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**Plant community assembly 15-37 years after clearcutting,
clearcutting plus prescribed burning, and wildfire in jack
pine (*Pinus banksiana* Lamb.) forests of central Canada.**

Keri L. Pidgen

**A thesis submitted in partial fulfillment of the requirements for
the degree of Master of Science in Biology**

Department of Biology

**Lakehead University
Thunder Bay, Ontario**

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Abstract

It has been suggested that clearcutting be followed by prescribed burning as a means of reconciling effects of clearcutting and wildfire on plant communities. To address the effectiveness of clearcutting followed by prescribed burning (PB), I assessed understorey communities in northwestern Ontario using fifty 10 x 10 m plots, located in 15-37 year old jack pine (*Pinus banksiana* Lamb.) stands established after clearcutting, PB, and wildfire. My findings are presented in two chapters, first I examined structural and compositional differences in plant communities originating from the three disturbance types, and secondly I examined the relationship of species' traits to disturbance type. In Chapter 1, I hypothesized that understorey communities established after PB would resemble those established after wildfire more closely than those established after clearcutting alone. However, I found that all three disturbance types had similar understorey species richness and diversity, while species composition within PB sites differed significantly from clearcut and wildfire sites. Compositional differences associated with PB were comparable to those found after successive short-interval wildfires. Indicator species of PB sites were mostly ruderal and disturbance tolerant species; suggesting that PB created a compound effect on plant communities. Since application of prescribed burning after clearcutting does not involve a novel disturbance, compositional differences may be related to the short-interval between clearcutting and PB. In Chapter 2, I hypothesized that compositional differences between communities originating from PB correspond to the interaction of short-interval disturbance with species' life history and regeneration traits. I analyzed traits related to post-disturbance regeneration to quantify relationships with disturbance type. For trait analysis I used the abundance-weighted analyses RLQ, Fourth-Corner Analysis, calculation of functional diversity indices (functional richness, evenness, and dispersion), and community weighted means. I found no significant relationship between the suite of traits and disturbance type. However I found significant relationships between PB and species' traits such as Raunkiaer's lifeform, seed banking, wind dispersal, deciduous foliage, rosettes and alien status. My hypothesis was supported by the prevalence of seed banking and wind dispersal in the PB sites, both of which are known to increase with short-interval disturbances. From these results I conclude that application of PB following clearcutting causes compositional differences that result from disturbance-mediated plant trait selection by short-interval disturbances.

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Introduction

Boreal forests are disturbance-driven ecosystems and perturbations are required to maintain boreal forest communities. For example, the role of severe wildfire in maintaining successional trajectories in jack pine forests (Frelich and Reich 1995) and black spruce-ericaceous forest systems in eastern Canada (Mallik 2003). In Canada, boreal forests are subjected to extensive stand-replacing disturbances, such as insect defoliation, wildfire, and clearcut harvesting. Crown fires are a key natural and historical stand-replacing disturbance agent of the boreal forest. However with the advent of clearcutting and fire suppression, clearcutting has become more extensive than wildfire in the managed area of Ontario (OMNR 2004). Wildfire imparts specific effects on site conditions and vegetation communities (Certini et al. 2003; Neff et al. 2005). Fires vary in their severity, but typically kill the majority of mature trees (Smirnova et al. 2008) and in extreme cases can incinerate all forest floor organic matter (Neff et al. 2005). Boreal plant species have adapted to the conditions imposed by wildfire, since it has been a selective force on vegetation communities for millennia. Species tolerant of recurring fire have attributes enabling survival and recolonization in post-fire habitats (Rowe 1983; Allen 2008). For example, most boreal tree species are adapted to early successional conditions with high light and altered seedbeds.

Clearcutting constitutes the removal of nearly all trees within an area. In much of the boreal forest it represents an extensive anthropogenic disturbance; yearly almost 200,000 hectares in Ontario alone are cleared of trees by clearcutting (OMNR 2008). Clearcutting, though often considered a single event, may actually represent a number of discrete disturbances. After harvesting, cut areas are often site prepared using mechanical

treatment (scarification) to facilitate planting and create favourable seedbeds for germination and establishment. Planting is often followed by herbicide application to reduce competition from broad-leaved species (OMNR 2007). Approximately half of clearcut areas in Ontario are replanted with jack pine (*Pinus banksiana* Lamb.) or black spruce (*Picea mariana* Mill.), depending on the pre-disturbance community and site conditions (OMNR 2004).

There are a number of differences between wildfire and clearcutting that directly affect survival and colonization of flora. Fire combusts organic matter, which impacts two key factors that can encourage survival or colonization. First, combustion of living matter causes death and damage to individuals. Typically all above-ground vegetation is killed, but depending on fire severity, belowground plant tissue may or may not survive (Rowe 1983). This is largely dependent on root and rhizome position in the soil, which is linked to heat exposure and survival (Flinn and Wein 1977). With clearcutting, there is no heat associated damage to plant tissues, although mechanical damage may occur. A second difference between fire and clearcutting is fire's role in creating favourable seedbeds by consuming organic matter (Wang and Kembell 2005). Thick organic matter presents different (and generally lower quality) conditions than shallow organic matter or exposed mineral soil for seed germination and seedling establishment (Charron and Greene 2002). Due to high porosity of organic matter it dries much more readily than does mineral soil with smaller pore spaces, and as such is not conducive to seed germination and seedling establishment (Charron and Greene 2002). In addition to the direct effects of organic matter combustion on plant survival and establishment, fire also recycles nutrients that have been bound within the organic matter. Combustion of organic matter results in a flush of biologically

available nutrients that can affect plant growth particularly directly after disturbance (Prescott et al. 2000). These intrinsic differences in the effects of clearcutting and wildfire coupled with the usurpation of wildfire by clearcutting, has led to concerns for biodiversity conservation in the boreal forest (Bradshaw et al. 2009).

Boreal plant species have adapted to wildfire, through traits enabling survival and recolonization. These adaptations have led ecologists to question whether conditions created by clearcutting enable maintenance of the structure and composition of forest communities that evolved in the presence of wildfire. This question has prompted study of similarities and differences between the effects of fire and clearcutting on plant communities (Reich et al. 2001; Haeussler and Bergeron 2004). Natural disturbance emulation, whereby forest managers attempt to emulate the spatio-temporal patterns of wildfire through clearcut silviculture, has received much attention regarding the effects on plant communities (McRae et al. 2001; Nitsche 2005; Kembell et al. 2006; LeDuc and Rothstein 2007). However, this type of management emulates spatial patterns with limited opportunity to address site characteristic differences that occur between clearcutting and wildfire (Thiffault et al. 2007). Since wildfire disturbance is so central to boreal ecosystems, it has been suggested that application of prescribed burning after clearcutting may further emulate wildfire, increase species richness, and provide habitat for fire-dependent species, such as *Leptobryum pyriforme* (Whittle et al. 1997; Rees and Juday 2002). However, application of prescribed burning, typically occurring 2 to 3 years after clearcutting, introduces additional disturbance to clearcut sites. The impact of two such disturbances in close proximity on plant communities remains unclear. Temporal variation in disturbance-free interval can have strong effects on plant communities. For example, short-interval fire

events favour different species assemblages than long-interval disturbances (Donato et al. 2009). Each disturbance filters species based on their traits and successive disturbances result in increased filtering of species. In clearcuts followed by prescribed burning species assemblages must pass through the filter related to each disturbance as well as that imposed by the short-interval between disturbances.

There are some limited studies on vegetation communities developed following clearcutting plus prescribed burning, but the most focus on short-term effects comparing burned with unburned clearcuts (Abrams and Dickman 1982; Whittle et al. 1997). The presence of permanent OMNR plots within jack pine forests originating after clearcutting and planting, clearcutting plus prescribed burning and planting, and naturally regenerating forest after wildfire, provided an excellent opportunity to study the comparatively long-term effects (15 to 37 years) of these disturbances on plant communities. My objective was to compare understory vegetation communities developed after clearcutting plus prescribed burning with those of clearcut only and wildfire. The findings of this study are presented in the following two chapters. The first chapter deals with the response of understory plant communities to clearcutting, clearcutting plus prescribed burning, and wildfire disturbance. The second chapter examines the interaction between species' traits and disturbance types to explain the observed differences in community composition.

Chapter 1

Plant community assembly 15-37 years after wildfire, clearcutting, and clearcutting followed by prescribed burning in jack pine forests.

1.1 Abstract

Application of prescribed fire after clearcutting has been suggested as a means of reconciling differential effects of clearcutting and wildfire on plant communities. I assessed understorey communities in northwestern Ontario using fifty 100 m² plots, located in 15-37 year old jack pine stands established after clearcutting, clearcutting with prescribed burning, and through natural regeneration after wildfire. I hypothesized that understories at sites established after clearcutting with prescribed burning would resemble those of natural wildfire origin stands more closely than those of clearcutting alone. However, I found that understorey communities of all three disturbance types had similar species richness and diversity. Furthermore, species composition within prescribed burned sites differed significantly from both clearcut and wildfire sites, which were similar. Use of prescribed burning after clearcutting resulted in compositional differences comparable to those found after short-interval wildfires. Eleven indicator species were identified for the prescribed burned sites, while only two were identified for the wildfire and clearcut sites. Indicator species of prescribed burned sites were mostly ruderal and disturbance tolerant species, suggesting that clearcutting and prescribed burning created a compound effect on plant communities. The short-interval between disturbances (clearcutting and prescribed burning) may have caused increased damage and death of vegetation, which provided colonizable space for invading early successional species than the communities originating from only clearcutting or wildfire.

1.2 Introduction

Community dynamics and species composition are often a function of disturbance (Sousa 1984). Disturbances can be small-scale, such as individual plant death, through to large-scale, such as crown fires. In addition to spatial scale, the type, frequency, and severity of disturbance affect survival, propagule availability, colonization, and establishment in a post-disturbance community (Connell 1978; Roberts 2004; Johnstone 2006; Roberts 2007; Fraterrigo and Rusak 2008; Smirnova et al. 2008). Disturbances can provide opportunities for less-competitive species to maintain populations, by creating colonizable space and reductions in abundance of highly competitive species (Sousa 1984; Gardner and Engelhardt 2008). Furthermore, disturbance may provide opportunity for increased colonization by ruderal, early successional species (Kemball et al. 2006 and references within; Laughlin and Fule 2008). As a result, species diversity is often higher in disturbed communities than in climax communities (Huston 1979; Denslow 1980; Gardner and Engelhardt 2008). However, frequent disturbance can reduce species diversity (Gardner and Engelhardt 2008) or alter community composition by favouring disturbance specialists (Paine et al. 1998; Frelich 2002; Donato et al. 2009). Resilience of communities to disturbance, defined as the ability of an ecosystem to return to pre-disturbance state, is the result of interplay between the community and disturbance characteristics (Halpern 1988). Ecosystems vary in their resilience, but those with frequent disturbance such as those of the boreal forest, tend to be highly resilient, due in part to high plant and propagule survival rates (Morgan and Neuenschwander 1988; Wang and Kemball 2005).

The boreal forest is among the largest intact forested biomes on the planet, spanning much of the northern hemisphere. Intactness, however, does not infer

homogeneity. Though the Canadian boreal forest is considered largely unfragmented, it is actually comprised of a mosaic of forest types and ages. This mosaic results from the intrinsic presence of disturbance, where stand-replacing natural disturbances are spatially and temporally variable. The boreal forest has historically been disturbed by windthrow, insect defoliation, and most significantly stand-replacing wildfire (Johnson 1992; Burton et al. 2003; Johnstone and Chapin 2006; Kembail et al. 2006). Typical fire return intervals range from 20 to 500 years through most of the boreal forest in Canada (Flannigan and Harrington 1988; McRae et al. 2001). In northwestern Ontario the fire return interval has been estimated at an average of 200 years (Li et al. 1997). Notably, regional fire return intervals are generally derived from composite fire regimes, incorporating all ecosystem types to derive an average (Rowe 1983). Ecosystems such as jack pine (*Pinus banksiana* Lamb.) dominated forests, are often highly prone to fire and experience more frequent fire events (Lesieur et al. 2002). Though severe disturbance seems to be an inherently destabilizing force, in the case of jack pine stands, severe fires can actually be viewed as a community stabilizing agent (Frelich and Reich 1999). In the absence of fires, which remove the canopy and existing trees, the disturbance regime would shift to low-severity events such as individual tree fall. Under such a scenario, fire-dependent jack pine would have no means of re-colonization and a shift to dominance by late successional species would result (Frelich and Reich 1995).

Many boreal plants are adapted both to disturbance and a wide range of site conditions (Hart and Chen 2006). Thus, post-disturbance species composition often varies little from pre-disturbance, though species abundances may differ (Wang and Kembail 2006). As fire is the primary stand-replacing natural disturbance agent in this forest region,

many boreal plant species have developed adaptations to fire in particular, the most apparent and documented of which are their regeneration strategies (Shafi and Yarranton 1973; Rowe 1983). In the boreal forests of Ontario, the epitome of such adaptations is the jack pine. Jack pine is a short-lived species preferring xeric conditions, and as with most boreal trees, is early successional, requiring full light to grow. There are two further adaptations that exemplify this niche, a requirement for exposed mineral soil (or thin residual organic matter) for seed germination (de Groot et al. 2004; Greene et al. 2007) and cone serotiny (Gauthier et al. 1996). In fire-disturbed systems adaptations allowing survival or rapid colonization have been favoured through the filter of recurrent fire disturbance (Rowe 1983). Regeneration after fire can be from germination by seed or through sprouting and expansion by surviving underground structures, the relative importance of either strategy depends largely on fire severity. For example, increases in fire severity correspond with increases in recolonization by jack pine due to heat-mediated release of seeds and the availability of favourable germination sites. Alternatively, boreal understorey and hardwood species often depend on resprouting ability of buried structures to recolonize post-fire habitats (Hart and Chen 2008).

Human expansion, technological advances, and the need for fibre prompted extensive harvesting of trees for timber and biomass in the boreal forests of Ontario over the last century. Extensive forest harvesting coupled with fire suppression for protection of resources and human properties have shifted the disturbance regime within the managed boreal forest of Canada. In fact in the managed area of Ontario, clearcutting has surpassed wildfire as the predominant disturbance (OMNR 2004). With increases in environmental awareness through the last half of the 20th century, concerns were raised regarding

sustainability of forest harvesting practices, including maintenance of boreal biodiversity. Recently, much attention has been paid to the effects of wildfire and clearcutting on understorey species (Nguyen-Xuan et al. 2000; Reich et al. 2001; Rees and Juday 2002; Haussler and Bergeron 2004; Kemball et al. 2006; Elson et al. 2007; Hart and Chen 2008). In response to concerns for biodiversity, natural disturbance emulation (NDE) guidelines have been put in place in Ontario (OMNR 2006). NDE is a silvicultural method meant to spatially mimic natural disturbances, particularly wildfire. While this practice may provide benefits to wildlife (OMNR 2001), it does not address the effects of disparity between clearcutting and wildfire on other lifeforms. For example, the understorey of boreal forests provides much of the species diversity in these relatively species poor systems (Hart and Chen 2006). It has been well recognized that natural disturbance emulation is deficient in its ability to emulate natural fire regimes, spatially, temporally, and in specific effects on edaphic and biological features (Thiffault et al. 2007). Fire is a physiochemical process involving combustion of carbon with oxygen. Clearcutting on the other hand, provides only physical disturbance with little direct chemical change. Differential effects of clearcutting and wildfire on edaphic and biological aspects on these ecosystems are largely a function of disturbance severity. It has been well-recognized that severity of forest floor disturbance is among the most critical for affecting community composition (Nguyen-Xuan et al. 2000).

Crown fires burn intensely resulting in high fire severity (Sabo et al. 2009), often measured as the amount of organic matter (duff) combusted (Van Wagner 1972; Brais et al. 2000; Rydgren et al. 2004; Wang and Kemball 2005). The heat produced by a fire (intensity) and the combustion of organic matter (severity) affect the survival of the pre-disturbance community (Flinn and Wein 1977; Mallik and Gimingham 1985; Schimmel and Granstrom

1996; USDA 2000). Much of the carbon in boreal forests is tied up in the forest floor organic matter. Short growing seasons with long, cold winters and highly lignified conifer litter result in an accumulation of organic matter on the forest floor. Accumulation of organic matter can reduce species diversity by reductions in seed germination and seedling establishment and by nutrient lock-up in recalcitrant humus (Prescott 2000). Fire brings rejuvenation through removal of organic matter thus providing opportunities for seed germination and a flush of available nutrients (Prescott 2000; Greene et al. 2007). As a result of organic matter combustion during wildfire seedbed conditions are enhanced, potentially resulting in an increase in species richness due to colonization by early successional ruderals (Rees and Juday 2002; Kemball et al. 2006). Clearcut harvesting does not offer the same advantages since forest floor disturbance is less complete. With clearcutting much of the forest floor biomass remains intact, though it may be buried or scattered by mechanical site preparation.

Differences between fire and harvesting result in differential survival of plants, which can cause differences in post-disturbance community structure (heights and abundances of lifeforms) and composition (e.g. Kemball et al. 2006). Fire, which has greater impacts on above ground plant biomass than clearcutting, has been associated with comparatively reduced shrub cover (Haeussler and Bergeron 2004). However, even with damage to above ground portions, most boreal species are capable of regenerating through underground reproductive parts such as rhizomes, intact root systems, buried buds, and seeds (Granstrom and Schimmel 1993). Without the heat required to damage or kill pre-harvest communities a greater proportion of the late successional species may persist, resulting in increased competition as well as reduced space for colonization in clearcut

versus burned sites (Haeussler and Bergeron 2004; Kemball et al. 2006). In central Alaska, Rees and Juday (2002), found higher species turnover rates after wildfire compared to clearcutting, implying higher survival of pre-disturbance individuals in clearcut communities. In a very intense/severe fire all individuals and propagules may be destroyed. More often, fires burn in a patchy pattern, with certain areas burning at a greater severity than others, based on site and weather conditions, vegetation qualities, and time of year (Greene et al. 2005; Perera et al. 2009). As such, communities are rarely completely removed by fire and post-fire recolonization is largely attributed to survival of underground vegetative buds (Rowe 1983; Kemball et al. 2006).

Though there is some disparity in findings, studies show significant species diversity and compositional differences between post-fire and post-clearcutting communities (Nguyen-Xuan et al. 2000; Rees and Juday 2002; Kemball et al. 2006; Elson et al. 2007). Some studies found specific, age and lifeform dependent differences between communities developed after clearcutting and wildfire. Reich et al. (2001), noted similarity between post-fire and post-logging communities, with the exception of vascular plant diversity and composition in young jack pine and aspen stands (up to 30 years). Similarly, Hart and Chen (2008) found higher diversity and abundance of vascular plants and a corresponding reduction in nonvascular plants in stands 21-30 years after clearcutting compared with wildfire. Rees and Juday (2002) found a greater richness of lichens and bryophytes in clearcut compared to wildfire origin stands less than 38 years old, after which no differences in species richness were found. These differences were attributed to vegetation survival and colonization in post-disturbance communities, which have been traced to aforementioned intrinsic differences in disturbance type.

One management option with promise to not only prepare for planting after harvest, but to potentially advance natural disturbance emulation is the implementation of prescribed burning. Prescribed burning (PB) has been used to manage parcels of land in North America for more than ten millennia (Fowler and Konopek 2007). In the context of clearcut silviculture, PB is occasionally used to prepare harvested land for renewal by using the effects of fire, such as removal of organic matter to facilitate natural seeding or planting and to reduce competition (Luke et al. 2000). It has been proposed that PB be used to treat ~~clearcut sites~~ as a means of improving natural disturbance emulation (OMNR 2001; Burton et al. 2003) and managing for understorey plant diversity and providing habitat for fire-specialist species (Whittle et al 1997; Rees and Judav 2002). This recommendation followed findings that species assemblages and successional turnover differed between naturally burned and clearcut sites, including increased diversity and species turnover in burned sites (Rees and Judav 2002). Similarly, Johnston and Elliot (1996) found increased compositional similarity among communities arising from naturally burned black spruce (*Picea mariana* Mill.) cutovers and wildfire compared with harvesting alone. Whittle et al. (1997) examined the effects of PB after harvesting a jack pine forest on re-vegetation; they found six species unique to burned plots, and only one to unburned plots. Abrams and Dickman (1982), found consistently increased species richness on young (<5 years) burned jack pine cutover compared with unburned cutovers in Michigan. Similarly, Tellier and Duchesne (1995) found transient differences one year after PB, including an increase in species richness in the burned treatment, which did not persist into the second growing season.

A central tenet of biodiversity conservation is to maintain comparable species composition to unmanaged natural areas. It is therefore pertinent to ask whether application of prescribed burning after harvesting results in communities more similar to wildfire than clearcutting alone. It has been acknowledged that species composition differs in the early stages of succession, but little information exists of vegetation differences extending into the crown closure stage of stand development. There are limited studies contrasting vegetation communities in clearcuts and clearcuts with PB, however these are largely restricted to recent disturbances (Tellier and Duchesne 1995; Whittle et al. 1997). Community divergence has been observed between clearcuts and prescribe-burned clearcuts in early post-disturbance communities of boreal systems (Tellier and Duchesne 1995; Whittle et al. 1997) and persistent differences (31-39 years) in other systems such as eucalypt forests of Australia (Turner and Kirkpatrick 2009). A single study comparing the early effects (<10 years) of wildfire, clearcutting, and clearcutting with prescribed burning in black spruce forests demonstrated compositional similarity of burned cutovers with wildfire compared with unburned cutovers (Johnston and Elliot 1996). To my knowledge, no study has compared post-canopy closure differences in boreal understorey species diversity and composition after clearcutting, clearcutting followed by prescribed burning, and natural wildfire. Since prescribed burning has been suggested as a means of natural disturbance emulation, it is important to understand the effects of prescribed burning after clearcutting on plant communities. The presence of permanent plots within a number of jack pine plantations established after clearcutting, clearcutting with prescribed burning, and natural wildfire origin jack pine stands between the ages of 15 and 37, provided an excellent opportunity to assess comparatively long-term differences in understorey regeneration following these disturbances. Since jack pine dominated communities are disposed to

wildfire, these ecosystems are likely to have greater adaptation to fire than most other boreal plant communities. As a result of these adaptations, I hypothesized that understorey communities of jack pine developed after clearcutting with prescribed burning would be more similar to wildfire origin communities than those developed after clearcutting alone.

1.3 Methods

1.3.1 Study area

I conducted my study within the boreal forest of northwestern Ontario, Canada. Study sites ranged from 48° 11' 12" in the south to 51° 12' 27" in the north and from -94° 30' 18" in the west to -86° 24' 32" in the east (Figure 1-1). Average annual precipitation and temperature across this area ranges from 640 to 705 mm, and 0.9°C to 2.6°C, respectively (Environment Canada 2009). Common plant species of this area include; *Pinus banksiana* (Lamb.), *Picea mariana* (Mill.), *Populus tremuloides* (Michx.), *Betula papyrifera* (Marsh.), *Abies balsamea* ((L.) Mill.), *Acer spicatum* (Lam.), *Corylus cornuta* (Marsh.), *Diervilla lonicera* (L.), *Vaccinium* spp., *Cornus canadensis* (L.), *Pleurozium schreberi* ((Brid.) Mitt.), *Cladonia* spp. (Canadian Forest Service 2007). Geology in northwestern Ontario is variable, due to glaciations and past water movements. Harvesting began in this region in the 1920s, since then large expanses of land have been harvested and in many cases planted with jack pine (OMNR 2006). Beginning in the late 1970s prescribed burning has been used occasionally after clearcut harvesting to prepare sites for planting, largely on a trial basis.

1.3.2 Study design

1.3.2.1 Study sites

Northwestern Ontario is a large and geographically diverse area. In an attempt to control for this variation, comparable study sites of each disturbance type were selected as geographically close as possible; and in most cases equivalent numbers of study sites of each disturbance type were located within the same ecozone (Table 1-1). Additional criteria for site selection were soil and ecosite types as per the Ontario Forest Ecosystem Classification System (Simms et al. 1997) that integrates vegetation and environmental data, such as moisture and nutrient regimes and regional climate (Table 1-1). Although there was variation in soil and ecosite types, the range of variation was similar among the clearcut, clearcut followed by prescribed burning (hereafter referred to as PB), and wildfire sites. Using preliminary data collected in the summer of 2007, the required sample size for statistical accuracy was calculated (Equation 1). I calculated that the minimum required number of study sites was 20 within each disturbance type, for a total of 60 sites. However, due to logistical problems, particularly accessibility, I sampled a total of fifty study sites.

$$n = (S_p^2 / \delta)^2 * (t_{\alpha(2)df} + t_{\alpha(2)df})^2 \quad \text{Equation 1.}$$

Where S_p is standard deviation of the population, δ is the minimum detectable difference, and t is the value taken from the statistical t -distribution table.

I focused on jack pine communities established after clearcut, PB, and wildfire, ranging from 15 to 37 years post-disturbance. Sites within this age bracket had achieved canopy closure and although there was variation in the stand ages, due to limited study site availabilities, similar age ranges were captured within each disturbance type (Figure 1-2).

Study sites were selected from Ontario Ministry of Natural Resources databases of Permanent Growth Plots (PGPs), which are traditionally used to study tree growth. All sites were predominantly jack pine, selected at a threshold of >70% basal area. Of the 50 study sites, 18 were clearcut, 17 PB, and 15 wildfire origin. Stand details including origin, tree composition and corresponding basal area, age, ecosite type, soil type, and ecoregion were documented in OMNR databases and in the case of wildfire origin sites also within OMNR GIS fire databases. Although I have no quantitative wildfire severity data, it was assumed that natural stands of pure jack pine were the result of high severity fire (Smirnova et al. 2008).

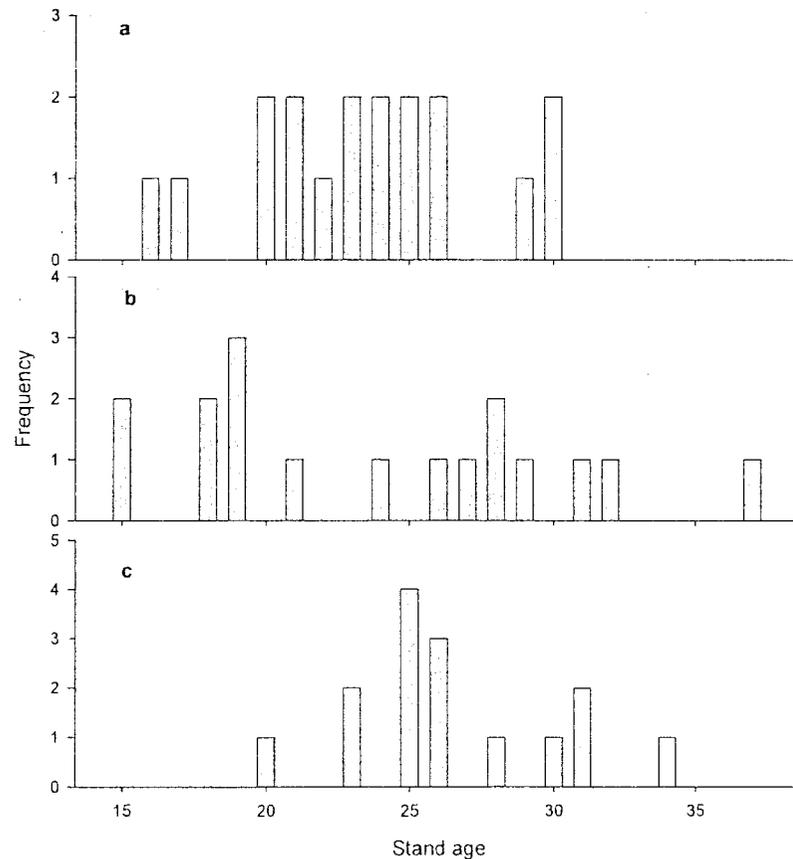


Figure 1-1. Frequency of stand ages for a) clearcut (n=18), b) PB (n=17), and c) wildfire (n=15), ranging from 15 to 37 years.

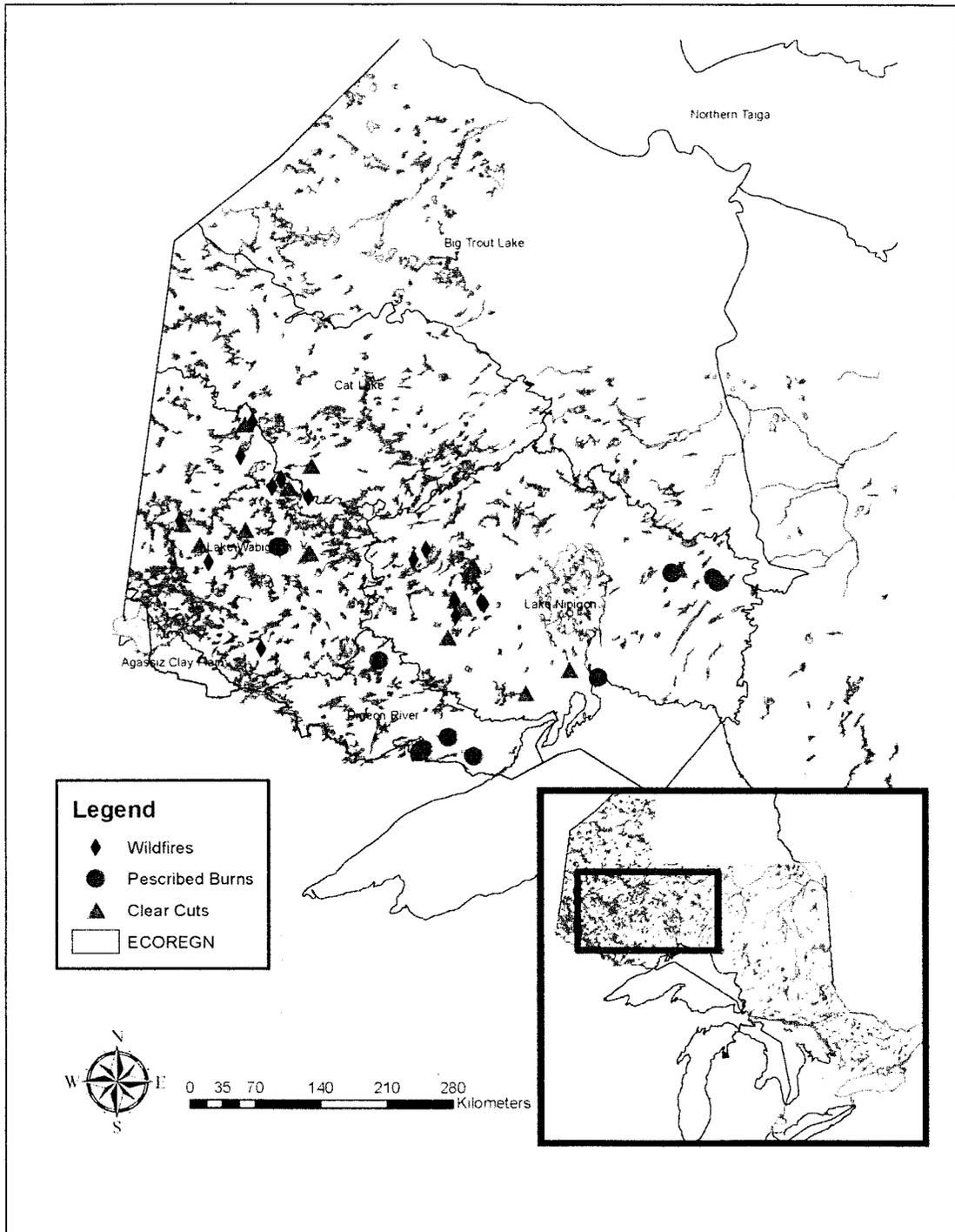


Figure 1-2. Map of study area and location of study sites clearcut (n=18), PB (n=17), and wildfire (n=15) in northwestern Ontario.

Table 1-1. Ecosite, and soil types of study sites in the clearcut, PB, and wildfire origin stands. Bracketed numbers indicate number of plots in each Ecosite and soil type and Ecoregion.

Treatment	Ecosite type	Soil type	Ecoregion
Clearcut	ES13(7), ES14(4), ES20(6), ES21(1)	S1(1), S2(5), S3(1), SS5(6), SS6(5)	3W (10), 3S (1), 4W (0), 4S(7)
PB	ES13(6), ES20(10), ES21(1)	S2(4), S3(5), SS5(3), SS6(5)	3W (6), 3S (0), 4W (7), 4S(4)
Wildfire	ES12(1), ES13(5), ES14(1), ES20(7), ES36(1)	S1(2), S2(5), S3(2), SS5(4), SS6(2), SS7(1)	3W (7), 3S (3), 4W (0), 4S(5)

1.3.2.2 Plot design

Habitat and vegetation data were collected during the peak vegetation period in July and August of 2008. Two plot sizes were used at each site. A single 10 x 10 m vegetation plot was installed in each site, in which I measured all site characteristics, structural layers, species presence-absence, and abundance of large shrubs and trees. To collect species abundance data I installed twelve 1 x 1 m quadrats randomly within the vegetation plot. For this I divided the vegetation plot into four quadrants and randomly (using a grid and random number system) sampled three quadrats in each quadrant.

1.3.2.3 Site parameters

Site parameters were measured to ensure that they were not an underlying cause for community differences (i.e. mesotopography and canopy cover) and/or to determine whether disturbance-related site differences that can alter post-disturbance communities were persistent (i.e. organic matter depths and pH). I quantified mesotopography through degree of slope, aspect, and position of the plot on a slope. Slope characteristics,

particularly aspect, interacts with disturbance type altering effects on site conditions and community response (Astrom et al. 2007). Slope positions were recorded as a value between one and six, with 'one' indicating slope crest and 'six' indicating level terrain. Canopy cover was measured using a spherical densiometer, following the methods of Strickler (1959), who determined a directional procedure for estimating canopy cover using a spherical densiometer without the overlap that occurs with traditional methods. I took four measurements from the plot centre, one facing each of the cardinal directions. I took three measurements of organic matter depths and pH at each site; one within every fourth 1 x 1 m quadrat. Depths of the litter, fibric, and humic organic layers were measured individually. Litter refers to relatively undecomposed matter, such as leaves and needles. Fibric material is decomposed further than litter, although is still identifiable. Humic material is the most decomposed of the surface organic matter horizons; at this stage all semblance to the original material is absent. Soil pH was measured in the field with an IQ150 pH metre, in both the humic organic layer and the 'A' horizon of the mineral soil, as most changes in chemical composition are limited to the surface soil horizon (Neff et al. 2005).

1.3.2.4 Community structure

I measured vegetation structure using percent cover estimates of lifeforms (lichens, bryophytes, pteridophytes, graminoids, herbaceous species, shrubs, hardwood trees, and conifer trees). Percent cover of woody lifeforms was estimated within height classes as follows; <0.5 m, 0.5-2 m, 2-4 m, and subsequently in 2 m intervals to a maximum observed height of 14 m.

1.3.2.5 Community composition

Species nomenclature followed those employed within the Ontario Plant List (NHIC 2008). Species abundance data were measured as percent cover. For small shrubs and trees (<1.3 m), herbaceous plants, and nonvascular species, I estimated abundance in 12 random 1 x 1 m quadrats. Quadrat level abundances were averaged to obtain plot level values. I recorded presence-absence data for all terrestrial species as well as abundance of larger trees and shrubs (>1.3 m) within the 10 x 10 m vegetation plot. Some graminoids lacked sufficient material to allow for identification and some species of moss e.g. *Brachythecium* spp. were not identified to species level. By recording presence-absence data I was able to capture some species that were missed in the 1 x 1 m quadrat sampling due to patchy distribution or species rarity.

1.3.3 Data analysis

Multivariate Analysis of Variance (MANOVA) was used to detect disturbance-level differences in site characteristics and to test the relationship of each site characteristic on species richness and Shannon's diversity. Structural layer data did not conform to assumptions of normality or homogeneity of variance. Since these assumptions could not be met through data transformation, Kruskal-Wallis rank sum tests were used to analyze for differences in structural layers among disturbance types. Statistically significant differences were further tested using pairwise Kruskal-Wallis rank sum tests, to determine significant structural differences between disturbance types. ANOVA and Kruskal-Wallis rank sum tests were performed using the Stats Package in R (R Development Core Team 2009). Vegetation abundance data were organized in a species-by-site abundance matrix based on the plot-averaged abundance data. Species richness was calculated using presence-absence data

collected from the 10 x 10 m vegetation plot. Shannon's diversity index was calculated using averaged plot-level abundance data of all species encountered in the twelve 1 x 1 m quadrats (Equation 2). Shannon's diversity index is a commonly used index of diversity. This index incorporates species evenness to provide a value representing community entropy, which provides a valuable index to diversity (Jost 2006). Species richness and diversity data did not conform to normal distributions, and were log transformed for parametric analysis. I tested the hypothesis of no richness and Shannon's diversity differences between disturbance types with one-way ANOVA.

$$H' = - \sum_{i=1}^S p_i \ln p_i \quad \text{Equation 2.}$$

Where H' is Shannon's index, and p_i is the proportion of abundance of the i th species.

To test the hypothesis of no compositional difference between treatments, I performed Nonparametric Multi-response Permutation Procedure (MRPP) using Sørensen distance, with PC-Ord Version 5 (McCune and Mefford 2006). The A-statistic derived from MRPP provided an estimate of within-group homogeneity in species composition, relative to that expected through random data partitioning (McCune and Grace 2002). The P -value estimated the probability of the derived A-statistic being the result of chance. Further MRPP analyses were run for lifeform subsets to identify lifeform-specific compositional differences among the disturbance types.

To identify which species were indicative of disturbance-based community differences for all species and within lifeforms, I conducted an Indicator Species Analysis (ISA) using PC-Ord software version 5 (Dufrene and Legendre 1997; McCune and Mefford 2006). ISA uses relative frequency and abundance data to calculate an indicator value that represents the strength of association of species to *a priori* identified groups (McCune and Grace 2002). Indicator values may range from 0 to 100; with 0 representing no association and 100 representing complete association. Monte Carlo randomization tests, using 1000 test runs, provided *P*-values that signified whether the probability of derived indicator values were stronger than expected by chance. In addition, a Reverse Indicator Species Analysis (RISA) was conducted to determine missing or relatively absent species within disturbance types. For the RISA an inverse abundance matrix was used; calculated by subtracting the abundance value from its highest potential value (100%). For example, a species with an abundance of 5% would score a 95% in the inverse abundance matrix (100% - 5% = 95%). This approach allowed for identification of species with comparatively reduced abundances in a particular disturbance type (clearcut, PB, or wildfire), in the same way that a traditional ISA identifies species with relatively high abundances in a particular group.

I ran a Nonmetric Multidimensional Scaling (NMS) ordination using PC-Ord (Version 5; McCune and Mefford 2006). NMS employs an iterative procedure that reduces the dimensionality of a dataset while minimizing the 'stress' value. NMS is valuable for nonlinear data, often found in community data, which tends towards an abundance of zero values. I ran the NMS calculations using Sørensen distance measure, with a random starting configuration and 250 runs with the real data. Axes were selected using a Monte Carlo procedure, using 100 runs with randomized data. The NMS outcome is assessed using the

final stress value; low stress values indicate that dimensionality was reduced without a great loss of information. Two matrices were used, a species-by-site abundance matrix and a plot-by-site characteristics matrix. Ordination was performed using the species-abundance matrix; I overlaid the site characteristics matrix on the ordination based on a threshold Pearson correlation value of 0.2.

1.4 Results

1.4.1 Vegetation structure

No structural differences were found among most woody layers (Figure 1-3a,b,c). Structural differences were found in the conifer 8-10 m height layer between the PB and clearcut sites ($H=6.7$, $P=0.001$) as well as the PB and wildfire sites ($H=5.6$, $P=0.018$), with PB sites having lower cover (Figure 1-3a). Although there was lower cover of 8-10 m conifer height class, there was a corresponding increase in the height classes directly beneath (6-8 m) and above (10-12 m) (Figure 1-3a). Other differences among conifers included the 0.5-2 m height layer between the PB and clearcut sites ($H=6.3$, $P=0.012$) and the PB and wildfire sites ($H=10.4$, $P=0.001$), as well as between the PB and wildfire <0.5 m height layer ($H=5.2$, $P=0.022$), in all cases the PB sites had lower conifer cover. Hardwoods within the 8-10 m layer showed significant cover differences among the wildfire and clearcut sites ($H=3.7$, $P=0.032$) and the wildfire and PB sites ($H=7.2$, $P=0.007$), in both instances the wildfire sites had higher cover in the 8-10 m hardwood tree layer (Figure 1-2b). Bryophyte lifeform cover differed significantly between the PB and clearcut sites ($H=12.1$, $P=0.000$) and the PB and wildfire sites ($H=4.6$, $P=0.031$) (Figure 1-4). Other nonwoody lifeforms, herbs, pteridophytes, graminoids, and lichens showed no significant differences in percent cover (Figure 1-4) (see also Appendix I).

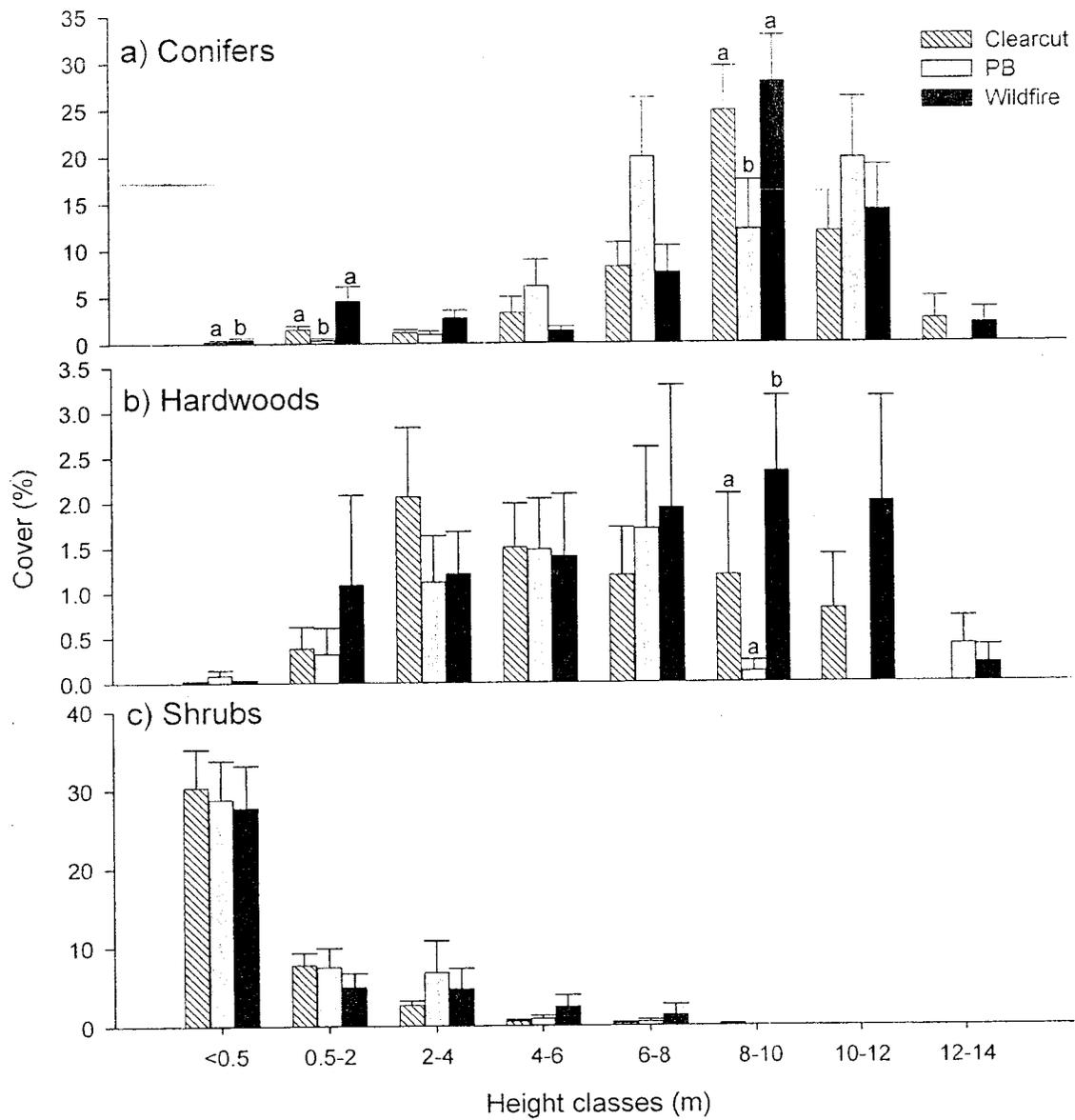


Figure 1-3. Mean and standard error for percent cover within height classes of woody vegetation structural layers among clearcut (n=18), PB (n=17), and wildfire (n=15) sites. Unlike letters within height classes denote statistical significance at $\alpha=0.05$.

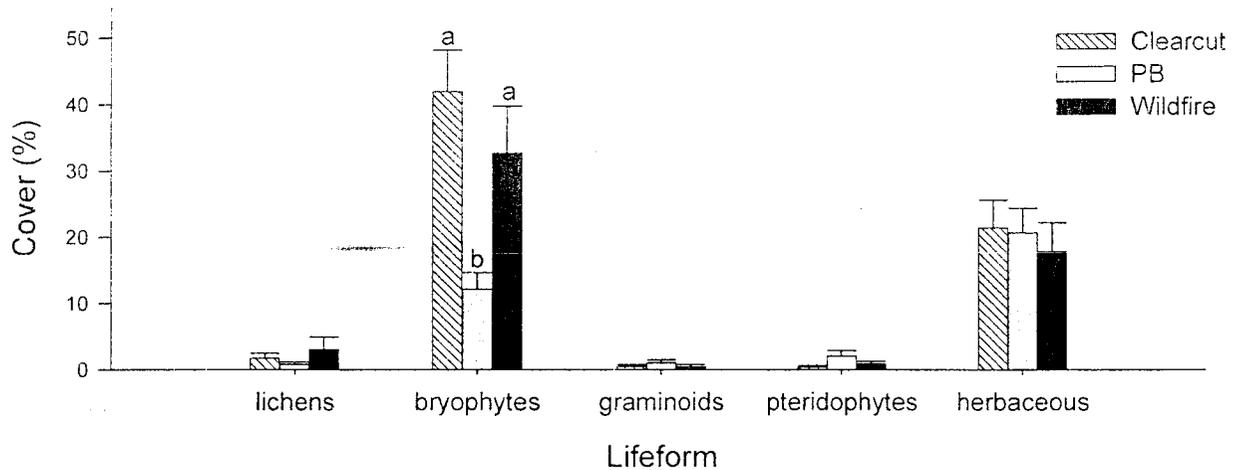


Figure 1-4. Mean and standard error for percent cover within non-woody structural layers among clearcut (n=18), PB (n=17), and wildfire (n=15) sites. Unlike letters within lifeform layers denote statistical significance at $\alpha=0.05$.

1.4.2 Species richness and diversity

I recorded 155 species among the 50 sites: 6 trees, 38 shrubs, 43 herbs, 9 graminoids, 11 pteridophytes, 28 lichens, and 20 bryophytes. No differences in species richness were found among the clearcut, PB, and the wildfire origin sites ($F_{2,48}=1.344$, $P=0.271$). Similarly, no significant differences were found among the disturbance types with respect to Shannon's Diversity Index ($F_{2,48}=0.503$, $P=0.608$). With both measures of diversity (richness and Shannon's diversity index) the PB sites showed slightly higher values, which were not statistically significant (Table 1-2). Alpha diversity (site level) varied from 5 to 42 in the clearcut sites, 7 to 43 in the PB, and 12 to 30 in the wildfire sites. Total disturbance-level species diversity was 113 in clearcut, 118 in PB, and 105 in wildfire disturbance. The PB sites had fewer total species of shrubs and greater lichen richness than clearcut or wildfire sites. Other than these cases, treatment level diversity among life forms was similar (Table 1-3).

Table 1-2. Mean Shannon's diversity values (H') and species richness (\pm standard error) for clearcut (n=18), PB (n=17), and wildfire (n=15) sites.

Diversity	Clearcut	PB	Wildfire
H'	1.758(0.078)	1.813 (0.090)	1.708 (0.114)
Richness	20.778 (1.830)	24.824 (1.914)	21.200 (1.471)

Table 1-3. Disturbance level species richness of lifeforms, trees, shrubs, herbs, graminoids, pteridophytes, bryophytes, and lichens for clearcut (n=18), PB (n=17), and wildfire (n=15) sites.

Treat- ment	Trees	Shrubs	Herbs	Graminoids	Pteridophytes	Bryophytes	Lichens	Total
Clearcut	4	31	32	6	11	17	12	113
PB	5	23	32	9	9	17	23	118
Wildfire	6	32	27	5	5	19	11	105

1.4.3 Species composition

Species composition differed among the three disturbance types; clearcut, PB and wildfire (MRPP, $A=0.027$, $P=0.007$). Pairwise comparisons of species composition among disturbance types showed that the PB sites differed from both clearcut and wildfire sites (Table 1-4). Within-group agreement values (A), derived from comparisons of PB with clearcut and with wildfire, were positive and statistically significant at a 99.9% confidence level, indicating that within-group compositions were more similar than among groups. However, the clearcut and wildfire sites were not significantly different, indicating similar compositions. Although the A value derived through pairwise comparison of clearcut and wildfire sites was not significant, it was notably a negative value, inferring that greater compositional differences exist within than among the disturbance types.

Table 1-4. Pairwise MRPP test statistics, within-group agreements, and probabilities among understory communities within clearcut (n=18), PB (n=17), and wildfire (n=15) sites.

Treatments	Test statistic (T)	Within-group agreement (A)	P
Clearcut x PB	-4.72	0.067	0.001
PB x Wildfire	-4.16	0.068	0.001
Clearcut x Wildfire	1.04	-0.018	0.875

A total of 15 indicator species were identified through ISA; two for both the clearcut and wildfire sites, and 11 for the PB sites (Table 1-5). Significant indicator species were considered at $\alpha=0.1$. Three of the four indicator species were bryophytes in the clearcut and wildfire sites; *Dicranum polysetum*, *D. montanum*, and *Brachythecium salebrosum*. While in the PB sites no bryophyte indicators were found. Eight species were identified through RISA to be significantly absent from a disturbance type, four species were in clearcut, three in PB, and one in wildfire (Table 1-6).

Analysis of species composition by life form revealed that the greatest compositional differences were in bryophytes (MRPP, $A=0.055$, $P=0.003$). Significant indicator bryophytes were *Dicranum polysetum* and *D. montanum* for the clearcut sites, and *Brachythecium salebrosum* for the wildfire sites (Table 1-5). No bryophyte indicator species were found for the PB sites. Composition of medium-sized shrubs (0.5 to 1.3 m) differed significantly among disturbance types (MRPP, $A=0.033$, $P=0.051$), while low shrubs (<0.5 m) differed significantly at $\alpha=0.1$ ($A=0.027$, $P=0.099$). However, neither life form group resulted in any statistically significant indicator species. Other life forms analyzed were lichens ($A=0.012$, $P=0.727$) and herbs ($A=0.006$, $P=0.270$).

Table 1-5. Indicator species significant at $\alpha=0.1$ with corresponding indicator and probability values for the clearcut (n=18), PB (n=17), and wildfire (n=15) sites.

Species	Indicator Value (IV)	P
<u>Clearcut</u>		
<i>Dicranum polysetum</i>	51.4	0.046
<i>Dicranum montanum</i>	27.3	0.081
<u>PB</u>		
<i>Cladonia gracilis</i>	45.8	0.058
<i>Cladonia verticillata</i>	45.4	0.092
<i>Aster sagittifolia</i>	45.0	0.000
<i>Hieracium caespitosum</i>	35.5	0.005
<i>Aster macrophyllus</i>	32.7	0.053
<i>Viola renifolia</i>	26.5	0.038
<i>Lathyrus ochroleucus</i>	23.5	0.015
<i>Fragaria virginiana</i>	23.0	0.065
<i>Anaphalis margaritacea</i>	17.6	0.058
<i>Schizachne purpurescens</i>	17.6	0.063
<i>Osmunda claytoniana</i>	17.6	0.095
<u>Wildfire</u>		
<i>Picea mariana</i> (seedling)	49.2	0.003
<i>Brachythecium salebrosum</i>	13.3	0.082

Table 1-6. Missing species derived from Reverse Indicator Species Analysis, significant at $\alpha=0.1$ with corresponding indicator and probability values for the clearcut (n=18), PB (n=17), and wildfire (n=15) sites.

Species	Reverse Indicator Value (IV)	P
<u>Clearcut</u>		
<i>Aster sagittifolia</i>	33.3	0.050
<i>Hieracium pratense</i>	33.4	0.084
<i>Brachythecium salebrosum</i>	33.3	0.089
<i>Apocynum androsaemifolium</i>	33.3	0.096
<u>PB</u>		
<i>Dicranum polysetum</i>	34.2	0.000
<i>Pleurozium schreberi</i>	36.7	0.001
<i>Vaccinium caespitosum</i>	33.6	0.018
<u>Wildfire</u>		
<i>Viola</i> spp.	33.3	0.089

Community analysis using NMS identified a three-axis solution with a final stress level of 14.66, after 153 iterations. The R^2 values for the three axes were 0.168, 0.206, and 0.374 respectively. The ordination diagram demonstrated an aggregation of PB sites somewhat separated from the clearcut and wildfire sites mostly along the second axis (Figure 1-5). Only the second axis was correlated with any site variables. Axis 2 was negatively associated with organic matter pH ($r=-0.534$). The PB sites were grouped toward the lower end of axis 2, indicating a correlation with increased organic matter pH. Wildfire and clearcut sites showed little distinction from one another along the second axis; however, the wildfire sites were situated almost entirely on the low end of axis 1.

1.4.4 Site parameters

Disturbance type did not demonstrate any significant effects on the measured site parameters ($F_{4,45}= 0.938$, $P=0.451$) (Table 1-7). Additionally none of the measured variables demonstrated a significant relationship (MANOVA) to species richness or diversity, stand age ($F_{2,47}= 0.504$ $P= 0.607$), degree of slope ($F_{2,47}= 2.710$ $P= 0.078$), canopy cover ($F_{2,47}= 0.740$ $P= 0.483$), depths of litter ($F_{2,47}= 2.618$ $P= 0.084$), fibric ($F_{2,47}= 1.289$ $P= 0.285$) and humic organic layers ($F_{2,47}= 0.711$ $P= 0.496$), or mineral soil pH ($F_{2,47}= 0.469$ $P= 0.629$). Organic matter pHs were not used due to missing data from plots with little or no recognizable humic layer. Ecoregion did have a significant effect on diversity ($F_{6,92}=3.816$, $P= 0.002$), caused by ecoregion effects on species richness ($F_{3,46}= 8.278$, $P=0.000$), but not Shannon's diversity index ($F_{3,46}= 1.881$, $P=0.146$). This effect was caused by differences between ecosites 3W and 3S ($P=0.010$) and ecosites 3W and 4W ($P=0.001$). These differences provide some cause for concern, particularly since only PB sites were located in ecoregion 4W.

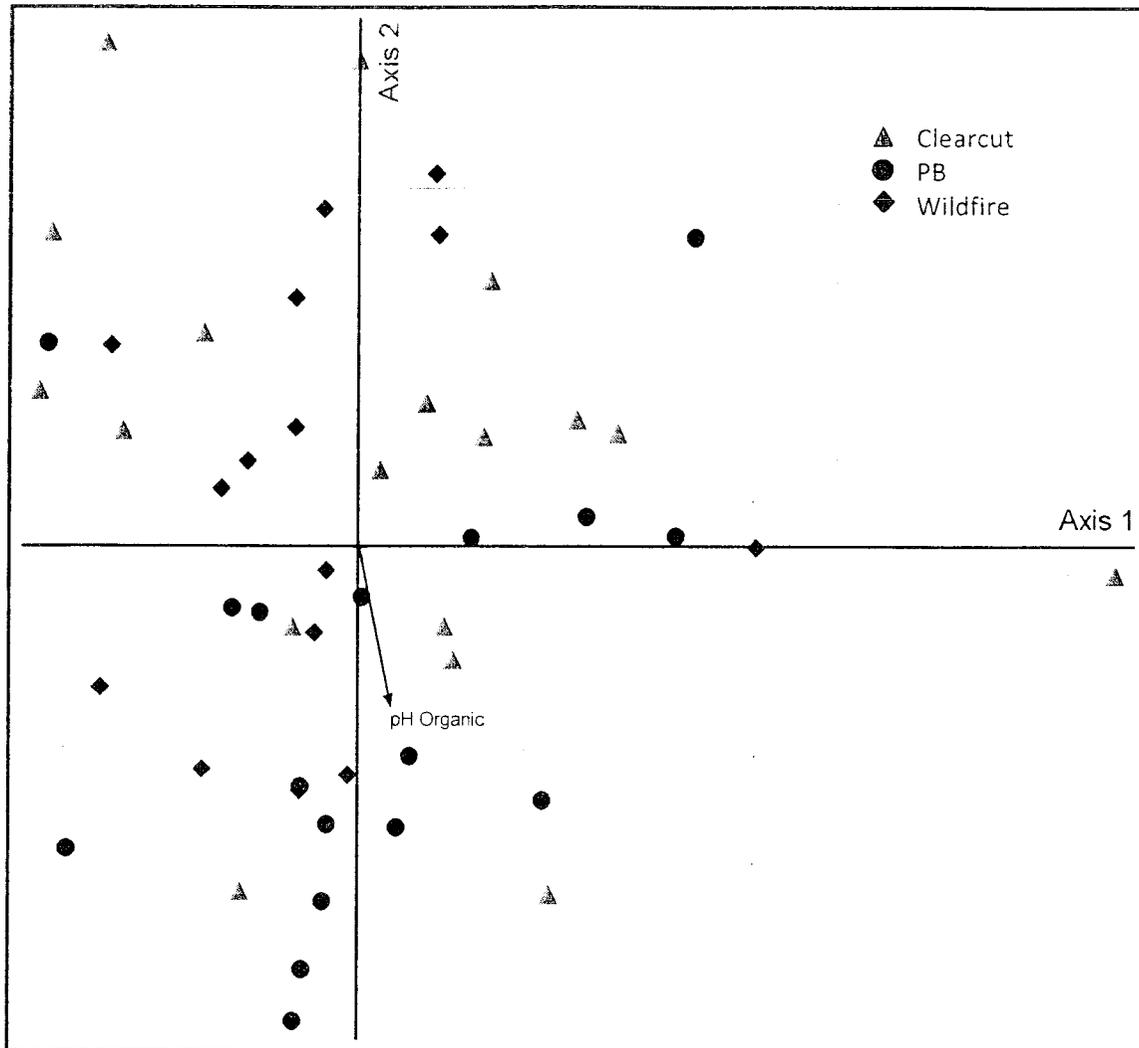


Figure 1-5. Nonmetric Multidimensional Scaling axes 1 and 2, showing clearcut (n=18), PB (n=17), and wildfire (n=15) sites, overlain with organic matter pH, the significant site characteristic at a correlation coefficient of $r = 0.2$. Each data point represents a site level mean derived from twelve 1 m² quadrats for a total of n=50.

The number of sites in 3W was similar among disturbance types (10 in 6 in PB, and 7 in wildfire). Although only PB sites were located in ecoregion 4W, this was in part the result of a trade off with sites in ecoregions 4S and 3S (higher frequencies in clearcut and wildfire sites), which did not differ from 4W significantly in richness. Further, since species richness and Shannon's diversity index were not significantly affected by disturbance type, I presume that ecoregion effects on my results were minimal. I have discussed the potential effects of this spatial limitation in further detail in the general conclusions (pg. 72).

Table 1-7. Mean (\pm standard error) of quantitative site characteristics at clearcut (n=18), PB (n=17), and wildfire (n=15) sites.

	Clearcut		PB		Wildfire	
Stand age	20.778	(1.830)	24.824	(1.914)	21.200	(1.471)
Slope	4.667	(0.676)	7.118	(1.745)	4.667	(0.960)
Aspect	139.722	(0.676)	138.824	(28.382)	137.800	(27.403)
Canopy cover	47.600	(1.640)	49.200	(1.520)	45.700	(2.010)
Litter depth	0.807	(1.410)	0.992	(0.130)	0.816	(0.133)
Fibric depth	3.680	(0.420)	2.600	(0.390)	3.540	(0.570)
Humic depth	0.650	(0.220)	0.330	(0.090)	0.680	(0.105)
pH Organic	4.523	(0.121)	4.849	(0.139)	4.163	(0.156)
pH mineral	4.651	(0.166)	4.937	(0.178)	4.419	(0.143)

1.5 Discussion

My hypothesis that application of prescribed burning after clearcutting has resulted in vegetation communities more like wildfire than clearcutting alone, was not supported. In terms of species richness and Shannon's diversity there were no detectable differences among the disturbance types, similar to findings of Reich et al. (2001) where total species diversity and richness did not differ among clearcut and wildfire origin stands, though lifeform specific differences were found. Other studies have found higher diversity after wildfire compared with clearcutting (Rees and Juday 2002) or conversely short term increases in diversity after clearcutting (Tellier and Duchesne 1995). However, it is often the case that species richness does not differ, but abundances of species may differ as reflected in composition/abundance data (Wang and Kembell 2006). This similarity in species diversity indicates that the effects of disturbance type were not responsible for the number of species inhabiting these sites. However, purely quantitative data, such as species richness and diversity provide little insight toward community characteristics. Arguably, species richness and Shannon's diversity index are crude plant community measures; a simple count of the number of species offers little insight into a community's composition. For example, a site with 10 graminoid species cannot be considered equivalent to a site with 10 bryophyte species. It was necessary to delve further into the actual community composition to determine whether the communities differed.

At 15-37 years, with respect to species diversity and composition, the communities of clearcut and wildfire originated sites appear to have converged. Perhaps it is not surprising, since recovery of species composition following disturbance in fire-adapted ecosystems is mainly through regeneration of surviving individuals and persistent seed

banks (Halpern 1988). However, these findings contradict those of Reich et al. (2001), who found differences in richness, Shannon's diversity, and community composition of vascular plants (though not when analyzed using all species) among similarly aged (25 – 40 year old) clearcut and wildfire origin jack pine stands, in northern Minnesota. I found that application of prescribed burning after clearcutting resulted in dissimilar community composition compared to both the clearcut and wildfire sites. These findings differ from those of Johnston and Elliot (1996) where application of prescribed burning after clearcutting in black spruce forest resulted in composition more similar to wildfire than clearcutting alone. However, in addition to a small sample size, the clearcut site in their study was not subjected to post-harvest site preparation treatments and their study was conducted less than 10 years post-disturbance. Not only were the PB sites compositionally different, but they had a greater number of species on a treatment level and a greater number of indicator species. Therefore, PB sites held a number of species that were underrepresented in wildfire and clearcut sites. Compositional differences with PB cannot be explained by the persistent site effects I examined, although they may provide evidence of site differences that occurred at the time of disturbance.

These results can be explained with respect to the compounding effects of successive short-interval disturbances. In this case prescribed burning was applied approximately two years after clearcutting, providing little time for community recuperation prior to the second disturbance, PB. The short-interval second disturbance (PB) may have further reduced survival and compounded disturbance effects on site conditions. Short-interval disturbances can have severe effects on community composition (Paine et al. 1998), while not necessarily on values of diversity (Schoennagel et al. 2004). In areas with high-

severity fires, a major stand replacing fire is sometimes followed by short-interval successive burns or 're-burns' (Donato et al. 2009 and references therein). Occurrence of these successive burns has been found to alter community composition and successional trajectory. Corresponding reductions in species groups can create gaps for recruitment of early successional species. For example, Donato et al. (2009) found that occurrence of a short-interval fire resulted in high representation of early successional species, attributed to a reduction in broad-leaved woody species. Much of the effects of fire on vegetation results from destruction of woody species that do not resprout; with short-interval fires only resprouting species can effectively persist due to their ability to survive underground (Frelich 2002). Significantly lower cover of hardwood species in the canopy of PB sites exemplified this effect. Additionally, disturbance level shrub diversity though not abundance, was reduced in PB sites. This indicates that removal of woody species provided space for the remaining woody species to expand into the available space. Current shrub abundance may be similar among disturbance types as a result of the time since disturbance, allowing for recovery from initial declines. Additionally, both the clearcut and the PB sites were treated with mechanical site preparation (scarification) and herbicides, which might have reduced shrub abundance (Bell and Newmaster 2002). It is possible that in absence of these treatments higher shrub densities would have been found in the clearcut sites. Though the application of PB following clearcutting is a different combination of disturbance than 're-burns', similar results were found in this study, indicating that clearcutting with prescribed burning acts as a compound disturbance.

Altered species compositions in PB sites support this theory, considering reduced abundance and richness of bryophytes as well as greater richness of lichen species.

Newmaster and Bell (2002) found both lower bryophyte and lichen diversity (lasting at least 5 years) with increasing silvicultural disturbance. The compounding of disturbance on the PB sites might have resulted in greater disturbance effects on communities than occurred on either the wildfire or clearcut sites. The multiple disturbance filters imposed on the PB community likely resulted in increases disturbance-tolerant species (E.g. *Cladonia* spp.). Furthermore, the vascular indicator species for the PB sites were largely seed disseminated ruderal, early successional species. Additionally, none of the PB indicator species were of the bryophyte lifeform. The PB sites could be expected to have lost much of the bryophyte cover as a result of the multiple disturbances. Bryophytes are highly flammable when dry and with canopy removal these nonvascular species would have been subjected to desiccation (Hylander 2009). Many bryophytes require specific substrates, such as downed wood to establish (Mills and Macdonald 2004). This substrate in particular would have been lacking due to removal of biomass after harvesting and PB.

As with many post-hoc studies, some aspects of the history of study sites were unknown, such as detailed pre-disturbance species composition, although the sites were characteristic of those occupied by jack pine communities. The wildfire plots, being nearly pure jack pine ensures that regeneration occurred from the cone seed bank present on the site at the time of wildfire. It is important to note, that although species composition of wildfire and clearcut stands appear to have converged, it is possible that early successional pathways may have differed (Rees and Juday 2002; Whittle et al. 1997). Further, the clearcutting in these study sites were not discrete events. Planted clearcuts typically undergo mechanical site preparation the year after harvesting, prior to planting, and chemical herbicides are often applied within 10 years afterward. The PB sites experienced

further disturbance through burning within two years of harvesting, prior to both mechanical and chemical site preparation. Variability in the timing and specifics of such events is common and could not be controlled for in the scope of this study.

1.6 Conclusions

Contrary to my hypothesis, PB sites have demonstrated community divergence at the 15-37 year time period examined within this study, while clearcut and wildfire sites showed community convergence. Application of PB after clearcutting resulted in communities similar to those that originate from short-interval disturbances. It could be argued that the observed compositional similarity of clearcut and wildfire sites and their dissimilarity with PB sites could be the result of spatial separation of the PB study sites. However, compositional differences were exemplified by early successional, ruderal and disturbance-tolerant indicator species, and not those with a high degree of geographic variation. These findings indicate that fire-prone boreal jack pine communities demonstrate a high degree of resilience with regard to disturbance type, while disturbance frequency can have lasting effects on species composition. In the context of plant community composition and structure, it appears that application of PB after clearcut harvesting does not further natural disturbance emulation. In the next chapter I examine the role of the short interval between disturbances on these plant communities using a trait analysis approach.

Chapter 2

Short-interval disturbance effects on community trait composition: the influence of prescribed burning after clearcutting in jack pine forests.

2.1 Abstract

Application of prescribed burning after clearcutting (PB) resulted in persistent community composition differences compared with clearcutting alone and wildfire 15-37 years after disturbance. Since application of PB does not involve a novel disturbance, compositional differences may be related to the short-interval between clearcutting and prescribed burning. I hypothesized that compositional differences found in the PB sites correspond to the interaction of short-interval disturbance with species' life history and regeneration traits. Disturbance related plant traits were analyzed to quantify relationships to disturbance type using abundance-weighted trait analyses, consisting of RLQ ordination, Fourth-Corner Analysis, functional diversity indices, and community weighted means. RLQ is a three-way ordination that links trait and environment using species abundance data. I used RLQ to assess for a relationship between a species' trait matrix and disturbance type. Fourth Corner Analysis was used to evaluate the relationship of specific traits with disturbance type, again using a species-abundance matrix as a link. I calculated three functional diversity indices; functional richness, evenness, and dispersion for relationship to disturbance type. I analyzed community weighted trait means for differences in dominant trait expression among disturbance types. I found significant relationships for Raunkiaer's life form, seed banking, wind dispersal, deciduous foliage, rosette growth form and alien status with PB. However, most traits were not related to a specific disturbance type, and no significant relationship was found between the suite of traits and disturbance. My hypothesis was supported by the prevalence of seed banking and wind dispersal in the PB sites, both of which are known to increase with short-interval disturbances. From these results I conclude that application of PB following clearcutting causes compositional differences that result from disturbance-mediated plant trait selection by short-interval disturbances.

2.2 Introduction

Traits are species' attributes, and certain traits enable species to inhabit specific environmental conditions. Species' traits or rather interaction of traits with extrinsic forces (i.e. disturbance) are suggested to be the underlying causes of differences in community composition across environmental gradients (Halpern 1989a; Crane 2005; Fraterrigo et al. 2006). Species traits may represent ecological functions provided by species (Garnier et al. 2004). There is a growing understanding that species diversity may be less important than functional diversity, in affecting ecosystem processes and community resilience (Tilman 1997). Therefore it has been argued that species conservation *per se* may not be as important as conservation of traits (Tilman 1997, Loreau 2000). In an attempt to explain plant community composition, dynamics, and general ecological trends there has been a shift in focus from description and classification toward trait analysis (Halpern 1989b; Tilman 1997; Eviner and Chapin 2003; Austerheim et al. 2005; Pausas and Verdu 2005; Keith et al. 2007). Species' trait approaches follow a central tenet of community ecology in the search for generalizations that identify key processes that shape community assemblages. Studies of community ecology often require data reduction as a means of removing noise and natural variability within the data. Trait analysis provides a means of reducing complexity of natural systems, resulting in simplified data allowing for identification of general patterns (Diaz and Cabido 1997). Responses of community composition and dynamics to disturbance lend themselves well to trait analyses (Halpern 1989; McIntyre et al. 1995; Lavorel et al. 1997; Kleyer 1999; Pausas et al. 2004), since species' traits interact with disturbance to determine survival, post-disturbance colonization, and growth. Species' traits such as life form, mode of vegetative and sexual reproduction, resprouting ability, propagule dispersal, and growth rate are important drivers of post-disturbance community

composition (Donato et al. 2009; McIntyre et al. 1995). With respect to fire disturbance, Noble and Slatyer (1980) refer to this category of traits as 'vital attributes', i.e. traits that are vital to post-fire succession. Vital attributes fall into three categories; method of arrival or persistence after disturbance, ability to establish and grow to maturity, and time taken to reach critical life stages.

A species trait approach can be used for *post hoc* assessment of the biotic and abiotic filters imposed upon a community. Biotic and abiotic filters selectively encourage or discourage species survival, colonization, and establishment based on their traits (Lavorel and Garnier 2002). For example, clearcutting in the boreal forests of Ontario filters species through changes in growing conditions, mechanical and chemical damage to individuals, and degree of forest floor disturbance (Nguyen-Xuan et al. 2000; Haeussler et al. 2004; Newmaster et al. 2006). This filtering effect causes differences among pre- and post-clearcut communities through losses and gains of species (e.g. Roberts and Zhu 2002). Compositional changes result partly from availability of colonization sites; with increased available space for early successional species that may provide compositional changes (Rees and Juday 2002). Degree of compositional change has been shown to correlate with the degree of disturbance severity (Frelich and Reich 1999; Haussler et al. 2004; Rydgren et al. 2004). However, regardless of disturbance type and severity, boreal forest communities tend toward convergence after disturbance (Haeussler et al. 2004). Typically disturbances in the boreal forest are single, relatively discrete events. However, in fire-prone ecosystems such as those of the boreal, wildfires may occur in relatively rapid succession (Johnstone 2006; Donato et al. 2009). Immediately after disturbance community assembly is governed primarily by plant regeneration processes either through vegetative or sexual means,

followed by competition as available space becomes depleted (Noble and Slatyer 1980). Occurrence of subsequent disturbances prior to community convergence may result in further filtering of the regenerating community by compound effects on the community (Frelich and Reich 1999; Donato et al. 2009). Several authors have shown that temporal variation in disturbance-free interval can affect post-disturbance communities (Sousa 1984; Paine et al. 1998; Ross et al. 2004). Short-interval disturbances support a particular trait assemblage, including obligate seeding, re-sprouting, early successional, short-lived, and alien species (Rowe 1983; Peterson and Carson 1996; Johnstone 2006; Donato et al. 2009). Donato et al. (2009) found that fast-maturing seed banking species in particular, were highly represented after short-interval fires. Successive disturbances impart multiple biotic and abiotic filters that control post-disturbance community assembly.

Since the boreal forest is largely a fire-disturbed system, traits such as the 'vital attributes' described by Noble and Slatyer (1980), play a role in its high degree of resilience. Forest fires of this region are typically crown fires of high severity, causing death of all aboveground vegetation (Van Wagner 1978). The resiliency of the boreal forest implies that, by and large, boreal vegetation have mechanisms enabling persistence through disturbance and/or colonization after disturbance (Rowe 1983). As a result, boreal plants depend on seed and vegetative sprouting; the relative role that each plays is dependent on disturbance characteristics. Although historically the most extensive stand-replacing natural disturbance affecting this biome was wildfire, the disturbance regime in much of the Canadian boreal forest has shifted in the last century due to fire suppression and clearcutting (OMNR 2004). Despite current governmental attempts at encouraging natural disturbance emulation to promote maintenance of natural fire patterns, wildfire and clearcutting differ intrinsically

(OMNR 2001). Wildfire and clearcutting vary in their effects on post-disturbance communities, biomass, forest floor conditions, and nutrient cycling (Nguyen-Xuan et al. 2000; Rees and Juday 2002; Kembell et al. 2006; Thiffault et al. 2007). In spite of these differences boreal plant communities have shown resilience, as communities originating from various disturbances tend to converge (Haeussler et al. 2004). For example, Reich et al. (2001) reported vascular species composition differences in jack pine forests for up to 30 years, but not in older stands.

I demonstrated in Chapter 1 that plant communities developed after clearcutting and wildfire had similar understorey species compositions at 15 to 37 years post-disturbance. However, the addition of prescribed burning after clearcutting resulted in different composition 15 to 37 years post-disturbance. Since clearcutting followed by prescribed burning is a combination of fire and harvesting, no new disturbance type was added that could explain the observed community differences. However, this community difference may be attributed to application of two disturbances within a short interval. Use of prescribed burning as a means of site preparation typically occurs within two years of harvesting. Application of prescribed burning results in further death and damage to individuals, resulting in increased space for colonization. At this juncture, most species have not recovered enough to reproduce, and so new colonization can be expected to occur from fast-reproducing species present on the site, soil seed bank, wind dispersion, and vegetative expansion (Donato et al. 2009). By analyzing the relationship of plant traits to disturbance type, underlying causes for compositional differences can be examined.

I examined community composition differences found in sites subjected to clearcutting followed by prescribed burning compared with those subjected to only

clearcutting and to wildfire using a species' trait approach. As a result of the compounded community filtering associated with successive short-interval disturbances, I hypothesized that application of prescribed burning after clearcutting would result in a specific trait assemblage representative of the imposed filters.

2.3 Methods

For analysis of traits I used the species abundance data collected for Chapter 1. Data were collected from fifty 10 x 10 m plots. In each plot I sampled twelve 1 x 1 m quadrats, for a total of 600 quadrats. However; one plot of the clearcut sites was removed due to exceptionally low species abundance (8.8% total abundance), compared to the mean disturbance-type total abundance of 79.5%. It is possible that further silvicultural disturbance occurred (i.e. re-application of herbicides) or some other unidentified force further disturbed this particular community, resulting in very low total plant cover. Since the total abundance of the plot in question was greater than two standard deviations away from the mean, it was excluded from this study. As a result, species abundances from 588 quadrats were used for the purposes of trait analysis. Among these 17 were clearcut, 17 were prescribe-burned (PB), and 15 were wildfire origin plots (See Chapter 1 for complete description of study area and study design).

2.3.1 Trait selection

I considered species traits based on their relation to persistence, colonization (dispersal), and establishment (Weiher et al. 1999) after clearcutting and/or wildfire, as well as on availability of trait data. Persistence through a clearcutting or wildfire event may be indicated by expression of the following traits (see Table 2-1); Raunkaier's life form,

vegetative reproduction (stolon and rhizome), re-sprouting ability, fire resistance, and fire tolerance (Rowe 1983; Donato et al. 2009). Colonization after disturbance may be indicated by seed banking, specific dispersal agents, and propagule type (Rowe 1983; McIntyre 1999; Johnstone 2006). Leaf retention, carbon: nitrogen ratio, growth rate, growth form, and shade tolerance relate to species' ability to establish.

Trait data were compiled from a number of sources including the USDA plants database and fire effects database, field guides, journal articles, as well as online floras (see Appendix II). Some data on shade tolerance and Raunkaier's Life form were inferred from species' habitat preferences and morphology. All trait data were categorical.

2.3.2 Data analyses

Data were first analyzed to demonstrate compositional differences among clearcut, PB, and wildfire sites, using MRPP (McCune and Mefford 2005). Sørensen's distance measure was used with the autopilot mode set at slow and thorough using 1000 randomly seeded runs. I used a direct approach to analyze the communities for differential expression of traits based on disturbance type consisting of functional diversity indices, community weighted means, Fourth-Corner Analysis, and RLQ ordination (described below). Community weighted means of traits that showed a relationship with disturbance type were further analyzed by Chi square tests of independence, adjusted using Holm's correction for multiple comparisons. All data analyses were conducted using the free-ware statistical program R (R development core team 2009). RLQ and Fourth Corner Analysis can be found in the 'ADE4' package, while functional diversity indices and community weighted means can be calculated using the 'FD' package.

Table 2-1. Species' traits (16), trait descriptions, and species examples.

Trait	Description	Importance	Examples
Raunkiaer life form	Based on location of regenerative buds (phanerophyte, chamaephyte, hemicryptophyte, geophyte, therophyte).	Bud placement relative to forest floor affects ability to survive disturbance	Geophyte- <i>Anemone quinquefolia</i>
Stolon	Above ground means of clonal growth (binary)	Allows for rapid recolonization from surviving individuals or colonizers	<i>Fragaria virginiana</i> , <i>Hieracium caespitosum</i>
Rhizome	Below ground means of clonal growth (binary)	Allows for recolonization from surviving buried structures	<i>Achillea millefolium</i> , <i>Apocynum androsaemifolium</i>
Re-sprouting	Resprouting of woody species following top removal (binary)	Allows regrowth following top kill	<i>Rubus idaeas</i> , <i>Corylus cornuta</i>
Fire resistance	Known to resist burning (binary) (USDA 2009)	Affects survival through fire	<i>Chimaphila umbellata</i>
Fire tolerance	Relative ability to resprout, re-grow, or re-establish from residual seed after fire (low, medium, high) (USDA 2009)	Affects survival through fire	High- <i>Prunus pensylvannica</i> , low- <i>Sorbus americana</i>
Seed banking	Storage of seed in forest floor or mineral soil (binary)	Allows reestablishment	<i>Rubus idaeas</i>
Seed dispersal	Mechanism of seed dispersal (animal, gravity, wind)	Potential for invasion	wind- <i>Epilobium angustifolium</i>
Propagule type	Spore or seed	Sexual propagule survival (seed>spore)	Spore- <i>Lycopodium annotinum</i> , seed- <i>Eurybia macrophylla</i>
Leaf retention	Deciduous, evergreen, or partial evergreen	Competition or stress tolerance strategy	Deciduous- <i>Gaium triflorum</i> , evergreen- <i>Chimaphila umbellata</i>
C:N	% Organic carbon / % total nitrogen in above ground organic material (Low: <23; Medium: 23 – 59; High: >59). (USDA 2009)	Competition or stress tolerance strategy	High- <i>Acer spicatum</i> , low- <i>Vaccinium vitis-idaea</i>
Growth rate	Growth rate after successful establishment relative to other species with the same growth habit (slow, medium, rapid) (USDA 2009)	Competitive ability	Rapid- <i>Anaphalis margaritacea</i> , slow- <i>Cornus canadensis</i>
Rosette	Basal growth form (binary)	Competitive ability	<i>Hieracium caespitosum</i>
Prostrate	Creeping growth form (binary)	Competitive ability	<i>Gaultheria hispidula</i>
Shade tolerance	Relative tolerance (intolerant, intermediate, tolerant)	Affects competitiveness	Tolerant- <i>Viola blanda</i>
Alien status	Native or alien	Disturbance has been shown to increase abundance of alien species	Alien- <i>Hieracium caespitosum</i>

RLQ, a three way ordination, was used to determine the relationship between traits and disturbance type (Dolédec et al. 1996). RLQ uses three matrices to assess the trait-environment relationship; site x environment (R), species x trait (Q), and site x species abundance (L) matrices, hence the name RLQ. Abundance and environment data are linked through sites, while trait and site data are linked by species composition. I used the three disturbance types as environmental variables, so my site x environment matrix consisted of site and disturbance type (clearcut, PB, and wildfire). RLQ uses three distinct ordinations to create a co-inertia table with the greatest degree of covariation between the environment and trait data. Significance of the detected relationship between R (environment) and Q (traits) was assessed using a Monte Carlo randomized permutation procedure. The Monte Carlo procedure permutes the rows of the R and Q matrices and compares this with inertia in the RLQ analysis (Dolédec et al. 1996).

Fourth Corner Analysis is similar to RLQ in that it directly quantifies the link between species' traits and environment, using the same three matrices in a one step analysis (Dray and Legendre 2008). However, Fourth corner differs from RLQ in that, while RLQ identifies relationships between the two matrices as a whole, Fourth Corner enables examination of the relationship of each trait individually with disturbance type. As with the RLQ analysis the environmental matrix consisted of plots and disturbance types (clearcut, PB, and wildfire). Though the original Fourth-Corner Analysis developed by Legendre et al. (1998) was suitable only for binary species data, a new version allows the use of abundance data (Dray and Legendre 2008). Fourth Corner Analysis allows for hypothesis testing using five potential models to test different hypotheses. I used the first model, which permutes values for each species independently (Dray et al. 2007).

Villegger et al. (2008) proposed three indices to describe functional diversity of communities; functional richness, evenness, and dispersion. Functional diversity indices were calculated to quantitatively assess the representation of life history and reproductive traits expected to enable or inhibit recolonization. In the case of multivariate analysis, these indices reflect community distribution in multidimensional functional space, using species abundance and trait data (Villegger et al. 2008). Often functional diversity is estimated through use of functional groups (species with like traits), however that approach results in information loss. Functional diversity indices provide quantitative values describing community trait assemblage patterns allowing for comparison among communities, using continuous or categorical trait variables. These indices use PCoA axes derived from a Gower dissimilarity matrix. Functional richness is defined as the volume of the multidimensional functional space that a community occupies. Functional evenness represents the distributional regularity within the occupied space. Functional dispersion measures dissimilarity of communities within the multidimensional functional space (Villegger et al. 2008). These indices were used to capture variation in prevalence and distribution of selected traits within and among clearcut, PB, and wildfire origin sites. Community values of functional richness, evenness, and dispersion were analyzed using ANOVA to test the hypothesis of no differences in functional richness, evenness, or dispersion among the disturbance types.

The FD package was used to calculate community weighted mean trait values (Laliberté 2009). Community weighted means represent the central tendency of trait expression within a site. Since the traits used in this study were categorical, the community weighted mean is expressed as a modal average. Community weighted means were

assessed using Chi squared tests of independence to test for disturbance-specific trait dominance. Chi squared tests of independence compare the frequencies of one nominal variable for different values of a second nominal variable. The Chi square test of independence tests the null hypothesis that the relative proportions of a variable are independent of the second variable. In this case, the null hypothesis is that the frequency of a nominal trait is not related to the disturbance type.

2.4 Results

2.4.1 Species composition and functional diversity

Species composition differed among the three disturbance types ($A=0.034$; $P=0.031$). This difference was driven by compositional deviation of the PB sites from both the clearcut and wildfire sites (Table 2-2). The clearcut and wildfire sites had similar species composition, indicated by a T statistic close to zero and a slightly negative A (within group chance-corrected agreement), indicating that variation within groups was slightly greater than variation among clearcut and wildfire origin sites.

Table 2-2. MRPP T statistics, within-group agreement (A), and probabilities for pair wise comparisons of composition in clearcut, PB, and wildfire sites (n=49).

Treatment	T	A	P
Clearcut vs. PB	-2.927	0.047	0.011
Clearcut vs. Wildfire	0.992	-0.016	0.852
Wildfire vs. PB	-2.588	0.043	0.02

Functional diversity indices, functional richness ($F_{2,46}=1.49$; $P=0.24$), functional evenness ($F_{2,46}=1.37$; $P=0.26$), and functional dispersion ($F_{2,46}=0.04$; $P=0.95$) were statistically similar among the clearcut, PB, and wildfire sites (Table 2-3).

Table 2-3. Mean (\pm standard error) of functional richness, evenness, and dispersion of clearcut, PB, and wildfire sites ($n=49$).

Treatment	Richness	Evenness	Dispersion
Clearcut	0.142 (0.016)	0.375 (0.034)	0.263 (0.013)
PB	0.166 (0.013)	0.439 (0.027)	0.261 (0.016)
Wildfire	0.133 (0.011)	0.433 (0.030)	0.267 (0.009)

2.4.2 Specific trait relationships with disturbance types

Fourth Corner Analysis demonstrated statistically significant ($\alpha < 0.05$) relationships between the PB disturbance type and specific traits (Table 2-4; Appendix II). Of the analyzed traits, Raunkiaer's lifeform ($\chi^2=1.056$, $P=0.018$), leaf retention ($\chi^2=4.414$, $P=0.018$) dispersal agent ($\chi^2=2.542$, $P=0.018$), rosette growth form ($\chi^2=0.972$, $P=0.018$), and marginally alien origin ($\chi^2=1.987$, $P=0.052$) were significantly related to the PB sites. No significant species' trait relationships were identified for the clearcut or wildfire disturbance types.

Central tendencies of disturbance-level categorical and ordinal traits from the community weighted means are presented in Table 2-5. Only seed banking ($\chi^2=9.808$, $P=0.009$) showed significant disturbance specific dominance (Table 2-5). Seed banking was a significantly more dominant trait on the PB sites than on either clearcut ($\chi^2=6.348$, $P=0.049$) or wildfire sites ($\chi^2=11.484$, $P=0.002$).

Table 2-4. Statistically significant results ($\alpha=0.05$) from the Fourth-Corner Analysis, where species' traits are positively (+) or negatively (-) associated with the PB disturbance type. Blanks indicate a non-significant relationship.

Trait	State	Relationship with PB	<i>P</i>
Raunkaier	Chaemophyte	(-)	0.005
	Geophyte		
	Hemicryptophyte		
	Phanerophyte		
	Therophyte		
sexual	Seed	(-)	0.002
	Spore		
leaf	Deciduous	(-)	0.001
	Evergreen		
	Partial evergreen		
seed bank			
C.N	high		
	low		
	medium		
	medium		
growth	rapid		
	slow		
stolon			
rhizome			
sprouting			
fire resistance			
fire tolerance	high		
	low		
	medium		
	none		
shade	intolerant		
	midtolerant		
	tolerant		
dispersal	animal	(-)	0.001
	gravity		
	wind		
rosette		(+)	0.006
prostrate			
alien		(+)	0.020

Species' traits that were found to be significantly related to PB were further examined through dominant trait states identified within community weighted means. The PB sites were dominated by species with deciduous foliage, while the clearcut and wildfire sites were dominated by deciduous and evergreen species in similar proportions. PB plots showed a greater proportion of wind and gravity dispersal that corresponded to a reduction in animal dispersal. Three of the PB sites had wind dispersal as the community weighted mean contrasted with one site for both the clearcut and wildfire origin sites. The proportion of plots dominated by gravity dispersed seed was similar though slightly greater in PB (0.35) than in clearcut (0.29), and wildfire sites (0.27). Phanerophytes were the predominant Raunkiaer life form in the clearcut, PB, and wildfire sites, with some domination by chaemophytes, hemicryptophytes and in one instance within the PB group, geophytes. Both rosette and alien species were minor components of all communities, and as such expressed no dominance within a community.

2.4.3 Trait matrix relationship with disturbance types

I used RLQ to determine whether a general relationship exists between trait composition and disturbance type. I found no significant relationship between trait and disturbance matrices ($P=0.434$). However, the RLQ results can be used to facilitate understanding of the relationship among traits and disturbance type already found to be significant by the Fourth-Corner Analysis and analysis of community weighted means. A solution with two axes was produced, with eigenvalues of 0.351 and 0.141 (Figure 2-3). Axis one was most negatively correlated with alien species and partial leaf retention, and most positively correlated with low fire tolerance (Table 2-6). Axis two was most negatively

correlated with spore production, wind dispersal, and medium C: N ratios, and positively with no fire resistance and chaemophytes (Table 2-6). The most notable aspect of this ordination is the proximity of clearcutting and wildfire on the positive end of the first axis, which accounted for 67.8 % of the variance explained. The PB sites separated from the clearcut and wildfire toward the negative end of the first axis (Table 2-7). The second axis, which represented 32 % of the total explained variation, showed separation of wildfire from the PB and clearcut disturbance type.

Chaemophytes, phanerophytes, seed banking, leaf retention, dispersal agent, rosette growth form and alien status were demonstrated to significantly differ among the disturbance types based on the analysis of community weighted means and/or Fourth Corner Analysis, and merited further examination through the RLQ findings. Graphical representation of the ordination of traits within species-trait space demonstrates some of the relationships (Figure 2-3). Seed banking, partial leaf retention, wind dispersal, and alien status, (all identified as have a relationship with the PB sites) occupied the negative end of the first axis corresponding to the PB sites (Figure 2-3).

Table 2-5. Relationship between traits and disturbance types using community weighted means of clearcut (n=17), PB (n=17), and wildfire (n=15) sites, described by proportion of sites expressing the study wide dominant trait state, Chi square test statistics and associated probability values (P); bold values indicate statistical significance at $\alpha=0.05$, blank values indicate a single level of trait state among all communities.

Trait	Dominant state	Clearcut			PB			Wildfire		
		Proportion	Proportion	Proportion	Proportion	Proportion	Proportion	Proportion	χ^2	P
Raunkaier	chaemophyte	0.71	0.59	0.67	3.582	0.856				
Sexual rep.	seed	1	1	0.93	2.314	0.306				
Leaf retention	deciduous	0.53	0.82	0.53	5.027	0.088				
Seed bank	present	0.18	0.52	0.07	9.808	0.006				
C:N	high	0.24	0.47	0.33	9.839	0.138				
Growth rate	slow	0.59	0.47	0.53	1.852	0.797				
Stolon	absent	1	1	0.87	4.726	0.092				
Rhizome	present	0.71	0.65	0.53	2.91	0.632				
Sprouting	present	0.65	0.77	0.6	3.332	0.523				
Fire resistance	absent	0.41	0.59	0.47	3.858	0.45				
Fire tolerance	high	0.41	0.71	0.47	7.584	0.297				
Shade										
intolerant	tolerant	0.29	0.47	0.6	3.42	0.514				
Dispersal agent	animal	0.65	0.47	0.67	2.276	0.732				
Rosette	absent	1	1	1	-	-				
Prostrate	absent	1	1	0.93	2.314	0.318				
Alien status	native	1	1	1	-	-				

Table 2-6. RLQ scores for traits expressions based on abundance of species with those traits for axis 1 and 2. scores from RLQ associated with Axes 1 and 2. Bold values indicate traits selected as significantly related to disturbance type by Fourth Corner Analysis.

Trait	Axis 1	Axis 2
alien	-1.620	0.071
animal	0.165	-0.007
chaemophyte	0.255	0.283
competitive	0.138	-0.114
deciduous	-0.148	0.000
evergreen	0.230	-0.001
fire resistant	0.280	-0.057
geophyte	-0.124	-0.081
gravity dispersal	-0.224	0.103
hemicryptophyte	0.046	-0.070
high C:N	-0.312	0.112
high fire tolerance	-0.161	0.045
intolerant (shade)	0.082	-0.047
low C:N	0.275	0.064
low fire tolerance	0.703	0.032
medium C:N	-0.060	-0.352
medium fire tolerance	0.147	-0.250
medium growth	0.065	-0.175
midtolerant (shade)	-0.148	-0.054
native	0.004	0.000
no fire resistance	-0.190	-0.004
no rosette	0.009	0.006
no seed bank	0.193	0.057
no stolon	-0.007	-0.001
not competitive	-0.095	0.078
not fire resistant	0.276	1.266
not prostrate	-0.002	-0.007
not rhizomatous	-0.124	0.062
not sprouting	0.181	-0.063
partial leaf retention	-0.735	0.091
phanerophyte	-0.037	0.016
prostrate	0.033	0.140
rapid growth	-0.474	-0.082
rhizomatous	0.093	-0.043
rosette	-0.389	-0.271
seed	0.002	0.021
seed banking	-0.328	-0.094
slow growth	-0.003	0.042
spore	-0.062	-0.536
sprouting	-0.042	-0.017
stolon	0.103	0.013
therophyte	-0.123	0.134
tolerant (shade)	0.065	0.073
wind dispersal	-0.404	-0.335

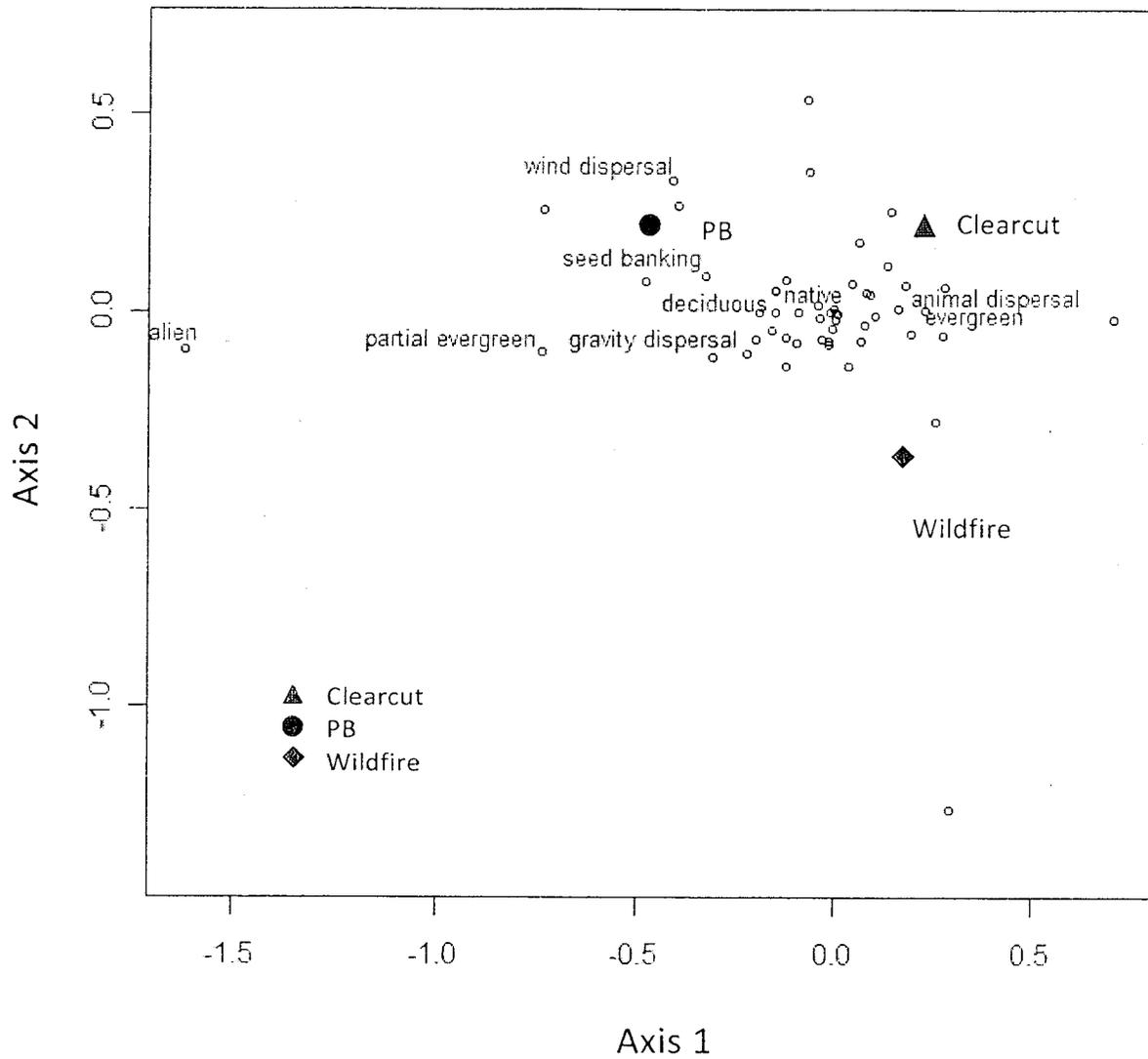


Figure 2-1. RLQ axes 1 and 2, illustrating traits and disturbance type in ordination space. Labelled trait points represent those traits demonstrated as significantly related to the PB sites through Fourth-Corner Analysis.

Table 2-7. RLQ scores for the disturbance types (clearcut, PB, and wildfire) based on species abundances for axes 1 and 2.

Disturbance type	Axis 1	Axis 2
Clearcut	0.486	-0.624
PB	-0.827	-0.102
Wildfire	0.283	0.775

2.5 Discussion

Boreal forests, particularly xeric components such as jack pine ecosystems, are highly prone to fire. This has resulted in communities that are highly resilient to both natural and anthropogenic disturbance. The species' trait matrix showed no significant relationship with disturbance type and most of the individual traits examined did not show any relationship to clearcutting, PB, or wildfire. Furthermore, there were no detectable differences in functional richness, evenness, or dispersion among disturbance types. This implies that the majority of understorey species' functional traits are capable of surviving varying disturbance types and regimes. However, frequency of such traits can vary depending on site specific conditions and disturbance history potentially with significant impacts on post-disturbance community composition.

My findings demonstrate that 15-37 years after disturbance, species composition of clearcut and wildfire origin jack pine sites were similar. However, application of prescribed burning within a couple of years after clearcutting altered plant community composition from that of clearcut and wildfire sites. These compositional differences were associated with differences in species' traits. My results support the hypothesis that trait associations with PB sites relate to the filtering effects of successive disturbances on post-disturbance

communities. Traits that showed a relationship with PB were Raunkiaer's lifeform, leaf retention, alien status, dispersal agent, rosette growth form, and seed banking. No traits were significantly related to clearcutting or wildfire disturbance.

The reproductive traits, seed banking and dispersal agent (reduction in animal and corresponding increase in wind dispersal), were significantly related to PB sites. Prevalence of seed banking and wind dispersal has been found to play a critical role in recolonization after successive fire disturbance (Donato et al. 2009). Increased dependence on seed regeneration (both wind dispersed and banked seed) can be related to disturbance effects on soil and the biotic community (Roberts 2004). The success of obligate seed banking species after disturbance depends on time to reach maturity (i.e. seed production during disturbance-free interval), seed survival through disturbance, and suitability of the post-disturbance site (Pausas et al. 2004). Since seed banking allows for long-term survival of species within the soil, it can play a major role in the post-disturbance community composition and diversity (Roberts 1981; Hills and Morris 1992). It has been suggested that clearcutting results in accumulation of larger seed banks than fire as an effect of heat damage to banked seeds by fire (Archibold 1989). However, in this study prevalence of seed banking species was higher in PB sites than clearcut and wildfire sites, indicating that the increases in seed banking species relate to the additive effect of two successive disturbances. Donato et al. (2009) suggested that short intervals between disturbances favour species capable of storing seed in the seed bank. As in the present study, prescribed burning after clearcutting has been shown to favour seed banking species compared with clearcutting alone (Whittle et al. 1997).

Species filtering associated with clearcutting followed by prescribed burning provides an explanation for the prevalence of seed banking and wind dispersal traits. In the current study, clearcutting involved canopy removal followed by mechanical and chemical site preparation. This treatment would have provided colonization opportunities for wind dispersed and buried seeds, by killing and damaging the existing understorey community and exposing mineral soil (Bell and Newmaster 2002). However, a major source for species re-establishment in this community would be through resprouting of species by underground vegetative propagules (Hart and Chen 2008). New colonization would have occurred within the first couple of years after disturbance, while competition-free colonizable spaces were still available. The addition of a second disturbance by prescribed burning would further damage individuals, reduce organic matter depths, and consequently increase colonizable space once again. This increase in forest floor disturbance would further stimulate germination of buried seed and provide establishment opportunities for plant propagules dispersed from nearby unburned patches. No relationships were found between sprouting or vegetative reproduction and disturbance type. This lack of relationship may have occurred because species of all three disturbance types would benefit from the ability to re-sprout. Clearcut, PB, and wildfire sites were all dominated by rhizomatous and sprouting species. This trend relates to the prevalence of wildfire disturbance in these ecosystems; vegetative reproduction through rhizomes and basal sprouts are common traits allowing for survival and post-fire establishment (Rowe 1983; Mallik 1994).

In addition to the reproductive traits, there were three non-reproductive traits that showed a positive relationship to PB: Raunkiaer's lifeform, leaf retention, and alien status.

Although all sites were dominated by chaemophytes, the PB disturbance type was negatively related to both chaemophytes and phanerophytes (shrubs and trees), both of which maintain buds above the forest floor interface. Regenerative tissues located aboveground are more susceptible to the effects of fire than belowground (Rowe 1983). Both clearcutting (with site treatments) and wildfire are known to reduce shrub cover in post-disturbance communities (Kemball et al. 2006; Redburn and Strong 2008). As such, it is understandable that some species of chaemophytes and phanerophytes would be filtered out through additive effects of clearcutting and wildfire. Similar reductions in woody species were found in early post-disturbance jack pine communities after clearcutting with and without prescribed burning (Tellier and Duchesne 1995). Further, the short time interval between these disturbances may not have allowed for recovery of damaged individuals prior to the second disturbance. The PB sites were dominated by deciduous species while clearcut and wildfire sites demonstrated equivalent dominance by deciduous and evergreen species. There is evidence relating leaf longevity to nutrient availability; leaf retention has been shown to negatively correlate with soil nitrogen (Reich et al. 1992). Further, early successional and competitive species often have deciduous foliage, while stress tolerant species often exhibit evergreen leaf retention (Chapin 1980). It is most likely that the relatively high representation of deciduous foliage in PB disturbance type relates to increases in early successional and ruderal species as demonstrated in Chapter 1. Alien origin, though important, cannot be expected to have any direct effect on disturbance survival or post-disturbance colonization. However, the strong positive relationship between alien origin and PB sites was the result of increases in abundance of *Hieracium caespitosum*. This species exhibits the other traits found to relate positively and significantly

to PB sites; seed banking, wind dispersal, rosette growth form, and deciduous foliage. The boreal forests of this region do not host an abundance of non-native species, and alien species constituted only a small portion of the total abundance in the study sites. The only non-native species documented within this study were *Bromus inermis* ssp. *inermis*, *Hieracium caespitosum* and *H. piloselloides*. *B. Inermis* ssp. *inermis* was rare throughout the study sites. However, both *Hieracium* species were relatively abundant in the PB sites and all but absent in the clearcut and wildfire sites (*H. caespitosum* present at 0.08% in one clearcut site; *H. piloselloides* present at 0.5% in one wildfire site). These alien species exemplify the significant traits found in this study to relate to short-interval disturbance. Perhaps this is what led to their successful colonization of new habitats.

2.6 Conclusions

The compositional divergence that occurs with prescribed burning after clearcutting is in accordance with typical effects of short-interval fires. It can be argued that the successive nature of clearcutting followed by prescribed burning resulted in altered community composition compared with clearcutting and wildfire disturbance composition. The prevalence of seed banking and wind dispersal within the PB sites demonstrated that the compositional differences were partly related to differential colonization opportunities. Although the disturbance types were mixed (i.e. clearcutting and prescribed burning) the compounding effect of the two disturbances resulted in similar trait relationships to those reported for short-interval fires.

Although the RLQ ordination of plant traits did not yield significant separation of traits or disturbance types, analysis of individual traits through Fourth-Corner Analysis and analysis of community weighted means showed relationships between disturbance specific traits and disturbance type. This exemplifies the importance of appropriate trait selection. Important trait relationships can be missed through incorporation of too many traits, especially those that do not relate to the ecological problem being examined (Bernhardt-Rommerman et al. 2008). Trait selection is highly subjective and often desirable trait data are not available, resulting in a biased trait selection that can affect whether or not relationships are detected (Bernhardt-Rommerman et al. 2008).

General discussion and conclusions

The objective of this study was to determine the relatively long-term effects of prescribed burning after clearcutting on understorey communities, compared with clearcutting alone and wildfire. I hypothesized that understorey communities on sites exposed to clearcutting plus prescribed burning would be more similar to wildfire origin communities than those originating from clearcutting alone, due to species' adaptations to fire. Secondly, I hypothesized that community differences could be explained by the filtering effects of clearcutting followed by prescribed burning on disturbance-specific species' traits.

I found that clearcutting with prescribed burning resulted in different community composition compared with clearcut and wildfire origin communities at 15 to 37 years since disturbance. The PB communities were characterized by early successional and disturbance-tolerant indicator species. Since the PB sites were not exposed to novel disturbances, I postulate that the species compositional difference is related to the compounded effects of short-interval disturbances. Multiple perturbations can result in trait assemblages that differ from those of single disturbances (Johnson 2006; Donato et al. 2009). I suggest that species trait expression in PB sites would be indicative of the filtering effects of short-interval fire disturbance. Assessment of disturbance-specific life history traits supported this hypothesis. I found positive relationships between seed banking, wind dispersal, deciduous foliage, rosette growth form, and alien origin with PB sites. As well as reductions in chaemophyte and phanerophyte species. Seed banking and wind dispersal directly relate to the effects of multiple perturbations on seed dependence and colonization opportunities (Donato et al. 2009). This relationship demonstrates that community differences are indeed

associated with effects of post-disturbance colonization, and more specifically with effects similar to those of short-interval wildfire disturbances (Johnstone 2006; Donato et al. 2009). Neither clearcutting nor wildfire disturbance had a significant relationship to the selected traits. This absence of relationship indicates that trait filters imposed on communities by clearcutting and wildfire disturbances are similar enough to result in comparable community composition. Based on the findings of this study, I conclude that application of prescribed burning after clearcutting does not mimic the effects of wildfire on understorey communities 15 to 37 years after disturbance. Furthermore, prescribed burning significantly increased abundance of a common non-native species, *Hieracium caespitosum*. This alien species exemplifies the traits that are favoured by short-interval disturbances.

As noted in Chapter 1, spatial separation of PB sites from clearcut and wildfire sites may have confounded compositional differences due to regional variation in species pools. Though the potential confoundment cannot be eliminated, I suggest that geographic variation constitutes only a minor role in observed community dissimilarity for the following reasons. Although analysis of diversity values based on Ecoregion demonstrated significant differences in richness, there were no corresponding differences in richness based on disturbance type. Further, Indicator Species Analysis, which was used to assess association of species with disturbance types, did not support compositional differences resulting from geographic variation. All indicator species associated with PB were widespread boreal species and most of which are typical of recently disturbed conditions and not of regional variation. In addition, using a species' trait approach in conjunction with a taxonomic approach provides comparative ability across regions and even continents (Duckworth et al. 2000; Diaz et al. 2004). Plant traits analyses are less sensitive to biogeographical differences

than taxonomic approaches, since they examine underlying mechanisms for community assembly, such as those driving post disturbance communities. Using these two approaches I have shown that community divergence of PB sites from clearcut and wildfire are the result of disturbance type influence on post-disturbance community assembly.

The implicit assumption of my conclusion, that application of prescribed burning does not improve natural disturbance emulation with regard to understorey communities, is that within the confines of this study clearcut sites were mechanically site prepared, planted, and chemically treated. However, assisted regeneration after clearcutting (as in this study) occurs in approximately 50% of clearcut areas in Ontario. In the remaining half of clearcut areas are left to naturally regenerate and thus experience fewer disturbances than their managed counterparts, in which case community composition can be expected to differ (Bell and Newmaster 2002; Redburn and Strong 2008).

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Appendix I. Structural data

Mean cover and standard error of structural layers within clearcut (n=18), PB (n=17), and wildfire (n=15) sites, with Kruskal-Wallis test statistics (H) and associated probabilities (P), significant values bolded, $\alpha=0.05$.

Structural layer	Clearcut		PB		Wildfire		H	P
	Mean	SE	Mean	SE	Mean	SE		
Conifer								
<0.5	0.038	0.012	0.194	0.176	0.387	0.227	6.188	0.045
0.5 to 2.0	1.500	0.394	0.359	0.190	4.540	1.572	12.018	0.003
2.1 to 4.0	1.125	0.354	0.941	0.369	2.667	0.843	4.376	0.112
4.1 to 6.0	3.200	1.735	6.059	2.815	1.267	0.452	1.334	0.513
6.1 to 8.0	8.125	2.578	19.824	6.315	7.467	2.890	0.163	0.922
8.1 to 10.0	24.750	4.743	12.059	5.258	27.800	4.968	8.328	0.016
10.1 to 12.0	11.875	4.214	19.706	6.438	14.133	4.834	0.332	0.847
12.1 to 14.0	2.500	2.357	0.000	0.000	2.000	1.676	2.270	0.322
Deciduous								
<0.5	0.013	0.008	0.082	0.058	0.020	0.011	1.560	0.458
0.5 to 2.0	0.381	0.241	0.318	0.293	1.087	0.996	0.703	0.704
2.1 to 4.0	2.063	0.767	1.118	0.514	1.207	0.469	1.838	0.399
4.1 to 6.0	1.500	0.487	1.476	0.562	1.400	0.689	0.161	0.923
6.1 to 8.0	1.188	0.532	1.706	0.898	1.933	1.354	0.274	0.872
8.1 to 10.0	1.188	0.899	0.118	0.118	2.333	0.838	8.814	0.012
10.1 to 12.0	0.813	0.604	0.000	0.000	2.000	1.159	5.098	0.078
12.1 to 14.0	0.000	0.000	0.412	0.310	0.200	0.200	1.910	0.385
Shrub								
<0.5	30.313	4.873	28.824	4.936	27.733	5.385	0.118	0.943
0.5 to 2.0	7.750	1.553	7.482	2.411	4.940	1.735	3.202	0.202
2.1 to 4.0	2.631	0.568	6.771	4.027	4.667	2.625	0.416	0.812
4.1 to 6.0	0.563	0.192	0.888	0.427	2.400	1.463	0.263	0.877
6.1 to 8.0	0.250	0.161	0.471	0.286	1.333	1.333	0.739	0.691
8.1 to 10.0	0.125	0.118	0.000	0.000	0.000	0.000	2.000	0.368
Herbaceous	21.450	4.184	20.706	3.696	17.873	4.385	0.851	0.653
Graminoid	0.400	0.187	2.035	0.848	0.847	0.386	5.380	0.679
Pteridophyte	0.481	0.294	1.053	0.412	0.440	0.332	1.608	0.448
Bryophyte	41.875	6.293	12.176	2.451	32.673	7.100	12.095	0.002
Lichen	1.681	0.777	0.800	0.318	3.060	1.850	0.551	0.759

Appendix II. Fourth Corner supplemental data

Relationship of species' traits to disturbance type including Chi squared test statistic and probability for each trait, and pseudofrequency, associated sign (above or below expected value) and probability for each trait state.

Trait	State		CC	PB	WF	
Raunkiaer		χ^2	0.126	1.056	0.498	
		<i>P</i>	1.000	0.018	0.782	
	Chaemophyte	Pseudofrequency	0.113 +	0.072 -	0.120 +	
		<i>P</i>	0.885	0.005	0.963	
	Geophyte	Pseudofrequency	0.114 -	0.126 +	0.105 -	
		<i>P</i>	0.318	0.897	0.124	
	Hemicryptophyte	Pseudofrequency	0.302 -	0.350 +	0.283 -	
		<i>P</i>	0.060	0.990	0.016	
	Phanerophyte	Pseudofrequency	0.450 +	0.402 -	0.460 +	
		<i>P</i>	0.877	0.020	0.917	
	Therophyte	Pseudofrequency	0.016 +	0.014 -	0.018 +	
		<i>P</i>	0.454	0.273	0.796	
	sexual		χ^2	0.035	0.058	0.198
			<i>P</i>	1.000	1.000	1.000
Seed		Pseudofrequency	0.952 +	0.947 -	0.957 +	
		<i>P</i>	0.503	0.278	0.703	
Spore		Pseudofrequency	0.048 +	0.052 +	0.042 -	
		<i>P</i>	0.499	0.751	0.302	
leaf		χ^2	0.916	4.414	1.334	
		<i>P</i>	0.170	0.018	0.072	
	Deciduous	Pseudofrequency	0.573 -	0.656 +	0.557 -	
		<i>P</i>	0.003	1.000	0.004	
	Evergreen	Pseudofrequency	0.394 +	0.255 -	0.409 +	
		<i>P</i>	0.999	0.001	0.998	
	Partial evergreen	Pseudofrequency	0.018 -	0.024 +	0.014 -	
		<i>P</i>	0.120	0.579	0.042	
seed bank		χ^2	0.071	1.231	0.776	
		<i>P</i>	1.000	0.216	0.900	
	present	Pseudofrequency	0.314 -	0.342 +	0.289 -	
		<i>P</i>	0.258	0.969	0.029	

Trait	State		CC	PB	WF
C.N		χ^2	0.464	0.480	0.318
		<i>P</i>	1.000	0.976	1.000
	high	Pseudofrequency	0.224 -	0.260 +	0.260 +
		<i>P</i>	0.053	0.843	0.717
	low	Pseudofrequency	0.146 +	0.110 -	0.150 +
		<i>P</i>	0.902	0.012	0.917
medium	Pseudofrequency	0.188 +	0.189 +	0.158 -	
	<i>P</i>	0.789	0.772	0.053	
growth		χ^2	0.067	0.266	0.285
		<i>P</i>	1.000	1.000	1.000
	medium	Pseudofrequency	0.263 +	0.256 +	0.231 -
		<i>P</i>	0.844	0.589	0.128
	rapid	Pseudofrequency	0.053 -	0.063 +	0.055 -
		<i>P</i>	0.162	0.887	0.280
slow	Pseudofrequency	0.308 -	0.287 -	0.336 +	
	<i>P</i>	0.441	0.075	0.974	
stolon		χ^2	0.003	0.156	0.221
		<i>P</i>	1.000	1.000	1.000
	present	Pseudofrequency	0.121 -	0.116 -	0.134 +
		<i>P</i>	0.374	0.256	0.855
rhizome		χ^2	0.343	0.308	0.292
		<i>P</i>	1.000	1.000	1.000
	present	Pseudofrequency	0.573 +	0.540 -	0.538 -
		<i>P</i>	0.949	0.206	0.210
sprouting		χ^2	0.002	0.074	0.103
		<i>P</i>	1.000	1.000	1.000
	present	Pseudofrequency	0.450 +	0.431 -	0.455 +
		<i>P</i>	0.661	0.181	0.739
fire resistance		χ^2	0.401	0.634	0.074
		<i>P</i>	1.000	0.860	1.000
	present	Pseudofrequency	0.196 +	0.150 -	0.188 +
		<i>P</i>	0.969	0.022	0.751
fire tolerance		χ^2	0.623	0.674	0.637
		<i>P</i>	0.714	0.407	1.000
	high	Pseudofrequency	0.306 -	0.357 +	0.329 -
		<i>P</i>	0.031	0.971	0.347
	low	Pseudofrequency	0.042 +	0.022 -	0.043 +
		<i>P</i>	0.922	0.103	0.816
	medium	Pseudofrequency	0.243 +	0.192 -	0.210 -
		<i>P</i>	0.998	0.033	0.270
	none	Pseudofrequency	0.016 -	0.018 -	0.029 +
		<i>P</i>	0.053	0.126	0.664

Trait	State		CC	PB	WF
shade		χ^2	0.294	0.240	0.064
		<i>P</i>	1.000	1.000	1.000
	intolerant	Pseudofrequency	0.282 +	0.249 -	0.263 -
		<i>P</i>	0.953	0.101	0.422
	midtolerant	Pseudofrequency	0.261 +	0.266 +	0.246 -
		<i>P</i>	0.562	0.719	0.212
	tolerant	Pseudofrequency	0.452 -	0.481 +	0.489 +
		<i>P</i>	0.044	0.702	0.834
	dispersal		χ^2	0.873	2.452
		<i>P</i>	0.108	0.018	1.000
animal		Pseudofrequency	0.593 +	0.493 -	0.576 +
		<i>P</i>	1.000	0.001	0.876
gravity		Pseudofrequency	0.236 -	0.268 +	0.269 +
		<i>P</i>	0.055	0.800	0.751
wind		Pseudofrequency	0.152 -	0.199 +	0.147 -
		<i>P</i>	0.008	0.959	0.013
rosette			χ^2	0.069	0.972
		<i>P</i>	1.000	0.018	0.782
	absent	Pseudofrequency	0.944 +	0.925 -	0.951 +
		<i>P</i>	0.877	0.006	0.992
prostrate		χ^2	0.085	0.322	0.084
		<i>P</i>	1.000	1.000	1.000
	present	Pseudofrequency	0.093 +	0.079 -	0.096 +
		<i>P</i>	0.698	0.138	0.765
alien status		χ^2	0.659	1.987	0.393
		<i>P</i>	1.000	0.052	1.000
	native	Pseudofrequency	0.992 +	0.978 -	0.992 +
		<i>P</i>	0.023	0.159	0.111

Appendix III. Species abundance matrix

<i>Oryzopsis asperifolia</i>	0.000	0.000	0.010	0.092	0.083	0.008	0.000	0.000	0.000	0.017	0.000	0.092
<i>Oryzopsis pungens</i>	0.000	0.000	0.110	0.000	0.000	0.000	0.100	0.000	0.000	0.000	0.000	0.000
<i>Osmunda claytoniana</i>	0.000	0.000	0.000	0.000	0.000	6.425	0.000	0.083	0.417	0.000	0.000	0.000
<i>Petastites frigidus</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
<i>Picea mariana</i>	0.000	0.267	0.000	0.000	0.000	0.000	1.667	0.000	0.000	0.000	0.000	0.000
<i>Pinus banksiana</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
<i>Platanthera macrophylla</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
<i>Poa pratensis</i>	0.000	0.000	0.320	0.092	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
<i>Polygala pauciflora</i>	0.340	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
<i>Populus tremuloidea</i>	0.000	0.000	0.000	0.083	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
<i>Potentilla tridentata</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
<i>Prunus pennsylvannica</i>	0.000	0.000	0.000	0.000	0.000	0.000	3.000	0.750	0.000	2.000	0.000	0.000
<i>Pteridium aquilinum</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
<i>Pyrola asarifolia</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
<i>Pyrola chlorantha</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
<i>Pyrola minor</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
<i>Rhamnus ainifolia</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
<i>Ribes glandulosum</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
<i>Rosa acicularis</i>	0.000	0.008	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.842
<i>Rubus idaeus</i>	0.000	0.000	0.000	0.833	0.000	0.000	0.083	0.017	0.083	0.000	0.000	0.000
<i>Rubus pubescens</i>	0.000	1.192	0.000	0.000	0.000	0.000	0.000	0.333	3.417	1.167	0.000	0.000
<i>Salix humilis</i>	0.200	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
<i>Schizachne purpurascens</i>	0.110	0.000	0.000	0.000	0.000	0.000	0.250	0.000	0.000	0.000	0.000	0.000
<i>Solidago hispida</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
<i>Solidago nemoralis</i> var. <i>nemoralis</i>	0.200	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
<i>Sorbus americana</i>	0.100	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
<i>Sorbus decora</i>	0.000	0.000	0.258	0.000	0.167	0.000	0.000	0.083	0.333	0.000	0.000	0.000
<i>Spirea alba</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
<i>Streptopus lanceolatus</i>	0.000	0.000	0.167	0.000	0.000	0.833	0.000	0.000	0.000	0.008	0.000	0.000
<i>Taraxium officinalis</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
<i>Trientalis borealis</i>	0.110	0.000	0.083	0.000	0.000	0.000	0.000	0.025	0.692	0.000	0.000	0.000
<i>Trifolium repens</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
<i>Vaccinium angustifolium</i>	0.000	0.000	0.000	0.000	0.000	0.000	1.667	0.000	0.000	0.000	0.000	0.000
<i>Vaccinium caespitosum</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
<i>Vaccinium myrtilloides</i>	0.010	0.000	0.000	0.000	0.000	0.000	32.000	5.667	0.000	0.000	0.000	0.000

Appendix IV. Species' trait matrix

Species' trait matrix legend

Raunkaier life form	Pphanerophyte (p), chaemophyte (c), hemicryptophyte (h), geophyte (g), therophyte (t)
Propagule type	Spore (sp) or seed (s)
Leaf retention	Deciduous (d), evergreen (e), or partial evergreen (p)
Seed banking	Binary (y/n)
C:N	Low (l), Medium (m), High (h)
Growth rate	Slow (s), medium (m), rapid (r)
Stolon	Binary (y/n)
Rhizome	Binary (y/n)
Re-sprouting	Binary (y/n)
Fire resistance	Binary (y/n)
Fire tolerance	Low (l), medium (m), high (h)
Shade tolerance	Intolerant (i), intermediate (m), tolerant (t)
Dispersal vector	Animal (a), gravity (g), wind (w)
Rosette	Binary (y/n)
Prostrate	Binary (y/n)
Alien status	Native (n) or alien (y)
Competitiveness	Binary (y/n)

Raunkaier	spore/seed	leaf retention	seed bank	C:N ³	growth rate ³	stolon ⁴	rhizome ³	sprouting ³	fire resistance ³	fire tolerance ³	shade tolerance	dispersal vector	rosette	prostrate	alien ²	competitive ¹
<i>Abies balsamea</i>	p	s	e	h	s	n	n	n	n	l	t ³	w	n	n	n	n
<i>Acer rubrum</i>	p	s	d	h	r	y ³	y	y	n	l	t ³	w	n	n	n	n
<i>Acer spicatum</i>	p	s	d	h	m	n	n	y	n	h	t ³	w ⁶	n	n	n	n
<i>Achillea millefolium</i>	h ⁹	s	d	y ¹⁰	m	n	y ⁹	y ⁹	n	h ⁹	t ³	g ⁹	n	n	n	y
<i>Alnus incana</i>	p	s	d	h	r	n	n	n	n	h	m ³	g ⁸	n	n	n	n
<i>Alnus viridis</i>	p	s	d	h	r	n	n	y	n	m	m ³	w ⁸	n	n	n	y
<i>Amelanchier alnifolia</i>	p	s	d	y	m	n	y ⁵	y	n	h	m ³	a	n	n	n	y
<i>Amelanchier bartramiana</i>	p	s	d	y		n	y ⁶		n		m	a	n	n	n	n
<i>Amelanchier humilis</i>	p	s	d	y		n	y		n		m	a	n	n	n	y
<i>Amelanchier laevis</i>	p	s	d	y	m	n	y ⁶	y	n	m	t	a	n	n	n	y
<i>Amelanchier sanguinea</i>	p	s	d	y	m	n	y ⁶	y	n	h	t ³	a	n	n	n	y
<i>Anaphalis margaritacea</i>	g	s	d	l	r	n	y	y	n	n	m ³	w	n	n	n	y
<i>Andromeda polifolia</i> var. <i>glaucophylla</i>	p	s	e			n			n		m	w	n	n	n	n
<i>Anemone quinquefolia</i>	g	s	d			n	y		n		t	g	n	n	n	n
<i>Apocynum androsaemifolium</i>	g	s	d		m	n	y ⁷	y		m	m ⁷	w	n	n	n	n
<i>Aralia nudicaulis</i>	h	s	d	m	m	n	y			m	t ³	a ⁹	n	n	n	n
<i>Arctostaphylos uva-ursi</i>	c	s	e	h	m	y	n	n	n	l	m ³	a	n	y	n	n
<i>Athyrium filix-femina</i>	g ⁹	sp	d	m	m	n	y		n	l	t	w	n	n	n	n
<i>Betula papyrifera</i>	p ⁹	s	d	m	r	n	n	y	n	m	t ³	w	n	n	n	y
<i>Bromus inermis</i> ssp. <i>inermis</i>	h	s	d	m	m	n	y	n	n	h	l	w	n	n	y	n
<i>Calamagrostis canadensis</i>	h	s	d		m	n	y		n	l	l	w	n	n	n	y
<i>Chimaphila umbellata</i>	c	s	e	m	s	n	y	n	y	h	t ³	g	n	n	n	n
<i>Cinna latifolia</i>	h	s	d	m		n			y	h	m	g	n	n	n	n
<i>Clintonia borealis</i>	h	s	d	m	m	n	y	n	n	m	t ³	a	n	n	n	n
<i>Comptonia peregrina</i>	p	s	e	h	s	n	y ⁸	y	n	h	t ³	g	n	n	n	n
<i>Coptis trifolia</i>	h	s	e	l	s	n	y	y	y	h	m ⁹	g	n	n	n	n
<i>Cornus canadensis</i>	h	s	d	h	m	n	y	y	y	h	t ³	a	n	n	n	n
<i>Cornus sericea</i>	p	s	d	h	m	n	n	y	n	l	m ³	a	n	n	n	n
<i>Corylus cornuta</i>	p	s	d		m	n	n	y	n	h	t ³	g	n	n	n	y
<i>Cypripedium acaule</i>	g	s	d			n			n		t	w	n	n	n	n
<i>Danthonia spicata</i>	c ⁹	s	d			n					m	g	n	n	n	n

	Raunkaier	spore/seed	leaf retention ⁴	seed bank	C:N ³	growth rate ³	stolon ⁴	rhizome ³	sprouting ³	fire resistance ³	fire tolerance ³	shade tolerance	dispersal vector	rosette	prostrate	alien ²	competitive ¹
<i>Diervilla lonicera</i>	p	s	d	y ¹¹	h	s	n	n	y	n	h	m ³	g	n	n	n	n
<i>Dryopteris carthusiana</i>	h	sp	p					y				t	w	n	n	n	n
<i>Epilobium angustifolium</i>	h ⁹	s	d	y ¹⁶	m	r	n	y	n	n	h	m ²	w	n	n	n	y
<i>Equisetum arvense</i>	g ⁹	sp	d				n	y				m	w	n	n	n	n
<i>Equisetum sylvaticum</i>	g ⁹	sp	d				n	y				t	w	n	n	n	n
<i>Eurybia macrophylla</i>	h	s	d		h	m	n	y	n	n	h	t ³	w	n	n	n	y
<i>Fragaria virginiana</i>	h	s	d	y ¹⁰			y	y			l	i	a	y	n	n	n
<i>Galium boreale</i>	g ⁹	s	d		m	m	n	n	n	n	l	m ³	g	n	n	n	n
<i>Galium triflorum</i>	g ⁹	s	d	y ⁵			n				h	t ⁷	g	n	y	n	n
<i>Gaultheria hispidula</i>	c	s	e		h	s	y	n	y	n	h	t ³	a	n	y	n	n
<i>Gaultheria procumbens</i>	c	s	e		h	s	y	y	y	n	h	t ³	a	n	n	n	n
<i>Goodyera spp.</i>	h ⁹	s	e				n	y				t	w	y	n	n	n
<i>Gymnocarpium dryopteris</i>	g ⁹	sp	p				n	y				t	w	n	n	n	n
<i>Hieracium caespitosum</i>	h	s	d	y ^{19,20}			y	y				i	w	y	n	y	n
<i>Hieracium canadense</i>	h	s	d	y			n					i	w	n	n	n	n
<i>Hieracium piloselloides</i>	h	s	d	y ^{19,20}			n					i	w	y	n	n	n
<i>Hieracium scabrum</i>	h	s	d	y			n					i	w	y	n	n	n
<i>Juniperus communis</i>	p	s	e		h	s	n	n	n	n	l	j ³	a	n	n	n	n
<i>Kalmia polifolia</i>	c	s	e				n	y			m	i	g	n	n	n	n
<i>Lathyrus ochroleucus</i>	h	s	d				n	y				m	g	n	n	n	n
<i>Ledum groenlandicum</i>	p	s	e			s	n	n	n	y	m	m ³	g	n	n	n	y
<i>Linnaea borealis</i>	c	s	e				y					t	g	n	y	n	n
<i>Lonicera canadensis</i>	p	s	d				n					t	a	n	n	n	n
<i>Lonicera dioica</i>	p	s	d				n					m	a	n	n	n	n
<i>Luzula multiflora</i>	h	s	p				n					t	g	n	n	n	n
<i>Lycopodium annotinum</i>	h ⁹	sp	e				y					t	w	n	y	n	n
<i>Lycopodium clavatum</i>	h	sp	e				y					t	w	n	y	n	n
<i>Lycopodium dendroideum</i>	h	sp	e				y	y				t	w	n	n	n	n
<i>Lycopodium obscurum</i>	h	sp	e				y	y				t	w	n	n	n	n

Raunkaier	spore /seed	leaf retention ⁴	seed bank	C:N ⁵	Growth rate ¹	stratig. ²	rhizome ³	sp. cur. long ⁷	fire resistance ²	fire tolerance ³	shade tolerance	dispersal vector	rosette	prostrate	alien ²	competitive ¹
<i>Maianthemum canadense</i>	B	s	d	Y ¹³	n	n	y				t	a	n	n	n	n
<i>Melampyrum lineare</i>	t	s	d		n	n	n				m	w	n	n	n	n
<i>Monesit uniflora</i>	h	s	p		n	n	n				t	w	n	n	n	n
<i>Monotropa uniflora</i>	g	s	n		n	n	n				t	w	n	n	n	n
<i>Oryzopsis aperifolia</i>	h	s	p		n	n	n				t	B	Y	n	n	n
<i>Osmunda claytoniana</i>	h	sp	d		n	n	n				m	w	n	n	n	n
<i>Petasites frigidus</i>	g	s	d		n	n	n				m	w	n	n	n	n
<i>Picea mariana</i>	p	s	e		h	s	n	n	n	n	t ³	g	n	n	n	n
<i>Pinus banksiana</i>	p	s	e		h	r	n	n	n	n	t ³	g	n	n	n	n
<i>Piptatherum pungens</i>	h	s	p				n	n			t	g	Y	n	n	n
<i>Poa pratensis</i>	h	s	d				n	n			t	g	n	n	n	n
<i>Polygala paucifolia</i>	h	s	p				n	n			t	g	n	n	n	n
<i>Populus tremuloides</i>	p	s	d		m	r	n	y	n	h	t ³	w	n	n	n	Y
<i>Prunus pennsylvanica</i>	p	s	d		h	r	n	y	n	h	t ³	a	n	n	n	Y
<i>Pteridium aquilinum</i>	g	sp	d				n	n			m	w	n	n	n	Y
<i>Pyrola asarifolia</i>	h	s	e				n	n			t	w	Y	n	n	Y
<i>Pyrola chlorantha</i>	h	s	n				n	n			t	w	Y	n	n	n
<i>Pyrola minor</i>	h	s	e				n	n			t	w	Y	n	n	n
<i>Rhamnus alnifolia</i>	p	s	d				n	n			m	a	n	n	n	n
<i>Ribes glandulosum</i>	p	s	d				n	n			m	a	n	n	n	Y
<i>Rosa acicularis</i>	p	s	d		m	r	n	n	y	h	t ³	a	n	n	n	Y
<i>Rubus idaeus</i>	h ⁹	s	d		m	m	n	y	y	m	t ³	a	n	n	n	Y
<i>Rubus pubescens</i>	c	s	d				Y	Y			t	a	n	Y	n	n
<i>Salix humilis</i>	p	s	d		h	r	n	y	n	h	m ³	w	n	n	n	Y
<i>Schizachne purpurascens</i>	h	s	d				n	n			t	g	n	n	n	n
<i>Sibbaldiaopsis tridentata</i>	h	s	e				n	n			t	g	n	n	n	n
<i>Solidago hispida</i>	h	s	d				n	n			t	w	n	n	n	n
<i>Solidago nemoralis</i>	h	s	d				n	n			t	w	n	n	n	n
<i>Solidago nemoralis</i> var. <i>nemoralis</i>	h	s	d		m	r	n	n	n	h	t ³	w	n	n	n	n
<i>Sorbus americana</i>	p	s	d		h	m	n	y	n	h	m ³	a	n	n	n	n
<i>Sorbus decora</i>	p	s	d		h	s	n	n	n	m	t ³	a	n	n	n	n
<i>Spirea alba</i>	p	s	d				n	n			t	g	n	n	n	n
<i>Streptopus lanceolatus</i>	g	s	d				n	n			t	a	n	n	n	n

	Raunkaier	spore/seed	leaf retention ⁴	seed bank	C:N ³	growth rate ³	stolon ⁴	rhizome ³	sprouting ³	fire resistance ³	fire tolerance ³	shade tolerance ³	dispersal vector	rosette	prostrate	alien ²	competitive ¹
<i>Symphyotrichum ciliolatum</i>	h	s	d				n	y				i	w	n	n	n	n
<i>Symphyotrichum urophyllum</i>	h	s	d		m	m	n	y		n		i ³	w	n	n	n	n
<i>Trientalis borealis</i>	g	s	d				n					t	g	n	n	n	n
<i>Vaccinium angustifolium</i>	p	s	e	y	m	m	n	y ⁶	y	n		i ³	a	n	n	n	y
<i>Vaccinium cespitosum</i>	c	s	d				n					m	a	n	n	n	n
<i>Vaccinium myrtilloides</i>	p	s	e				n	y ⁶				i	a	n	n	n	y
<i>Vaccinium vitis-idaea</i>	c	s	e		l	m	n	y	y	n		i ³	a	n	n	n	n
<i>Viola adunca</i>	c	s	d	y ^{6,18}			n					t	a	y	n	n	n
<i>Viola blanda</i>	c	s	d				n					t	a	y	n	n	n
<i>Viola canadensis</i>	c	s	d	y ⁵			n					t	a	y	n	n	n
<i>Viola pubescens</i> var. <i>pubescens</i>	c	s	d	y ¹⁸			n					t	a	y	n	n	n
<i>Viola renifolia</i>	c	s	d	y ⁵			n					t	a	y	n	n	n

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Note: unreferenced trait expressions were inferred from species descriptions.