Spatial and temporal stand dynamics of mature lodgepole pine forests of the Canadian Rocky Mountains

by

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Abstract

In forest ecosystems, structure and species composition change over time as a function of ageing and minor disturbances and it is important to understand these changes for predicting forest productivity and habitat suitability for other plant and animal biota. Disturbances play a major role in controlling these changes and in many forest ecosystems disturbance regimes have recently changed due to either the influence of climate or human management. The reduced fire frequency and recent mountain pine beetle (MPB) outbreak in lodgepole pine forests of Alberta are a good example of such changes. These forests were historically characterized by relatively frequent stand-initiating disturbance but previous studies have recognized a variety of post-fire successional pathways. We have a limited understanding of the pattern and underlying processes of stand dynamics of these forests, particularly in mature forests as they proceed towards the canopy breakup stage. To better understand the dynamics of both the understory and overstory communities of mature lodgepole pine forest I used data from spatially explicit long term permanent plots in the Rocky Mountains of Alberta, Canada to determine the mechanisms or processes responsible for the observed patterns in community composition and structure as well as how these patterns changed in time. I also used dendrochronology to reconstruct the timing of establishment and disturbance history to assess how they influenced stand dynamics. I first assessed whether canopy closure led to the homogenization and convergence of understory communities and if the processes spatially structuring these communities changed during stand development. I also assessed what was driving mortality of lodgepole pine trees and if mortality in different canopy positions was affected by different processes. Finally I assessed which factors were influencing the establishment and survival of regeneration throughout stand development.

I was able to demonstrate that following canopy closure understory communities homogenized within and between sites. Dispersal limitation was the most important factor driving structuring the understory communities and following canopy closure it increased in importance relative to environmental control processes. Environmental control nonetheless played an important role, especially in more xeric environments. Overall, tree mortality was a density-dependent process, suggesting that self-thinning was still ongoing even 140 years following the last stand replacing disturbance. This was likely a reflection of either a prolonged establishment period or slow growth due to surface fires or higher elevation respectively. Mortality of larger dominant trees, on the other hand, was a random process suggesting that in future developmental stages density independent processes might control tree mortality. Lodgepole pine establishment mainly occurred quickly post-fire while shade tolerant species started establishing soon after fire on moister sites but their establishment was mostly delayed on the drier sites even though there was evidence that seed was available in the early post-fire period. The spatial distribution and composition of the pioneer tree cohort and moisture limitations played an important role in regulating subsequent recruitment of regeneration.

Overall, my thesis provides valuable new information on various aspects of the stand dynamics of mature lodgepole pine forest such as understory communities, tree mortality and regeneration. This information can be used as a benchmark to assess the impacts of future changes in climate or disturbance regimes on these ecosystems as well as the impact of management decisions on stand dynamics.

Preface

The research conducted for this thesis would not have been possible without the collaboration and efforts of Roger Hnatiuk and John Stadt who provided valuable data from previous sampling periods as well as Dr. G.H. La Roi who initiated this study in 1967 and supervised both Roger and John. Chapter 2 of this thesis has been published as B. Gendreau-Berthiaume, S. E. Macdonald, J. J. Stadt and R. J. Hnatiuk. 2015. Ecosphere. 6: art27. I was responsible for the most recent data collection, all analyses and manuscript composition for Chapter 2 and subsequent chapters presented in this thesis. Dr. S. E. Macdonald was the supervisory author and guided me through the design, data analyses and manuscript composition of all chapters. J.J. Stadt and R. Hnatiuk provided valuable comments on earlier versions of the Chapter 2 and J.J. Stadt also provided comments on Chapter 3.

Dedication

I dedicate my thesis to family: my parents who have always been supportive throughout my academic journey and to my wife and son who have stood by me during this adventure.

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Chapter 1. Introduction to the successional dynamics and ecology of lodgepole pine ecosystems

In forest ecosystems, structure and species composition (tree and understory species) change over time as a function of ageing and minor disturbances in the stand (Brulisauer et al. 1996, Bergeron 2000, Clark et al. 2003, Hart and Chen 2006a). It is important to understand these changes for predicting forest productivity and habitat suitability for other plant and animal biota. It is also important to understand the changes in understory communities as they are an important component of biodiversity, they serve as food sources and habitat for many other life forms, they play an important role in nutrient cycling, and they also influence regeneration of tree species (Nilsson and Wardle 2005, Gilliam 2007).

Lodgepole pine (*Pinus contorta* var *latifolia*) forests have a broad distribution throughout the Rocky Mountains from southern Yukon in Canada to the southern United States (Burns and Honkala 1990c). Lodgepole pine is also a commercial species through most of its range rendering the understanding of these ecosystems ecologically as well as economically important (La Roi et al. 1988, Burns and Honkala 1990c). The abundant seed supply of lodgepole pine from serotinous cones and their rapid growth rates enable this species to dominate the canopy following a stand replacing fire. Many studies have found that the majority of lodgepole pines establish within 10 to 30 years following fire (Moir 1969, Day 1972, Johnson and Fryer 1989, Antos and Parish 2002a, Clark et al. 2003). Depending on the proximity of seed sources in unburned areas, Engelmann spruce (*Picea engelmanii*) and subalpine fir (*Abies lasiocarpa*) can also establish immediately following fire (albeit at lower levels than pine) but continue to establish throughout succession due to their higher shade tolerance and there is evidence that they could eventually replace the declining lodgepole pine canopy (Antos and Parish 2002a, Clark et al. 2003). These shade tolerant species can also develop a sapling bank that can persist in a suppressed stage for long periods (Antos et al. 2000). Subalpine fir usually establishes at lower levels than spruce following fires, likely due to its larger seed size (Knapp and Smith 1982) which can limit its dispersal (Greene and Johnson 1993) but its establishment usually increases or remains constant throughout stand development and it typically dominates the understory of older forests (Knapp and Smith 1982, Antos and Parish 2002a, Clark et al. 2003). However differences in life history strategies between Subalpine fir and Engelmann spruce - such as abundant regeneration (fir) vs longer longevity (spruce) - allows these species to coexist (Cattelino et al. 1979, Antos et al. 2000). Engelmann spruce could also be maintained in older stands due to its greater ability to respond to canopy openings as well as faster release in growth of the sapling bank (Antos et al. 2000, Antos and Parish 2002a).

Besides the classical successional model described above, different studies have found evidence of “climax” self-perpetuating lodgepole pine forest in Yellowstone National Park (Despain 1983), in the Central Sierra Nevada (Parker 1986), in south central Oregon (Stuart et al. 1989) and in the Colorado Front Range (Moir 1969, Whipple and Dix 1979) indicating that the phenomenon is widespread across the ecological distribution of the species. Although such “climax” lodgepole pine stands have been documented, they have been found only on limited portions of some landscapes while the classical lodgepole pine transitioning to a spruce-fir “climax” was more prominent (Whipple and Dix 1979).

An important feature of the “climax” lodgepole pine stands is the presence of pine regeneration in the understory combined with the absence or low number of regeneration from shade tolerant species that could grow under lodgepole pine and eventually replace it. Low levels of regeneration from shade tolerant species are usually attributed to a lack of seed sources, unfavourable seedbeds, or inadequate microsite conditions due to a lack of shade, dry soils, or poor nutrient regimes (Whipple and Dix 1979, Despain 1983, Stuart et al. 1989). The absence of late successional species in stands under 100 years (Moir 1969) should however be interpreted with caution since it can sometimes take up to 100 years or more for spruce and fir to invade lodgepole pine stands (Whipple and Dix 1979). Xeric sites, open canopy conditions and the occurrence of surface fires have been suggested as potential factors allowing the presence of uneven aged self-perpetuating lodgepole pine or jack pine (*Pinus banksiana*) stands (Moir 1969, Gauthier et al. 1993). In “climax” lodgepole pine stands, regeneration has been reported to be limited by light; thus on-going pine regeneration occurs primarily in gaps (Parker 1986) or under sparse overstories (Despain 1983). However another study found that soil moisture was the environmental factor limiting lodgepole pine seedling establishment and survival (Stuart et al. 1989). Thus, although different successional pathways have been found in lodgepole pine forests the mechanisms driving these different pathways are still not well understood.

The dynamics of lodgepole pine or spruce-fir forests might be driven by disturbances (Johnson and Fryer 1989, Antos and Parish 2002a) or by endogenous factors

(Antos and Parish 2002b) and which of these factors is important is not always revealed in the size structure of the trees (Antos and Parish 2002a, b). Many studies have emphasised the importance of examining age structure, patterns of tree growth, and spatial structure in order to better understand the dynamics of forest ecosystems (Moeur 1993, Anto and Parish 2002a, b). The spatial arrangement of living and dead trees can also reveal important information on stand dynamics; for example how far along in the self-thinning process a stand is (Kenkel 1988) and whether mortality is driven by disturbance vs endogenous factors (Park et al. 2005). Thus, to adequately evaluate the processes underlying different successional pathways it is important to have a good understanding of disturbance history as well as the factors driving tree mortality.

Although many studies have looked at the stand dynamics and successional pathways of trees species in lodgepole pine forests, much less information is available about the successional dynamics of the understory vegetation in these ecosystems. Cormack (1953) described the understory vegetation in lodgepole pine stands in different stages of succession for the eastern slopes of the Canadian Rockies. However this study was descriptive and the described “scheme is an arbitrary one and its confirmation or negation await further study” (Cormack 1953). Horton (1956) found wider variation in composition of understory communities in young lodgepole pine stands than was reported by Cormack (1953). This wide variation is a reflection of numerous factors such as stand density, stand moisture and nutrient conditions, as well as effects of repeated fires and burning intensity (Moss 1955). In the 1980’s, five major understory community types were described for the lodgepole pine forests of Banff and Jasper National Parks across a moisture/elevation gradient (La Roi and Hnatiuk 1980). These authors suggested that the understory communities stabilized 70 years after fire, with understory composition and structure resembling the “climax” forests of the habitat type on which they occur. However, the La Roi and Hnatiuk (1980) study had a limited range of stand ages; 80 % of the stands they sampled were younger than 100 years old and only one stand was older than 125 years old. This limited their ability to evaluate the stability of understory communities throughout succession. Brulisauer et al. (1996) evaluated understory community organization of lodgepole pine forest using a 300+ year chronosequence and found that these communities change even after 100 years following fire, especially on drier sites. Thus, although few studies have looked at the long term changes in these understory communities there is evidence suggesting that they remain dynamic throughout succession.

Early stand dynamics of forest understory communities have been described often and in different conifer forests (Halpern 1988, Bainbridge and Strong 2005, Kayes et al. 2010). Following disturbances, understory communities are usually dominated by shade intolerant species that regenerate from seed or underground rhizomes (Halpern 1989, Hart and Chen 2006b) but can also include remnants from the pre-disturbance communities (Halpern 1989, Anderson and Romme 1991, Nieppola 1992). Following canopy closure, understory communities gradually shift towards increasing relative abundance of shade tolerant species (Taylor et al. 1988, De Grandpré et al. 1993, Nygaard and Ødegaard 1999). The successional changes of overstory species have also been found to influence the understory communities in the boreal forests (Hart and Chen 2006a) and these successional changes could also play an important role in ageing lodgepole pine forest. By controlling understory light levels (usually the most limiting resource affecting understory vegetation), forest canopy cover influenced understory communities in coastal forests of British Columbia and Washington (Klinka et al. 1996, McKenzie et al. 2000) but poor correlations were found between the two vegetation layers in coniferous forests of Montana (McCune and Antos 1981). Few studies have, however, looked at the influence of overstory attributes, and how these change over time, on the dynamics of understory communities in mature lodgepole pine forests.

Besides the effects of the overstory on light levels or other environmental conditions, dispersal limitations can also play an important role in structuring understory communities in mature forests (Ehrlén and Eriksson 2000, Frelich et al. 2003, Karst et al. 2005, Burton et al. 2011) since many understory species have limited dispersal abilities (Matlack 1994, Cain et al. 1998). However, few studies have looked at the relative importance of environmental control *versus* dispersal limitation processes for forest understory communities (however see Karst et al. 2005, Burton et al. 2011) and none that we are aware of have been based on longitudinal sequences throughout stand development. Such studies could contribute to a better understanding of the processes driving successional changes in the understory communities of mature lodgepole pine forests.

Lodgepole pine ecosystems have historically been dominated by relatively frequent stand-initiating fires and these forests thus most often exist as relatively young, heavily pine-dominated stands that rarely proceed to the canopy breakup stage of succession (Johnson and Fryer 1989). However, lodgepole pine forests in different parts of the species' range have recently been experiencing lower fire frequencies either due to natural or anthropogenic causes (Anderson et al. 1987, Masters 1990, Johnson and Larsen

1991, Van Wagner et al. 2006). This has led to large tracts of mature lodgepole pine forest experiencing significant canopy decline and successional transition (Rhemtulla et al. 2002). These forests have also been increasingly affected by less severe disturbances that do not directly affect the understory community or forest floor; for example the recent epidemic of Mountain Pine Beetle (MPB; *Dendroctonus ponderosae* Hopkins (Coleoptera: Curculionidae, Scolytinae) (Mathey and Nelson 2010). These changes in disturbance regimes make it even more important to understand the mechanisms driving different successional pathways as well as the natural dynamics in ageing lodgepole pine stands; a subject which has received insufficient attention.

Most studies looking at succession of either understory vegetation (De Grandpré et al. 1993, Brulisauer et al. 1996, Coxson and Marsh 2001) or tree species (Johnson and Fryer 1989, Bergeron 2000, Clark et al. 2003) have employed a chronosequence approach, in which successional patterns are reconstructed by using similar stands of different ages, which are inferred to represent a temporal sequence (Johnson and Fryer 1989, Brulisauer et al. 1996, Bergeron 2000, Clark et al. 2003). These studies make the assumption that each of the sites differs only by age and are otherwise similar in terms of abiotic (soil, climate, etc) and biotic components (microbial communities, vegetation, fauna, etc) (Johnson and Miyanishi 2008). However these assumptions are rarely tested and inferences made by many different chronosequence studies have since been proven incorrect due to the fact these basic assumptions were invalid (Johnson and Miyanishi 2008). Furthermore, chronosequence studies are poorly suited to evaluating the processes or mechanisms driving observed successional patterns (Johnson and Miyanishi 2008). The use of long term permanent plots is much preferred for studies aimed at determining the processes driving successional change or stand dynamics because they avoid the problem of substituting space for time and thus allow for direct interpretations (Kenkel et al. 1997, Nygaard and Ødegaard 1999, Lutz and Halpern 2006, Halpern and Lutz 2013). However such long term permanent plots studies are nonetheless rare due to logistical and time constraints.

For my PhD thesis I'm fortunate to have access to data from spatially explicit long-term permanent plots established in mature lodgepole pine stands of the Canadian Rocky Mountains chosen to cover a wide range of moisture and elevation. The main goal of my thesis work was to provide information about the processes driving the dynamics of understory communities, tree mortality and regeneration of the main tree species in these ageing lodgepole pine forests. This information will be especially valuable as climate continues to change and disturbance regimes are altered as it can allow us to better anticipate the impacts of these changes. By documenting the natural dynamics in unaffected mature stands this could also allow future studies to better assess the impacts of these new disturbances and environmental condition on stand dynamics. Through the following chapters, I provide insights about: 1) the processes structuring understory communities in these lodgepole pine forests and how these change following canopy closure; 2) the processes driving mortality in mature stands; and 3) the factors controlling regeneration success throughout stand development.

Chapter 2 - How dynamic are understory communities and the processes structuring them in mature conifer forests? - assessed whether understory communities showed within plot homogenization and between plot convergence following canopy closure and if compositional changes observed were supportive of either the initial or relay floristics model. This chapter also evaluated the relative importance of the environment vs. dispersal limitations in structuring these understory communities and how this changes over time.

Chapter 3* - *Untangling the processes driving mortality in mature conifer forests **-** determined the processes driving mortality in mature lodgepole pine stands of the Canadian Rocky Mountains. More specifically we tested the hypothesis that the studied stands had completed the self-thinning/density-dependent mortality stage of succession and assessed whether or not mortality of trees in different canopy positions can be affected by different processes.

Chapter 4* - *Factors influencing regeneration establishment and survival following stand initiation in lodgepole pine forests – investigated the processes driving regeneration throughout stand development of lodgepole pine forests and how these influence successional pathways in these ecosystems. More specifically we assessed the importance of the composition and spatial distribution of the initial post disturbance establishment and microsite conditions on subsequent regeneration in mature lodgepole pine stands.

In my concluding chapter I summarize and link the results from my different chapters, discuss management implications of the knowledge gained as well as suggest future research questions that could be answered with the substantial data set gathered during my thesis.

Chapter 2. How dynamic are understory communities and the processes structuring them in mature conifer forests?

Abstract - Even though understory plant communities play important roles in northern forest ecosystems, our understanding of their long term successional dynamics and the associated driving processes is still limited. This study used spatially explicit data from five, long-term, permanent plots in mature lodgepole pine (*Pinus contorta*) stands in the Canadian Rocky Mountains to: 1) assess whether understory communities showed homogenization over time either within or between plots and if compositional changes observed were supportive of either the initial or relay floristics model; and 2) evaluate the relative importance of the environment *versus* dispersal limitations in structuring these understory communities and how this changes over time. We found between-plot convergence and within-plot homogenization over time, largely due to increasing cover of mosses and later successional species. These changes were mainly in relative abundance, thus supporting the initial floristic model. However, the appearance of late successional species and the disappearance of early successional species over the study period suggested that the relay floristic model was also important. Most of the variation in understory species composition and richness was explained by spatial variables that were independent of environmental factors, suggesting that dispersal limitation was important in these communities. However, environmental variables explained an important fraction of the variation in species richness and composition, especially in more xeric environments; from this we infer that deterministic processes still played an important role in structuring these communities. In most plots, our results also showed increasing importance of dispersal limitations following canopy closure and we attribute this to both the homogenisation of the understory environment and increased abundance of later successional species which were more dispersal limited.

2.1. Introduction

The structure and species composition (tree and understory species) of forest ecosystems change over time as a function of ageing and minor disturbances (Brulisauer et al. 1996, Clark et al. 2003, Hart and Chen 2006b). Understanding the dynamics of understory plant communities is important in northern forests since they represent most of plant biodiversity, provide food and habitat for many other life forms, as well as influence nutrient cycling and regeneration of tree species (Nilsson and Wardle 2005, Gilliam 2007).

Many studies have described the dynamics of forest understory communities in the early post-disturbance stages (Halpern 1988, Bainbridge and Strong 2005, Kayes et al. 2010). Initial post-disturbance understory communities are typically dominated by shade intolerant species that colonize from seed or underground rhizomes (Halpern 1989, Hart and Chen 2006b) but can also include remnants of the pre-disturbance community that gradually increase in abundance over time (Halpern 1989, Anderson and Romme 1991, Nieppola 1992). Following canopy closure, understory communities gradually shift towards increasing relative abundance of shade tolerant species (Taylor et al. 1988, De Grandpré et al. 1993, Nygaard and Ødegaard 1999). However, the few long term permanent plot studies of mature forest understory communities showed that no new species established during this phase (Nieppola 1992, Nygaard and Ødegaard 1999). This suggests that understory communities follow the complete initial floristic model *sensu* Wilson et al. (1992) which proposes that all the species present throughout succession are present at the beginning, although their relative importance changes over time. However, we still have a poor understanding of the fine scale dynamics of understory vegetation in mature forests and later successional stages (Nygaard and Ødegaard 1999, Frelich et al. 2003) as the canopy breaks up or changes in composition.

In these later successional stages there could be a transition in understory species composition characterized by new establishment of later-successional species, conforming to the relay floristics or facilitation model (Egler 1954, Connell and Slatyer 1977). This model assumes that early successional species modify the environment such that it becomes more suitable for establishment of late successional species. However, the relay floristic model doesn’t consider dispersal limitations which could also influence the timing of species arrival following disturbances; determining the driving processes of relay floristics can be challenging (Finegan 1984). On the other hand the complete initial floristic model assumes that most species are not dispersal limited and are well adapted to return following disturbance which is a reasonable assumption for many fire adapted forested landscapes (Halpern 1989, Anderson and Romme 1991, Nieppola 1992). While both complete initial and relay floristics are likely at play in most forest ecosystems, few studies have been able to address their relative importance throughout successional development or examine the processes driving dynamics of forest understory communities over the long term. Understanding the spatial patterns of species and their relationship to environmental factors can give insight into the mechanisms structuring understory communities (Dale 1999). If environmental conditions are responsible for the observed patterns of understory communities, this suggests that the classical model of environmental control (or niche theory) is important (Hutchinson 1957). The spatial structure of understory communities could, alternatively, be driven mainly by dispersal limitations which would generate spatial autocorrelation in the species data (Legendre et al. 2009). Few studies have looked at the relative importance of these different processes for forest understory communities (however see Karst et al. 2005, Burton et al. 2011) and none that we are aware of are based on longitudinal sequences throughout stand development. Indeed, most studies of understory community dynamics have used a chronosequence approach (e.g., Taylor et al. 1988, De Grandpré et al. 1993, Brulisauer et al. 1996, Bainbridge and Strong 2005), which limits our ability to answer these questions. The use of long term permanent plots are rare (however see Nygaard and Ødegaard (1999)) but they can allow a rigorous assessment of successional dynamics while also providing insight into potential underlying mechanisms – particularly if they are spatially-explicit.

Lodgepole pine ecosystems are dominated by relatively frequent stand-initiating wildfire and thus most often exist as relatively young, heavily pine-dominated stands that rarely proceed to the canopy breakup stage of succession (Johnson and Fryer 1989). These forests are, however, increasingly affected by less severe disturbances that do not directly affect the understory community or forest floor; for example, the recent Mountain Pine Beetle epidemic (Mathey and Nelson 2010). Furthermore, lower fire frequencies in recent decades (Van Wagner et al. 2006), whether due to natural or anthropogenic causes, have led to large tracts of mature lodgepole pine forest that are experiencing significant canopy decline and successional transition (Rhemtulla et al. 2002). Understanding the vegetation dynamics of understory communities in these aging lodgepole pine ecosystems is critical for assessing the biodiversity impacts and management implications of these changes in disturbance regime.

In the research presented herein, we used spatially explicit data from five long-term permanent plots in mature lodgepole pine (*Pinus contorta* Douglas ex Loudon) stands in the Canadian Rocky Mountains to: 1) examine complete initial *versus* relay floristics; and 2) explore the importance of deterministic processes versus dispersal limitation in influencing understory community composition over time. Changes in community composition due to changes in relative abundance would support the complete initial floristic model, whereas the appearance of new species over the study period would support the relay floristic model. The environmental control hypothesis would be supported by correlations between the environment (canopy, microtopography) and understory community composition whereas a spatial structure that is independent of environmental variables would support the importance of dispersal limitations. We expected that homogenization of the understory environment following canopy closure would be accompanied by homogenization of understory communities due to reduced abundance of pioneer species and increased abundance of shade tolerant or late successional species. In turn, this was expected to lead to decreased importance of environmental control but increasing importance of dispersal limitations over time. Canopy break-up (due to disturbances or decline of pioneer tree canopy), on the other hand, would increase heterogeneity in the understory environment resulting in greater heterogeneity in understory communities with increasing abundance of pioneer species in gaps. In turn, this was expected to lead to increased importance of environmental control.

2.2. Methods

Study area

The research was conducted in five mature lodgepole pine dominated forests in Banff and Jasper National Parks, Canada (Table 2-1) . These forests were selected following an extensive survey of lodgepole pine dominated forests in these parks and were chosen to cover a wide range of moisture/elevation and to represent a range of lodgepole pine forest types found in these parks (Hnatiuk 1969, La Roi and Hnatiuk 1980). In 1967, a 1 ha permanent plot configured as a 20 x 20 grid of 5x5m contiguous quadrats was established in each forest (*i.e.* a total of 400 quadrats per forest). Each of these forests had already reached the canopy closure stage of succession in 1967. The plots were permanently marked in 1967 using railway spikes placed every 5 m around the plot boundary and every 20m within the plot. Relocation of the railway spikes using a metal detector allowed for a precise repeated measurement of the same quadrats in 1989 and 2012. Between 1971 and 2000 the weather stations closest to the low (Athabasca) and high (Hector) elevation plots recorded mean annual temperatures of 3.3°C and -0.3°C and mean annual precipitation of 398mm and 569mm, respectively (Canadian Climate Normals). However, the environmental conditions at each of our sites might vary from these weather stations as the geographical location in these mountains ranges can greatly influence precipitation and temperature.

Understory vegetation

Understory vegetation was sampled at each plot in 1967, 1989, and 2012 except for the Spray River plot, which was not sampled in 1989 (due to access constraints) but was sampled in 2010. In each study year, sampling was carried out between the middle of June and the third week of August, sampling dates for each plot were similar between years. For this study, nomenclature follows the USDA PLANT database (USDA, NRCS 2014); we aligned species identifications between sampling periods as some species changed names over the last 45 years. Estimates of percent cover for each vascular species and the main forest floor bryophyte and lichens species were made in each 5x5m quadrat using a modification of the Braun-Blanquet approach (Hnatiuk 1969) which included eight cover classes (<0.1%, 0.1-1%, 1-5% cover, 5-15% cover, 15-25% cover, 25-50% cover, 50-75% cover and 75-100% cover). These cover classes were then converted to mid-point values (respectively 0.1%, 0.5%, 3%, 10%, 20%, 38%, 63%, 88%) for use in subsequent analyses. In 1989 and 2012 more precise estimates of percent cover were made but for the purpose of this study they were converted back to mid-points of cover classes to allow comparison with the 1967 data. We acknowledge that differences in cover estimates between the different observers could have been a potential source of variation in this study although the use of broad cover classes limits this concern. Due to identification uncertainties or errors in 1967 or 1989 the following taxa were considered at the genus level for analyses: *Salix* spp., *Carex* spp., *Antennaria* spp. (includes *A. parvifolia*, *A. racemosa* and *A. rosea*), *Packera* spp. (includes *P. subnuda* and *P. streptanthifolia)*, *Solidago* spp. (includes *S. spatulatha* and *S. multiradiata*), *Vaccinium* spp. (includes *V. scoparium*, *V. myrtillus*, *V. membranaceum* and *V. myrtilloides*; although mainly *V. scoparium* and *V. myrtillus*), *Phyllodoce* spp. and *Empetrum nigrum*, *Cladonia* spp., *Cladina* spp., *Peltigera* spp., *Stereocaulon* spp. In 1967, three quadrats were not sampled in the Athabasca plot and were therefore excluded from the analysis for that year. Also in 1967 in the Athabasca plot only total percent cover of mosses and lichens was recorded and in the Whirlpool plot only lichens of the genus *Peltigera* were sampled. Furthermore, in 1967 *Cladina* species were classified as part of the *Cladonia* genus but in 1989 and 2012 *Cladina* and *Cladonia* were considered as two separate genera and percent cover was therefore estimated separately for each. Species richness and alpha diversity (Shannon-Wiener index) were calculated for each quadrat and the changes in species identified in the different years were taken into account when calculating average species richness and alpha diversity (see footnote of Table 2-3).

Overstory, topography and soils

Trees were counted by species and size classes in each quadrat. Stems with a diameter at breast height (DBH) greater than 2.54 cm (one inch, as used in the 1967 sampling) were placed in size classes (seven classes each spanning 7.62 cm DBH or three inches) while individuals less than 2.54 cm DBH but taller than 30cm were called 'transgressives' (Hnatiuk 1969). Canopy cover was measured using a Lemmon Model A Convex Spherical Densiometer at each quadrat corner and the average of the four corners was used as the canopy cover value for a given 5 x 5m quadrat. These data were unfortunately lost for 1967. The relative micro-elevation (hereafter referred to only as elevation) of each quadrat corner was determined in 1967 by measuring the slope between each quadrat corner using a Haga altimeter (Hnatiuk 1969). From the elevation of quadrat corners, four topographic attributes were calculated for each quadrat: elevation, convexity, slope and aspect. Following Legendre et al. (2009), elevation of each quadrat was calculated as the mean elevation of the four quadrat corners. Convexity was the mean elevation of a quadrat minus the average elevation of the eight surrounding quadrats. For quadrats on the edge of the plot, convexity was calculated using only those surrounding quadrats that were within the plot. ArcGIS version 10.1 (ESRI) natural neighbour interpolation was used to create a digital elevation model from which slope and aspect were calculated for each quadrat and which formed the basis for creation of micro-elevation topographic maps (Figure 2-1). For subsequent analyses, aspect was converted to northing [sin (aspect)] and easting [cos (aspect)] values.

In 2013, two soil pits were dug in the periphery of each plot to describe and classify the soils. They were located in areas representative of the interior of the plot and were positioned to sample different topographical features present within the plot (Figure 2-1, Table 2-2). For each soil profile, the thickness, texture, and color of each horizon were determined in the field (Soil Classification Working Group 1998). The pH of each horizon was also measured using water as a suspension medium (Kalra and Maynard 1991) and air dried color of each horizon was noted in the lab. Complete soil profile descriptions are presented in Appendix 2-A.

Data analysis

To examine the variation in understory species composition within and between plots over time, we used principal component analyses (PCA) on species composition data from all plots and all sampling periods. Total moss and lichen cover was calculated and used for all plots and sampling periods because of previously described data limitations for these groups in 1967. All understory community composition analyses were performed on Hellinger transformed species mid-point percent cover data (hereafter referred to as species composition data) which allowed us to use species abundance data in PCA and canonical redundancy analysis (RDA) (Legendre and Gallagher 2001). Following the PCA, the centroids and 95% confidence ellipses of each plot at each sampling period were calculated and displayed in ordination space to visualize the convergence of community composition between plots and within-plot homogenisation over time, respectively. We then formally tested between-plot convergence and within-plot homogenisation using a distance-based test of homogeneity of multivariate dispersion based on distance to centroid values (Anderson 2006). The average of

Euclidian distances for each quadrat to the centroid of all plots was compared between sampling periods (1967, 1989 and 2012) to test between plot convergence. The average distance for each quadrat to the centroid of the plot it was in was compared among sampling periods to test within-plot homogenization. To further assess how the understory communities were changing in time and whether these changes were mainly in relative abundance or if new species were establishing, we calculated the frequencies of all species in each plot at each sampling period.

We used variation partitioning to examine the relative influence of overstory, topography and spatial structure on species richness and alpha diversity (analogous to partial regressions) and on understory species composition (using partial RDAs) (Borcard et al. 1992). Adjusted R^2 are presented for the variation partitioning analysis which allows us to better compare the amount of variation explained by different types of variables as it adjusts for the number of variables used (Peres-Neto et al. 2006). Confidence intervals were calculated for adjusted R^2 values to allow for comparison of the fractions between sampling periods (Peres-Neto et al. 2006). Spatial patterns of the understory communities were determined using the principle coordinates of neighbour matrices (PCNM) method described by Borcard and Legendre (2002) since it has been found to be one of the most efficient methods in capturing complex spatial structures (Smith and Lundholm 2010). This method generates spatial patterns at multiple scales specific to the sampling design and in our study it generated 209 PCNM eigenfunctions with positive autocorrelation; these were submitted to a forward selection procedure, as described below, to choose a subset for inclusion in the variation partitioning analyses.

Variation partitioning was done for each plot and each sampling period separately and we retained the species at the level they were identified to in each year. Since the results from the variation partitioning of species richness and alpha diversity were similar, only the results for species richness are presented. Before conducting variation partitioning we used forward selection to choose the overstory and topography variables as well as the PCNM eigenfunctions that were most strongly related to the response variable. Significant (α=0.05) variables were selected using the forward selection procedure described in Blanchet et al. (2008). Using simulated data, Gilbert and Bennett (2010) found that variation partitioning with PCNM variables inflates the Adjusted R^2 due to the inclusion of superfluous canonical axes that model random noise. Thus we present the amount of variation explained by the first axis and the following 5 significant axes to determine the importance of this potential inflation. Unconstrained ordination (PCA), tests of multivariate dispersion, constrained ordination (RDA), and variation partitioning were conducted using the “vegan” package (Oksanen et al. 2013), PCNM variables were constructed using the “spacemakeR” package (Dray et al. 2006), and forward selection was computed using the “packfor” package (Dray 2009) of the R statistical language (R Development Core Team 2007).

2.3. Results

Temporal dynamics of understory communities

A total of 112 understory species occurred in the five plots, and species per stand varied from 31 to 66 (Table 2-3, Appendix 2-B). The first PCA axis can be interpreted as a gradient from the xeric (Athabasca) plot, where species such as *Arctostaphylos uva-ursi*, *Shepherdia canadensis*, *Leymus innovatus* and *Juniperus communis* were present in high cover, to moister plots (Hector and Spray River) which were associated with a higher cover of mosses, *Vaccinium* species, *Menziesia ferruginea* and *Arnica cordifolia* (Figure 2-2, Table 2-3). The mesic Sunwapta plot and the Whirlpool plot were intermediate between these two. Over time all plots (except Whirlpool) had substantial increases in moss cover (Table 2-3) and this can be seen in Figure 2b where, with time, all plots are moving in the direction of mosses (Figure 2-2a & b). The five plots were converging over time; the average distance for each quadrat to the overall centroid of all plots decreased significantly ($p<0.001$) over time from 0.67 to 0.56 and 0.51 in 1967, 1989 and 2012 respectively. We also found evidence of within-plot homogenization. For all plots except Whirlpool, the 95% confidence ellipses of all plots shrank over time (Figure 2-2) and the average distance in ordination space between quadrats and centroids of each plot generally decreased over time (Athabasca 0.48, 0.40, 0.32; Sunwapta 0.49, 0.35, 0.31; Hector 0.40, 0.27, 0.26; Spray River 0.40, 0.28) (all significant ($p<0.001$) except Hector between 1989 and 2012). In contrast, at Whirlpool the average distance in ordination space between quadrats and the plot centroid increased significantly after 1989 (0.30, 0.32, 0.36 for 1967, 1989, 2012 respectively). The Whirlpool plot was affected by severe wind disturbances over the last 20 years which considerably altered the structure of the stand (out of 2281 total standing stems with DBH > 2.54cm living and dead in 1989, 721 were either blown down or snapped). Most of the canopy blowdown occurred over 10 years prior to 2012 and a more detailed description of this disturbance and its effect on the structure and composition of this stand will be presented in a subsequent manuscript.

In most plots, total species richness and average species richness per 5 x 5m quadrat was stable over time; the exceptions were for total species richness which increased by more than 50% from 1989 to 2012 at the Athabasca plot, but showed a minor (~16%) decrease at the Spray River plot from 1967 to 2010 (Table 2-3). In contrast, mean alpha diversity per quadrat increased over time at every plot; together these results suggest an increase in evenness. The community dynamics underlying these trends in richness and diversity were characterized by complex patterns of increases and decreases in cover and frequency of individual species (Tables 2-3 & 2-4). Understory community composition in these plots was dynamic; a large number of species increased or decreased in frequency by at least 25% over the last 45 years (Table 2-4). Most of the taxa that decreased in frequency were ones associated with open or dry micro-habitats such as *Packera* spp., *Antennaria* spp., *Senecio lugens*, *Solidago* spp., *Stereocaulon* spp., *Calamagrostis purpurascens*, *Trisetum spicatum*, and *Castilleja miniata*. On the other hand most of the species increasing in frequency were ones associated with moist or closed forest micro-habitats such as *Orthilia secunda*, *Chimaphila umbellata*, *Geocaulon lividum*, *Hylocomium splendens*, *M. ferruginea*, *Cornus canadensis*, *Moneses uniflora* and many orchid species adapted to moist habitats (*Dactylorhiza viridis*, *Piperia unalascensis*, *Platanthera obtusata*, *Listera cordata*). Micro-habitat preferences were verified using the USDA PLANT database and local flora (Moss 1983). Some species showed different responses among the plots (Table 2-4). For example, *Dicranum polysetum* increased in the Athabasca and Sunwapta plots, but decreased in the two moist plots (Hector and Spray River); and *Polytrichum juniperinum* increased in the Athabasca and Whirlpool plots, but decreased in all the other plots.

In addition to species changes in abundance and frequency, there were several instances of new species appearing or disappearing over time. The xeric Athabasca plot had a total of 18 newly established species over the study period, most of which are later successional or moist adapted species such as *C. umbellata*, *G. lividum*, *Goodyera oblongifolia*, *D. viridis*, *Platanthera orbiculata*, *M. uniflora*, *Vaccinium cespitosum*, *Vaccinium vitis-idaea*, *Viburnum edule*, *Ribes lacustre*, *Rubus pubescens* and *Ptilium crista-castrensis* (Appendix 2-B). In the Whirlpool plot, 10 species appeared over time, most of which established in the drier upper terrace of the plot and included late successional or moist adapted species such as *Lonicera involucrata*, *V. vitis-idaea*, *P. orbiculata* and *Stellaria calycantha,* while in the mesic Sunwapta plot five species appeared over time including late successional or moist adapted species such as *V. edule*, *P. orbiculata* and *Lycopodium annotinum*. In contrast, there were few newly establishing species in the moist Hector and Spray River plots (one and three respectively) and the latter had 14 species which disappeared from the plot over the study period, many of which were early successional or open habitat species such as *Dasiphora fruticosa*, *Achillea millefolium*, *Agoseris glauca*, *Antennaria neglecta*, *Campanula rotundifolia*, *Erigeron peregrinus*, *Gentianella amarella*, *Heracleum maximum* and *Hieracium albiflorum* and *Solidago* species. In the other plots fewer species disappeared (3, 6, 6, 2 in the Athabasca, Sunwapta, Whirlpool and Hector plots, respectively). Of all the species that established over the study period approximately half reproduces mainly by seed while the other half reproduces mainly vegetatively (Appendix 2-B).

Processes structuring understory communities

All plots had spatially structured understory communities, with the PCNM variables always explaining the most variation (adjusted R^2) in understory community composition (between 20-56%; Figure 2-3a to 2-7a) and understory species richness (between 23-

64%; Figure 2-3c to 2-7c). However, the relative importance of the environmental variables (overstory and topography) varied between plots. Further, the relative importance of spatial and environmental variables was constant in time for some plots (Hector/ Spray River) but varied over time for others (Athabasca/Sunwapta/Whirlpool).

In all plots, there was considerable overlap in the variation in species composition and richness explained by the environmental variables and the PCNM variables. In the Athabasca and Whirlpool plots there was also a high degree of overlap between overstory and topography in terms of the explained variation in understory composition, suggesting they both had similar spatial structure and explained the same spatial pattern (Figure 2-3a & c, 2-5a & c). In the Sunwapta, Hector and Spray River plots there was more independence between overstory and topography in terms of the explained variation in understory composition and richness, although both showed shared variation with the spatial variables. This suggests they are both spatially structured but that this structure explains different aspects of the spatial pattern (Figure 2-4a & c, 2-6a & c, 2-7a & c). Detailed results (species scores and scores for constraining variables) for RDAs with environmental variables are presented in Appendix 2-C.

In the RDAs of understory community with overstory, topography or PCNM variables (referred hereafter as RDA-over, RDA-topo and RDA-PCNM respectively), the first axis always explained most of the variation in species composition and represented the most ecologically meaningful gradients. Therefore only the first axis will be presented in more detail. The only exception was for the Spray River plot in 2010 where the second axis of the RDA-PCNM is presented because it explained almost as much variation as the first axis (5.3% vs 5.7%) and showed a spatial pattern similar to the first axis of the RDA-PCNM in 1967 (see Figure 2-7b).

Xeric plot (Athabasca)

Community composition.—In the Athabasca plot, around 40% of variation in understory composition was explained by space (i.e., PCNM variables) in 1967 and 1989 but this decreased to 29% in 2012 with no overlap of confidence intervals between 2012 and the previous sampling periods (Figure 2-3a). The amount of variation in the understory composition explained by the overstory was around 19% in both 1967 and 1989 and then dropped in 2012 (11%) while the amount explained by topography gradually decreased over time (14% in 1967 to 5% in 2012) and the confidence intervals barely overlap for these variables (Figure 2-3a). To better evaluate the relative influence of PCNM and environmental variables on understory community composition and richness we also calculated the proportion of explained variance accounted for by these variables. This was done by dividing the sum of all fractions representing respectively environmental variables (topography and overstory) and PCNM variables by the total of variation explained. Over time, the proportion of the explained variance that was due to PCNM variables remained stable (93%, 94%, 90%) while the proportion due to environmental variables decreased (54%, 46% and 40%).

The importance of the main spatial structure of the understory composition (i.e. Axis 1 of RDA-PCNM) declined across the 3 sampling periods (Figure 2-3b); the spatial pattern itself was similar in 1967 and 1989 but then changed in 2012. The main spatial structure explained 27.1%, 20.2% and 11.2% of the variation in 1967, 1989 and 2012 respectively (Figure 2-3b); while together, secondary spatial structures (the five following significant axes of RDA-PCNM) explained together 10.8%, 16.9% and 13.7% of the variation in 1967, 1989 and 2012, respectively. These results suggest a potential inflation by 2, 6 and 4% of variation explained by spatial variables. The main structure captured the contrast between quadrats with high *A. uva-ursi* cover vs high moss cover (open circles vs closed circles respectively in Figure 2-3b). This gradient in species composition was also captured in the first axis of the RDA-over and RDA-topo (Appendix 2-C).

A. uva-ursi cover was higher in quadrats which had larger lodgepole pine trees (both had negative scores on the first axis of RDA-over) while high moss cover in quadrats was associated with a high density of small lodgepole pine trees (living or dead) and high canopy cover in all time periods (all had positive scores on the first axis of RDA-over) (Appendix 2-C, Table 2-5). In these latter quadrats, high densities of small lodgepole pine grew along with smaller black or Engelmann spruce trees and transgressives (all had positive scores on the first axis of RDA-over; Table 2-5, Appendix 2-C: Table 2-C1) and over time densities of these small spruce became the most important overstory variables (higher positive scores on first axis of RDA-over in 2012; Appendix 2-C: Table 2-C1). High *A. uva-ursi* cover was also associated with higher elevation and convex quadrats (all had negative scores on the first axis of RDA-topo) while moss cover was higher in lower elevation and concave quadrats (moss score on the first axis of RDA-topo was positive) (Table 2-6, Appendix 2-C: Table 2-C2). The soil from the lower elevation/concave topographical element was more well-developed and eluviated (presence of Ae horizon, thicker solum, redder hues and higher color values and chromas, Table 2-2) than in the higher elevation/convex area; this suggests more movement of water through the soils of these lower elevation/concave areas (Rahman et al. 1996).

The lower amount of variation in understory composition explained by the overstory in 2012 is due in part to declining density of smaller lodgepole pine trees in areas that earlier had quite high density (PC1 was not selected during the forward selection procedure in 2012, Table 2-5; also see PC1 and PC2 in Appendix 2-D) and to the spread and increase in cover of mosses and *A. uva-ursi* across the whole plot (Appendix 2-D). The latter also contributed to the gradual decrease in variation explained by topography over time (reduction of species scores on the first axis of RDA-topo, Appendix 2-C) and the reduction in variation explained by space in 2012 (reduction of species score on the first axis of RDA-PCNM, Figure 2-3b).

Richness.—In contrast to community composition, the amount of variation in understory species richness explained by space (or PCNM variables) increased over time, from 36% in 1967 to 62% in 2012 with no overlap of confidence intervals between 2012 and previous sampling periods. (Figure 2-3c). The amount of variation in species richness explained by the overstory also increased over time, from around 8% in 1967 to 34% in 2012 while the amount explained by topography was not significant in 1967 but gradually increased to 9% in 2012 although the confidence intervals included zero in both 1989 and 2012 (Figure 2-3c). Over time, the proportion of explained variance due to PCNM variables remained stable (96%, 93%, 95%) while the proportion due to environmental variables increased (22%, 35%, 54%).

From 1967 to 2012 the spatial structure of species richness (Figure 2-3d) gradually changed into a pattern that was very similar to the main spatial structure of understory community composition in 1967 and 1989. The areas of low species richness in 2012 corresponded very well with the areas of higher moss cover in 1967 and 1989 (Figure 2-3b & d). Richness was usually negatively correlated with the density of small lodgepole pine trees (e.g., density of small dead trees (1967), small living pine (1989, 2012), and canopy cover (2012)) and positively correlated with the density of lodgepole pine transgressives (1989, 2012) (Table 2-5) which are characteristic of more open areas (more abundant in quadrats which had lower densities of pine trees larger than 7.63cm DBH in the southwest and south central parts of the plot and in a small northeast section of the plot, see PC2-5 in Appendix 2-D). Species richness was always positively correlated with elevation but was negatively correlated with slope in 1967 and 2012 (Table 2-6); i.e., quadrats in higher elevation spots (usually also more open) had higher richness and those on steeper slopes and lower elevation had lower richness.

The increases over time in the amount of variation in species richness that was explained by both spatial pattern and overstory were due to: 1) species like *G. amarella*, *A. neglecta* and taxa such as *Stereocolon, Solidago*, *Packera* and *Carex* species which were initially present more or less throughout the plot being gradually excluded from the dense band of small pines, particularly by 2012 (Appendix 2-D); 2) species like *D. viridis*, *Amelanchier alnifolia*, *C. miniata*, *Festuca saximontana* and *Viola adunca* that were initially found mainly in the more open areas increasing in frequency in open areas in 2012 (Appendix 2-D); and 3) species previously restricted to the dense areas - like *O. secunda* in 1967 and 1989 or the different moss species sampled in 1989 - having spread out into more open areas and thus contributing to increased species richness in these areas (Appendix 2-D). Together, these resulted in increased species richness in open areas and reduced richness in dense areas, leading to a stronger spatial pattern for richness in 2012 (Figure 2-3d). This also contributed to the slight increase in the amount of variation in richness that was explained by topography in 2012 compared to 1967 and 1989 since the more open areas of the plot were also at higher elevations.

Mesic plot (Sunwapta)

Community composition.—In the Sunwapta plot, the amount of variation in understory composition explained by space (or PCNM variables) was more or less stable around 35% in 1967 and 1989 but increased to 55% in 2012 with no overlap of the confidence intervals between 2012 and previous sampling years (Figure 2-4a). The amount of variation in the understory composition explained by overstory and topography was more or less constant throughout the study period with values around 12% and 5% respectively and substantial overlap of confidence intervals between sampling periods (Figure 2-4a). Over time, the proportion of explained variance that was due to PCNM variables increased (88%, 93% and 97%) while the proportion due to environmental variables decreased (39%, 41% and 29%).

The main spatial structure of the understory composition (i.e. Axis 1 of RDA-PCNM) was relatively constant during the study period and the main species associated with this structure remained more or less the same (Figure 2-4b). The main spatial structure explained 12.6%, 18.8% and 25.8% of the variation in 1967, 1989 and 2012 respectively (Figure 2-4b) while together, secondary spatial structures (five following significant axes of RDA-PCNM) explained together: 15.5%, 11.9% and 12.4% of the variation in 1967, 1989 and 2012, respectively. These results suggest a potential inflation by 5, 6 and 12% of variation explained by spatial variables. The main spatial structure captured the contrast between quadrats with high cover of species associated with moist micro-habitats or that have low drought tolerance (positively correlated with the first axis of RDA-PCNM in Figure 2-4b) vs quadrats with high cover of species associated with more open micro-habitats or having higher drought tolerance (negatively correlated with the first axis of RDA-PCNM in Figure 2-4b). Interestingly, *Pleurozium schreberi* was initially on the moist side of the gradient in 1967 and 1989 and changed to the drier side of the gradient in 2012. The increase in amount of variation in species composition explained by space in 2012 is due to: 1) the strengthening of the main spatial structure (first axis of RDA-PCNM) due to the reinforcement of the spatial patterns of many species associated with this structure (Figure 2-4b, Appendix 2-E); and 2) the increased importance of secondary spatial structure of the understory communities.

The cover of species associated with moist micro-habitats such as *V. vitis-idaea*, *M. ferruginea*, *P. schreberi*, *P. crista-castrensis*, *H. splendens* was usually higher in areas with higher density of live lodgepole pine transgressives, high canopy cover in 1989 and high density of dead transgressives in 2012 (all had positive scores on the first axis of RDA-over; Table 2-5, Appendix 2-C: Table 2-C1). On the other hand, the cover of dry or open micro-habitat species was associated (although weakly in 1989 and 2012) with higher density of larger lodgepole pine trees (all had negative scores on the first axis of RDA-over; Appendix 2-C: Table 2-C1). The cover of mosses and species associated with moist micro-habitats was also usually associated with lower elevation, east facing slopes and concave quadrats (positive scores for these species and convexity on the first axis of RDA-topo while elevation and the sine of aspect had negative scores; Table 2-6, Appendix 2-C: Table 2-C2). However, in 2012, *P. schreberi* switched to a negative score on the first axis of RDA-topo and was thus associated with quadrats in higher elevation, west facing and convex (Appendix 2-C: Table 2-C2). Similar to the Athabasca plot, soils from the lower elevation topographical element (east side of the plot, Figure 2-1) were more developed (presence of Ae horizon, thicker solum, Table 2-2) than in the higher elevation areas; this suggests, once again, more movement of water through the soils of these lower elevation areas.

Richness.—In contrast to species composition, the amount of variation in understory species richness explained by space (or PCNM variables) decreased from 64% in 1967 to 50 and 54% in 1989 and 2012, respectively (Figure 2-4c) with minimal overlap of confidence intervals between 1967 and subsequent sampling periods. Also in contrast with species composition is that the amount of variation in species richness explained by the overstory decreased over time from around 20% in 1967 and 1989 to 11% in 2012 while the amount explained by topography decreased from 12% to 2% between 1967 and 1989 and then increased to 6% in 2012 (Figure 2-4c), although there was substantial overlap of confidence intervals between sampling periods for these variables. Over time, the proportion of explained variance due to PCNM variables decreased only slightly (99%, 92% and 95%) while the proportion due to environmental variables decreased (50%, 44% and 32%).

Species richness was positively correlated with the density of lodgepole pine transgressives (living in 1967 and 1989, dead in 2012), with the density of trembling aspen transgressives in 1967 and 1989, and was negatively correlated with the density of larger lodgepole pine trees in each year (Table 2-5). Species richness was negatively correlated with elevation in 1967 and 2012 but positively correlated with elevation in

1989 (although the amount of variation explained in 1989 was very low). Richness was also consistently negatively correlated with the sine of aspect (i.e., easting; Table 2-6). Thus, generally west facing quadrats at lower elevations had higher species richness than east facing quadrats at higher elevation, at least in 1967 and 2012.

The decreased amount of variation in richness explained by space after 1967 can be explained by the spread of species such as *H. splendens*, *V. vitis-idaea, C. umbellata;* these originally had low frequencies and were mainly present on the east moist side of the plot but by 1989 and 2012 they were also present in low abundance in quadrats on the western drier side of the plot (Appendix 2-E: Fig. 2-E1). There were two processes underlying the decreased amount of variation in richness explained by the overstory in 2012. Firstly, species (like *C. canadensis*, *V. vitis-idaea*, and *C. umbellata*) that were initially present mainly in quadrats with higher densities of lodgepole pine transgressives or in more open areas with low densities of large trees were spreading into the rest of the plot (Appendix 2-E: Fig. 2-E1). Secondly, species (like *Packera* spp., *Solidago* spp. and *Antennaria* spp.) originally occupying quadrats with low densities of big trees were becoming less frequent in these open areas (Appendix 2-E: Fig. 2-E1).

Moist/xeric plot (Whirlpool)

Community composition.—In the Whirlpool plot, the amount of variation in understory composition explained by space was stable during the study period at about 55% (with overlap of confidence intervals between all sampling periods). The amount explained by the overstory decreased from 21% and 24% in 1967 and 1989 to 18% in 2012 (Figure 2-5a) while the amount explained by topography decreased from 25% in 1967 to 16% in 2012 with only small confidence interval overlap (Figure 2-5a). Over time, the proportion of the explained variance that was attributable to PCNM variables remained at 97% while the proportion attributable to environmental variables decreased (55%, 54% and 46%).

The understory composition main spatial structure (i.e. Axis 1 of RDA-PCNM) was also stable in time (Figure 2-5b). However, the amount of variation that it explained in understory composition, gradually decreased from 40.4% in 1967 to 21.4% in 2012 (Figure 2-5b) while together, secondary spatial structures (five following significant axes of RDA-PCNM) explained, together, 13.5%, 14.1% and 23.0% of the variation in 1967, 1989 and 2012, respectively. These results suggest a potential inflation by 3%, 10% and 10% of variation explained by spatial variables in 1967, 1989 and 2012 respectively. The main spatial structure captured the contrast between quadrats with high cover of *H. splendens*, *P. crista-castrensis* and other species with low drought tolerance or associated with moist micro-habitats (*C. canadensis*, *A. cordifolia*, *Chamerion angustifolium* and *Ledum groenlandicum*) vs quadrats with high cover of *P. schreberi* (only in 1967 and 1989) and species associated with more open micro-habitats or with higher drought tolerance (*A. uva-ursi*, *J. communis*, *S. canadensis* and *V. cespitosum*, *Cladonia* spp.) (Figure 2-5b). The reduction in variation explained by the main spatial structure is due to the gradual spread of the main pleurocarpous moss species and *C. canadensis* throughout the plot (Appendix 2-F: Fig. 2-F1).

The cover of species with high drought tolerance or associated with open micro-habitats, as well as *P. schreberi,* was higher in quadrats with larger lodgepole pine trees (all had negative scores along the first axis of RDA-over; Table 2-5, Appendix 2-C: Table 2-C1) and higher elevation (all had negative scores on the first axis of RDA-topo; Table 2-6, Appendix 2-C: Table 2-C2) although this was only true in 1967 and 1989 for *P.*

schreberi. The cover of *H. splendens*, *P. crista-castrensis* or species associated with moist micro-habitats such as *C. canadensis* and *A. cordifolia* was higher in quadrats with high density of black spruce transgressives and trees, higher canopy cover (in 1989 and 2012), high density of dead trees (6 to 9 inch DBH) and dead transgressives in 2012 (all had positive scores along the first axis of RDA-over; Table 2-5, Appendix 2-C: Table 2-C1) and lower elevation (positive score on the first axis of RDA-topo; Table 2-6, Appendix 2-C: Table 2-C2). Once again, soils from the lower elevation topographical elements had characteristics suggesting more movement of water (presence of Ae horizon, thicker solum, redder hues and higher color values and chromas, Table 2-2). Furthermore there were mottles in the lower horizons of the soils from the lower terrace (Appendix 2-A) which suggests the water table reached these lower horizons for at least part of the year.

Richness.—Unlike with species composition, the amount of variation in understory species richness explained by space (PCNMs), overstory and topography increased from 1967 to 1989 and then decreased in 2012 (Figure 2-5c). Confidence intervals did not overlap for the PCNM variables but slightly overlapped for environmental variables between 1967 and 1989 and more so between 1989 and 2012. Over time, the proportion of explained variance due to PCNM variables remained stable (99%, 98% and 96%) while the proportion due to environmental variables increased overall (33%, 59% and 48%). Species richness was always positively correlated with elevation, with lodgepole pine transgressive density and with slope in 1967 and 1989 and with trembling aspen transgressive density in 2012 (Tables 2-5 & 2-6). Species richness was always negatively correlated with the density of black spruce trees or transgressives and also with canopy cover in 1989 (Table 2-5). Richness was also consistently negatively correlated with the cosine of aspect (i.e., northing) and with the sine of aspect (i.e., easting) in 1989 and 2012 (Table 2-6). Thus areas on the upper terrace with southern or western orientations usually had higher richness than on the lower terrace where black spruce trees and transgressives were dominant (Figure 2-5d, Appendix 2-F: Fig. 2-F1).

The increase in amount of variation in richness explained by overstory and topography between 1967 and 1989 is due to: 1) species that decreased in frequency on the lower terrace (west side of the plot; Figure 2-1c) from 1967 to 1989 (i.e. *D. polysetum*, *Pyrola chlorantha* and *C. rotundifolia*; see Appendix 2-F: Fig. 2-F2); and 2) species that increased in frequency on the upper terrace from 1967 to 1989 (i.e. *J. communis*, *C. umbellata* and *G. oblongifolia*; see Appendix 2-F: Fig. 2-F2). Overall this resulted in greater contrast in richness between the two terraces in 1989 (Figure 2-5d). The decrease in variation in richness explained by the overstory and topography between 1989 and 2012 is due to: 1) species that decreased in frequency on the upper terrace (east side of plot, Figure 2-1c) (i.e. *A. uva-ursi*, *G. oblongifolia*, *P. chlorantha* and *C. bulbosa*; Table 2-4, Appendix 2-F: Fig 2-F3); and 2) species that increased in frequency on the lower terrace from 1989 to 2012 (i.e., *P. crista-castrensis*, *D. polysetum*, *C.angustifolium*, *C. rotundifolia* and *Cladonia* spp. (Appendix 2-F). Overall this reduced the contrast in species richness between the upper and the lower terrace in 2012 compared to 1989 (Figure 2-5d).

Moist plots (Hector and Spray River)

Community composition.—In the two moist plots (Hector and Spray River), the amount of variation in understory composition explained by space (or PCNM variables) increased over the study period (Figure 2-6a & 2-7a) although the confidence intervals overlapped in the Spray River site. The amount of variation in species composition explained by space was higher in the Hector (between 38-49%) compared to the Spray River (21-26%) plot. The amount of variation in species composition explained by the overstory was constant in time around 7% and 4% for the Hector and Spray River plots, respectively, while topography always explained less than 4% for these plots. For both these plots the confidence intervals of the adjusted R^2 of the environmental variables overlapped substantially between sampling periods and always encompassed zero. Over time, the proportion of explained variance due to PCNM variables remained stable (Hector always 98% ; Spray River 93% and 98%) while the proportion due to environmental variables was stable (Hector 19%, 18% and 18%) or decreased (Spray River 26% and 19%).

In the Hector plot the main spatial structure explained 26.4%, 29.2% and 29.5% of the variation in community composition in 1967, 1989 and 2012 respectively (Figure 2-6b) while together, secondary spatial structures (five following significant axes of RDA-PCNM) explained together 9.7%, 15.6% and 16.6% of the variation in 1967, 1989 and 2012, respectively. These results suggest a potential inflation by 1, 3 and 3% of variation explained by spatial variables in 1967, 1989 and 2012 respectively. The main spatial structure of the Hector plot captured the gradient between quadrats with high cover of *M. ferruginea* and *P. schreberi* vs quadrats with high cover of *S. canadensis* and other drought tolerant species (Figure 2-6b). The cover of *M. ferruginea* and *P. schreberi* was higher in quadrats with high density of transgressives or small trees of later successional species (Engelmann spruce and subalpine fir) as well as high canopy cover in 1989 (all had positive scores on the first axis of RDA-over; Table 2-5, Appendix 2-C,

Table 2-C1). On the other hand, the cover of *S. canadensis* and other drought tolerant species was higher in quadrats with high density of small to medium size live or dead lodgepole pine trees (all had negative scores on the first axis of RDA-over; Table 2-5, Appendix 2-C, Table 2-C1). The soil profiles sampled were located near the two ends of this gradient (Figure 2-1; Figure 2-6b) and there were signs of higher water movement through the soils (thicker Ae horizon and deeper solum depth, Table 2-2) of the pits down slope near the moist side of the gradient (northwest corner of the plot).

In the Spray River plot the main spatial structure (first and second axis of RDA-PCNM in 1967 and 2010 respectively) explained 9.2% and 5.3% of the variation in 1967 and 2010 respectively (Figure 2-7b) while together, secondary spatial structures (five following significant axis of RDA-PCNM) explained together 9.1%, 12.8% of the variation in 1967and 2012, respectively. These results suggest a potential inflation by 2 and 8% of variation explained by spatial variables in 1967 and 2010, respectively. The main spatial structure once again captured the gradient between quadrats with higher cover of mosses or moist adapted species *versus* the drought tolerant shrub *S. canadensis* (and other open habitat species in 1967). As with the Sunwapta plot, *P. schreberi* started on the moist side of the gradient in 1967 but ended up on the drier side of the gradient along with *S. canadensis* in 2010. There was some variation in Ae horizon and solum depth between the two soil profiles around this plot but the differences were not as striking as in some of the other plots previously described (Table 2-2). The amount of variation explained by the environmental variables was too low to justify a detailed description of the few significant relations.

Richness.—In the Hector plot the amount of variation in species richness explained by space (PCNM variables) initially decreased from 1967 to 1989 and then increased in 2012 while it increased from 23% to 33% over the study period in the Spray River plot. Both overstory and topography consistently explained only a small fraction (≤3%) of the variation in species richness (Figure 2-6c & 2-7c). In both these plots all the adjusted R^2 confidence intervals for all variables overlapped substantially between sampling periods. These results suggest that the understory species richness in the moist plots was spatially structured but that this structure is unlikely to be the result of the environmental factors measured.

2.4. Discussion

To our knowledge, this was the first long term study of understory communities in mature forests looking at both temporal and spatial changes in community composition and diversity using permanent plots. As expected, we found between-plot convergence and within-plot homogenization over time (Figure 2-2), largely due to increasing cover of mosses and later successional species. These changes were mainly due to changes in relative abundance, which supports the complete initial floristics model. However, over the study period some late successional species appeared (especially in drier environments) which suggests that the relay floristics model is also important, especially in harsher environments. The majority of the variation in understory species composition and richness was explained by spatial variables that were independent from environmental factors, suggesting that dispersal limitation was a dominant structuring process in these communities. Nevertheless environmental control played an important role in structuring these communities since environmental variables often explained an important fraction of the variation in species richness and composition, especially in more xeric environments. In most plots studied, our results also suggest that dispersal limitations were becoming more important following canopy closure (Figure 2-3 to 2-7), which supports our initial hypothesis. However, deterministic processes became more important for species richness in two of the plots, which had suffered canopy decline (Figure 2-3c and 2-5c); this agrees with the expected increase in importance of environmental control processes following canopy break-up.

Are understory communities stable in mature lodgepole pine stands?

Over the study period there was both between plot convergence towards later successional composition and within plot homogenization of the understory communities (in all stands except Whirlpool) (Figure 2-2). This supports our initial hypothesis that canopy closure would be followed by a homogenisation of the understory communities and is consistent with previous studies, which demonstrated that increasing evenness and/or declining variation in composition of understory communities follows canopy closure (Shafi and Yarranton 1973, De Grandpré et al. 1993). However, ours is the first study to demonstrate this using permanent sample plots. There wasn’t homogenisation of the understory community in the Whirlpool plot; this is probably because the canopy was 40 to 75 years older than in the other plots and thus had potentially already reached a more mature understory community in 1967. The increase in variability in community composition between 1989 and 2012 in this plot is likely the result of the recent wind disturbances which had significantly affected the canopy.

The convergence and homogenization observed were largely driven by the spread of mosses throughout the plots (Table 2-2, Figure 2-2), but declines in frequency of open micro-habitat species, increases in frequency and cover of species associated with closed forest or moist micro-habitats, and increasing evenness (in quadrats) also contributed to these processes (Table 2-4). Previous studies that did not observe such convergence of understory communities over time examined forest stands with different overstory species (Christensen and Peet 1984, Hunt et al. 2003, Hart and Chen 2008). Our results agree with Woods (2007) who found convergence to be prevalent between patches of similar habitats while not as important between different habitat types. Our results also agree with previous studies which found that the major compositional change in understory communities, throughout the later successional stages after canopy closure in coniferous forests, was the increase in mosses (Økland 2000, Bainbridge and Strong 2005, Uotila et al. 2005). Further, many of the species that increased in frequency or cover over time in our plots (such as *C. canadensis*, *C. umbellata*, *G. oblongifolia, L. annotinum, M. uniflora*, *O. secunda*, *V. vitis-idaea*, *H. splendens*, *P. crista-castrensis*) had been previously classified as intermediate or late seral species (Kauppi et al. 1978, McKenzie et al. 2000) or had appeared later in stand development (De Grandpré et al. 1993, Uotila et al. 2005, Hart and Chen 2006b).

Our results also support our hypothesis about the predominance of the complete initial floristics model, as understory community composition dynamics were mostly due to changes in relative abundance. This is in accordance with previous studies in northern conifer forests that mainly found changes in relative abundances, especially in the later successional stages after canopy closure (Taylor et al. 1988, De Grandpré et al. 1993, Nygaard and Ødegaard 1999). However, we did see new late successional/moist adapted species gradually appear over the study period in most plots and this supports the idea that relay floristics can become important later in stand successional development. The number of newly established species was especially notable in the xeric Athabasca plot and on the drier upper terrace of the Whirlpool plot while fewer newly established species were found in the moister plots (lower terrace of Whirlpool, Sunwapta, Hector and Spray River). Since most of these species were associated with moist or closed forest habitats and established in areas of high tree and moss cover in the Athabasca plot, this suggests that the facilitation process for establishment of later successional species played an important role in that xeric plot. However, some newly established species were associated with open habitats and established in the more open areas of the Athabasca and Whirlpool plot suggesting that low levels of competition could also have contributed to the establishment of some species in the xeric plots. Furthermore, the fact that half of the newly established species mainly reproduce sexually through seed dispersal supports the hypothesis of facilitation since it suggests that dispersal limitations were unlikely preventing these species from establishing in these plots. However since the other half of the newly established species reproduces mainly vegetatively this suggest that dispersal limitation was also likely responsible for the delayed arrival of some of the species in this study.

For two of the later successional species that appeared in the Athabasca plot (*C. umbellata* and *G. oblongifolia*) previous studies had identified them as ones that appear only later following disturbance (Halpern 1989, De Grandpré et al. 1993). Also, according to Klimešová (2007) and Hynson et al. (2009), many of the late successional species that appeared or increased in abundance over our study period (*C. umbellata, M. uniflora, O. secunda, P. chlorantha, L. cordata*) are partial mycoheterotrophs, which obtain part of their carbon from surrounding autotrophic plants through shared mycorrhizal fungi (Selosse et al. 2006). Furthermore, most orchid species (as well as *O. secunda*; Beatty et al. (2008)) rely upon mycorrizhal associations for carbon and nutrients, at least during their early establishment phase (Leake 1994, Hynson et al. 2013). Thus the reliance of these species on an established mycorrhizal network and other pre-established vegetation could explain their later establishment or expansion in these plots. This is in agreement with the fact that early successional species are less frequently mycoheterotrophic (Janos 1980). The later recruitment of some species could, however, also be due to dispersal limitations and their slow growth rates (Matlack 1994, Halpern and Spies 1995, Jules 1998).

The Spray River plot had a particularly large number of early successional or open habitat species that disappeared from the stand over the last 45 years. Previous studies showed that compositional change is most important in the few decades following fire (De Grandpré et al. 1993, Økland 2000, Hart and Chen 2006b, Halpern and Lutz 2013). At the first (1967) sampling, the Spray river plot was the youngest plot, with a dense tree canopy, and this could explain its notable declines in early seral successional species over the subsequent four decades. The Athabasca and Sunwapta plots both had more open canopies than the other plots and this likely allowed more early successional species to maintain their presence, even if they were declining in frequency. These results suggest that the exclusion of early seral species can occur faster in stands with dense canopies while more open forests can maintain early seral species for longer periods. Our study is the first one to provide empirical evidence of the importance of the relay floristics model in understory communities of mature forest ecosystems, since previous studies supporting this model focused mainly on short time periods (less than 25 years) after major disturbances (Halpern 1988, Kayes et al. 2010).

Overall our results suggest that these forest understory communities are still dynamic, even nearly 200 years following stand replacing disturbances. This supports Brulisauer et al.'s (1996) conclusions, but seemingly contradicts La Roi and Hnatiuk's (1980) finding that understory communities were stable 70 years following fire in lodgepole pine forest. In the latter study only one out of the 63 study stands was over 125 years of age; thus they had limited ability to evaluate the long term understory dynamics. The results from our study demonstrate the usefulness of permanent plots in studying understory community dynamics and in evaluating the relative importance of different successional theories and the timing of species turnover throughout stand development.

Correlates and driving processes of understory communities: Dispersal limitations

Space always explained most of the variation in understory community composition and richness in all study plots (even when considering the potential inflation of the adjusted R^2 of PCNM variables), although the importance and stability over time of the spatial structures varied among plots (Figure 2-3 to 2-7). These results are consistent with a previous study which also found that spatial variables explained most of the variation in understory fern community composition at fine scales similar to our study (Karst et al. 2005). Other studies also found that spatial variables explained most of the variation in understory composition, diversity and cover (Jones et al. 2008, Gazol and Ibáñez 2009) although results can be influenced by scale (Karst et al. 2005, López-Martínez et al. 2013) and the way spatial variables were determined (Gilbert and Bennett 2010, Smith and Lundholm 2010).

The fact that variation explained by space was mostly independent from environmental variables suggests: 1) that other spatially structured environmental variables uncorrelated with overstory or topography contributed to the observed spatial structures; and/or 2) that the structuring effects due to dispersal limitations were responsible for the observed spatial structures. Previous studies have found that spatially structured soil characteristics were important environmental variables explaining understory composition (Karst et al. 2005, Jones et al. 2008), cover and diversity (Gazol and Ibáñez 2009). Thus the variation that we observed, as explained by space independent of environmental variables, could be due to spatially-structured, unmeasured, soil properties (also suggested by La Roi and Hnatiuk (1980)). However, in most of these previous studies, variation explained by soil properties was largely shared with topographic variables; thus, we expect that the topographic variables used in our study are reasonable proxies for soil conditions. This is supported by the differences in soil properties we documented among microtopographic elements within each stand. Furthermore, understory communities in pine forests at scales similar to ours were found to be only moderately influenced by soil nitrogen and light, while spatial patterning was most likely influenced by other factors such as dispersal limitation (Frelich et al. 2003). Ehrlén and Eriksson (2000) also found that dispersal limitation was an important structuring factor in herb communities of mature temperate forests and many understory species have been found to have limited dispersal abilities (Matlack 1994, Brunet and Von Oheimb 1998, Cain et al. 1998). In our study, most (21/27) of the species associated with the main spatial structure were those that reproduce mainly by vegetative means (see Appendix 2-B); this further supports the hypothesis that the amount of variation in understory composition explained by space but not environment is reflecting dispersal limitation.

In the two moist plots (Hector and Spray River), a particularly large proportion of the spatial structure was independent from any measured environmental variables, despite the Hector plot being on a very steep slope and the Spray River plot being almost flat. These results suggest that dispersal limitations are more important in more productive or less environmentally limited ecosystems, which agrees with Chase (2010). Overall, our results support the growing body of evidence for the importance of dispersal limitations in structuring forest understory communities at local scales (Karst et al. 2005, Jones et al. 2008, Gazol and Ibáñez 2009, López-Martínez et al. 2013).

Correlates and driving processes of understory communities: Deterministic processes

Despite our evidence for the importance of dispersal limitations in structuring these understory communities, the fact that environmental variables did explain a notable proportion of the variation in composition and richness suggests that deterministic processes also play an important role (Figure 2-3 to 2-7). The important deterministic processes likely include: canopy closure, increasing abundance of later successional tree species, competition among understory species, moisture availability, organic matter accumulation, and the influence of past disturbance. Our results are thus consistent with many previous studies that found both deterministic and dispersal limitation to be important in structuring understory communities (Karst et al. 2005, Jones et al. 2008, Burton et al. 2011).

Canopy closure and later successional trees.—The overstory variables (including smaller trees in the subcanopy) explained a substantial fraction of the variation in understory community composition and species richness for three of the plots (Athabasca, Sunwapta and Whirlpool) suggesting their importance in structuring understory communities. In these plots, species richness was higher in quadrats in open micro-habitats and lowest in areas with large trees, higher canopy cover or high densities of later successional tree species. Since lower species richness was associated with closed canopy and a lack of early successional species, these results support the importance of canopy closure excluding early successional understory species as an underlying process driving understory dynamics.

We also observed increasing presence of later successional conifer tree species (*Picea engelmanii*, *Abies lasiocarpa* or *Picea mariana)* in all study plots and this is consistent with previous studies in similar ecosystems (Taylor et al. 1988, Nygaard and Ødegaard 1999, Clark et al. 2003). These species seem to have a particularly important influence on the understory. In plots where the overstory explained variation in understory composition and richness, late successional tree species were amongst the important explanatory variables and when they increased in abundance over time, they usually also became stronger explanatory variables (Athabasca, Sunwapta and Whirlpool plots). For example, in the Whirlpool plot, quadrats with higher canopy cover or higher density of black spruce stems had lower species richness. In the Athabasca plot, quadrats that had lower species richness in 2012 were those in low elevation/concave areas that had denser tree canopies in 1967 and 1989, and by 2012 had declining densities of lodgepole pine but increasing presence of late successional tree species. This effect is likely caused through influence on light attenuation, since shade tolerant, late successional tree species reduce light transmission to the understory more than shade intolerant deciduous or conifer species (Messier et al. 1998). Augusto et al. (2003) also found that the understory vegetation under pioneer pine species had higher Ellenberg indicator values for light than under later successional *Picea* species and the increased abundance of the latter species in the overstory reduced species richness over time (Nygaard and Ødegaard 1999). Overall our results suggest that light was an important limiting factor for understory vegetation, although the influence of canopy or later successional tree species on other components of understory microenvironment, such as soil properties or competition for water and nutrients could also have been at play (Finzi et al. 1998, Augusto et al. 2003, Reich et al. 2012, Halpern and Lutz 2013).

Competitive exclusion by other understory plants.—The results from two of our study plots could be partially explained by competitive exclusion of open habitat/early successional understory species by mosses and shrubs. At the Athabasca plot, the quadrats with lower richness in 2012, mentioned above, were also characterized by increasing cover of mosses and tall shrubs over the whole study period. This could have also contributed to the competitive exclusion of early successional species from these areas of the plot. In the Sunwapta plot, declining frequency of open and dry micro-habitat species in open areas was associated with increasing cover of mosses and tall shrubs. High moss cover has been implicated in competitive exclusion of early seral vascular species in lodgepole pine ecosystems (Bainbridge and Strong 2005), possibly through their effectiveness in absorbing available nutrients (Zackrisson et al. 1999). Many studies have also demonstrated that dominant shrubs can affect the composition and richness of understory herbaceous communities (Frelich et al. 2003, Chávez and Macdonald 2010, Reich et al. 2012, Halpern and Lutz 2013).

Moisture availability.—In all plots the main spatial structure in understory composition contrasted quadrats with high cover of moist adapted species versus high cover of species usually associated with dry or open micro-habitats. This suggests that moisture availability was a driving force in structuring these communities. In all plots, the soil profiles from the different topographic elements support the moisture gradient hypothesis as the soil profile sampled near quadrats that had higher cover of moist adapted species showed evidence of higher moisture availability (more developed soils; mottles present in the Whirlpool plot). Furthermore in plots where topography explained part of the variation in understory composition (Athabasca, Sunwapta and Whirlpool) quadrats with high cover of moist adapted species were always associated with environmental variables representative of higher moisture availability (lower topographic position). At the Whirlpool plot, the presence of black spruce on the lower terrace further supports that this area had higher moisture (Laidlaw 1971), as did its location so close to the adjacent river. This micro-structuring of the understory species mirrors the importance of moisture in structuring variation in lodgepole pine vegetation types at the landscape scale (Hnatiuk 1969, La Roi and Hnatiuk 1980). It was that moisture gradient that formed the basis for selecting the five plots for the long term study of the current work.

The influence of moisture on the understory could have also been partly associated with effects of the tree layer(s). In the Sunwapta plot, areas with lower canopy density but high densities of lodgepole pine transgressives were mainly associated with moist adapted species. Quadrats with large trees had high cover of open/dry habitats species and this could be due to canopy interception of precipitation (Anderson et al.

1969, Økland et al. 1999, Pina Poujol 2013). Our results, however, suggest that this influence decreases in time as some moist adapted species were spreading into areas with large lodgepole pine trees, possibly through other mechanisms that increased moisture availability, such as the gradual accumulation of organic matter (see below).

Organic matter accumulation.—In the Athabasca plot, moist-adapted species (*O. secunda* and *D. viridis*) were spreading into the more open micro-habitats while in the Sunwapta plot other moist-adapted species (*C. canadensis*, *V. vitis-idaea*, and *C. umbellata*) were also spreading into previously unoccupied quadrats under large lodgepole pine trees. Moisture was likely the limiting factor for these shade tolerant species under these large trees, and gradual accumulation of organic matter in the humus layer could be the process whereby moisture conditions improved over time in these quadrats (De Grandpré et al. 1993, Emmer 1995, Hart and Chen 2006b). Økland (2000) found that nutrient and light demanding species were associated with plots with thin humus layers, while shade tolerant late successional species were associated with plots with thicker humus layers. It is thus likely that organic matter accumulation contributed to the expansion of later successional species in previously inhospitable areas of the Athabasca and Sunwapta plots. This mechanism could have contributed to within plot homogenization, as previously discussed, particularly in more xeric environments where moisture is more of a limiting factor.

Disturbance history.—Finally, the disturbance history also seemed to play an important role in structuring the understory community in the Athabasca plot. In this plot, the quadrats with lower richness in 2012, mentioned above, correspond to an area where no trees had fire scars suggesting that the surface fire which occurred in 1889 in this plot may not have been as intense in this area. Thus, more survivors from the previous community could have been present, and reduction in the depth of the forest floor may have been less. Lower fire severity could also explain the much higher tree density in this area of the plot (Anderson and Romme 1991). The presence of surviving trees, the reduced organic matter consumption, and dense lodgepole pine regeneration in this less intensively burned area could have all contributed to an earlier return to an understory community more typical of mature or closed forest conditions (higher moss cover, lower species richness). These results suggest that previous non-stand replacing disturbances can have a strong influence on understory spatial structure even after 100 years.

Change in the relative importance of processes in time

For all plots, our composition results support our hypothesis that, following canopy closure, dispersal limitations were increasing in importance relative to environmental control processes (the proportion of explained variation due to space vs environment increased over time). However in the Spray River plot the confidence interval of the adjusted R^2 of the spatial variables overlapped between sampling periods suggesting the increase in variation explained was not significant (Figure 2-7c). In all plots (except Whirlpool), homogenisation of the understory environment through the different mechanisms discussed above (reduction in understory light, accumulation of organic matter, increased moss and shrub cover) could explain the decreasing importance of deterministic processes or limited importance over the whole study period in moist plots (Hector and Spray River). However, the increasing frequency and cover of later successional species, which often have lower dispersal abilities than early successional species (Bazzaz 1979, Rydin and Borgegard 1991), could also have contributed to the increasing importance of dispersal limitation.

For the Sunwapta and Spray River plots the species richness results also supported our initial hypothesis that dispersal limitation would increase in importance following canopy closure. For the Hector plot, the confidence interval of the adjusted R^2 for spatial variables in the species richness analysis overlapped considerably suggesting the decreases in variation explained were not significant (Figure 2-6c). Finally, for the Athabasca and Whirlpool plots the proportion of variation in species richness explained by space vs environment decreased over time suggesting that deterministic processes were increasing in importance relative to dispersal limitations. For example in the Athabasca plot even though the amount of variation in species richness explained by spatial variables increased over time, proportionally the amount explained by environmental variables increased more, suggesting that environmental control processes were becoming relatively more important over the study period.

Interestingly, the two plots with increasing importance of deterministic processes for species richness were both plots which have sustained substantial canopy mortality over the study period from either windthrow (Whirlpool) or general canopy decline (in the Athabasca plot 80% of lodgepole pine stems with DBH ≥ one inch in 1967 died by 2012). These results lend support to our second hypothesis that deterministic processes can gain importance following canopy break up or secondary disturbances, but this seemed to be true only in terms of species richness. This difference can be explained by the fact that understory community composition can have a lagged response to a change in canopy cover while species richness has been found to respond more quickly (Thomas et al. 1999).

2.5. Conclusion

As we postulated, understory communities in these mature lodgepole pine forests were homogenising within and converging between the five study plots, suggesting these communities were still undergoing compositional change even nearly 200 years since the last stand replacing disturbance. Understory dynamics were largely due to declining abundance of open-habitat species and increasing abundance of shade tolerant and moist-adapted species – notably mosses. Our results show the dynamic interplay between both the complete initial floristics model and the relay floristics model, demonstrating that both are important in the long-term development and change of the understory of these pine dominated forests. The understory communities studied are likely to continue changing in the future as the initial post-disturbance cohort of *Pinus contorta* is replaced by later successional tree species such as *Picea engelmanii*, *Abies lasiocarpa* or *Picea mariana,* which further modify the understory microenvironment. Continued accumulation of organic matter and increases in moss cover will also play a role in future understory community dynamics.

This study was the first to demonstrate that the relative importance of deterministic processes vs dispersal limitation in structuring understory communities can change within the same ecosystem throughout succession or stand development. Overall, dispersal limitation seemed to explain the bulk of the variation in understory community composition and richness, and their importance increased over the past 45 years in most of the forests studied, which ranged in age from ~110 to 185 years in 2012. We attribute this largely to the influence of later successional species which have primarily vegetative reproduction and are more dispersal limited. The homogenisation of the understory environment following canopy closure, and the increased abundance of later successional species, both contributed to the increased importance of dispersal limitation in structuring these communities following canopy closure. Our study also showed that deterministic processes could increase in importance with regards to species richness but further monitoring is need to determine whether or not these process will also become more important for community composition over time. However, our results suggest that deterministic processes continue to be important in structuring understory communities especially when considering species richness. More work is still needed to understand the complex interplay of these processes following canopy breakup since most of the plots studied had not yet reached, or were just starting to reach, this successional stage. A fourth re-sampling of these five sites should be done around 2030-32 to test the nature of the further development of the understory of these five types of lodgepole pine forests.

2.6. Acknowledgments

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Table 2-1. Description and location of the five plots studied in Banff and Jasper National Parks

Characteristics	Athabasca†	Sunwapta	Whirlpool	Hector†	Spray River
National Park	Jasper	Jasper	Jasper	Banff	Banff
Moisture class‡	Xeric	Mesic	Moist/xeric§	Moist	Moist
Ecoregion ¶	Montane	Lower Subalpine	Montane	Lower Subalpine	Lower Subalpine
Elevation (m a.s.l.)	1100	1300	1130	1860	1720
Stand age (in 2012) #	146 (114)‖	136	186	140	111
Vegetation type‡	*Artcostaphylos uva-ursi*	*Sheperdia canadensis*	*Hylocomium splendens*	*Menziesia ferruginea*	*Vaccinium scoparium*
Landform genetic material¶	Glacio-fluvial	Glacio-fluvial	Glacio-fluvial	Morainal > fen	Glacio-fluvial
Longitude (N)	117° 58’	117° 42’	117° 55’	116° 15’	115° 23’
Latitude (W)	52° 45’	52° 33’	52° 42’	51° 30’	50° 54’

† The weather station near the Athabasca plot was located at 52°53' N, 118°04' W at 1062 m.a.s.l. while the one near the Hector plot was located at 51°26' N, 116°13' W at 1524 m.a.s.l.

‡ According to Hnatiuk (1969).

§ The Whirlpool plot had a drier upper micro-elevation terrace and a more moist lower terrace on the east and west portion of the plot respectively (see Figure 2-1).

¶ According to Holland and Coen (1982).

Age of oldest lodgepole pine cohort. Determined using tree cores (at 30cm height) from two dominant trees in 25 randomly selected quadrats throughout each 1 ha plot.

‖ In the Athabasca site two cohorts were present: an older one with fire scars and a younger one without fire scars.

Table 2-2. Key morphological features of soils (Ae horizon and solum thickness, upper Bm horizon color in the field and air dried) sampled at two topographic elements on the periphery of each plot (see Figure 2-1 for sampling location). The topographic elements sampled and the soil classifications are also presented. Full descriptions of soil profiles are presented in Appendix 2-A.

Sites/Pit	Topo element†	Soil subgroup‡	Ae (cm)	Solum (cm)	Upper Bm color in the field§	Upper Bm color air dried§
Athabasca						
Pit a	Upper micro elevation	Orthic Eutric Brunisol	--	21	5YR 3/3	10YR 6/4
Pit b	Lower micro elevation	Brunisolic Grey Luvisol	6	47	7.5YR 4/4	10YR 6/4
Sunwapta						
Pit a	Upper micro elevation	Orthic Eutric Brunisol	--	30	5YR 4/6	10YR 6/6
Pit b	Lower micro elevation	Eluviated Eutric Brunisol	6	40	5YR 4/6	10YR 6/6
Whirlpool						
Pit a	Upper terrace	Orthic Eutric Brunisol	--	39	10YR 5/6	10YR 7/6
Pit b	Lower terrace	Gleyed Eutric Brunisol	8	53	7.5YR 5/6	10YR 8/3
Hector						
Pit a	Upper slope	Eluviated Dystric Brunisol	3	15	7.5YR 4/6	10YR 6/6
Pit b	Bottom of slope	Eluviated Dystric Brunisol	8	53	5YR 4/6	10YR 6/6
Spray River						
Pit a	Flat ground	Eluviated Eutric Brunisol	3	18	7.5YR 5/8	10YR 6/6
Pit b	Flat ground	Eluviated Dystric Brunisol	5	10	10YR 5/8	10YR 6/6

† Topographic feature sampled.
‡ See Soil Classification Working Group (1998).
§ Munsell Soil Color Charts.

Table 2-3. Mean percent cover and frequency (number of occupied 5x5 m quadrats out of 400 per plot) for each plot and sampling period for species with a score > |0.2| with PCA axis 1 or 2 (see Figure 2-2 in which the four letter code represents species name). Also given are: total richness (number of species encountered in the 1 ha plot), mean species richness and mean alpha diversity (Shannon-Wiener index) per 5 x 5 m quadrat.

	Athabasca			Sunwapta			Whirlpool			Hector			Spray River	
Species	1967	1989	2012	1967	1989	2012	1967	1989	2012	1967	1989	2012	1967	2010
Tall shrubs														
Juniperus communis (JUCO)	0.29	2.34	8.78	1.13	4.56	13.8	0.57	1.88	5.20	0.03	0.02	0.11	0.04	0.27
	138	287	380	359	370	399	191	251	284	39	32	34	115	95
Menziesia ferruginea (MEFE)	-	-	-	0.01	0.03	0.37	-	-	-	31.8	26.7	29.2	0.20	2.82
				21	22	56				385	387	388	114	225
Rosa acicularis (ROAC)	0.13	2.76	2.30	0.19	0.50	1.91	0.09	0.56	1.97	-	-	-	0.01	0.06
	342	353	384	341	331	357	335	332	369				30	36
Shepherdia canadensis (SHCA)	0.71	7.68	7.82	9.37	9.77	12.7	0.37	5.35	6.53	3.40	2.30	3.97	1.66	7.34
	319	388	398	397	400	400	352	363	359	283	297	275	254	344
Dwarf shrubs														
Arctostaphylos uva-ursi (ARUV)	8.59	26.98	40.9	0.42	2.09	4.95	0.37	2.30	4.19	-	-	<0.01	0.01	<0.01
	397	400	398	370	379	375	277	240	189			1	32	5
Linnaea borealis (LIBO)	0.76	5.45	6.70	1.11	4.06	5.52	1.10	3.16	2.26	0.14	0.34	0.96	0.27	3.16
	262	307	394	399	399	400	399	394	397	229	252	314	400	400
Vaccinium cespitosum (VACE)	-	-	0.03	0.34	1.34	3.45	0.64	3.02	5.43	-	-	-	-	-
			4	382	372	400	336	330	380					
Vaccinium spp. (Vacc sp) †	-	-	-	0.04	0.02	0.29	0.01	0.02	0.04	3.08	1.54	3.39	3.36	5.38
				71	62	141	5	12	8	400	400	400	400	400
Herbaceous species														
Arnica cordifolia (ARCO)	-	-	-	0.04	0.05	0.11	0.07	0.58	0.74	0.47	0.83	1.47	1.60	3.38
				73	57	65	141	138	173	362	358	362	399	389
Cornus canadensis (COCA)	-	-	-	0.07	0.38	1.56	0.75	4.48	5.49	0.04	0.26	0.54	0.53	6.11
				120	136	256	342	373	392	95	111	125	398	399
Fragaria virginiana (FRVI)	0.12	1.78	1.79	0.19	1.23	0.39	0.01	0.10	0.05	<0.01	<0.01	-	0.01	0.01
	390	387	399	375	373	345	41	46	41	1	1		21	19
Leymus innovatus (LEIN)	0.19	8.82	8.90	0.36	3.21	9.21	0.19	3.51	6.08	<0.01	<0.01	<0.01	0.18	2.94
	396	399	399	399	399	400	400	398	400	2	2	2	398	396
Mosses	6.32	10.6	28.1	5.68	35.4	69.5	35.6	51.9	57.6	6.27	36.6	70.1	17.6	85.7
	395	384	400	392	400	400	400	400	400	389	400	400	400	400
Lichens	2.84	6.52	5.06	1.69	2.06	3.73	0.78	3.61	3.01	2.57	1.13	2.60	1.73	2.76
	396	399	400	400	398	396	400	398	399	398	400	400	400	400
Total richness (nbr/ 1ha) ‡	39	36	53	62	57	63	46	49	52	32	31	31	66	55
Mean richness (nbr / 25m^2)‡	13.5	12.6	12.6	21.2	18.6	22.5	14.1	13.4	15.1	11.4	11.0	11.0	21.4	20.3
Mean α diversity ‡	1.27	1.59	1.68	1.75	1.64	1.99	1.10	1.57	1.86	1.02	1.06	1.13	1.59	1.63

† Includes *Vaccinium scoparium|myrthillus|membranaceum|mythilloides* (mainly *scoparium* and *myrthillus*).

‡ For the Athabasca plot different moss and lichen species were not identified in 1967 and thus were not considered in calculations of richness or diversity.For 1989 and 2012 the *Cladina* and *Cladonia* species were pooled for calculations of richness and diversity because the two genera were not distinguished in 1967; at the Whirlpool plot only *Peltigera* spp. was recorded in 1967 thus *Cladonia*, *Cladina* and *Stereocaulon* were excluded for calculations of richness and diversity for this plot.

Table 2-4. Change in species occurrence from 1967 to 2012 for the five study plots (ATH: Athabasca, SUN: Sunwapta, WHI: Whirlpool; HEC: Hector; SPR: Spray River) calculated as the ratio of 2012 frequency/1967 frequency (number of occupied 5x5 m quadrats out of 400 sampled per plot). The ratios are presented for species that increased (left column) or decreased (upper right column) in frequency and those that had plot-specific changes in frequencies (lower right column). Ratios are presented only for species present in at least 20 quadrats per 1 ha plot for at least one sampling period (otherwise marked as uncommon (u)) and that had a 25 percent increase (ratio ≥ 1.25) or decrease (≤0.75) in frequency in a least one plot (otherwise marked as stable (s)). Species absent from a plot are indicated by "-". See Appendix 2-B for a complete list of species frequencies for each plot and sampling time.

	ATH	SUN	WHI	HEC	SPR		ATH	SUN	WHI	HEC	SPR
Species that increased						Species that decreased					
Dactylorhiza viridis	6.22[†]	-	-	-	-	*Antennaria* spp.[‡]	0.46	0.07	u	-	u
Orthilia secunda	2.89	1.47	1.29	1.35	1.33	*Solidago* spp.[‡]	0.52	0.40	s	-	u
Juniperus communis	2.75	s	1.49	s	s	*Calamagrostis purpurascens*	0.63	-	-	-	0.57
Festuca saximontana	2.02	-	-	-	-	*Packera* spp.[‡]	0.65	0.09	-	-	-
Viola adunca	1.85	-	u	-	-	*Senecio lugens*	-	-	-	-	0.21
Amelanchier alnifolia	1.76	u	u	-	u	*Trisetum spicatum*	-	0.14	u	-	-
Linnaea borealis	1.50	s	s	1.37	s	*Antennaria neglecta*	s	0.33	-	-	u
Hylocomium splendens	1.29[†]	5.34	s	7.88	1.31	*Stereocolon* spp.[‡]	s[†]	0.48	u[†]	0.08	0.15
Geocaulon lividum	u[†]	116[§]	3.73	-	-	*Castilleja miniata*	u[†]	0.59	-	-	0.39
Piperia unalascensis	-	52[§]	-	-	-	*Achillea millefolium*	s	0.75	s	-	u
Lycopodium complanatum	-	26.9	6.0	u	s	*Arctostaphylos uva-ursi*	s	s	0.68	u	0.16
Platanthera obtusata	u	3.44	u	-	u	*Symphyotrichum ciliolatum*	u	s	0.70	u	s
Vaccinium vitis-idaea	-	3.27	u[†]	-	-	*Carex* spp.[‡]	s	u	u[†]	0.21	0.22
Chimaphila umbellata	u[†]	2.72	2.65	-	3.23	*Salix* spp.[‡]	u	s	u	s	0.07
Menziesia ferruginea	-	2.67	-	s	1.97	*Equisetum scirpoides*	-	-	-	-	0.74
Cornus canadensis	-	2.13	s	1.32	s	Species with plot-specific changes					
Vaccinium spp.[‡]	-	1.99	u	s	s	*Corallorhiza trifida*	7.00	0.34	u	-	u
Agoseris glauca	-	1.27	u[†]	-	u	*Calypso bulbosa*	8.89	1.47	0.14	-	u
Rhododendron albiflorum	-	u	-	1.30	1.59	*Gentianella amarelle*	2.16	0.22	-	-	u
Moneses uniflora	u[†]	-	-	-	14.40	*Dicranum*	1.31[†]	1.33	s	0.07	0.40

						polysetum					
Listera cordata	-	u	u	-	10.06	*Polytrichum juniperinum*	1.89[†]	0.26	6.94[†]	0.23	0.28
Lycopodium annotinum	-	u[†]	u	u	1.78	*Goodyera oblongifolia*	u[†]	5.06	0.69	u	s
Shepherdia Canadensis	s	s	s	s	1.35	*Phyllodoce* spp./ *Empetrum nigrum*[‡]	-	3.00	-	0.54	s
Ledum groenlandicum	-	u	s	s	1.31	*Epilobium angustifolium*	u[†]	s	1.91	0.52	s
						Ptilium crista-castrensis	u	0.73	3.20	1.94	s
						Cladonia spp.[‡]	s[†]	s[†]	2.12[†]	s[†]	s[†]
						Pyrola chlorantha	s	s	0.23	u	1.52
						Cladina spp.[‡]	1.62[†]	s[†]	s[†]	0.65[†]	u[†]

† In these plots, these species appeared over the study period or were not recorded in 1967 (*Cladonia* spp., *Cladina* spp., *Stereocolon* spp., *Dicranum polysetum* and *Polytrichum juniperinum*) and thus the ratios were calculated between 1989 and 2012.

‡ These taxa were not identified to species or were not differentiated (see methods for details).

§ These ratios are extremely high because these species were found in only one quadrat in 1967.

Table 2-5. Tree densities and relationship of these with understory community richness and composition as determined by multiple regression and the RDA constrained by overstory, respectively. Shown are densities (stems ha^{-1}) for each overstory species by size class† along with mean canopy cover (Can Cov %) for each plot and sampling year. Overstory variables in **bold** were chosen during forward selection based on their correlation with either understory composition or species richness, as indicated by the sub- or super-script. The sign of the relationship between these densities (at the scale of the 5 x 5 m quadrats) and the main gradient in understory composition (C, the first axis of the RDA with overstory variable; open habitat species on the negative side of the axis and moist habitat species on the positive side of the axis) or species richness (R) is also indicated. Positive relationships are identified with C^{+} and R^{+} while negative relationships are identified with C^{-} and R^{-}. "na" indicates that data for that species and size class were not available in that plot for that year. "0" indicates the species and size class was not present in the plot in that year.

	Athabasca			Sunwapta			Whirlpool			Hector			Spray River	
	1967	1989	2012	1967	1989	2012	1967	1989	2012	1967	1989	2012	1967	2010
Pinus contorta (PC)														
PCTRA	392	$\mathbf{349}^{R+}$	$\mathbf{414}^{R+}_{C-}$	$\mathbf{2784}^{R+}_{C+}$	$\mathbf{4122}^{R+}_{C+}$	$\mathbf{3026}_{C+}$	$\mathbf{367}^{R+}_{C-}$	$\mathbf{769}^{R+}_{C-}$	$\mathbf{303}_{C-}$	31	10	1	$\mathbf{9}^{R+}$	45
PC1	$\mathbf{1941}_{C+}$	$\mathbf{511}^{R-}_{C+}$	84	302	156	202	34	1	8	$\mathbf{956}_{C-}$	$\mathbf{454}^{R+}$	180	$\mathbf{428}_{C+}$	$\mathbf{31}_{C+}$
PC2	$\mathbf{672}_{C+}$	$\mathbf{817}^{R-}_{C+}$	$\mathbf{288}^{R-}_{C+}$	127	74	$\mathbf{48}^{R+}$	273	81	$\mathbf{15}^{R+}$	$\mathbf{1750}^{R+}$	$\mathbf{1458}^{R+}_{C-}$	$\mathbf{1061}_{C-}$	$\mathbf{2912}_{C+}$	803
PC3	$\mathbf{102}_{C-}$	$\mathbf{146}^{R-}_{C-}$	$\mathbf{141}^{R-}$	$\mathbf{176}_{C-}$	110	75	$\mathbf{595}^{R-}$	$\mathbf{315}_{C-}$	103	$\mathbf{476}_{C-}$	$\mathbf{844}^{R+}$	952	$\mathbf{293}^{R+}_{C-}$	867
PC4	$\mathbf{55}_{C-}$	$\mathbf{59}_{C-}$	$\mathbf{43}_{C-}$	$\mathbf{98}^{R-}_{C-}$	$\mathbf{145}^{R-}_{C-}$	$\mathbf{128}^{R-}_{C-}$	145	205	123	8	79	163	3	$\mathbf{184}_{C-}$
PC5	9	$\mathbf{8}^{R-}_{C-}$	8	$\mathbf{34}_{C-}$	$\mathbf{87}^{R-}_{C-}$	$\mathbf{98}^{R-}_{C+}$	$\mathbf{31}_{C-}$	$\mathbf{38}_{C-}$	$\mathbf{34}_{C-}$	0	0	2	0	1
PC6	0	0	0	$\mathbf{3}_{C-}$	9	20	0	1	$\mathbf{2}_{C-}$	0	0	0	0	0
Picea mariana (PM)														
PMTRA	9	26	$\mathbf{87}_{C+}$	0	0	0	$\mathbf{2856}_{C+}$	$\mathbf{1775}^{R-}_{C+}$	$\mathbf{4735}^{R-}_{C+}$	0	0	0	0	0
PM1	$\mathbf{2}_{C+}$	2	$\mathbf{13}_{C+}$	0	0	2	$\mathbf{99}^{R-}$	$\mathbf{353}_{C+}$	$\mathbf{835}^{R-}_{C+}$	0	0	0	0	0
PM2	**2**	$\mathbf{3}_{C+}$	1	0	0	0	$\mathbf{124}^{R-}_{C+}$	105	65	0	0	0	0	0
PM3	0	1	1	0	0	0	$\mathbf{37}^{R-}_{C+}$	$\mathbf{97}^{R-}_{C+}$	$\mathbf{21}_{C+}$	0	0	0	0	0
PM4	0	0	1	0	0	0	0	4	2	0	0	0	0	0
Picea engelmannii (PG)														
PGTRA	5	42	$\mathbf{124}^{R-}_{C+}$	3	5	$\mathbf{36}^{R-}$	$\mathbf{7}^{R+}$	8	17	$\mathbf{1647}^{R+}_{C+}$	1149	$\mathbf{1468}_{C+}$	437	305

PG1	0	**4_{C+}**	**61_{C+}**	0	**2_{C-}**	**3_{C+}**	4	11	13	170	**455_{C+}**	**604^{R-}_{C+}**	180	270
PG2	0	**1_{C+}**	**10_{C+}**	0	0	2	1	1	4	18	71	131	71	197
PG3	1	1	0	0	0	0	0	2	**8_{C-}**	4	6	12	0	**67^{R-}**
PG4	0	0	1	0	0	0	0	0	1	2	4	3	0	3
PG5	0	0	0	0	0	0	0	0	1	0	0	1	0	0
Abies lasiocarpa (AL)														
ALTRA	1	**16_{C+}**	**156^{R-}**	1	**15^{R+}**	**103_{C+}**	**28^{R+}**	47	**368_{C+}**	525	357	652	27	216
AL1	0	0	12	0	1	12	0	12	38	45	170	**264^{R-}_{C+}**	1	23
AL2	0	0	0	0	0	0	0	2	10	**11_{C+}**	**27_{C+}**	66	0	8
AL3	0	0	0	0	0	0	0	0	5	2	3	8	0	0
Populus tremuloides (PT)														
PTTRA	0	**18_{C+}**	30	**28^{R+}_{C+}**	**4^{R+}**	2	23	**26_{C-}**	**339^{R+}_{C-}**	0	0	0	3	0
PT1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
PT2	0	0	0	0	0	0	9	0	0	0	0	0	0	0
PT3	0	0	0	0	0	0	7	**5_{C-}**	0	0	0	0	0	0
PT4	0	0	0	0	0	0	2	4	2	0	0	0	0	0
PT5	0	0	0	0	0	0	0	1	3	0	0	0	0	0
Can Cov	Na	**51.3_{C+}**	**43.2^{R-}_{C+}**	na	**61.3_{C+}**	**57.7^{R+}_{C-}**	na	**70.4^{R-}_{C+}**	**49.6_{C+}**	na	**73.5^{R+}_{C+}**	**84.9^{R-}**	na	**78.6_{C+}**
Dead snags (D)														
D_TRA	1010	Na	84	160	na	**1562^{R+}_{C+}**	11	na	**375^{R+}_{C+}**	24	na	**150_{C+}**	166	44
D_1	**1196^{R-}_{C+}**	503	**250_{C+}**	31	40	84	241	44	76	**106_{C-}**	**316_{C-}**	456	**833_{C+}**	**454_{C+}**
D_2	10	**127_{C-}**	319	4	9	22	197	154	52	15	61	232	80	433
D_3	2	21	65	1	8	13	58	**114^{R-}**	**130^{R-}_{C+}**	15	5	**11^{R-}_{C+}**	1	27
D_4	2	**11^{R-}**	15	0	1	6	**5_{C-}**	15	49	**3_{C+}**	1	1	1	1
D_5	0	0	3	0	0	4	0	0	**6_{C-}**	11	3	2	4	0
D_6	0	0	0	0	0	1	0	0	1	3	2	1	1	0

†Size classes: “TRA” = individuals <2.54 cm diameter at breast height (DBH) but taller than 30cm, 1 = 2.54cm to 7.62cm DBH, 2 = 7.63cm to 15.24cm DBH, 3 = 15.25cm to 22.86cm DBH, 4= 22.87cm to 30.48cm DBH, 5 = 30.49cm to 38.1cm DBH, 6 = 38.11cm to 45.72cm DBH).

Table 2-6. Relationship of topography variables with the understory community composition and richness as determined by the RDA constrained by topography variables and multiple regression, respectively. Topography variables were chosen during forward selection based on their correlation with either understory composition (C) or species richness (R). The sign of the relationship between these topography variables (at the scale of the 5 x 5 m quadrats) and the main gradient in understory composition (the first axis of the RDA with topographic variables; open habitat species on the negative side of the axis and moist habitat species on the positive side of the axis) or species richness is also indicated. Positive relationships are identified with C^+ and R^+ while negative relationships are identified with C^- and R^-. “-” indicates the topography variable was not selected for either understory composition or species richness.

	Athabasca			Sunwapta			Whirlpool			Hector			Spray River	
	1967	1989	2012	1967	1989	2012	1967	1989	2012	1967	1989	2012	1967	2010
Elevation	C^-	R^+C^-	R^+C^-	R^-C^-	R^+C^-	R^-C^-	R^+C^-	R^+C^-	R^+C^-	R^+	R^+C^-	C^-	R^-C^-	C^-
Slope	C^+	C^+	R^-	-	-	-	R^+C^-	R^+C^-	C^-	-	-	-	-	C^+
Convexity†	-	C^-	C^-	C^+	C^+	C^+	R^-C^-	R^-C^-	C^-	R^+	C^+	C^+	C^-	-
Sin.aspect E-W‡	C^-	C^-	R^+C^-	R^-C^-	R^-C^-	R^-C^-	$^-$	R^-	R^-	-	-	-	R^+	C^-
Cos.aspect N-S‡	-	R^+	-	-	-	-	R^-	R^-	R^-	C^+	R^-C^+	C^+	-	C^-

† Convexity is calculated as the elevation of a quadrat minus the average elevation of surrounding quadrats.

‡ Sin aspect represents the east-west orientation with values of 1 and -1 respectively representing an east and west facing slope. Cos aspect represents the north-south orientation with values of 1 and -1 respectively representing a north and south facing slope.

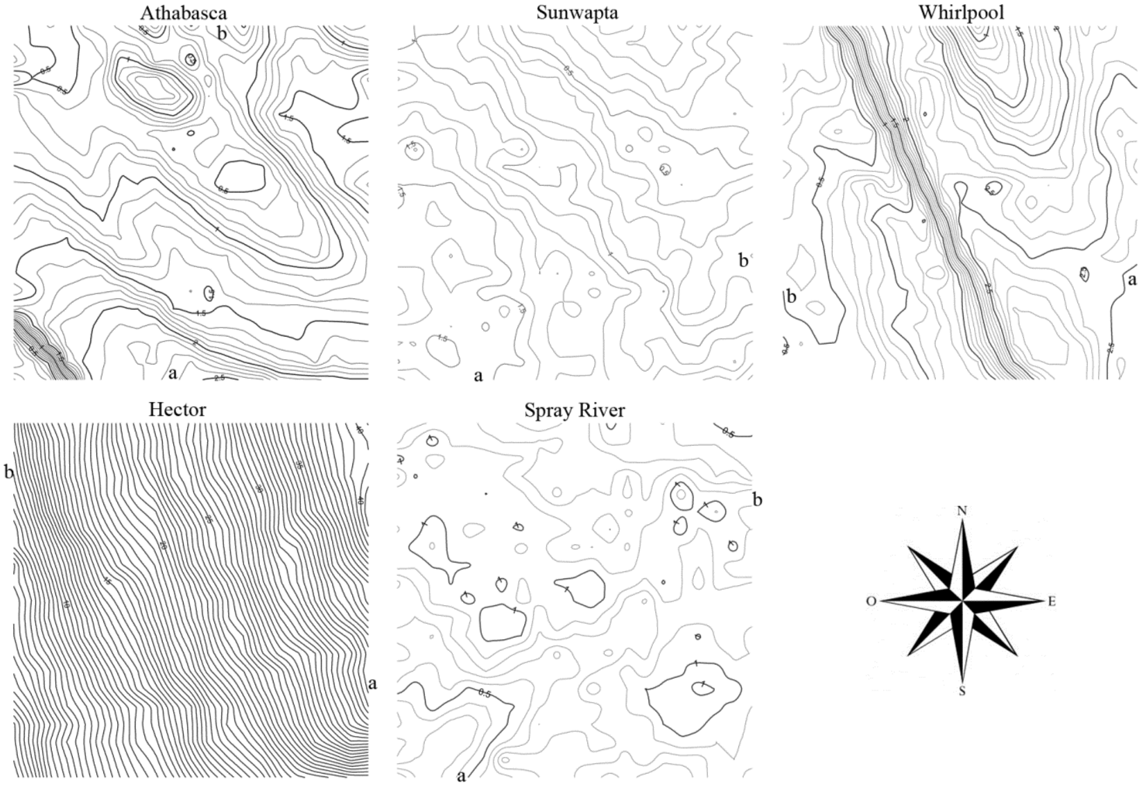

Figure 2-1. Topographic maps of the five 1 ha plots (100m x 100m) with 10cm contours lines except the Hector site which has 50cm contour lines. North is oriented towards the top of all maps. The approximate locations near the plot periphery where the two soil pits were sampled are indicated with a and b.

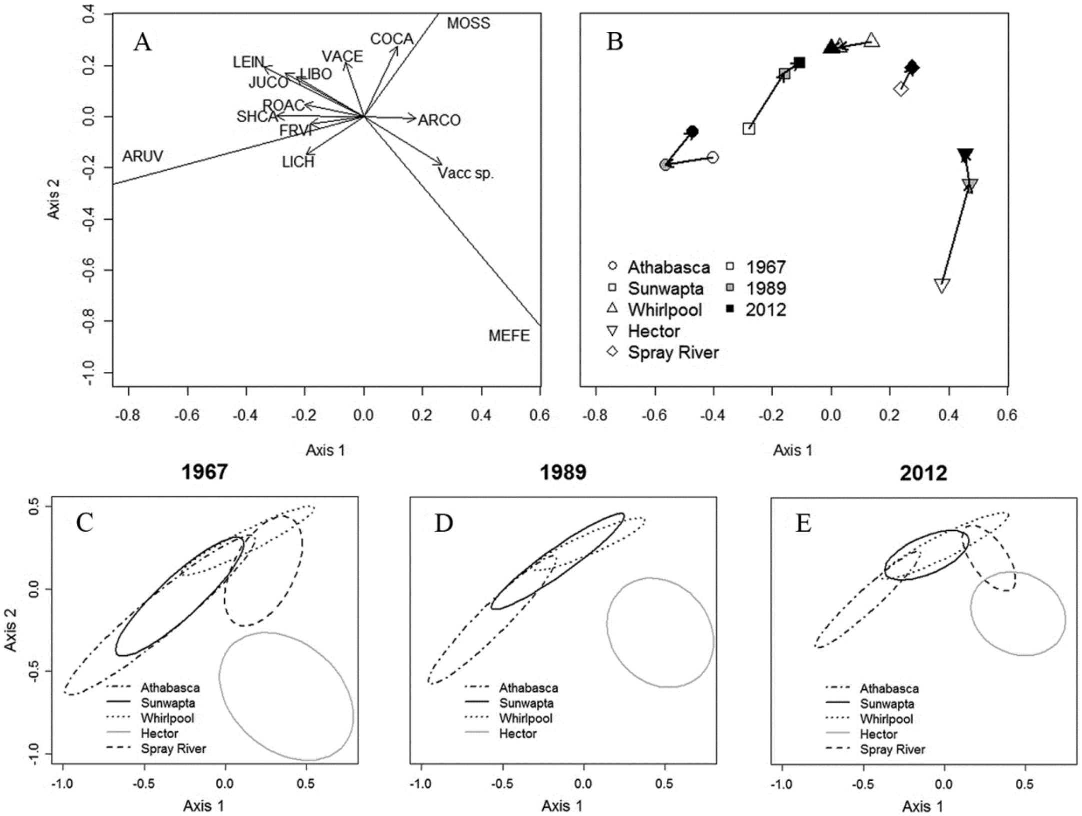

Figure 2-2. Principal components analysis (PCA) on Hellinger transformed species mid-point percent cover data from all plots and all sampling periods: A) Vectors of species with scores > |0.2| on PCA axis 1 or 2 (ARUV, MEFE and MOSS had the highest scores and their vectors were not completely plotted on the graph to facilitate the interpretation of species with shorter vectors); B) Centroids of each plot at each sampling period (vectors indicate change over time for each plot); C-E) 95% confidence interval ellipses for each plot at each sampling period. The first and second PCA axes explained 35% and 22% of the variation, respectively. For taxa identified to species the codes represent the first two letters of the genus and the species epithet while for taxa not identified to species the code is an abbreviation of the genus (see Table 2-3 for complete species names).

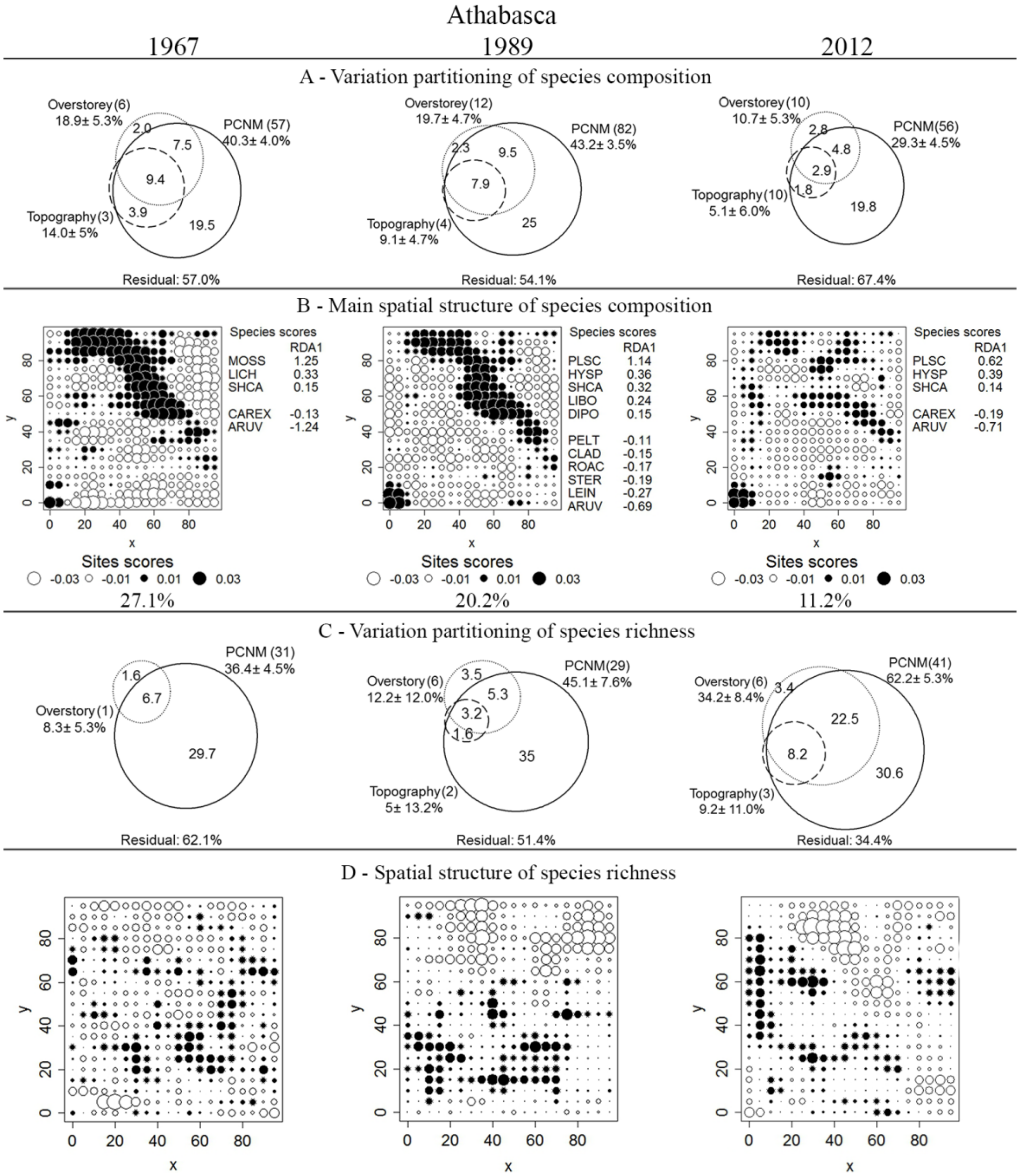

Figure 2-3. Variation partitioning and spatial structure of the understory community at the Athabasca plot. Given is the percent of variation explained (Adjusted R^2) by overstory variables, topography variables and the principle coordinates of neighbour matrices (PCNM) eigenvectors for A) understory community composition; and C) species richness. The number of variables used in the analysis is presented between brackets and confidence intervals are presented for the Adjusted R^2 for each type of variable. Components explaining less than 1% of variation are not presented. The diagrams in B show the main spatial structure in understory community composition based on the RDA with PCNM eigenvectors. The amount of variation explained (Adjusted R^2) by the first RDA axis for each sampling period is presented below the main spatial structure. Species with scores of at least 0.1 in absolute values along the first RDA axis are

presented beside the main spatial structure. Circle size and color represents positive (closed circles) or negative (open circles) site scores of each quadrat along the first RDA axis. The diagrams in D represent the spatial structure of species richness expressed as the scaled predicted values of the multiple regression of species richness on the PCNM eigenvectors. Species richness is higher in quadrats represented by large black circles and lower in quadrats represented by large white circles. The three quadrats not sampled in this plot in 1967 can be seen in the lower left part of the diagrams in B and D. See Figure 2-2 for species codes.

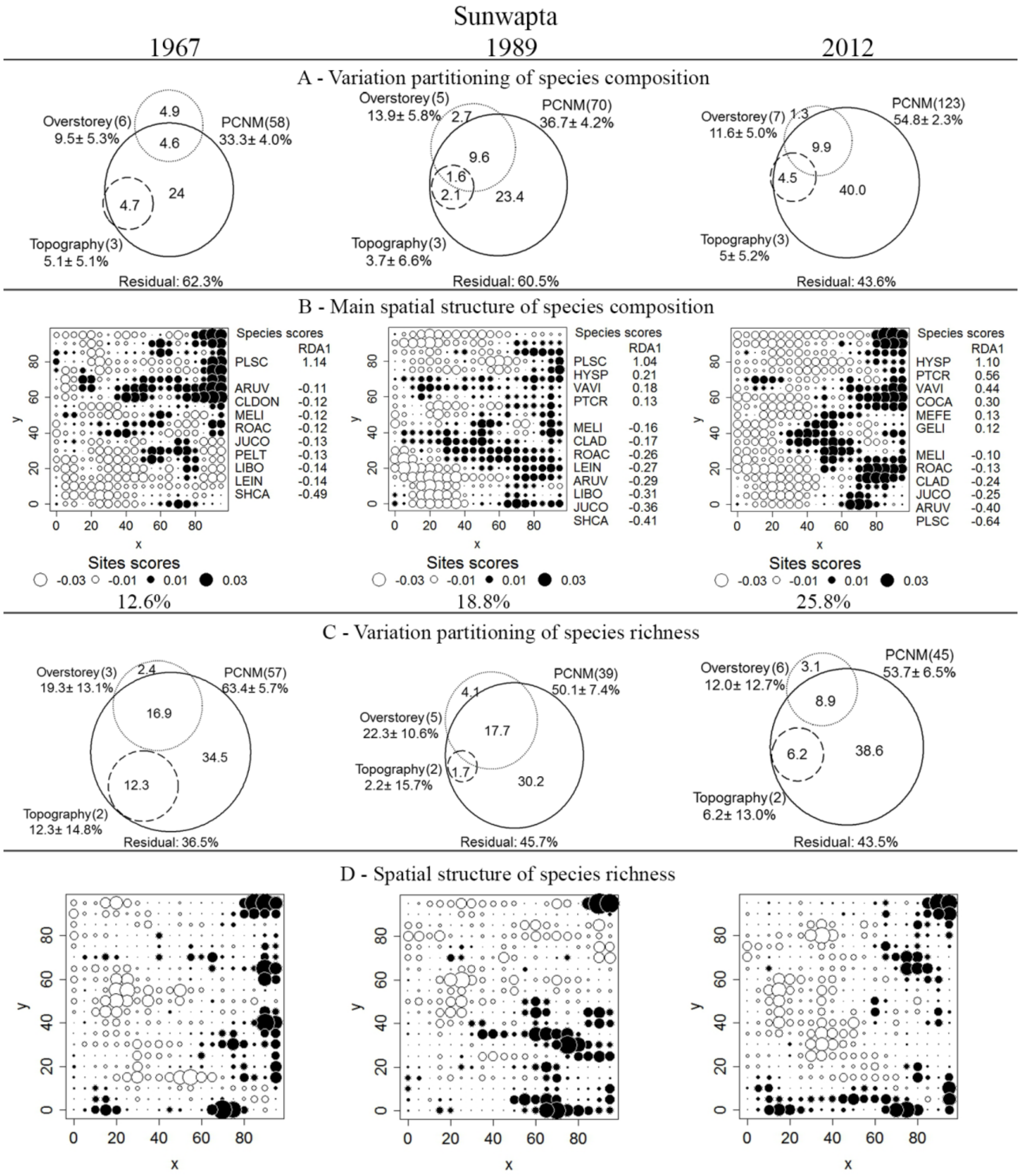

Figure 2-4. Variation partitioning and spatial structure of the understory community at the Sunwapta plot. See Figure 2-3 for details.

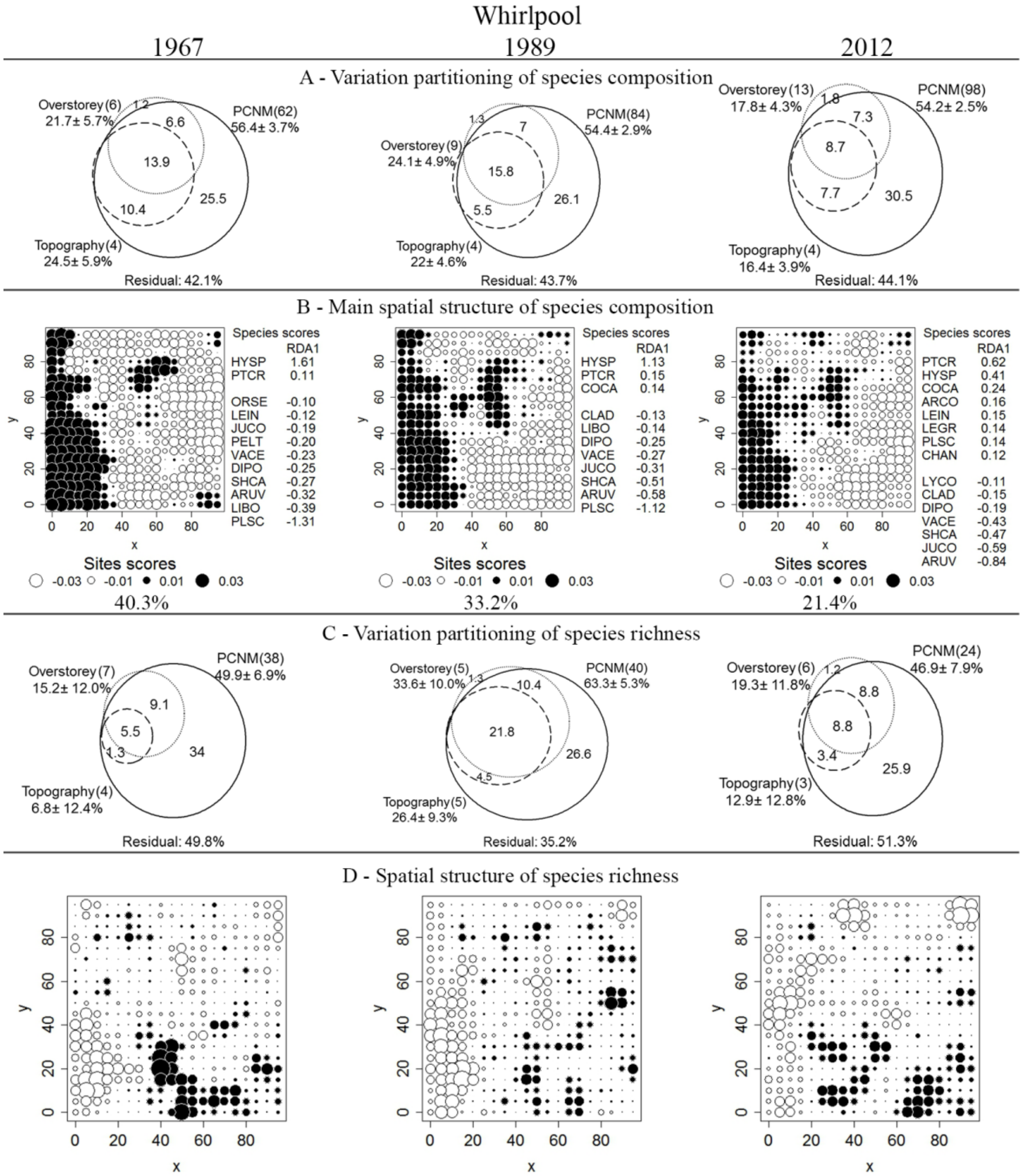

Figure 2-5. Variation partitioning and spatial structure of the understory community at the Whirlpool plot. See Figure 2-3 for details.

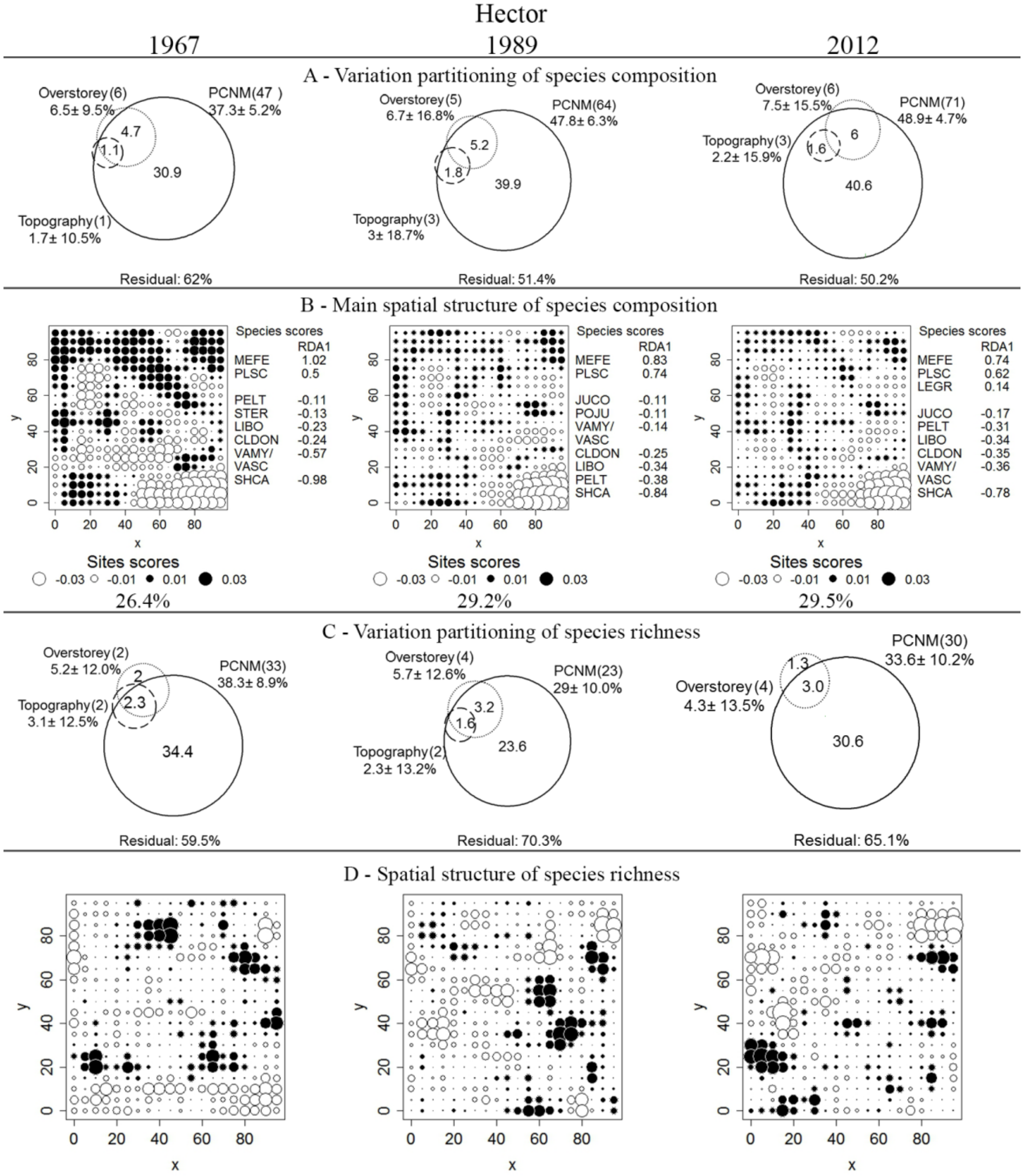

Figure 2-6. Variation partitioning and spatial structure of the understory community at the Hector plot. See Figure 2-3 for details.

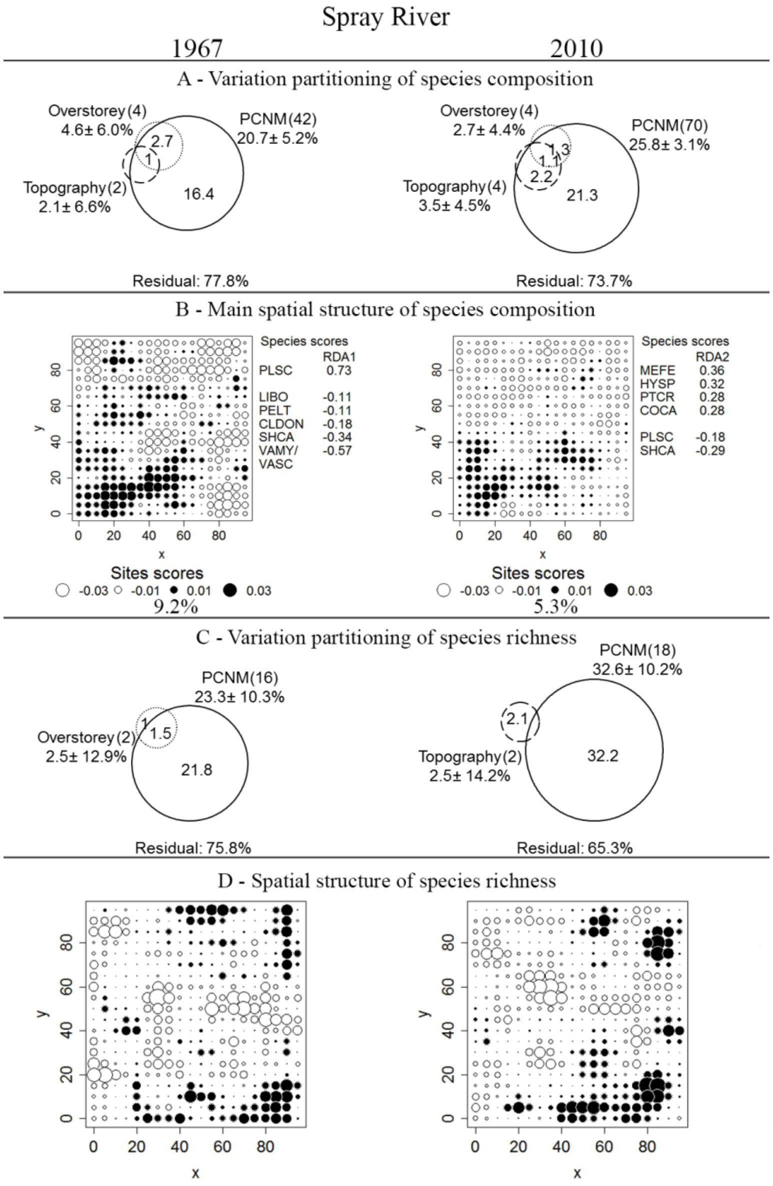

Figure 2-7. Variation partitioning and spatial structure of the understory community at the Spray River plot. See Figure 2-3 for further details.

2.7. Appendixes

Appendix 2-A. Detailed description (horizon depth, soil texture and pH) of soil profiles sampled at each plot.

Table 2-A1. Descriptions by horizon - depth, soil texture and pH - for soil profiles in two different topographic elements present in each plot. Refer to Figure 2-1 for the sampling locations at each plot. For horizon samples of less than 50 grams, soil textures are underlined and were assessed using the modified pipette method (Miller and Miller 1987) while the rest were assessed using the hydrometer methods (Kalra and Maynard 1991).

Sites	Pit A				Pit B			
	Horizon†	Horizon depth (cm)	Soil texture‡	pH§	Horizon name	Horizon depth	Soil texture	pH
Athabasca	LF	10-0	O	--	LF	2-0	O	--
	Bm1	0-7	SL	6.07	Ahe	0-6	SL	5.01
	Bm2	7-21	SL	6.23	Bm1	6-17	SL	6.1
	C	21-55	LS	6.96	Bm2	17-30	SL	6.66
	Ck	55+	LS	7.46	Bt	30-47	SCL	6.85
					IICk	47+	SL	7.8
Sunwapta	LF	5-0	O	--	FH	5-0	O	--
	Bm1	0-12	SiL	6.34	Ae	0-6	SiL	5.6
	Bm2	12-30	L	6.4	Bm	6-20	SL	5.84
	IICk	30-50	LS	7.98	IIBm	20-40	LS	6.57
	IIICk	50+	LS	8.28	IICk	40-50	SL	7.9
					IIICk	50+	S	8.55
Whirlpool	LF	2-0	O	--	LF	8-0	O	--
	Ah	0-3	SiL	5.08	Ahe	0-2	SL	4.95
	Bm1	3-24	SL	6.06	Bm1	2-18	SiL	5.8
	Bm2	24-39	SL	6.41	Bm2	18-28	L	6.1
	C	39+	SL	7.54	Bmg	28-42	SL	6.66
					Ckg	42-60	L	8.48
					IICk	60+	SL	8.47
Hector	LF	2-0	O	--	LF	5-0	O	--
	Ae	0-3	SL	4.16	Ae	0-8	SiL	3.97
	Bm1	3-15	SL	5.54	Bm1	8-15	SL	5.25
	C	15+	SL	6.64	Bm2	15-53	LS	5.93
					C	53+	SL	6.12
Spray River	LF	7-0	O	--	LF	5-0	O	--
	Ae	0-3	SiL	4.27	Ae	0-5	SiL	4.03
	Bm1	3-10	SL	6.11	Bm1	5-10	SL	5.44
	Bm2	10-18	SL	6.33	IICk	15-30	SL	6.8
	IICk	18-31	SL	7.21	IIICk	30+	LS	8.2
	IIICk	31+	LS	8.64				

† See Soil Classification Working Group (1998)

‡ O-Organic; SiL-Silt Loam; L-Loam; SL-Sandy Loam; LS-Loamy Sand; S-Sand; SCL-Sandy Clay Loam.

§ pH determined using water as suspension medium, methods described in Kalra and Maynard (1991).

Appendix 2-B. Mean percent cover and frequency of all species present in each plot for each sampling period.

Table 2-B1. Mean percent cover and frequency (number of occupied 5x5 m quadrats out of 400 per plot) of all species present in each plot for each sampling period. **Bolded** species appeared (A) or disappeared (D) over the study period in at least one plot; underlined species where associated with the main spatial structure of at least one plot. The super-script of underlined and **bolded** species represents the main reproductive strategy of that species (s = seed, sp = spore, v = vegetative) determined from the USDA PLANT database (USDA, NRCS 2014). Species names follow USDA PLANT database.

	Athabasca			**Sunwapta**			**Whirlpool**			**Hector**			**Spray River**	
Species	**67**	**89**	**12**	**67**	**89**	**12**	**67**	**89**	**12**	**67**	**89**	**12**	**67**	**10**
Shrubs														
Alnus viridis* subsp. *Crispa^{s} **(D)**				0.01 7	0.06 7	0.27 13	<0.01 1	0.01 1						
Amelanchier alnifolia	0.01 21	0.02 15	0.10 37	<0.01 6		<0.01 1	<0.01 10	<0.01 2	0.04 12				<0.01 1	0.01 3
Dasiphora fruticosa* subsp. *floribunda^{s} **(D)**	<0.01 1	<0.01 1	<0.01 2										<0.01 1	
Juniperus communis^{s}	0.29 138	2.34 287	8.78 380	1.13 359	4.56 370	13.8 399	0.57 191	1.88 251	5.20 284	0.03 39	0.02 32	0.11 34	0.04 115	0.27 95
Juniperus horizontalis^{v} **(A)**		<0.01 11	<0.01 8	<0.01 3	0.01 16	0.02 17								
Ledum groenlandicum^{s}				0.01 10	0.03 14	0.20 18	0.02 23	0.11 21	0.43 28	0.18 179	0.21 190	0.57 190	0.05 68	0.55 89
Lonicera dioica^{s} **(A)**	<0.01 1	<0.01 1	<0.01 8			<0.01 1			<0.01 3					
Lonicera involucrata^{s} **(A)**				<0.01 2		<0.01 1		<0.01 1	0.01 1	0.01 42	0.01 21	0.11 36	0.45 345	1.32 305
Lonicera tartarica^{s} **(A)**			0.01 3											
Menziesia ferruginea^{s}				0.01 21	0.03 22	0.37 56				31.8 385	26.7 387	29.2 388	0.20 114	2.82 225
Rhododendron albiflorum^{v}				<0.01 3	<0.01 1	0.03 8				0.10 20	0.05 15	0.15 26	0.05 39	0.47 62
Ribes lacustre^{s} **(A)**			<0.01 2							<0.01 3	<0.01 2	0.02 3	<0.01 4	0.01 10

Rosa acicularis^{v}	0.13 342	2.76 353	2.30 384	0.19 341	0.50 331	1.91 357	0.09 335	0.56 332	1.97 369				0.01 30	0.06 36
Salix spp.	0.01 14	0.01 18	0.03 15	0.02 67	0.02 43	0.12 68	<0.01 16	0.01 16	0.02 10	0.01 29	<0.01 16	0.03 22	0.10 213	0.01 15
Shepherdia canadensis^{s}	0.71 319	7.68 388	7.82 398	9.37 397	9.77 400	12.7 400	0.37 352	5.35 363	6.53 359	3.40 283	2.30 297	3.97 275	1.66 254	7.34 344
Sorbus scopulina^{s} **(D)**							<0.01 1	<0.01 1						
Sorbus sitchensis^{s} **(A)**														0.02 2
Spiraea betulifolia^{v} **(D)**	<0.01 2						0.02 64	0.05 65	0.16 62	0.01 12	<0.01 7	0.04 13		
Dwarf shrubs														
Arctostaphylos rubra				<0.01 1		<0.01 2								
Arctostaphylos uva-ursi^{v} **(A)**	8.59 397	27.0 400	40.9 398	0.42 370	2.09 379	4.95 375	0.37 277	2.30 240	4.19 189			<0.01 1	0.01 32	<0.01 5
Cassiope mertensiana					<0.01 1									
Cassiope tetragena^{v} **(D)**													<0.01 1	
Linnaea borealis^{v}	0.76 262	5.45 307	6.70 394	1.11 399	4.06 399	5.52 400	1.10 399	3.16 394	2.26 397	0.14 229	0.34 252	0.96 314	0.27 400	3.16 400
Phyllodoce empetriformis/ Empetrum nigrum				<0.01 7	0.01 13	0.09 21				0.02 35	0.01 27	0.02 19	0.02 41	0.11 41
Vaccinium cespitosum^{v} **(A)**			0.03 4	0.34 382	1.34 372	3.45 400	0.64 336	3.02 330	5.43 380					
Vaccinium myrtillus/ scoparium/myrtilloides/ membranaceum^{v}				0.04 71	0.02 62	0.29 141	0.01 5	0.02 12	0.04 8	3.08 400	1.54 400	3.39 400	3.36 400	5.38 400
Vaccinium vitis-idaea^{v} **(A)**				0.07 96	0.62 158	4.42 314			0.01 1					
Viburnum edule^{s} **(A)**			<0.01 1		<0.01 1	<0.01 2	0.01 17	0.02 16	0.07 18					
Herbaceous species														
Achillea millefolium^{v} **(D)**	0.10 346	0.10 335	0.36 365	0.02 71	0.01 20	0.02 53	0.01 35	0.01 33	0.01 35				<0.01 9	
Agoseris glauca^{s} **(A-D)**				0.01 33	<0.01 9	0.02 42		<0.01 1	<0.01 2				<0.01 1	
Androsace chamaejasme^{s} **(D)**	<0.01 2													
Anemone multifida^{s} **(D)**	<0.01 5	<0.01 5	<0.01 5	<0.01 1	<0.01 1									

***Anemone parviflora*^{s} (D)**				<0.01 2		<0.01 1								
***Antennaria neglecta*^{s} (D)**	0.06 241	0.09 191	0.36 290	0.09 272	0.05 126	0.03 90							<0.01 1	
***Antennaria parvifolia/ racemosa/rosea*^{s} (D)**	0.02 52	0.01 33	0.02 24	0.03 130	<0.01 17	<0.01 9	<0.01 1						0.01 17	<0.01 4
***Aquilegia formosa*^{v} (A)**						<0.01 2								
Arnica cordifolia^{v}				0.04 73	0.05 57	0.11 65	0.07 141	0.58 138	0.74 173	0.47 362	0.83 358	1.47 362	1.60 399	3.38 389
***Calypso bulbosa*^{s} (D)**	0.01 36	0.02 62	0.11 320	0.01 17	<0.01 2	0.01 25	0.02 85	0.01 24	<0.01 12				<0.01 7	
***Castilleja miniata*^{v} (A)**		<0.01 1	0.01 10	0.01 44	0.01 35	0.02 26							0.01 23	<0.01 9
***Campanula rotundifolia*^{s} (D)**	0.02 73	0.01 29	0.02 84				0.01 57	<0.01 18	0.02 60				<0.01 5	
***Chamerion angustifolium* subsp. *angustifolium*^{v} (A)**			<0.01 1	0.01 37	0.02 29	0.14 42	0.01 34	0.01 31	0.17 65	0.05 198	0.03 116	0.04 102	0.12 400	1.53 392
***Chimaphila umbellata*^{v} (A)**			<0.01 6	0.03 87	0.04 96	0.39 237	0.01 31	0.03 39	0.10 82				0.02 52	0.21 168
Clematis occidentalis													0.01 7	0.02 11
Cornus canadensis^{v}				0.07 120	0.38 136	1.56 256	0.75 342	4.48 373	5.49 392	0.04 95	0.26 111	0.54 125	0.53 398	6.11 399
***Corallorhiza trifida*^{s} (D)**	<0.01 4	<0.01 9	0.01 28	0.01 29	<0.01 11	<0.01 10	<0.01 7	<0.01 0	<0.01 2				<0.01 1	
***Dactylorhiza viridis*^{s} (A)**		<0.01 9	0.03 56											
***Erigeron peregrinus*^{s} (D)**													<0.01 4	
Eurybia conspicua				0.04 103	0.06 95	0.38 112	0.06 177	0.21 178	0.42 192				0.15 89	0.42 106
***Fragaria virginiana*^{v} (D)**	0.12 390	1.78 387	1.79 399	0.19 375	1.23 373	0.39 345	0.01 41	0.10 46	0.05 41	<0.01 1	<0.01 1		0.01 21	0.01 19
***Gentianella amarella*^{s} (D)**	0.04 140	0.02 60	0.09 303	0.05 194	0.01 34	0.01 42							<0.01 4	
***Geocaulon lividum*^{v} (A)**			0.03 10	<0.01 1	0.01 11	0.32 116	0.02 44	0.12 89	0.36 164					
Gentianella propinqua					<0.01 1									
***Geum triflorum*^{s} (D)**	<0.01 1													
***Goodyera oblongifolia*^{v} (A)**			<0.01 1	0.02 54	0.04 151	0.09 273	0.01 48	0.02 83	0.01 33	<0.01 1		<0.01 3	0.02 44	0.01 37

Goodyera repens^{v} **(D)**				<0.01 5									<0.01 1	<0.01 4
Hedysarum alpinum	<0.01 1		<0.01 2										<0.01 3	<0.01 2
Heracleum maximum^{s} **(D)**													<0.01 1	
Hieracium albiflorum^{s} **(D)**	<0.01 3		<0.01 3	<0.01 16	<0.01 1	<0.01 3				<0.01 3		<0.01 1	<0.01 1	
Lathyrus ochroleucus							<0.01 15	0.01 17	0.03 19					
Listera cordata^{s} **(D)**				<0.01 3	<0.01 2	<0.01 16	<0.01 3						0.01 17	0.08 171
Melampyrum lineare^{s}				0.24 389	0.47 381	2.93 398								
Mitella nuda													<0.01 2	<0.01 2
Moneses uniflora^{s} **(A)**			<0.01 1										<0.01 5	0.02 72
Orthilia secunda^{v}	0.03 74	0.02 61	0.14 214	0.12 262	0.20 288	0.31 384	0.08 231	0.19 236	0.14 297	0.03 96	0.02 77	0.12 130	0.08 178	0.16 236
Osmorhiza depauperata													<0.01 3	0.01 9
Packera streptanthifolia/ subnuda	0.05 193	0.09 221	0.06 126	0.02 95	<0.01 1	<0.01 9								
Parnassia palustris^{s} **(D)**				<0.01 2										
Piperia unalascensis				<0.01 1	<0.01 10	0.01 52								
Platanthera hyperborea					<0.01 7									
Platanthera obtusata **subsp.** ***obtusata***^{s} ***(D)***	<0.01 3		<0.01 10	0.01 9	<0.01 18	0.01 31	<0.01 1		<0.01 1				<0.01 1	
Platanthera orbiculata^{s} **(A)**			0.01 18			0.01 18		<0.01 1	<0.01 7					
Pyrola chlorantha	0.08 266	0.03 116	0.07 216	0.09 368	0.08 305	0.10 355	0.05 216	0.03 102	0.01 50	<0.01 3	<0.01 1	<0.01 11	0.05 168	0.11 253
Rubus pedatus^{v} **(A)**														0.01 7
Rubus pubescens^{v} **(A)**			<0.01 1				<0.01 1		<0.01 1					
Senecio lugens													0.01 48	<0.01 10
Solidago simplex **subsp.** ***simplex var. spathulata/ Solidago multiradiata***^{s} **(D)**	0.07 286	0.10 261	0.08 150	0.06 234	0.03 101	0.08 94	0.01 32	0.02 24	0.03 28				<0.01 11	

***Spiranthes romanzoffiana*^{S} (D)**				<0.01 1										
***Stellaria calycantha*^{S} (A)**									<0.01 2					
Stellaria longipes	<0.01 2		<0.01 12											
Stenanthium occidentale													0.01 27	0.01 28
Symphyotrichum ciliolatum	<0.01 2	<0.01 2	0.01 1	0.02 60	0.02 51	0.05 58	0.01 20	0.01 15	0.01 14		<0.01 2		0.30 395	0.63 357
***Taraxacum officinale*^{S} (A)**		<0.01 2	<0.01 3											
Thalictrum occidentale													<0.01 13	0.02 13
***Trifolium repens*^{S} (A-D)**		<0.01 2	<0.01 6	<0.01 1			<0.01 3	<0.01 1						
Viola adunca	0.04 164	0.05 170	0.22 303				<0.01 4	<0.01 2	<0.01 8					
Vicia Americana	<0.01 2	<0.01 5	0.01 5											
Zigadenus elegans								<0.01 1					<0.01 3	<0.01 1
Grasses and sedges														
Bromus inermis	<0.01 3		0.02 6											
Calamagrostis purpurascens	0.03 86	0.02 38	0.03 54										0.03 72	0.15 41
***Carex* spp.^{V} (A)**	0.40 234	0.03 35	0.74 259	<0.01 4		<0.01 2			0.02 2	0.06 201	0.01 24	0.01 42	0.09 370	0.02 81
Festuca saximontana	0.05 125	0.04 59	0.09 253											
***Festuca altaica*^{S} (D)**				<0.01 1										
***Festuca idahoensis*^{S} (A)**			0.20 74											
Leymus innovates^{V}	0.19 396	8.82 399	8.90 399	0.36 399	3.21 399	9.21 400	0.19 400	3.51 398	6.08 400	<0.01 2	<0.01 2	<0.01 2	0.18 398	2.94 396
***Poa palustris*^{S} (A)**			<0.01 1											
***Poa pratensis*^{S} (A)**			0.01 8						0.01 2					
Trisetum cernuum														0.11 14

Trisetum spicatum^{s} **(D)**				0.01 28	<0.01 1	<0.01 4	<0.01 1	<0.01 1						
Pteridophytes														
Dryopteris expansa													<0.01 1	<0.01 2
Equisetum pratense^{v} **(A)**									<0.01 1					
Equisetum scirpoides													0.09 348	0.11 259
Lycopodium annotinum^{v} **(A)**						<0.01 5	<0.01 1	0.01 2	<0.01 7	<0.01 4	<0.01 3	<0.01 3	0.05 105	0.67 187
Lycopodium complanatum^{v} **(D)**				<0.01 7	0.05 39	1.70 188	0.01 6	0.11 14	0.32 36	<0.01 3	<0.01 1		0.07 145	0.35 160
Mosses														
Dicranum polysetum^{v}		0.34 301	2.27 395	0.12 291	0.12 249	0.67 387	0.33 377	0.63 233	0.69 344	0.15 227	<0.01 10	<0.01 16	0.23 389	0.08 155
Hylocomium splendens^{v}		2.49 298	4.36 384	0.02 64	0.86 191	14.34 342	24.0 400	38.6 397	28.2 400	0.03 32	0.27 110	0.88 252	0.23 302	5.79 395
Pleurozium schreberi^{v}		7.39 345	19.5 400	4.94 366	35.1 397	52.2 400	12.0 400	13.1 358	24.6 400	6.03 378	36.5 392	69.9 400	17.5 400	75.0 400
Polytrichum juniperinum^{sp}		0.04 142	0.13 268	0.09 360	0.04 152	0.04 95		0.01 16	0.15 111	0.08 197	0.04 121	0.02 46	0.12 366	0.06 102
Ptilium crista-castrensis^{v} **(A)**			0.01 2	0.19 266	0.37 121	2.72 193	0.15 46	0.40 36	1.95 147	0.08 186	0.22 226	1.55 361	0.34 391	8.52 398
Total mosses	6.32 395	10.6 384	28.1 400	5.68 392	35.4 400	69.5 400	35.6 400	51.9 400	57.6 400	6.27 389	36.6 400	70.1 400	17.6 400	85.7 400
Lichens														
Cladina spp.^{v}		0.10 154	0.31 249		0.36 343	0.89 289		0.27 228	0.24 185		0.01 23	<0.01 15		<0.01 6
Cladonia spp.†		0.14 259	0.19 259	0.33 398	0.09 289	0.08 211		0.04 136	0.08 288	1.30 394	0.21 400	0.45 399	0.44 400	0.57 398
Peltigera spp.^{v}		5.03 388	4.29 400	0.71 400	0.94 386	2.21 392	0.78 400	3.34 398	2.43 394	0.82 347	0.83 400	1.87 399	0.44 375	1.89 396
Stereocolon spp.^{v}		0.70 319	0.32 267	0.08 271	0.06 208	0.07 131		0.01 18	0.01 19	0.09 188	0.02 70	<0.01 15	0.02 66	<0.01 10
Total lichens	2.84 396	6.52 399	5.06 400	1.69 400	2.06 398	3.73 396	0.78 400	3.61 398	3.01 399	2.57 398	1.13 400	2.60 400	1.73 400	2.76 400

† In 1967 the result represents the frequency and mean cover of *Cladina* and *Cladonia* together since these genera were not distinguished in that sampling year.

Appendix 2-C. Detailed results of the constrained ordination (RDA) for the understory community data constrained by the overstory and topography variables.

Table 2-C1. Detailed results of the RDA for the understory community data constrained by the overstory variables. Species scores and scores for constraining variables are presented for the first axis (p<0.01) of the RDA for each plot and each sampling year. Only scores with absolute values > 0.1 are presented. The percent of variation in understory community composition explained by the first RDA axis is presented in the first row. Overstory variables include the species and size class (see explanation below table).

	Athabasca			**Sunwapta**			**Whirlpool**			**Hector**			**Spray River**	
	67	**89**	**12**	**67**	**89**	**12**	**67**	**89**	**12**	**67**	**89**	**12**	**67**	**10**
Percent explained by first axis	16	16	6	7	11	09	19	22	13	5	5	5	4	2
Shrubs														
Juniperus communis				0.15	-0.25	-0.18	-0.16	-0.29	-0.47					
Menziesia ferruginea						0.14				0.42	0.32	0.14		0.13
Shepherdia canadensis	0.15	0.20		-0.7	-0.23		-0.22	-0.47	-0.38	-0.41	-0.41	-0.46	-0.14	
Rosa acicularis		-0.14			-0.15									
Dwarf shrubs														
Arctostaphylos uva-ursi	-0.89	-0.58	-0.51		-0.24	-0.23	-0.28	-0.55	-0.55					
Linnaea borealis		0.27			-0.26		-0.32	-0.13			-0.11			
Vaccinium cespitosum							-0.25	-0.32	-0.34					
Vaccinium myrtillus/ scoparium/myrtilloides/ membranaceum										-0.35			-0.38	
Vaccinium vitis-idaea					0.19	0.18								
Forbs														
Antennaria neglecta				0.12										
Arnica cordifolia								0.12	0.14					
Cornus canadensis					0.11			0.13	0.12			0.15		0.13
Fragaria virginiana				0.13										
Geocaulon lividum														
Melampyrum lineare					-0.15									
Packera streptanthifolia/ subnuda	-0.10													
Solidago simplex subsp. *simplex* var. *spathulata/ Solidago multiradiata*	-0.12													
Carex spp.	-0.15		-0.11											
Leymus innovatus		-0.24			-0.19		-0.11							
Mosses	0.93†													
Dicranum polysetum		0.13		0.12			-0.19	-0.21	-0.13					

Hylocomium splendens		0.28	0.36		0.21	0.63	1.10	0.87	0.31					0.19
Pleurozium schreberi		0.96	0.36	0.44	0.67	-0.29	-0.74	-0.73	0.15	0.25	0.22	0.19	0.4	-0.11
Ptilium crista-castrensis					0.14	0.34		0.12	0.53					0.2
Lichens	0.17†													
Cladonia spp. ‡				0.18						-0.17		-0.12	-0.13	
Cladina spp.		-0.12			-0.16	-0.12		-0.12	-0.11					
Peltigera spp.							-0.18							
Stereocolon spp.		-0.16												
Overstory variables§														
AL_TRA		0.29				0.23								
AL_1												0.41		
AL_2										0.28	0.31			
PG_TRA			0.41							0.77		0.70		
PG_1		0.16	0.39			0.12					0.68	0.84		
PG_2		0.17	0.32											
PM_TRA			0.63				0.79	0.81	0.76					
PM_1	0.23		0.52					0.45	0.84					
PM_2		0.25					0.70							
PM_3							0.48	0.58	0.31					
PT_TRA		0.31		0.11					-0.33					
PT_3								-0.16						
PC_TRA				0.61	0.46	0.9	-0.28	-0.56	-0.46					
PC_1	0.82	0.63								-0.35			0.51	0.46
PC_2	0.35	0.56	0.32								-0.40	-0.38	0.67	
PC_3	-0.38	-0.20		-0.58				0.11		-0.39			-0.5	
PC_4	-0.49	-0.33	-0.26	-0.59	-0.1	-0.1								-0.75
PC_5				-0.37			-0.30	-0.26	-0.12					
PC_6				-0.22					-0.15					
dead_TRA						0.69			0.35			0.35		
dead_1	0.87		0.36							-0.42	-0.35		0.88	0.64
dead_3									0.26			0.20		
dead_4										0.20				
dead_5									-0.12					
Canopy Cover		0.78	0.26		0.82			0.78	0.25		0.61			0.25

†For the Athabasca plot different moss and lichen species were not identified in 1967 and thus total moss and lichen cover was used for that sampling year.

‡ In 1967 the *Cladonia* spp. results represent the *Cladina* and *Cladonia* species together since these genera were not distinguished in that sampling year.

§Species code: PC = *Pinus contorta*, PM = *Picea mariana*, PG = *Picea glauca/engelmannii,* AL = *Abies lasiocarpa*, PT = *Populus tremuloides*. Size classes: "TRA" = individuals <2.54 cm diameter at breast height (DBH) but taller than 30cm, 1 = 2.54cm to 7.62cm DBH, 2 = 7.63cm to 15.24cm DBH, 3 = 15.25cm to 22.86cm DBH, 4= 22.87cm to 30.48cm DBH, 5 = 30.49cm to 38.1cm DBH, 6 = 38.11cm to 45.72cm DBH.

Table 2-C2. Detailed results of the RDA for the understory community data constrained by the topographic variables. Species scores and scores for constraining variables are presented for the first axis (p<0.01) of the RDA for each plot and each sampling year. Only scores with absolute values greater than 0.1 are presented. The percent of variation in understory community explained by the first RDA axis is presented in the first row.

	Athabasca			**Sunwapta**			**Whirlpool**			**Hector**			**Spray River**	
	67	**89**	**12**	**67**	**89**	**12**	**67**	**89**	**12**	**67**	**89**	**12**	**67**	**10**
Percent explained by first axis	12	8	4	4	3	4	24	20	14	2	2	1	2	2
Shrubs														
Juniperus communis				-0.11	-0.19	-0.11	-0.16	-0.22	-0.38					
Ledum groenlandicum									0.14					
Menziesia ferruginea										0.26	0.14	0.10		
Shepherdia canadensis	0.14	0.22	0.17		-0.18		-0.21	-0.40	-0.35	-0.20	-0.15	-0.17	-0.21	-0.12
Rosa acicularis		-0.17		-0.11										
Dwarf shrubs														
Arctostaphylos uva-ursi	-0.71	-0.41	-0.33	-0.21		-0.12	-0.33	-0.47	-0.59					
Linnaea borealis	-0.20	0.12	0.10	-0.10			-0.31	-0.13			-0.13			
Vaccinium cespitosum							-0.27	-0.32	-0.36					
Vaccinium myrtillus/ scoparium/myrtilloides/ membranaceum										-0.20	-0.16	-0.13	-0.15	
Vaccinium vitis-idaea					0.14	0.23								
Forbs														
Arnica cordifolia								0.15	0.22		-0.15		0.12	
Chamerion angustifolium subsp. *Angustifolium*									0.10					
Cornus canadensis					0.10	0.20	0.12	0.25	0.29			-0.10		
Fragaria virginiana					0.13									
Melampyrum lineare					-0.10									
Carex spp.			-0.20											
Leymus innovatus		-0.15		-0.10			-0.11							
Lycopodium complanatum									-0.10					
Mosses	0.85†													
Dicranum polysetum		0.10					-0.17	-0.19	-0.12					
Hylocomium splendens		0.14	0.27			0.37	1.15	0.75	0.13					0.22
Pleurozium schreberi		0.65	0.22	0.54	0.31	-0.29	-0.92	-0.76	0.13		0.21	0.16	0.17	-0.15
Ptilium crista-castrensis						0.16	0.11	0.18	0.54					0.24
Lichens	0.22†													
Cladina sp								-0.12	-0.12					
Cladonia sp‡				-0.13									-0.10	
Peltigera sp		-0.11					-0.14		0.12					

Topography variables														
Elevation	-0.96	-0.89	-0.89	-0.81	-0.83	-0.89	-0.92	-0.95	-0.95		-0.83	-0.80	-0.99	-0.85
Convexity§		-0.64	-0.76	0.36	0.25	0.11	-0.19	-0.18	-0.21		0.32	0.41	-0.30	
Slope	0.17	0.32					-0.32	-0.19	-0.11					0.28
Sin.aspect§	-0.19	-0.22	-0.23	-0.25	-0.44	-0.44								-0.51
Cos.aspect§										1.00	0.37	0.36		-0.21

†For the Athabasca plot different moss and lichen species were not identified in 1967 and thus total moss and lichen cover was used for that sampling year.

‡ In 1967 the *Cladonia* spp. result represent the *Cladina* and *Cladonia* species together since these genera were not distinguished in that sampling year.

§ Convexity is calculated as the elevation of a quadrat minus the average elevation of surrounding quadrats. Sin aspect represents the east-west orientation with values of 1 and -1 respectively representing an east and west facing slope. Cos aspect represents the north-south orientation with values of 1 and -1 respectively representing a north and south facing slope.

Appendix 2-D. Spatial distribution of overstory variables and understory species mentioned in the results section for the Athabasca plot.

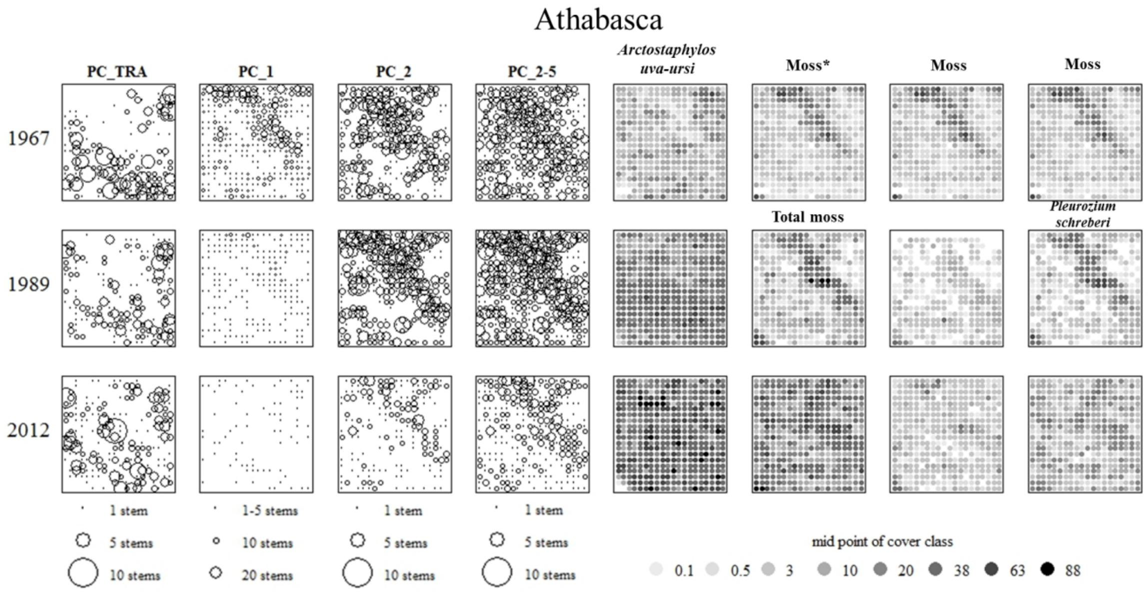

Figure 2-D1. Spatial distribution of *Pinus contorta* (PC) stems of different size classes as well as *Arctostaphylos uva-ursi* and main moss species in the Athabasca plot over the study period. Size classes presented include "TRA" = individuals <2.54 cm diameter at breast height (DBH) but taller than 30cm, 1 = 2.54cm to 7.62cm DBH, 2 = 7.63cm to 15.24cm DBH, 2-5 = ≥ to DBH. * For the Athabasca plot different moss species were not identified in 1967 and thus only total moss cover is presented for 1967.

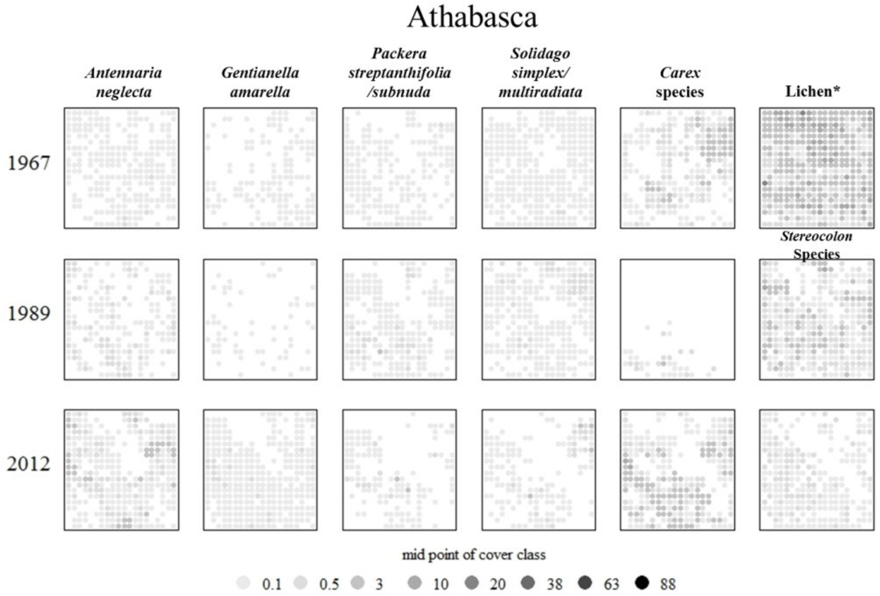

Figure 2-D2. Spatial distribution of different understory species that were gradually excluded from the dense band of small pines (see Figure 2-D1), particularly by 2012. *For the Athabasca plot different lichen species were not identified in 1967 and thus only total lichen cover is presented for 1967 and *Stereocolon* species afterwards in 1989 and 2012.

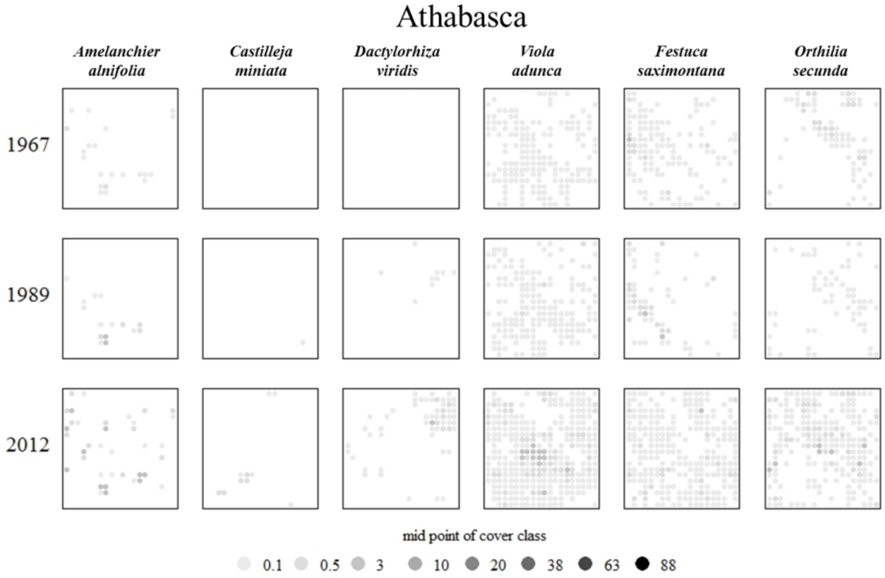

Figure 2-D3. Spatial distribution of different understory species that increased in frequency in open areas of the Athabasca plot (see Figure 2-D1) over the study period, especially in 2012.

Appendix 2-E. Spatial distribution of overstory variables and species mentioned in the result section for the Sunwapta plot.

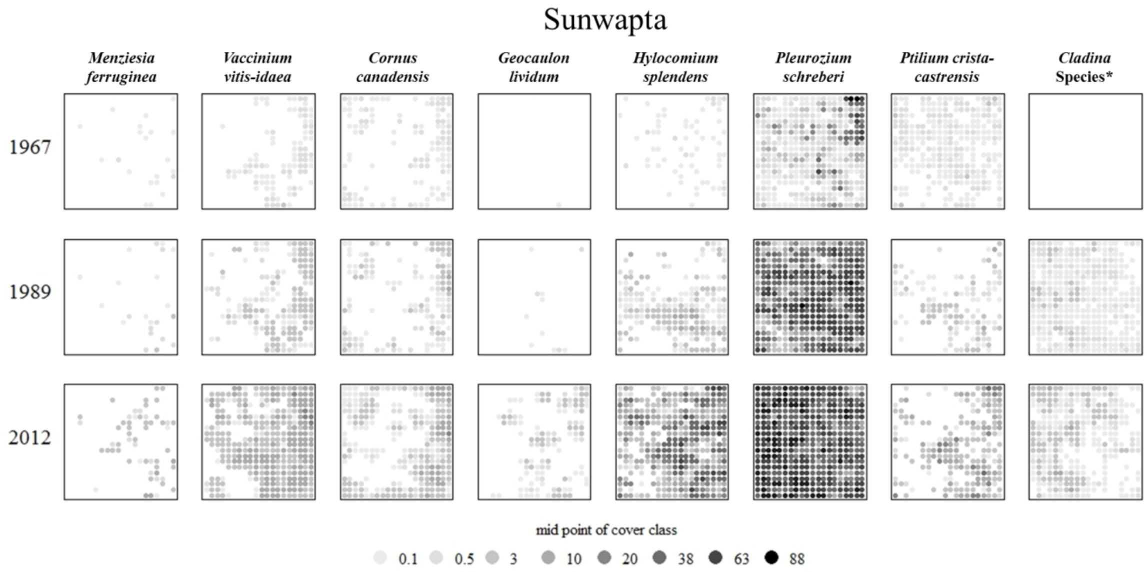

Figure 2-E1. Spatial distribution of understory species in the Sunwapta plot that contributed to a strengthening of the spatial pattern over time and thus an increase in the amount of variation in understory community explained by spatial variables (PCNM) in 2012.

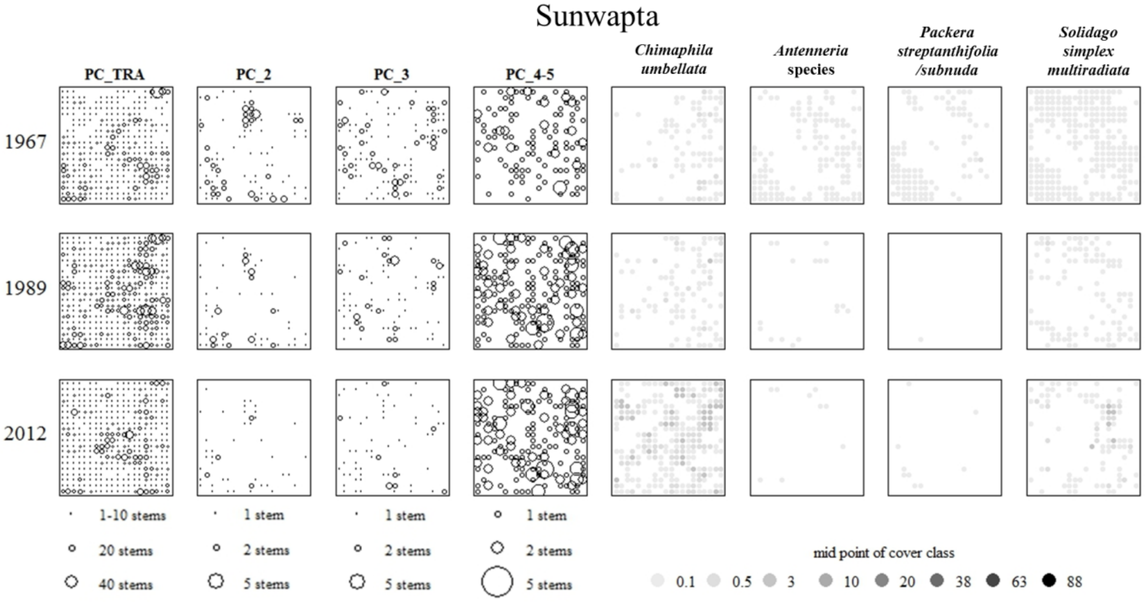

Figure 2-E2. Spatial distribution of *Pinus contorta* (PC) stems of different size classes in the Sunwapta plot as well as *C. umbellata* (which like *H. splendens* and *V. vitis-idaea* was mainly present on the east side of the plot in 1967 and spread to the western drier side in 1989 and 2012, see Figure 2-E1) and other species originally present in quadrats with low densities of big trees (southwest corner of plot and southeast of the center of the plot) but which became less frequent in these open areas. Size classes code : “TRA” = individuals <2.54 cm diameter at breast height (DBH) but taller than 30cm, 2 = 7.63cm to 15.24cm DBH, 3 = 15.25cm to 22.86cm DBH, 4-5 22.87cm to 38.1cm DBH.

Appendix 2-F. Spatial distribution of overstory variables and species mentioned in the result section for the Whirlpool plot.

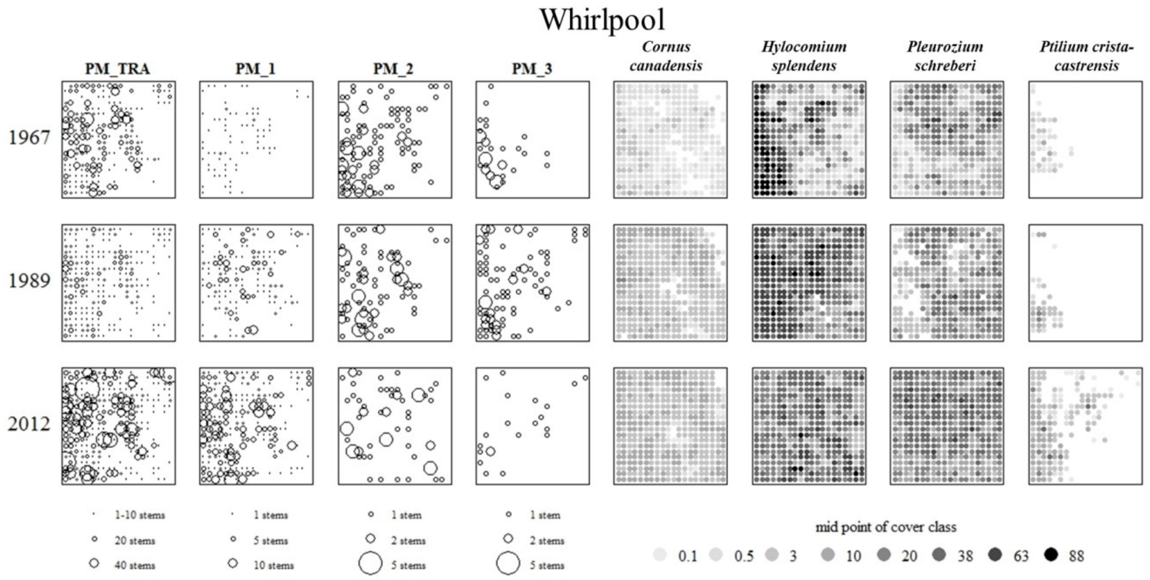

Figure 2-F1. Spatial distribution of *Picea mariana* (PM) stems of different size classes in the Whirlpool plot and of species spreading or increasing their cover throughout the plot over the study period. Size classes code: "TRA" = individuals <2.54 cm diameter at breast height (DBH) but taller than 30cm, 2 = 7.63cm to 15.24cm DBH, 3 = 15.25cm to 22.86cm DBH.

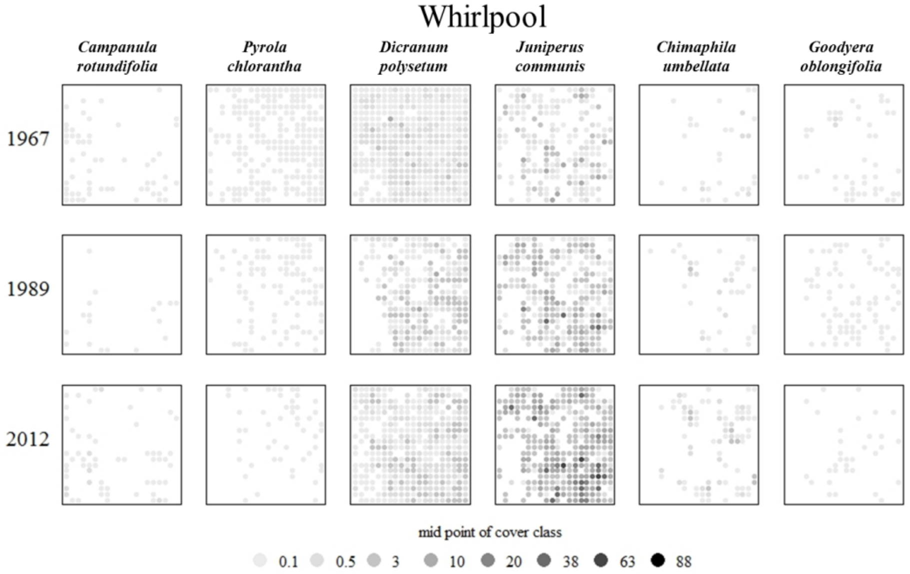

Figure 2-F2. Spatial distribution of species that decreased in frequency on the lower terrace of the Whirlpool plot (western half of plot) from 1967 to 1989 (*Campanula rotundifolia*, *Pyrola chlorantha* and *Dicranum polysetum*) as well as species that increased in frequency mainly on the upper terrace (eastern half of plot) from 1967 to 1989 (*Juniperus communis*, *Chimaphila umbellata* and *Goodyera oblongifolia*).

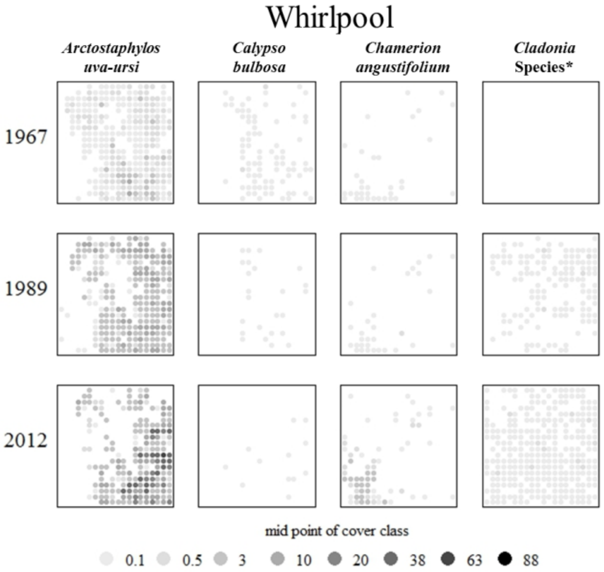

Figure 2-F3. Spatial distribution of species that decreased in frequency on the upper terrace of the Whirlpool plot (eastern half of plot) over the study period or in 2012 compared to 1989 (*A. uva-ursi* and *Calypso bulbosa;* see also *G. oblongifolia*, *P. chlorantha* in Figure 2-F2) as well as species that increased in frequency on the lower terrace from 1989 to 2012 (*C. angustifolium* and *Cladonia* spp.*;* see also *P. crista-castrensis* in Figure 2-F1 and *D. polysetum and C. rotundifolia in Figure 2-F2*).

Chapter 3. Untangling the processes driving mortality in mature conifer forests

Abstract - Understanding the processes driving mortality in forests is important for our comprehension of natural stand dynamics as well as for the development of natural disturbance or ecosystem based management. The objective of this study was to determine the processes driving mortality in five mature *Pinus contorta* stands of the Canadian Rocky Mountains ranging in age from 111 to 186 years old in 2012. We used data from five spatially explicit large permanent plots (repeated measurement over a 45 year period), dendrochronological information and point pattern analysis to test the hypothesis that these stands had completed the self-thinning/density-dependent mortality stage of succession. Our results showed that contrary to our expectation the self-thinning phase can persist for more than 140 years following stand establishment due to two different processes 1) prolonged post-fire establishment periods due to surface fires and 2) slow growth which delays the onset of competition. Different evidence pointed toward the importance of density-dependent mortality in the studied stands over the study period. The diameter distribution of individuals changed from an initially right-skewed distribution towards normality as a result of mortality of smaller diameter stems and individuals of lower canopy positions were proportionally more affected by mortality indicating that competition for light was important. Also when compared to the pre-mortality pattern, surviving stems in all stands had an increasingly more uniform spatial distribution suggesting the importance of density-dependent mortality. In two of the plots, recent windthrow and/or ingrowth initially hindered our ability to detect density-dependent mortality but our dendrochronological sampling and permanent plot data allow us to untangle the different processes at play and demonstrate for the first time how density-independent process can mask underlying density-dependent mortality processes in older stands. Mortality of larger dominant canopy trees increased over the study period and mortality of dominant stems was a random process in all stands suggesting they were approaching the end of the self-thinning stage and that density-independent process might become more important in the following stages of stand development.

3.1. Introduction

Understanding the processes driving mortality in forests plays an important role in our comprehension of stand dynamics (Franklin et al 1987). Mortality can be driven by density-dependent and density-independent processes and the relative importance of these processes can vary with stand age. It is generally accepted that density-dependent competition is the main process driving mortality during the early self-thinning stage of forest development (Oliver and Larson 1996, Brassard and Chen 2006) while in later stages it is often assumed that density-independent process become more important (Szwagrzyk and Czerwczak 1993, Aakala et al. 2012). However, very few studies have tested these assumptions using long term surveys (but see Kenkel et al (1997)) and few have been over long enough periods to determine the length of the self-thinning stage (however see Harper et al (2005) who used a chronosequence approach). Understanding the processes driving mortality in different successional stages is also important to inform forest management following natural disturbance emulation approaches such as ecosystem-based management (Bergeron and Harvey 1997, Niemelä 1999).

Many studies in young forests have concluded that mortality is driven by density-dependent competition or suppression (Kenkel 1988, Kenkel et al. 1997, Lutz and Halpern 2006), but others found that mortality was random (Getzin et al. 2006, Metsaranta and Lieffers 2008). There is, however, some evidence that even in the early stages of stand development, density-independent processes may be more important than previously thought (Lutz and Halpern 2006, Metsaranta and Lieffers 2008, Donato et al. 2012) and this could have long lasting effects on the structure of forests. In old-growth forests some studies have found that mortality can still be driven by density-dependent processes (Moeur 1993, He and Duncan 2000, Castagneri et al. 2010, Svoboda et al. 2010, Lutz et al. 2014) while others have shown that it is mainly a random process (Szwagrzyk and Czerwczak 1993, Das et al. 2011, Aakala et al. 2012, Silver et al. 2013). Some authors have suggested that in old-growth forest, density-independent processes such as insect outbreaks, surface fires, pathogens and windthrow could mask the influence of competition-induced mortality (Szwagrzyk and Czerwczak 1993, Aakala et al. 2012) thus potentially contributing to the appearance of random mortality; however, this has never been demonstrated explicitly. The range of findings from studies looking at the processes driving mortality in both young and old-growth forests also demonstrates the need for more studies linking the processes driving mortality to the spatial structure of the surviving and dead stems in forests.

Most studies assessing the importance of density-dependent mortality in forest ecosystems have relied on inferences based on the spatial distribution of living and dead trees at a fixed point in time (Kenkel 1988, Szwagrzyk and Czerwczak 1993, Getzin et al. 2006, Das et al. 2011). During the self-thinning stage of succession, if higher mortality occurs in denser areas (suggesting density-dependent mortality) this then leads to more regularly spaced survivors (Peet and Christensen 1987, Kenkel 1988, Chen and Popadiouk 2002). Thus by looking at the change in the spatial pattern between all stems (living and dead) and surviving stems it is possible to assess the importance of density-dependent mortality. To use these methods however, requires information on the age structure or timing of establishment of the population studied, since the presence of recently established stems (for example ingrowth into gaps) can influence the results. For example, a study in an old-growth forest found that tree mortality was followed by ingrowth within gaps and that this then led to a more clustered pattern of the shade intolerant *Pseudotsuga menziesii* trees (Getzin et al. 2006). This demonstrates how the presence of ingrowth can limit the ability to detect the processes driving mortality (Aakala et al. 2012).

Permanent plots and information on the age structure of trees can take factors such as ingrowth into consideration, thus allowing a more rigorous evaluation of the factors driving mortality. Information on the size structure of living and dead trees and how this changes in time can also provide valuable insight into the process driving mortality (Kenkel et al. 1997, He and Duncan 2000, Aakala et al. 2012). After stand establishment, asymmetric competition for light would result in size distribution becoming increasingly positively skewed (Weiner and Thomas 1986, Kenkel et al. 1997). During self-thinning, then, mortality of smaller size classes would gradually bring the size distribution back towards normality (Kenkel et al. 1997). This is supported by evidence that in old-growth stands the size distribution of early successional species has been found to be very close to normal (He and Duncan 2000, Lutz et al. 2014). On the other hand if mortality is distributed equally across all size classes or is proportionally more important in larger size classes the skewness of the size distribution would remain the same or become more skewed; this would indicate that mortality was not from self-thinning (Canham et al. 2001, Aakala et al. 2012). Combining information from changes in both size structure and spatial patterns can provide a more complete understanding of processes driving stand dynamics (Kenkel et al. 1997).

In this study we used data from spatially explicit large permanent plots to determine which processes were driving mortality in mature *Pinus contorta* stands of the

Canadian Rocky Mountains ranging from 111 and 186 years old in 2012. In these ecosystems the shade intolerant *Pinus contorta* is well adapted to fires with serotinous cones, and thus establishes rapidly following stand replacing wildfires; while later successional species, such as *Picea engelmannii* and *Abies lasiocarpa*, generally establish a few decades later (Day 1972, Antos and Parish 2002a, Clark et al. 2003). *Pinus contorta* ecosystems are widely distributed in North America (Burns and Honkala 1990a) and are used in this study to test hypotheses about the processes driving mortality in the mid to later successional stages. We combined dendrochronological information, repeated plot measurement over a 45 year period and spatial analysis to test the hypothesis that the studied stands had mostly finished the self-thinning/density-dependent mortality stage of succession and thus that mortality had become a random process. Evidence in support of this hypothesis would be that 1) The skewness of the diameter distribution of individuals was not moving towards normality over time 2) Individuals of lower canopy positions were not proportionally more affected by mortality suggesting that competition for light was not a driving factor of mortality and 3) When compared to the pre-mortality pattern, surviving stems had a random spatial distribution. If evidence of density-dependent mortality was found we then tested the hypothesis that mortality of dominant canopy trees was a random process to assess whether mortality of trees in different canopy positions can be affected by different processes. The use of permanent plots and dendrochronology allowed us to account for effects of ingrowth and recent disturbances which could have influenced our interpretation of processes driving tree mortality in these forests.

3.2. Methods

Study area

This study was conducted in five mature *Pinus contorta* dominated forests in Banff and Jasper National Parks, Canada. These forests were selected following an extensive survey of *Pinus contorta* dominated forests in these parks and were chosen to represent a range of forest types as well as cover a wide range of moisture/elevation (Hnatiuk 1969, La Roi and Hnatiuk 1980). In 1967, a one hectare plot configured as a 20x20 grid of 5x5m contiguous quadrats was established in each forest (*i.e.* a total of 400 quadrats per forest) and permanently marked with railway spikes placed every 5 m around the plot boundary and every 20m within the plot. Relocation of the railway spikes using a metal detector allowed for a precise repeated measurement of the same quadrats in 1989 and 2012. In 1967, the Athabasca, Sunwapta, Whirlpool, Hector and Spray River plots were respectively 101, 91, 141, 95 and 66 years old. For a more detailed description of the plots see Gendreau-Berthiaume et al. (2015). Between 1971 and 2000 the weather stations closest to the low (Athabasca) and high (Hector) elevation plots recorded mean annual temperatures of 3.3° and -0.3° and mean annual precipitation of 398mm and 569mm, respectively (Canadian Climate Normals). However, the environmental conditions at each of our sites might vary from these weather stations as the geographical location in these mountains ranges can greatly influence precipitation and temperature.

Data collection

In 1967 and 1989, live stems and standing snags were counted by species and size classes in each quadrat. Stems with a diameter at breast height (DBH) greater than 2.54 cm (one inch, as used in the 1967 sampling) were placed in seven classes each spanning 7.62 cm

DBH (or three inches) except the smallest tree size class which only spans 2 inches (from 1 to 3 inches) (Hnatiuk 1969). In 2012 all dead and live stems greater than 2.54cm DBH were stem-mapped, identified to species and their DBH was recorded (Figure 3-1). Stems over 9cm DBH were classified as dominant/codominant or suppressed based on their position in the canopy (stems 3m below the dominant canopy were considered suppressed) and stems less than 9cm DBH were classified as saplings. In 2012 dead stems were identified as standing dead stems or fallen logs (to allow comparison with previous sampling periods) and the presence of needles or small twigs were noted to indicate that mortality occurred recently. Signs such as fire scars or char on the stems were also noted to help identify remnants from the previous stand replacing disturbances.

In 2012 one living stem over 5cm DBH of each species and each canopy position (dominant/codominant, suppressed, sapling) was randomly selected in each of 100 10 x10 m subplots per plot; these were cored and their heights were measured. Two perpendicular cores were taken on each stem at a height of 30cm except for stems ≤ 6cm DBH which were cored once. For the Athabasca plot, disks from two snags with fire scars were collected on each side of the plot (total of eight disks with fire scars) to date the fires. For the Whirlpool plot, which had recently suffered severe windthrow, disks from five recently uprooted or snapped (still had needles or small twigs) *Pinus contorta* and *Picea* (all *mariana* except one *engelmannii*) stems were collected on each side of the plot and when possible recently fallen trees were cored within the plot to determine when the recent blowdown occurred. Recent windthrow was also present in the Sunwapta site, although to a lesser extent, and recently fallen trees within this plot were also cored when possible. All samples were scanned with an Epson V750 Pro at a resolution between

2400-4800 dpi (depending on ring width) and rings were measured on the images using the CooRecorder software (Larsson 2008b). The CDendro software (Larsson 2008a) was then used to cross-date samples by comparing every sample to the average plot chronology to find measurement mistakes, missing rings, determine years with fire scars (Athabasca) or determine timing of mortality (Whirlpool, Sunwapta). When the pith was not present on a core, we estimated the number of missing rings near the center by: 1) estimating the distance between the last ring measured and the pith by aligning three concentric circles to the three inner most rings measured (using a tool available in the CooRecorder software); and 2) by dividing this distance by the average ring width of the last three years measured. We evaluated the accuracy of this method by comparing cores with piths to ones from the same tree without piths and found that in most cases it was accurate within 1-2 years. We used the age of the oldest of the two cores for each stem (always using a core with the pith when available) to estimate year of establishment.

Stand structure and composition data analysis

Establishment dates for all trees cored allowed us to reconstruct the age structure of each plot and to determine the timing of establishment of each species. The number of live stems of each species and total number of dead stems was counted at each sampling period to provide information about stand composition and density and how these changed over time. For each sampling period diameter distributions of early successional species (all *Pinus contorta* except 11 *Populus tremuloides* stems in Whirlpool) and later successional species (*Abies lasiocarpa*, *Picea engelmannii* and *Picea mariana*) were constructed for live stems (L), live stems and standing dead snags (L+S), and for live stems, standing snags and fallen logs (L+S+F) for 2012. For each of these categories we determined the mean DBH, skewness of the distribution and the coefficient of variation using the mid-point of DBH classes for each stem since in the previous sampling periods DBH was not recorded for each stem. We evaluated the effect of using mid-points (vs actual DBH) for these metrics by comparing to calculations using actual DBH values from the 2012 data and found that use of the mid-points of classes produced acceptable results. To better describe the stand structure of the plots in 2012 we used the DBH measurements of all live stems and the data from height measurements made on cored trees to determine the average DBH and height of trees from each canopy position (dominant/codominant, suppressed, saplings) for both early successional and late successional species separately. Finally the percentage of dead stems in each of these categories was also calculated. For the purpose of this analysis highly degraded snags and fallen stems were assigned a canopy position of dominant/co-dominant or suppressed using a DBH cut-off equal to the average DBH of living dominant/co-dominant trees minus the standard deviation. For these and later analyses, care was taken not to include remnant stems that most likely died during the last stand replacing disturbance such as dead stems with char and/or with a DBH substantially greater than any living trees in the plot. Such remnant trees were only found in the higher elevation plots (82 in Hector and 20 in Spray River), likely because decay processes are slower at higher elevations (Kueppers et al. 2004). Finally in the Spray River plots some trees had been logged and these were also excluded from our analyses (n=84).

Spatial analyses

To evaluate if live stems had a clustered, random or uniform spatial distribution we calculated the Morisita index of dispersion (Morisita 1959) for 5 spatial scales (25m^2,

$100m^2$, $400m^2$, $625m^2$ and $2500m^2$) using the quadrat level data of each sampling period More specifically, we were interested in the change of spatial distribution over time as we expected that mortality during self-thinning would gradually lead to a less clustered and potentially more uniform distribution of surviving stems. To determine if spatial patterns were significantly different from complete spatial randomness (CSR) we used the dispindmorisita function of the "vegan" package in the R statistical language (R Development Core Team. 2011) which tests for deviation from the null hypothesis of CSR using critical values of the Chi-square distribution with n-1 degree of freedom (Oksanen et al. 2014).

The stem maps of all living and dead stems from 2012 allowed us to analyse their spatial distributions in more detail using marked point pattern analysis. For these analyses we used the commonly used L-function $L(r)$, which is a square root transformation of Ripley's K-function that stabilizes its variance (Ripley 1977). However the K-function and its transformation $L(r)$ are cumulative, meaning that clustering at short distances can influence the value of the statistic at larger scales (Condit et al. 2000, Perry et al. 2006). Thus we complemented $L(r)$ with the pair correlation function $g(r)$ (Stoyan and Stoyan 1994) also known as the O-ring statistic (Wiegand and Moloney 2004) or the Neighbourhood density function (Perry et al. 2006) which is non-cumulative and thus has the potential to more accurately determine the scale at which the deviance from the null model occurs (Wiegand and Moloney 2004, Perry et al. 2006). All subsequent analyses were conducted with both $L(r)$ and $g(r)$ but we refer to only $L(r)$ in the following paragraphs for simplicity as interpretations are the same for both functions.

We tested the random mortality hypothesis using the univariate random labelling approach. This approach is often used in ecology to determine whether intra-specific competition leads to a more regular post-mortality spatial pattern (an indication of self-thinning) while accounting for first order heterogeneity in the initial pattern (Kenkel 1988, Getzin et al. 2006, Das et al. 2011). We thus randomly resampled sets of dead trees within the initial pre-mortality pattern (live and dead trees) to produce Monte Carlo simulation envelopes representing the spatial distribution of surviving trees under random mortality. We tested the statistical significance of the departure from our null model (random mortality) using the goodness-of-fit statistic developed by Loosmore and Ford (2006). Most previous studies determined significance using departure from simulation envelopes but this was found to inflate type I error rates (Loosmore and Ford 2006); thus we based our interpretation on goodness-of-fit statistics (although we present the simulation envelopes to facilitate comparison with earlier studies). We tested for significant departure from our null model for 5m distance classes (0-5, 5-10, 10-15, 15-20 and 20-25). Due to multiple tests at each distance class we used a Bonferroni corrected alpha level (five comparison, $\alpha = 0.01$). For each test, we ran 1521 simulations in order to constrain the uncertainty around the exact p value of the goodness-of-fit statistic between 0.005 and 0.015 (see Loosemore and Ford (2006) for details).

We present these results as the difference between the spatial distribution of the pre-mortality pattern $L_{\text{initial}}(r)$ and the post-mortality pattern $L_{\text{live}}(r)$ to emphasise the change in spatial pattern over time. Under random mortality $L_{\text{initial}}(r) - L_{\text{live}}(r) = 0$ whereas $L_{\text{initial}}(r) - L_{\text{live}}(r) > 0$ is an indication that there are fewer live trees around live trees in the current distribution compared to the initial pre-mortality distribution (live trees were becoming more uniformly distributed). On the other hand $L_{\text{initial}}(r) - L_{\text{live}}(r) < 0$ suggest that live trees are more frequent around live trees in the current distribution as compared to the initial distribution – an indication that mortality occurred in areas of lower tree density. We repeated this analysis for dominant/co-dominant stems in all plots to determine whether tree death of larger overstory trees was spatially random. All analyses of the stem mapped data were completed in R (R Development Core Team. 2011) using the “spatstat” package (Baddeley and Turner 2005).

3.3. Results

Composition, age structure and disturbance history

All plots were strongly dominated by *Pinus contorta* with later successional species increasing in importance over the study period, although the increase in later successional species was more important in the Whirlpool, Hector and Spray River plots (Table 3-1). The age structure of early successional species followed a bimodal distribution for the Athabasca, Sunwapta and Whirlpool plots (Figure 3-2). In the Athabasca plot, the disks sampled all had fire scars dating to 1889 (one disk had a second scar in 1859), in the Sunwapta plot eight of the cores sampled also had fire scars in 1889 and in the Whirlpool plot four cores had fire scars dated to 1836. Together this suggests that non stand-replacing fires were responsible for the second pulse of pine regeneration in all these stands (Figure 3-2). In the Hector and Spray River plots, pine establishment followed a single pulse of regeneration and occurred mainly within a decade after the last stand replacing disturbance (Figure 3-2). Late successional species established mainly 60-90 years after the last stand-replacing disturbance in the Athabasca, Sunwapta and Whirlpool plots although in the Whirlpool plot some establishment of these species occurred in the decades immediately following the stand-initiating disturbance. In the Hector and Spray River plots establishment of late successional species started immediately following the last stand-replacing fire and for the Hector plot the presence of surviving late successional stems in the NW corner of the plot likely contributed to the early return of these species (Figure 3-2).

In the Whirlpool plot, 53% of the disks and cores sampled from recently fallen trees (n=76) indicated a year of disturbance of 2009 and 77% indicated the disturbance was between 2009 and 2011; this suggests a major event in 2009 with some amount of subsequent mortality. However, only 21% and 9% of late and early successional stems, respectively, that were uprooted or snapped in 2012 still had needles or small twigs suggesting that most of the fallen trees were probably already dead when the windthrow occurred at this site. In the Sunwapta plot, 9 out of the 10 recently fallen trees that were cored fell in 2009 suggesting that recent windthrow at this site also occurred in 2009

Description of mortality

The Athabasca, Hector and Spray River plot all had initial *Pinus contorta* stem densities (all living and standing dead stems) of > 3000 stems/ha while the Sunwapta and Whirlpool plot had densities of 776 stems/ha and 1862 stems/ha respectively (Table 3-1). Over the study period, the density of living pines decreased in all plots although rates of mortality were higher in the Athabasca and Whirlpool plots where respectively 80 % and 73% of the pine stems that were alive in 1967 died by 2012. This is in contrast with the Sunwapta, Hector and Spray River plots where 23%, 26% and 48%, respectively, of the initial living pine stems died over the study period. However in the Sunwapta plot the percentage of initial stems that died is likely underestimated because some of the later-recruiting stems grew into the smallest size class sampled in this study between1989 and 2012 (Figure 3-3). The use of the permanent plots also allowed us to recognize that some of the standing dead stems of smaller size classes present in 1967 had decomposed beyond recognition by 2012, especially in the Athabasca, Whirlpool and Spray River plots (Figure 3-3). Mortality of later successional species was absent or minimal in all plots except Whirlpool which recently suffered extensive mortality, especially in larger size classes, due to the recent windthrow (Figure 3-1 & 3-4).

Throughout the study period, mortality of early successional species was mainly found in the lower diameter classes and this led to an increase in average diameter of living stems compared to living and dead stems (L+S & L+S+F) in all sampling periods (Figure 3-3). This also had the predicted effect of decreasing the skewness of the diameter distribution of living early successional species over time, except between 1989 and 2012 for the Sunwapta and Whirlpool plots (Figure 3-3). For the Sunwapta plot the ingrowth of pine stems into the smallest size class sampled increased the skewness of live stems while in the Whirlpool plot the diameter distribution of live stems was pretty close to normal in 1989 (skew = 0.21) and the subsequent mortality generated a left skew distribution of surviving stems by 2012 (skew = -0.33; Figure 3-3). In the last sampling period mortality in large size classes started to increase in all plots, although more so in the Whirlpool plot. The diameter distributions of late successional species were strongly right-skewed in all plots and this skewness increased over time as more stems of late successional species grew into the smaller size classes (Figure 3-4).

In all plots, suppressed pine trees were more or less 5m shorter than the average dominant/codominant pines of the canopy except in the Sunwapta site where they were almost 9m shorter (Table 3-2). Pine saplings were another 3-5m shorter than the suppressed pines, except in Sunwapta where they were on average 10m shorter; in the Whirlpool plot none were cored (all < 5cm DBH) and thus heights were not recorded (Table 3-2). In all plots suppressed canopy trees and saplings (< 9cm DBH) of early successional species suffered proportionally greater mortality compared to dominant trees. In the Athabasca, Hector and Spray River plots saplings suffered proportionally more mortality than suppressed trees but at Sunwapta these two experienced similar mortality and at Whirlpool saplings had lower mortality than suppressed trees (Table 3-2). Late successional species in all canopy positions suffered very low mortality except in the Whirlpool plot where 91% and 68% of dominant/co-dominant and suppressed stems, respectively, died mainly due to the recent windthrow event in this plot.

Spatial analyses

The Morisita index analysis showed that in all plots the spatial distribution of living stems was moving towards uniformity over time (from clustered to less clustered or random) although this trend was stronger at smaller scales (Figure 3-5). For the Athabasca, Sunwapta and Spray River plots the spatial distribution of living pines moved from a clustered distribution in 1967 to a random distribution in 2012 at small scales. In the Hector plot the spatial distribution of living pines was still clustered in 2012 but less so than in 1967. Finally in the oldest plot, Whirlpool, the spatial distribution of living pines was already significantly more uniform than random at small scales in 1967 and it became even more uniform over time.

Our random mortality analysis using the 2012 stem mapped data of living and dead stems supports the Morisita index analysis. In all plots, $L(r)$ results suggest that the pattern of all current living trees was more uniform than if random mortality had occurred within the initial tree population (Figure 3-6); however the scale at which we found a significant departure from our null model of random mortality varied between plots. With *g*(*r*) we found similar results for three of our plots (Athabasca, Hector, and Spray River) although with this analysis significant departure from our null model of random mortality was only found for the smaller distances class of 0-5m. These results demonstrate the cumulative nature of *L*(*r*) compared to *g*(*r*). For the Sunwapta and Whirlpool plots the *g*(*r*) results suggest that mortality was random. However for these two plots, when trees recently affected by windthrow were considered as still alive (to remove the mortality effect of this last recent disturbance), and when ingrowth in the Sunwapta plot was accounted for by removing living trees with a DBH of 3cm or less, we found that mortality differed significantly from random for both *L*(*r*) and *g*(*r*) (Figure 3-7). Looking only at the dominant trees, both *L*(*r*) and *g*(*r*) results showed that mortality was random at all scales in the Athabasca, Sunwapta and Whirlpool plots (Figure 3-8). For dominant trees at the Hector and Spray River plots, both the *L*(*r*) and *g*(*r*) results suggested that mortality was random at smaller scales but significantly more uniform than random at larger scales; this resulted in the surviving dominant trees being more clustered in 2012 compared to the initial population (Figure 3-8).

3.4. Discussion

Our study has shown that, contrary to our initial hypothesis, the mature stands studied were still going through the self-thinning/density-dependent mortality stage of succession. The diameter distribution of individuals changed from an initially right-skewed distribution towards normality as a result of mortality of smaller diameter stems and individuals of lower canopy positions were proportionally more affected by mortality indicating that competition for light was important. Also, when compared to the pre-mortality pattern, surviving stems had an increasingly more uniform spatial distribution suggesting the importance of density-dependent mortality. Mortality of larger dominant canopy trees increased over the study period and mortality of dominant stems was a random process suggesting that density-independent processes might become more important following the self-thinning stage of stand development.

By testing the random mortality hypothesis using the random labeling approach we could better evaluate whether mortality was random or not than by using the common approach of looking at the spatial distribution of living and dead trees separately (Antos and Parish 2002a, Castagneri et al. 2010). The results from this study provide evidence that the self-thinning phase can persist for many decades, in this case for more than 140 years following stand establishment. Our results contrast with those of Kenkel et al (1997) who found that the self-thinning phase in forests of a similar species *Pinus banksiana* was mostly completed within 60 years of stand establishment. These contrasting results can be explained by either prolonged post-fire establishment periods (Athabasca, Sunwapta and Whirlpool) or due to slow growth which delays the onset of competition (Hector and Spray River). In our case the prolonged establishment periods were associated with surface fires occurring relatively early on following the stand-initiating fire. This could also explain why density-dependent mortality was not found in a 39-year-old *Pseudotsuga menziesii* forest (Getzin et al. 2006) since these ecosystems are also prone to extended establishment periods (Peet and Christensen 1987). Delayed establishment could also help explain the observation of density-dependent mortality in

250 year-old *Pseudotsuga menziesii* forest (He and Duncan 2000) while in much older forests (at least 500 years) mortality of this species was observed to be a random process (Lutz et al. 2014). The fact that three of our sites had bimodal age structures driven by surface fires also echo's findings from Kuuluvainen and Aakala (2011) who suggested that a cohort like structure due to low intensity fires might be more common than traditionally thought. These results also demonstrate how density-independent processes in the early stage of stand development can have long lasting effects on stand development (Lutz and Halpern 2006, Donato et al. 2012).

For the Hector and Spray River plots which had relatively short periods of initial establishment, the moist conditions and slower growing conditions at these higher elevation sites might have delayed the onset of competition, thus extending the self-thinning stage for longer periods. In the dry site studied by Kenkel et al (1997) establishment also occurred quickly after a stand replacing fire, but competition for resources most likely became a limiting factor earlier on. In moist *Picea mariana* forests of the boreal forest the self-thinning stage can be absent altogether due to slow establishment and slow growth (Harper et al. 2005). This interpretation is further supported by studies in high elevation *Picea abies* forest who found that the self-thinning phase extended beyond 150-180 years following stand establishment (Castagneri et al. 2010, Svoboda et al. 2010). However, *Picea abies* is a much more shade tolerant and slower growing species than *Pinus contorta* and thus the extended self-thinning stage in these forests is less surprising. Although extended self-thinning stages have been observed previously in systems affected by extended establishment periods (He and Duncan 2000), this study is the first to demonstrate that this phenomenon can also occur in early successional shade intolerant species even when delayed establishment is not a contributing factor.

Both the Sunwapta and Whirlpool plot had confounding factors that initially hindered our ability to detect a strong effect of density-dependent mortality. Early in the study period, mortality was constrained to smaller size classes suggesting that mortality was mainly driven by competition, while the recent windthrow in both plots mainly affected larger pines. In the Sunwapta plot, the use of permanent plots allowed us to detect in-growth of smaller stems between the last two sampling periods. This influenced the skewness of the diameter distribution in 2012 and since most of this recent in-growth was clustered in gaps it prevented us from detecting (with $g(r)$) the more uniform pattern of surviving stems. When we accounted for the recent windthrow disturbances (for both Sunwapta and Whirlpool) and the in-growth (for Sunwapta) we found that surviving stems were more uniformly distributed at small scales (results for both $L(r)$ and $g(r)$). These results emphasize the importance in accounting for in-growth when using random labeling approaches to analysis and support previous suggestions that the presence of density-independent mortality processes in later successional stages can mask density-dependent mortality effects (Szwagrzyk and Czerwczak 1993, Aakala et al. 2012). Although, these previous authors suggested that the presence of density-independent processes can mask an underlying pattern of density-dependent mortality and thus explain observations of random mortality in old-growth forests, ours is the first study to explicitly demonstrate this phenomenon. The increasing mortality of larger *Pinus contorta* stems over the study period in all plots and the fact that mortality of dominant trees in all plots was a random process also supports this interpretation. Later successional species were also becoming more abundant over the study period suggesting these stands were entering the canopy transition stage of succession (Chen and Popadiouk 2002). Our finding that density-independent processes were increasing in importance in some of our plots thus supports the notion that these processes increase in importance as stands approach the canopy transition stage of succession (Peet and Christensen 1987). Still it was surprising that density-dependent mortality still seemed to be an important process in these stands considering their age.

The disappearance over the study period of standing dead stems of smaller size classes present in 1967 might have also influenced our results and potentially contributed to the lack of significant results with *g*(*r*) in Sunwapta and Whirlpool. These smaller dead stems likely died due to competitive exclusion; if they had been included as part of the "actual" initial distribution of trees the surviving stems would have appeared even more uniform in comparison. The fact that in most plots we still found convincing evidence of density-dependent mortality even with the disappearance of some smaller dead stems (especially in the Athabasca and Spray River plot) demonstrates the importance of competition induced mortality as a process driving mortality in these mature stands.

Recent increases in tree mortality in temperate forests have been attributed to drought associated with increased temperatures (van Mantgem and Stephenson 2007, van Mantgem et al. 2009, Allen et al. 2010, Das et al. 2013). However this process is unlikely to be important in our plots as trees adapted to drier environments have been found to be better adapter to lower water availability (Bréda et al. 2006, Choat et al. 2012). Furthermore, Thorpe and Daniels (2012) found that mortality in *Pinus contorta* forests was a function of tree size and competition environment with no effects of increasing temperature over the last 50 years and Bigler et al. (2007) found that *Pinus contorta* mortality was unaffected by droughts. Finally another study found that competition was the main factor driving mortality of the closely related *Pinus banksiana* (Chen et al. 2008). Since *Pinus contorta* is highly shade intolerant (Burns and Honkala 1990a) and our finding that stems of lower canopy position were more likely to die suggests that competition for light likely contributed to the observed mortality in our plots over the last 45 years although below ground competition could also have contributed to mortality.

Our finding that density-dependent mortality still occurs in mature stands of this shade-intolerant, early-successional, fire-adapted species demonstrate that the absence of thinning treatments in such stands can reduce stand yields for an extended period of time. Thinning in forests of this type is most often recommended to be made in relatively young stands with high stem densities (Tappeiner et al. 1997). Although we agree that the benefits of thinning treatments are greatest when applied earlier in stand development, our results suggest that for mature stands with delayed self-thinning stages (either due to a slow establishment phase or slow growing conditions) thinning later in stand development might still pre-empt some mortality. Thinning treatments in mature stands could also be used to accelerate the successional development of the stands towards old-growth forest structure as well as reduce fuel loads and thus help prevent higher intensity fires (Sturtevant et al. 2004). Prescribed surfaces fires have also been used to meet these objectives (Yu et al. 2009) and are often used in landscapes where timber management is not permitted such as conservation areas (Ryan et al. 2013). Our results suggest that the use of prescribed surface fires in relatively young stands could mimic the natural processes of prolonged establishment periods and better reflect the range of conditions found in natural systems (Donato et al. 2012). In turn this would increase structural diversity early in stand development which could have biodiversity benefits (Hansen et al. 1991).

3.5. Conclusion

The combined use of stem mapped data, permanent sampling plots and dendrochronological analyses allowed us to account for confounding factors such as ingrowth and other disturbances, thus allowing us to better untangle the factors driving mortality as well as develop a in depth understanding of the stand dynamics in the studied plots. Our study demonstrates that the self-thinning stage in *Pinus contorta* forests can last for over 140 years (due to delayed establishment periods or slow growing condition) after which evidence of canopy transition starts to become apparent. This study also contributes to the growing body of literature suggesting that traditional models of stand development might be overly simplistic. For example, a finding that arose from this research is that a stochastic (density independent) event such as a surface fire can occur early in succession and have long term impacts on stand development such as prolonging the self-thinning stage of stand development. Future monitoring of these plots will allow us to assess whether or not density-dependent mortality is still important in the following stages of stand development or if mortality now becomes driven more by density-independent processes, as expected.

3.6. Acknowledgement

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Table 3-1. Number of living stems > 2.54 cm in DBH for each species, the total number of living stems and the number of standing snags (and fallen logs in 2012) in each plot for each sampling period. Plot locations (Longitude/ Latitude) are presented in brackets beside plot names while site index (SI, height at breast height age 50) are presented for Pinus contorta.

	1967	1989	2012
Athabasca (117° 58'/ 52° 45')			
Pinus contorta (SI-11.1) ‡	2779	1541	566
Picea mariana	4	6	16
Picea engelmannii	1	6	72
Abies lasiocarpa	0	0	12
Standing snags/logs†	1210	662	652/637
Sunwapta (117° 42'/52° 33')			
Pinus contorta (SI-19.0)	740	582	572
Picea mariana	0	0	2
Picea Engelmannii	0	2	5
Abies lasiocarpa	0	1	12
Standing snags/logs	36	58	130/84
Whirlpool (117° 55'/52° 42')			
Pinus contorta (SI-17.4)	1078	641	283
Picea mariana	260	559	923
Picea Engelmannii	5	14	27
Abies lasiocarpa	0	14	53
Populus tremuloides	18	10	5
Standing snags/logs	501	327	314/676
Hector (116° 15'/51° 30')			
Pinus contorta (SI-14.1)	3190	2835	2358
Picea Engelmannii	194	536	751
Abies lasiocarpa	58	200	338
Standing snags/logs	153	389	703/367
Spray River (115° 23'/50° 54')			
Pinus contorta (SI-16.8)	3636	-	1886
Picea Engelmannii	251	-	537
Abies lasiocarpa	1	-	31
Standing snags/logs	920	-	915/579

Note: The Spray River plot was only sampled in 1967 and 2012.

† Fallen dead trees where only counted in the last measurement period. Some of these dead trees were classified as remnants from the previous stand and were removed from spatial analyses (see Methods for details).
‡ Calculated using the height and age of the five largest trees in each plot and following the equation presented in Shongming et al. (2009). Ages at coring height were however converted to age at breast height by removing 10 years.

Table 3-2. Mean diameter at 1.3 m height (DBH) and height (standard deviation in parentheses), the total number of stems (Nbr stems) and mortality (% dead) in 2012 for each canopy position for early and late successional species[†].

	Early successional[†]				Late successional[†]			
	DBH	Height	Nbr stems	% dead	DBH	Height	Nbr stems	% dead
Athabasca								
Dominant	20.2 (5.1)	14.9 (2.8)	304	36.8	24.5 (5.0)	18.3 (2.1)	3	0
Suppressed	12.5 (2.3)	9.4 (1.9)	691	62.7	11.0 (2.4)	7.9 (1.7)	8	12.5
Sapling	6.3 (1.9)	5.8 (1.8)	856	86.4	4.3 (1.6)	5.2 (1.3)	80	2.5
Sunwapta								
Dominant	30.2 (5.4)	25.5 (3.0)	297	10.1	--	--	--	--
Suppressed	16.4 (4.4)	16.7 (3.5)	146	37.0	10.2 (0.2)	8.1 (0.0)	2	0
Sapling	4.1 (1.6)	6.4 (2.2)	343	37.9	3.8 (1.2)	5.5 (0.3)	17	0
Whirlpool								
Dominant	26.0 (4.6)	22.1 (3.1)	441	50.6	26.2 (7.3)	21.2 (1.8)	44	90.9
Suppressed	18.2 (3.2)	16.7 (2.1)	477	87.6	14.3 (4.0)	11.2 (3.1)	207	67.6
Sapling	3.3 (0.6)	--	40	80.0	4.3 (1.5)	5.7 (1.3)	1048	12.5
Hector								
Dominant	19.0	18.8	1280	6.0	23.0	19.9	13	0

	(3.4)	(1.8)			(4.9)	(2.2)		
Suppressed	12.2	14.4	1036	19.0	11.7	11.0	152	2.0
	(2.0)	(2.2)			(2.2)	(2.5)		
Sapling	6.9	9.9	1027	69.3	4.7	6.2	933	0.6
	(1.6)	(2.8)			(1.7)	(1.4)		
Spray River								
Dominant	19.4	18.9	1194	3.9	19.1	18.5	37	0
	(3.5)	(1.7)			(3.0)	(1.9)		
Suppressed	12.3	14.5	1100	41.8	12.9	10.4	187	0.5
	(1.9)	(1.7)			(3.2)	(2.5)		
Sapling	7.8	11.4	977	90.0	5.6	5.6	351	1.7
	(1.1)	(2.0)			(1.8)	(1.6)		

†Late successional species include *Picea mariana*, *Picea engelmannii* and *Abies lasiocarpa* while early successional species include *Pinus contorta* and *Populus tremuloides*

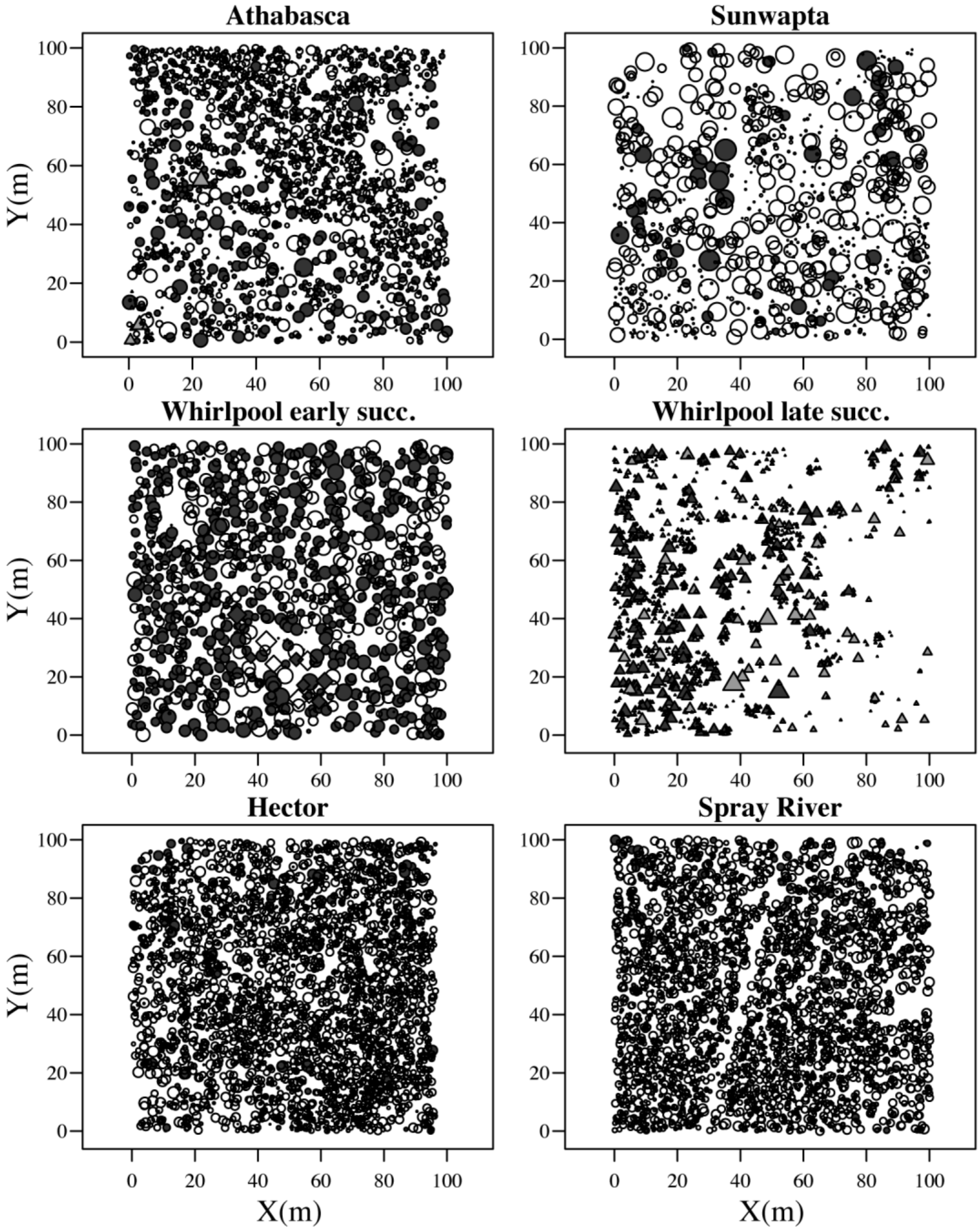

Figure 3-1. Map of stems over 2.54cm diameter at 1.3 m height (DBH) in each plot. White circles and diamonds represent live stems of *Pinus contorta* and *Populus tremuloides*, respectively, while light grey triangles represent live late successional species (*Abies lasiocarpa*, *Picea mariana* and *Picea engelmannii*). Symbol sizes are proportional to the DBH. Dark grey symbols represent dead stems. Early and late successional species are presented separately for Whirlpool to show the extent of mortality at this site while late successional species are not presented for Hector and Spray River because densities of early successional species were too high.

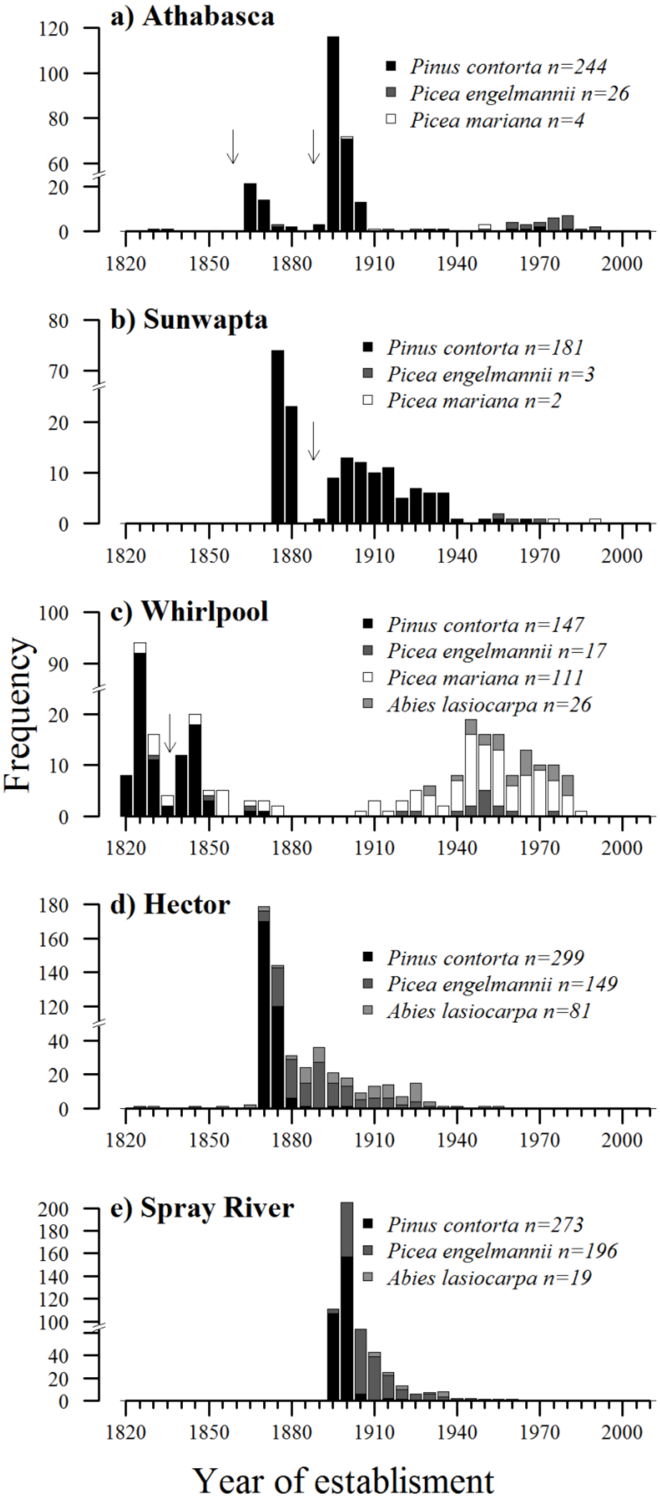

Figure 3-2. Year of establishment for trees cored in each plot. Arrows represent years for which evidence of fire was present on disk or core samples; the number of samples cored for each species in each plot is also presented (n).

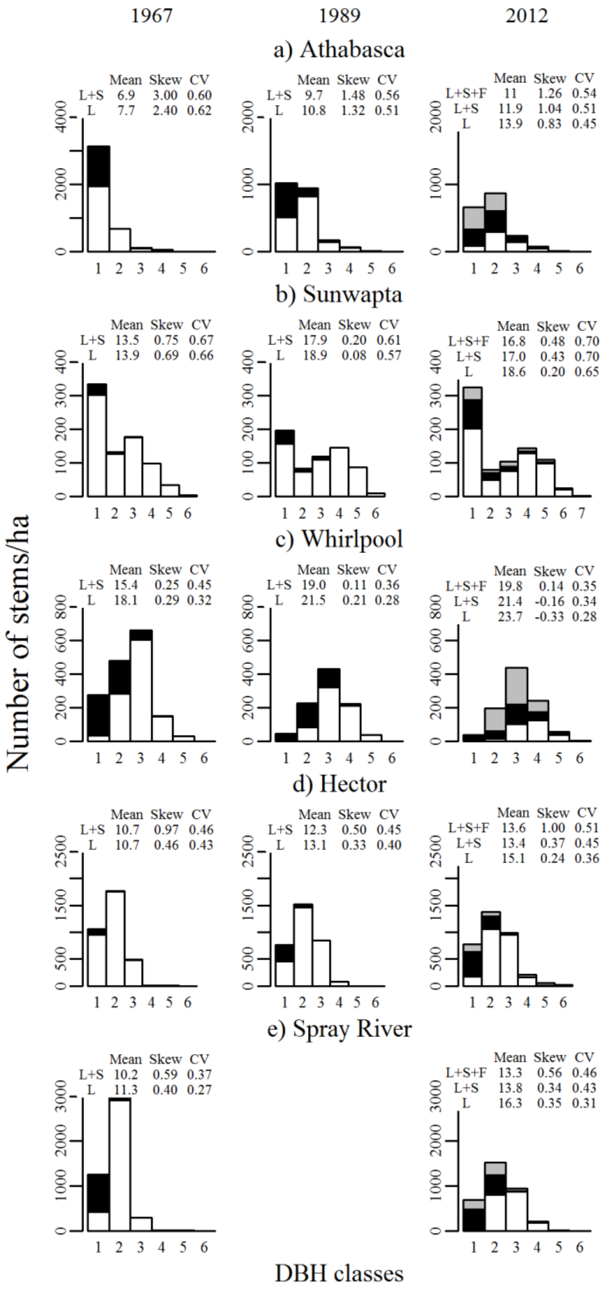

Figure 3-3. Diameter distribution of early successional species (all *Pinus contorta* except for 11 stems of *Populus tremuloides* in Whirlpool) in all plots at each sampling period. White, black and grey bars represent live, standing dead and fallen logs, respectively. Mean DBH (Mean), skewness of the distribution (Skew) and coefficient of variation of DBH (CV) are presented for live stems (L) and for live and standing dead stems combined (L+S) for each plot and sampling period. In 2012 these statistics were also calculated for live, standing dead and fallen logs combined (L+S+F). DBH classes

represent: 1 = 2.54 to 7.62cm, 2 = 7.63 to 15.24cm, 3 = 15.25 to 22.86cm, 4= 22.87 to 30.48cm, 5 = 30.49 to 38.1cm, 6 = 38.11 to 45.72cm, 7 = 45.73 to 53.34cm.

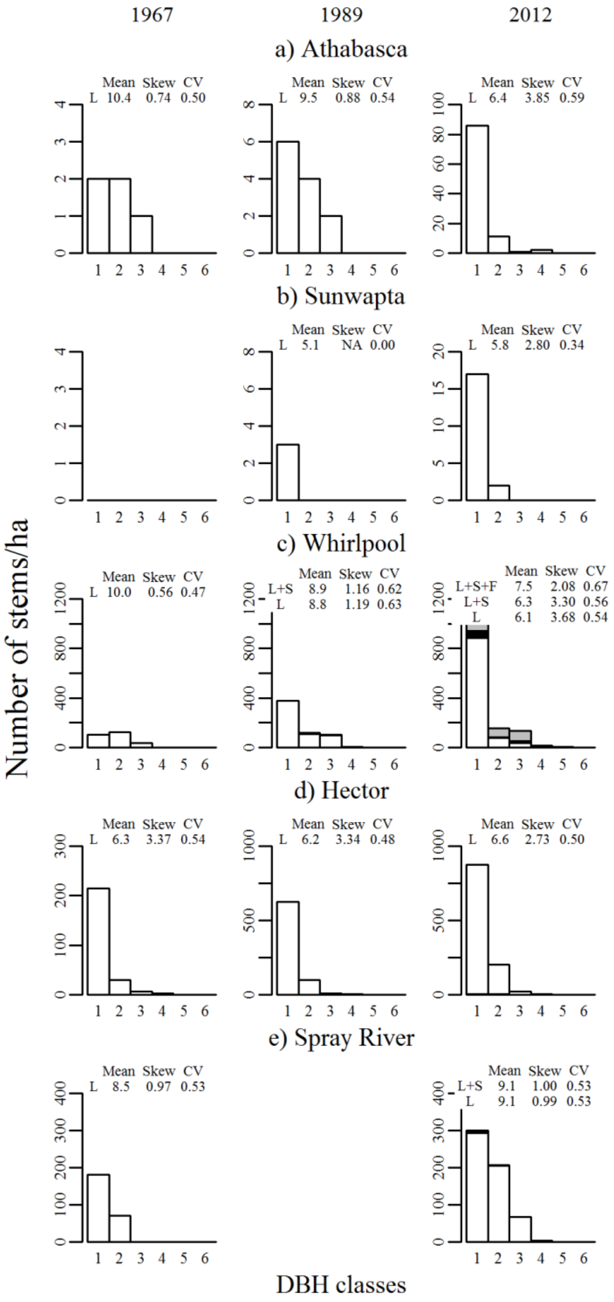

Figure 3-4. Diameter distribution of late successional species (*Picea mariana*, *Picea engelmannii* and *Abies lasiocarpa*) in all plots at each sampling period. See Figure 3-3 for details.

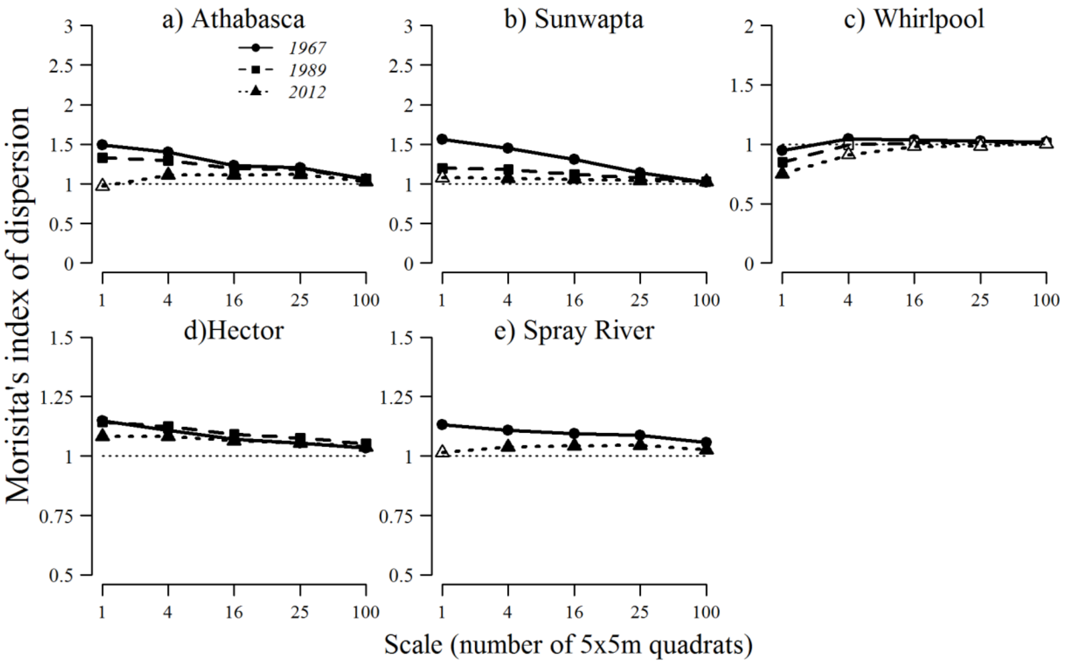

Figure 3-5. Values of Morisita's index of dispersion at different scales for live *Pinus contorta* in each of the five study plots and for each sampling period. Values significantly greater or lower than 1 (black symbols) represent clustered and over dispersed spatial patterns, respectively, as compared to complete spatial randomness.

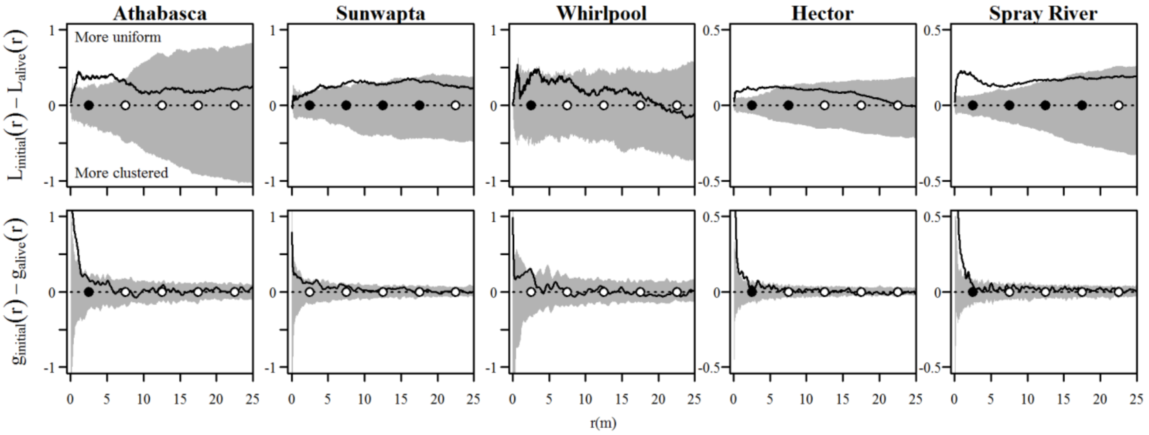

Figure 3-6. Change in spatial pattern of *Pinus contorta* stems over 2.54cm DBH between initial and surviving stems as a function of distance r compared to the null model of random mortality quantified with both the L- and g- functions. Significant deviation from our null model was assessed using goodness-of-fit statistics (see methods) and is shown with black circles along the x-axis on each graph. Critical bands from the Monte Carlo simulation are shaded and are presented for comparison with previous studies.

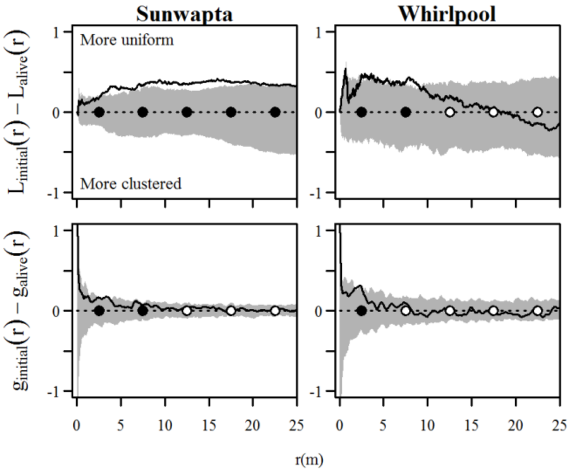

Figure 3-7. Change in spatial pattern of *Pinus contorta* stems over 2.54cm DBH between initial and surviving stems as a function of distance r in the Sunwapta and Whirlpool plot once recent mortality was accounted for (i.e. trees that had died recently were considered to be still alive) and ingrowth was removed in the Sunwapta plot (remove living stems ≤ 3cm DBH). Interpretation is as in Figure 3-6.

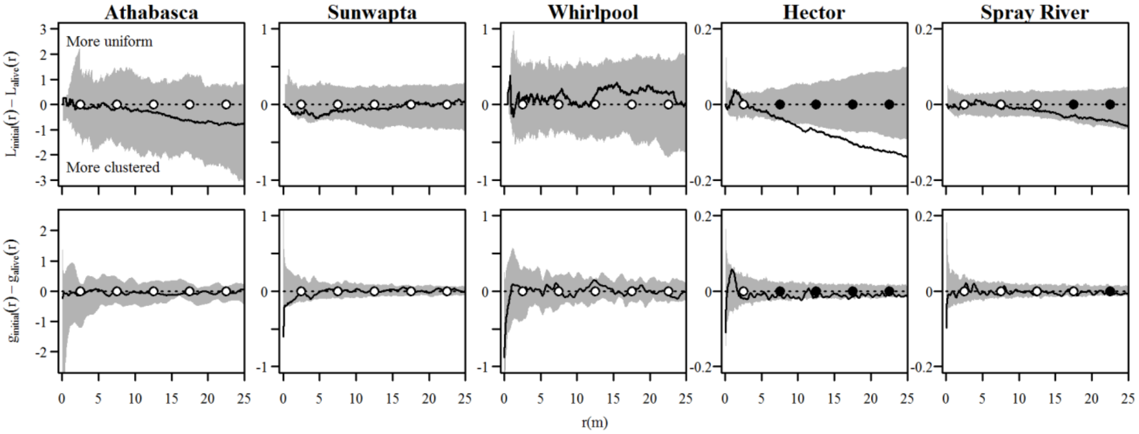

Figure 3-8. Change in spatial pattern of dominant/co-dominant *Pinus contorta* between initial and surviving stems as a function of distance r in all plots compared to the null model of random mortality quantified with both the L- and g- functions. Interpretation is as in Figure 3-6.

Chapter 4. Factors influencing tree regeneration and survival following the initial establishment phase of stand development in lodgepole pine forests

Abstract - There are a variety of possible successional pathways in *Pinus contorta* forests including some in which forests reach the canopy break-up stage, at which point they could be self-perpetuating or might transition to other more shade tolerant species such as *Picea engelmannii* and *Abies lasiocarpa*. In landscapes dominated by *Pinus contorta* forests, disturbance regimes are changing (less frequent fire, partial disturbances becoming more common) and this will influence which successional pathways are occurring. The objective of this study was to describe the patterns of post-disturbance (PD) regeneration following the last stand replacing fire as well as the patterns of subsequent post-establishment (PE) regeneration in these forests and determine factors driving these patterns. We address this objective through the use of five long-term permanent plots, dendrochronological stand reconstruction and detailed spatial analysis of stem mapped data. Establishment of shade intolerant species (mostly *Pinus contorta* but some *Populus tremuloides*) mainly occurred within 20 years post-fire but important later (i.e., PE) recruitment of these species was observed in the drier plots, primarily in gaps in these stands which had more open canopies. In one of the plots, establishment of shade intolerant PE regeneration seemed to also be limited by low moisture while in two other plots, drier conditions seemed to benefit shade intolerant PE regeneration by reducing the cover of understory species such as shrubs and mosses. Shade tolerant species started establishing soon after the most recent stand-initiating fire in moister plots while in the drier plots their establishment was mostly delayed, presumably because of moisture limitation and the lack of shaded microsites. The presence of surface fires, which occurred shortly after the stand-initiating fire, in the drier plots also would have contributed to these delays in establishment. Shade tolerant PE regeneration was clustered around shade tolerant trees that had established immediately post-disturbance; this suggests the latter served as seed sources and perhaps created favorable microsites for establishment. Shade tolerant PE regeneration was also associated with moist

microsites in all plots, suggesting that moisture is important for successful establishment and survival of these species. Although initial studies in these stands had suggested some of the stands could potentially be self-perpetuating *Pinus contorta* forest, our results suggest that all plots studied will likely transition towards shade tolerant species but that the rate of this transition will be slower in the drier sites compared to the moister sites.

4.1. Introduction

Understanding the changes in forest structure and composition over time following stand initiating disturbances has been of interest to forest ecologists for a long time. There has been considerable debate regarding patterns, processes and possible end points (climax communities) of succession but it is now widely accepted that multiple successional pathways can occur for one forest type and these pathways can lead to different end point communities (Cattelino et al. 1979, Pickett et al. 1987, Bergeron et al. 2014). Instead of only describing successional transition of species, process-based approaches have considerably improved our understanding of succession by providing insight on the processes responsible for such transitions (Bergeron 2000). The intensity and frequency of stand-initiating disturbances is the first factor to consider as it influences the establishment of the initial post-disturbance (PD) cohort which in turn influences subsequent post-establishment (PE) regeneration (Stewart 1986). Following stand initiating disturbances and throughout stand development, species are filtered by their ecological characteristics such as dispersal abilities, regeneration niche, shade tolerance, competitive ability and longevity (Knapp and Smith 1982, Johnson and Fryer 1989, Galipeau et al. 1997, Wright et al. 1998). Understanding the factors influencing PE regeneration is key to our understanding of stand structure and composition in later successional stages.

Many landscapes historically dominated by frequent stand replacing fires have experienced lower fire frequencies during the 20th century, either due to natural or anthropogenic causes (Anderson et al. 1987, Masters 1990, Johnson and Larsen 1991, Van Wagner et al. 2006). In these landscapes, this has led to large tracts of mature forest experiencing canopy decline and successional transition (Rhemtulla et al. 2002), processes that were previously uncommon due to the high frequency of stand replacing disturbances (Johnson and Fryer 1989). In landscapes with lower frequencies of stand replacing fires, secondary disturbances such as insect outbreaks (Anderson et al. 1987, Veblen et al. 1994, Burton 2010, Jenkins et al. 2014) or windthrow disturbances (Veblen et al. 1991) become increasingly important. *Pinus contorta* is a fire adapted (serotinous cones), shade intolerant, commercially important species which as a broad distribution in western North America (Burns and Honkala 1990a). *Pinus contorta* forests have experienced such reductions in fire frequencies which have allowed successional transition to occur on large portions of the landscape (Barrett et al. 1991, Van Wagner et al. 2006). A process-based approach to factors controlling post-establishment regeneration is key to understanding possible future successional pathways/outcomes in these forests.

The classical successional pathway in *Pinus contorta* forests starts with rapid post-disturbance pine establishment, usually within the first two decades following fire (Moir 1969, Day 1972, Johnson and Fryer 1989, Antos and Parish 2002a, Clark et al. 2003). The abundant seed supply of *Pinus contorta* from serotinous cones and rapid growth rates enable this species to dominate the canopy of initial post-fire stands (Burns and Honkala 1990a). Shade tolerant species such as *Picea engelmannii* and *Abies* *lasiocarpa* can establish immediately following fire (albeit at lower levels than pine) if seed sources are available but, they might also continue to establish throughout succession due to their ability to establish and survive in the understory (Day 1972, Johnson and Fryer 1989, Antos and Parish 2002a, Clark et al. 2003). As the initial *Pinus contorta* canopy declines, it is usually replaced by *Picea engelmannii* which can grow faster in the understory and has a longer life span than *Abies lasiocarpa* (Oosting and Reed 1952, Moss 1955, Antos et al. 2000, Antos and Parish 2002b). With on-going regeneration, *Abies lasiocarpa* can increase in importance over time leading to an all-aged sub-canopy tree layer including coexistence of both shade tolerant species (Day 1972, Antos and Parish 2002a). This is not the only possible successional pathway for lodgepole pine forest, however. Some studies, have found evidence of self-perpetuating *Pinus contorta* stands in various part of its range (Whipple and Dix 1979, Despain 1983, Parker 1986, Stuart et al. 1989). These types of stands usually have low levels of shade tolerant regeneration and this is usually attributed to a lack of seed sources or unfavourable site conditions, such as dry soils or poor nutrient regimes (Whipple and Dix 1979, Despain 1983, Stuart et al. 1989). Within these apparently self-perpetuating stands, *Pinus contorta* regeneration has been reported to be limited by light, thus occurring primarily in gaps (Parker 1986) or under sparse overstories (Despain 1983), or by soil moisture (Stuart et al. 1989). Overall mechanisms driving these different successional pathways in *Pinus contorta* forests are still not well understood.

Our objective was to determine the processes driving regeneration at the stand initiation (post-disturbance PD) stage and throughout stand development (post-establishment PE) in *Pinus contorta* forests in order to better understand how changes in disturbance regimes might alter successional dynamics in temperate coniferous forest ecosystems. Most of our understanding regarding successional pathways comes from chronosequence studies which, although useful, have numerous limitations especially for evaluating the processes or mechanism driving the observed patterns (Johnson and Miyanishi 2008). We were fortunate in having available long term, spatially-explicit, permanent plots, in which we used dendrochronology to reconstruct timing of establishment and point pattern analyses of stem mapped data to test hypotheses about the processes driving PD and PE regeneration. Our first hypothesis was that most *Pinus contorta* establishment occurred within 20 years post-fire while shade tolerant species started establishing quickly following fires if seed sources were available but continued recruiting throughout stand development. Our second hypothesis was that the composition and spatial distribution of the PD cohorts will play an important role in the composition and spatial distribution of PE regeneration. Evidence in support of this hypothesis would be: 1) significant spatial segregation between shade intolerant PE regeneration and trees of the PD cohort; 2) clustering between shade tolerant regeneration and trees of the PD cohort; and 3) higher survival of shade intolerant and tolerant PE regeneration in their preferred microhabitats (open and shade respectively). Finally the third hypothesis tested was that edaphic factors also play an important role in determining the composition and density of PE regeneration, especially in moisture limited environments.

4.2. Methods

Study area

This study was conducted in five mature *Pinus contorta* dominated forests in Banff and Jasper National Parks, Canada. These forests were selected following an extensive survey of *Pinus contorta* dominated forests in these parks and were chosen to represent a range of forest types as well as to cover a wide range of moisture/elevation (Hnatiuk 1969, La Roi and Hnatiuk 1980). The initial moisture class of the plots (Hnatiuk 1969) which was later confirmed by a study of the understory communities in these plots (Chapter 2) places the Athabasca and Sunwapta plots respectively on xeric and mesic sites while the Hector and Spray River plots were on moist sites. The Whirlpool plot had a striking moisture gradient within the plot itself with a dry upper terrace (similar to the Athabasca plot) on the eastern part of the plot and moist lower terrace on the western part of the plot (Chapter 2). In 1967, a 1 ha plot configured as a 20x20 grid of 5x5m contiguous quadrats was established at each forest site (i.e., a total of 400 quadrats per site) and permanently marked with railway spikes placed every 5 m around the plot boundary and every 20m within the plot. Relocation of the railway spikes using a metal detector allowed for a precise repeated measurement of the same quadrats in 1989 and 2012. In 1967, the Athabasca, Sunwapta, Whirlpool, Hector and Spray River plots were 101, 91, 141, 95 and 66 years old, respectively. For a more detailed description of the plots see Chapter 2. Between 1971 and 2000 the weather stations closest to the low (Athabasca) and high (Hector) elevation plots recorded mean annual temperatures of 3.3° and -0.3° and mean annual precipitation of 398mm and 569mm, respectively (Canadian Climate Normals). However, the environmental conditions at each of our sites might vary from these weather stations as the geographical location in these mountains ranges can greatly influence precipitation and temperature.

Data collection

In 1967 and 1989, live stems and standing snags were counted by species and size classes in each quadrat. Stems < 30 cm in height were classified as seedlings while stems >30cm in height but with a diameter at breast height (DBH) < 2.54 cm diameter (1 inch, as used in the 1967 sampling) were classified as “transgressives”. Stems with a DBH ≥ 2.54 cm were placed in seven size classes each spanning 7.62 cm DBH (3 inches) (Hnatiuk 1969). In 2012, seedlings and “transgressives” were further classified as layers when they were connected with the parent tree and at least one foot of the branch was buried underground. This was not done for *Picea mariana* at the Whirlpool plot because the recent blowdown combined with the large quantities of *Picea mariana* regeneration made it impossible to separate layers from seedlings with confidence. In 2012 all dead and live stems were stem-mapped, identified to species and DBH was recorded on stems taller than 1.3m. Stems over 9cm DBH were classified as dominant/codominant or suppressed based on their position in the canopy (stems 3m below the dominant canopy were considered suppressed) and stems less than 9cm DBH were classified as saplings. Signs such as fire scars or char on the stems were also noted to help identify residuals from the previous stand replacing disturbance (these stems were not included in the analyses).

A comprehensive dendrochronological sampling was conducted within each plot to determine timing of establishment of trees over 5cm DBH as well as determine the timing of post-disturbance establishment. In 2012 one living stem over 5cm DBH of each species and each canopy position (dominant/codominant, suppressed, sapling < 9cm

DBH) was randomly selected in each of 100 10 x10 m subplots per plot. Two perpendicular cores were taken on each stem at a height of 30cm except for stems ≤ 6cm DBH which were cored once. For the Athabasca plot, disks from two snags with fire scars were collected on each side just outside of the plot (total of eight disks with fire scars) to date the fires. All cores plus the disks with fire scars were scanned with an Epson V750 Pro at a resolution between 2400-4800 dpi (depending on ring width) and rings were measured on the images using the CooRecorder software (Larsson 2008b). The CDendro software (Larsson 2008a) was then used to cross-date samples using the average plot chronology to find measurement mistakes or missing rings and to determine years with fire scars when they were present on samples. For more details on the procedures used to estimate establishment when the pith was not present on core samples see Chapter 3. To determine the timing of post-establishment regeneration while preserving the integrity of the permanent plots we sampled along four 100m transects 25m away and parallel to each plot boundary. Five stems < 5cm DBH of each species and height class (< 30cm, 31cm-1m, 1-2m, 2-4m) were destructively sampled from each transect by taking disks at the base and also at 30cm to estimate the potential number of rings missing at coring height in the sampling of post-disturbance regeneration described above. The number of rings on these disks was counted on two different rays with a special attention to incomplete rings.

Data analyses

Stand structure and composition ─ Establishment dates from dendrochronoloical samples allowed us to reconstruct the age structure of each plot and separate individuals into either the post-disturbance (PD) or the post-establishment (PE) cohort. Shade intolerant species (*Pinus contorta*, *Populus tremuloides*) and shade tolerant species (*Picea mariana*, *Picea engelmannii*, *Abies lasiocarpa*) were considered part of the post-disturbance cohort (hereafter referred to as "PD trees") if the estimated year of establishment was within 20 or 30 years of the last fire, respectively. An extra 10 years was added for shade tolerant species due to their slower growth compared to the shade intolerant species thus better accounting for the likely underestimation of the year of establishment using cores at 30cm. Individuals establishing later than the post-disturbance period were considered as post-establishment regeneration (hereafter referred to as "PE regeneration"). The diameter distribution for each species was determined for each sampling period to provide information about stand composition as well as to support the dendrochronological results. For these and later analyses, care was taken not to include remnant stems that most likely died during the last stand replacing disturbance such as dead stems with char and/or with a DBH substantially greater than any living trees in the plot. Such remnant trees were only found in the higher elevation plots (82 in Hector and 20 in Spray River), likely because decay processes are slower at higher elevations (Kueppers et al. 2004). Finally in the Spray River plots some trees had been logged and these were also excluded from our analyses (n=84).

Spatial analyses — To determine the influence of PD trees (live and dead) on PE regeneration we examined the spatial relationship between these two cohorts. This was done by means of point patterns analysis using the commonly used L-function *L*(*r*), which is a square root transformation of Ripley's K-function that stabilizes its variance (Ripley 1977). However the K-function and its transformation *L*(*r*) are cumulative, meaning that clustering at short distances can influence the value of the statistic at larger scales (Condit et al. 2000, Perry et al. 2006). Thus we complemented $L(r)$ with the pair correlation function $g(r)$ (Stoyan and Stoyan 1994) which is non-cumulative and thus can more accurately determine the scale at which the deviance from the null model occurs (Wiegand and Moloney 2004, Perry et al. 2006). All subsequent analyses were conducted with both $L(r)$ and $g(r)$ but we refer only to $g(r)$ in the following paragraphs for simplicity as interpretations are the same for both functions.

We completed the following analyses separately for shade intolerant (*Pinus contorta* and *Populus tremuloides*) and shade tolerant (*Picea mariana*, *Picea engelmannii* and *Abies lasiocarpa*) PE regeneration since different processes could control these different groups of species. We used both living and dead stems of PE regeneration to assess the factors influencing their establishment. We determined if there was a spatial relationship between the PE regeneration and: live shade intolerant stems, live shade tolerant stems, and dead stems of the PD tree cohort using the toroidal shift null model of independence. This null model preserves the structure of each pattern but shifts them relative to one another. We thus randomly shifted the spatial pattern of the PE regeneration, while maintaining the pattern of the PD tree cohort constant, to produce Monte Carlo simulation envelopes representing the spatial relationship under the null model of independence.

We investigated the processes influencing survival of PE regeneration by testing the random mortality hypothesis. This approach is often used in ecology to determine whether intra-specific competition (which leads to a more regular post-mortality spatial pattern) is an important cause of mortality while accounting for first order heterogeneity in the initial pattern (Kenkel 1988, Getzin et al. 2006, Das et al. 2011). This hypothesis was tested in all plots for shade intolerant PE regeneration and only in the Whirlpool plot for shade tolerant PE regeneration, since mortality was too low for these species in other plots (<5%). We used the univariate random labelling approach to determine whether mortality of PE regeneration was a random process. To achieve this we randomly resampled sets of dead stems within the initial pre-mortality pattern (live and dead stems) to produce Monte Carlo simulation envelopes representing the spatial distribution of surviving trees under random mortality. Results of the analyses are presented as the difference between the spatial distribution of the pre-mortality pattern $g_{\text{initial}}(r)$ and the post-mortality pattern $g_{\text{live}}(r)$ to emphasise the change in spatial pattern over time. Under random mortality $g_{\text{initial}}(r) - g_{\text{live}}(r) = 0$ whereas $g_{\text{initial}}(r) - g_{\text{live}}(r) > 0$ is an indication that there are fewer live stems around other live stems in the current distribution compared to the initial pre-mortality distribution (live stems were becoming more uniformly distributed suggesting intra-specific competition). On the other hand $g_{\text{initial}}(r) - g_{\text{live}}(r) < 0$ suggests that live stems are more frequent around live stems in the current distribution as compared to the initial distribution – an indication that mortality occurred in areas of lower stem density.

We tested the statistical significance of the departure from our null model (independence and random mortality) using the goodness-of-fit statistic developed by Loosmore and Ford (2006). Most previous studies determined significance using departure from simulation envelopes but this was found to inflate type I error rates (Loosmore and Ford 2006); thus we based our interpretation on goodness-of-fit statistics (although we also present the simulation envelopes to facilitate comparison with earlier studies). We tested for significant departure from our null model for 5m distance classes

(0-5, 5-10, 10-15, 15-20 and 20-25) and corrected for multiple test using a Bonferroni correction of alpha. Due to the large number of stems sampled in each plot (Table 1), our initial alpha level was set at 0.1 (thus correct alpha was 0.10/5 = 0.02) to reduce the number of simulations required and thus computation time when following the method proposed by Loosemore and Ford (2006). For each test, we ran 335 simulations in order to constrain the uncertainty around the exact p value of the goodness-of-fit statistic between 0.03 and 0.01 (see Loosemore and Ford (2006) for details). All analyses of the stem mapped data were completed in R (R Development Core Team. 2011) using the "spatstat" package (Baddeley and Turner 2005).

Finally, we used variation partitioning (Borcard et al. 1992) to explore the potential influence of factors other than the PD tree cohort (e.g., edaphic conditions) on the spatial structure of PE regeneration (living and dead stems) at the 5x5m quadrat scale. The spatial structure of the quadrat-based data of PE regeneration was determined using the principle coordinates of neighbour matrices (PCNM) method described by Bocard and Legendre (2002) since it has been found to be one of the most efficient methods in capturing complex spatial structures (Smith and Lundholm 2010). This method generates spatial patterns at multiple scales specific to the sampling design; in our study it generated 209 PCNM eigenfunctions with positive autocorrelation. PD tree variables consisted of the number of living and dead PD trees of shade intolerant and tolerant species by 10cm DBH classes, the total number of shade intolerant and tolerant PD trees, and the total number of PD dead trees. Edaphic variables consisted of topographic variables (micro-elevation, convexity, slope, aspect; see Chapter 2 for more details) as well as the significant spatial structures of the understory communities found in these plot which mainly represented gradients between moist adapted and dry adapted species (Chapter 2). These understory spatial structures were the significant RDA axes between understory community composition data and PCNM variables presented in Chapter 2 (12, 26, 21, 14, 18 significant RDA axes in the Athabasca, Sunwapta, Whirlpool, Hector and Spray River plot respectively). Before conducting variation partitioning we used forward selection to choose a reduced set of variables from among the PD trees and edaphic variables as well as the PCNM eigenfunctions choosing those that were most strongly related to the response variable (density of PE regeneration). Significant ($\alpha=0.05$) variables were selected using the forward selection procedure described in Blanchet et al. (2008). Adjusted R^2 values were calculated for the variation partitioning analysis allowing us to better compare the amount of variation explained by different types of variables as it adjusts for the number of variables used (Peres-Neto et al. 2006). Variation partitioning was conducted using the ‘‘vegan’’ package (Oksanen et al. 2014), PCNM variables were constructed using the ‘‘spacemakeR’’ package (Dray et al. 2006), and forward selection was computed using the ‘‘packfor’’ package (Dray 2009) of the R statistical language (R Development Core Team. 2011).

4.3. Results

Temporal patterns of species establishment

In the Sunwapta, Whirlpool, Hector and Spray River plots we estimated the year of the last stand replacing fire as the year before the establishment of the oldest lodgepole pine tree which was in 1874, 1822, 1870 and 1896, respectively (Figure 4-1). In the Athabasca plot, one of the disks with fires scars had two scars, one in 1859 (last stand replacing fire) and a second in 1889 suggesting a surface fire (Figure 4-1). Evidence of surface fires were also present on cores sampled in the Sunwapta and Whirlpool plots and occurred in 1889 and 1836, respectively (Figure 4-1). Although burnt snags were present in the Hector and Spray River plots, none of the samples collected had fires scars. In all plots *Pinus contorta* establishment was mainly confined to within 20 years following the last stand replacing disturbance except in the Athabasca plot where most of the pine establishment was following the subsequent surface fire (Figure 4-1). In the Athabasca and Sunwapta plots *Pinus contorta* establishment also continued throughout stand development while in the Whirlpool plot there was a period of pine establishment 100 to 160 years following stand initiation. In the Hector and Spray River plots there was relatively little pine regeneration after the initial PD cohort except in recent decades in Spray River (Figure 4-1). In the Athabasca plot, *Populus tremuloides* regeneration < 2.5cm DBH was present only since 1989 and densities increased slightly in 2012 (Figure 4-2). In the Sunwapta plot *Populus tremuloides* densities decreased gradually since 1967 and only 2 stems were found in the whole plot in 2012 (Figure 4-2). In the Whirlpool plot, *Populus tremuloides* regeneration < 2.5cm DBH was present over the whole study period but densities increased dramactially in 2012 (Figure 4-2). *Populus tremuloides* regeneration never grew above 2.5cm DBH in any of the plots (Figure 4-2).

In the Athabasca, Sunwapta and Whirlpool plots the shade tolerant species mostly started establishing between 70-90 years following the last surface fire or 100-120 years after stand initiation and showed continuous recruitment over several decades (Figure 4-1). However, in the Athabasca and Whirlpool plots a few stems of *Picea engelmannii* and *P. mariana* established soon after stand initiation and survived the subsequent surface fire; these species also had regeneration occurring shortly after the surface fire (Figure 4-

1). In the Hector and Spray River plots shade tolerant species established immediately following stand initiation; in the Spray River plot *Picea engelmannii* established slightly earlier than *Abies lasiocarpa* (Figure 4-1). In the northwestern corner of the Hector plot, there were a few shade tolerant trees that were older than the last fire (Figure 1) and outside the plot near that corner four *Picea engelmanii* and three *Abies lasiocarpa* trees cored were between 179-330 years old; this suggests seed sources for these species were available at the time of stand initiation.

Determining post-disturbance (PD) and post-establishment (PE) cohorts

The establishment dates determined for stems < 5cm DBH sampled on the transects (Figure 1) were consistent with the changes in densities observed within the permanent plots over the last 45 years (Figure 4-2); this confirms that the samples we collected on the transects where representative of the regeneration present within the plots. Due to the surface fires in the Athabasca, Sunwapta and Whirlpool plots which occurred in 1889, 1889 and 1836, respectively (Figure 4-1), we considered that the post-disturbance (PD) establishment periods ended in 1909, 1909 and 1856, respectively, for shade intolerant species and 10 years later for shade tolerant species. For the Hector and Spray River plots the last stand replacing fire was estimated to be in 1870 and 1896, respectively (Figure 4-1) and thus the PD period was considered to have ended in 1890 and 1916, respectively, for shade intolerant species and 10 years later for shade tolerant species. Using these dates and our dendrochonological samples we determined which stems sampled within the plots should be placed in the PD or PE cohorts.

For cored stems we used the estimated year of establishment while un-cored trees and stems < 5 cm DBH were placed in either cohort based on rules determined for each species in each plot (Table 4-1, Figure 4-1). These rules were chosen to minimise the number of misclassified stems when applied to the cores and regeneration disk samples and the accuracy of the chosen rules is presented in Table 4-1. Sampled shade tolerant stems < 5 cm DBH took an average of between 15 to 31 years to reach 30cm in height in the different plots while shade intolerant stems took on average between 10-18 years. Although we recognize that the growing conditions for these later establishing stems were likely different than earlier in stand development, these results provide support to our decision to add an extra 10 years to the establishment period of shade tolerant species to account for their slower growing habits during the seedling stage. Stem maps of the PD tree and PE regeneration cohorts of shade intolerant and tolerant species are presented in Appendix A. Since the Hector plot had only 58 stems of shade intolerant PE regeneration and 60% of those stems were dead, analyses of these data are not presented since any interpretation from them would have limited utility. Similarly, as the shade tolerant PD cohorts in the Sunwapta plot was absent and comprised of only 4 stems in the Athabasca plot (Table 1) subsequent analyses of the spatial relationships between this cohort and PE regeneration are not presented.

Spatial analyses

Results from both the $L(r)$ and $g(r)$ function were similar (except that the cumulative property of the $L(r)$ function was apparent in most analyses) and thus only the g(r) function results are presented (see Appendix B for $L(r)$ results). Shade intolerant PE regeneration was segregated from shade intolerant PD trees at small scales (between 0-10m) in the Athabasca, Sunwapta and Whirlpool plots and independent from shade intolerant PD trees in the Spray River plot (Figure 4-3). Shade intolerant PE regeneration was independent from shade tolerant PD trees in the Whirlpool (although there was a trend towards segregation at small scales) and segregated from them at small scales in the Spray River plot (Figure 4-3). Shade intolerant PE regeneration was also segregated from dead trees at small scales in the Athabasca, Sunwapta and Whirlpool plots while independent from dead PD trees in the Spray River plot (Figure 4-3).

Shade tolerant PE regeneration was independent from shade intolerant PD trees at all scales in the Athabasca, Whirlpool and Spray River plot but aggregated with them at scales around 10m in the Sunwapta plot, and segregated from them at large scales (15-25m) in the Hector plot (Figure 4-4). Shade tolerant PE regeneration was aggregated with shade tolerant PD trees at most scales in the Whirlpool and Hector plots but independent at all scales in the Spray River plot. In the Athabasca, Sunwapta, Hector and Spray River plots, respectively, 34%, 10%, 4% and 19% of shade tolerant regeneration less than 2.5cm DBH was classified as layers while in the Whirlpool plot 70% were layers even without accounting for *Picea mariana* (due to assessment difficulties in this plot - see methods). Finally, shade tolerant PE regeneration were independent from dead PD trees in the Athabasca, Sunwapta and Spray River plots but aggregated with them at small and medium scales (0-15m) in the Whirlpool plot and segregated from them at large scales (20-25m) in the Hector plot.

For all plots except Sunwapta our random mortality results suggest that the spatial distribution of surviving shade intolerant PE regeneration was significantly more clustered than if mortality had occurred randomly within the initial regeneration population (Figure 4-5). These results were significant at most scales in the Athabasca and Whirlpool plots (0-20m) and significant at small (0-5m) and large scales (15-20m) in the Spray River plot. In the Sunwapta plots, surviving shade intolerant PE regeneration were more uniformly distributed at all scales than if mortality had occurred randomly; this suggests that intraspecific competition led to density-dependent mortality within this cohort. Finally the spatial distribution of surviving shade tolerant PE regeneration in the Whirlpool plot was also significantly more clustered at small scales (0-5m) than if mortality had occurred randomly.

Variation partitioning

Using variation partitioning we found that in most plots PE regeneration at the 5x5m quadrat scale was spatially structured, with PCNM variables explaining most of the variation (adjusted R^2) in PE regeneration densities (Figure 4-6). In all plots, there was also considerable overlap in the variation in PE regeneration densities explained by both the PD trees and edaphic variables with the PCNM variables suggesting both sets of variables contributed to the observed spatial structure (Figure 4-6). Our results, however, suggest that edaphic factors played an important role that was partially independent of the influence of the PD trees as a sizeable fraction of variation explained by these two types of variables didn't overlap (Figure 4-6). Furthermore, in some plots edaphic variables explained more variation (as compared to PD trees) in the density of the shade intolerant post-establishment cohort (Athabasca, Sunwapta and Whirlpool) and shade tolerant post-establishment cohort (Sunwapta, Whirlpool and Hector) (Figure 4-6). In almost all plots the main spatial structures of the understory communities (first RDA axis as described in Chapter 2) were amongst the most important within the set of edaphic variables explaining the variation in PE regeneration; this suggests that our interpretation of these variables as edaphic proxies is correct.

In the Sunwapta plot, PD trees didn't explain a significant fraction of the variation in shade tolerant PE regeneration (Figure 4-6) even though we found a significant spatial relationship between these two cohorts using point pattern analyses (Figure 4-4). In the Athabasca plot although only four shade tolerant PD trees were present (Table 4-1), densities of these at the quadrat level explained 22% of the variation in shade tolerant PE regeneration. The remaining significant PD trees variables used in the variation partitioning analyses will not be described further as they mainly echoed findings presented using the point pattern analyses such as the segregation of shade intolerant PE regeneration relative to PD trees and the clustering of shade tolerant PE regeneration near shade tolerant PD trees (See Appendix 4-C for details).

In the Athabasca plot, dry microsites had higher densities of shade intolerant PE regeneration whereas moist microsites had higher densities of shade tolerant PE regeneration. The most important edaphic variables explaining the variation in shade intolerant PE regeneration densities were RDA axes 7, 2 and 4 as well as convexity (together accounting for 19.6% of the 20.3% explained by edaphic variables, Figure 4-6). The most important edaphic factors explaining the variation in shade tolerant PE regeneration densities were RDA axes 1 and 12, convexity and sin aspect together explaining 11.6% of the variation (Figure 4-6). Dry microsites were convex areas with high cover of *Fragaria virginiana*, *Linnaea borealis*, *Antennaria neglecta, Carex* species and *Arctostaphylos uva-ursi* while moist microsites where concave west facing areas with high cover of mosses (*Pleurozium schreberi*, *Hylocomium splendens* and *Dicranum polysetum*), *Shepherdia canadensis* and *Peltigera* species (Appendix 4-D). Although *Shepherdia canadensis* is usually considered a species adapted to dry environments in this xeric plot it was shown to be associated with the moister areas of the plot (Chapter 2).

In the Sunwapta plot, moist microsites had higher densities of both shade intolerant and shade tolerant PE regeneration. The most important edaphic variables explaining the variation in shade intolerant PE regeneration densities were RDA 1, 8, 7 and 9 (together accounting for 19.1% of the 32.5% explained by edaphic variables, Figure 4-6). The most important edaphic variables explaining variation in shade tolerant PE regeneration densities were RDA axes 1, 4, 7 and 10 (together explaining 10.8% of the 11.6% explained by edaphic variables, Figure 4-6). Dry microsites had high cover of drought adapted species such as *Shepherdia canadensis*, *Juniperus communis, Cladonia* species, *Arctostaphylos uva-ursi* and *Pleurozium schreberi* whereas moist microsites had high cover of moist adapted species such as *Vaccinium vitis-idaea*,, *Geocaulon lividum*, and *Cornus canadensis* and mosses (*Ptilium crista-castrensis* and *Hylocomium splendens*) (Appendix 4-D).

In the Whirlpool plot, dry microsites had higher densities of shade intolerant PE regeneration while moist microsites had higher densities of shade tolerant PE regeneration. The most important edaphic variables explaining the variation in shade intolerant PE regeneration densities were RDA axes 1, 4, 7 and 2 (together explaining 32.0% of the 41.5% explained by edaphic variables, Figure 4-6). The most important edaphic variables explaining the variation in shade tolerant PE regeneration densities were RDA axes 1, 4, 19 and cos aspect (together explaining 27.0% of the 31.3% explained by edaphic variables, Figure 4-6). Dry microsites had high cover of drought adapted species such as *Juniperus communis* and *Arctostaphylos uva*-ursi whereas moist microsites had high cover of mosses *(Pleurozium schreberi, Ptilium crista-castrensis* and *Hylocomium splendens*) and other moist adapted species (*Ledum groenlandicum*, *Arnica cordifolia, Viburnum edule* and *Chamerion angustifolium*) (Appendix D).

In the Hector plot, moist microsites had high densities of shade tolerant PE regeneration. The most important edaphic variables explaining the variation in shade tolerant PE regeneration densities were RDA axes 2, 3, 1 and 6 (together explaining 35.9% of the 40.2% explained by edaphic variables, Figure 4-6). Dry microsites had high cover of *Juniperus communis, Shepherdia canadensis*, *Linnaea borealis*, *Cladonia* and *Peltigera* species whereas moist microsites had high cover of mosses (*Pleurozium schreberi, Hylocomium splendens, Ptilium crista-castrensis*) and other moist adapted species such as *Menziesia ferruginea*, *Cornus canadensis*, *Ledum groenlandicum* (Appendix 4-D). The significant edaphic variables in this plot also represent a gradient from moist condition in the northwestern corner toward drier conditions in the southeastern corner of the plot. In the Spray River plot edaphic variables explained only 3.8% of the variation in shade intolerant PE regeneration densities and were not significant for shade tolerant PE regeneration (Figure 4-6).

4.4. Discussion

Our results demonstrated that the post-disturbance (PD) establishment patterns in *Pinus contorta* forest can vary more than initially anticipated. As hypothesized *Pinus contorta* establishment mainly occurred soon after fire while shade tolerant species started establishing quickly following fires on moister sites but their establishment was mostly delayed in the drier sites, despite apparent seed source availability after the stand-initiating fire. Our results support our hypothesis that the spatial distribution and composition of the PD tree cohort played an important role in structuring subsequent PE regeneration as in most plots PE regeneration was segregated (shade intolerant) or aggregated (shade tolerant) with different groups of species of the PD cohort. Finally our variation partitioning analyses support our hypothesis that edaphic conditions also played an important role in structuring the PE regeneration in these forests, especially for shade tolerant species on drier sites.

Factors influencing the establishment and survival of shade intolerant species

Pinus contorta established primarily within 20 years following fires as expected due to its ability to store seeds in serotinous cones (Burns and Honkala 1990a); this is consistent with previous studies (Day 1972, Johnson and Fryer 1989, Antos and Parish 2002a). In the two moist plots (Hector and Spray River) there was relatively little shade intolerant regeneration after the initial PD cohort. Subsequent shade intolerant regeneration did, however, occur throughout stand development in the Athabasca and Sunwapta plots as well as between 100 to 160 years following the last surface fire in the Whirlpool plot.

There are a number of factors that likely contributed to this pattern of on-going / later-stage shade intolerant recruitment in the three drier plots (Athabasca, Sunwapta and Whirlpool). Firstly, these drier plots had much lower PD trees densities and large gaps in the overstory compared to the two moist plots (Hector and Spray River) allowing more light to reach the understory. In the drier plots shade intolerant PE regeneration (mainly *Pinus contorta* but also some *Populus tremuloides*) were segregated from shade intolerant PD trees supporting the generally accepted assumption that these species have difficulty establishing under the shade of a mature canopy (Burns and Honkala 1990a, b). As tree mortality in these plots mainly occurred in areas of high tree density (Chapter 3) the segregation between shade intolerant PE regeneration and dead PD trees further supports the importance of gaps for the establishment of these species. The fact that segregation between shade intolerant PE regeneration and shade intolerant PD trees was only found at small scales (10m or less) suggests that relatively small gaps might be sufficient to allow establishment. During the initial sampling of the Whirlpool plot, Hnatiuk (1969) observed large numbers of standing dead *Pinus contorta* trees and this decline of the overstory, which continued over the whole study (Stadt 1993, Chapter 2), likely contributed to the establishment of shade intolerant regeneration in this plot over the length of the study period.

The importance of gaps for shade intolerant PE regeneration was also supported by our analyses of random mortality. The increased clustering of surviving shade intolerant PE regeneration (Athabasca and Whirlpool plots) suggests that mortality occurred more often in areas of high tree density (outside gaps) leaving surviving shade intolerant PE regeneration clustered within gaps. In the Sunwapta plot, the more uniform distribution of surviving shade intolerant PE regeneration was due to the extremely high densities establishing in gaps which likely resulted in strong intra-specific competition and higher levels of mortality within gaps compared to elsewhere under the canopy. This is interesting as it suggests there could be a second self-thinning phase within the understory *Pinus contorta* regeneration cohort, a phenomenon not previously described in the literature. Our results thus support previous studies in self-perpetuating *Pinus contorta* forest in which regeneration occurred primarily in gaps (Parker 1986) or under sparse overstories (Despain 1983).

Late successional tree species reduce light transmission to the understory more than shade intolerant conifer species (Messier et al. 1998). Thus, the low numbers of shade tolerant PD trees in the three drier plots likely resulted in sufficient light penetration to the understory for establishment of shade intolerant regeneration. Besides the dense shade intolerant PD cohorts present in the two moist plots (Hector and Spray River) they also had substantial shade tolerant PD cohorts, further contributing to lower light levels in the understory and thus inhibiting establishment of shade intolerant PE regeneration. The segregation of shade intolerant PE regeneration with shade tolerant PD trees in the Spray River as well as the trend towards segregation between these cohorts in the Whirlpool plot also support this interpretation.

Edaphic factors were also important for shade intolerant PE regeneration especially in the drier plots which had large PE cohorts. Drier microsites favored the establishment of shade intolerant PE regeneration in two of these drier plots (Athabasca and Whirlpool) whereas moist microsites favoured it in the Sunwapta plot. The presence of feather mosses and tall shrubs on the moist microsite of the Athabasca and Whirlpool plots, respectively, likely contributed to the lower densities of shade intolerant PE regeneration in these microsites. Feather mosses are considered to be a poor substrate for *Pinus contorta* seedling establishment (Wright et al. 1998, LePage et al. 2000) while tall shrubs could have competed with regenerating tree seedlings for light (Shropshire et al. 2001). On the more mesic Sunwapta plot however, the dominant feather mosses (*Pleurozium schreberi*) and shrubs were most abundant on drier microsites and thus shade intolerant regeneration was more abundant on moist microsites. Finally in the Spray River plot, the edaphic variables did not explain much variation in shade intolerant

PE regeneration densities, likely because the understory communities lacked an important spatial structure (suggesting more homogenous moisture conditions) and the topography was quite flat (Chapter 2). Overall, results from the Sunwapta plot agree with a previous study suggesting that lodgepole pine regeneration in self-perpetuating forests could be limited by moisture (Stuart et al. 1989), but the results from the Athabasca and Whirlpool plot, on the other hand, suggest that moisture limitation can also be beneficial by preventing the establishment of competitive species, such as shrubs and mosses, that might inhibit tree establishment.

Although the three drier plots (Athabasca, Sunwapta and Whirlpool) had on-going and later-stage recruitment of shade intolerant regeneration, only in the Sunwapta plot was there evidence of growth of this regeneration into larger size classes (see Chapter 3). In the Spray River plot the age structure of shade intolerant PE regeneration suggests that establishment occurred only after 1980. However shade intolerant seedlings were present in the Spray River plot in 1967 suggesting that most of the seedlings present during the earlier sampling periods since died. Although the shade intolerant seedlings currently present in the understory had low levels of mortality (12%) it seems unlikely that they will survive and grow into the large size class given the heavily shaded condition they are in. The result in the Spray River plot highlighted the potential hazards in interpreting static age structures to infer stand dynamics (Johnson et al. 1994). Without the information from the permanent plots we could have interpreted the age structure as a recent pulse in shade intolerant regeneration while it is more likely that there is actually a high turnover of *Pinus contorta* regeneration in the understory. Overall our results are consistent with a study by Johnson and Fryer (1989) who found that understory *Pinus* *contorta* cohorts can exist but that survival and chances of reaching the canopy are low. Shade intolerant regeneration in the studied plots thus seems to serve as a sapling bank that could perhaps release in the presence of secondary disturbances such as insect outbreaks (Axelson et al. 2010). The results of the Sunwapta plot, however, suggest that in some conditions understory *Pinus contorta* could grow into the canopy.

Populus tremuloides PE regeneration was only present in the three drier plots and although the process previously described for shade intolerant species also apply to this species, additional factors have likely contributed to its regeneration dynamics. The recent pulse in *Populus tremuloides* regeneration in the Whirlpool plot was likely triggered by the recent windthrow disturbance since in 2012 six out of the 11 *Populus tremuloides* trees present in this plot had been recently snapped or uprooted, a process that promotes suckering in this species (Frey et al. 2003). The decreasing densities over the study period in the Sunwapta plot and the fact that none of the *Populus tremuloides* regeneration in the Athabasca and Sunwapta plots grew into larger size classes, even though they were present in previous sampling periods, could be attributed to elk (*Cervus elaphus* Linnaeus) browsing (Beschta and Ripple 2007). This is supported by the many signs of elk, such as antler injuries on trees as well as many well maintained trails, that were present throughout the study period in these plots (Hnatiuk 1969, Stadt 1993).

Factor influencing the establishment and survival of shade tolerant species

In the Hector plot, shade tolerant stems surviving the last stand replacing disturbance in the northwestern corner of the plot provided seeds immediately following stand initiation and contributed to the quick return of these species. The moist condition in the northwestern corner (on the moist end of the understory gradient, was downslope and soils near this corner had thicker Ae horizon and deeper solum depth, Chapter 2) likely contributed to the survival of this post-disturbance regeneration. While in the Spray River plot no sampled trees had survived the last stand replacing fire, the rapid post-disturbance establishment of *Picea engelmanii* and *Abies lasiocarpa* clearly indicates that seed sources were present at the time of stand initiation. Since smaller seed size is usually associated with better dispersal abilities (Greene and Johnson 1993), the smaller seed size of *Picea engelmannii* compared to *Abies lasiocarpa* could explain its slightly earlier return (Galipeau et al. 1997, LePage et al. 2000). The earlier return of *Picea engelmannii* also agrees with previous studies in these ecosystems (Day 1972, Antos and Parish 2002b, Clark et al. 2003).

In the three drier plots (Athabasca, Sunwapta and Whirlpool) the delayed establishment of shade tolerant species didn’t seem to be caused by a lack of seed availability. In the Athabasca and Whirlpool plots a few stems of shade tolerant species established soon after the fires suggesting seed sources were available following stand initiation and the subsequent surface fires. Although there were no signs suggesting the presence of seed availability following fires in the Sunwapta plot (no initial establishment and no nearby seed sources observed in the field) the similar temporal delay in establishment as in the other two dry plots (around 70-90 years following the last surface fire) suggests some other common processes could potentially be responsible for the delayed establishment pattern.

The occurrence of surface fires early following stand initiation likely contributed to delayed establishment of shade tolerant species in the three drier plots (Athabasca, Sunwapta and Whirlpool) and surface fires have previously been found to be more abundant in drier *Pinus contorta* sites compared to moister ones (Barrett et al. 1991). Besides killing established seedlings, these surface fires could also have removed coarse or fine woody debris generated from the stand initiating disturbance, both of which have been found to be important for seedling establishment following fires in dry open environments (Little et al. 1994, Castro et al. 2011). The lack of coarse woody debris has also previously been suggested as a potential explanation for the delayed establishment of shade tolerant regeneration in another subalpine forest (Agee and Smith 1984).

The drier environmental conditions in the drier plots could also have contributed to delayed establishment of shade tolerant species. Different studies concluded that drought stress was an important cause of *Picea engelmannii* and *Abies lasiocarpa* seedling mortality since they established mainly in shaded environments and on substrates that retained moisture (Day 1963, Day 1964, Noble and Alexander 1977). This interpretation is further supported by the fact that in the drier plots shade tolerant PE regeneration was always associated with the moist microsites, which were mainly areas of high cover of mosses and other moist adapted species. Although feather mosses are generally considered unfavourable seedbeds for *Picea* species (Coates et al. 1994, Hörnberg et al. 1997) our results agree with a study by Day (1964) who found shade tolerant conifer seedlings establish on moss seedbeds because mosses occurred in moist, shaded microsites. The fact that most of the shade tolerant species present in the Whirlpool plot (especially *Picea mariana*) established on the moister lower terrace (Appendix A2) also supports this interpretation. In our study area, *Picea mariana* is usually found on wet poorly drained sites (Laidlaw 1971) like the lower terrace of the Whirlpool plot which had evidence of poor drainage (presence of mottles in the lower horizons, Chapter 2). Over time, the gradual increase in understory vegetation cover in the drier plots (Chapter 2) likely provided more shaded microsites thus limiting drought stress while having a limited negative impact on shade tolerant conifer seedling survival (Coates et al. 1994, Little et al. 1994, Feller 1998). In the Hector plot shade tolerant PE regeneration also occurred in moist microsites dominated by mosses which in this plot also meant in proximity to available seed sources following stand initiation. It is, however, difficult to determine the driving factor although it is fair to assume that both distance to seed sources and moist microsites were important for shade tolerant PE regeneration establishment and survival on the Hector site.

Shade tolerant PE regeneration was mostly independent from shade intolerant PD trees suggesting that shade from the overstory didn’t prevent recruitment of these species in the understory. This is consistent with previous studies that found establishment of *Picea engelmannii* and *Abies lasiocarpa* in the understory is not limited by light (Knapp and Smith 1981). The strong layering habits of *Abies lasiocarpa* and *Picea mariana* could have contributed to the spatial aggregation of shade tolerant PE regeneration around shade tolerant PD trees. However in the Hector plot very few layers were found, suggesting that other processes contributed to this spatial aggregation. Shade tolerant trees usually have relatively limited seed dispersal (Galipeau et al. 1997) especially under closed canopies (LePage et al. 2000) and thus seed dispersal near parent trees could also have contributed to these aggregation patterns. As layering and the clustering of seedlings around parent trees are both process that can take long periods of time to unfold, the younger age of the Spray River plot could explain why no significant clustering of shade tolerant PE regeneration was found around shade tolerant PD trees.

Besides serving as seed sources, early establishing shade tolerant trees could also provide favorable shaded microsites for the recruitment and survival of these species (Little et al. 1994). This latter explanation is supported by the results in the Whirlpool plot. In this plot shade tolerant PE regeneration was strongly clustered around PD shade tolerant species and our random mortality results suggested that surviving stems were even more clustered, suggesting that survival was higher in these clusters around a parent tree. This might have been especially important in the Whirlpool plot as the dominant pine canopy was breaking down over the past 45 years thus increasing light and potential moisture stresses in the understory. The clustering of shade tolerant PE regeneration around dead PD trees in the Whirlpool plot is due to the contribution of fallen dead trees (majority of dead trees in Whirlpool, see Chapter 3) to the layering of *Picea mariana* PE regeneration in this plot.

Successional status and pathways in these plots

Our results suggest that the initial composition and spatial distribution of the pioneer trees played an important role in determining the future composition of these stands, either by allowing shade intolerant regeneration to persist in drier environments or by favoring a faster transition towards shade tolerant species in moister conditions. Stewart (1986) also found that pioneer tree establishment following disturbances in conifer forests had important effects on subsequent tree regeneration. Our finding that all tree species established following stand initiation in the moist plots supports the complete initial floristic model of succession (Egler 1954, Wilson et al. 1992) while in our drier plots the delayed establishment periods of shade tolerant species lends support to the relay floristics model of succession (Egler 1954, Connell and Slatyer 1977). This is especially true in the Sunwapta plot where there was no evidence of immediate post-disturbance establishment of any shade tolerant species. The fact that shade tolerant species did not establish early in the drier plots and that the later post-establishment regeneration preferred moist shaded microsites in these plots supports the facilitation model of succession presented by Connell and Slatyer (1977). Overall, the recruitment of shade tolerant species and their low levels of mortality suggests that, given enough time, all of the plots studied will likely transition towards the dominance of *Picea* and *Abies*. As these shade tolerant species increase in abundance they will further limit the recruitment of shade intolerant regeneration in the understory. However our study suggests that the speed of this transition will be faster in moister sites while on drier sites shade intolerant regeneration may persist for longer periods. These drier stands may even develop into structurally more complex stands with different cohorts of shade intolerant regeneration before shade tolerant species dominate. The historically shorter fire cycles in these forests likely contributed to the maintenance of *Pinus contorta* dominated forest in this landscape. A lengthening of the fire cycle will likely increase the importance of the shade tolerant species on these landscapes especially in dry environments.

4.5. Acknowledgement

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Table 4-1. Years and DBH thresholds used to separate post-disturbance and post-establishment cohorts as well as the efficiency of these rules for shade intolerant and shade tolerant species. The number of stems and percentage of dead stems within each cohort are also presented. When DBH thresholds were different between species of the same shade tolerance group they are presented for each species (Abies lasiocarpa-AbL, Picea engelmannii-PiE, Picea mariana-PiM).

Plots	Year threshold	DBH threshold (cm)	Nbr of stems sampled by cores/disks	Percent of stems misclassified cores/disk (%)	Nbr of post-dist. stems (% dead)	Nbr of post-estab. stems (% dead)
Shade intolerant species						
Athabasca	1909	5	244/99	2.9 / 4.0	1633 (67.7%)	2162 (13.1%)
Sunwapta	1909	10	181/79	11.6 / 0	412 (29.2%)	5670 (30.7%)
Whirlpool	1856	5	147/60	1.3 / 0	945 (70.3 %)	887 (22.0%)
Hector	1890	2.5	299/12	0.3 / 0†	3342 (29.5%)	58 (60.3%)
Spray River	1916	2.5	273/39	0.7 / 0	3271 (42.3%)	307 (12.1%)
Shade tolerant species						
Athabasca	1919	‡	30/138	0 / 0	4 (0%)	678 (2.4%)
Sunwapta	1919	10	3/118	0 / 0	0	194 (0.5%)
Whirlpool	1866	AbL 20 PiE 25 PiM 15	26/66 17/27 111/107	0 / 0 5.8 / 0 8.1 / 0	148 (81.8%)	7480 (6.8%)
Hector	1900	6	230/159	28.7/ 13.2[¶]	371 (1.3%)	3929 (3.7%)
Spray River	1926	5	215/161	7.7[#] / 12.4	413 (1.0%)	1109 (1.5%)

† Three stems between 2.5 and 5cm DBH sampled on the transects were initially dated, based on ring counts, to just after 1890 (see Figure 4-1). However, the presence of very narrow rings near the end of these samples made us suspicious of missing rings. After measuring and cross-dating these samples it was found that they all had multiple missing rings and thus established well before 1890.

‡ Only 2 *Picea engelmannii* and 2 *Picea mariana* ≥ 5cm DBH established before 1919 and these stems were already in larger size classes in 1967 (See Figure 4-2).

¶ Most of the stems that were misclassified were near the northwest corner of the plot near the fire margin and are thus not representative of the majority of the plot.

This percent misclassification only applied to Engelmann spruce since all subalpine fir stems >5cm DBH in the plot were cored and thus their estimated year of establishment was used for classification.

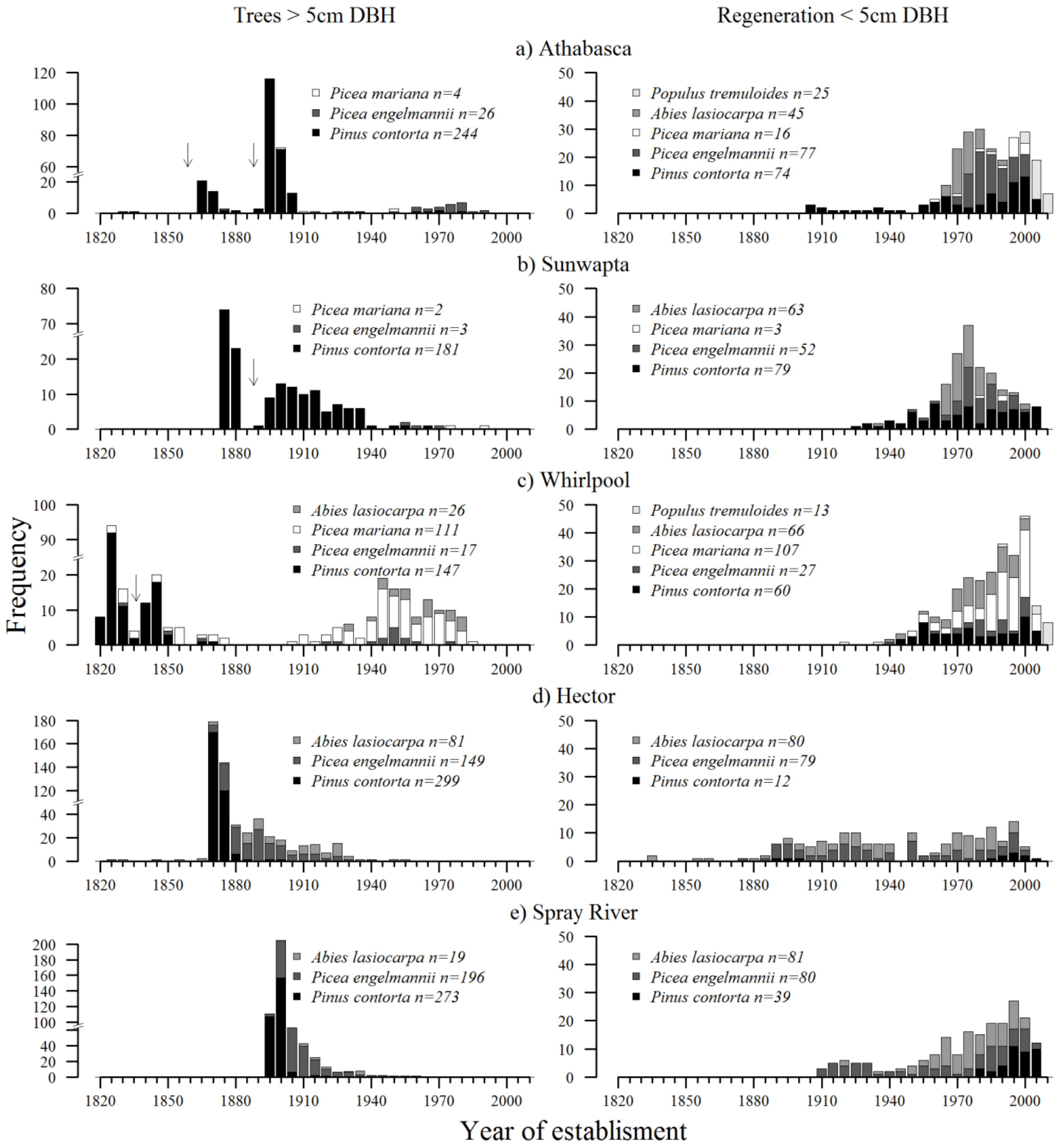

Figure 4-1. Year of establishment for trees over 5cm DBH cored in each plot and stems less than 5cm DBH sampled on the 4 x 100m transect surrounding each plot. Arrows represent years for which evidence of fire was present on disk or core samples (see Chapter 3 for details); the number of samples cored for each species in each plot is also presented (n). Surface fires occurred in the Athabasca, Sunwapta and Whirlpool plots in 1889, 1889 and 1836, respectively. In the Athabasca plot only two Picea engelmannii and two Picea mariana stem established following the fires making it hard to see them on the figure.

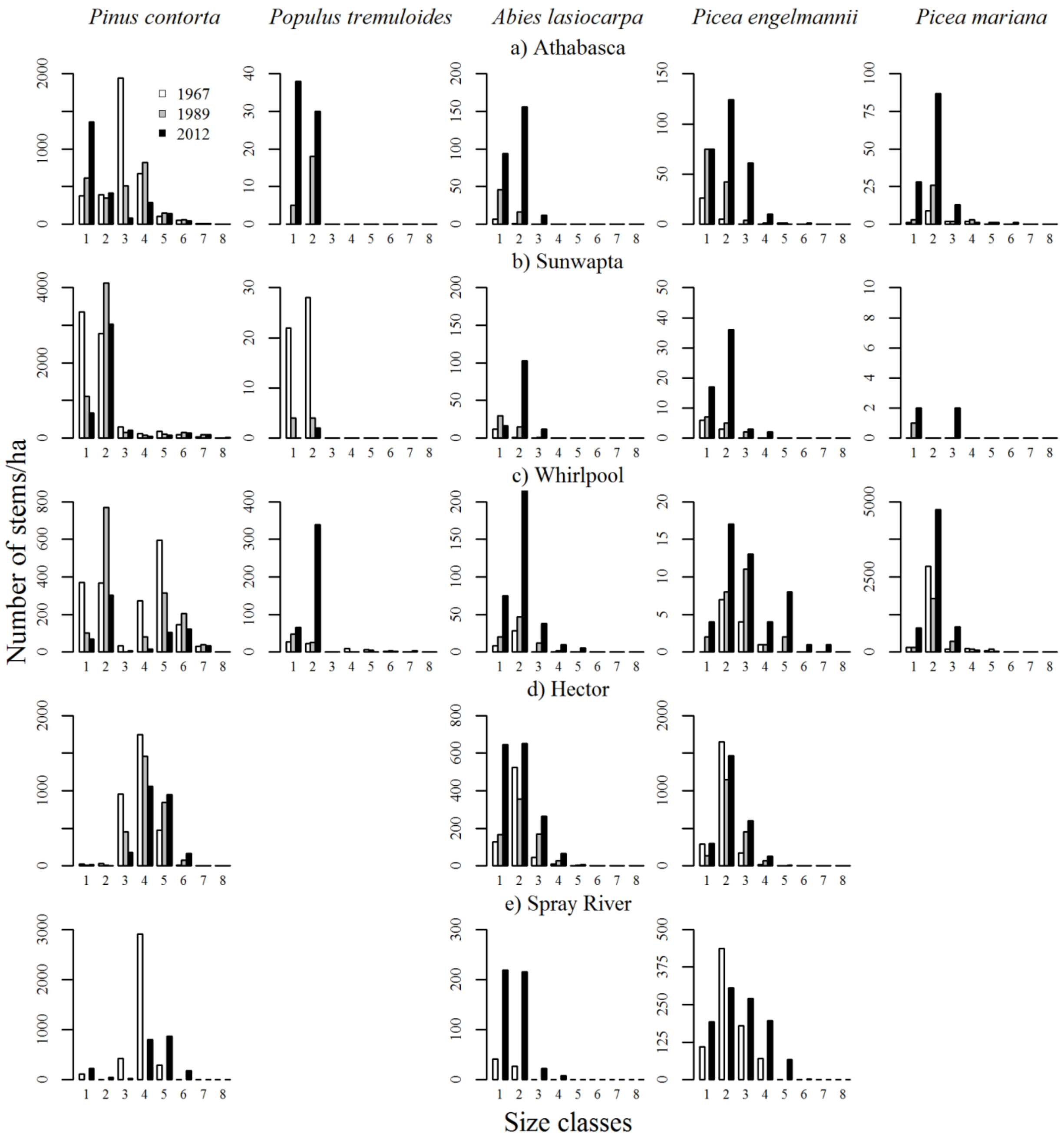

Figure 4-2. Size class distribution of all tree species in all plots at each sampling period. Size classes represent: 1 = < 30 cm in height, 2 = >30cm in height but with a diameter at breast height (DBH) < 2.54 cm diameter, 3 = 2.54 to 7.62cm DBH, 4 = 7.63 to 15.24cm DBH, 5 = 15.25 to 22.86cm DBH, 6= 22.87 to 30.48cm DBH, 7 = 30.49 to 38.1cm DBH, 8 > 38.11 DBH.

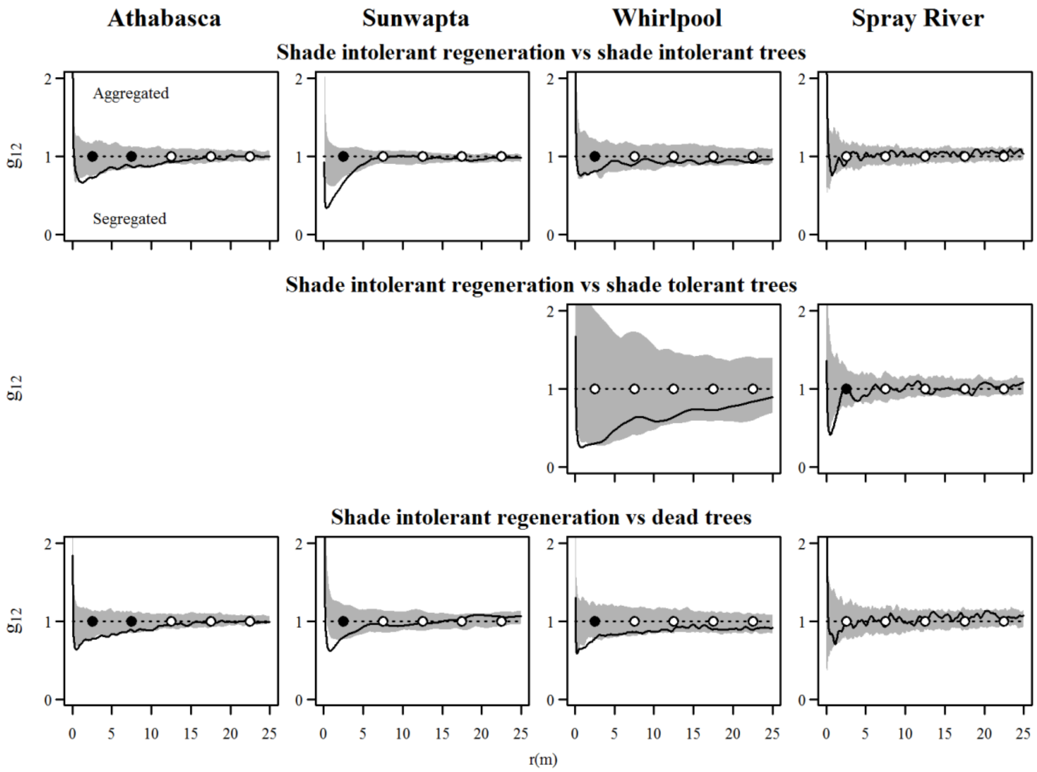

Figure 4-3. Spatial relationship (aggregated, independent or segregated) as a function of distance r between shade intolerant post-establishment regeneration and trees from the post-disturbance cohort: living shade intolerant, living shade tolerant, and dead. Spatial relationships were quantified using the bivariate pair correlation function g12(r). Significant deviation from our null model of independence was assessed using goodness-of-fit statistics (see methods) and is shown with black circles along the x-axis on each graph. Critical bands from the Monte Carlo simulation are shaded and are presented for comparison with previous studies. Results are not presented for Hector because there was little shade intolerant regeneration in this plot.

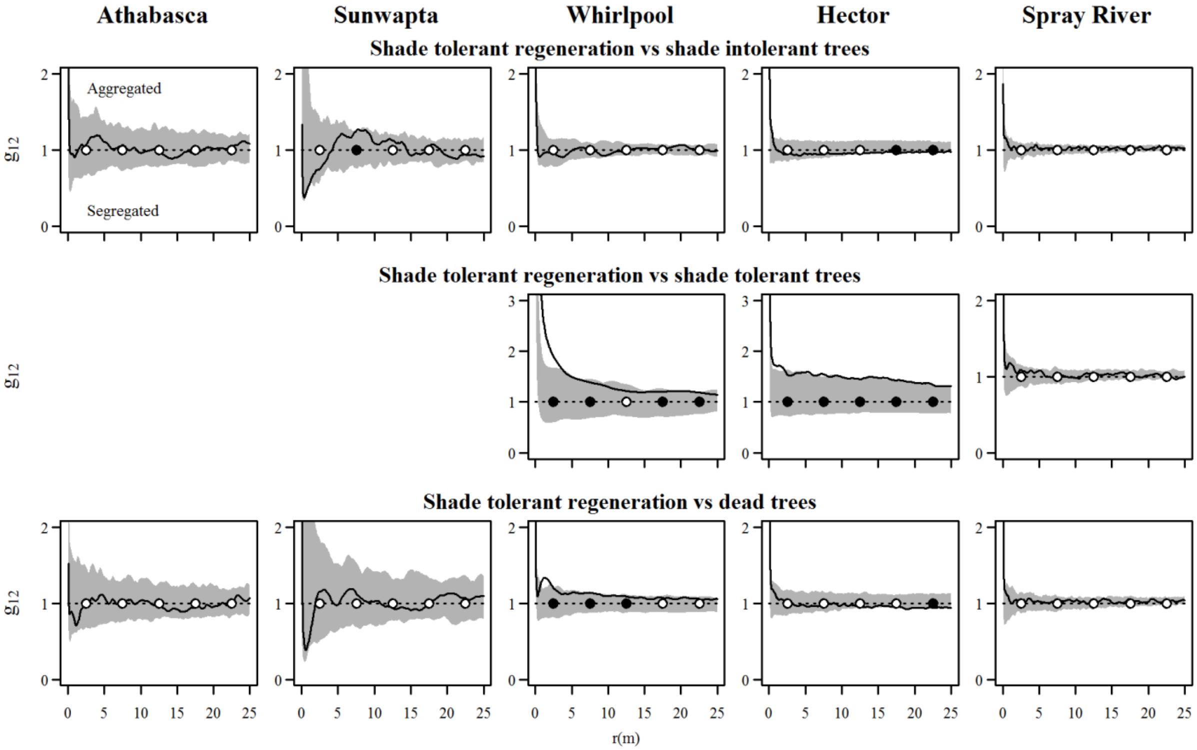

Figure 4-4. Spatial relationship (aggregated, independent or segregated) as a function of distance r between shade tolerant post-establishment regeneration and trees from the post-disturbance cohort: living shade intolerant, living shade tolerant, and dead. Spatial relationships were quantified using the bivariate pair correlation function $g_{12}(r)$. Interpretation is as in Figure 4-3.

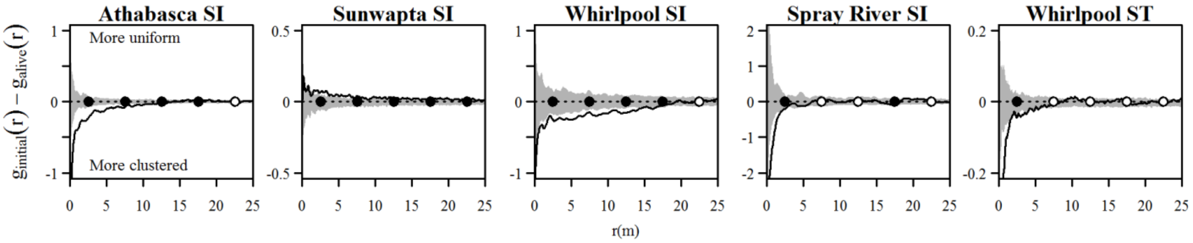

Figure 4-5. Change in spatial pattern (became more uniform, more clustered or unchanged) between initial (ginitial) and surviving (galive) post-establishment regeneration stems as a function of distance r compared to the null model of random mortality. Spatial patterns were quantified using the univariate pair correlation function g(r). Results are for shade intolerant (SI) species except for the Whirlpool plot for which results of shade tolerant (ST) species are also presented due to sufficient mortality in this plot. Interpretation of significance and simulation bands is as in Figure 4-3. Results are not presented for Hector because there was little shade intolerant regeneration in this plot.

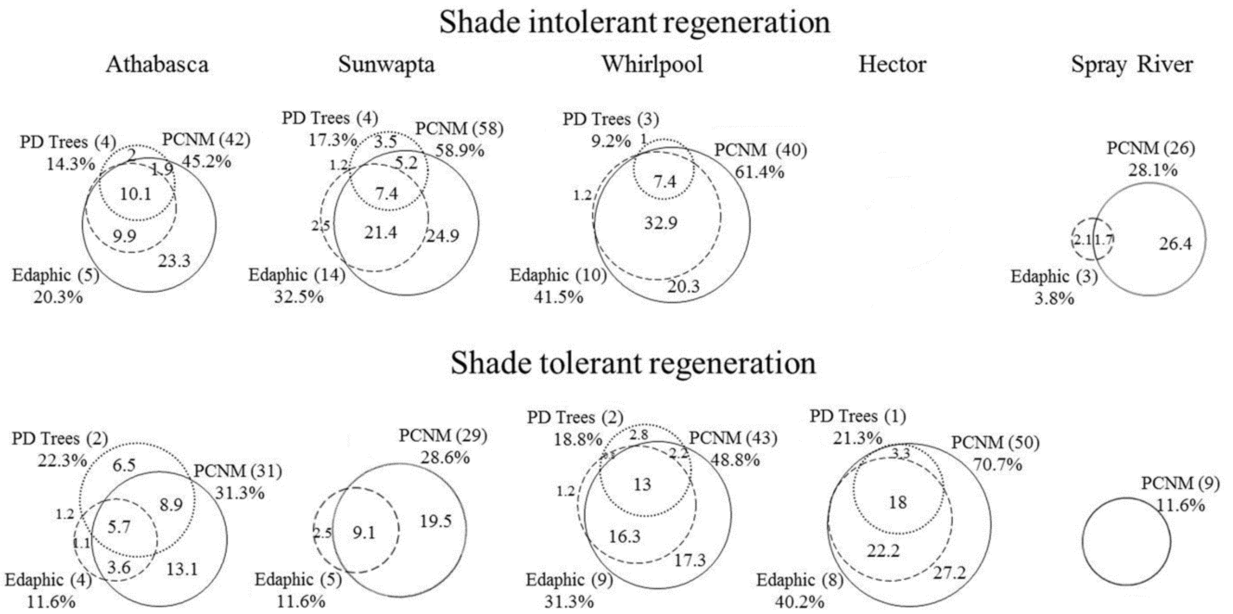

Figure 4-6. Results of variation partitioning analyses. Given is the percent of variation (adjusted R^2) in shade intolerant and shade tolerant post-establishment regeneration densities explained by post-disturbances (PD) trees variables, edaphic variables and spatial variables (principle coordinates of neighbour matrices (PCNM) eigenvectors). The number of variables used in the analysis is presented in brackets. Components explaining less than 1% of variation are not presented. Results are not presented for Hector because there was little shade intolerant regeneration in this plot.

4.6. Appendixes

Appendix 4-A. Map of shade intolerant and shade tolerant stems from the post-disturbance and post-establishment cohort.

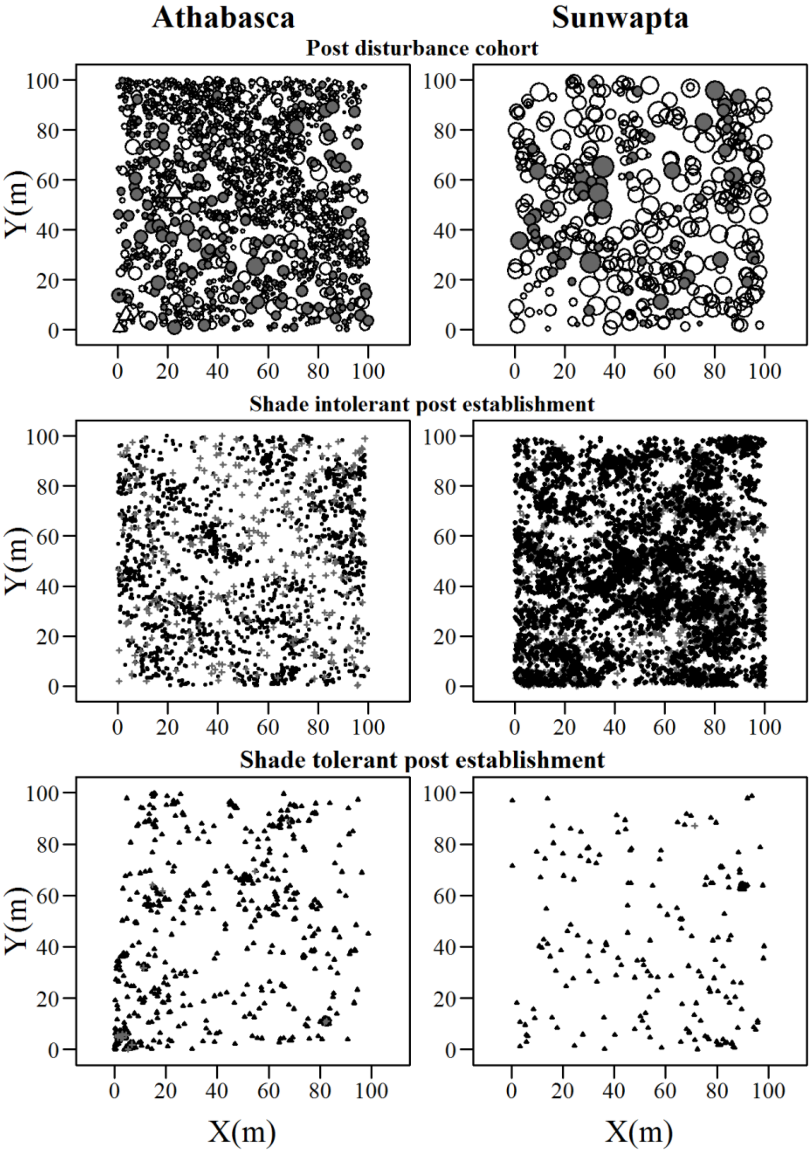

Figure 4-A1. Stem maps from the Athabasca and Sunwapta plots (north oriented towards the top of all maps). Presented are the stems from the post disturbance cohorts (both shade tolerant and shade intolerant on the same maps) as well as shade intolerant and shade tolerant stems from the post establishment cohort presented on separate graphs. Circles and triangles represent shade intolerant and shade tolerant species, respectively. For the post disturbance cohort, white circles represent live stems while dark grey circles represent dead stems and circle size is proportional to the DBH of the stem. For the post establishment cohort black circles represent live stems while light grey crosses represent dead stems.

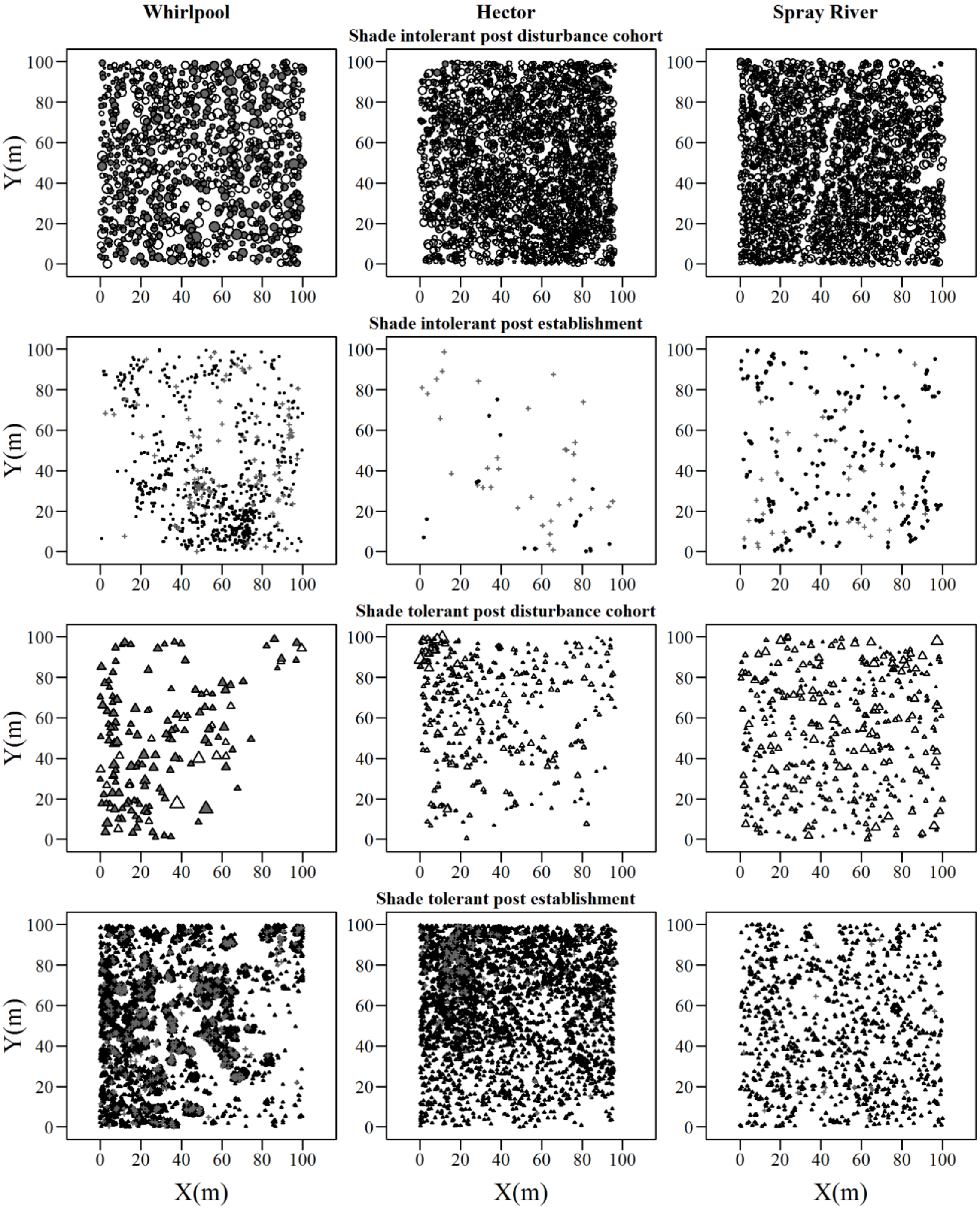

Figure 4-A2. Stem maps from the Whirlpool, Hector and Spray River plots (north oriented towards the top of all maps). Presented are shade intolerant and shade tolerant stems from the post disturbance (PD) and the post establishment (PE) cohort. Circles and triangles represent shade intolerant and shade tolerant species, respectively. For the PD cohort, white symbols represent live stems while dark grey symbols represent dead stems and symbol size is proportional to the DBH of the stems. For the PE cohort black symbols represent live stems while light grey crosses represent dead stems.

Appendix 4-B. Spatial analysis results with L(r). Test of independence and random mortality.

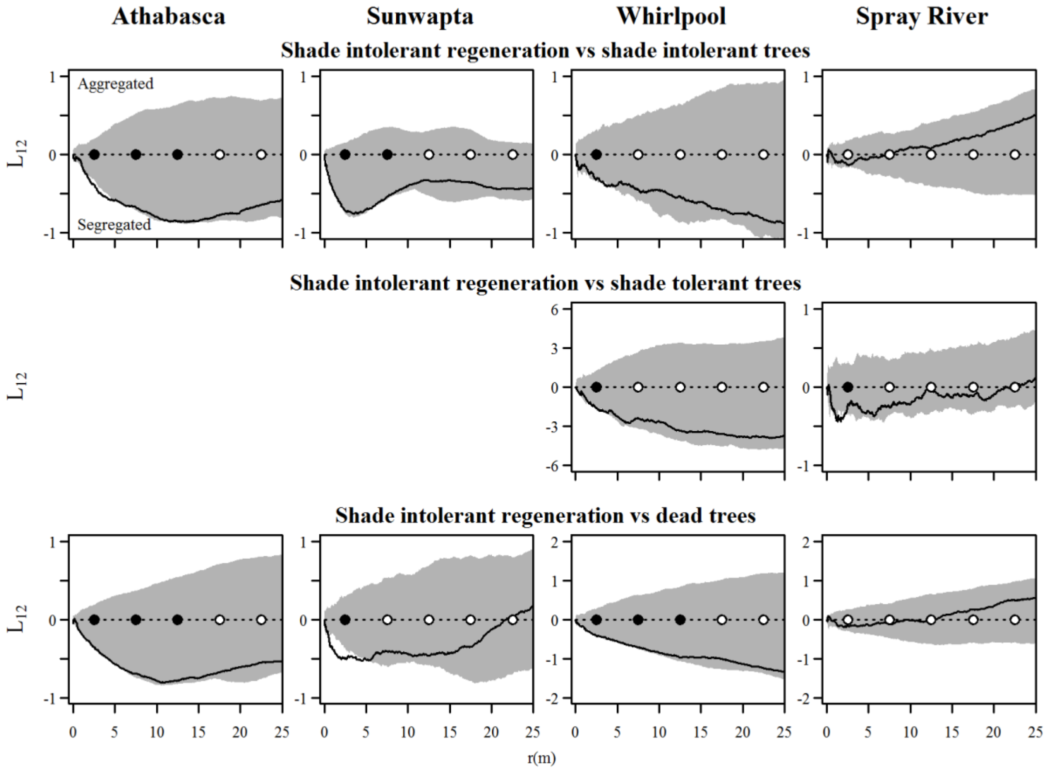

Figure 4-B1. Spatial relationship (aggregated, independent or segregated) as a function of distance r between shade intolerant post-establishment regeneration and trees from the post-disturbance cohort: living shade intolerant, living shade tolerant, and dead. Spatial relationships were quantified using the bivariate L_{12} function. Significant deviation from our null model of independence was assessed using goodness-of-fit statistics (see methods) and is shown with black circles along the x-axis on each graph. Critical bands from the Monte Carlo simulation are shaded and are presented for comparison with previous studies. Results are not presented for Hector because there was little shade intolerant regeneration in this plot.

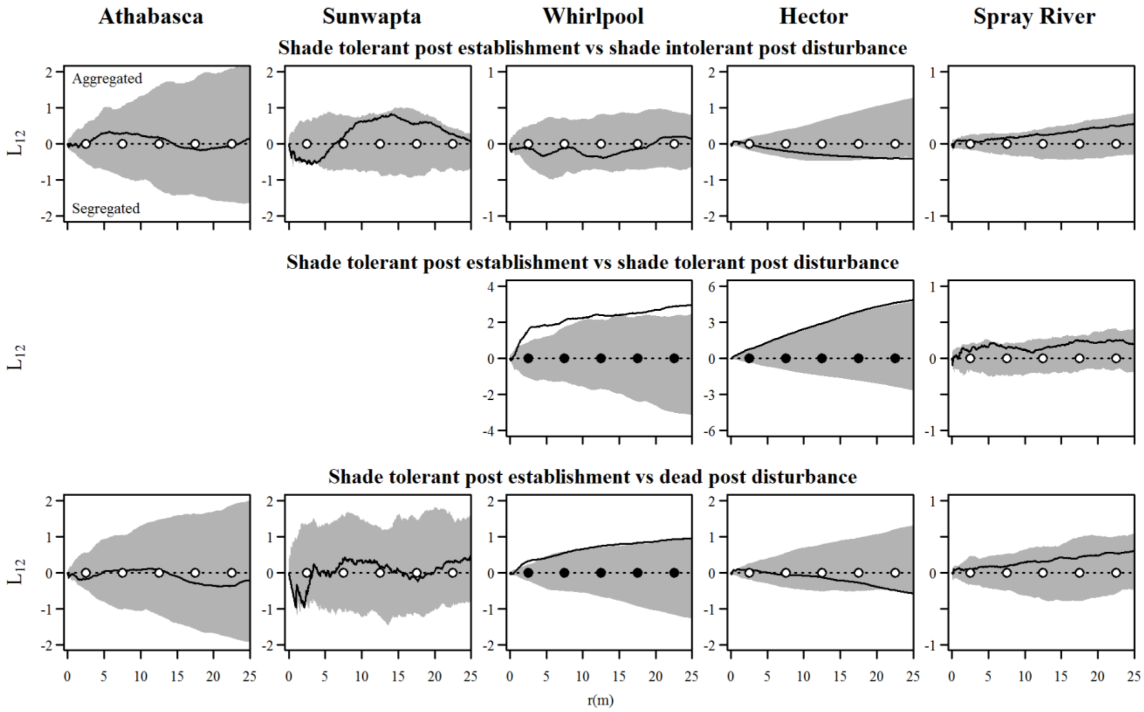

Figure 4-B2. Spatial relationship (aggregated, independent or segregated) as a function of distance r between shade tolerant post-establishment regeneration and trees from the post-disturbance cohort: living shade intolerant, living shade tolerant, and dead. Spatial relationships were quantified using the bivariate L_{12} function. Interpretation is as in Figure 4-B1.

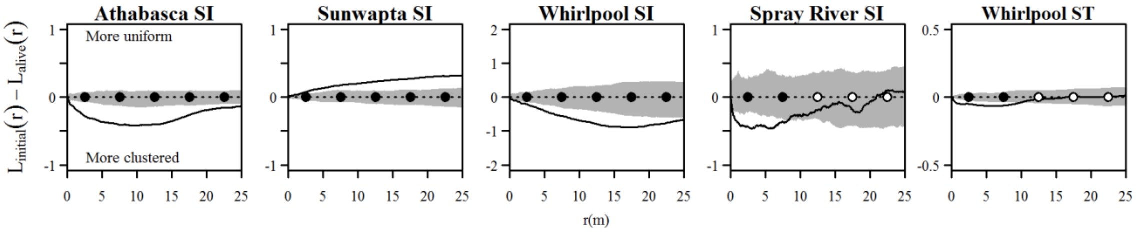

Figure 4-B3. Change in spatial pattern (became more uniform, more clustered or unchanged) between initial (L_{initial}) and surviving (L_{alive}) post-establishment regeneration stems as a function of distance r compared to the null model of random mortality. Spatial patterns were quantified using the univariate *L* function. Results are for shade intolerant (SI) species except for the Whirlpool plot for which results of shade tolerant (ST) species are also presented due to sufficient mortality in this plot. Interpretation of significance and simulation bands is as in Figure 4-B1. Results are not presented for Hector because there was little shade intolerant regeneration in this plot.

Appendix 4-C. Description of the post disturbance tree variables explaining a significant amount of the variation in shade tolerant and intolerant post establishment regeneration densities.

Athabasca: the density of dead and living post disturbance (PD) stems together explained 11.6% of the variation in post establishment (PE) shade intolerant regeneration densities (all significant post-disturbance variables explained 14.3%, Figure 4-6) and the density of living shade tolerant PD stems 22.3% of the variation in PE shade tolerant regeneration densities (Figure 4-6).

Sunwapta: the density of living PD stems explained 12.2% of the variation in shade intolerant PE regeneration (all significant variables explained 17.3%, Figure 4-6). PD overstory variables did not explain a significant amount of variation in PE shade tolerant regeneration (Figure 4-6).

Whirlpool: the density of dead stems and of living shade intolerant PD stems explained 9.2% of the variation in PE shade intolerant regeneration. The density of dead stems and of living shade tolerant PD stems explained 18.8% of the variation in post establishment shade intolerant regeneration (Figure 4-6).

Hector: the density of living and dead PD lodgepole pine stems explained 7.8% of the variation in PE shade intolerant regeneration while the density of living shade tolerant PD trees explained 21.3% of the variation in PE shade tolerant regeneration (Figure 4-6).

Spray River: PD tree variables did not explain a significant amount of variation in either shade intolerant or shade tolerant PE regeneration (Figure 4-6).

Appendix 4-D. Understory vegetation associated with the RDA axes selected in the variation partitioning analysis of shade intolerant and shade tolerant post establishment regeneration.

Table 4-D1. Understory vegetation associated with the most important RDA axes (inferred as edaphic variables) selected in the variation partitioning analyses of shade intolerant post establishment (PE) regeneration. Only species with absolute score values greater than 0.1 on the original RDA axes from Chapter 2 are presented. Species with a + and – sign were associated with areas or high and low regeneration densities, respectively. The percent variation in shade intolerant PE regeneration densities explained by each RDA axis is presented in the first row.

Species	Athabasca			Sunwapta				Whirlpool				Hector		Spray River		
RDA axes	7	2	4	1	8	7	9	1	4	7	2	9	1	17^*	10^*	5
Percent explained by axes (%)	6.4	5.3	4.5	9.8	3.8	3.1	2.4	17.8	6.1	4.1	4.0	2.2	1.1	1.6	1.3	0.8
Tall shrubs																
Juniperus communis		+	-	-				+	+				+			
Ledum groenlandicum								-	+		+		-			+
Menziesia ferruginea				+									-			
Rosa acicularis				-		-										
Shepherdia canadensis		-	-			-		+	-	-	-		+			
Dwarf shrubs																
Arctostaphylos uva-ursi		-	-	-				+		+	+					
Linnaea borealis			+		-		+		-			-	+			
Vaccinium cespitosum								+	-	+						
Vaccinium spp.													+			
Vaccinium vitis-idaea				+												
Forbs																
Antennaria neglecta		+														
Arnica cordifolia								-		-	-					
Cornus canadensis				+			-	-	-							
Chamerion angustifolium								-								
Fragaria virginiana	+															
Geocaulon lividum				+						+						

Melampyrum lineare				-												
Grasses and sedges																
Carex spp.		+	+													
Leymus innovates		-	+		+		-	-	-	-				+		
Pteridophytes																
Lycopodium complanatum								+								-
Lycopodium annotinum																-
Mosses & Lichens																
Cladina spp.				-				+								
Cladonia spp.													+			
Dicranum polysetum								+								
Hylocomium splendens	+		-	+				-			+	+				+
Peltigera spp.	-	+				+							+		-	
Pleurozium schreberi				-				-			-		-			
Ptilium crista-castrensis				+	+		+	-	+	+						

* These axis did not have any species with scores above 0.1 and thus the species with the highest absolute scores are presented.

Table 4-D2. Understory vegetation associated with the most important RDA axes (inferred as edaphic variables) selected in the variation partitioning analyses of shade tolerant post establishment regeneration. Only species with absolute score values greater than 0.1 on the original RDA axes from Chapter 2 are presented. Species with a + and – sign were associated with areas or high and low regeneration densities, respectively. The percent variation in shade intolerant post establishment regeneration densities explained by each RDA axis is presented in the first row.

Species	Athabcasca		Sunwapta				Whirlpool			Hector			
RDA axes	1	12*	1	4	7	10	1	4	19	2	3	1	6
Variation explained	6.7	0.9	5.3	2.5	2.0	1.1	23.7	1.4	0.9	24.8	4.3	4.3	2.6
Tall shrubs													
Juniperus communis			-	-			-	+				-	
Ledum groenlandicum							+	+			+	+	
Menziesia ferruginea			+							-	+	+	+
Rosa acicularis			-		-								
Shepherdia canadensis	+				-		-	-		-	-	-	
Viburnum edule									+				
Dwarf shrubs													
Arctostaphylos uva-ursi	-		-				-						
Linnaea borealis								-				-	
Vaccinium cespitosum							-	-					
Vaccinium spp.											+	-	
Vaccinium vitis-idaea			+	-									
Forbs													
Arnica cordifolia							+						-
Cornus canadensis			+	+			+	-		+	+		
Chamerion angustifolium							+						
Geocaulon lividum			+										
Melampyrum lineare			-										
Grasses and sedges													
Leymus innovates						+	+	-					
Pteridophytes													

Lycopodium complanatum				+			-						
Mosses & Lichens													
Cladina spp.			-			-	-						
Cladonia spp.												-	
Dicranum polysetum		+					-						
Hylocomium splendens	+		+				+			+			+
Peltigera spp.					+					+	+	-	+
Pleurozium schreberi	+		-				+			+	-	+	
Ptilium crista-castrensis			+				+	+					+

* These axis did not have any species with scores above 0.1 and thus only the species with the highest absolute scores are presented.

Chapter 5. General conclusions

The research presented in this thesis provides new insights regarding the processes structuring the understory and overstory communities in mature lodgepole pine forests. We demonstrated that the processes driving the understory community change following canopy closure, that self-thinning can persist for over 140 years in lodgepole pine forests, and that the initial post-disturbance establishment and moisture availability play a crucial role in determining the rate of successional change in these ecosystems. By understanding the processes responsible for the observed spatial patterns of different communities or populations this thesis contributes to the growing body of literature demonstrating how spatial autocorrelation or spatially structured data can be considered a useful tool, more than a nuisance in ecology (Legendre 1993).

In the second chapter, we first demonstrated that understory communities in mature lodgepole pine forest were still dynamic even more than 140 years following the last stand replacing disturbance (Figure 5-1). After canopy closure, the understory communities homogenized due to the decline of pioneer shade intolerant species and increased abundance of shade tolerant moist adapted species, a pattern often found in chronosequence studies but rarely demonstrated using long term permanent plots. These processes also contributed to the convergence of the different plots along the moisture/elevation gradient and the increasing abundance of mosses was driving most of this convergence. Most of the changes in community composition were in relative abundance, thus supporting the complete initial floristics model of succession, but we also found evidence of relay floristics especially in drier environments. Many of the species that appeared or increased considerably over time in the drier sites (for example: *Chimaphila umbellata*, *Moneses uniflora*, *Orthilia secunda*, *Pyrola chlorantha*, *Listera cordata*, *Geocaulon lividum*, *Piperia unalascensis*) are indicators of later successional stages and can thus be used by managers assessing the level of disturbance in forests impacted by either humans or natural disturbances.

Our ability to observe relay floristics was not only due to the fact that the same plots were sampled over a 45 year time period; it was also due to the large size and contiguous nature of the sampling design since many of these later successional species were infrequent and could have easily been missed on smaller dispersed sampling plots which are often used in understory vegetation studies. Although chronosequence studies can provide information about general characteristics of the understory communities, conclusions about succession models (relay vs initial) are usually avoided due to the inability to assess how differences between sites contributed to observed changes in species composition. Previous long-term studies have demonstrated the importance of relay floristics in the decades following disturbance but this thesis is the first study that we are aware of to demonstrate the importance of relay floristic in understory communities in later stand development stages following canopy closure.

Looking at processes spatially structuring the composition and richness of the understory community provided support for our hypothesis that deterministic processes would be decreasing in importance following canopy closure while dispersal limitation would increase in importance. We are not aware of any previous published studies that demonstrated how the relative importance of these two processes can not only differ depending on different environmental conditions (xeric vs moist) but can also change during stand development. Although dispersal limitation was a driving force in structuring the understory communities in these forests, deterministic processes still played an important role, especially in the drier plots studied. These deterministic processes were canopy closure, increasing abundance of later successional tree species, competition among understory species, moisture availability, organic matter accumulation, and the influence of past disturbance. Although not assessed in this thesis we recommend that future monitoring of these plots incorporate information on fine scale soil properties and below-ground processes, as these have been found to be important in structuring understory communities in mature lodgepole pine stands (McIntosh 2013).

Many of the deterministic processes structuring the understory community also played important roles in other aspects of stand dynamics (Figure 5-1). Variation in moisture availability within and between plots and the presence of shade tolerant tree species also influenced the establishment of pioneer trees and later regeneration. The disturbance history in three of the plots studied (presence of surface fires) influenced post-disturbance establishment and subsequently the length of the self-thinning stage (Chapter 3) as well as the composition and density of subsequent regeneration (Chapter 4). The fact that three out of the five plots I sampled experienced surface fires a few decades following stand initiation was an unexpected result from this thesis. Obvious fire scars on larger trees at the Athabasca plot clearly showed evidence of surface fires, however this evidence was initially much less obvious at the Sunwapta and Whirlpool plot. Although signs of such disturbances were present in the age structure of lodgepole pine in these sites, without the extensive dendrochronological survey we conducted, these fires would have gone unidentified.

These findings contribute to the growing body of evidence that besides stand replacing fires, non-lethal surface fires or mixed-severity fire regimes play an important role in lodgepole pine ecosystems especially in the lower elevation drier environments in the Canadian Rockies. These results could be used by managers responsible for prescribed fire programs, such as in National Parks, to justify the use of prescribed fires in recently burnt forests (either naturally or from a previous prescribed burn) to replicate natural stand dynamics as well as reduce fuels on the landscape. An important side finding of this thesis is that three decades following stand initiation would be sufficient for pioneer lodgepole pine regeneration to reach large sizes enabling them to survive surface fires. The use of presecribed surface fires could also be used to slow down the successional transition towards more shade tolerant tree species, a process likely to increase in lodgepole pine forests as disturbance regimes change. Our finding that disturbances were important in many aspects of stand dynamics also contribute to the now generally accepted view that natural disturbances play a prominent role in structuring most ecosystems. Thus management strategies based on our understanding of disturbance regimes and their influence on stand dynamics are warranted.

Our finding that self-thinning was still ongoing in all of the plots was another unexpected but interesting result of this thesis (Chapter 3). In some plots this was due to a delayed establishment periods due to surface fires while in other plots (Hector and Spray River) it was due to slow growing conditions that postponed the advent of competition between stems (Figure 5-1). The influence of competition on tree growth wasn't covered in the current thesis but warrants future research to assess its role as the actual process prolonging the self-thinning stage in the Hector and Spray River plots. Following stand initiation, the growth of pioneer trees increases or remains high until most stems reach a size at which they start competing with each other for light, space and nutrients. Determining if this decline in growth occurs later in the Hector and Spray River plot compared to stands of similar densities that completed the self-thinning stage earlier could provide support to our hypothesis that slow growth was responsible for the delayed self-thinning stage. Better understanding how competition influences the growth of the different tree species and how this changes throughout stand development could also provide information valuable for forest management. For example this could help predict future yields as well as help plan silvicultural treatments that could favor different species. Future research on the potential relationships between climate and tree growth of the different species in these plots would also be interesting as this could help predict how future climate changes could affect the successional dynamics in these stands. The chronologies developed in this thesis combined with the spatial and temporal nature of the data collected over the years could be used to answer these questions in the near future.

Although we demonstrated that most of the mortality was in trees of the smaller size classes and was thus due to self-thinning (Chapter 3), the oldest plot studied (Whirlpool) experienced some canopy decline over the study period even before the more recent windthrow. This gradual decline of the canopy did not lead to a reduction in cover of shade tolerant species (they actually increased) or to increases of shade intolerant understory species (Chapter 2) a pattern observed a previous chronosequence study (De Grandpré et al. 1993). The impact of the recent windthrow also didn’t have a noticeable impact on the understory community at this site although this could be because it occurred too recently (2009) and there was a lag in response of understory communities to the overstory disturbance (Thomas et al. 1999). Early signs of community reorganisation were however visible in the Whirlpool plot as the understory community increased in heterogeneity in 2012 while it decreased in all other plots.

Although the canopy decline and recent windthrow disturbance in the Whirlpool plot did not cause an important response of the understory community both these events influenced the establishment of shade intolerant trees. This suggests that, compared to understory communities, regeneration of shade intolerant tree species can respond to lower levels of canopy decline and also respond more quickly following important canopy disturbances. However, since the process of canopy break-up had not yet or had only recently started in most of the plots studied, future monitoring of these plots is required to better determine the impact of canopy decline on both the understory communities and regeneration. This would also allow a better evaluation of the potential impacts of mountain pine beetle (MPB) outbreaks in lodgepole pine forests in this region on the stand dynamics of both the understory community and regeneration compared to unaffected stands.

A recent study by Edwards et al. (2015) has recently shown that mortality following the recent mountain pine beetle (MPB) outbreak in lodgepole pine forests decreased the cover of many species of the understory community within 8 years, especially mosses and other shade tolerant species and that subsequent fire in these same stands had even more drastic effects and generated new pioneer communities. When compared to the findings in the Whirlpool plot this suggests that MPB outbreaks might change the composition of understory communities to a greater degree than does the process of canopy break-up in unaffected stands. Other studies found that in the first decade following MPB outbreaks new tree regeneration was limited (Astrup et al. 2008, McIntosh and Macdonald 2013) while in later decades pulses of regeneration have been observed (Amoroso et al. 2013). The faster response of tree regeneration following the windthrow disturbances in the Whirlpool plot (Chapter 4) is likely due to a much more rapid opening of the canopy compared to what happens following MPB. In MPB-attacked stands trees die slowly over one to two years, slowly lose their needles over three to five years and maintain standing snags for long periods of time thus the amount of light reaching the understory can be limited for up to a decade or more post-attack (Simard et al. 2011).

In previous studies, new tree recruitment following MPB was mostly dominated by shade tolerant species (Axelson et al. 2009, Diskin et al. 2011, Hawkins et al. 2012, Pelz and Smith 2012) but higher canopy mortality or dry conditions has led to recruitment of shade intolerant species (Nigh et al. 2008, Axelson et al. 2009, 2010). This variability in regeneration dynamics has led to a diversity of successional pathways following MPB (Astrup et al. 2008, Hawkins et al. 2012, Amoroso et al. 2013) as well as to more structurally and compositionally complex stands with important recruitment of shade intolerant tree species in the understory (Axelson et al. 2009, 2010, Hawkins et al. 2012, Amoroso et al. 2013). MPB outbreaks however will mostly accelerate the transition of lodgepole pine dominated stands towards shade tolerant tree species (Astrup et al. 2008, Hawkins et al. 2012, Amoroso et al. 2013). Thus overall the variability in regeneration dynamics and diversity of successional pathways described following MPB is similar to the ones described in these unaffected stands studied in this thesis.

Although successional pathways are likely to converge amongst all the plots studied, the time required for the different plots to converge towards dominance of shade tolerant tree species will vary depending on moisture conditions. Thus, in drier more open conditions structurally more complex stands of lodgepole pine can develop before this transition takes place. I found that even the Sunwapta plot which was initially thought of as a potential “climax” lodgepole pine stand (Hnatiuk 1969, Stadt 1993) will likely transition towards the more common successional pathway of dominance by shade tolerant tree species. This supports comments from a previous study that the successional status or stability of lodgepole pine forest shouldn’t be assessed in stands less than 100 years old as establishment of shade tolerant tree species can be delayed for long periods (Whipple and Dix 1979), as was the case in some of the plots I studied.

Overall, the historically shorter fire cycles in these forests and the presence of mixed severity fire regimes on the drier sites likely contributed to the maintenance of lodgepole pine dominated forest on these landscapes. A lengthening of the fire cycles will thus likely increase the importance of shade tolerant tree species on the landscape. Since the presence of shade tolerant tree species had an important impact on the understory community (Chapter 2), these changes in disturbance regimes could also have an indirect impact on these communities.

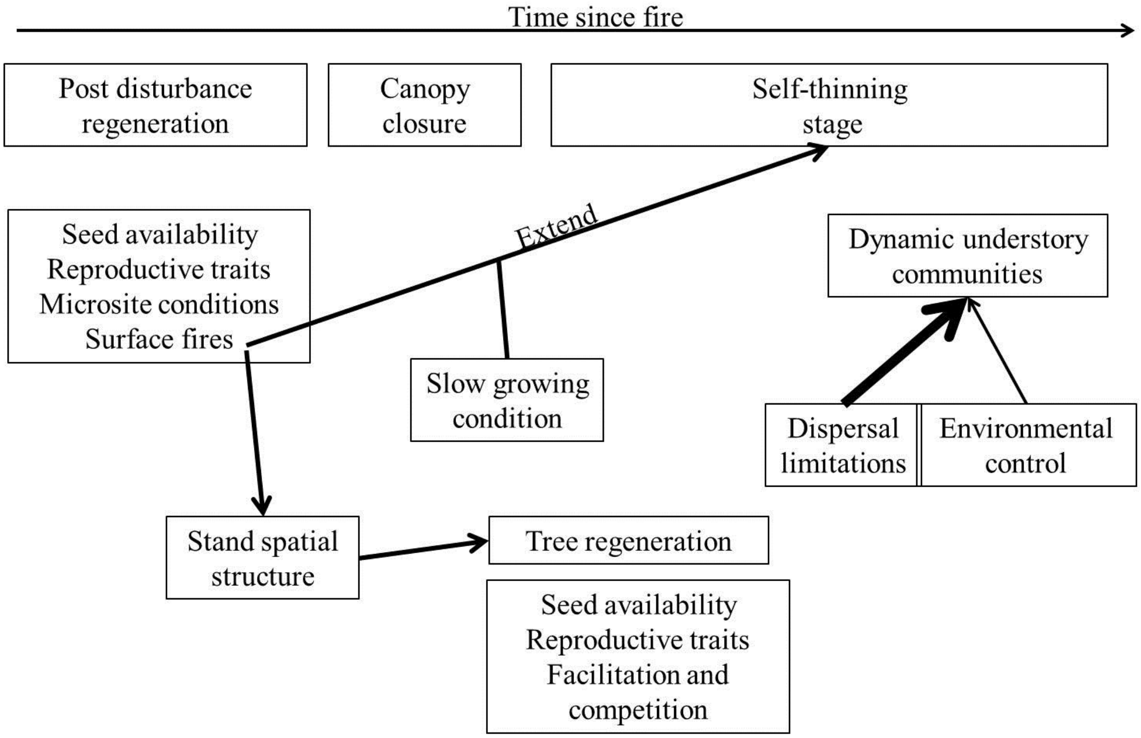

Figure 5-1. Main conclusions of this thesis linked in a conceptual diagram.

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