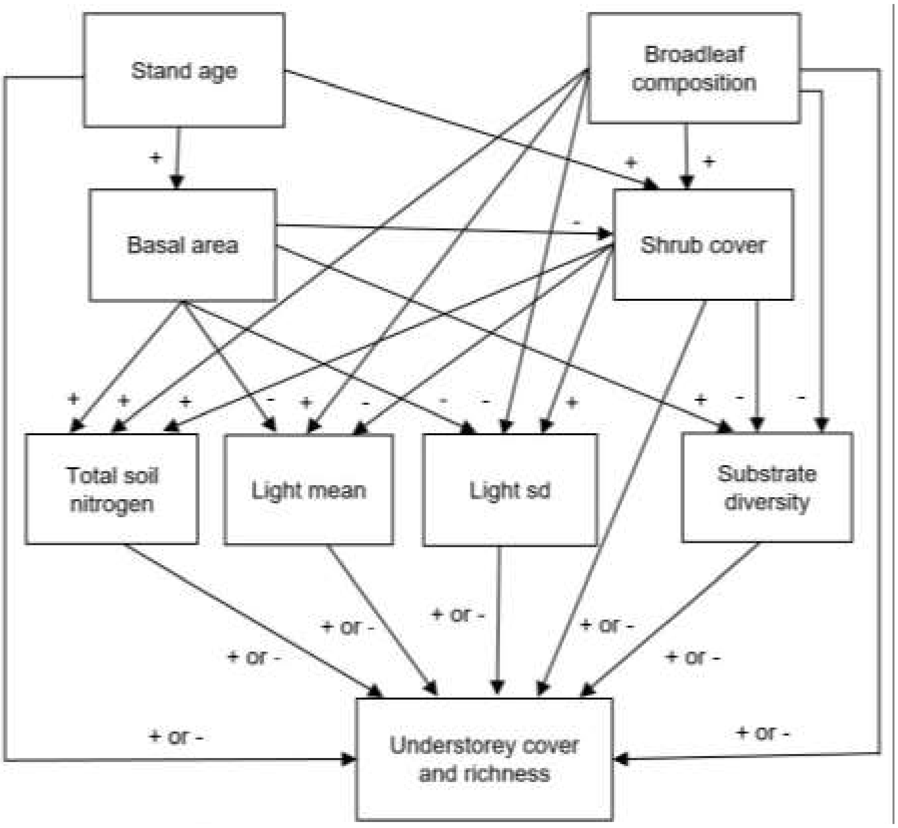

Figure S4.4. Alternative model with stand basal area linking the effect of stand development on stand basal area and its influences on soil nitrogen, light mean, light standard deviation, and substrate diversity, allowing stand age isolated to represent the effect of time since colonization on shrub cover and understorey cover or richness. Signs ('+' or '− ') indicate direction of relationships that expected to vary with understorey plant group under study.

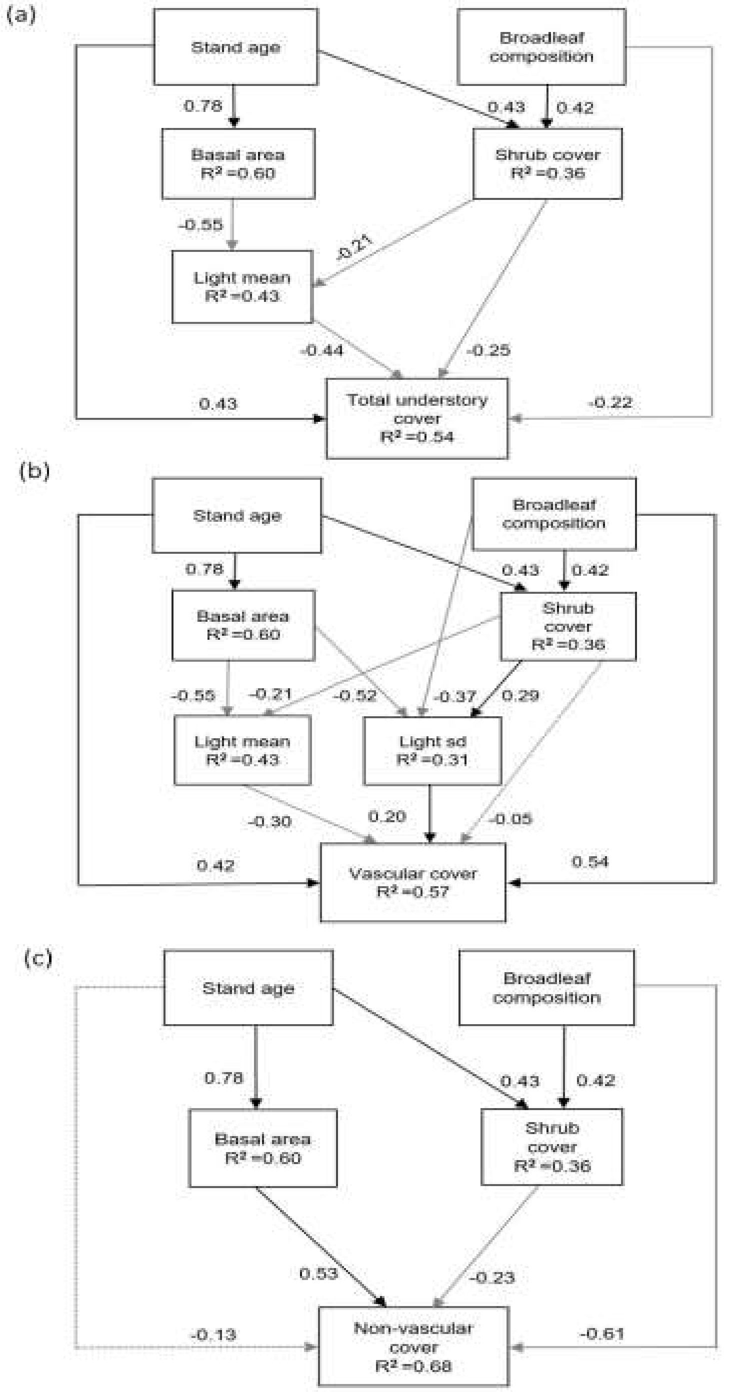

Figure S4.5. Structural equation models (SEM) with stand basal area linking the effect of stand development on stand basal area and its influences on light mean, light standard deviation, and substrate diversity to total, non-vascular and vascular understorey species cover. Solid lines represent statistically significant positive paths and grey lines show the significant negative paths at ($P \leq 0.05$), except for the path between shrub cover and light availability ($P = 0.06$). Dashed arrows indicate non-significant paths ($P > 0.05$) that were necessary to include in order obtaining the most parsimonious model. The coefficients are standardized for each causal path.

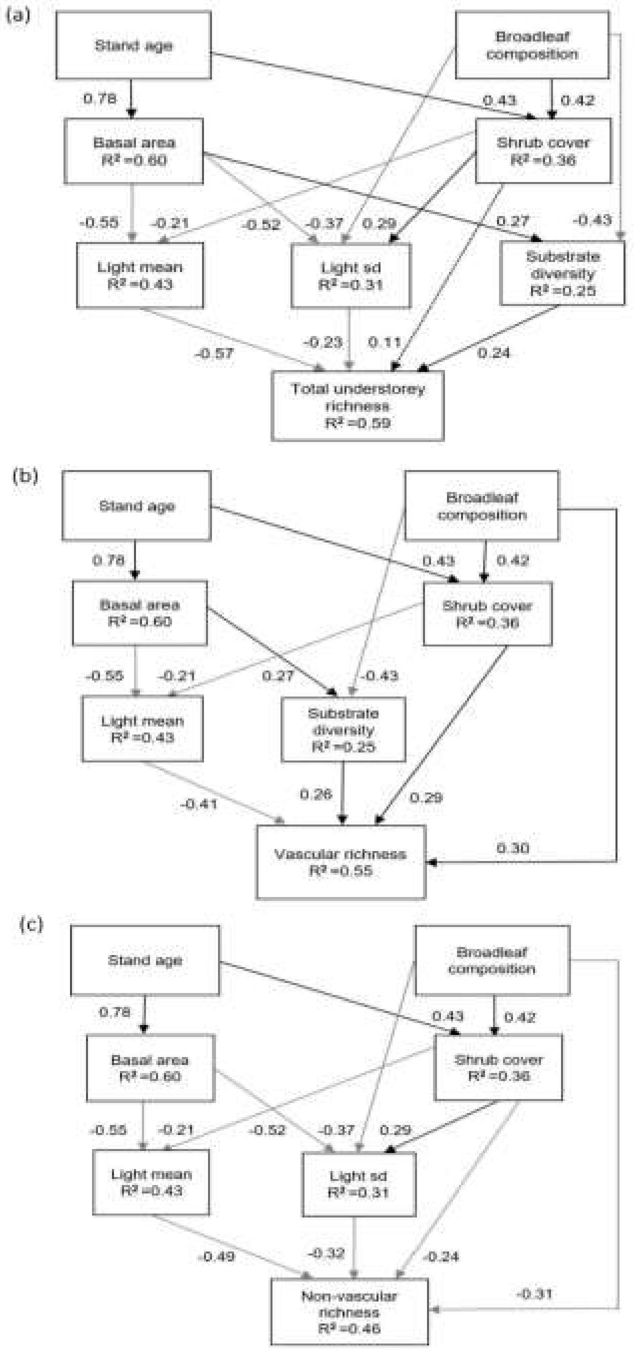

Figure S4.6. Structural equation models (SEM) with stand basal area linking the effect of stand development on stand basal area and its influences on light mean, light standard deviation, and substrate diversity to total, non-vascular and vascular understorey species richness. Solid lines represent statistically significant positive paths and grey lines show the significant negative paths at ($P \leq 0.05$), except for the path between shrub cover and light availability ($P = 0.06$). Dashed arrows indicate non-significant paths ($P > 0.05$) that were necessary to include in order obtaining the most parsimonious model. The coefficients are standardized for each causal path.

APPENDIX IV. SUPPLEMENTAL INFORMATION FOR CHAPTER 5

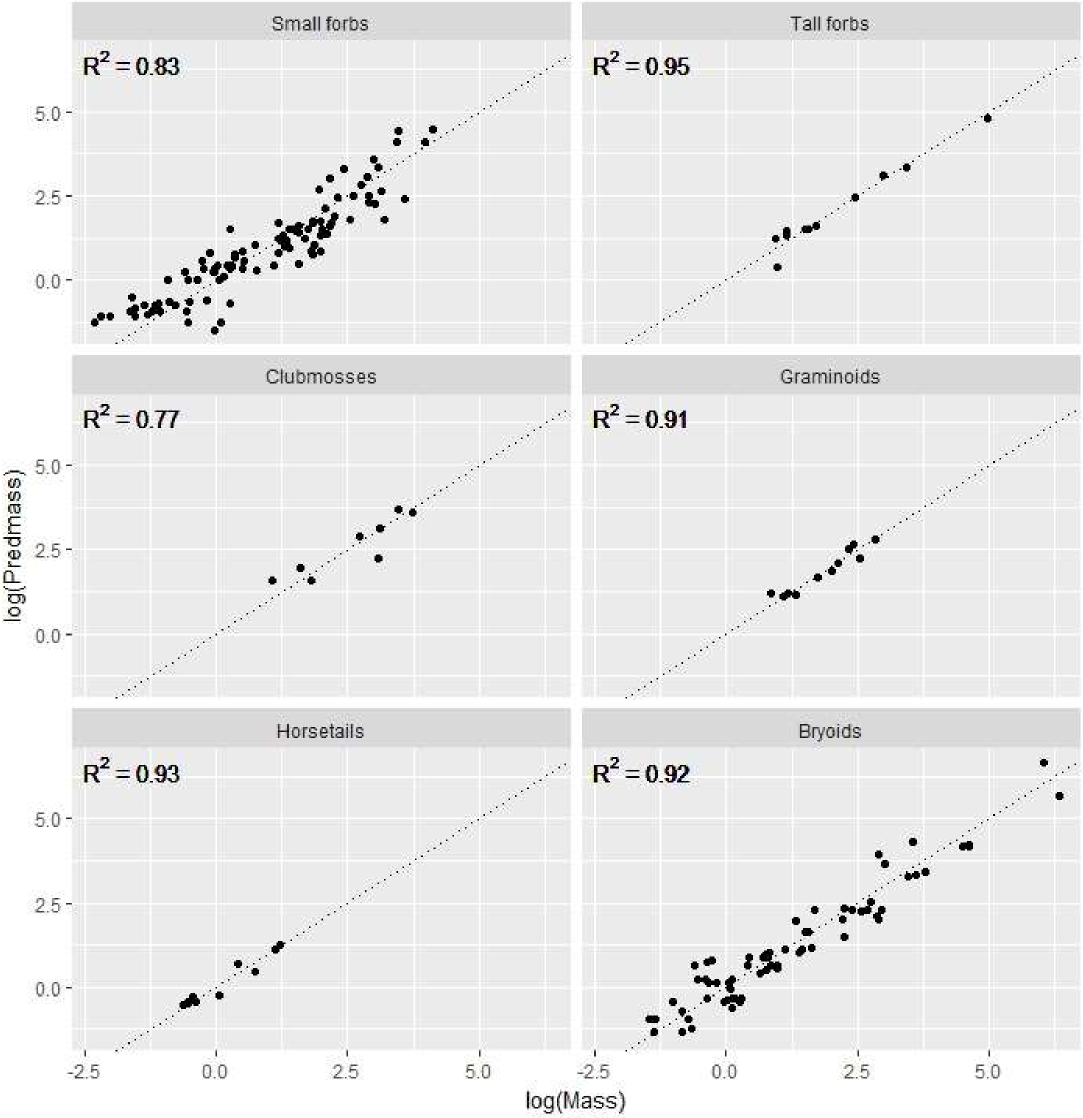

Figure S5.1. Predicted versus measured biomass values at the quadrat level for understorey growth forms.