Impacts of multiple fires and wind disturbance on forest community composition, succession and diversity in the Boundary Waters Canoe Area Wilderness.

A DISSERTATION

SUBMITTED TO THE FACULTY OF THE GRADUATE SCHOOL

OF THE UNIVERSITY OF MINNESOTA

BY

ELIAS RASCH ANOSZKO

IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE DEGREE OF
DOCTOR OF PHILOSOPHY

Peter B. Reich PhD. & Lee E. Felich PhD., Advisors

January 2018

Acknowledgements

Abstract

Under a warming climate, the Boundary Waters Canoe Area Wilderness (BWCAW) of Northern MN is expected to see an increase in the frequency of disturbances including wildfires and severe windstorms. While boreal forests such as those of the BWCAW are generally considered disturbance adapted, it is uncertain how changing disturbance regimes will impact these forests. We used a series of recent disturbances in the BWCAW ranging from areas affected by wind or fire only, to areas affected by wind followed by fire, or multiple fires, to examine how predicted changes in boreal disturbance regimes are likely to impact these forests. We found that multiple disturbances typically had greater cumulative disturbance severity than single disturbance events and in the case of wind+fire combinations also tended to burn with greater intensity, and fire severity relative to areas affected by a single fire only. While diversity-severity relationships varied in shape, we found that diversity was generally lower at high disturbance severity relative to moderate severities. Multiple disturbances had modestly reduced diversity relative to single disturbances, but this relationship varied depending on the spatial scale of inquiry. Despite only modest impacts on diversity, multiple disturbances did have a pronounced impact on succession and composition. Regardless of pre-disturbance composition, multiple disturbances resulted in succession to aspen and paper birch, with birch being more dominant in areas burned in late season fires and aspen more dominant in areas burned by early season fires. Stands subjected to single disturbance events exhibited multiple successional pathways and mix of forest types. Our results suggest that

predicted changes in boreal disturbance regimes are likely to have minor impacts on woody plant diversity, but could adversely affect disturbance adverse species, and alter the age structure and composition of forests by reducing long-lived boreal conifers and increasing the dominance of aspen and paper birch.

Table of Contents

List of Tables

List of Figures

ix

Chapter 1

How do multiple disturbances shape the diversity-severity relationship in recently disturbed boreal forests?

with
Lee Frelich
Peter B. Reich

Synopsis

The intermediate disturbance hypothesis predicts that disturbances of intermediate severity should result in the greatest biodiversity, yet many studies have failed to find the hypothesized hump shaped diversity-disturbance relationship. Here we use a case study of wind and fire disturbances in the southern boreal forest of Minnesota, USA to examine the roles that disturbance severity, and interactions among multiple disturbances play in influencing woody plant diversity post-disturbance. We examined multiple aspects of disturbance severity across a range of spatial scales and across a gradient of disturbances ranging from areas affected by single fires or wind storm to areas experiencing a rapid series of disturbance events including wind, prescribed fire and wildfire. We measured the diversity of regeneration following disturbance by counting and identifying trees and woody shrubs. We found modest evidence that regeneration diversity showed a peaked or humped-shaped distribution with increasing total (aggregate) disturbance severity at the scale of a 3-m regeneration plot. While there was considerable variation in the shape of the diversity-disturbance relationship, almost all relationships had lower diversity at the highest severity levels. In some instances, multiple disturbances had greater disturbance severity and reduced diversity when compared to single disturbance events, but these patterns varied depending on the spatial scale of inquiry. Differences in diversity between single and multiple disturbances were generally less than those between disturbed and undisturbed areas. Overall, we found that the woody plant community of the disturbance-adapted boreal forest is likely to be somewhat

2

resilient to predicted increases in disturbance frequency and severity, such as may occur under climate change. Our results also highlight the importance of considering spatial scale and disturbance complexity as factors when examining diversity-disturbance relationships.

Introduction

Disturbance events in forests, whether they occur at the level of individual tree fall gaps or large-scale wildfires, are thought to exert an important influence on biodiversity. Disturbances are generally defined as discrete events that result in the mortality, displacement or damaging of individuals, but disturbances often increase resource availability and provide opportunities for new establishment and growth (Sousa 1984). Successional changes in community composition following disturbance events can result in the maintenance or increasing abundance of some species and the decline or extirpation of others. Such changes can have a pronounced impact on biodiversity and thereby ecosystem functioning (Hooper et al. 2005). Because of their central importance to ecology, disturbances and subsequent succession have long been a focus of ecological research (Cowles 1899, Clements 1916, Gleason 1926), but despite an extensive body of literature documenting the relationship between biodiversity and disturbance, the exact nature of the relationship remains contentious (Makey and Currie 2001; Hughes et al. 2007).

The intermediate disturbance hypothesis (IDH) variously proposed by Grime (1973) and Connell (1978), asserts that local species diversity is maximized by disturbances of intermediate severity and frequency. While the IDH is a highly cited hypothesis, many empirical studies have failed to find evidence of humped disturbance-biodiversity relationships (Schwilk et al. 1997; Mackey and Curie 2001; Hughes et al. 2007)—but not all (Peterson and Reich 2008). More recently,

some have argued that the basic assumptions of the IDH are flawed (Fox 2013).

Others recognize that biodiversity-disturbance relationships may be variously

positive, negative or humped (Hall et al. 2012) and that the shape of this

relationship depends on how such relationships are constructed (Miller et al.

2011). Because disturbance intensity and frequency are themselves related, it is

possible that two researchers studying the same system may report different

disturbance-diversity relationships if they do not investigate the same aspect of

disturbance (Miller et al. 2011). Differences among research studies may be

further exacerbated because there are no universally agreed upon metrics of

either biodiversity or disturbance severity. Further complicating matters, the

relationship between diversity and disturbance is often discussed as if it were

scale independent, despite the fact many ecological patterns vary with spatial

scale (Bunnell and Huggard 1999). Although there is no current consensus as to

how diversity-severity relationships might vary across spatial scales, it is possible

that ecologists investigating similar aspects of disturbance and diversity at

different spatial scales could reach different conclusions (Dumbrell et al. 2008).

Although the relationship between disturbance and biodiversity continues to be

imperfectly understood, the realities of a changing climate make understanding

the relationship all the more important. Across large portions of the globe, climate

change may increase or has already increased, the frequency and intensity of

forest fires (Fauria and Johnson 2008; Flannigan et al. 2009; Van Bellen et al.

2010). In addition, climate change is also expected to increase the frequency of

severe storms, insect and disease outbreaks and other forest disturbances across the globe (IPCC 2014; Frelich and Reich 2010; Peterson 2000; Diffenbaugh 2012). The increased frequency of disturbance events sets the stage for increased incidence of multiple disturbance events, where two or more disturbances overlap, creating novel disturbances with potentially extreme severity with unknown impacts on biodiversity (Paine et. al 1998; Buma and Wessman 2011). The predicted increases in disturbance frequency and severity along with the increased potential for compounding multiple disturbance events mean that it has never been more important to understand how disturbance events affect diversity.

One possible way to advance understanding of these issues is to examine multiple aspects of disturbance and diversity across a wide range of conditions and across spatial scales to see if universal patterns such as the IDH emerge or if patterns of diversity and disturbance are idiosyncratic. Meta-analyses such as those of Makey and Currie (2001) and Hughes et al. (2007) are one way to examine diversity-disturbance relationships, but experiments, natural or planned, are also needed to help further define and develop theory about the role of disturbance in biodiversity. Here we propose using instances of multiple and single disturbance events that co-occurred in close spatial and temporal proximity within the Boundary Waters Canoe Area Wilderness (BWCAW) of Northern MN USA as a natural experiment to examine the diversity-disturbance relationship within a forest ecosystem.

Specifically, this paper seeks to answer the following questions as they relate to disturbance theory.

1) How does disturbance severity affect the diversity of the regeneration post-disturbance?

We defined regeneration as seedlings and saplings of trees and woody shrubs established post-disturbance as well as advanced regeneration that survived a disturbance event. In line with the predictions of the IDH, we hypothesized that regeneration diversity, would exhibit a humped relationship with disturbance severity. We expected diversity would be low with low disturbance severity because disturbance-adapted early-successional species would have difficulty establishing due to lack of suitable seedbeds or light conditions. At high disturbance severities, we also expected diversity would be low because such disturbances might eliminate seed sources and propagules of disturbance-averse, late-successional species. We expected that at moderate disturbance severities diversity would be maximized, because disturbances of this severity would create suitable growing conditions for disturbance adapted early-successional species, but not be so severe as to eliminate the propagules and seed sources of late-successional species.

2) Are wind and fire disturbance functionally different in their effect on diversity?

We hypothesized that disturbance type would not have a pronounced effect on the relationship between diversity and severity. In many cases, differences in the physical effects of different disturbance types limit the utility of severity metrics when comparing diversity relationships across different disturbance types. For example, measures such as burn depth have no equivalent metric for disturbances such as windstorms. However, where comparable metrics existed we expected that the effects of disturbance severity on diversity would not differ significantly between disturbance types.

3) Do multiple disturbances within a short period of time result in reduced diversity when compared to single disturbance events?

Multiple disturbances are likely to have a greater impact on biodiversity than single disturbances by increasing the cumulative severity experienced by the system, particularly when cumulative severity is intermediate (where diversity would be enhanced by multiple disturbances) or very high (where diversity would be reduced by multiple disturbances). We hypothesized that the latter is more likely given the tendency for high disturbance severity in southern boreal forest. For example, if disturbances occur in close temporal proximity, the later disturbance may reduce the abundance of seed sources and propagules available to colonize a newly disturbed area. Depending on the relative severities of the disturbances and their timing, which we expect to be high, instances of multiple disturbances can conceivably restrict the available species pool and therefore limit the diversity of a recovering system. We expected therefore, that

areas experiencing multiple disturbances would be less diverse than areas affected by single disturbances. We hypothesized that mechanistically, differences in impacts between single and multiple disturbance events would come from differences in disturbance severity and not from fundamental differences in the shape of diversity-severity relationships between single and multiple disturbances, i.e. at similar cumulative severity levels we expected single and multiple disturbances to have similar levels of diversity. We expected instances of multiple disturbances to have lower diversity because of the higher average cumulative severity than for single disturbances. We note that one can envision scenarios where multiple disturbances might have greater or conversely less effect on diversity than single disturbances of similar cumulative severity, but we do not expect those to be a regular enough or predictable enough occurrence to alter our hypothesis.

4) Do the effects of disturbance frequency and severity on diversity vary with spatial scale?

We expected diversity-disturbance relationships would vary across spatial scales. At local scales, we hypothesized disturbance-diversity relationships would exhibit the humped shape predicted by the IDH and that instances of multiple disturbances would have lower diversity than areas affected by single disturbances. With increasing spatial scale, we hypothesized that there would be increasing incorporation of different patches with an increased range of disturbance severities and increased beta diversity. We hypothesized that the

9

incorporation of more patches at higher spatial scales would decrease

differences in diversity between multiple disturbances and single disturbance

events, as compared to differences at smaller spatial scales (Collins and Glenn

1997; Roxburgh et al. 2004; Limberger and Wickman 2012). In essence, we

hypothesize that beta diversity of species richness and composition would mirror

beta diversity (i.e. heterogeneity) of disturbance severity, on top of the underlying

impact of location on the 'humped' alpha scale gradient.

Methods

The study area (15,000 ha) is centered at 90°56′W and 48°08′N lies within the BWCAW and adjacent areas of the Superior National Forest, Cook County, MN USA. The BWCAW is a 400,000 ha federally designated wilderness area that stretches for 177 km along the US-Canadian border. Approximately 168,000 ha of the BWCAW are primeval fire-origin forests that have never been logged (Heinselman 1996).

The geology of the BWCAW is mostly Canadian Shield bedrock of pre-Cambrian granite with areas of metamorphosed volcanic and sedimentary rocks. Soils are typically thin, derived from glacial till, and coarse-loamy to coarse in texture (MN DNR ECS). Past glaciation has left a landscape with low total relief (400-580 m above sea level) but with numerous hills and rocky cliffs of 10-50 m local relief (Rich et al. 2007). The landscape is bisected by over 1,000 lakes greater than 4 ha in size totaling an area of 69,000 ha (Heinselman 1973). The climate is cold-temperate continental with a mean frost-free growing season of 100 days. Mean annual precipitation is 64 cm, ranging from 38 to 100 cm with 64% falling as rain during the growing season (Heinselman 1973). The mean July temperature is 17°C and the mean January temperature is –8°C with an average annual temperature of 2°C (Heinselman 1996).

The BWCAW is classified as Laurentian Mixed Forest, border lakes subsection, which occupies an ecotonal transition area between the temperate and boreal forest (MN DNR ECS). Common boreal species include Jack pine (*Pinus banksiana* Lamb), quaking aspen (*Populus tremuloides* Michx), balsam poplar (*Populus balsamifera* L.), paper birch (*Betula papyrifera* Marshall), black spruce (*Picea mariana* (Mill.) Britton, Sterns & Poggenb.), white spruce (*Picea glauca* (Moench) Voss), balsam fir (*Abies balsamea* (L.) Mill.), tamarack (*Larix laricina* (Du Roi) K. Koch), and northern white cedar (*Thuja occidentalis* L.). Common temperate species include, red pine (*Pinus resinosa* Aiton), white pine (*Pinus strobus* L.), red maple (*Acer rubrum* L.), black ash (*Fraxinus nigra* Marshall), bigtooth aspen (*Populus grandidentata* Michx.), and northern red oak (*Quercus rubra* L.). While all of the above species except northern red oak were found within the study area, the overall composition is near-boreal. In the study area, many stands are composed exclusively of boreal tree species and these made up over 90% of the total basal area measured in this study.

Prior to and during European settlement, high intensity crown fires occurred during periodic drought years, with an average fire rotation of ≈100 years for the BWCAW. Jack pine, aspen and birch stands likely experienced crown fires with return intervals of 50-100 years while red pine and white pine stands likely experienced frequent surface fires (return interval <50 years) punctuated with crown fires on intervals of 150-250 years (Heinselman 1973). After European settlement, fire frequency declined due to changes in land use outside the

BWCAW, climate and fire suppression. In 1986, the Superior National Forest adopted a wildland fire use policy that allows naturally ignited fires in the BWCAW to burn so long as they do not threaten life or property outside the wilderness (Heinselman 1996). In contrast to fire, wind disturbances including tornados and derechos are historically rare events that likely had recurrence intervals >1000 years (Rich et al. 2005).

The Upper Gunflint Trail area of the BWCAW has experienced a series of overlapping disturbance events that have created a unique matrix of disturbance conditions ranging from areas affected by a single disturbance event to areas that have experienced 3 significant disturbance events within a single decade. Major disturbances in the area include two small wildfires in 1974 (407 ha) and 1995 (5,100 ha), a severe windstorm in 1999 (193,000 ha), numerous prescribed crown fires and small wildfires from 2001 to 2006 (13,000 ha in total), and several large wildfires in 2006 and 2007 (45,000 ha in total). In many cases these disturbances overlapped in space creating unique patches of disturbance combinations that range from areas affected by wind alone or single fires, to areas that have experienced combinations of wind and fire or two or three fires within a short period of time (Table 1-1). This mosaic of disturbance severities and combinations has been superimposed upon an existing mosaic of fire-origin stands with known fire histories (Heinselman 1973). The range of variability in the timing, severity and combination of disturbance events across an area with relatively uniform physiographic conditions is to our knowledge, unprecedented.

Impacts of multiple disturbances on biodiversity were quantified across 850 plots on 67 transects. Exact transect locations were random, but stratified with regard to disturbance type or combination and stand origin dates from Heinselman (1973). The starting locations of transects were determined before sampling using US Geologic Survey 7 1/2 min topographic maps or Minnesota Department of Natural Resources 1:100,000 Lakes and Rivers digital shapefiles. Fire perimeter maps and storm damage maps generated from remotely sensed data (USFS 2001, Rich et al. 2010) were used to assign transects and stratify plots, and field-collected measurements of disturbance severity were used to categorize plots by disturbance type or combination for analysis (Table 1-1). Because nearly all portions of the study area showed some evidence of wind disturbance from the 1999 blowdown, we had difficulty locating areas where wind disturbance was completely absent. We therefore needed an arbitrary cutoff to divide plots where wind was a significant disturbance from those where it was not. Based on the distribution of measured wind severity for plots outside of the main storm path, we chose 25% wind killed basal area as our threshold value. Plots with measured wind severity of ≥ 25% basal area killed were classified as having been disturbed by wind, while those with measured wind severity <25% were considered to be relatively unaffected by wind disturbance; within this category the mean wind severity value was 9.2% wind caused mortality expressed as the relative change in basal area. Any plot with >0% fire severity was considered disturbed by fire. Disturbance types and combinations include

single fires, wind disturbance, wind followed by single fire, wind followed by 2 fires, 2 or 3 fires, and lightly disturbed areas that have not experienced significant fire or wind disturbance in the past 40 years.

Transects originated from lakeshores or adjacent to roads and ran upslope to capture the natural pattern of vegetation differences between lakeshores and hilltops. Circular plots were spaced at 25 m intervals along a transect ranging from 150 m to 400 m in length, with the first plot on lake-originating transects being a semicircular plot. Because 80% of the land area in the BWCAW exists within 500 m of a lakeshore, and the pattern of variation in forest communities is a gradient from lakeshore to ridge top, these transects provided a representative sample of the landscape (Rich et al. 2007). Transect length varied but generally covered a variety of hillslope and aspect combinations from lakeshores and bogs, to backslopes and summits.

Four hundred forty-six plots were established in 2001-2002 following the 1999 windstorm with the aim of quantifying the impacts of wind disturbance on the forest community. These plots were subsequently resampled in 2007 and 2011 after fire. An additional 404 plots were added in 2012, in areas largely outside the main storm path that had been recently burned in the Ham Lake Fire, Redeye Lake Fire or Famine Lake Fire of 2006-2007. Eighty-two plots were located outside the formal wilderness boundary, but all plots were established in areas of primary forest that have never been logged and were not salvage logged following disturbance. Plot centers were marked with a 50 cm piece of 3/8" steel

rebar and GPS coordinates were recorded via a Garmin eTrex Vista HCx. Exact plot centers were found in 51.5% of plots during re-survey, if the exact plot center could not be found, GPS coordinates were used along with plot description to approximate actual plot center with an estimated accuracy of +/- 3 m.

Plots were nested with fixed radii of 12.5 m, 5 m, and 3 m. Within the coarse scale plot (12.5 m radius) all trees greater than 5 cm in dbh were tallied according to species, whether they were live, dead, or fallen and dead, and diameter size classes (5-15 cm, 15-25cm or >25 cm dbh). Within the fine scale plot (5 m radius) all trees greater than 2.5 cm dbh were tallied according to species, measured diameter, canopy class, vitality, potential mortality agent, decay class and whether they were live, standing dead or fallen and dead. Canopy class, and decay class were based on categories developed for the USFS Common Stand Exam (CSE) procedure and the CSE was used as a model for data collection protocols (USFS 2003). Within the 3 m radius regeneration plot, all trees and tree-like shrubs less than 2.5 cm in dbh were counted. For multi stemmed species, branching above breast height was considered one individual, where branching occurred below breast height we tallied the number of stems and for analysis purposes considered each stem an individual. Across the 12.5m plot area, percent area burned was recorded by ocularly assessing the proportion of the plot area burned. A plot was considered partially burned if there were patches of unburnt vegetation or fuel greater than 1% of the plot area and less than 100% of the plot area. Char height was

16

recorded by occularly estimating the vertical extent of charring from the root crown to the uppermost extent of continuous charring on the bole of the 4 trees closest to plot center and then taking the mean. Five of the 850 plots had no regeneration within the 3 m radius plot and were excluded from further analysis.

In cases where we lacked pre-fire data (403 plots), mortality agents were determined using a combination of a priori knowledge, direct observations and qualitative measures of disturbance severity. (See Appendix)

Live basal areas were calculated for each plot by summing the cross sectional area of all live trees greater than or equal to 5 cm dbh within a 12.5 m radius of plot center. Because diameters of trees in coarse scale plots were not measured directly, but instead placed in size categories, quadratic mean diameters (QMDs) were used to obtain estimates of basal areas. QMDs were calculated for each species and size class from measured trees in fine scale plots. Live basal area in 1999 prior to the windstorm was calculated by summing the cross-sectional areas of all trees, live and dead in the 2011-2012 survey. Live basal area in 2000, following the windstorm, was measured directly for plots surveyed in 2000-2001 and reconstructed for plots added to the study in 2011-2012. For plots added in 2011-2012, live basal area in the year 2000 was defined as the sum of the cross-sectional areas of all live trees minus the cross-sectional area of dead trees where wind was determined to be the mortality agent (See Appendix).

Because tree growth rates in the BWCAW are generally very slow we assumed that any growth between 1999 and 2012 would be minimal and within the margin of error for our methods.

Regeneration-class density was defined as the sum of all tree and tree-like shrub stems <5 cm in dbh and included new germinants, seedlings and saplings. Tree-like shrubs included species of *Alnus*, *Amelanchier* and *Sorbus* that can grow to several meters in height. Because of difficulty in identifying seedlings to species, we grouped 2 subspecies of *Alnus* into a single group for analysis and also combined all *Amelanchier* sp into a single taxonomic group. Occasionally we were unable to distinguish between the two different species of *Picea*. In the field, these were recorded as genus *Picea* and for the purposes of analysis these trees were assumed to belong to the more common *Picea mariana* species.

Disturbance severity is well defined theoretically (Sousa 1984; White and Pickett 1985), but in practice, no universally accepted metrics exist to quantify the severity of a disturbance. To address this issue, we used a variety of commonly used severity metrics including both quantitative and categorical measures that were assessed at the 12.5 m plot scale. Qualitative categorical measures included ground fire severity, wind disturbance severity and tree crown fire severity, hereafter referred to as ground fire severity, categorical wind severity and crown fire severity. Ground fire and crown fire severity classes were after

Carlson et al. (2011) and included 6 and 5 levels respectively (Table 1-2).

Quantitative fire, and wind severity were after Rich et al. (2005), and Peterson

and Leach (2008) and obtained by calculating the relative change in basal area

pre- and post-disturbance using basal area and tree mortality measures from the

coarse and fine scale plots; hereafter these measures of severity are referred to

as fire severity ΔBA, and wind severity ΔBA. Other quantitative severity

measures included char height in meters and percent of plot area burned.

We analyzed the effects of disturbance severity on tree and woody shrub

regeneration diversity across multiple spatial scales: alpha, beta and gamma.

Alpha diversity was defined as the diversity at the 3m plot scale. Alpha diversity

was quantified using both species richness defined as the number of species per

regeneration plot and a modified Shannon-Weiner Index after Jost (2006) to

obtain a true diversity value measured in units of effective number of species,

referred to here as Shannon's true diversity. Shannon Weiner indices and

species richness were calculated for all plots using the Vegan package for R

(Oksanen et al. 2011). Beta diversity and Gamma diversity were after Jost (2007)

where beta diversity is the quotient of true gamma diversity divided by true alpha

diversity. Gamma diversity was defined in this context as the mean Shannon's

true diversity of a randomly selected sample of 50 3m plots selected from the

total population of plots using a Monte Carlo process.

The relationships between alpha diversity and continuous measures of disturbance severity were analyzed using general linear regression models in R. If residual plots indicated curvature or lack of fit, we evaluated models with a quadratic term and used Akaike information criterion to select the most parsimonious model. We tested both species richness and Shannon's true diversity against continuous measures including fire severity ΔBA, wind severity ΔBA, percent area burned, and char height. ANOVA tests and Tukey's honest significant difference tests were used to compare diversity and richness values for categorical measures of disturbance severity. We used one way ANOVA tests and Tukey's HSD tests to compare the diversity of categorical measures of disturbance severity and compare the diversity of various disturbance types. We tested for interactions between disturbance type and disturbance severity by comparing the slopes of diversity-severity relationships. We used basal area based severity metrics to compare the shape of relationships between different disturbance types.

At the beta and gamma level, all continuous measures of disturbance severity were first converted to categorical severity measures so that individual plots could be aggregated to calculate gamma diversity at a given severity level with a minimum of 20 plots at each level. Fire severity ΔBA and wind severity ΔBA were both converted to 3 tiered categorical variables in order to analyze them by gamma diversity. Breakpoints for fire and wind severity were <33%, 33-66% and >66%. Char height was converted to a 4 tiered categorical variable with

increments of 2 m. Bootstrap resampling was used to create 1000 replicate samples of 50 randomly chosen regeneration plots. Within each 50-plot sample, species abundances were calculated by summing the number of stems by species for all plots. Shannon's true diversity was then calculated for each replicate using the same methods as for alpha diversity. An estimate of mean Shannon's true gamma diversity was then obtained by calculating the mean across all 1000 replicates. Beta diversity was calculated by dividing the mean Shannon's true gamma diversity for a given disturbance type or severity level by the Shannon's true alpha diversity of individual plots within that level or disturbance type: $D(H_\gamma) = D(H_\alpha) \cdot D(H_\beta)$ (Jost 2007). ANOVA and Tukey's HSD tests were used to detect significant differences in beta diversity. No inferential statistics were used to compare gamma diversity because the effective sample size for most disturbance types/severity levels was less than 5. We did, however, compare the overall shape of the diversity-severity relationship at the gamma level to the shape of the relationship at the alpha level to detect changing patterns across spatial scales.

Results

Across all 845 plots and across a range of disturbance types and combinations we counted approximately 66,000 tree and shrub saplings and seedlings. We encountered 14 tree species, with quaking aspen and paper birch occurring most frequently (38.5% and 38.1% of plots respectively) and black ash and red pine occurring most infrequently (0.8% and 0.9% of plots respectively). We encountered 16 species of tree-like woody shrubs with pin cherry *Prunus pennsylvanica* L. f*.* occurring most frequently (28% of plots) and fireberry hawthorn *Crategus chrysocarpa* Ashe. and high bush cranberry *Viburnum edule* (Michx.) found most infrequently (0.1% of plots). To our knowledge, our sample plots included all species of trees and tree-like woody shrubs known to occur within our study area with the exception of bur oak *Quercus macrocarpa* Michx., northern red oak *Quercus rubra* L. and Canada yew *Taxus canadensis* Marshall.

Severity of disturbances varied widely from plots with single treefalls to plots where all trees were dead and fallen, and fires had partially or fully consumed litter and duff layers. Instances of wind followed by single fire, wind followed by 2 fires, and 2 or 3 fires all tended to have higher fire severity ∆BA, and ground fire severity than did instances of single fires, while char height was highest for wind followed by single fires. Char height for other multiple disturbance events tended to be less than that of single fires. Mean wind severity ∆BA was generally less than mean fire severity ∆BA across either single or multiple disturbance scenarios (Table 1-3).

Effects of continuous measures of disturbance severity on alpha diversity

For plots in which wind was the only disturbance, we found no statistically significant relationships between either species richness or Shannon's true diversity and disturbance severity (wind severity ΔBA). However, in areas of wind followed by fire, both Shannon's true diversity and species richness had weak and slightly humped to declining relationships with wind severity ΔBA (Figure 1-1).

Diversity metrics showed a generally humped relationship with fire severity measures. When all plots experiencing fire were pooled, Shannon's true diversity and species richness had a modestly humped relationship with fire severity ΔBA, where diversity values were lowest at high and low disturbance severities. The shape of this relationship held when examining the relationship by disturbance combination. Both single fire plots and plots experiencing wind followed by fire had significant, humped relationships between fire severity ΔBA and Shannon's true diversity and species richness (Figure 1-1). The effect of char height on local diversity was also examined but we found no statistically significant relationship between char height and Shannon's true diversity and species richness.

Fire severity ΔBA was significantly related to percent of plot area burned ($r^2 = 0.5644$; $P < 0.0001$, n = 50) and the hump shaped relationship for fire plots may reflect two different underlying patterns. When partially burned plots were

23

examined separately, there were positive linear relationships between diversity

metrics for both fire severity and percent area burned (Figure 1-2). Contrastingly,

on completely burned plots, Shannon's true diversity had a significant but weak

negative linear relationship with fire severity ΔBA ($r^2 = 0.0196$, $P = 0.0002$, $n =$

631), and fire severity ΔBA was not a significant predictor of species richness.

The humped response seen in the full set of burned plots may therefore reflect

the positive linear trend for partially burned plots and the neutral to slight

negative response for fully burned plots.

Effects of categorical measures of disturbance severity on alpha diversity

Categorical measures of disturbance severity were analyzed for differences in

alpha diversity using one way ANOVA and Tukey's honest significant difference

test. Crown fire severity of 4 was only recorded on 6 plots, so these severity

values were grouped with crown fire severity of 3 for analysis. Ground fire

severities ranged from 0 for unburned plots to 5 for plots where fires had

completely consumed the ground litter and duff layers, leaving only bare mineral

soil. Alpha diversity measures exhibited a hump shaped distribution for species

richness and ground fire severity and a plateau shaped distribution for Shannon's

true diversity and ground fire severity (Figure 1-3). One way ANOVA tests found

differences among ground severity classes to be significant for both species

richness ($F_{4, 691} = 34.97$; $P < 0.0001$) and Shannon's true diversity ($F_{(4, 691)} =$

19.16; $P < 0.0001$)). Post hoc comparisons using Tukey's HSD test for

Shannon's true diversity and ground fire severity class indicated that ground

severity of 5 resulted in significantly lower Shannon's true diversity (mean = 2.63; se = 0.11) than for all other ground severities and ground severity of 4 resulted in a significantly lower Shannon's true diversity (mean = 3.18; se = 0.07) than for ground severity of 2 (mean = 3.80; se = 0.13) or 3 (mean = 3.87; se = 0.10) (Figure 1-3).

Post hoc comparisons using Tukey's HSD test indicated that species richness was significantly higher for ground severity 3 (mean = 6.36; se = 0.15) than for other severity levels, except 2 (mean = 6.05; se = 0.19). Ground severity of 5 resulted in significantly lower richness (mean = 3.75; se = 0.19) when compared to all other severity levels. (Figure 1-3).

Diversity measures showed a threshold relationship with crown fire severity, where diversity was high for crown severity of 1 and 2, which corresponded to areas where fires only caused scorching or consumption of some fine branches, while diversity was lower for crown fire severity of 3, where all fine branches had been consumed by fire. One-way ANOVA tests found differences among crown fire severity classes to be significant for both species richness ($F = _{(2, 5.796)}$; $P = 0.0032$)) and Shannon's true diversity ($F = _{(2, 4.685)}$; $P = 0.0095$)). Tukey's HSD test found both species richness and Shannon's diversity were significantly lower for plots with a crown fire severity of 3, than for crown severity of 1 or 2 (Figure 1-4).

Effects of single versus multiple disturbances on alpha diversity

We found modest evidence of differences in regeneration diversity between disturbance types/combinations. Comparisons of species richness by disturbance type/combination using a one way ANOVA showed significant differences between disturbances ($F_{(5, 839)} = 6.5702$; $P < 0.0001$)). A post hoc Tukey's HSD test found that single fire plots (mean = 6.01; se = 0.13) had significantly higher richness than did plots experiencing wind followed by single fire (mean = 5.02; se = 0.11), or wind followed by 2 fires (mean = 4.94; se = 0.26), but that all other disturbance types did not differ significantly (Figure 1-5). A one-way ANOVA test for Shannon's true diversity by disturbance type/combination failed to find significant differences amongst disturbance types ($F_{(5, 839)} = 1.64$; $P = 0.1458$)).

We did not see evidence of significant difference in the shape of the severity-diversity relationship across different disturbance types. While wind severity ΔBA did not have a significant relationship with either diversity metric, the curved best fit line for wind severity ΔBA for wind only plots had significant overlap with the curved best fit line for fire severity ΔBA for single fire plots (Figure 1-6). We failed to detect significant differences between the shapes of diversity-severity curves for single disturbances and multiple disturbances when compared across basal area based severity metrics.

Variation in effects of multiple disturbances and severity on diversity across spatial scales

We examined whether differences in disturbance type/combination or disturbance severity varied across spatial scales by fractionating diversity into alpha, beta and gamma components. Beta diversity in this context is a measure of how different diversity is from one regeneration plot to another or more specifically it is the average number of uniquely different plots in a pool of 50 plots. In most instances, we failed to detect significant differences in beta diversity by either disturbance type/combination or disturbance severity. A one-way ANOVA test of beta diversity by disturbance type/combination found no significant differences in Shannon's true beta between disturbance types/combinations. Similarly, almost all severity metrics examined, including fire severity ΔBA, ground fire severity, crown fire severity, and char height did not differ significantly in beta diversity across severity levels. Wind severity ΔBA for all plots was the only severity metric where we detected significant differences in beta diversity by severity ($F_{(2, 833)} = 10.65$, $P < 0.0001$). A Tukey's HSD found that wind severities of >66% had significantly higher true beta diversity than did lower severity levels (Figure 1-7). This relationship contrasted with that found for alpha diversity where alpha diversity was lowest for plots with high wind severity and showed a humped to declining relationship with increasing wind severity. Differences in beta diversity by wind severity ΔBA were not statistically significant when examining wind only plots and the relative magnitude of differences for beta diversity were small.

We examined gamma diversity at the scale of 50 plots. Similar to the alpha level, there were modest differences in diversity between disturbance types/combinations. Lightly disturbed plots had the highest gamma diversity followed by wind-only plots. All other disturbance types/combinations had similarly lower gamma diversity, except for single fires, which had the lowest gamma diversity of any type/combination (Figure 1-8). This contrasted with the relationship at the alpha level where all disturbance types/combinations had similar true diversity and single fire plots had statistically greater richness but not Shannon's diversity than did wind followed by single fire or wind followed by 2 fires.

Gamma diversity and disturbance severity

Diversity-severity relationships were mixed, but sometimes pronounced, at the gamma level; of the 6 we examined 2 were sharply declining, 2 were humped, and 2 were flat (Figure 1-9). The hump shaped diversity-severity relationship of fire severity ΔBA found at the alpha level held at the gamma level with the middle range of fire severity values having the highest gamma diversity (Figure 1-9B). Crown fire severity and gamma diversity had a relationship that was similar to their relationship at the alpha level, where low and mid crown fire severity values had similar diversity values and high crown fire severity values were associated with reduced diversity (Figure 1-9F). Similar to the alpha level, there was no relationship between char height and diversity at the gamma level (Figure 1-9E).

28

Other severity metrics had diversity-severity relationships at the gamma level that differed from those at the alpha level. Ground severity, which had a humped to plateaued relationship with diversity at the alpha level, showed a declining relationship at the gamma level, where the highest severity levels were associated with lower gamma diversity (Figure 1-9C). Gamma diversity had a declining relationship with wind severity ΔBA for wind only plots which contrasts with the relationships observed at the alpha level where there was no significant between diversity and wind severity for wind only plots (Figure 1-9D). Gamma diversity had a humped to declining relationship with wind severity ΔBA when all plots were examined together, which was similar to the relationship at the alpha level (Figure 1-9A)

Discussion

We used a series of multiple disturbances in the BWCAW as a case study to examine the relationship between disturbance severity and diversity as a test of current ecological theory. Moreover, we used multiple measures of disturbance severity and diversity across a range of spatial scales and disturbance combinations to examine the nature and shape of the disturbance severity-diversity relationships. At the alpha diversity level, we found the relationships between disturbance severity and diversity were complex and individualistic. Similar to Miller et al. (2011), we found that depending on the measure of disturbance severity used, diversity-disturbance relationships were variously positive, negative, or humped. Aggregating across spatial scales, we found little evidence of significant relationships between disturbance severity and beta diversity and variable relationships between gamma diversity and disturbance severity. Differences in diversity between disturbance types/combinations were generally weak. While in some instances, multiple disturbances had lower diversity than single disturbance events, relative differences between single and multiple disturbances were small. In all cases, lightly disturbed plots, or those experiencing no major disturbances, had higher alpha and gamma diversity than recently disturbed plots, likely reflecting the greater stand-age variation of these plots. Across spatial scales, there were often variations in the shape of diversity-severity relationships from the alpha to the gamma scale, indicating that spatial scale is an important factor in assessing the relationship between disturbance and diversity.

Effects of disturbance severity on alpha diversity

Although we found humped diversity-severity relationships for the majority of severity metrics, the relationships were modest and not universal; we also found instances of linear and flat relationships and cliff or plateau shaped relationships indicative of a threshold response. The linear relationships found for partially burned plots and completely burned plots can be viewed as segments of an overall humped relationship. Assuming that the IDH were a universally true relationship, one would expect that by constraining the range on severity values examined, one could produce linear relationships between severity and diversity as segments of a curve that may appear relatively straight. Examining only partially burned or only completely burned plots effectively truncates the range of severity values analyzed and may therefore create two linear trends from an overall modestly humped relationship.

Cliff or plateau shaped relationships may reflect threshold responses of a community to disturbance severity, where severity has little effect on diversity until a threshold is crossed after which increased severity is associated with reduced diversity. For ground fire severity, a severity value of 5, where all litter and duff was consumed by fire, was consistently associated with low regeneration diversity. Similarly, for crown fire severity, severities of 3, which corresponded to fires where all fine branches were consumed, were associated with reduced diversity for both Shannon's true diversity and species richness. In both cases, the highest observed severity values are associated with significantly

reduced diversity when compared to lower severities. In the case of ground fire

severity, high ground fire severities likely reduced the availability of propagules

by damaging the roots and meristems of suckering and sprouting species and

depleting the seedbanks of species which bank dormant seeds in litter and duff

layers. High crown fire severities may lead to loss of aerial seed banks for

serotinous species. In both cases, high severities may limit the potential species

pool to shade intolerant pioneer species

Despite finding many examples of humped or cliff shaped diversity-severity

relationships, some severity metrics appeared to have little or no effect on

diversity. Char height had no relation to any diversity measures we examined. As

most boreal tree species regenerate from either below ground vegetative

mechanisms and seed banks or aerially stored seed banks, char height which

measures fire intensity but does not account for the residence time or total heat

exposure, relates poorly to measures of regeneration success and diversity. In

brief, disturbance metrics that integrate the physical effects of fire over its

duration appear to be more useful as predictors of diversity.

Wind severity ΔBA had no significant effect on diversity of regeneration following

the 1999 windstorm, at least at the alpha level. While wind severity did not have

any direct effect on regeneration alpha diversity for unburned areas, in areas that

subsequently experienced fire, there was a humped to declining relationship

between increasing wind severity and alpha diversity. Wind disturbance from the 1999 storm substantially increased fuel loads in affected stands (Woodall and Nagel 2007) and fire managers have reported increased fire intensity and extreme fire behavior in these areas (Fites et al. 2007). Our results reinforce this conclusion. Because high fire severity and very high ground fire severities were both associated with lower biodiversity, wind disturbance may indirectly impact biodiversity in cases of wind followed by fire via disturbance interactions that increase the relative severity of subsequent fires.

Wind disturbance likely also has direct impacts on diversity in wind-fire combinations. One possible mechanism for the long-lasting influence of wind severity on diversity in cases of wind followed by fire is the reduction in abundance of many early successional tree species that tend to be less wind firm than late successional species (Rich et al. 2007). High mortality of species such as jack pine following wind disturbance may have eliminated or greatly reduced the seed sources for species that typically are important components of post-fire regeneration (Heinselman 1996). Jack pine seed viability declines significantly after about 5 years (Beaufait 1960) and in our study many jack pines killed by wind had been dead for 5+ years at the time of fire. The notable absence of these species in wind-fire combinations, may partially explain some of the negative association between high wind disturbance and biodiversity in wind-fire combinations. Differences between boreal tree susceptibility to wind throw and the relative resilience to wind of many temperate species may in part explain

differences in our findings compared to those of Peterson and Leach (2008) who found a marginal increase in tree regeneration diversity with increasing cumulative severity from combinations of wind and logging in an investigation of temperate forests in Tennessee, USA.

Overall, the forests examined in this study appear to be relatively resilient to disturbances with modest to negligible differences in diversity between different disturbance types and combinations. This is consistent with other independent studies of southern boreal forests which found no difference in diversity (or productivity) of similarly aged boreal forests established following either timber harvesting or wildfire (Reich et al. 2001; Hart and Chen 2008). To exist in a landscape dominated by high severity fires trees must have adaptations to disturbance; while disturbance may reorganize communities, even severe or overlapping disturbances are unlikely to eliminate disturbance adapted species.

Variation in diversity-severity relationships across spatial scales

We hypothesized that diversity-severity relationships would become less pronounced with increasing spatial scale, and generally become flatter. While several relationships became flatter from the alpha to the gamma scale, others that had non-significant relationships at the alpha level had relatively large differences at the gamma scale, and still others had relationships that changed shape across spatial scales. Both crown fire severity and fire severity ΔBA had

diversity-severity relationships at the gamma scale with the same shape as those at the alpha scale. Gamma diversity had a relatively flat relationship with wind severity ΔBA for burned plots, and a declining relationship with wind severity ΔBA for wind only plots. This contrasts with patterns at alpha level where diversity metrics had a humped to declining pattern with wind severity.

Changing diversity-severity relationships across spatial scales may be one reason why universal diversity-severity relationships are hard to find empirically (Makey and Currie 2001). The variation in patterns of diversity-severity relationships across spatial scales in our study demonstrates how different researchers investigating diversity-severity relationships in the same system could conceivably reach very different conclusions about the shape of the diversity-severity relationship if they used different spatial scales.

One consistent trend we observed across spatial scales was reduced diversity at the highest severity levels. While we found all types of possible patterns, monotonic increasing patterns were only found in cases of truncated disturbance severity. All other trends, across spatial scales were either flat, humped or cliff shaped. While there may be considerable variation in the response of diversity to low and mid-severity disturbances, our results suggest that the highest disturbance severities consistently result in lower diversity. In this way, high

disturbance severity may act as an ecological filter, which reduces the potential species pool of a site.

Other studies in the boreal forest examining understory diversity have found that disturbances have far more impact on community composition than diversity which may in part explain our results. Haeussler et al. (2002) proposed that as disturbance severity increases different guilds of species are favored. At low disturbance severity composition may be dominated by species that survive the disturbance, as disturbance severity increases survivors are reduced and replaced by species regenerating vegetatively or from seedbanks, and at still higher levels of severity seed dispersing species dominate. At the highest severity levels survivors are eliminated, and only those species capable of long distance dispersal can recolonize a site. Thus, although disturbance can impact diversity, its effect is somewhat masked by large changes in composition that occur between different reproductive guilds, and only at the highest severity levels are differences in diversity readily apparent.

Effects of disturbance type and multiple disturbances on diversity

We found weak to modest evidence that instances of multiple disturbances result in reduced diversity when compared to single disturbance events. We did not see strong evidence of interactions between disturbance severity and disturbance type and diversity, rather instances of multiple disturbances tended to have

higher mean severity values than cases of single disturbances. Where we could compare fire and wind disturbance using comparable diversity metrics, the overall shape of the diversity-severity relationships had a large amount of overlap and did not appear to differ significantly based on wind vs fire disturbance. Multiple disturbance events in our study generally had higher ground fire severity and fire severity ΔBA, than did single disturbances. Although high ground fire severities and high fire severities were both associated with reduced diversity, only in the case of species richness did we find significant differences between single and combined multiple disturbances. Single fire plots had greater species richness than either wind followed by fire or wind followed by 2 fires, but there were no other statistically significant differences in diversity by disturbance type or combination for species richness and no significant differences in Shannon's true diversity by disturbance type. In addition, the relative magnitude of differences in diversity between disturbance types were small, suggesting that even where statistically significant differences between disturbance types exist, their ecological impacts are likely to be minimal.

At the gamma scale, single fire plots had lower Shannon's true diversity than did wind followed by fire or wind followed by 2 fires, although again the relative magnitude of any difference in diversity between disturbance types was small. Across spatial scales, differences between single and multiple disturbances appeared to be less than those between lightly disturbed plots and all other plots. While disturbance itself may reduce diversity in these systems, the differences

37

between the diversity of common disturbances like crown fire and much less common multiple disturbance incidents appear to be relatively small where they exist at all. In the context of Liang et al. (2015), the magnitude of differences in diversity across severities or between disturbance types in this study do not appear to be large enough to lead to declines in productivity.

Although in some cases multiple disturbances had higher average severity than single disturbances, the failure to find consistent differences between the diversity of single and multiple disturbances suggests that while multiple disturbances may be more severe than single disturbance events, there is considerable variation in severity and/or its impacts over the landscape scale. Even in cases of multiple fires or wind followed by fire, low and mid severity patches exist that likely mitigate to some extent the diversity loss that would be expected from their high overall disturbance severity. The overall heterogeneity and patchiness of natural disturbances in this study suggests that the boreal forest may be relatively resilient to even seemingly extreme combinations of disturbance, at least in terms of tree and shrub diversity. It is unknown whether initial differences in diversity post-disturbance will persist as stands in this study age and develop. Work by Hart and Chen (2008) suggest that patterns in diversity do change over time and that richness gradually increases over time, at least until the point of stand maturity, and that initial differences in composition and richness between disturbance types tend to converge over time. If similar

trends occur in this study, initial differences between different disturbances types and severities may become less significant over time.

In this study, we did not examine differences in community composition between disturbance types/combinations or severity levels. Although our results suggest that overall differences in diversity of trees and shrubs are small, changes in community composition observed but not reported on in this work could have significant impacts on ecological functioning in this system. In addition, increased disturbance severity or multiple disturbances within a short period of time could still impair the diversity of other functional groups or trophic levels beyond those examined in this study (Reich et al. 2012). At this time, it is unknown what relationship exists between trees species diversity and understory diversity or the diversity of other organisms such as invertebrates, fungi or vertebrates within the community. Our results were generally similar to those of other researchers examining the effects of disturbances on understory diversity (Hart and Chen 2008) without further investigation it is difficult to know if the effects we observed of disturbance on the tree and woody plant community are similar for other functional groups and guilds within the boreal forest. In addition, increasing disturbance frequency may still adversely impact species that depend on late successional stand types and forest structure if disturbances become frequent enough to shift the overall landscape stand age distribution.

Although our results suggest that predicted increases in disturbance occurrence and the possibility of increasing frequency of multiple disturbance events may perhaps pose less risk than expected to the resilience of the boreal forest under climate change, additional compounding impacts including physiological stress (Reich et al. 2015), increased incidence of drought (Peng et al. 2011) or insect outbreaks (Volney et al. 2000) along with changing age structure could still negatively impact the overall diversity and resilience of this system. In addition, while the natural multiple disturbance events encountered in this study did not appear to decrease diversity, high disturbance severity did. Conceivably human disturbances could create disturbances that are more uniform in their severity than the natural disturbances encountered in this study. Across a landscape scale, the creation of large blocks or relatively uniform disturbance severity might result in reduced diversity compared to natural disturbances with their high degree of patchiness and severity variability. Management actions like salvage logging that tend to increase overall disturbance severity (Peterson and Leach 2008), could result in reduced diversity if they are applied across large spatial scales without reserve areas or if they are applied without regard for the inherent heterogeneity of naturally occurring multiple disturbances (Purdon et al. 2004). Although biodiversity has been a major area of focus of forest conservation and sustainable forestry it is important to remember that disturbances impact many aspects of ecosystem functioning beyond species diversity and that impacts of disturbances on community composition are also important to consider when evaluating the ecological impacts of a given disturbance (Haeussler et al. 2002).

Table 1-1. Disturbance events, and severity cut offs for disturbance types and combinations along the upper Gunflint Trail of BWCAW

Disturbances 1974 through 2007

Disturbance Type/ Combination	1974 Prayer Lake Fire and/or 1995 Saganaga Corridor Fire	1999 Blowdown	Prescribed Fires from 2002-2005	2006 Cavity Lake Fire	2007 Ham Lake Fire	2007 Redeye Lake Fire or 2007 Famine Lake Fire	Fire Severity ΔBA	Wind Severity ΔBA	Number of Plots (n=845)
Two or Three fires	yes	no	no	no	yes	no	>0	<25%	69
Wind followed by two fires	no	yes	yes	no	yes	no	>0	≥ 25%	53
Wind followed by single fire	no	yes	some plots	some plots	some plots	some plots	>0	≥ 25%	379
Single fire	no	no	some plots	some plots	some plots	some plots	>0	< 25%	233
Wind disturbance	no	yes	no	no	no	no	0	≥ 25%	45
Lightly Disturbed	no	no	no	no	no	no	0	<25%	66

Table 1-2. Categorical disturbance severity indices

	Crown Fire Severity Index	Ground Fire Severity Index
0	No damage	Unburned
1	Most needles scorched	Light scorching of surface litter
2	Most fine branches (<1cm) charred	1-50% of surface litter consumed
3	No fine branches remain	50-99% of surface litter consumed
4	Only main stem or branch stubs remain	100% of surface litter consumed, some duff consumed
5	N/A	All organic litter and duff consumed

Table 1-3. Disturbance severity of disturbance types and combinations. Number of observations equals number of plots except where otherwise noted in table

	Wind followed by 2 fires	2 or 3 fires	Wind followed by single fire	Single Fire	Wind Alone	Lightly disturbed
number of plots	53	70	382	234	45	66
Ground fire severity (mean)	3.0	2.9	3.7	2.8	NA	NA
Ground fire severity (SD)	0.9	1.0	0.9	1.2	NA	NA
Ground fire severity (number of observations)	51	63	362	233	NA	NA
Fire severity as % change in BA (mean)	98.2	93.4	96.5	86.3	NA	NA
Fire severity as % change in BA (SD)	6.3	14.1	16.3	23.3	NA	0
Wind severity as % change in BA (mean)	58	11	59	10	51	8
Wind severity as % change in BA (SD)	16.3	14.7	21.6	7.2	18.5	6.6
Char height in meters (mean)	NA	0.36	3.46	2.10	NA	NA
Char height in meters(SD)	NA	0.24	2.32	2.02	NA	NA
Char height (number of observations)	NA	45	140	206	NA	NA
Percent area burned (mean)	100.0	96.3	98.9	89.0	NA	NA
Percent burned (SD	0.00	17.0	8.1	25.9	NA	NA
Percent burned (number of observations)	48	63	368	221	NA	NA

Figure 1-1. Shannon' true diversity (A-D) and species richness (E-H) vs wind severity or fire severity expressed as the proportional change in basal area. Fits: A ($r^2 = 0.030$, $P < 0.0001$, $n = 729$), B($r^2 = 0.0302$, $P = 0.0110$, $n = 232$), C($r^2 = 0.0107$, $P = 0.0375$, $n = 428$), D ($r^2 = 0.018$, $P = 0.0005$, $n = 729$), E ($r^2 = 0.084$, $P < 0.0001$, $n = 729$), F($r^2 = 0.01706$, $P = 0.0515$, $n = 232$), G ($r^2 = 0.0257$, $P = 0.0015$, $n = 428$), H ($r^2 = 0.023$, $P < 0.0001$, $n = 729$). See Appendix Table 2 for regression equations. Points are jittered 0.1 in width for A-H and 0.25 in height for A-D. Shaded line represents 95% confidence interval for fit.

44
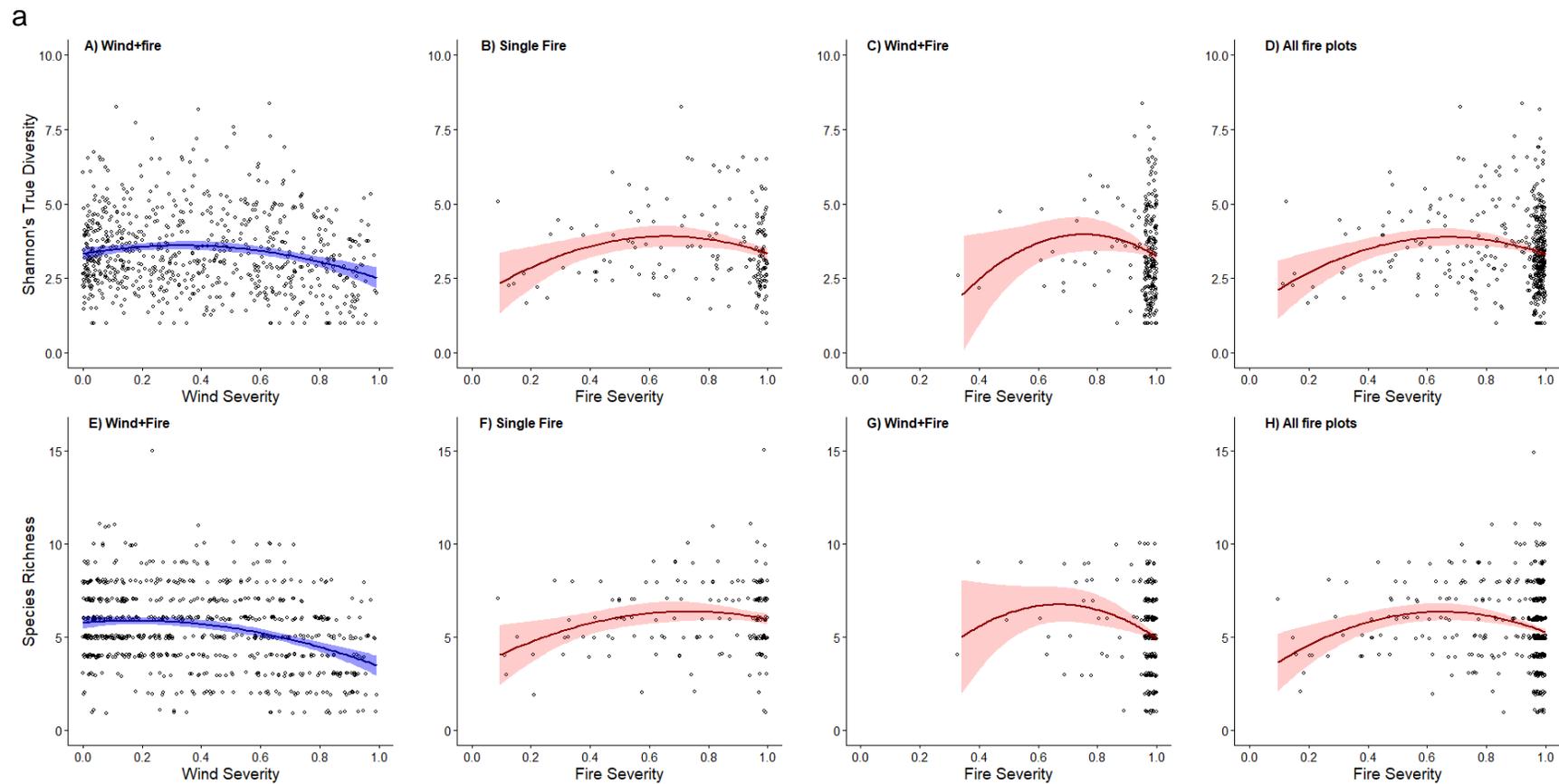
Figure 1-2. Species richness and Shannon's true diversity in relation to fire severity measured as the proportional change in basal area from 2000-2012 and % of plot area burned for partially burned plots. Fits were A. ($r^2 = 0.075$, $P = 0.0036$, $n = 98$), B($r^2 = 0.181$, $P = 0.0003$, $n = 98$), C. ($r^2 = 0.079$, $P = 0.0051$, $n = 98$), D. ($r^2 = 0.261$, $P < 0.0001$, $n = 98$), See Appendix Table 2 for regression equations. Points for figures C and D are jittered 0.25 in height. Shaded line represents 95% confidence interval for fit.
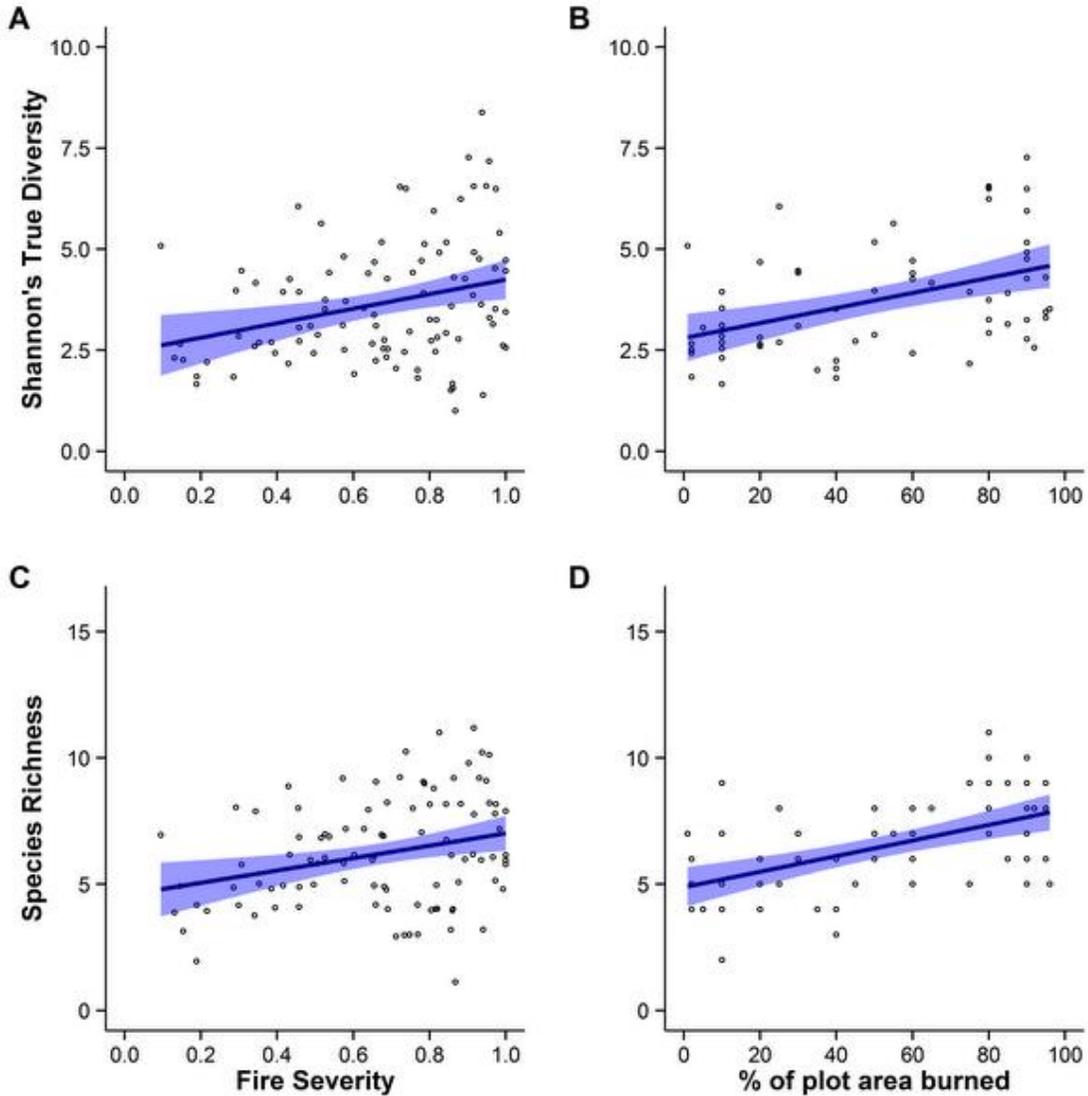
Figure 1-3. Box and whisker plots of Shannon's true diversity and species richness by ground fire severity class. Letters represent significant differences in mean diversity between ground fire severity classes (Tukey's HSD, $P < 0.05$). Box plots represent the median value and interquartile range at each severity level. The upper and lower hinges represent the inner quartile range (IQR) or the 25th and 75th percentiles while the middle bar represents the median or 50th percentile. The upper and lower whiskers extend to the highest and lowest values within 1.5*IQR. Data points beyond 1.5*IQR are considered outliers and represented as dots.
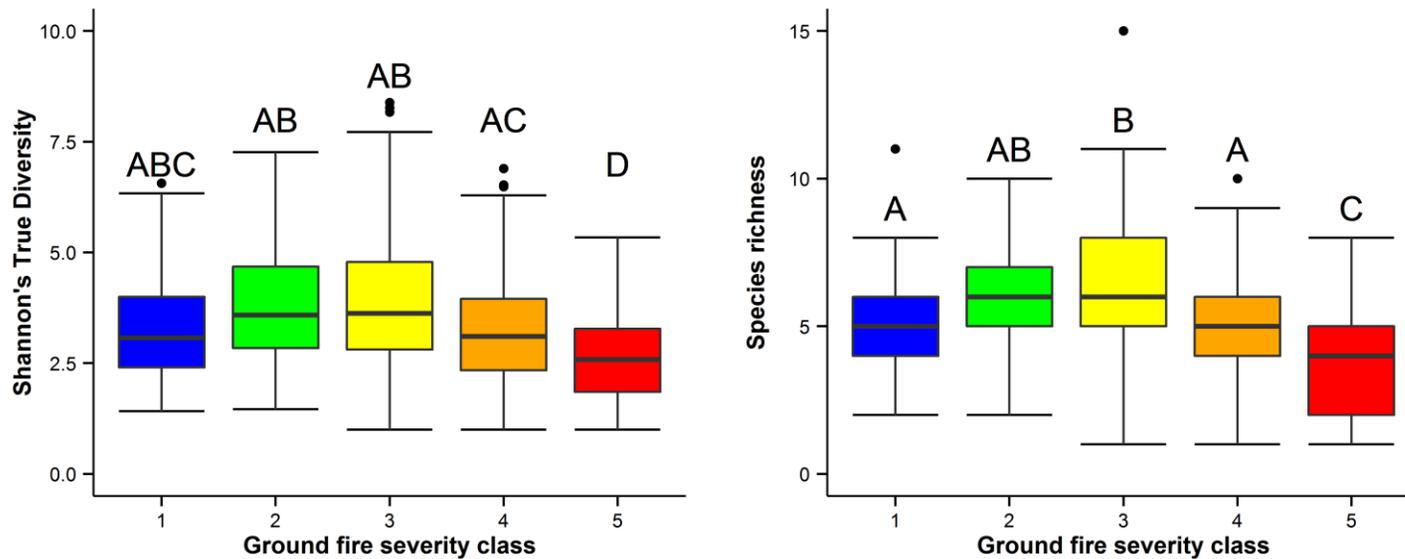
Figure 1-4. Box and whisker plots of Shannon's true diversity and species richness vs crown fire severity. Few plots (n=4) had crown severity values of 4 so these plots were combined with severity class 3 for analysis. Letters represent significant differences in mean diversity between crown fire severity classes (Tukey's HSD, $P < 0.05$) Box plots represent the median value and interquartile range at each severity level. The upper and lower hinges represent the inner quartile range (IQR) or the 25th and 75th percentiles while the middle bar represents the median or 50th percentile. The upper and lower whiskers extend to the highest and lowest values within 1.5*IQR. Data points beyond 1.5*IQR are considered outliers and represented as dots.
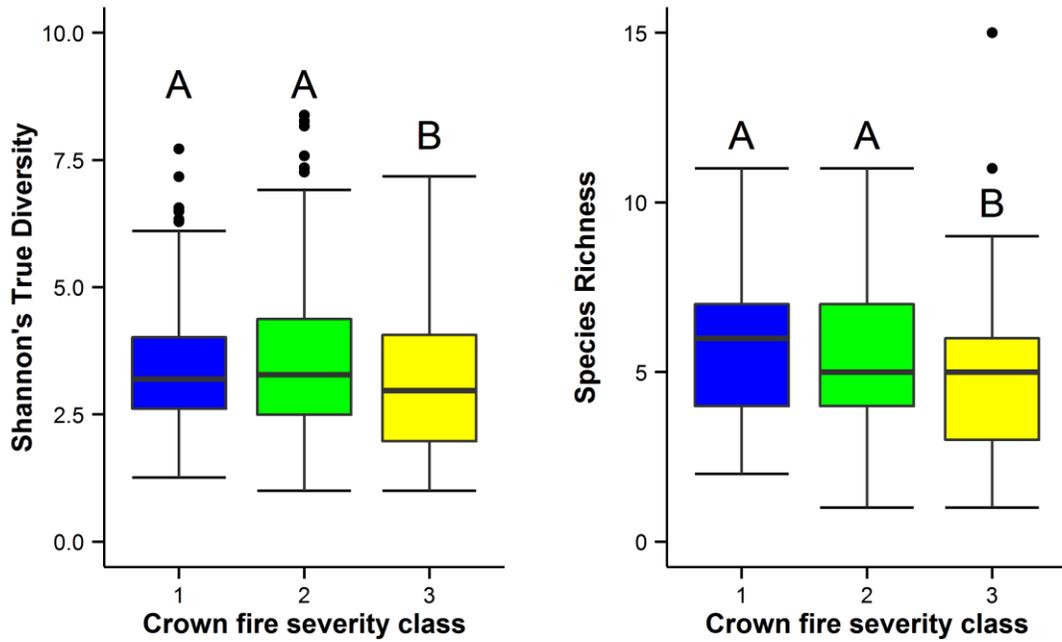
Figure 1-5. Box and whisker plot of species richness by disturbance type/combination. Letters represent significant differences in mean species richness between disturbance types/combinations (Tukey's HSD, $P < 0.05$). Box plots represent the median value and interquartile range at each severity level. The upper and lower hinges represent the inner quartile range (IQR) or the 25th and 75th percentiles while the middle bar represents the median or 50th percentile. The upper and lower whiskers extend to the highest and lowest values within 1.5*IQR. Data points beyond 1.5*IQR are considered outliers and represented as dots.
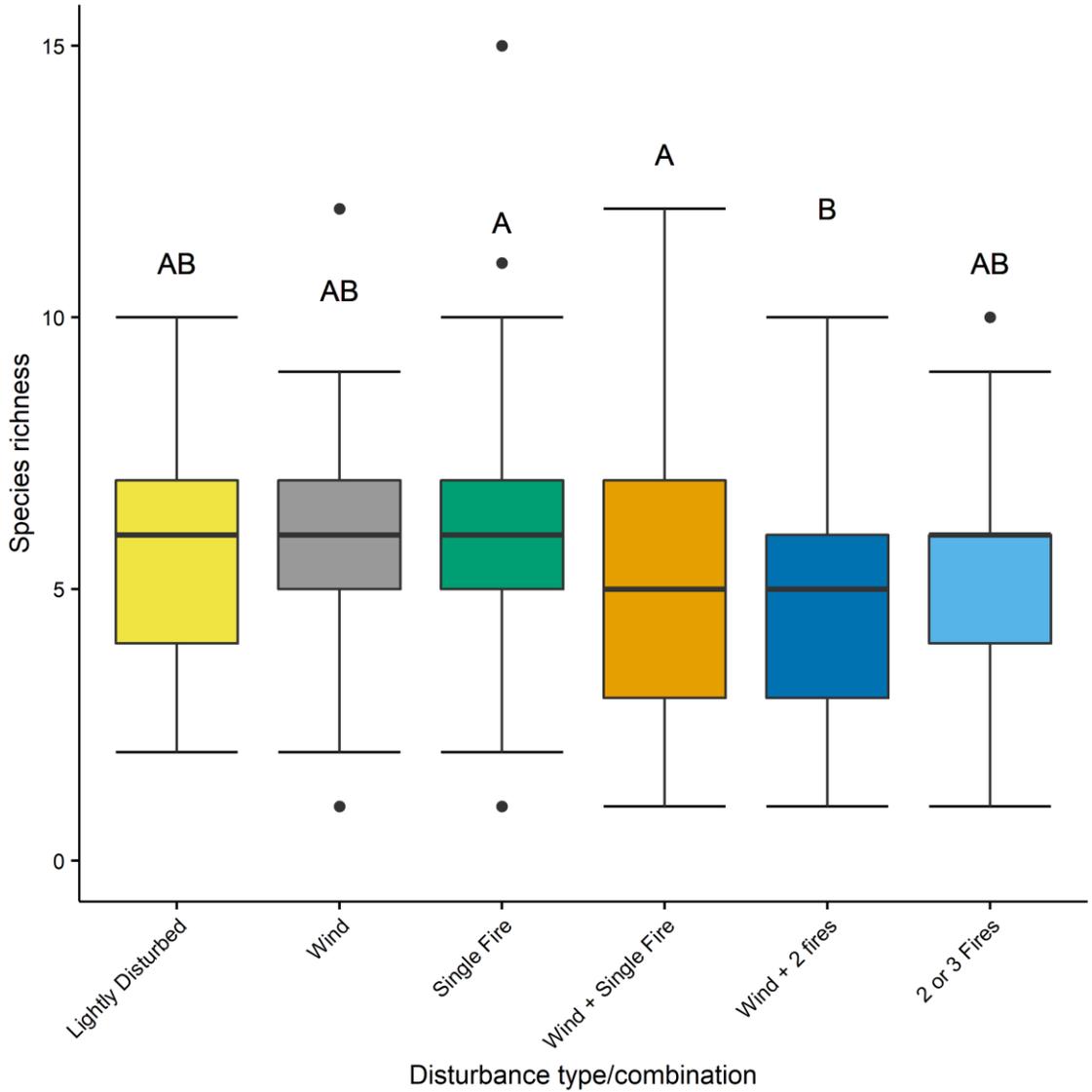
Figure 1-6. Comparison of relationships of diversity with fire severity vs. with wind severity for wind only and single fire plots. Wind severity was non-significant for both species richness (B) and Shannon's true diversity (A), while fire severity was significant for Shannon's true diversity p < 0.05 and marginally significant for species richness $P = 0.0515$. Points are jittered 0.1 in width. Shaded line represents 95% confidence interval for fit.
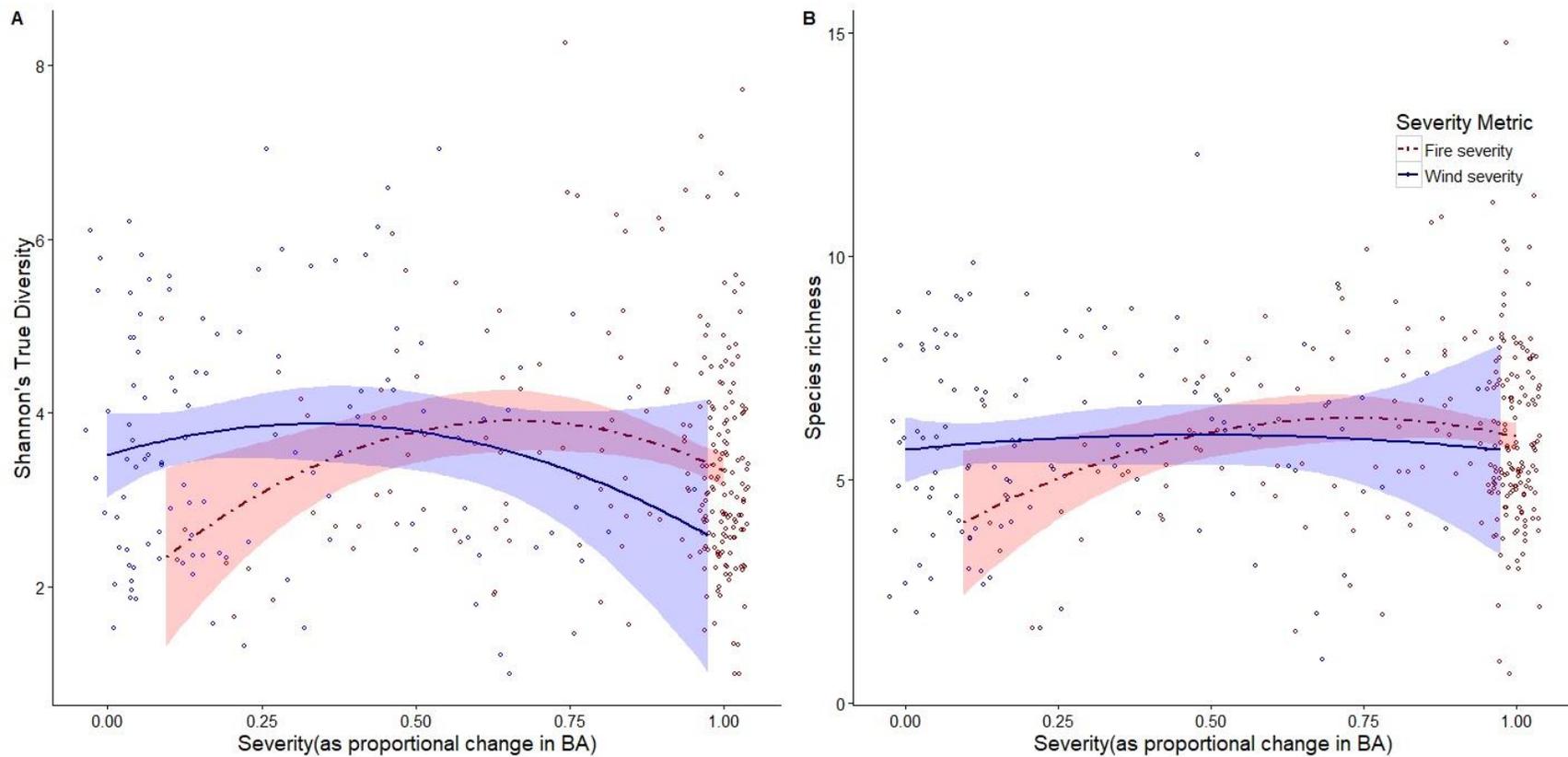
Figure 1-7. Shannon's true beta diversity by wind severity class for all plots. Means with different letters are significantly different (Tukey's HSD, *P* < 0.05). 21 points go beyond the y axis limit on this figure.
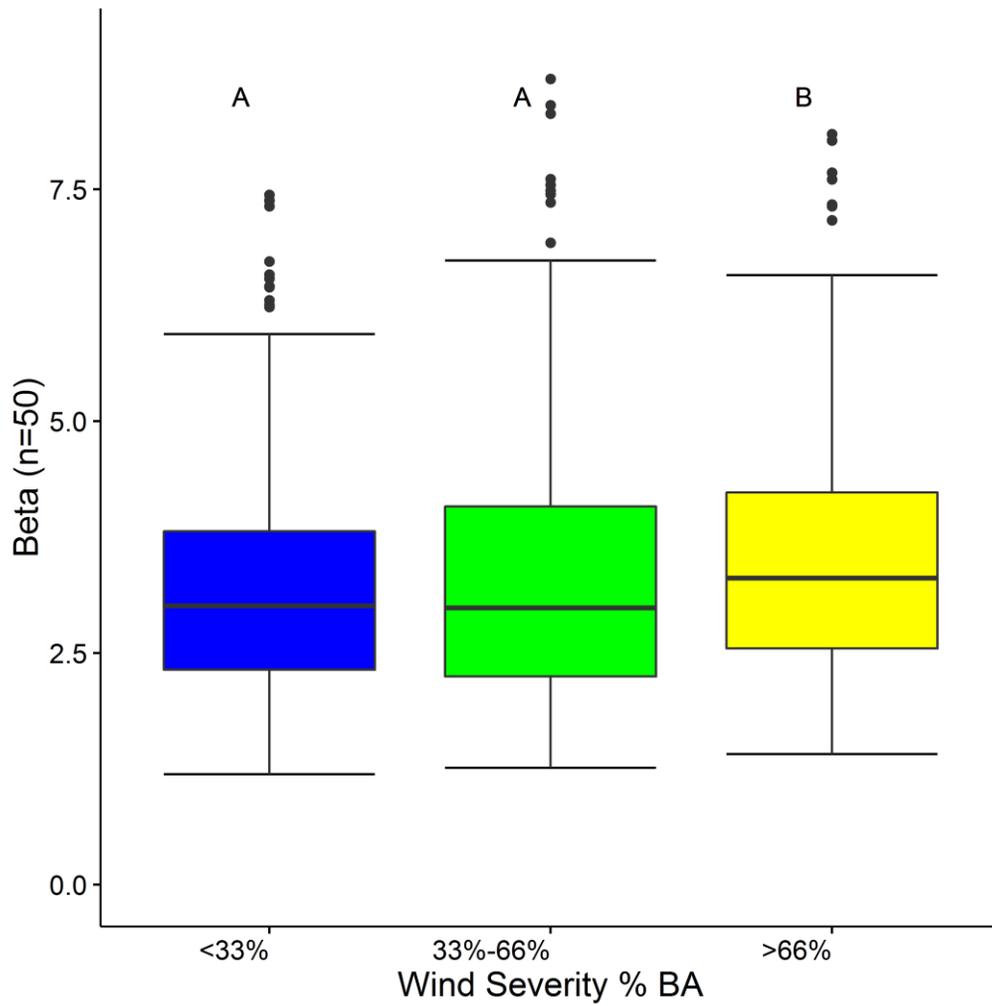
Figure 1-8. Gamma diversity by disturbance type/combination. Gamma diversity is measured as the mean Shannon's true diversity of a randomly selected group of fifty, 3 m radius regeneration plots (n=1000).
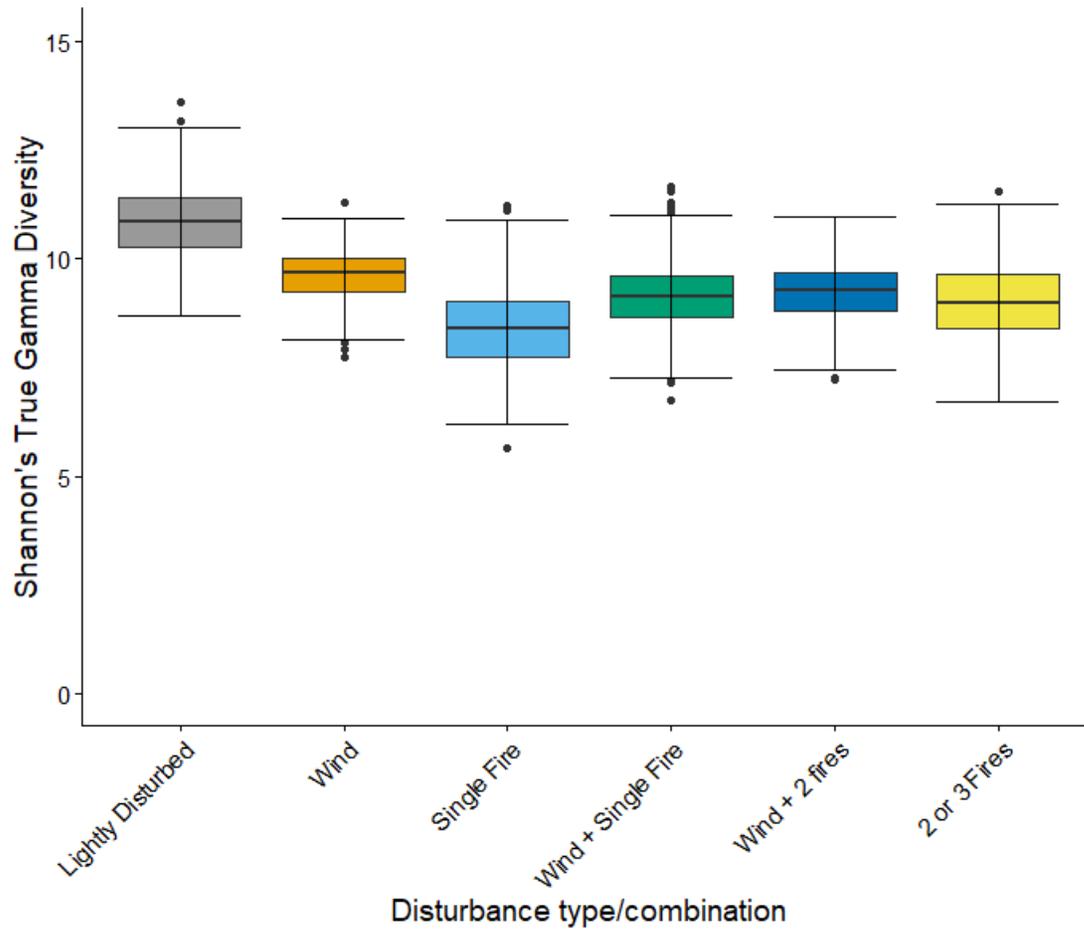
Figure 1-9. Gamma diversity by disturbance severity measures. Gamma diversity as the Shannon's true diversity of a randomly selected 50 plots sample drawn from each severity level, distributions are of 1000 bootstrap samples.
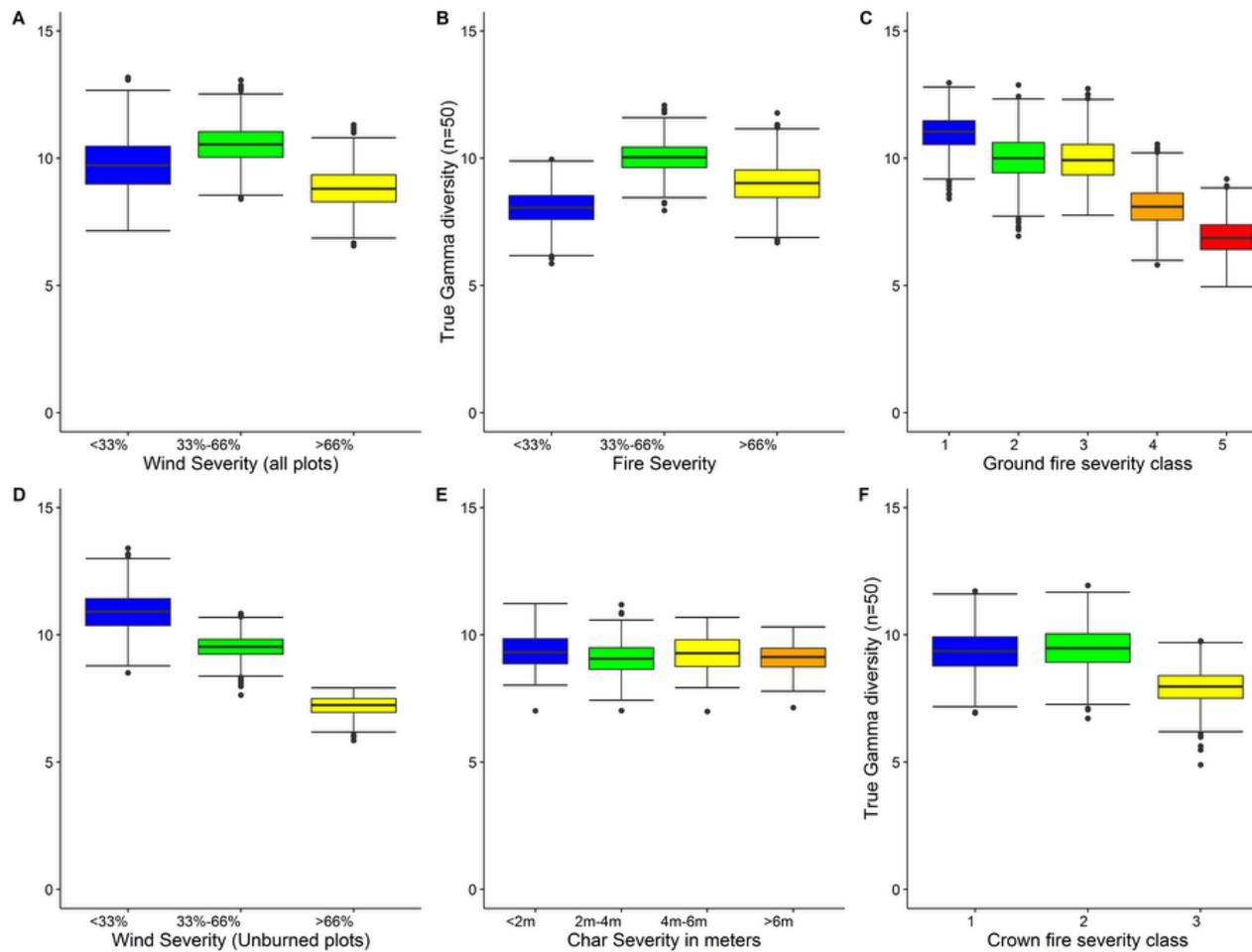
Chapter 2

Interactions between seasonal timing of fire and fire severity create alternate successional pathways in the southern boreal forest.

with
Lee Frelich
Peter B. Reich

Introduction

The seasonal timing of wildfires may exert a large influence over fire behavior and in turn, differentially impact plant communities (Heinselman 1973; Ohman and Grigal 1981; Knapp et al. 2009). In the boreal forest, fire occurrence is typically limited by fire weather conditions rather than fuel (Johnson et al. 2001), although the compositional make-up of the forest also influences patterns of severity (Carlson et al. 2011). The boreal fire regime has historically been characterized as high severity crown fires occurring on intervals of approximately 100 years (Heinselman 1973), but recent research suggests that boreal fire regimes are often complex and may include areas with frequent low and mid severity fires occurring on intervals of 4-50 years, as well as areas with considerably longer fire intervals (Johnson and Kipfmueller 2016). Fires are typically associated with extended periods of drought that occur on 10-20 year intervals (Heinselman 1973; Beverly and Martell 2005). While fires can occur in April or October, most fires occur from May through September. Fires that occur early in the season in May or early June typically occur within a window following snowmelt but preceding leaf-out when foliar moisture of conifers is very low (Chrosciewicz 1986). Dry conditions early in the season may allow fires to rapidly spread, and low foliar moisture may promote crown fires, but deep burning of the organic layer is uncommon in spring fires because of the limited window of drying (Heinselman 1981). Because of the relatively short window of drying, early season fires may be of lower severity, or leave more unburned patches when compared to fires that occur later in the fire season.

Late-season fires, which occur following prolonged dry periods, can result in much deeper burning and complete consumption of organic layers (Kasischke and Johnstone 2005), increased fire severity and fewer unburned patches compared to early season fires (Ohman and Grigal 1981; Heinselman 1996). Boreal forests are normally considered resilient to fire; while individual tree mortality is typically high in boreal fires, regeneration mechanisms such as serotinous cones, sprouts or seed refuges often result in composition post-fire that is very similar to pre-fire composition. However, extreme fire severity may disrupt resilience mechanisms leading to unexpected shifts in composition (Johnstone et al. 2010). Differences in fire effects between early and late-season fires may therefore make forests more or less resistant or resilient to fire disturbance.

Patterns of fire behavior including patchiness, burn depth and fire severity in turn influence the number and type of propagules available, nutrient levels, soil conditions and post-fire light levels all of which affect the establishment and relative success of species in the post-fire community. Parallel succession is defined as succession following a disturbance that may result in significant structural change but limited compositional change; instances of parallel succession often result in post-disturbance stands quickly resembling the pre-disturbance community with little or no change in composition. In the boreal

forest, parallel succession is common following stand-replacing fires (Heinselman 1973; Greene and Johnson 1999; Greene et al. 2004; Jayen et al. 2006), Parallel succession is also common in fire prone alpine systems of North America where post-fire composition often quickly resembles pre-fire composition (Lyon and Stickney 1976; Turner et al. 1997). However, characteristics of fires including their intensity, severity, and spatial extent and the composition of the pre-fire community can also interact to produce alternate successional pathways post-fire(Johnstone et al. 2010). Older stands that have undergone transitions toward late successional community types may show a strong convergent succession towards early successional community types if a fire is severe and leaves few residual trees. Alternatively, succession may be individualistic if a fire is of low intensity and severity creates a patchy burn pattern that leaves many residual trees. In such a scenario, there may be stands that undergo succession towards early successional community types as well as stands where self-replacement of late-successional community types occurs depending on the spatial patterns of fire severity and pre-fire composition.

In addition to influencing succession via fire effects, the seasonal timing of fires also directly impacts succession through its timing, relative to the phenological and seasonal biological states of plants. Vegetation may be differentially sensitive to or resilient to a fire at different times of year because of differences in dormancy cycles, exposure of meristematic tissues, carbohydrate storage, or the water content of plant tissues (Platt et al. 1988; Peterson and Ryan 1986; Ryan

2002). Thus, even a low severity fire could cause high mortality of fire adapted

species if the fire occurs during a phenological window of vulnerability. The

timing of a fire further influences succession by determining the season of initial

regeneration and the stage of a plants life cycle at which a fire occurs

(Heinselman 1981). Such direct effects of seasonality may be particularly

important for annual forbs or grasses (Howe 1994) but may also affect trees and

shrubs (Harrington 1987; Buckman 1964).

While prior studies have increased our understanding of how fire behavior and

burn characteristics influence succession (Heinselman 1973; Ohman and Grigal

1981; Knapp et al. 2009), accurately predicting patterns of succession following

fire remains a challenge. Additionally, a warming climate is likely to greatly alter

fire regimes across the North American boreal forest by increasing fire frequency,

increasing area burned, and lengthening the fire season (Flannigan et al. 2005;

Fauria and Johnson 2008; Le Goff et al. 2009; Krawchuck 2009; Wotton et al.

2010); and perhaps altering the distribution of early- and late-season fires

(Kasischke and Turetsky 2006). In order to predict and model how changing

disturbance regimes will affect boreal forest systems we need to better

understand the interplay between fire characteristics, including behavior, timing

and severity, and successional outcomes.

To this end, we studied a series of recent wildfires in the Boundary Waters

Canoe Area Wilderness (BWCAW) of Northern Minnesota, USA. This series of

wildfires includes both early and late-season fires of variable severity that occurred during the 2006 and 2007 fire seasons in areas with known stand origins and disturbance history across a range of community types. Using this dataset, we investigated how factors including stand age, pre-disturbance community type and seasonal timing of fire influenced fire severity and how these factors affected succession following fire. We investigated 1) whether late-season fires resulted in increased intensity, severity, depth of burning or decreased patchiness of burning relative to early season fires, 2) if differences in fire effects led to different successional pathways or whether differences could be explained by pre-fire composition, stand age or the seasonality of the fires. As we expected late-season fires to be of greater severity, we hypothesized that early season fires would show more variation in succession pathways, while late-season fires would tend toward greater successional convergence. We expected that fire severity and pre-fire disturbance community would exert a larger influence over succession than the seasonal timing of fire when accounting for differences in fire severity between early and late-season fires.

Study Area

The study area encompasses a 15,000 ha area centered at 90°56′W and 48°08′N that includes portions of the BWCAW and adjoining lands of the Superior National Forest. The forests of the area are at the southern ecotone of the boreal forest. While temperate species such as red maple (*Acer rubrum* L.), red pine (*Pinus resinosa* Aiton) and white pine (*Pinus strobus* L.) are present, 90% of the mature trees encountered are boreal species. The broader ecoregion is characterized as Canadian Shield. Soils are thin, acidic and post glacial in origin and exposed Pre-Cambrian bedrock is common. The climate is cold continental with a mean temperature of 2°C and an average of 100 frost free days (Heinselman 1996).

Sampling for this study was part of a broader investigation into disturbance dynamics within the BWCAW that included areas affected by wind disturbance as well as combinations of wind and fire disturbance. Research in this area began following the 1999 BWCA derecho, a large and severe wind event that disturbed a large portion of the BWCAW. This area was subsequently impacted by a series of prescribed fires and wildfires from 2002-2007. The entire community change dataset encompasses 1086 plots on 86 transects. In this paper, we examine a subset of that broader dataset looking at areas that were affected by single fire events. We define that subset to include areas that experienced only 1 fire in the last 40 years and were largely unaffected by significant wind disturbance. We define the latter as areas where wind disturbance did not lead to mortality above

59

25% of total basal area as measured at the plot level. This subset includes

portions of the 2006 Cavity Lake fire, and 2007 Ham Lake fire. Both fires burned

areas that were severely impacted by the 1999 derecho, however in this paper

we examine only those areas of these fires where evidence of wind disturbance

was minimal. In addition, this subset includes large portions of the 2006 Famine

Lake Fire and Redeye Lake Fire that were largely outside the main path of the

1999 BWCAW blowdown (Table 2-1 and Figure 2-1). All of these fires were

wildfires, and all fires except the Ham Lake fire were of natural origin.

Methods

The subset of plots affected by single fire events consists of 225 plots on 38

transects. Twenty-six of these plots were established in 2000 and 2001 following

the 1999 Derecho; the remaining 199 plots were established in 2011 following

the fires of 2006-07. The majority of these plots are located within the boundaries

of the BWCAW but 35 were located in adjoining areas of the Superior National

Forest. Plots within the BWCAW are arranged on transects that originate 5m

from a lake shore and run perpendicular to lake shores with plots spaced every

25m along the transects which range in length from 150-400m. Approximately

80% of the landscape within our study area is located within 400m of a lakeshore

(Rich et al. 2007). Plots outside the BWCAW were established in a similar

fashion except these transects originate 40-80m from roadsides but similarly

follow the natural slope direction. Transects were stratified with regard to stand

age and disturbance type, and the exact location of transect origins were

randomly selected prior to surveying.

We used a nested-circular plot design with fixed radii of 12.5 m, 5 m and 3 m for

a coarse-scale tree plot, fine-scale tree plot and regeneration plot, respectively.

Because transects within the BWCAW originate 5 m from lakeshores, the first

plot on these transects was semicircular. Within the radius of the coarse scale

plot all trees live and dead greater than 5 cm dbh were counted and classified

according to size class and species. We used size classes of 5-15 cm, >15-25

cm and >25 cm. Within the fine scale plot all live and dead trees >2.5 cm dbh

were measured for diameter and for dead trees we assigned a cause of mortality (fire, wind or other) based on the presence of bole breaks, decay, tip up mounds and/or the presence of charring (See Appendix). Within the 3m regeneration plot all trees and woody shrubs from new germinants to saplings less than 5 cm dbh were tallied by species. We counted stems branching above breast height as one individual, but counted stems branching below breast height as multiple individuals. Across the entire 12.5 m plot area we also estimated the percent cover by tree species for canopy trees (>2 m tall) and sub canopy trees (≤2 m tall) to the nearest percent and estimated the percentage of the plot area burned.

We analyzed changes in forest composition and succession by comparing the relative proportion and dominance of species before fire using relativized basal area and relativized stem counts of regeneration after fire. For the 26 plots that were established in 2000-01 before fire, we used estimates of basal area obtained from our sampling in 2001-01 to determine pre-fire composition. This was performed by summing the measured basal area of fine scale plots for trees >5 cm dbh with the estimated basal area of our coarse scale plots. The coarse scale estimated basal area was obtained by first calculating the quadratic mean diameter (qmd) for each species and size class of tree using the measured dbh of trees in the fine scale plot. These estimates of qmd were then multiplied by the corresponding number of stems for each species and size class of tree within a coarse scale plot to obtain a coarse scale estimate of basal area.

We characterized post-fire composition and fire severity for these plots based on regeneration surveys and measurements of surviving trees conducted during a 2011 resurvey. This work included re-surveys of coarse and fine scale plots in order to estimate the portion of basal area killed by fire as well conducting stem counts to categorize regeneration following fire. During the initial survey in 2000-01, plot centers were monumented with a 50 cm piece of 9.5 mm diameter steel rebar. During the 2011 resurvey we were able to find the exact plot center by relocating this rebar for 51.5% of plots. Where we could not positively find plot center we used GPS coordinates and plot description from the original survey to estimate plot center. Using a Garmin Etrex Vista HCx handheld GPS unit we estimated that our accuracy in locating true plot center was ±3 m for plots where we were unable to locate the original plot center marker.

Plots that were added to the dataset after the fires of 2006-07, were surveyed once in 2012. Because we lacked pre-disturbance data for these plots we used measurements of dead trees, stumps and the presence of any surviving trees to characterize pre-fire composition. Because of the pervasive influence of wind in our study area, we needed to carefully determine the cause of mortality to ensure that our estimates of fire mortality were accurate and not the result of prior wind disturbance in 1999. To this end, we surveyed all live and dead trees on the fine scale plot, making detailed observations of the cause of individual tree mortality based on patterns of charring, whether the dead tree was standing, broken or fallen and the level of decay. We also measured dbh for each tree in coarse

scale plots and determined its species based on branching morphology and bark. On the coarse scale plot we counted trees by species and size class and recorded whether trees were standing dead, fallen and dead or live. Across the entire plot area, we recorded categorical wind severity (Table 2-2). We then used the detailed estimates of tree mortality at the fine scale as well as measures of categorical wind severity to develop logistic regression equations that allowed us to predict the probability of a coarse scale tree being killed by fire or wind based on its size class, species, and the plot level categorical wind severity (See Appendix). Using these equations, we calculated the plot level proportion of coarse scale basal area killed by wind and fire respectively by fractionally assigning the basal area of coarse scale trees to each mortality agent and then summing at the plot level. Estimates of basal area at the coarse scale were then aggregated with the measured basal area of fine scale plots to obtain plot level estimates of live basal area by species, both before and after disturbance. The relative change in live basal area before and after a disturbance was used as a measure of quantitative disturbance severity after Rich et al (2005), and Peterson and Leach (2008). For example, if a fire killed 90% of the basal area within a plot that plot would have a fire severity of 0.90. We refer to these quantitative measures of disturbance severity as fire severity ΔBA, and wind severity ΔBA respectively.

Because there is no single severity metric that integrates for both mature trees and propagules we used a variety of severity metrics to analyze the severity of

disturbances. In addition to wind severity ΔBA and fire severity ΔBA we also recorded categorical measures of fire severity including crown fire severity and ground fire severity after Carlson (2011) and categorical wind severity (Table 2-2). Crown fire severity is useful for understanding the impact of fire on serotinous stored seedbanks, while ground fire severity is useful for characterizing the impacts of fire on forest floor seedbanks and root networks that can be important in vegetative reproduction. To increase replication for analysis of successional pathway by fire season and fire severity, we collapsed the 5 category ground fire severity metric devised by Carlson (2011) to a simple high/low severity where ground severities of 2 or less were considered low severity and ground severities of 3 or greater were considered high. We used mean char height as a proxy for fire intensity and recorded char height in meters for each plot by averaging char heights from the nearest tree in each cardinal direction.

We used a combination of hierarchical agglomerative cluster analysis (HCA) and nonmetric multidimensional scaling ordination (NMDS) to analyze and visualize changes in community composition and successional pathways in ordination space. This combination of methods allowed us to identify community types based on associations within our community dataset and follow changes in the distribution of those community types over time.

HCA is a method that uses ecological distance measures to compare composition between different plots and create clusters by maximizing between

group variation and minimizing within group variation (McCune and Grace 2002). NMDS is an unconstrained ordination technique used to visualized complex multidimensional community datasets. It is robust to non-normal community datasets (McCune and Grace 2002). NMDS uses an iterative search to find a solution that seeks to maximize distances in ordination space for plots that have the most dissimilar composition and minimize distances for plots that are most similar in composition.

We used a community matrix consisting of columns of species and rows of plots grouped by 3 time-steps of observation to run both HCA and NMDS. The first time-step was basal area based community composition in 1999 prior to wind disturbance, the second time-step was basal area based composition from 2000-2006 prior to fire disturbance, and the final step was community composition in 2012, 4-5 years after fire based on regeneration stem counts. In order to compare basal areas with stem counts we row-relativized to obtain a unit-less measure of proportional dominance for each species at each plot at each time-step. Because the initial matrix was quite sparse and difficult to analyze, where practical we grouped some species by genus and eliminated species that did not occur on at least 5% of all plots. Black ash black ash (*Fraxinus nigra* Marshall) and tamarack (*Larix laricina* (Du Roi) K. Koch) were uncommon enough that we did not include them in our analysis and we combined the 3 species of *Populus* into a single aspen category.

We considered adding a 4th time-step consisting of the community composition of surviving mature trees in 2012, but few plots (< 35%) had any surviving mature trees making this time-step of the matrix especially sparse and difficult to ordinate. We therefore eliminated this time-step but examined overlays of these data within the ordination solutions to confirm that excluding it did not significantly bias our results. In addition, we performed similar analyses using cover data instead of regeneration data for our last time-step, this allowed us to integrate surviving trees with regeneration. Solutions obtained from this method were similar to those obtained from stem count data, such that we do not believe excluding surviving trees from our analyses significantly biases our results.

We ran HCA in the program PC-Ord 5 (McCune and Grace) using the flexible beta (-0.25) method and Sørensen's distance, and using a community matrix of the full set of 1086 plots with three time-steps. The decision of where to trim a cluster dendrogram is an arbitrary one, we sought to create well defined clusters with 1 or 2 species clearly dominant in each community type. We examined the resultant community types produced by trimming the dendrogram at 7-10 community types and chose to trim the dendrogram at 8 (42% of info remaining) because at that level community types were well defined with 7 of the 8 having one species that made up the majority of the composition for those plots. This resulted in the following community types being defined by a single dominant species: aspen (*Populus tremuloides* Michx.), paper birch (*Betula papyrifera* Marshall), balsam fir (*Abies balsamea* (L.) Mill.), black spruce *(Picea mariana*

67

(Mill.) Britton, Sterns & Poggenb.), red maple, white cedar (*Thuja occidentalis* L.), and jack pine (*Pinus banksiana* Lamb.). Red pine and white pine often co-occur in the BWCAW and were defined as a mixed community type by the HCA. White spruce (*Picea glauca* (Moench) Voss)) was not abundant enough to appear as a distinct community type but was a minor component of the paper birch community type. The community types we identified using HCA were similar to those developed in other studies of southern boreal forest (Ohmann and Ream 1971, Grigal and Ohmann 1975, Frelich and Reich 1995, Heinselman 1996, Rich 2005).

NMDS ordinations were run in the program R using the VEGAN package (Oksanen 2007) and same community dataset used for our HCA. We used "bray" for our distance measure which is Bray-Curtis dissimilarity (aka Sørensen's distance) measure and performed 3000 runs with a 3-dimensional solution resulting in a final stress of 14.6411. A 3-dimensional solution was chosen after constructing a scree plot in PC-Ord 5 to test for optimal number of dimensions (Figure 2-2)

We used three-way ANOVA tests with interaction followed by Tukey's honest significant differences test as a post hoc, to test whether the seasonal timing of fire, stand age or the pre-fire community type influenced fire severity variables including fire severity ΔBA, char height, ground fire severity or crown fire severity.

ANOVA runs were first done with the full suite of variables and interactions and then re-run with only factors and interactions found to be significant, Tukey's HSD tests were then used as a post hoc. To assess changes in community type we examined the NMDS ordination solution using successional vectors that track the movement of plots in species space before and after fire. In addition, we constructed transition tables that documented the frequency of plots of each community type before and after fire. Along with successional vectors these transition tables allowed us to track successional pathways of individual plots before and after fire and compare whether patterns of succession differed based on the seasonal timing of fire, pre-fire community type, stand age or fire severity metrics. We also calculated Sørensen's distance for plots pre- and post-fire, using these data we used t-tests to examine whether there were significant differences in the average amount of community change for plots experiencing early season fires vs those experiencing late-season fires.

Results

Prior to the fires of 2006-2007 there were differences in age and composition among the 225 focal stands both within and across those that would subsequently be affected by early versus late-season fires. Early season fire stands ranged in age from 102 to 211 years old at the time of fire (mean = 166 yr, SD = 50 yr; median = 205 yr), based on Heinselman's stand origin maps (1994). Prior to fire, the landscape was a mosaic of different stands, typically dominated by a single species, with a high degree of evenness among stands of each community type (Shannon's equitability (EH) = 0.89). By basal area, jack pine was the most dominant species accounting for 18.6% of total basal area across all stands, followed by red pine (16.6%), paper birch (15.7%), balsam fir (15.3%), black spruce (14.9%), aspen (6.3%), white pine (6.2%), white cedar (5.8%), white spruce (0.6%), and red maple (0.1%). HCA classified these plots into 8 community types that roughly mirrored the dominance of individual tree species. Of the 112 plots, 25.0% were classified as jack pine community type, followed by black spruce (23.2%), paper birch (16.9%), red pine and white pine (16.9%), balsam fir (9.8%), aspen (3.6%), white cedar (3.6%) and red maple (<1%) (Figure 2-3).

Areas that experienced late-season fires tended to have a slightly older age distribution and greater dominance by late successional species pre-fire relative to areas that experienced early season fires. Stand ages ranged from 94 years old to 402 years old at the time of fire (mean = 226 yr., SD =83 yr.; median

=211). The pre-fire landscape of areas that experienced late-season fires consisted of a mosaic of typically mono-dominant stands with moderate evenness (EH = 0.74). These stands were dominated in terms of basal area by white cedar (31.3%), paper birch (29.2%), balsam fir (12.2%), jack pine (8.1%), black spruce (7.9%), aspen (3.3%), white spruce (2.6%), white pine (2.6%), red pine (2.3%), and red maple (0.5%). HCA classified the pre-fire composition of theses plots as follows: white cedar community type (37.1%), paper birch (31.0%), black spruce (18.5%), balsam fir (4.4%), red pine and white pine (3.5%), aspen (2.7%), jack pine (1.8%), and red maple (<1%) (Figure 2-3).

Effects of fire season, community type and stand age on fire severity metrics

Fire effects varied considerably within and among fires in our study; using three-way ANOVA tests we examined the interplay between stand age, fire season and pre-fire community type and how these factors influenced fire severity and in turn succession. Stand age was not a significant predictor of fire severityΔBA (p = 0.312, but there was a significant interaction between community type and fire season (F (7, 209) = 2.875; p = 0.00691). On average late-season fires had a mean fire severity ΔBA that was 0.92, which was 0.12 units greater than areas affected by early season fire (p = 0.003). Black spruce stands that burned in late-season fires also tended to have high mean fire severity ΔBA (m = 0.97) that was 0.28 higher than those that burned in early season fires (p = 0.001) and the difference was greater than the average difference in fire severity ΔBA between

early and late-season fires. There were no other significant differences in fire severity ΔBA by community type or statistically significant interactions.

Fire season, stand age and pre-fire community type were all significant predictors of ground fire severity and there was a significant interaction between community type and fire season (F (7, 207) = 2.382; p = 0.03). Mature stands (167-213yr) had significantly greater ground fire severity (m = 0.4; p = 0.0182) than did young (<167yr) or old aged stands (>213yr). Late-season fires had a mean ground fire severity of 3.09, which was 0.6 greater than that of the early season fire areas (m = 2.48; p < 0.00001) A post hoc Tukey's HSD test found that there was a significant interaction between balsam fir stands and fire season (p =0.0093) with late-season fire stands having a mean ground fire severity of 4.4 vs 2.4 for balsam fir stands burned in an early season fire. Even when controlling for season of fire and stand age, red pine/white pine stands and cedar stands had mean ground fire severities (m = 3.3, m =3.1 respectively) that were significantly greater than those of aspen (m =1.7) or black spruce stands (m = 2.36) (p < 0.02). All other differences were non-significant or unimportant.

Both community type (F (7, 204) = 3.728; p = 0.0008) and fire season (F (1, 204) = 11.29; p = 0.0009) were significant predictors of the % of plot area burned, but there was no significant interaction between these factors. On average, late-season fires burned 93.2% of the plot area, which was significantly greater (p = 0.0068) than the mean percent of plot areas burned in early season fire (m =

83.9%). Red pine and white pine stands tended to burn more completely (m = 99%) than did black spruce stands (m =77.9%; p = 0.02). Other differences in % of plot area burned between community types were non-significant.

Community type was also a useful predictor of char height (F (7, 209) = 2.875; p = 0.00691), but fire season and stand age were not significant predictors of char height. Jack pine stands had the greatest char heights (m = 3.6 m) followed by red pine and white pine stands (m = 3.2 m). Both jack pine stands and red and white pine stands had char heights that were significantly (p < 0.05) greater than those of paper birch (m = 1.4m) or black spruce stands (m = 1.1m), but all other differences in char height by community type were non-significant. Only stand age was a significant predictor of crown fire severity (F (2, 222) = 8.34; p = 0.0003). Young stands (<167yr) and mature stands (167-213yr) had mean crown fire severities (m = 1.6; m= 1.7) that were significantly greater (p < 0.005) than the mean crown fire severity (m = 1.1) of old stands (>213yr).

Effects of seasonal timing of fire on succession

Regeneration in early season fire plots was dominated by woody shrubs that made up 53.1% of the total stem count. Beaked hazel (*Corylus cornuta* Marshall) made up 23.8% of the shrub component followed by, alder species (*Alnus sp.* Mill.) (21.8%), mountain maple (*Acer spicatum* Lam.) (20.0%), pin cherry (*Prunus pennsylvanica* L. f.) (19.9%), willow species (*Salix sp.* L.) (7.6%), service berry species (*Amelanchier sp.* Medik.) (4.3%) and mountain ash (*Sorbus americana*

Marshall) (1.1%). The tree regeneration was dominated by aspen, which made up 30.2% of the total regenerating tree stems followed by jack pine (20.9%), paper birch (17.7%), black spruce (14.2%), balsam fir (11.2%), white pine (1.7%), white cedar (1.3%), red pine (0.8%), and red maple (0.6%). HCA classified the newly regenerating tree community as a mix of aspen (34.1%), jack pine (18.0%), paper birch (17.7%), black spruce (14.4%), balsam fir (12.6%), red maple (1.8%), white cedar (0.9%) and red pine/white pine (0.9%) community types (Figure 2-4). We note that these values were only modestly different when post-fire stands were classified with methods that incorporated residual surviving overstory trees, likely because < 14% of the total pre-fire basal area across all 225 plots survived.

Successional pathways for stands experiencing early season fire were varied (Figure 2-4). The abundance of aspen dominated stands increased significantly (30.7%) post fire, with the majority (68%) of former red and white pine and 45.5 % of balsam fir stands undergoing conversion towards this community type. Balsam fir community types also were more dominant following fire, increasing from 9.7% to 12.6%, whereas paper birch communities remained at ≈ 17% of the total. All other community types except red maple, which stayed the same, declined in dominance following fire. The red pine/white pine community type declined the most, where before fire 16.8% of plots were red pine/white pine plots, following fire this community type made up less than 1% of the total plots. Late successional species including black spruce and balsam fir regenerated

strongly and in some cases stands that had been aspen or paper birch dominated pre-fire shifted towards balsam fir or black spruce dominated stands post-fire. While self-replacement did occur for many early successional stands there was low stability and many early successional stands transitioned to competing early successional stand types. On the landscape scale, the evenness of stand types declined from to 0.89 pre-fire to 0.82 post fire.

In contrast, regeneration following late-season fires was significantly less shrubby with woody shrub species making up 15% of the total stem count for these plots (as opposed to 53% following early season fire). Beaked hazel was the most abundant shrub making up 37% of the total shrub stem count, followed by willow species (20.8%), mountain maple (20.7%), pin cherry (12.0%), alder species (3.8%), and service berry sp. (1.4%). The tree community was dominated by paper birch which made up 56.1% of the total tree stem count, followed by white cedar (20.2%), aspen (18.0%), jack pine (1.9 %), black spruce (1.7%), balsam fir (1.2%), white spruce (0.4%), red maple (0.2 %), white pine (0.07%) and red pine (0.007%). HCA classified the newly regenerating tree community as being dominated by the paper birch community type (59.2%), followed by white cedar (17.7%), aspen (16.8%), balsam fir (4.4%), and black spruce (1.8%) community types (Figure 2-4). Again, we note that values for HCA performed with the inclusion of surviving overstory trees via % cover instead of regeneration stem counts produced similar results because of the relatively low

numbers of surviving overstory trees. On the landscape scale stand evenness increased slightly from 0.74 to 0.82 post-fire.

Late-season fire stands showed a strong successional convergence toward a paper birch community type. Paper birch was the second most dominant community type pre-fire covering 31% of plots and increased to 59.3% of plots post-fire (Table 2-3). Whereas there was considerable variation among successional pathways by community type for early season fire plots there was a much more uniform trend towards paper birch for late-season fire plots. The aspen community type also increased in dominance post-fire and displaced paper birch in a minority of plots. Unlike the successional pathways for early season fire, there were few transitions towards late successional community types. White cedar was the most dominant community type pre-fire and although it declined in dominance, 38.1% of white cedar plots pre-fire were also classified as white cedar dominated post-fire. Other community types including red maple, red pine and white pine and jack pine were eliminated, although only a few plots were classified as these community types pre-fire. While balsam fir plots succeeded to aspen and paper birch post-fire, some black spruce, paper birch, red pine/white pine and white cedar plots succeeded to balsam fir dominated plots post-fire, so that the total proportion of the balsam fir community type did not change post-fire. Despite detecting different patterns of succession, we were not able to find any significant difference in mean Sørensen distance of plots pre-

and post-fire for early and late-season fire plots (t = 0.8695, df = 227.92, p = 0.385).

Interactions between fire severity, stand age and timing of fire and their effects on succession

Because our dataset was drawn from wildfires that occurred in areas with varied stand origins and community types we could not compare succession across all community types, stand ages and severities that existed within our study. Where we had enough replication to examine interactions by timing of fire and severity and community type we often found variation in successional patterns.

Trends in succession by disturbance severity were generally similar across severity metrics as many severity metrics were at least partially related. Here we have chosen to present only those results for ground fire severity as there was good replication across community types and severity levels and because general trends from low to high severity were largely consistent among ground fire severity, fire severityΔBA, char height crown fire severity and % of plot area burned. Here ground severity values of 2 or less, corresponding to areas where <50% of surface litter were consumed were considered low severity, while areas that had 50-100% of surface litter and or some duff consumption were considered high severity.

When accounting for differences in fire season and ground fire severity we did not find strong trends in succession by stand age. Old, mature and young aged stands of the same community type tended to respond similarly given the same timing of fire and fire severity. One exception was white cedar stands exposed to late-season fire and high ground severity, where old stands (>213yr) tended to have more white cedar regeneration than did mature stands (167-213yr) (Figure 2-5). In other instances, we either lacked replication or did not find differences by stand age when other factors such as community type, severity or fire season were accounted for.

Of the primary factors we examined, the seasonal timing of fire had the largest influence on succession, but we also observed differences in successional pathways between high and low ground fire severity when controlling for fire season (Figure 2-6). High severity fire resulted in increases in aspen and declines in balsam fir community types in both early and late-season fire areas. Black spruce and white cedar declined in dominance in both low and high severity fire areas, but declines were more pronounced in high severity areas.

Black spruce and paper birch stands were the only stand types where we had sufficient replication to fully examine the differences in succession by both timing of fire and fire severity. For black spruce stands that experienced early season fire there was a modest effect of fire severity. Both low and high severity areas had 40% of plots where black spruce exhibited self-replacement sufficient to be

classified as black spruce post fire, but there was more conversion to aspen and paper birch and less balsam fir in the areas experiencing high severity fire (Figure 2-7) (Table 2-4). For black spruce stands experiencing late-season fire there was little evidence of difference in successional pathways between high and low severity areas, in both cases black spruce stands were largely replaced by paper birch (Figure 2-7).

Paper birch stands experiencing early season fires showed modest evidence of differential succession by severity. Low severity areas had more balsam fir and less aspen regeneration than did high severity areas (Figure 2-7), but otherwise were similar (Table 2-5). Paper birch dominance on the landscape scale remained relatively constant in early season fire areas across severity levels, even though its self-replacement rate was less than 40% for both high and low severity areas. Late-season paper birch plots displayed a similar pattern with fire severity with high-severity areas having more aspen and less balsam fir than low-severity areas. However, there was a significant effect of fire severity on paper birch regeneration in late-season areas and paper birch increased in dominance more with high severity than low severity ground fire even though its rate of self-replacement was 9% lower in high severity areas than in low severity areas (Table 2-5).

We lacked data for early fire-season white cedar plots sufficient to examine patterns of succession by severity, but had data for late-season areas. In late-

season white cedar stands that were exposed to low severity fire there was considerable regeneration of white cedar (Figure 2-8), with 80% of plots having sufficient white cedar regeneration to be classified as white cedar stands post-fire (Table 2-5). In high severity areas there was reduced dominance of white cedar and conversion to aspen and especially paper birch community types. Fully 50% of the high-severity, late-season white cedar plots became paper birch plots post fire.

For jack pine, we lacked sufficient data to compare succession by both timing of fire and severity, but we had sufficient data to examine the effect of severity on early season jack pine plots. In these areas jack pine responded roughly twice as well to high severity fire as low severity fire (Figure 2-9) with 68.8% of jack pine plots exhibiting self-replacement in high severity areas and only 33.3% in low severity areas (Table 2-5). High severity areas also tended to have more conversion to aspen (25% vs 16.6%) and less conversion to paper birch (6.25% vs 33.3%). We lacked sufficient data to compare patterns of succession by severity for aspen, balsam fir, red maple and red pine and white pine dominated stands.

Discussion

The late-season fires in our study tended to have greater fire severity and leave fewer unburned patches than did our early season fire, but fire intensity was similar between early and late-season fires. The early season fire we examined, the Ham Lake Fire of 2007, was a very rapidly moving and intense fire that in one-day spread approximately 15 km. In contrast, the late-season fires we examined tended to spread and burn more slowly. The rapid spread of the Ham Lake Fire was driven by strong winds that also resulted in high intensity for this fire (Fites et al. 2007), but the rapid rate of spread also left many unburned patches of surviving trees. Typically, these patches occurred in low lying areas at the edges of wetlands and lakes. Although there were unburned pockets in the late-season fires we examined, these tended to be fewer than in the Ham Lake Fire likely because of both the slower rate of spread and relatively greater dryness experienced by similar sites within the late-season fires. The patchy burn pattern meant that fire severity, expressed in terms of the proportion of basal area killed by a fire, was less than that experienced by areas burned in late-season fires.

Late-season fires like the Cavity Lake, Redeye Lake and Famine Lake Fires typically occur when fuel moisture is very low, which often results in increased depth of burning. This was the case for the fires that we examined that had significantly greater ground fire severity than did our early season fire, the Ham Lake Fire. The overall effect size was modest if statistically significant,

corresponding with on average 0.6 points on a categorical scale, which roughly corresponds to the difference between a fire consuming 50% of the surface litter and a fire consuming 100% of the surface litter. The distributions of ground fire severity values were relatively similar, except late-season fires had 10% of plots with a ground fire severity of 5 corresponding to areas of complete litter and duff consumption, whereas the maximum ground fire severity for Ham Lake Fire plots was 4, corresponding to areas where all of the surface layer has been consumed but at least some duff remains following fire. While there was considerable variation in ground fire severity within both early and late-season fires, the most heavily burned sites in our late-season fires had duff and litter consumption that was an order of magnitude greater than the most heavily burned sites within our early season fire.

While there were differences in stand age between late-season and early season fire sites, we generally did not detect differences in fire severity or succession because of stand age. Mature stands tended to have slightly higher ground fire severity than did young or old stands and lower crown fire severity than other stands, but otherwise severity metrics were similar across stand ages. The oldest white cedar stands tended to have more white cedar regeneration even when accounting for differences in ground fire severity, but otherwise we failed to detect patterns in succession by stand age. In most cases pre-disturbance community type was a far better predictor of severity and successional pathway than stand age.

Differences in fire effects between early and late-season fires were associated with different patterns of succession. The seasonal timing of fire appeared to exert a stronger influence over succession than did fire severity. We found that plots of the same initial community type but different severity, were more similar in their successional pathways than plots of the same severity and pre-disturbance community type that experienced different fire seasons. Controlling for the timing of fire we found that high severity areas typically had greater self-replacement of early successional species including aspen and jack pine, although not paper birch. Paper birch increased in dominance following high severity fire, but mostly because of increased conversion of other stand types to paper birch as paper birch stands themselves were more likely to be replaced by aspen at high severity levels. In addition, high severity fires reduced the dominance of late successional species including balsam fir, white cedar and black spruce. While balsam fir and white cedar are not commonly thought of as being fire adapted, both species regenerated well with low severity fire. Balsam fir increased its dominance on the landscape post-fire by expanding into stands previously dominated by spruce and paper birch despite declining in dominance among the subset of pre-fire balsam fir stands. While white cedar declined in dominance in both high and low severity fires, in low ground severity and late-season fire areas it had a self-replacement rate that was similar to fire adapted species under favorable fire conditions. Unlike other fire adapted species, it was unable to expand into stands previously dominated by other species, so while

white cedar can successfully colonize recently burned areas it is often limited by lack of surviving trees and relatively short seed dispersal distances (Curtis 1959; Fowells 1965).

The relative success of aspen and birch in our study was strikingly different between areas affected by early and late-season fires. The more severe late-season fires provide a good seedbed for birch, which prefers bare mineral soil for germination (Johnstone and Chapin 2006), even though its rate of self-replacement was typically lower with high ground fire severity than for low. The favorable seedbed conditions created by late-season fire did allow paper birch to displace other community types. The success of aspen following early season fires is notable given that in both early and late-season fire areas aspen made up a similar portion of the landscape pre-fire and even when controlling for differences in fire severity we found greater dominance by aspen than paper birch in early season fire areas.

Early-season fires such as the Ham Lake Fire may favor aspen in part because litter and duff layers tend to have greater moisture early in the year and are less likely to be consumed by fire. Spring fires may be intense enough to top kill mature trees, but have little effect on aspen root networks, which readily sucker after fire. Previous work by Rowe (1953), Maclean (1960) and Heinselman (1996) suggested that aspen is generally favored over other species by early season fires in the BWCAW and the boreal mixedwood forests of Canada. Birch

also reproduces vegetatively post fire, but as a stump sprouter it does not produce the same abundance of new stems as root-suckering aspen. Birch may be more successful following late-season fires because the species produces seed in the fall, and these fires are much more likely to consume duff and litter layers, exposing mineral soil and in some cases killing aspen root systems.

Early season fire areas were also significantly shrubbier than areas affected by late-season fires. Many woody shrubs have similar regeneration strategies to quaking aspen and may be similarly favored by fire conditions typical of early season fires. Previous research by Buckman (1964) showed that early season burning results in vigorous resprouting of beaked hazel, while summer fires typically result in lower levels of resprouting of hazel, although repeated fires may eventually be able to reduce the vigor of beaked hazel regardless of the seasonality of fire. Although we lacked data on pre-disturbance shrub abundance and composition, our results generally confirm those of Buckman. It is hypothesized that differences in fuel moisture and fuel consumption is the predominate driver of differences in vegetatively reproducing shrubs between early and late season fires and that differences for seed bank species may be somewhat obscured as conditions that favor seed regeneration are often negatively correlated with vegetative reproduction (Kaufmann and Martin 1990).

One surprising finding was the generally poor recruitment of jack pine post fire. Jack pine is commonly thought of as one of the most fire adapted species in the

boreal forest and is often assumed to be among the most successful post fire. In this study, the vast majority (94.6%) of jack pine stands were situated within the Ham Lake Fire area and therefore, only experienced an early season fire. Although there were no significant differences in crown fire severity between early and late-season fires, the Ham Lake Fire caused significantly less scarification and generally did not expose large areas of mineral soil that jack pine requires to germinate (Chrosciewicz 1974). Observations of jack pine regeneration following fire in Saskatchewan have shown that consumption of litter and duff can be a critical factor in the success of jack pine regeneration and that light burning may create unfavorable seedbeds for jack pine (Jameson 1961). The median ground severity we recorded for the Ham Lake Fire was 3, which corresponds to a fire that consumed 50-99% surface litter, but did not consume duff and exposed no mineral soil. Previous work by Ohmann and Grigal in the BWCAW (1981) also found that jack pine regeneration after a spring fire was less than that of summer fire in part because of lack of duff consumption in a spring fire. In areas of the Ham Lake Fire that had high ground fire severity there was significantly more jack pine regeneration than in areas with low ground fire severity, but the rate of jack pine self-replacement was still below what would be considered typical for this species following stand replacing fire. Had there been more jack pine in the pre-fire forests affected by late-season fires, it seems likely we would have observed higher levels of jack pine self-replacement in these stands, as jack pine plots tended to burn with greater severity compared to other stand types and late-season stands also tended to burn with increased ground

fire severity. The combination of late-season and high ground fire severity would likely create conditions ideally suited to jack pine establishment, where seed sources exist.

The failure of the red and white pine community type to self-replace after fire also warrants some elaboration. Red pine and white pine stands in the BWCAW are thought to have commonly originated following stand replacing fires (Heinselman 1973) and both species have thick fire-resistant bark and can tolerate partial crown scorch. Despite the relatively moderate fire effects of the Ham Lake Fire, we found that only one of our 19 red and white pine dominated plots pre-fire had sufficient red and white pine regeneration to be considered red and white pine dominated post-fire. This result can partly be explained by our analysis methods that excluded surviving mature trees from our analysis. When we conducted similar analyses using cover data that accounted for surviving trees as well as the cover of regenerating seedlings we still found a decline in red and white pine dominated plots (80%), but the decline was less than that found using regeneration data alone (95.6%).

Regardless of method, the present decline in red pine and white pine stands in this area is significant, although the present decline may not preclude the possibility of future recolonization of former red and white pine sites by these species. Both species are long lived and have thick bark that makes them resistant to fire. Across the fires we examined approximately 14% of red and

white pines >2.5cm dbh survived and 34% of sites classified as red and white pine dominant pre-fire had at least 1 surviving mature pine after fire. It seems possible then that red pine, and white pine especially, may be able to continue to seed into developing post fire stands over the next 15 years. If this occurs, red pine and white pine may eventually regain co-dominance on stands where aspen and birch currently compose the majority of regeneration. Observations by Alhgren (1976) in a post-fire stand in the Quetico Wilderness, which adjoins the BWCAW on the Ontario side of the US-Canadian border, demonstrated that where good seed beds exist after fire, both white and red pine can continue to establish at least 15 years post-fire, leading to increased stocking through the early stage of stand development. However, the success of delayed regeneration by these species is highly dependent on the level of competition from competing trees, woody shrubs and forbs (Dovčiak et al. 2003) and there is no guarantee that either species will re-colonize former sites even where scattered surviving trees exist. Early season fire sites had generally less exposed mineral soil seedbeds and more shrub regeneration and it seems unlikely for red and white pine to do well in these areas in the future despite these areas also having the majority of surviving red pines and white pines.

The use of fire as a tool for vegetation management depends on a detailed understanding of the interplay between vegetation, weather patterns and their effects on fire behavior. Our results suggest that while fire severity can exert a large influence on the relative success of species post-fire, the seasonal effects

of fire go beyond direct effects of severity on propagule availability. As was the case with paper birch and aspen, even though the late-season fires in our study generally burned with greater severity than our early season fire and even though aspen generally responded better to high severity fire, paper birch was still the more successful species in late-season fires likely because of advantages gained by its seeds arriving sooner post-fire relative to aspen. Thus, land managers should consider both the direct effects of season on fire severity as well as how the phenology and life cycles of vegetation can interact with the timing of fire events. If management goals include regeneration of pines, reduction of shrubs and aspen, then late season fires should be strongly preferred to early season fires. Likewise, where increasing paper birch is a management objective, late season fires or scarification during late summer and early fall should help create optimal conditions for paper birch regeneration. White cedar has often proven to be a difficult species to regenerate in the lake states, but our results suggest that low severity fires carried out during late season conditions with ample seed sources may be an effective means of regenerating white cedar stands.

More broadly, climate change is predicted to increase the length of the fire season across the N. American boreal forest, which could result in increased late-season fires (Kasischke and Turetsky 2006). Along with direct effects on species, altered disturbance regimes could have major impacts on succession following fire in the boreal forest. Our study shows that late-season fires typically have increased fire severity and may result in strongly convergent succession

when compared to early season fires. Paper birch in particular may be favored by a shift to late-season fires, although in an area such as the BWCAW the climate may be unsuitable in the future for this species even if favored by changing disturbance regimes. To successfully manage forests, managers need to consider both the physiological effects of climate change as well as changing disturbance regimes.

Table 2-1. Fires of the Eastern BWCAW from 2006 through 2007.

Fire	Year	Active months	Description	Total Area (Ha)	Approximate area affected by only 1 fire and largely unaffected by wind (Ha)	Total Number of Plots	Subset of plots affected only by a single fire event
Cavity Lake Fire	2006	July and August	Lightning ignited wildfire that burned areas heavily impacted by the 1999 BWCA Derecho	10000	1216	263	32
Red Eye Lake Fire	2006	September	Lightning ignited wildfire that burned areas largely unaffected by the 1999 BWCA Derecho	1650	1500	33	30
Famine Lake Fire	2006	September	Lightning ignited wildfire that burned areas largely unaffected by the 1999 BWCA Derecho	1000	822	62	51
Ham Lake Fire	2007	May	Human ignited wildfire that burned areas affected and unaffected by the 1999 BWCA Derecho	30000	11275	298	112

Table 2-2. Categorical disturbance severity classes

Level	Ground Fire Severity Classes	Categorical Wind Severity Classes	Crown Fire Severity Class
0	Unburned	No evidence of major wind damage, all trees are still standing, branches may be broken	No evidence of crown fire
1	Light scorching of surface litter	Minor evidence of wind damage, most trees standing, but larger individuals and more wind susceptible species may have fallen or suffered bole breakage (<10% of canopy)	Scorching of needles, but no consumption of branches
2	1-50% of surface litter consumed	<50% of canopy trees have broken boles or have fallen and most wind firm species are undamaged	Needles consumed, and fine branches (<1 cm) charred
3	50-99% of surface litter consumed	>50% of canopy trees have broken boles or have fallen, only wind tolerant species remain in canopy (although some may suffer damage or have fallen)	Needles, and fine branches (<1 cm) consumed, charring of larger branches
4	100% of surface litter consumed, some duff consumed	Wind damage extensive. All canopy trees have broken boles or have fallen, sub-canopy of wind firm species may remain intact	Only main stem or branch stubs remain
5	All organic litter and duff consumed	All canopy trees and most sub-canopy trees are broken or have fallen, only standing stumps and immature trees (less than 5m in height) remain.	NA

Table 2-3. Community transitions for late-season fires. Data shown are the % of plots that were a community type pre- and post-fire and the % of plots staying a community type or succeeding to a new one.

		Post Fire Community Types										
		Aspen	Balsam Fir	Black Spruce	Jack Pine	Paper Birch	Red Maple	Red Pine/White Pine	White Cedar	Pre-Fire % of landscape	Post-Fire % of landscape	Net Change
Pre-Fire Community Types	Aspen	33.3	0	0	0	66.7	0	0	0	2.7	16.8	14.2
	Balsam Fir	60	0	0	0	40	0	0	0	4.4	4.4	0
	Black Spruce	0	4.8	0	0	81	0	0	14.3	18.6	1.8	-16.8
	Jack Pine	50	0	0	0	50	0	0	0	1.8	0	-1.8
	Paper Birch	17.1	5.7	0	0	74.3	0	0	2.9	31	59.3	28.3
	Red Maple	0	0	0	0	100	0	0	0	0.9	0	-0.9
	Red Pine/White Pine	50	25	0	0	25	0	0	0	3.5	0	-3.5
	White Cedar	14.3	2.4	4.8	0	40.5	0	0	38.1	37.2	17.7	-19.5

Table 2-4. Community transitions for white cedar plots experiencing late-season fire and high severity ground fire by stand age. Data shown are the % of plots that were a community type pre- and post-fire and the % of plots staying a community type or succeeding to a new one.

	Aspen	Balsam Fir	Black Spruce	Jack Pine	Paper Birch	Red Maple	Red Pine/White Pine	White Cedar
Mature (167-213 yr)	26.667	0.000	0.000	0.000	66.667	0.000	0.000	6.667
Old (>213 yr)	0.000	5.556	0.000	0.000	33.333	0.000	0.000	61.111

Table 2-5. Community transitions by community type, fire season and ground fire severity level. Low ground fire severity is defined as surface burning that consumes less than 50% of surface litter and no duff, while high ground fire severity consumed 50-100% of surface litter and some duff. Data shown are the % of plots that were a community type pre- and post-fire and the % of plots staying a community type or succeeding to a new one.

		Post Fire Community Type										
	Early Season- Low Severity	Aspen	Balsam Fir	Black Spruce	Jack Pine	Paper Birch	Red Maple	Red Pine/ White Pine	White Cedar	Pre-Fire % of landscape	Post-Fire % of landscape	Net Change
Pre Fire Community Type	Aspen	50.0	0.0	25.0	0.0	25.0	0.0	0.0	0.0	7.3	20.4	13.1
	Balsam Fir	37.5	37.5	12.5	0.0	12.5	0.0	0.0	0.0	14.5	22.2	7.7
	Black Spruce	6.7	33.3	40.0	13.3	6.7	0.0	0.0	0.0	29.1	16.7	-12.4
	Jack Pine	16.7	8.3	0.0	33.3	33.3	8.3	0.0	0.0	21.8	13.0	-8.9
	Paper Birch	27.3	27.3	0.0	9.1	36.4	0.0	0.0	0.0	20.0	22.2	2.2
	Red Maple	0.0	0.0	0.0	0.0	0.0	100.0	0.0	0.0	1.8	3.7	1.9
	Red Pine/White Pine	0.0	0.0	0.0	0.0	0.0	0.0	0.0	100.0	1.8	0.0	-1.8
	White Cedar	0.0	0.0	50.0	0.0	50.0	0.0	0.0	0.0	3.6	1.9	-1.8
	Early Season High Severity											
	Aspen	NA	NA	NA	NA	NA	NA	NA	NA	0.0	49.1	49.1
	Balsam Fir	66.67	0.00	0.00	33.33	0.00	0.00	0.00	0.00	5.5	3.6	-1.8
	Black Spruce	30.00	10.00	40.00	0.00	20.00	0.00	0.00	0.00	18.2	12.7	-5.5
	Jack Pine	25.00	0.00	0.00	68.75	6.25	0.00	0.00	0.00	29.1	23.6	-5.5
	Paper Birch	50.00	0.00	0.00	12.50	37.50	0.00	0.00	0.00	14.5	12.7	-1.8
	Red Maple	NA	NA	NA	NA	NA	NA	NA	NA	0.0	0.0	0.0
	Red Pine/White Pine	72.2	5.6	16.7	0.0	0.0	0.0	5.6	0.0	32.7	1.8	-30.9
	White Cedar	50.0	0.0	0.0	0.0	50.0	0.0	0.0	0.0	3.6	0.0	-3.6

Table 2-5 Continued.

		Post Fire Community Type								Pre-Fire % of landscape	Post-Fire % of landscape	Net Change
	Early Season- Low Severity	Aspen	Balsam Fir	Black Spruce	Jack Pine	Paper Birch	Red Maple	Red Pine/ White Pine	White Cedar			
Pre-Fire Community Type	Aspen	100.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	4.8	4.8	0.0
	Balsam Fir	NA	NA	NA	NA	NA	NA	NA	NA	0.0	19.0	19.0
	Black Spruce	0	12.5	0	0	75	0	0	12.5	38.1	4.8	-33.3
	Jack Pine	NA	NA	NA	NA	NA	NA	NA	NA	0.0	0.0	0.0
	Paper Birch	0.0	18.2	0.0	0.0	81.8	0.0	0.0	0.0	52.4	76.2	23.8
	Red Maple	NA	NA	NA	NA	NA	NA	NA	NA	0.0	0.0	0.0
	Red Pine/White Pine	0.0	100.0	0.0	0.0	0.0	0.0	0.0	0.0	4.8	0.0	-4.8
	White Cedar	0.0	0.0	10.0	0.0	10.0	0.0	0.0	80.0	47.6	42.9	-4.8
	Late Season High Severity											
	Aspen	0.0	0.0	0.0	0.0	100.0	0.0	0.0	0.0	2.4	22.0	19.5
	Balsam Fir	60.0	0.0	0.0	0.0	40.0	0.0	0.0	0.0	6.1	1.2	-4.9
	Black Spruce	0.0	0.0	0.0	0.0	84.6	0.0	0.0	15.4	15.9	1.2	-14.6
	Jack Pine	50.0	0.0	0.0	0.0	50.0	0.0	0.0	0.0	2.4	0.0	-2.4
	Paper Birch	25.0	0.0	0.0	0.0	70.8	0.0	0.0	4.2	29.3	62.2	32.9
	Red Maple	0.0	0.0	0.0	0.0	100.0	0.0	0.0	0.0	1.2	0.0	-1.2
	Red Pine/White Pine	66.7	0.0	0.0	0.0	33.3	0.0	0.0	0.0	3.7	0.0	-3.7
	White Cedar	18.8	3.1	3.1	0.0	50.0	0.0	0.0	25.0	39.0	13.4	-25.6

Figure 2-1. Location of fires and research plots within the BWCAW of Northern MN, USA.
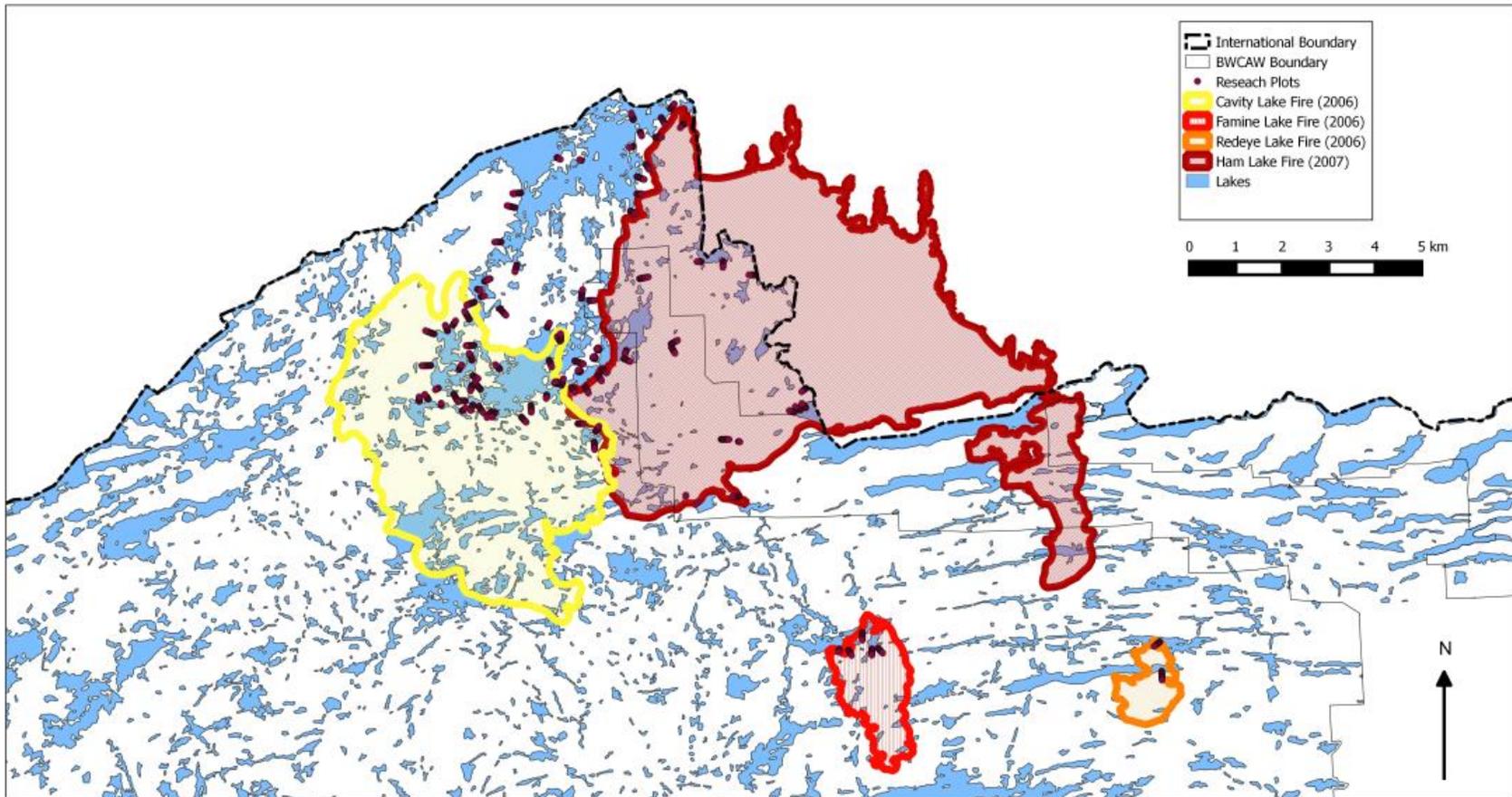
Figure 2-2. Scree plot of dimensions vs stress constructed in PC-Ord 5 using 25 runs of real and simulated data.
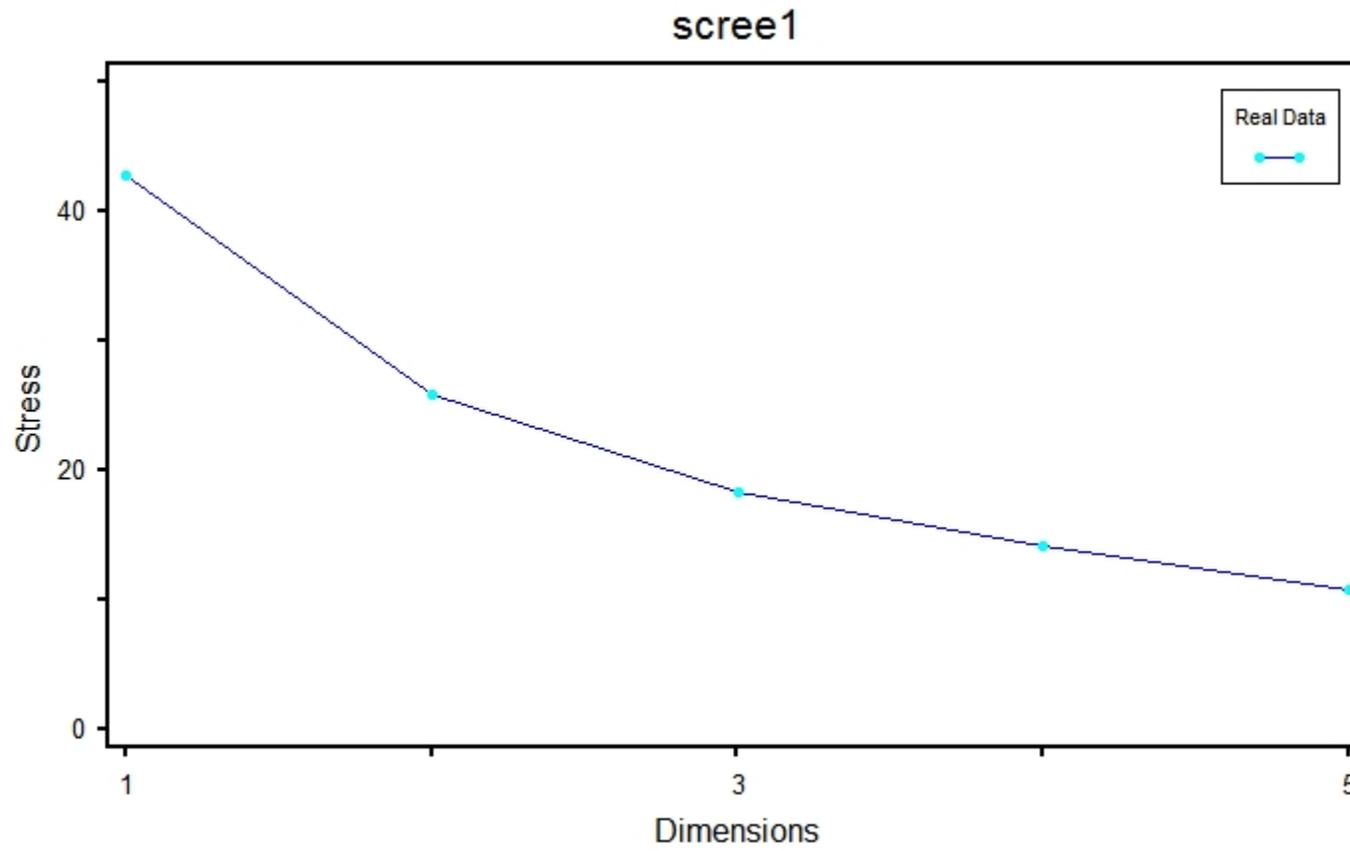
Figure 2-3. NMDS ordination showing pre- and post-fire distribution of plots by community type and fire season in ordination space. Labeled points are centroids for each community type.
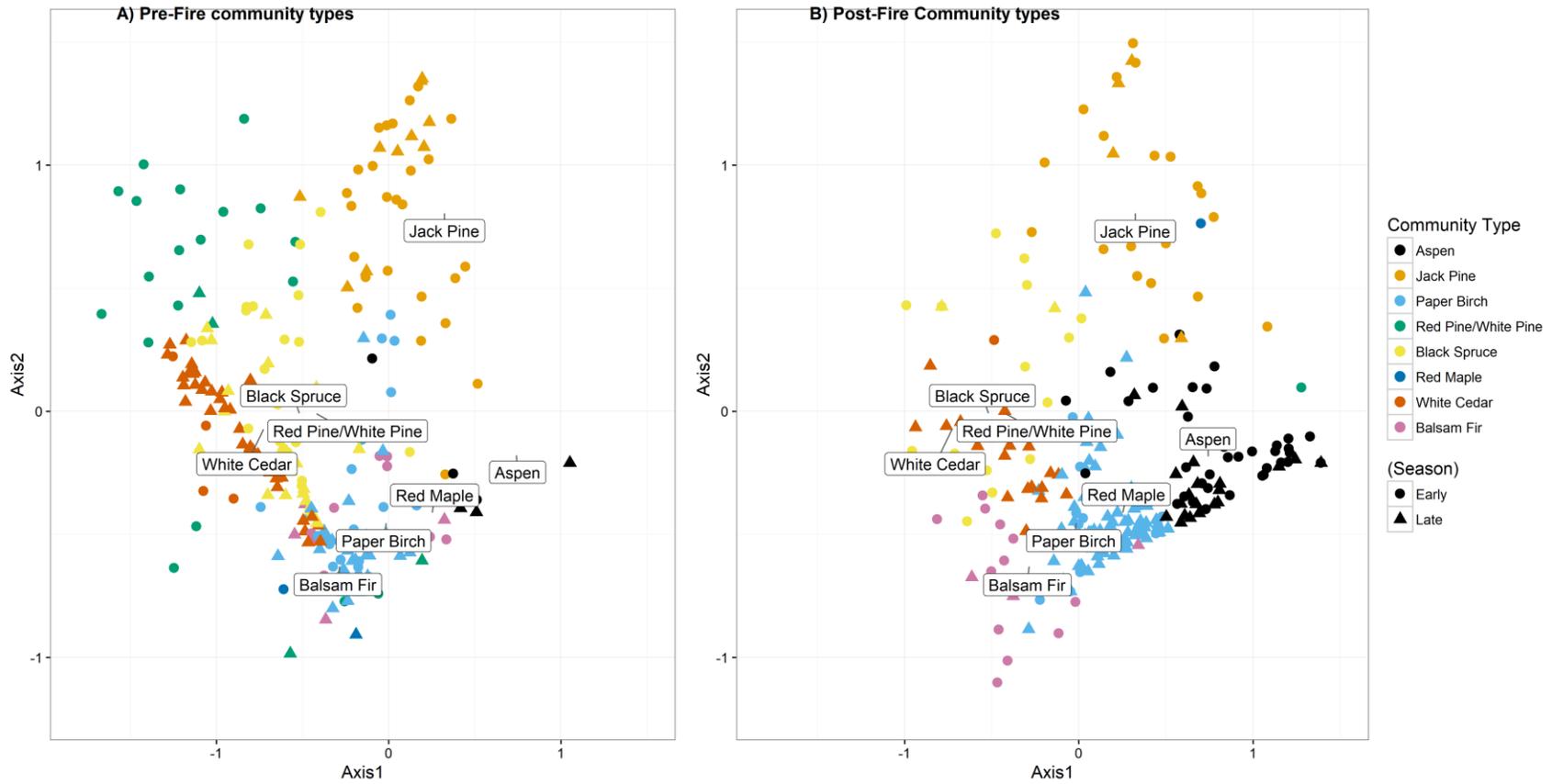
Figure 2-4. Successional pathways for A) early and B) late-season fire plots grouped by community type pre-fire, color of arrow indicates post fire community type. Origin of an arrow is the position in ordination space of a plot pre-fire, head of the arrow is the position of that plot in ordination space after fire.

A) Successional pathways for early season fire plots
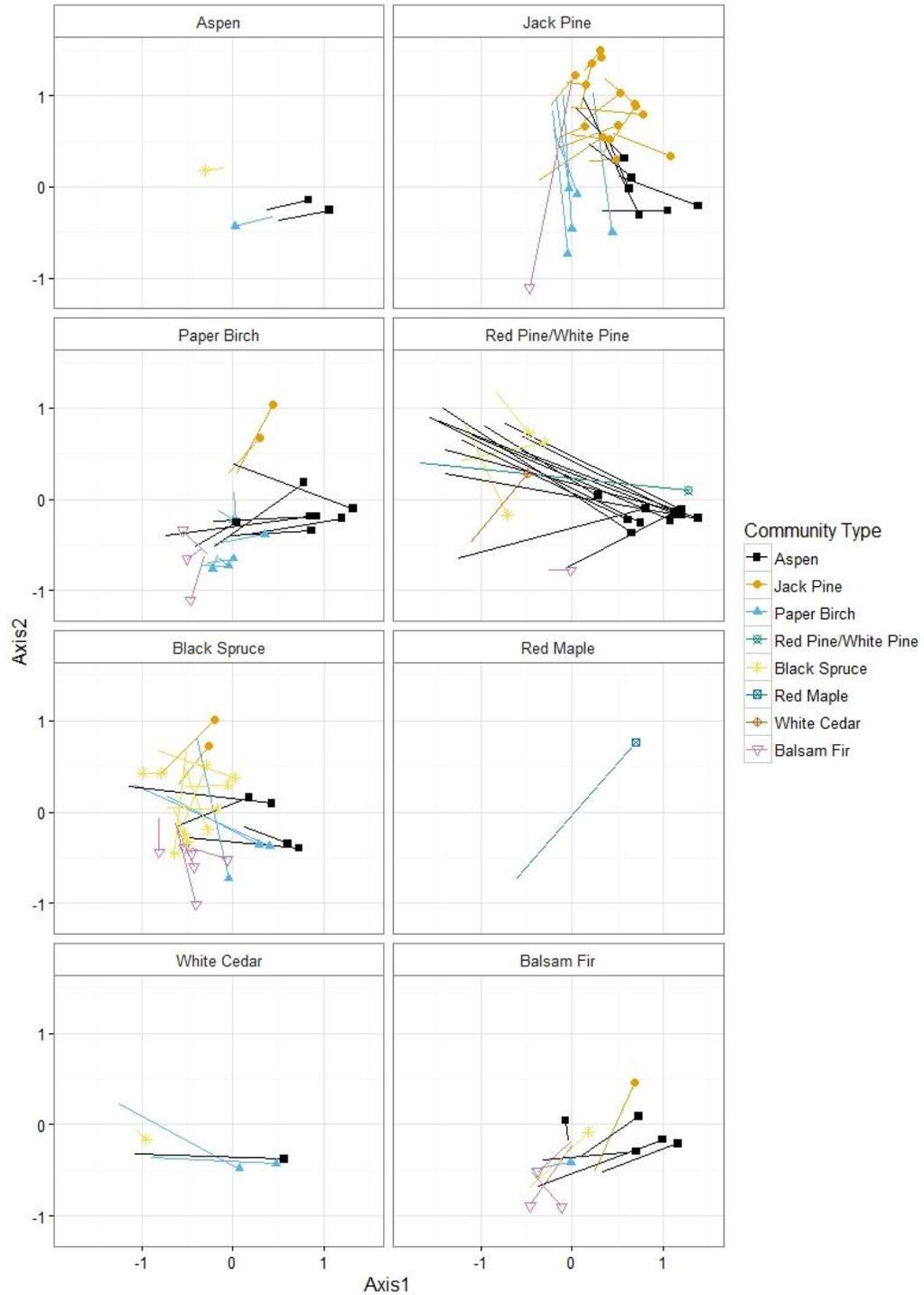
B) Successional pathways for late season fire plots
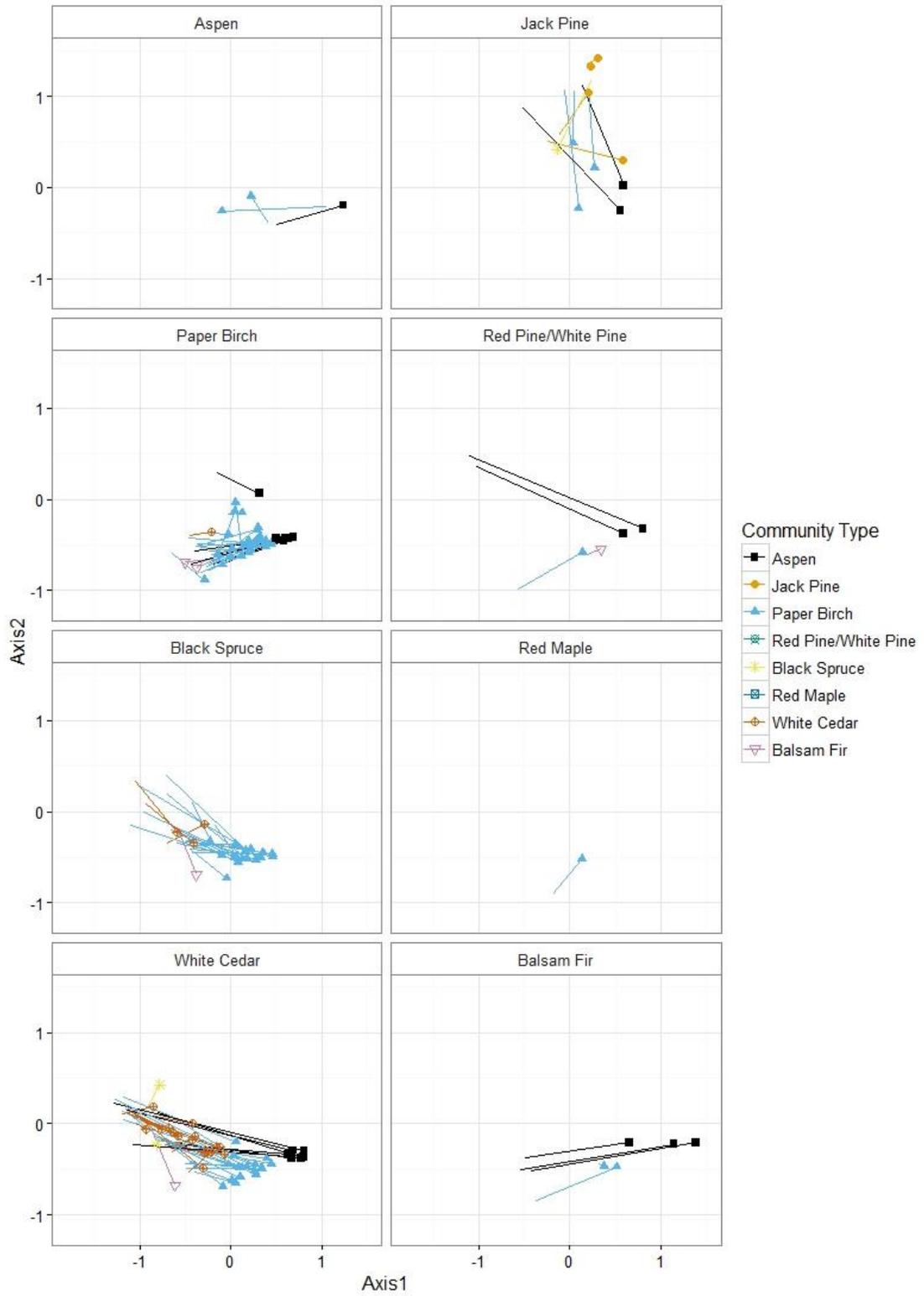
Figure 2-5. Successional pathways for white cedar plots experiencing late-season fire sorted by stand age.
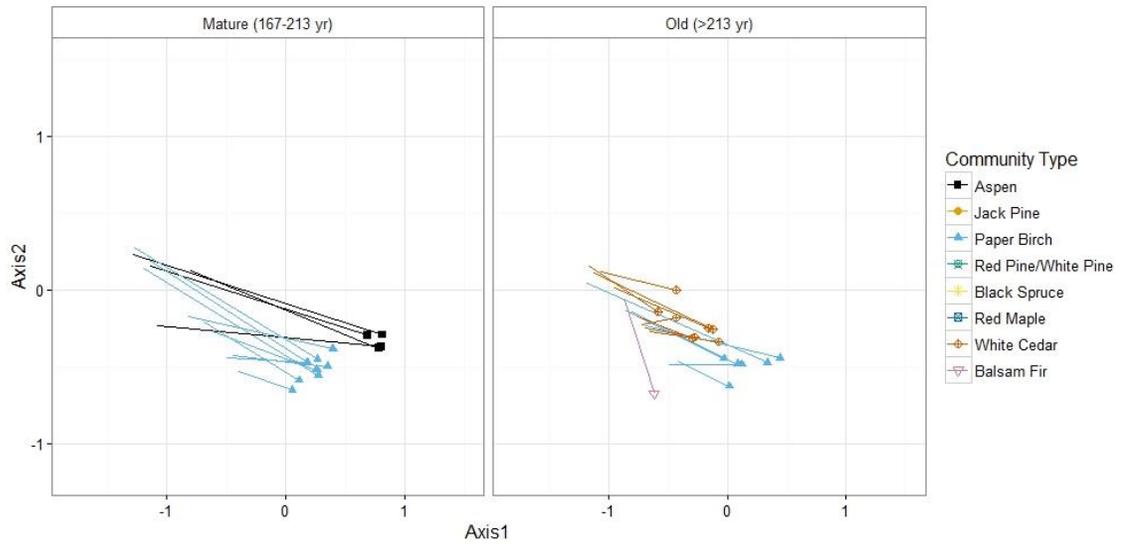
Figure 2-6. Successional pathways for early and late-season fire plots sorted by ground fire severity. Low ground fire severity is defined as surface burning that consumes less than 50% of surface litter and no duff, while high ground fire severity consumed 50-100% of surface litter and some duff.
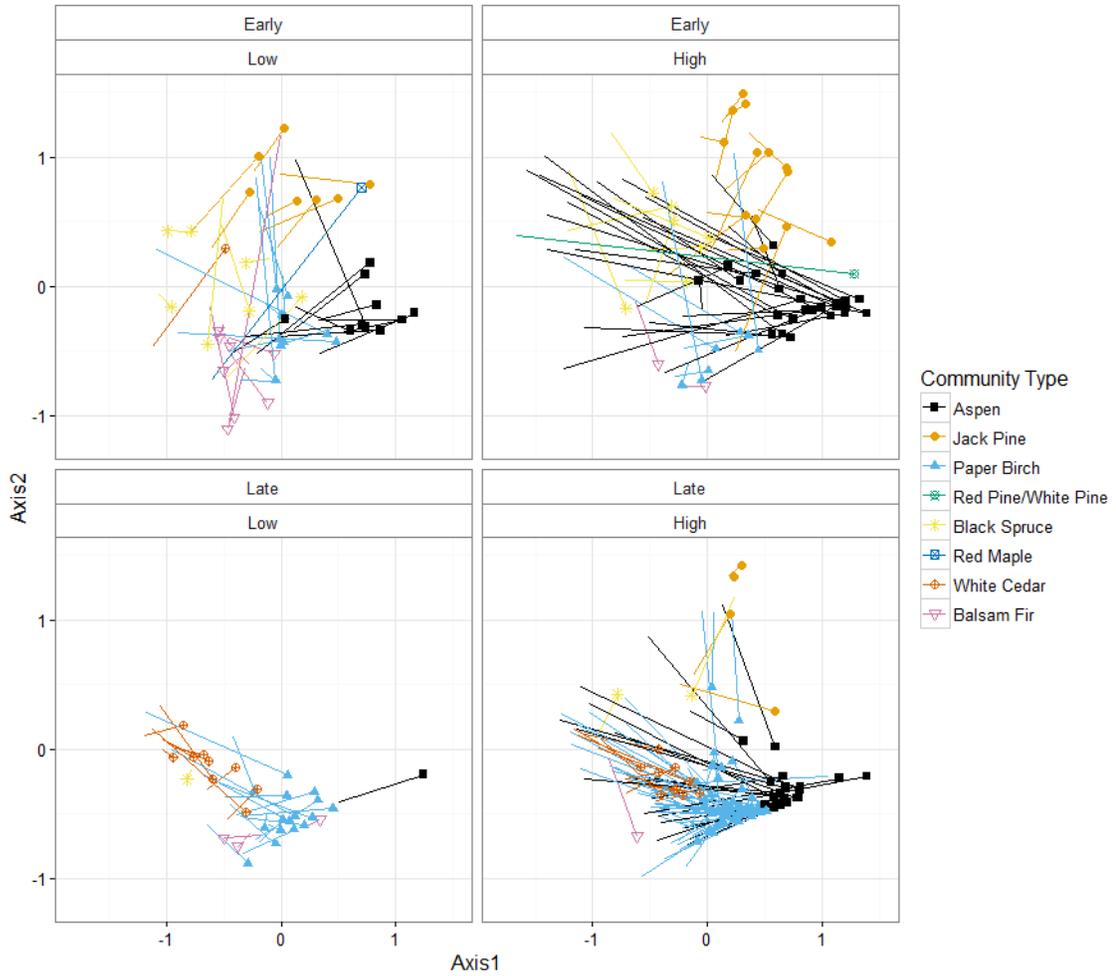
Figure 2-7. Successional pathways by community type, fire season and ground fire severity. Low ground fire severity is defined as surface burning that consumes less than 50% of surface litter and no duff, while high ground fire severity consumed 50-100% of surface litter and some duff.
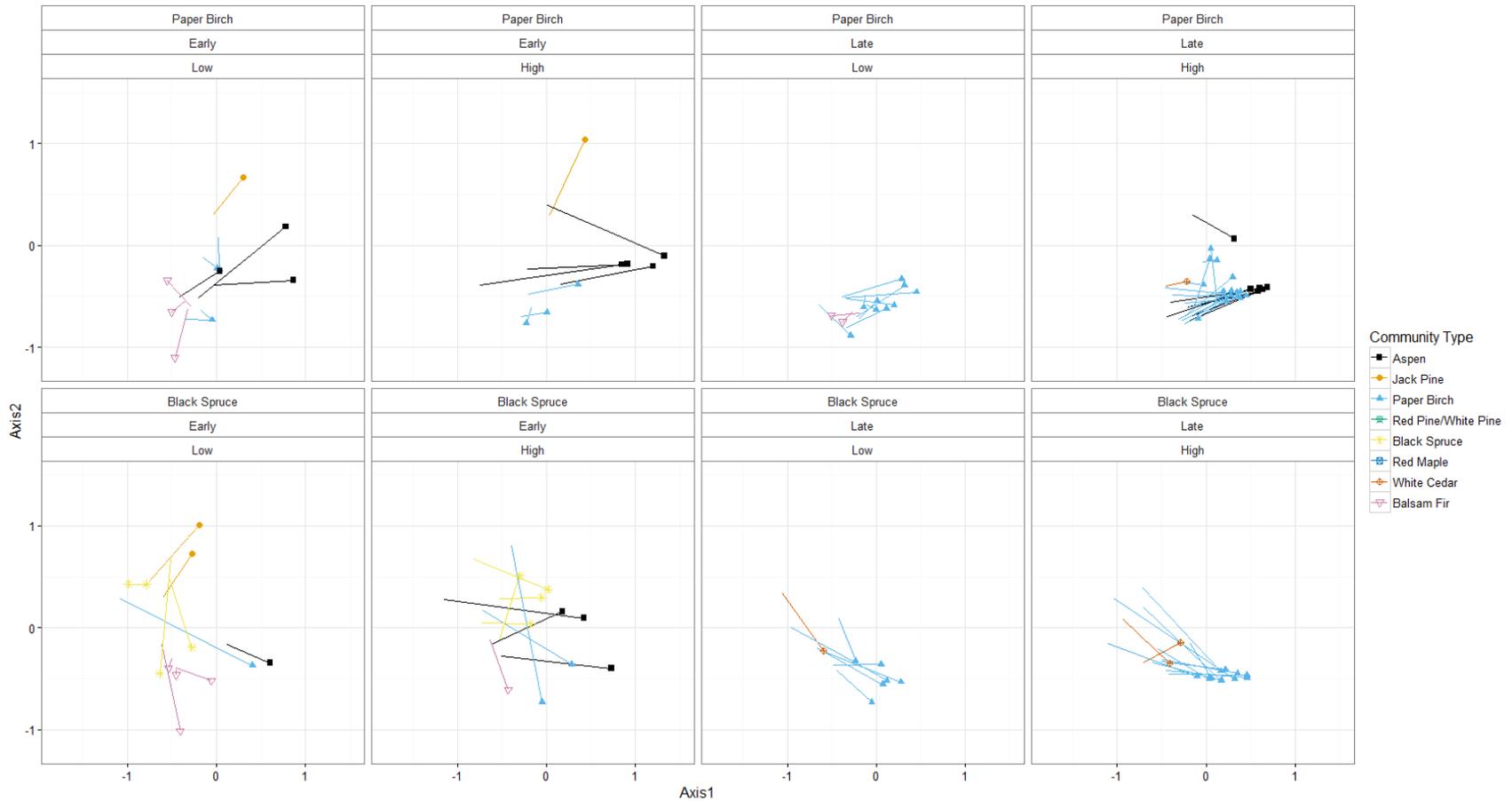
Figure 2-8. Successional pathways for late-season white cedar plots by ground fire severity. Low ground fire severity is defined as surface burning that consumes less than 50% of surface litter and no duff, while high ground fire severity consumed 50-100% of surface litter and some duff.
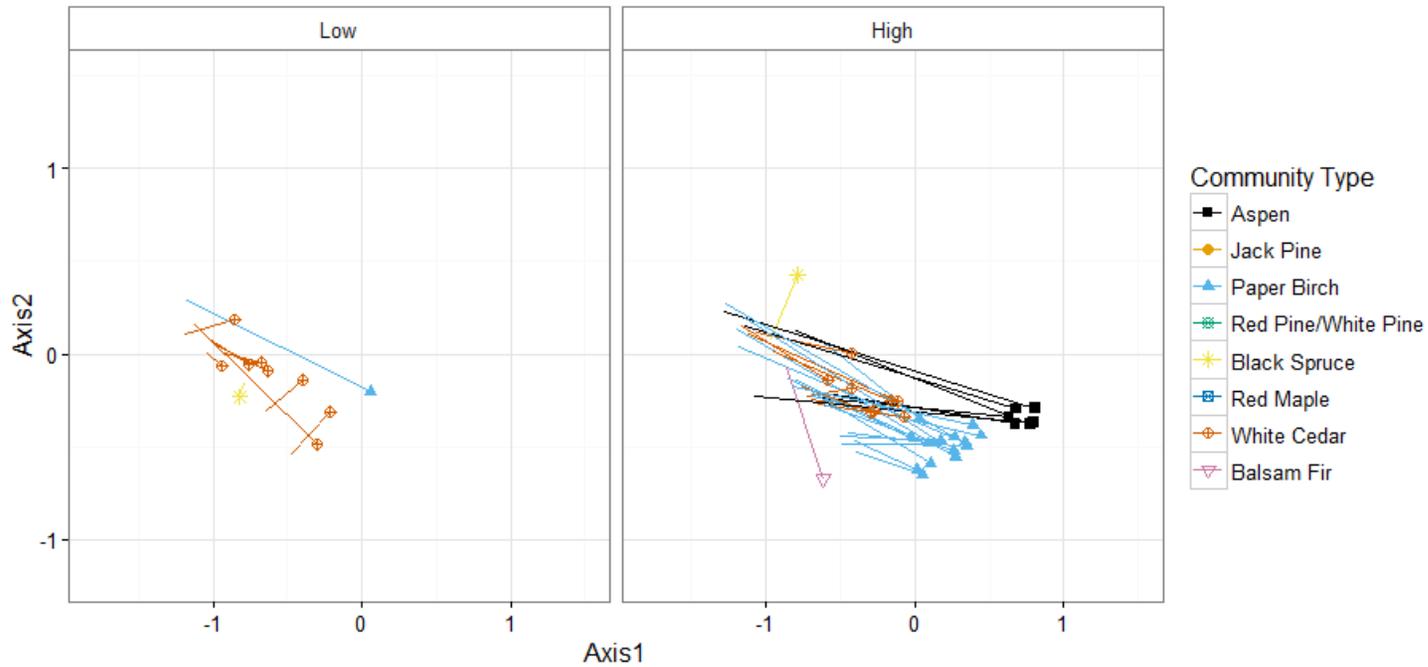
Figure 2-9. Successional pathways for early season jack pine plots. Low ground fire severity is defined as surface burning that consumes less than 50% of surface litter and no duff, while high ground fire severity consumed 50-100% of surface litter and some duff.
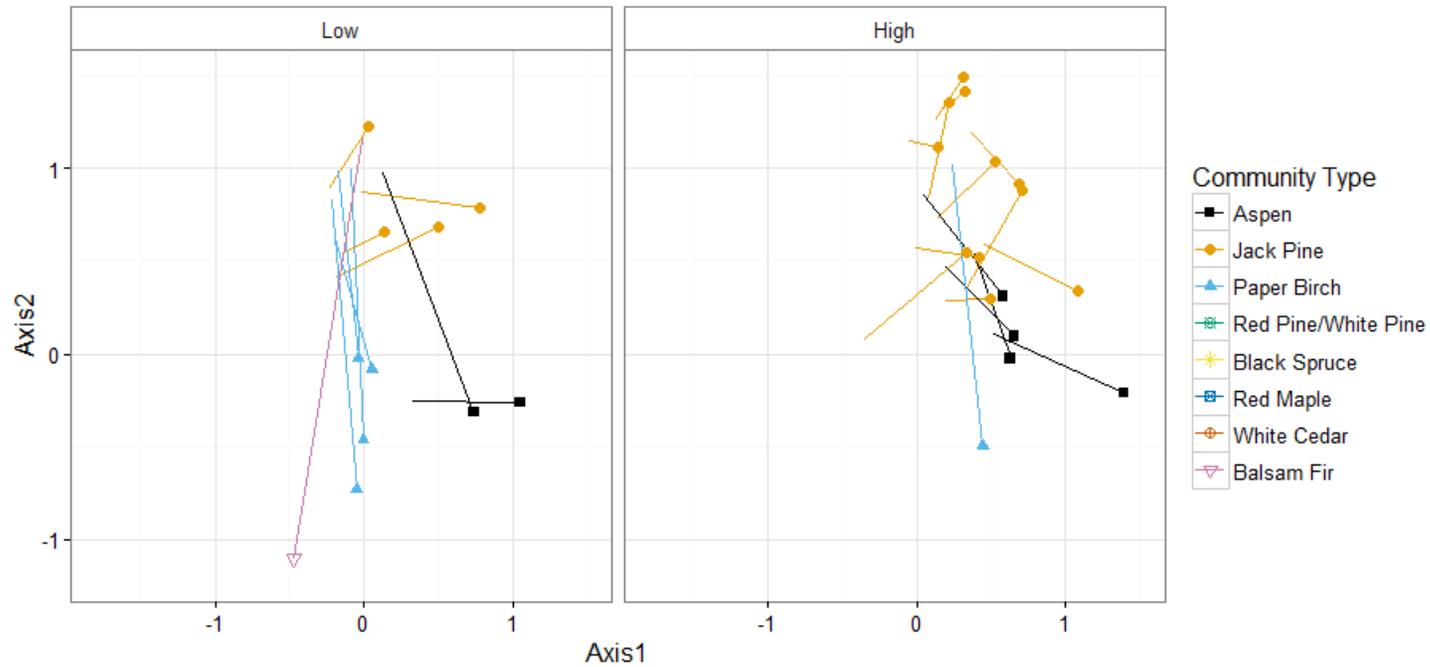
Chapter 3

Wind and fire: rapid shifts in community composition following multiple disturbances in the southern boreal forest

with
Roy Rich
Lee Frelich
Peter B. Reich

Synopsis

Under a warming climate, the southern boreal forest is expected to see an increase in the frequency of forest disturbances such as wildfires and severe windstorms. Although boreal forests are considered fire adapted, projected increases in disturbance frequency could result in novel combinations of disturbances with severities and impacts on community composition outside historic norms. Using a network of repeatedly measured vegetation monitoring plots we followed changes in forest community composition in areas of the Boundary Waters Canoe Area Wilderness (BWCAW), in Minnesota, USA experiencing disturbances ranging from severe windstorms or wildfires to areas affected by wind followed by fire or multiple fires within a short period of time. Using non-metric multidimensional scaling ordination, hierarchical cluster analysis and permutational analysis of variance we compared successional pathways across different disturbance types and combinations to test whether multiple disturbances had altered successional pathways or caused greater convergence (decreased community dispersion) relative to single disturbances. We found that instances of multiple disturbances often resulted in strong shifts towards wind-dispersed early successional forest types, while single disturbances tended to have multiple successional pathways that favored both late and early successional species. All disturbances in our study resulted in significant shifts in composition, but we generally failed to find statistical evidence of changes in community dispersion. Our results suggest that predicted changes in boreal disturbance regimes could alter patterns of succession and shift future

composition from diverse mixtures of fire adapted pines and late successional

conifers to dominance by disturbance adapted deciduous angiosperm species.

Introduction

The boreal forest of central North America is a fire dominated ecosystem characterized by stand replacing crown fires that occur on intervals ranging from 50-150 years (Heinselman 1973). Recent research has suggested that climate change will lead to warmer temperatures and more frequent droughts across much of boreal North America (IPCC 2013; Fauria and Johnson 2008; Flannigan et al. 2009; Van Bellen et al. 2010). Fire frequency is predicted to rise concomitantly with temperature and drought, leading to a predicted doubling or tripling in fire occurrence by the late 21st Century (Flannigan et al. 2005; Le Goff et al. 2009; Krawchuck 2009; Wotton et al. 2010). In addition, a warming climate is expected to increase the frequency and intensity of large-scale windstorms or derecho events that have been historically rare in the North American boreal forest (Peterson 2000; Frelich and Reich 2010; Diffenbaugh 2012). Under historic disturbance regimes, single disturbance events over intermediate time scales (such as 50 years) were common in the North American boreal forest. However, with increases in both fire and wind frequency, multiple compounding disturbance events, such as wind followed by fire or multiple fires within a short period of time (<50 years) could become more common. Furthermore, there is also the possibility of synergistic interaction between disturbance events (Buma 2015). Windstorms that are more frequent could increase coarse woody debris and fine fuel loadings, making forests more susceptible to fire and increase the intensity and severity of future fire events (Woodall and Nagel 2007; Mitchell 2012). Alternatively, frequent fire events could reduce the number of old, wind

susceptible stands on the landscape and reduce the severity of disturbance from future windstorms.

The increasing frequency and intensity of wind and fire disturbance within the boreal forest is likely to have far-reaching consequences for forest succession and could fundamentally alter the underlying structure and dynamics of the boreal forest ecosystem. Under current disturbance regimes, stand self-replacement is common but not ubiquitous after crown fire (Heinselman 1996), but rapidly compounding disturbances may leave fewer disturbance legacies in their wake, and erode ecosystem resilience (Paine et al. 1998; Johnstone et al. 2016). If combined disturbances exceed the disturbance regime that species within a community are adapted to there may be novel successional outcomes, altered ecosystem states, and disruptions in ecosystem functioning (Paine et al. 1998; Buma 2015; Johnstone et al. 2016). In the boreal forest, potential impacts of multiple disturbances include reduced average stand age and conversion of long-lived boreal conifer stands to stands dominated by deciduous species (Brown and Johnstone 2006; Johnstone and Chapin 2006). Shifts in forest age and composition could have a pronounced negative impact on species that depend on old forest habitats. In addition, increasing boreal forest disturbances have the potential to dramatically increase terrestrial carbon emissions and convert one of earth's largest terrestrial carbon sinks to a potential source by centuries end (Kasischke et al. 1995; Kurz et. al 2008; Balshi et al. 2009; Pan et al. 2011).

Because of the global importance of the boreal forest for biodiversity, conservation and carbon sequestration, it is imperative that we better understand not only how disturbance dynamics in the boreal forest are changing but also the ecological consequences of these shifting disturbance regimes. In this paper, we focus on the successional dynamics and interactions of fires and a severe windstorm within the southern boreal forest. While succession following single fires in the boreal forest has been extensively studied (Heinselman 1973; Ohman and Grigal 1981; Carlson et al. 2011), the successional dynamics of wind disturbance in the boreal forest (Rich et al. 2007) and the dynamics of multiple and compounding disturbances remain an area of evolving research (Paine et al. 1998; Johnstone and Chapin 2006; Brown and Johnstone 2011; D'Amato et al. 2011; Fraver et al. 2011; Buma et al. 2015; Johnstone et al. 2016).

Succession following disturbance may be characterized by several potential models, including cyclic, convergent, divergent, parallel or idiosyncratic (Frelich and Reich 1995, Frelich 2002). The actual model of succession may depend on neighborhood effects (Frelich and Reich 1999) and the spatial scale at which succession is observed, as well as stochastic factors. Heinselman (1973) reported that historically, parallel succession was typical for aspen (*Populus tremuloides* Michx.) and jack pine (*Pinus banksiana* Lamb.) stands in the southern boreal forest following stand replacing crown fires (Heinselman 1973; Ohman and Grigal 1981). Both species have strong positive disturbance-

activated neighborhood effects that lead to compositional stability when fires

occur on intervals of 50-150 years (Frelich and Reich 1999). In the absence of

fire disturbance, stands of aspen and or jack pine are unable to self-replace and

may undergo divergent or convergent succession (depending on the spatial scale

of inquiry) to more shade tolerant species such as black spruce (*Picea mariana*

(Mill.) Britton, Sterns & Poggenb.), balsam fir (*Abies balsamea* (L.) Mill.), white

cedar (*Thuja occidentalis* L.), and paper birch (*Betula papyrifera* Marshall)

(Frelich and Reich 1995; Chen and Taylor 2011) with white cedar becoming a

potential climax community type (Grigal and Ohmann 1975). Wind disturbance is

likely to accelerate the succession from early successional community types to

late by removing species including jack pine and aspen that are both shade

intolerant and susceptible to wind disturbance (Rich et al. 2007).

Successional patterns can be driven by both changes in community dispersion

(changes in the variability of composition) as well as directional shifts in

composition. Community dispersion is a measure of the beta diversity of the

patches or stands that make up a given unit of ecological observation (Anderson

et al. 2006). In this paper, we use the term community dispersion to refer to the

variability in community composition across plots exposed to a given disturbance

type/combination; this definition is similar to the definition used by Houseman et

al. (2008). Following a disturbance, a community may have a more variable

composition, i.e., an increase in dispersion, or alternatively a disturbance may act

like a filter and select against certain species leading to a new composition that is

more homogenous post-disturbance. Changes in composition can also be directional in nature, independent of changes in community dispersion. For example, a mixed forest of paper birch and black spruce could become a mono-dominant stand of aspen following disturbance, resulting in a community that has both lower dispersion and markedly shifted composition. Alternatively, a mixed stand of aspen and fir could succeed to a monodominant stand of aspen following fire resulting in a decline in dispersion, but only a minor shift in composition, or a monodominant fir stand could succeed to a mixed stand of aspen and birch, resulting in both an increase in dispersion and a shift in composition.

In this paper we sought to 1) determine how patterns of succession differ between single and multiple disturbances and 2) determine whether instances of multiple disturbances lead to greater successional convergence relative to single disturbance events. We used a series of recent disturbance events in the Boundary Waters Canoe Area Wilderness (BWCAW) of northern Minnesota U.S.A. as a case study to examine how changing disturbance regimes may impact boreal forest composition and succession. These disturbances include wildfires in 1974, 1995, 2006 and 2007, a large windstorm in 1999 and prescribed fires in 2002-2004. These disturbances have created a matrix of stands affected by different disturbance combinations including none, wind alone, fire alone, wind followed by single fire, wind followed by 2 fires, and multiple (2 or 3) fires within a 35-year period. Using this matrix of disturbances we sought to

characterize tree community response to disturbances ranging from windstorms and single fires to instances of combined multiple disturbances, and to address the following questions and hypotheses.

Q1) How do patterns of succession differ between single and multiple disturbances?

H1: Different types of disturbances act as ecological filters, with each disturbance in some way (but not necessarily the same way) limiting the potential post-disturbance community. In cases of single fires, we expected composition to be dominated by a mix of early successional species including aspen, paper birch, jack pine and red pine (*Pinus resinosa* Aiton) and white pine (*Pinus strobus* L.), with late successional species like black spruce occasionally present. In areas affected by wind alone we hypothesized that regeneration would consist of mainly shade tolerant advanced regeneration of species such as balsam fir, white cedar, red maple (*Acer rubrum* L.) and black spruce. We expected that regeneration following combinations of disturbance such as wind followed by fire or multiple fires would be composed of species that were either tolerant of both wind and fire such as paper birch and red maple, or capable of long distance seed dispersal or vegetative reproduction such as quaking aspen.

Q2) Do instances of multiple disturbances lead to greater successional convergence relative to single disturbance events?

H2: We expected areas experiencing multiple disturbances would undergo

successional convergence towards disturbance-adapted early successional

species, as disturbance averse species were expected to be reduced or

eliminated. In turn, we expected this would lead to a more homogenous

landscape resulting in both decreased dispersion and shifts in community

composition. In contrast, we expected single disturbances would result in

divergent succession and multiple successional pathways depending on the

specific disturbance and the pre-disturbance community type. We expected that

wind or fire alone would favor some community types, but that all community

types would persist so that the net result would be increased community

dispersion, but variable shifts in composition.

Methods

Our research area (≈15,000 ha) is centered at 90°56′W and 48°08′N and located within the BWCAW and adjoining lands of the Superior National Forest in northern, MN USA and consists of areas affected by the 1999 windstorm, various wild and prescribed fires from 2002-2007 and adjoining undisturbed stands with similar physiographic conditions. The landscape of the BWCAW is post glacial in origin with thin, acidic soils derived from glacial till on top of granitic bedrock of the Canadian Shield. The climate is cold continental with a mean July temperature of 17°C and a mean January temperature of –8°C. The average annual temperature is 2°C with approximately 64 cm of annual precipitation (Heinselman 1996). The forests of the BWCAW are near boreal in composition, but include several common temperate species such as red maple (*Acer rubrum* L.), red pine, white pine, and black ash (*Fraxinus nigra* Marshall). In our study area, 90% of mature trees encountered are considered boreal species.

Like much of the boreal forest, disturbance regimes in the BWCAW were historically characterized by severe crown fires with average return intervals of 50-150 years (Heinselman 1973). However, fire return intervals lengthened during the 20th century due to climate change, fire exclusion and suppression (Heinselman 1996). Over the last 40 years the forest surrounding the Seagull Lake and the Saganaga Lake Corridor has seen significant disturbance. Today within a 25km radius of Seagull Lake there are an unprecedented array of forest stands that have been variously affected by wind, single fires, wind followed by

117

single fire, wind followed by 2 fires, and stands that have been burned 2 or 3 times within a 33-year period (Table 3-1).

We used a network of 1086 vegetation monitoring plots arranged on 82 transects to track changes in forest composition. Six hundred eighty-two plots were established in 2000-2001 following the 1999 windstorm, while the remaining plots were established in 2010-2011 following the major fire events of 2006 and 2007. We used a stratified sampling approach with stand age and disturbance type to locate transects. Most transects originated at lakeshores and ran perpendicular to shore with plots spaced every 25 m. Several transects were established outside the BWCAW and these transects originated near roadsides but similarly followed the natural slope direction. Transect length varied but ranged between 150 m and 400 m; because 80% of the BWCAW landscape is within 500 m of a lakeshore (Rich 2005) this sampling approach provides a representative sample of the forest landscape in the BWCAW.

Plots were circular and centered at 25 m intervals along transects with the first plot on a transect originating 5 m from the lakeshore; the first plot of a lake-originating transect was semicircular. Plot centers were marked with a piece of 3/8" steel rebar and GPS coordinates were recorded using a Trimble GeoExplorer or Garmin eTrex Vista HCx. We used a nested plot design with fixed plot radii of 12.5 m, 5 m and 3 m for a coarse-scale tree plot, fine-scale tree

plot and regeneration plot, respectively. On the coarse-scale tree plot, all trees live and dead greater than 5 cm dbh were counted and classified by size class and species. Our size classes were 5-15 cm, >15-25 cm and >25 cm. Also across the entire, coarse-scale plot we observed % cover for all trees that occupied least 1% of the plot area. We recorded cover separately for overstory trees and regeneration, with overstory trees defined as those greater than 2 m in height and regeneration defined as trees < 2 m in height. Cover measurements could stack such that each species could theoretically occupy >100% of the plot if they were vertically stratified. Cover estimates were then relativized at the plot scale by dividing the total cover of individual species by the total cover of the plot.

Within the fine-scale tree plot all live and dead trees >2.5 cm dbh were measured for diameter and for dead trees we assigned a cause of mortality as fire, wind or other. Mortality causes were determined by closely examining trees for the presence of bole breaks, decay, tip-up mounds and the presence or absence of charring on specific portions of the bole (See Appendix). In our 3m regeneration plot, all trees from new germinants to saplings were counted by species. Across the entire plot, we also recorded the percent of the plot area burned using ocular estimation, and categorical fire severity and wind severity (Table 2-2), after Carlson (2011).

Changes in forest composition and succession were analyzed by comparing the

relativized pre-disturbance composition (measured as basal area) with the

relativized post-disturbance composition (measured using stem counts of

regeneration and percent cover). We used repeated measures and inference of

past composition from dead trees to track changes in composition at the plot

level. All plots established in 2000-2001 were also resurveyed in 2007 and 2010.

During the 2010 resurvey, we were able to find exact plot center markers for

51.5% of plots. Where we were unable to find exact plot center we used GPS

coordinates and plot description to establish plot center with an estimated

accuracy of ±3 m.

For new plots added in 2011-2012 we inferred past composition by surveying all

live and dead trees within the fine-scale tree plot, and assigning a cause of

mortality for any standing snags or fallen dead trees. On the coarse-scale plots

we recorded the number of live, dead and fallen dead trees by species and size

class. We then used species-specific logistic regression equations that calculated

the probability of tree mortality by fire or wind. These equations were

parameterized using the detailed mortality data collected on fine scale plots

including, whether a tree was standing dead or fallen dead, its diameter and the

categorical wind severity of the plot (See Appendix). From these equations, we

were then able to calculate the fraction of basal area at the coarse scale that

would have been killed by wind or fire, and allocate that basal area as living or

dead at a given point in time. For example, if a given tree had a basal area of 1

m^2 and a 75% chance of being killed by fire, we allocated 0.75 m^2 of its basal

area as having been killed by fire and 0.25 m^2 of its basal area as having been

killed by wind. Individual tree basal areas were aggregate at the plot level to

create plot level estimates of living basal area by species before and after wind

disturbance and before and after fire disturbance.

While map data were used to stratify transects by disturbance types, we used

measured disturbance severity of plots to classify individual plots by disturbance

type for analysis. Disturbance severity was measured after Peterson and Leach

(2008) as the relative change in basal area pre- and post-disturbance. Because

the 1999 windstorm was diffuse in its spatial extent, there were few if any stands

in our study area that were completely unaffected by wind. We therefore used a

critical threshold of wind severity as a cutoff to designate plots on which we

considered wind to be an important influence. We classified plots where at least

25% of the basal area had been killed by wind as wind disturbed, while plots

where <25% of the basal area was killed by wind were not considered to have

been wind disturbed. We used fire history maps as well as on-the-ground

observations of charring to determine whether a plot had been burned, and by

which fires.

We assessed succession following disturbances by analyzing the frequency of

community transitions from one community type to another, interpretation of

nonmetric multidimensional scaling ordination (NMDS) plots and successional

vectors, and statistical techniques including permutational analysis of dispersion

(PERMDISP; Anderson 2006) and permutational analysis of variance

(PERMANOVA, McArdle and Anderson 2001). Together these techniques

provide a complimentary suite of tools to track changes in community

composition over time.

To visualize changes in community composition we used a combination of

hierarchical cluster analysis and nonmetric multidimensional scaling ordination

(NMDS) in the statistical software program Pc-Ord 5 (McCune and Grace 2002)

and the VEGAN package for R (Oksanen 2007). This approach allowed us to first

categorize sites into community types based on their composition and then follow

the changes in community composition over time via successional vectors in

ordination space. Hierarchical cluster analysis is a dimensionless approach for

classifying plots into community types based on the proportional contribution of

each species to overall plot composition. NMDS ordination is a data reduction

technique that reduces the dimensionality of a dataset, while enabling

visualization of complex relationships in a 2 or 3-dimensional solution. NMDS

ordination is particularly suited for analysis of ecological data because it is

statistically robust with non-normal and discontinuous datasets (McCune and

Grace 2002).

Successional vectors were created by running both hierarchical clustering and ordination analyses with a matrix containing 3 time-steps of community composition, that is 1086 plots with 3 time-steps ordinated as part of a single solution comparing the movement of plots within ordination space through time. The first time-step was community composition of trees in 1999, prior to the windstorm and prior to all fires except the 1974 Prayer Lake Fire and 1995 Sag Corridor Fire. For all plots except multiple fire plots the first time-step was effectively a pre-disturbance time-step. This was reconstructed from direct observations made during field work in 2000-2001 or logistical regression techniques for plots added to the study in 2011 (See Appendix). Basal areas were calculated by summing all trees > 5 cm dbh on each fine-scale plot with all trees on the coarse-scale plot. Because we used size classes for trees in the coarse-scale plots, we used quadratic mean diameters (QMD) for trees from fine-scale plots to estimate QMD for trees on coarse-scale plots. The second time-step was tree community composition in 2000-2001 as measured through direct observation during field work or estimated through logistic regression for plots added in 2010-2011. This time-step was represented as a matrix of basal area for trees larger than 5 cm dbh. The third time-step was the composition of tree regeneration in 2011-2012, 4-6 years post fire. Data for this time-step was obtained through direct observation of regeneration during field surveys in 2011 and 2012. This matrix consisted of stem counts for all trees, saplings and seedlings including new germinants less than 5 cm dbh by species by plot. Because the first two time-steps used basal area and the third time-step used

stem counts, a row relativization was performed to create unit-less measures of proportional dominance for each species. In areas that were unaffected by fire, the 2012 regeneration layer is hereafter referred to as the understory layer.

We considered adding an additional time-step that would have consisted of basal area of live trees over 5 cm dbh in 2011-2012, but because 65% of all plots had no surviving trees in this size category in 2011-2012, it would have created an especially sparse matrix that could not be ordinated with the other time-steps. To confirm that the exclusion of data on surviving trees would not bias our results we ran separate analyses of hierarchical cluster analysis and NMDS ordination using the same data for the first two time-steps, but relativized percent cover rather than regeneration stem counts for our third time-step. The overall solution for ordinations using % cover was similar to those produced using regeneration stem count data. Hierarchical cluster analysis classified some plots differently based on cover data, and there were some subtle differences between ordination runs with cover data vs those with regeneration data. There were slightly more plots identified as red pine/ white pine, aspen, balsam fir and black spruce community types when using cover data vs regeneration data and slightly fewer jack pine, paper birch, red maple and white cedar plots, but overall trends were consistent whether using cover data or regeneration data.

The species matrix was initially quite sparse, making stable ordination runs hard to obtain. To improve ordination stability, we excluded plots where one of the time-steps had no trees present (21 plots) and excluded or combined rare species from our analysis. We chose to exclude any species that was not present in at least 5% of plots, which eliminated both tamarack and black ash. We also combined 3 species of *Populus* in our study into a single aspen category.

Tree community types were determined using hierarchical cluster analysis in PC-Ord 5 with Sørensen's distance and a flexible beta of -0.25 (McCune and Grace). The cluster dendrogram was cut into 8 community types leaving 42% of information remaining. Although the choice of where to cut the dendrogram is an arbitrary one, we selected this level based on visual inspection with species overlays of an NMDS ordination output to identify community types based on species abundance that retained enough information to be useable, and avoid classifying sparse community types that could not be used in statistical analyses. Each cluster was defined as a community type after the most dominant 1 or 2 species in each cluster with the most dominant species ranging from 47-67% dominance among cluster types. We identified the following community types: aspen, paper birch, balsam fir, black spruce, red maple, white cedar, jack pine and red pine/white pine. These community types resemble those found in other studies of southern boreal forest (Ohmann and Ream 1971, Grigal and Ohmann 1975, Frelich and Reich 1995, Heinselman 1996, Rich 2005). In addition, the abundance of individual community types roughly mirrored the relative

dominance of the individual species obtained through basal area and regeneration data.

NMDS ordinations were run in the program R using the VEGAN package (Oksanen 2007). We used Bray-Curtis dissimilarity (Sørensen's distance) as our distance measure and performed 3000 runs with a 3-dimensional solution resulting in a final stress of 14.6411.

We tested for changes in community dispersion before and after disturbance using PERMDISP, which is a multivariate analogue of the Levene's (1960) test for homogeneity of variances. PERMDISP measures the distances of plots from centroid of a community type (the average position of a community type in multidimensional space). We used Bray-Curtis dissimilarity (Sørensen's distance) as our distance measure in the VEGAN package for R. We considered decreasing distance to centroid before and after disturbance as evidence of successional convergence, and increasing distances evidence of successional divergence.

We tested for shifts in composition using PERMANOVA. PERMANOVA is a multivariate analogue of an ANOVA that uses multivariate distance metrics (Anderson 2001). We used Bray-Curtis dissimilarity (Sørensen's distance) as our distance measure and tested significance with 9999 permutations using the

Adonis function in the VEGAN package for R. Because we used repeated measures our data were nested so we used the strata function to randomize only within each disturbance type. Statistically significant shifts in composition can be caused by changes in dispersion as well as shifts in composition; PERMANOVA is able to partition this variance. In cases where a PERMDISP test was not significant but a PERMANOVA test was we concluded that there was statistical evidence of shifting composition.

Results

Pre-Disturbance composition

Pre-disturbance composition was roughly similar between all landscape scale disturbance types/combinations and was dominated by a mix of jack pine, aspen, balsam fir and black spruce (Figure 3-1a). Red maple, and red pine/white pine community types were present but not abundant. Single fire affected areas had pre-disturbance community composition that was more paper birch and white cedar dominated and less aspen dominated than other disturbance types/combinations (Figure 3-1a).

Single disturbance: Severe Wind

Prior to the 1999 windstorm, areas that would subsequently experience wind disturbance were composed of old stands (median age 197 yr) dominated by a mix of jack pine (38% of plots), aspen (21%) and black spruce (17%) with paper birch (7%), red pine/white pine (6%), balsam fir (5%) and white cedar (5%) community types also present (Figure 3-2a). After the 1999 windstorm, community types followed multiple successional pathways, with a general net shift towards paper birch and later-successional (and more shade-tolerant) community types (Figure 3-2a). Aspen and red pine/white pine community types were heavily impacted by wind disturbance and declined significantly in dominance (Figure 3-3; Table 3-1). Black spruce and jack pine stands both experienced significant succession post-storm to other community types, but as

128

jack pine was twice as abundant prior to disturbance and many jack pine stands succeeded to black spruce, there was a modest net increase in black spruce dominance across the landscape and a large net decline for jack pine (Figure 3-3, Table 3-2). Paper birch, white cedar, red maple and balsam fir community types all experienced only slight shifts in composition following the 1999 windstorm (Table 3-2). These community types tended to be either dominated by wind firm species or have significant advanced regeneration whose composition was very similar to overstory composition so that even in areas of high wind severity there was little if any change in stand composition despite changes in stand structure.

Aspen and red pine/white pine community types both experienced varied succession following wind disturbance, with similar successional pathways. Only 26% of aspen dominated plots remained aspen dominated post-wind. Most aspen plots were converted to balsam fir (31%), paper birch (22%) and white cedar (7%), with the remainder succeeding to a mix of black spruce or red maple (Figure 3-3). Red pine/white pine stands experienced substantial compositional change with 37% of red pine and white pine plots remaining pine dominated

following wind disturbance and the remainder succeeding to balsam fir (22%), white cedar (15%), black spruce (15%) and paper birch dominated stands (11%).

Forty one percent of pre-wind jack pine plots remained jack pine dominated post-wind with the remainder succeeding to a mix of black spruce (18%), paper birch (16%) and white cedar (11%) (Figure 3-3). In contrast to aspen and red pine/white pine stands, succession to balsam fir was not an important successional pathway for jack pine stands, with only 8% of pre-wind jack pine plots succeeding to balsam fir. Roughly half of black spruce plots (53%) remained black spruce dominated following the windstorm but there was also significant conversion of black spruce to paper birch (27%) and white cedar (11%) (Figure 3-3).

Across the wind affected areas of our study composition changed from dominance by jack pine, aspen and black spruce, to a more mixed landscape dominated by paper birch (21% of plots), black spruce (19%), balsam fir (17%), jack pine (17%), and white cedar (13%) (Figure 3-2a). We found modest statistical evidence of successional divergence following the 1999 windstorm. A PERMDISP test found that median Sørensen's distance to centroid increased from 0.4500 pre-fire, to 0.4717 post-wind ($F_{(1, 1430)} = 11.51$; $p = 0.0007$). A

PERMANOVA test indicated significant differences in centroid locations before and after wind (F (1, 1430) = 48.857; p = 0.0001).

Single disturbance: Fire

Prior to fire, single fire sites were dominated by a mix of paper birch (23% of plots), black spruce (20%), white cedar (20%), balsam fir (19%), and jack pine (16%) stands, with, red pine/white pine (10%) and aspen (3%) also present (Figure 3-2b). Most of these stands were old with a median age of 211 years at the time of fire. Post-fire there was a general shift in community composition towards aspen and birch community types, but successional pathways were multiple and divergent (Figure 3-4, Table 3-3). Post-fire composition was heavily dominated by paper birch (65% of plots) and aspen (25%), with areas of jack pine (10%), cedar (9%), black spruce (8%), balsam fir (7%) and red pine and white pine stands also present (1%) (Figure 3-2b).

Half of pre-fire jack pine plots remained jack pine dominated post-single fire while others succeeded to a mix of aspen (21%) or birch (21%) following a single fire. Balsam fir, black spruce and paper birch stands also experienced some succession to jack pine following single fires (Figure 3-3), which partially offset conversions of jack pine stands to aspen or birch, in terms of jack pine abundance post-fire.

While the general successional pathway for single fire stands was toward early successional community types, some plots showed shifts in composition from early successional species towards late-successional community types such as balsam fir, black spruce and white cedar. In addition, those three community types also successfully self-replaced on 18-34% of plots. Red pine/white pine community type declined the most of any community type following single fires with significant self-replacement occurring on only 4% of red pine and white pine stands (Table 3-3). The majority (65%) of red pine/white pine dominated plots succeeded to aspen post-fire (Table 3-3). Other community types including cedar, black spruce and balsam fir declined in dominance post-fire but persisted across the landscape due to modest self-replacement following single fires (Figure 3-4, Table 3-3).

Single fire plots exhibited moderate successional convergence in ordination space relative to their pre-fire configuration. A PERMDISP test found that median Sørensen's distance to centroid decreased from 0.4866 pre-fire, to 0.4499 post-fire ($F(1, 465) = 5.7981$; $p = 0.01643$) indicating significant convergence. A PERMANOVA test indicated significant differences in centroid locations before and after fire ($F(1, 465) = 68.94$; $p = 0.0001$).

Multiple Disturbances: Wind followed by single fire

For portions of the landscape experiencing wind followed by single fire, the 1999 windstorm resulted in multiple successional pathways post-wind (Figure 3-5a), but following either the Cavity Lake Fire (2006) or the Ham Lake Fire (2007) there was strong convergent succession towards early-successional community types (Figure 3-5b). Aspen and birch were highly favored by this combination of disturbance events and many community types succeeded to aspen or birch regardless of their pre-disturbance composition (Figure 3-5b). Before the windstorm this subset of the broader landscape was composed of older stands (median age 148 yr) dominated by a mix of jack pine (37%), aspen (25%), and black spruce (14%), with areas of paper birch (7%), red pine/white pine (6%), white cedar (6%) and balsam fir (5%) also present. Post-wind composition shifted to stands dominated by paper birch (22%), balsam fir (18%), jack pine (18%), black spruce (15%), and white cedar (13%), with aspen (7%), red maple (4%) and red pine/white pine (2%) also present (Figure 3-2c, Table 3-4). Aspen, black spruce and cedar stands all underwent significant succession to paper birch following wind disturbance, increasing paper birch's dominance post-wind. Both aspen and birch community types increased dramatically following fire with aspen dominating 59% and paper birch 20% of this landscape post-wind and single fire. The remainder of the post-wind and single fire landscape was composed of jack pine (10%), red maple (6%), and black spruce (3%), with balsam fir, white cedar and red pine/white pine nearly absent (Figure 3-2c). Despite being heavily favored by the combination of wind followed by fire, neither

aspen nor birch exhibited strong self-replacement following fire (Figure 3-3b). Aspen was slightly more likely to succeed to aspen than paper birch after fire with 52% of post-wind aspen plots remaining aspen dominated vs 41% succeeding to paper birch. Paper birch was more likely to succeed to aspen than to self-replace with 66% of paper birch plots succeeding to aspen and only 28% self-replacing as paper birch following fire (Table 3-4b).

All community types except red maple, aspen and birch declined in dominance following the combination of wind and single fire (Table 3-4a). Jack pine was the most dominant community type pre-disturbance, but following the 1999 windstorm underwent significant succession to balsam fir, cedar and black spruce. This residual jack pine component had low self-replacement following fire (39%) causing the majority of post-wind jack pine plots to succeed to either aspen (39%) or paper birch (16%) (Table 3-4b.). After both wind and fire jack pine remained dominant on <10% of wind+single fire plots (Figure 3-2c).

Other coniferous community types including balsam fir, black spruce, white cedar and red pine/white pine also declined following the sequence of wind followed by single fire, although balsam fir, black spruce, and white cedar initially increased in dominance following the windstorm. Balsam fir, black spruce, white cedar and red pine/white pine community types together were dominant on 5% of wind+single fire plots after both wind and fire, relative to 30% of plots pre-

134

disturbance and 49% of plots post-wind (Figure 3-2c; Table 3-4a). Red maple

was a very minor (1%) component of this landscape pre-disturbance, but

increased to dominate 6% of wind+single fire plots following both wind and single

fire (Figure 3-2c; Table 3-4). Red maple stands were as likely to succeed to

aspen as self-replace, but some jack pine, balsam fir and white cedar stands

succeeded to red maple following fire (Figure 3-3b).

A PERMDISP test failed to find differences in dispersion before wind and after

wind and fire for plots experiencing wind followed by fire, indicating that although

certain community types became rarer on the landscape, there was still

significant variation among community types so that there was no significant

difference in dispersion before and after multiple disturbances. A PERMANOVA

test indicated that there were significant differences in centroid locations before

wind, after wind and before fire, and after wind and fire (F (2, 1131) = 60.958; p =

0.0001).

Multiple Disturbances: Wind followed by 2 fires

Areas subjected to wind followed by 2 fires had successional pathways similar to

areas experiencing wind followed by a single fire. Prior to wind disturbance these

stands were a mix of older stands (median age 148 yr) dominated by jack pine

(43% of plots), black spruce (31%), and aspen (11%), with balsam fir (4%), white

cedar (4%), paper birch (4%) and red maple (2%) also present (Figure 3-2d).

Following the 1999 windstorm there were multiple successional pathways and a shift toward late successional community types and concomitant declines in early successional community types. Post-wind/pre-fires this landscape was dominated by black spruce (31% of plots), white cedar (14%), paper birch (14%), jack pine (12%), aspen (12%), and balsam fir (12%) with areas of red maple (6%) also present (Figure 3-2d; Figure 6a). Following both prescribed fires in either 2002, 2003 or 2004 and the Ham Lake fire of 2007 there was a strong trend towards increasing aspen and birch regardless of pre-fire composition (Figure 3-6b). After wind and 2 fires this area was dominated by aspen (57% of plots) and paper birch (26%) with jack pine (6%) and white cedar (6%) also present, with red maple (4%) and black spruce (2%) present but minor components.

Aspen stands were a minor component of this landscape prior to wind, and declined further following the 1999 windstorm, but increased significantly following two fires. Likewise, paper birch was absent as a community type for this set of plots pre-disturbance, but following wind and two fires, paper birch was dominant on approximately one fourth of this landscape. Jack pine was the most dominant community type pre-disturbance, but was very susceptible to wind disturbance and, and largely failed to self-replace following repeated fires with only 17% of the residual post-wind jack pine plots remaining jack pine dominated after 2 fires (Figure 3-6; Table 3-5b).

Despite increasing overall, aspen had a low rate of self-replacement following repeated fires. One-third of post-wind aspen plots remained aspen dominated

after 2 fires, while 50% succeeded to paper birch. Paper birch self-replaced on 57% of post-wind paper birch plots with other post wind paper birch plots succeeding to aspen (43%) following repeated fires. Black spruce, balsam fir and white cedar community types all increased following wind, but were greatly reduced following repeated fires (Figure 3-2d, Table 3-5). Red maple was absent as a community type for areas affected by wind and 2 fires prior to disturbance, but increased following wind to 6% of plots. Following 2 fires there was a modest decline in red maple dominance, but sample size for this community type was very small (3 plots) (Table 3-5).

A PERMDISP test failed to find differences in dispersion before and after all disturbances for plots experiencing wind followed by two fires. A PERMANOVA test indicated that there were significant differences in centroid locations before wind, after wind, and after two fires ($F(2, 154) = 18.52$; $p = 0.0001$).

Multiple Disturbances: Two or three fires

In areas affected by 2 or 3 fires (and not by wind disturbance) we were only able to follow compositional changes before and after the final fire in the sequence, the 2007 Ham Lake Fire. Similar to other multiple disturbances, there was a successional shift towards aspen and birch following the final fire in the sequence, (Figure 3-6). Prior to the Ham Lake fire this portion of the landscape was composed of mostly young jack pine (50% of plots), black spruce (25%) and

aspen (20%) stands that had regenerated after either the 1974 Prayer lake fire or the 1995 Saganaga Corridor fire. Following the Ham Lake Fire, jack pine was able to self-replace on 31% of plots and was dominant on 17% of plots post-fire (Figure 3-7). There was significant succession of jack pine plots to aspen (56%) and paper birch (13%) community types. Paper birch was only a minor component (2% of plots) of this landscape prior to the Ham Lake Fire, but increased significantly following the Ham Lake Fire to dominate 22% of this landscape post-Ham Lake Fire (Figure 3-2e). Many stand types including black spruce, jack pine, balsam fir, and white cedar stands succeeded to paper birch after the Ham Lake Fire. Aspen increased significantly from 20% to 58% of plots following the Ham Lake Fire (Figure 3-2e) through a combination of high self-replacement (85%) and succession from jack pine and black spruce stands (Figure 3-6; Table 3-6). Black spruce self-replaced on 13% of black spruce plots and largely succeed to aspen (44%) and paper birch (25%). White cedar was a minor component of these stands pre- Ham Lake Fire (9% of plots) and declined significantly (2% of plots) post-fire (Figure 3-2d). White cedar stands largely succeeded to paper birch. Balsam fir, red maple and red pine/ white pine community types were not significant components of this landscape pre-fire and remained so following the Ham Lake Fire (Table 3-6).

A PERMDISP test failed to find differences in dispersion before and after the Ham Lake Fire for plots experiencing 2 or 3 fires. A PERMANOVA test indicated

that there were significant differences in centroid locations before and after the

Ham Lake Fire (F (1, 137) = 12.275; p = 0.0001).

Discussion

In our investigation of single and multiple disturbances in the BWCAW, we found that all species and all community types persisted following single disturbance events, but in instances of multiple disturbances we found that many coniferous community types were greatly reduced and aspen and birch community types increased dramatically, resulting in a landscape that was far more deciduously dominated post-disturbance. Here we discuss first the successional pathways of disturbance types and combinations and the degree to which different disturbances resulted in successional convergence vs divergence followed by the overall impact of these disturbances on specific community types.

Wind disturbance

Aspen and jack pine both experienced significant mortality during the 1999 windstorm (Rich et al. 2007) and these community types became much less dominant post-windstorm (Figure 3-2a and Figure 3-3). Shade-tolerant boreal species and their associated advanced regeneration are relatively wind firm (Rich et al. 2007). In many cases shade-tolerant species were able to survive the storm as scattered mature trees, and/or the selective removal of early successional species allowed shade tolerant advanced regeneration to become the new canopy layer following wind disturbance, in either case shade tolerant species became much more dominant on the landscape post-disturbance (Rich et al. 2007). Paper birch, however, was an outlier in that it is both shade intolerant and

wind firm (Rich et al. 2007), allowing it to increase in dominance, consistent with the observation by Frelich and Reich (1995) that it in the BWCAW, it is both an early- and late-successional species.

Because of differences in shade tolerance and wind firmness amongst the species in our study wind disturbance resulted in successional patterns that, like those for single fires, were both convergent and divergent depending upon the stand type examined. Jack pine and aspen stands underwent successional divergence to a mix of late successional stand types including balsam fir, cedar, black spruce and also paper birch. In contrast paper birch and white cedar community types experienced successional convergence as other community types succeeded to them. This combination of simultaneous successional convergence and divergence may help explain why we failed to detect statistically significant changes is community dispersion using PERMDISP.

Single Fires

The single fire events that we examined resulted in modest successional convergence towards early successional forest types. Shade intolerant and fast-growing species like aspen and paper birch increased in dominance post-fire as many late successional stands succeeded to these community types, but shade-tolerant and slow-growing species were not eliminated by single fires. Natural disturbances tend to be inherently patchy and in a landscape of broken

topography and numerous lakes and low-lying wetlands even large fires routinely

leave unburned islands, lakeshores or small patches of surviving trees that can

act as disturbance legacies (Heinselman 1996; Carlson 2011). Despite increased

dominance by aspen and birch, many post-fire stands had at least some shade-

tolerant boreal conifer component. Where ample seed sources existed some of

these species were locally dominant ensuring their continued presence of

patches of these community types on the landscape. Overall succession in the

case of single fire events exhibited multiple successional pathways with a

general shift towards early successional community types. Some stand types

such as red pine and white pine underwent strong convergence to aspen while

others such as jack pine experienced successional divergence to a mix of aspen,

birch and jack pine. Despite increases in dominance following fire, aspen and

paper birch both exhibited relatively week self-replacement and often were as

likely to succeed to each other as to self-replace resulting in divergence at the

stand level.

Multiple disturbances

Changes in composition following multiple disturbances tended to be more

pronounced than those occurring following single disturbances. With few

exceptions, birch and aspen were heavily favored, but not equally, by

combinations of wind and fire or multiple fires within a short period of time.

Intriguingly however, neither birch nor aspen were particularly strong at self-

replacement, often shifting to each other (Figures 3-4, 3-5, 3-6). At the same

time, multiple disturbances largely eliminated boreal conifers that had been among the most dominant community types pre-disturbance.

We observed subtle differences in composition and successional pathways between areas affected by wind followed by single fire and areas affected by wind followed by 2 fires. Both disturbance combinations tended to be heavily dominated by aspen and birch post-disturbance regardless of pre-disturbance composition. Areas affected by wind followed by 2 fires tended to have slightly more aspen and birch and slightly less jack pine and black spruce than areas affected by wind and single fire, but both these disturbance combinations had composition that was more like to each other than to any other disturbance type or combinations. We observed that areas that burned repeatedly tended to have lower fire intensity than areas burned by wind and single fire but also tended to burn more completely. The effect of a second fire in an area already affected by wind and fire was mainly to further reinforce aspen and birch dominance at the expense of boreal conifers but not to dramatically alter successional patterns originating after wind and fire disturbance. Likewise, in instances of multiple fires, but no wind disturbance, we found that the final fire in a sequence tended to reinforce aspen dominance and to a lesser extent paper birch at the expense of jack pine and black spruce.

Despite strong shifts toward aspen and birch community types following multiple disturbances we failed to find significant differences in community dispersion as measured by the PERMDISP procedure. There was a significant decrease in community dispersion for single fire plots, but not for other disturbance types/combinations that we investigated. While the results of our ordination runs indicated strong convergence, the results of PERMDISP tests suggest that although aspen and birch are the dominant community type, stands remain mixed and have not become significantly more homogenous post-disturbance. Differences between PERMDISP results and those of community transition tables can in part be explained by the different spatial scales used by each technique. PERMDISP accounts for dispersion or a measure of beta diversity between plots, while transition tables using hierarchical cluster analysis are aggregated data that show trends at a broader spatial scale. While we found little statistical evidence of convergence occurring at the plot scale, at the landscape scale aspen and birch forest types have greatly increased compared to their pre-disturbance abundance, regardless of their pre-disturbance community type, indicating a landscape-scale successional convergence. Although long-lived conifer species such as black spruce and white cedar are still present in many stands currently dominated by aspen and birch, black spruce and cedar community types have been greatly reduced in areas affected by multiple disturbances. If disturbance frequencies increase and multiple disturbances become more common, long-lived conifer community types may increasingly be

144

restricted to refuge positions such as lowlands and lakeshores where disturbance frequency and severity tend to be lower.

Effects of single and multiple disturbances: Aspen and birch community types

Aspen and paper birch were among the most successful community types across all fires and fire combinations we examined. Paper birch was also very successful following wind disturbance, unlike aspen which declined in dominance following the 1999 windstorm (Figure 3-8). Both community types were present prior to disturbance with aspen typically the second most dominant community type following jack pine.

Despite the large increase in aspen and birch dominance following fire and fire combinations, both birch and aspen often exhibited surprisingly weak self-replacement rates and in many instances birch stands were more likely to succeed to aspen following fire than to birch and vice-versa. The low rate of self-replacement could in theory be due in part to small shifts in composition in mixed stands but on average plots classified as paper birch dominated or aspen dominated were greater than 60% dominated by their nominal species, with the other (either aspen or birch) making up less than 10% of the total stand. The low self-replacement rates of aspen and birch following wind and fire combinations suggest that these species have neutral to negative neighborhood effects

whereby these species are unable to modify their local environment to favor their own regeneration over other species. In this case factors other than pre-fire composition such as seasonal timing of fire (Chapter 2) are likely more useful predictors of post-disturbance composition. One exception to the trend of low self-replacement following fire was paper birch stands affected by single fires. Most of the single fire sites we examined were burned in late season fires that are known to favor paper birch over aspen (Chapter 2). Conversely aspen stands had very high self-replacement in instances of multiple fires, where all samples were from the early season Ham Lake Fire; early season fires tend to favor aspen over paper birch even when accounting for differences in fire severity between early and late season fires (Chapter 2).

Because of narrow moisture and temperature requirements for aspen seedling establishment (Einsphar and Winton 1976; Perala 1990), it is possible that the large increase in aspen documented across burned areas in our study could in part be due to ample moisture following in the spring of 2007 when most post-fire recruitment occurred. Had the period following the 2007 Ham Lake fire been drier, it is possible aspen might have failed to reproduce sexually and been restricted to areas where it could sucker. Without this significant aspen seedling recruitment, overall regeneration may have been sparser and more paper birch dominated. The high severity nature of multiple combined disturbances also suggests that long-distance seed dispersal might be more important than

sprouting or suckering, especially in cases of large infrequent disturbances (Turner et al. 2003) or multiple disturbances within a short period of time.

Red maple community type

Red maple was an uncommon community type prior to disturbance, but increased in abundance following the 1999 windstorm, as it was relatively wind firm (Rich et al 2007) and a well distributed minor component of advanced regeneration across a variety of stand types. Following the fires of 2006-2007 red maple increased in abundance via both basal sprouts and seedlings. Like paper birch, red maple was one of the few community types that increased in dominance across virtually all disturbance types/combinations (Figure 3-8). Although red maple is commonly thought of as a fire sensitive species, our results are similar to at least one other study of combined disturbance in the Lake States that found red maple increased in relative abundance in a clear cut followed by fire (Scheiner et al. 1988). As red maple appears both tolerant of a wide variety of disturbances and is a temperate species well adapted for a warming boreal climate, it appears red maple could be among the most successful species under climate change scenarios that increase both temperatures and future disturbance frequency.

Jack pine community type.

Jack pine was the most common pre-disturbance stand type in our study area, however, representation of jack pine stands decreased after all disturbance types and combinations (Figure 3-8). Jack pine is typically regarded as a pyrophillic species because of its serotinous cones and its well documented tendency to self-replace with high density regeneration following stand-replacing boreal crown fires (Ahlgren 1959, Cayford 1963, Ohmann and Grigal 1979, Heinselman 1996). However, in this study jack pine was notably absent from regeneration in wind disturbed portions of the Cavity Lake and Ham Lake Fire and it was present but declining in dominance in areas experiencing single or multiple fires. In many cases jack pine stands subjected to wind followed by fire failed to regenerate to jack pine and were replaced by either aspen or birch. The paucity of jack pine regeneration following fire documented in this study is counter to the published literature on jack pine silvics and warrants careful examination. We hypothesize several possible explanations for why jack pine failed to regenerate following wind and fire. 1) Windstorm fueled fires may have burned with a greater intensity and duration, and/or the fallen crowns of jack pine may have placed aerially-stored seedbanks in areas of higher fire intensity and duration, either of which could have generated lethal temperatures that destroyed or consumed the serotinous cones and seeds. 2) Mortality of adult trees followed by a 3-8 year period of time until fires occurred may have reduced the viability of jack pine seed such that jack pine failed to regenerate. 3) Other stochastic factors such as

the seasonal timing of fire or unique fire behavior may have created seed bed conditions that placed jack pine at a competitive disadvantage.

There is no doubt that heavily wind-damaged areas of our study had greater fuel loads (Woodall and Nagel 2007) and consequently these areas tended to burn with greater intensity than non-windstorm areas, but it is unclear whether the increased intensity of blowdown-fueled fires alone was enough to cause mortality of jack pine seed. Serotinous jack pine cones are very tolerant of temperatures generated during forest fires and seed mortality typically occurs only when the cones themselves ignite. However, despite the increased temperature and duration of fires in windstorm fuels and proximity of fallen crowns and cones to the most intense part of the fire, field crews collecting data in the aftermath of the fire reported large numbers of open jack pine cones, indicating that windstorm fires did not always burn so hot as to consume all jack pine cones. Nonetheless, it is difficult to rule out the possibility that some jack pine seed was destroyed by fire. The consensus of forest management for jack pine is that burning slash following clear cutting does not typically lead to successful jack pine reproduction unless there are viable seed trees left after harvest because slash fires generally destroy seeds in slash even if they otherwise produce good seedbeds (Chrosciewicz 1959, Benzie 1977, McRae 1979, Chrosciewicz 1990). In our study, the combination of wind followed by fire may have created conditions similar to a clear cut followed by a slash fire without sufficient seed trees, partially explaining the failure of jack pine to regenerate in these areas.

149

Viability of jack pine seed declines with age and may be partially responsible for the failure of jack pine to regenerate following the windstorm fires in our study. Beaufait (1960) in a study of jack pine seed collected from Michigan, found that jack pine seed germination rates average about 76% for 1-2 year old cones, but that germination rates fall as low as 33% for cones 5 years and older. In our study, the majority of adult jack pine trees were killed in the July 4th derecho event. The first fires in our study occurred in 2002, 3 years following the windstorm and the last fires in our study occurred 8 years after the windstorm. There is anecdotal evidence to suggest that jack pine regeneration was more successful in areas that burned 3 years after the windstorm than areas that burned after 8 years. Two prescribed fires, the 2002 Threemile Island burn and the 2002 Magnetic Lake burn, both had relatively good regeneration of jack pine despite being significantly impacted by the 1999 blowdown; of 18 plots classified as jack pine prior to the pre-wind and fire, 10 (55%) remained jack pine post-wind and fire. This rate of self-replacement is closer to that of the single fire stands we observed where jack pine self-replaced on 50% of plots. In contrast, only 23% (n=151) of stands classified as jack pine before the windstorm remained jack pine dominated following burns in the windstorm affected portions of the Ham and Cavity Lake fires of 2006-2007. Although differences in regeneration success between these prescribed fires and the wildfires in our study could be due to differences in fire effects, all of these fires had mean ground fire severity values close to 4, indicating that there was on average, complete consumption of

the litter layer and at least partial consumption of the duff layer. This suggests that the timing of fire following windstorm and hence the viability of jack pine seed, may have played a role in successional outcomes of this study.

One surprising finding was that even in cases of single fire events there was a 37% decline in jack pine dominance. The seasonality of fire in our study may in part explain the decline of jack pine. The vast majority (94.6%) of jack pine plots experiencing single fire events were jack pine plots from the Ham Lake Fire. The Ham Lake Fire burned in May of 2007 before most vegetation had greened up and was very fast moving. As a result, the fire caused little scarification and did not expose large areas of mineral soil that jack pine requires to germinate (Chrosciewicz 1974). Observations of jack pine regeneration following fire in Saskatchewan have shown that consumption of litter and duff can be a critical factor in the success of jack pine regeneration and that light burning may create unfavorable seedbeds for jack pine (Jameson 1961).

Jack pine also declined in dominance in cases of multiple fires within a short period of time, although the reductions in jack pine were not as severe as in cases of wind+fire combinations. We observed jack pine in our study producing non-serotinous cones at 3 years of age although good seed crops and serotinous cones typically take >10 years to develop (Rudolph 1965). If a fire occurs before young trees develop sufficient serotinous cones there is little chance of reseeding

after fire unless significant refugia of surviving jack pine are present. Even in cases where jack pine is old enough to produce sufficient serotinous cones, the re-burn fire may burn with too low of an intensity and merely heat-girdle jack pines without generating sufficient heat to release serotinous cones. Both patterns were observed in our multiple fire sites where jack pine stands that originated after the 1995 Sag Corridor fire were reburned 12 years later by the Ham Lake Fire. Flame lengths were generally very low in this reburned area (<50cm) such that the few serotinous cones that existed at the time of the fire were observed to remain unopened following fire. The lack of sufficient jack pine seed source created conditions favorable for the invasion of light-seeded and long-dispersing aspen and birch. Similar regeneration failure occurred on sites experiencing wind followed by 2 fires where stands of jack pine that survived the windstorm had extremely low self-replacement rates after 2 fires (<15%). Although there have been few observations of jack pine following repeated fires, our results are similar to the observations of Eyre and LeBarron (1944), who noted that fires that occurred before jack pine can produce sufficient seed may convert jack pine stands to "a waste of brush and grass". In addition, our results are similar to those of Johnstone and Chapin (2006) who found that boreal conifer dominated stands in the Yukon and British Columbia were much more likely to succeed to aspen if fires occurred less than 25 years apart.

Red pine/white pine community types.

The failure of the red pine/white pine community type to self-replace after fire (Fig. 2, 8) also warrants some elaboration. Both species are susceptible to wind disturbance and experienced high mortality after the 1999 windstorm (Rich et al. 2007). In addition, both species lack serotinous cones and are largely dependent on episodic and sometimes sporadic mast events that often occur 3-7 years apart; as such they are highly dependent on post-fire survival of scattered mature individuals for successful establishment. In cases of wind+fire combinations, red pine/white pine regeneration was confined to lakeshore areas where scattered mature trees survived both wind and fire, and generally absent elsewhere. Red pine/white pine also declined in cases of single fire events, but not as extensively as in cases of wind and fire combinations. Furthermore, the regeneration data we used did not include surviving mature trees. Ordination runs and hierarchical cluster classifications based on cover data that incorporated surviving mature trees still showed a decline in red pine/white pine dominance (76%), but less than that found with when using regeneration data (95%). Both species are long lived and often take up to 20 years to establish post-fire (Ahlgren 1976). Where suitable microsites exist red pine and especially the more shade tolerant white pine may continue to establish under developing aspen stands.

Black spruce

Black spruce is relatively wind firm, especially when small in size, but larger trees have wind susceptibility similar to other wind vulnerable species like aspen and jack pine (Rich et al. 2007). While black spruce has semi-serotinous cones and is typically a component of post-fire regeneration in the boreal forest it typically is not as dominant post-fire as other fire adapted species such as aspen, birch or jack pine (Heinselman 1996). In this study, we found black spruce to increase in dominance moderately post-wind and decline in dominance post-fire (Fig 8). Similar to other fire adapted conifers in this study, black spruce declined more in instances of multiple disturbances than in single fires. The mechanism of black spruce regeneration failure in these cases is likely driven by the greater severity of windstorm fires and elimination of vulnerable young regeneration in the case of repeatedly burned stands. Our results are similar to those of Johnstone and Chapin who documented the conversion of black spruce stands to aspen following repeated fires in the Yukon Territory, Canada (2006).

Balsam fir

Balsam fir, like black spruce, is relatively wind-firm, especially when small, but vulnerable to wind when large (Rich et. al 2007). As a shade tolerant species, balsam fir was well established throughout pre-disturbance stands in our study. Most stands were greater than 100 years old and had already begun the demographic transition from typically monodominant stands of early successional

154

species to more mixed stands dominated by gap dynamics as shade tolerant advance regeneration succeeds the initial post-fire cohort (Frelich and Reich 1995). While balsam fir was not among the most dominant community types prior to disturbance, it was a well distributed component of early successional stand types. The 1999 windstorm greatly increased balsam fir's dominance on the landscape by selectively removing the remaining early successional jack pine and aspen components of stands and releasing advanced regeneration of fir. The effect of the windstorm was thus to accelerate the normal stand development process and accelerate the normal gap based process of understory reinitiation.

Unlike black spruce, balsam fir is both vulnerable to fire, and lacks fire adaptations such as serotinous cones and is therefore wholly dependent on surviving refuge populations for reestablishment post-fire. In areas burned in single fires balsam fir dominance declined modestly following fire, but declines were steep and dramatic for areas affected by wind-fire combinations. While balsam fir was more dominant post wind (Fig. 8), the increased fire intensity of the windstorm fueled fires left fewer unburned patches and fewer surviving trees, resulting in a loss of balsam fir seed sources. In the case of wind followed by single fires this resulted in a 78% decline in balsam fir dominance and in the case of wind followed by 2 fires balsam fir was practically eliminated (Fig. 2). There was a small increase in dominance following multiple fires as balsam fir was not a community type documented in these stands pre-fire, but post fire there was a

single balsam fir plot so this result could be due to a classification error or colonization of a lightly burned plot by an adjacent unburned fir stand and either way doesn't represent a significant increase in fir dominance.

White cedar

White cedar is both shade tolerant and long-lived, and was the most wind firm species in our study area; 92% of white cedar stands remained white cedar dominated following the 1999 windstorm. Like balsam fir, white cedar was a well distributed component of many stands and was typically an understory component of jack pine, black spruce and especially paper birch stands pre-disturbance. While paper birch was wind firm, the susceptibility of jack pine and large black spruce to wind allowed cedar advanced regeneration to be released in these stands following the 1999 windstorm. The relative stability of existing white cedar stands coupled with the conversion of other stand types to cedar following wind led to a significant increase in cedar dominance in wind affected areas. As cedar is also considered the longest lived species in our study area and has been proposed as a climax community type for the BWCAW landscape (Grigal and Ohman 1975) cedar dominance is likely to increase in the long-term absence of fire.

Although its bark is somewhat thicker than that of black spruce or balsam fir, cedar trees have shallow roots that are easily damaged by fire (Caulkins 1967).

156

Like balsam fir it is largely dependent on survival in unburned refuge areas for re-establishment post fire. Similar to balsam fir, white cedar abundance declined in dominance following single fire events but was largely eliminated as a community type by multiple fires, or wind fire combinations. The mechanism of cedar decline in the case of multiple disturbances is likely a combination of increased fire severity and less unburned area in the case of wind followed by a fire and less unburned area in cases of repeated fires.

Conclusion

All disturbances leave legacies in their wake whether they are material legacies like dead wood, propagules or nutrients or information legacies such as adaptations to disturbance within a community (Johnstone et al. 2016). Single disturbance events, unless of extreme severity or size, tend to leave ample disturbance legacies to ensure continuity of composition (Turner et al. 1998). Disturbances are inherently spatially heterogeneous and tend to leave mosaics that include patches of lightly disturbed and undisturbed areas where even those species ill-adapted to a given disturbance may persist. When two or more disturbances are combined, areas that escaped the first disturbance may not escape a second time. Multiple disturbance events can erode ecosystem resilience by reducing disturbance legacies (Paine et al. 1998; Johnstone et al. 2016). The reduction in disturbance legacies and loss of ecosystem resilience may lead to novel successional outcomes (Paine et al. 1998).

In this study, we documented dramatic shifts in community composition following both single and multiple disturbance events (Figs. 3- 8). Wind disturbance resulted in extensive mortality of mature aspen and jack pine releasing shade tolerant advanced regeneration of black spruce, balsam fir and cedar. Single fires resulted in conversion of many older conifer stands to aspen and birch but there were also significant areas of low severity fire enabling fire sensitive species such as balsam fir and white cedar to survive and often establish new stands of these community types. The multiple disturbance events we observed tended to

158

greatly reduce or eliminate coniferous community types and heavily favor deciduous species capable of long distance seed dispersal and vegetative reproduction. While there was still considerable variation in fire severity of the fires observed in multiple disturbance events, the combination of fires and wind or multiple fires tended to reduce or eliminate conifer seed sources that would likely persist following a single disturbance event.

Because of their relatively long ages to sexual maturity, many boreal conifers, are vulnerable to fire disturbance until the initial post-fire cohort can produce seeds. A second or third fire such as those that occurred on our multiple fire sites can easily eliminate any conifer regeneration and further reduce or eliminate disturbance legacies. In stands affected by multiple disturbances some community types such as jack pine and red pine and white pine were largely eliminated by the loss of disturbance legacies. In the boreal forest where single disturbances on rotation intervals of 50-150 years are common and forests tend to be dominated by serotinous conifers like black spruce and jack pine, a shift in disturbance regimes to one dominated by multiple interacting disturbances could result in conversions of large areas of boreal conifer forests to forests dominated by deciduous species capable of either long distance seed dispersal or vegetative reproduction.

The net effect of multiple disturbances, either multiple fires, or wind-fire combinations, on forest composition in the BWCAW has been the conversion of coniferous stands to deciduous stands (Fig 3-8). Aspen and birch both had dramatic increases in dominance following single fire events but were most prominent in wind-fire combinations and multiple fires within a short period of time (Fig 3-8). This large shift in composition, while not arising from a novel successional pathway, has led to novel composition at the landscape scale, where formerly boreal conifer dominated stands were rapidly converted to deciduous stands. The changes in composition we observed are unusual in that they occurred regardless of pre-disturbance community type and largely ignored the tendency of many boreal forest community types to self-replace following fire. The effects of wind + fire combinations and repeated fires on the BWCAW landscape is similar to the those that occurred outside the BWCAW in northern Minnesota during the big pine logging era (1895-1930) when extensive logging removed pine seed sources and subsequent slash fires eliminated advanced regeneration and further reduced residuals, leading to widespread conversion to aspen and birch community types (Heinselman 1996; Sterns 1997; Friedman and Reich 2005). These changes to the landscape outside the BWCAW have proven persistent (Friedman and Reich 2005) and it seems likely that the conversion of conifer forests to aspen and birch within the BWCAW is also likely to persist in the absence of the historic disturbance regime.

Both the direct effects of climate change, including both temperature and reduced soil moisture availability (Rich et al. 2015), and increased disturbance frequency are likely to favor boreal deciduous species over boreal coniferous species (Johnstone and Chapin 2006), although in ecotonal forests more southerly temperate species like red maple will benefit the most (Reich et al. 2015). While advanced regeneration of boreal conifer species such as black spruce and balsam fir are somewhat wind-firm (Rich et al. 2007) and generally favored by increasing wind disturbance, their vulnerability to fire in the case of balsam fir and short interval fires (Brown and Johnstone 2006) or wind-fire combinations in the case of black spruce, combined with their sensitivity to the physiological stresses of climate change (Reich et al. 2015), makes these species especially vulnerable to both the direct and indirect effects of climate change.

Aspen and birch are heavily favored by increasing disturbance frequency and both are better adapted than black spruce or balsam fir to the direct effects of climate change, but these species are still vulnerable to a warming climate (Reich and colleagues, unpublished). Along the prairie forest border, quaking aspen has experienced large diebacks due to extreme drought events that are thought likely to become increasingly common under climate change (Michaelian et al. 2011). In the Lake states, paper birch has already experienced large diebacks that are thought to be the result of interactions between climate stress and pest and pathogen activity (Jones et al. 1992). While aspen and birch may

be favored over jack pine, black spruce and balsam fir by increasing disturbances and may increase in dominance in the short term, with increased warming they too may experience increased stress and dieback.

Interactions between disturbances, climate change and forest communities may be further modified by herbivory and invasive species. Red maple was not an abundant community type prior to disturbance, but increased in dominance across a range of disturbances including wind alone, single fire and wind+fire combinations. As a temperate species, red maple is likely to become more dominant in the boreal forest under a warming climate, but in areas of high herbivore density, preferential browse of temperate species by ungulates may impede their migration northward (Fisichelli et al. 2012). In the upper great lakes region, areas of high deer density are often correlated with invasive plant species (Russel et al. 2017) and there is evidence that white tailed deer and invasive earthworms can have synergistic negative impacts on native forbs and tree seedlings while facilitating invasive plants (Fisichelli et al. 2013; Dávalos et al. 2015). While white tailed deer are not currently abundant within the BWCAW, but a warming climate and in particular, milder winters and shallower snowpack could increase their impact on temperate species that would otherwise be favored by the combination of increased disturbance frequency and a warming climate. Invasive earthworms currently have a very limited distribution within the BWCAW (Frelich and colleagues unpublished) and may be somewhat limited by

the often coarse and rocky soils of the BWCAW and may have less potential for impact on vegetation than white tailed deer.

To successfully manage forests in the face of climate change, managers will need to consider both a species potential physiological tolerances to warmer temperatures and their ability to adapt and tolerate changing disturbance regimes. Unfortunately, except for red maple, all the species in our study that increased in dominance following multiple disturbances, are also predicted and observed to be sensitive to the warmer temperatures and increased droughts that are likely under climate change (Handler et al. 2014, Fisichelli et al. 2012, Reich et al. 2015). Without assisted migration, modulation of future disturbance regimes or meaningful reductions in emissions, the forests of the BWCAW and the broader southern boreal region may be subject to forest dieback, loss of diversity and resilience and potential loss of ecosystem services (Frelich and Reich 2009).

With both fire and wind likely to increase in frequency over the next century, land managers need to take changing disturbance regimes into account when developing climate adaptation plans (Handler et al. 2014). Our results suggest that fast growing ruderal species rapidly expand following multiple disturbances and that to maintain complexity on a landscape scale, managers will need to find

ways to maintain refugia populations of species that are vulnerable to multiple

disturbances as well as to climate change itself.

Table 3-1. Major stand replacing disturbance events occurring within the Eastern BWCAW and adjoining Superior National Forest lands from 1974 through 2007. Total number of plots was 1086 but because some disturbances over lapped spatially some plots experienced more than one disturbance event.

Disturbance	Year	Size (Ha)	Description	Number of Plots
Prayer Lake Fire	1974	400	Human ignited wildfire	11
Saganaga Corridor Fire	1995	5100	Human ignited wildfire that reburned the majority of the area affected by the 1974 Prayer Lake Fire	38
BWCA Derecho	1999	193000	Extreme wind event producing straight line winds in excess of 190km/hr	627
BWCAW Fuel Reduction Treatments	2002-2005	1500	Prescribed fires initiated by the Superior National Forest aimed at reducing 100 hour fuels and creating barriers to fire spread within portions of the BWCAW heavily impacted by the 1999 BWCA Derecho.	108
Cavity Lake Fire	2006	10000	Lightning ignited wildfire that burned areas heavily impacted by the 1999 BWCA Derecho	262
Red Eye Lake Fire	2006	1650	Lightning ignited wildfire that burned areas largely unaffected by the 1999 BWCA Derecho	32
Famine Lake Fire	2006	1000	Lightning ignited wildfire that burned areas largely unaffected by the 1999 BWCA Derecho	61
Ham Lake Fire	2007	30000	Human ignited wildfire that reburned areas previously burned by the 1974 Prayer Lake Fire and 1995 Saganaga Corridor Fire. The fire also burned areas previously impacted by the 1999 BWCA Derecho and the fuel reduction burns of 2002-2005. The fire also burned some stands that largely escaped the impacts of the 1999 Derecho.	297

Table 3-2. Transition table for areas experiencing wind disturbance. Transitions reflect changes in community composition 1 year after wind disturbance.

| | | 2000 Community Type, Post-Wind | | | | | | | | Pre-Wind % of landscape | Post-Wind % of landscape | % change across landscape | #of plots 1999 (n=479) | #of plots 2000 (n=479) |
		Aspen	Jack Pine	Paper Birch	Red Pine/ White Pine	Black Spruce	Red Maple	White Cedar	Balsam Fir					
1999 Community Type Pre-Wind Disturbance	Aspen	25.5%	2.9%	21.6%	0.0%	5.9%	5.9%	6.9%	31.4%	21.3%	8.1%	-61.8%	102	39
	Jack Pine	5.0%	41.4%	15.5%	0.0%	17.7%	1.7%	11.0%	7.7%	37.8%	16.5%	-56.4%	181	79
	Paper Birch	0.0%	0.0%	74.2%	0.0%	6.5%	0.0%	6.5%	12.9%	6.5%	20.7%	219.4%	31	99
	Red Pine/ White Pine	0.0%	0.0%	11.1%	37.0%	14.8%	0.0%	14.8%	22.2%	5.6%	2.1%	-63.0%	27	10
	Black Spruce	1.2%	0.0%	27.2%	0.0%	53.1%	2.5%	11.1%	4.9%	16.9%	18.6%	9.9%	81	89
	Red Maple	0.0%	0.0%	0.0%	0.0%	0.0%	100.0%	0.0%	0.0%	1.7%	4.0%	137.5%	8	19
	White Cedar	0.0%	4.2%	0.0%	0.0%	4.2%	0.0%	91.7%	0.0%	5.0%	13.4%	166.7%	24	64
	Balsam Fir	12.0%	0.0%	4.0%	0.0%	4.0%	0.0%	0.0%	80.0%	5.2%	16.7%	220.0%	25	80

166

Table 3-3. Transition table for areas experiencing single fires

| | | 2012 Community Type, Post-Fire | | | | | | | | | | | |
		Aspen	Jack Pine	Paper Birch	White Pine/ Red Pine	Black Spruce	Red Maple	White Cedar	Balsam Fir	% of Landscape Pre-Fire	% of Landscape Post-Fire	% Change Across Landscape	#of Plots Pre-Fire (n= 233)	#of Plots Post-Fire (n= 233)
2006 Community Type Pre-Fire	Aspen	42.9%	0.0%	42.9%	0.0%	14.3%	0.0%	0.0%	0.0%	3.0%	24.9%	728.6%	7	58
	Jack Pine	21.1%	50.0%	21.1%	0.0%	2.6%	2.6%	0.0%	2.6%	16.3%	10.3%	-36.8%	38	24
	Paper Birch	24.1%	3.7%	61.1%	0.0%	0.0%	0.0%	1.9%	9.3%	23.2%	38.2%	64.8%	54	89
	White Pine/ Red Pine	65.2%	0.0%	4.3%	4.3%	13.0%	0.0%	4.3%	8.7%	9.9%	0.4%	-95.7%	23	1
	Black Spruce	8.7%	4.3%	43.5%	0.0%	21.7%	0.0%	6.5%	15.2%	19.7%	8.2%	-58.7%	46	19
	Red Maple	0.0%	0.0%	50.0%	0.0%	0.0%	50.0%	0.0%	0.0%	0.9%	0.9%	0.0%	2	2
	White Cedar	14.9%	0.0%	42.6%	0.0%	6.4%	0.0%	34.0%	2.1%	20.2%	9.0%	-55.3%	47	21
	Balsam Fir	50.0%	6.3%	18.8%	0.0%	6.3%	0.0%	0.0%	18.8%	6.9%	8.2%	18.8%	16	19

Table 3-4a. Net Transition table for changes in composition following wind and fire disturbance.

		2000 Community Type, Post-Wind Disturbance								% of landscape Pre-Wind	% of landscape Post-Wind	% change across landscape	#of Plots Pre-Wind (n=370)	#of plots Post-Wind (n=370)
		Aspen	Jack Pine	Paper Birch	Red Pine/ White Pine	Black Spruce	Red Maple	White Cedar	Balsam Fir					
1999 Community Type Pre-Wind Disturbance	Aspen	22.6%	2.2%	23.7%	0.0%	5.4%	5.4%	7.5%	33.3%	25.1%	7.3%	-71.0%	93	27
	Jack Pine	2.8%	45.1%	16.9%	0.0%	16.2%	2.1%	10.6%	6.3%	37.0%	17.6%	-52.6%	137	65
	Paper Birch	0.0%	0.0%	74.1%	0.0%	7.4%	0.0%	7.4%	11.1%	7.0%	22.4%	219.2%	26	83
	Red Pine/ White Pine	0.0%	0.0%	8.7%	34.8%	13.0%	0.0%	17.4%	26.1%	5.7%	1.9%	-66.7%	21	7
	Black Spruce	1.9%	0.0%	31.5%	0.0%	44.4%	1.9%	14.8%	5.6%	13.5%	14.6%	8.0%	50	54
	Red Maple	0.0%	0.0%	0.0%	0.0%	0.0%	100.0%	0.0%	0.0%	1.1%	3.5%	225.0%	4	13
	White Cedar	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	100.0%	0.0%	5.7%	14.9%	161.9%	21	55
	Balsam Fir	5.6%	0.0%	5.6%	0.0%	0.0%	0.0%	0.0%	88.9%	4.9%	17.8%	266.7%	18	66

Table 3-4b. Net Transition table for changes in composition following wind and fire disturbance.

| | | 2012 Community Type, Post-Fire+Wind Disturbance | | | | | | | | % of landscape Pre-Fire/ Post-Wind | % of landscape Post-Wind+ Fire | % change across landscape | #of Plots Pre-Fire/ Post-Wind (n=370) | #of plots Post-Fire (n=370) |
		Aspen	Jack Pine	Paper Birch	Red Pine/ White Pine	Black Spruce	Red Maple	White Cedar	Balsam Fir					
2000 Community Type, Post-Wind Disturbance	Aspen	51.9%	0.0%	40.7%	0.0%	3.7%	3.7%	0.0%	0.0%	7.3%	59.7%	718.5%	27	221
	Jack Pine	38.5%	38.5%	15.4%	0.0%	1.5%	6.2%	0.0%	0.0%	17.6%	3.8%	-46.2%	65	35
	Paper Birch	66.3%	2.4%	27.7%	0.0%	0.0%	2.4%	0.0%	1.2%	22.4%	6.8%	-8.4%	83	76
	Red Pine/ White Pine	57.1%	0.0%	28.6%	14.3%	0.0%	0.0%	0.0%	0.0%	1.9%	14.9%	-85.7%	7	1
	Black Spruce	48.1%	9.3%	25.9%	0.0%	9.3%	3.7%	0.0%	3.7%	14.6%	1.1%	-79.6%	54	11
	Red Maple	53.8%	0.0%	7.7%	0.0%	0.0%	38.5%	0.0%	0.0%	3.5%	7.0%	61.5%	13	21
	White Cedar	65.5%	5.5%	18.2%	0.0%	1.8%	7.3%	1.8%	0.0%	14.9%	1.9%	-98.2%	55	1
	Balsam Fir	81.8%	0.0%	7.6%	0.0%	4.5%	4.5%	0.0%	1.5%	17.8%	9.7%	-93.9%	66	4

Table 3-5a. Transition table for areas experiencing wind followed by 2 fires. Transitions in this table are those occurring following wind.

		2000 Community Type, Post-Wind Disturbance												
		Aspen	Jack Pine	Paper Birch	Red Pine/ White Pine	Black Spruce	Red Maple	White Cedar	Balsam Fir	% of landscape Pre-Wind	% of landscape Post-Wind	% change across landscape	#of Plots Pre-Wind (n=370)	#of plots Post-Wind (n=370)
1999 Community Type Pre-Wind Disturbance	Aspen	33.3%	16.7%	0.0%	0.0%	16.7%	16.7%	0.0%	16.7%	11.8%	11.8%	0.0%	6	6
	Jack Pine	18.2%	18.2%	4.5%	0.0%	27.3%	0.0%	22.7%	9.1%	45.1%	13.7%	-69.6%	22	6
	Paper Birch	0.0%	0.0%	100.0%	0.0%	0.0%	0.0%	0.0%	0.0%	3.9%	15.7%	300.0%	2	7
	Red Pine/ White Pine	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	NA	0	0
	Black Spruce	0.0%	0.0%	25.0%	0.0%	56.3%	6.3%	6.3%	6.3%	33.3%	31.4%	-5.9%	16	16
	Red Maple	0.0%	0.0%	0.0%	0.0%	0.0%	100.0%	0.0%	0.0%	2.0%	5.9%	200.0%	1	3
	White Cedar	0.0%	50.0%	0.0%	0.0%	0.0%	0.0%	50.0%	0.0%	3.9%	13.7%	250.0%	2	7
	Balsam Fir	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	100.0%	3.9%	11.8%	200.0%	2	6

Table 3-5b. Transition table for areas experiencing wind followed by 2 fires. Transitions in this table are those occurring following 2 fires.

		2012 Community Type, Post-2 Fires+Wind Disturbance								% of landscape Pre-Fire/ Post-Wind	% of landscape Post-Wind+2 Fires	% change across landscape	#of plots Post-Wind/ Pre-Fire (n=51)	#of plots after Wind+2Fires (n=51))
		Aspen	Jack Pine	Paper Birch	Red Pine/ White Pine	Black Spruce	Red Maple	White Cedar	Balsam Fir					
2000 Community Type, Post-Wind Disturbance	Aspen	33.3%	16.7%	50.0%	0.0%	0.0%	0.0%	0.0%	0.0%	11.8%	56.9%	383.3%	6	29
	Jack Pine	66.7%	16.7%	0.0%	0.0%	0.0%	0.0%	16.7%	0.0%	11.8%	5.9%	-50.0%	6	3
	Paper Birch	42.9%	0.0%	57.1%	0.0%	0.0%	0.0%	0.0%	0.0%	13.7%	25.5%	85.7%	7	13
	Red Pine/ White Pine	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	NA	0	0
	Black Spruce	75.0%	0.0%	12.5%	0.0%	6.3%	0.0%	6.3%	0.0%	31.4%	2.0%	-93.8%	16	1
	Red Maple	33.3%	0.0%	0.0%	0.0%	0.0%	66.7%	0.0%	0.0%	5.9%	3.9%	-33.3%	3	2
	White Cedar	57.1%	0.0%	28.6%	0.0%	0.0%	0.0%	14.3%	0.0%	13.7%	5.9%	-57.1%	7	3
	Balsam Fir	50.0%	16.7%	33.3%	0.0%	0.0%	0.0%	0.0%	0.0%	11.8%	0.0%	-100.0%	6	0

Table 3-6. Transition table for areas experiencing 2 or 3 fires. 2006 time-step is the community composition following either the 1995 Sag Corridor Fire, 1995 Sag Corridor and the 1974 Prayer Lake Fire, or prescribed fires in 2002-04. 2012 time-step is following the 2007 Ham Lake Fire and one of the previously mentioned fire scenarios.

		2012 Community Type, Post-Ham Lake Fire								Pre- Ham Lake Fire % of landscape	Post- ham Lake Fire % of landscape	% change across landscape	#of plots 2000 (n=69)	#of plots 2012 (n=69)
		Aspen	Jack Pine	Paper Birch	Red Pine/ White Pine	Black Spruce	Red Maple	White Cedar	Balsam Fir					
2006 Community Type, Pre-Ham Lake Fire	Aspen	84.6%	0.0%	7.7%	0.0%	7.7%	0.0%	0.0%	0.0%	20.3%	57.8%	184.6%	13	37
	Jack Pine	56.3%	31.3%	12.5%	0.0%	0.0%	0.0%	0.0%	0.0%	50.0%	17.2%	-65.6%	32	11
	Paper Birch	0.0%	0.0%	100.0%	0.0%	0.0%	0.0%	0.0%	0.0%	1.6%	21.9%	1300.0%	1	14
	White Pine/Red Pine	0.0%	0.0%	100.0%	0.0%	0.0%	0.0%	0.0%	0.0%	1.6%	0.0%	-100.0%	1	0
	Black Spruce	43.8%	6.3%	25.0%	0.0%	12.5%	6.3%	0.0%	6.3%	25.0%	6.3%	-75.0%	16	4
	Red Maple	NA	NA	NA	NA	NA	NA	NA	NA	0.0%	1.6%	NA	0	1
	White Cedar	16.7%	0.0%	50.0%	0.0%	16.7%	0.0%	16.7%	0.0%	9.4%	1.6%	-83.3%	6	1
	Balsam Fir	NA	NA	NA	NA	NA	NA	NA	NA	0.0%	1.6%	NA	0	1

Figure 3-1. Pre- and post-disturbance community composition by disturbance type/combination.
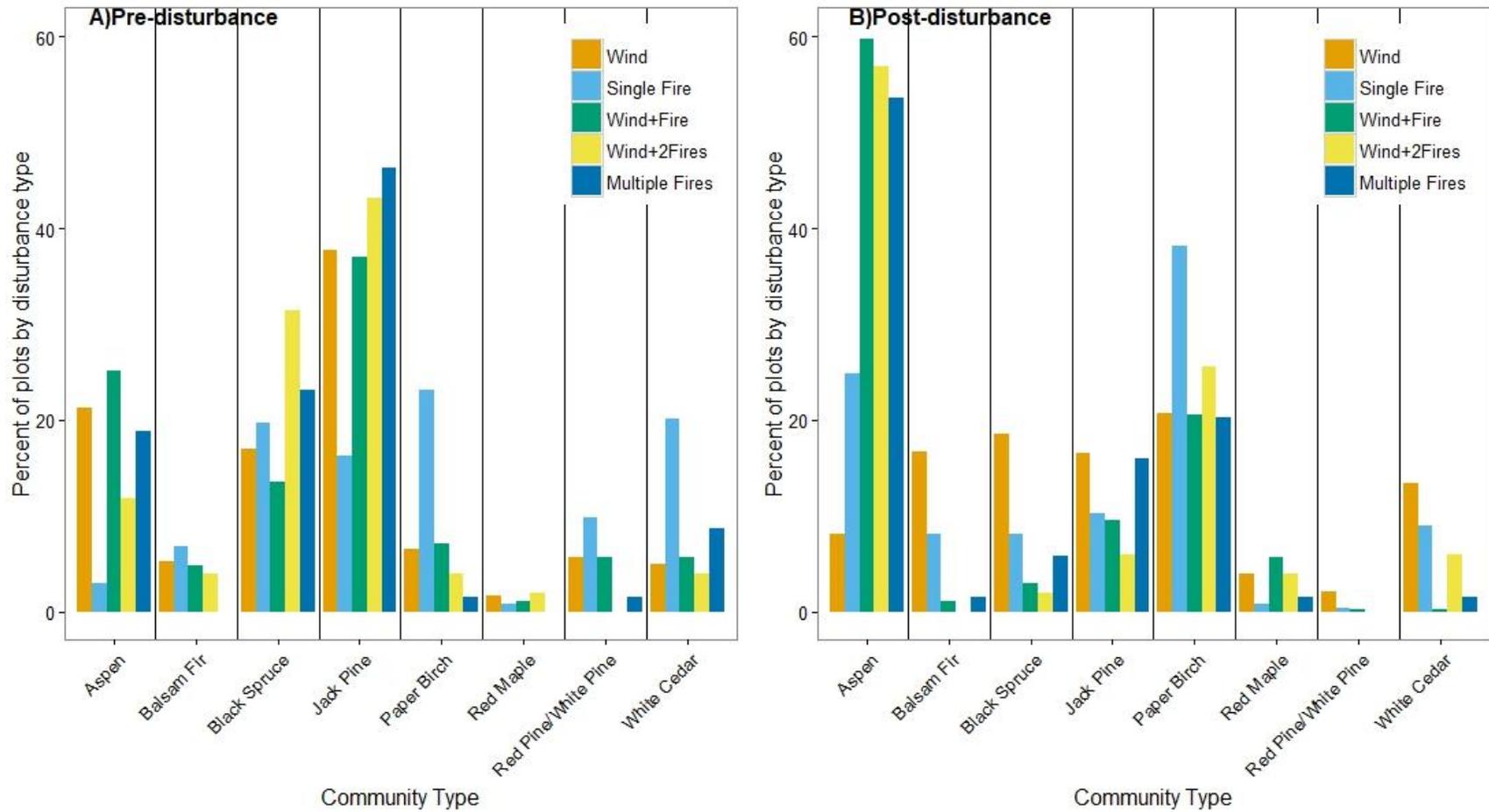
Figure 3-2. Change in community composition by disturbance type or disturbance combination.
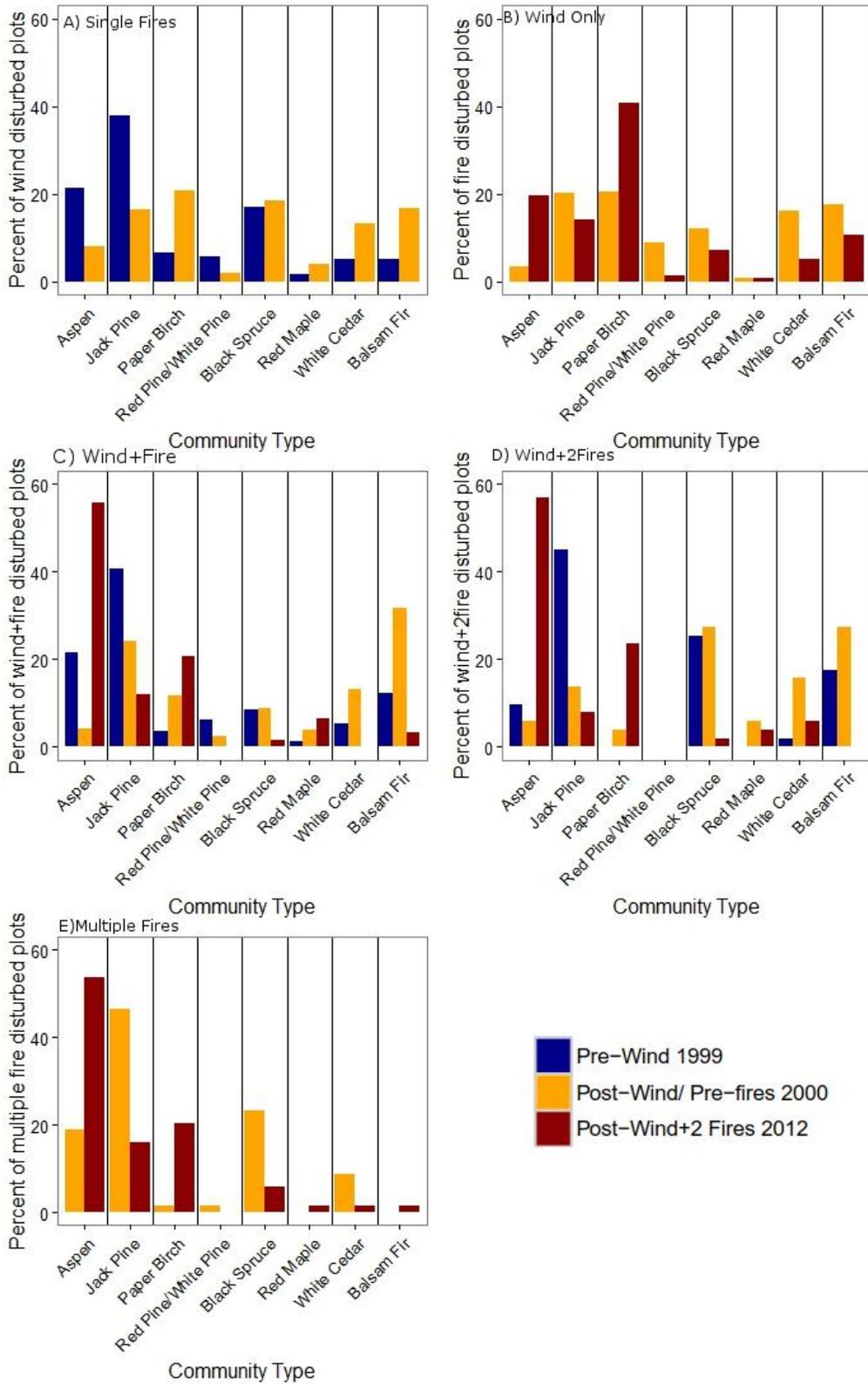
Figure 3-3. Community transitions before and after wind disturbance sorted by pre-wind community type. Colors represent community type following disturbance, symbols represent position of plots in ordination space post-wind, origins represent position in ordination space before wind. All panels are facets of the same overall ordination solution.
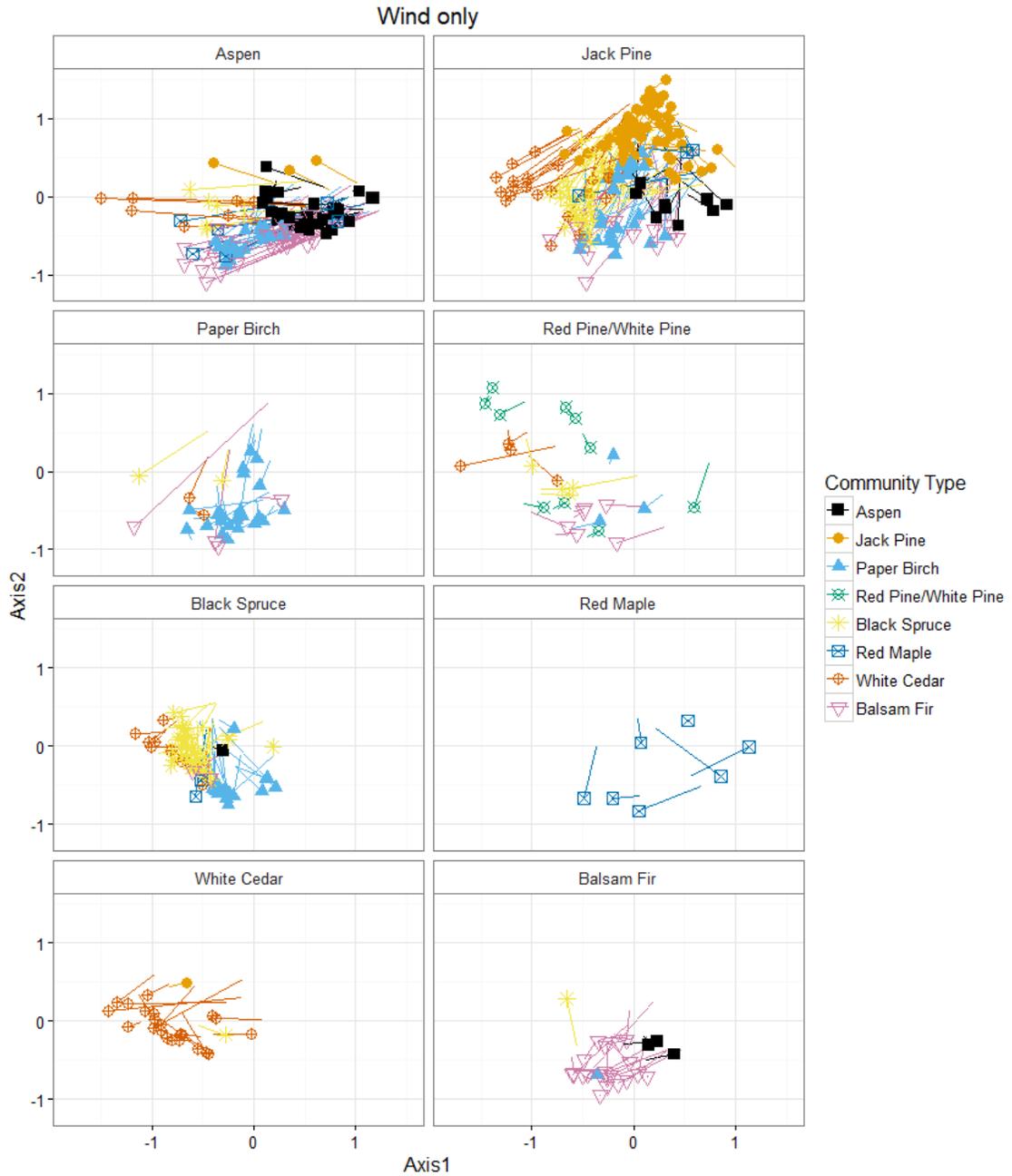
Figure 3-4. Community transitions before and after fire for plots experiencing single fires sorted by pre-fire community type. Colors represent community type following disturbance. All panels are facets of the same overall ordination solution.
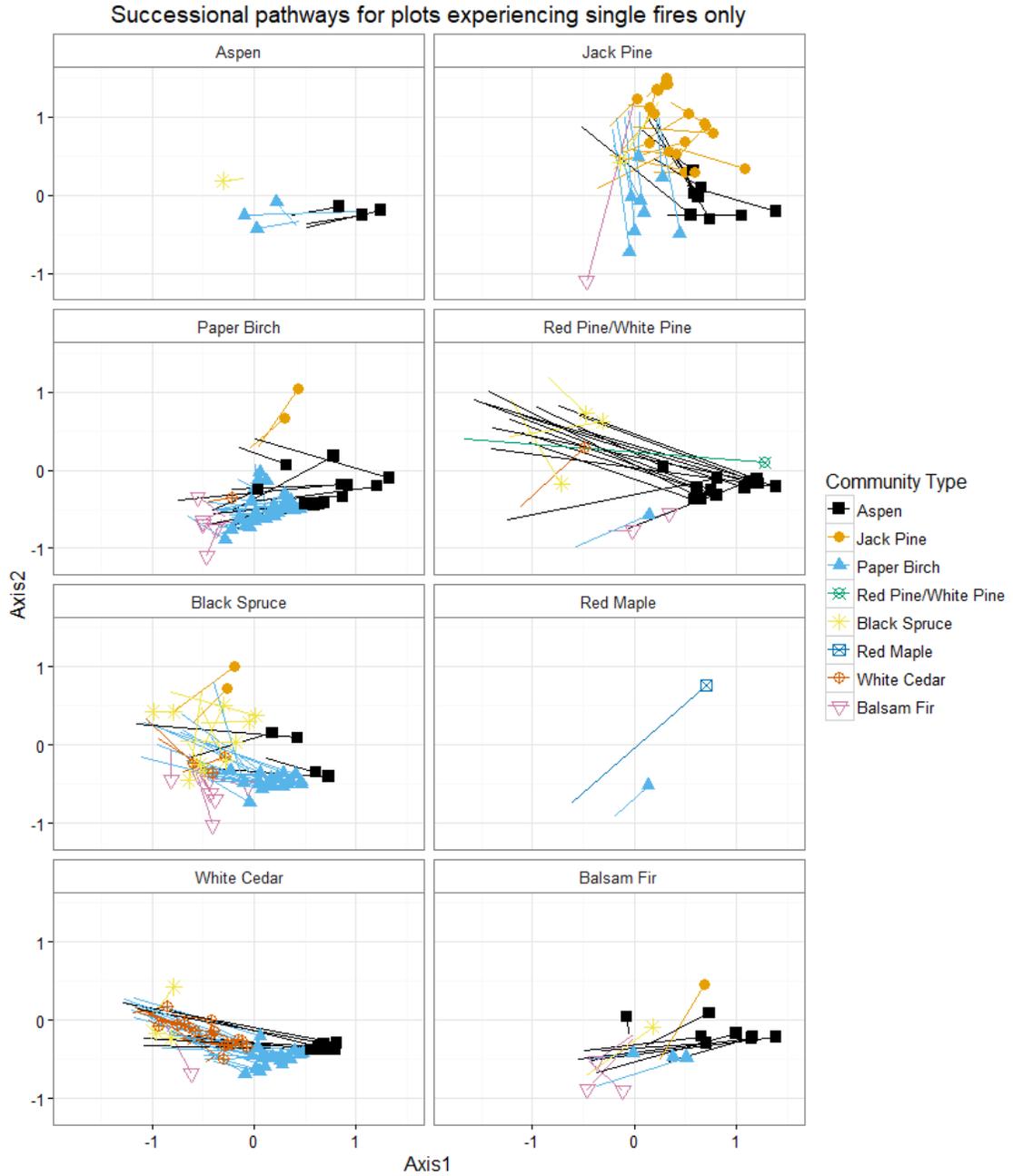
Figure 3-5. Community transitions for plots experiencing wind followed by fire sorted by pre-disturbance community type. A) Change in community composition following the 1999 windstorm sorted by the pre-wind community type. B) Change in community composition after either the 2006 Cavity Lake Fire, or the 2007 Ham Lake Fire sorted by the community type after the 1999 windstorm. Colors represent community type following disturbance. All panels are facets of the same overall ordination solution.

A
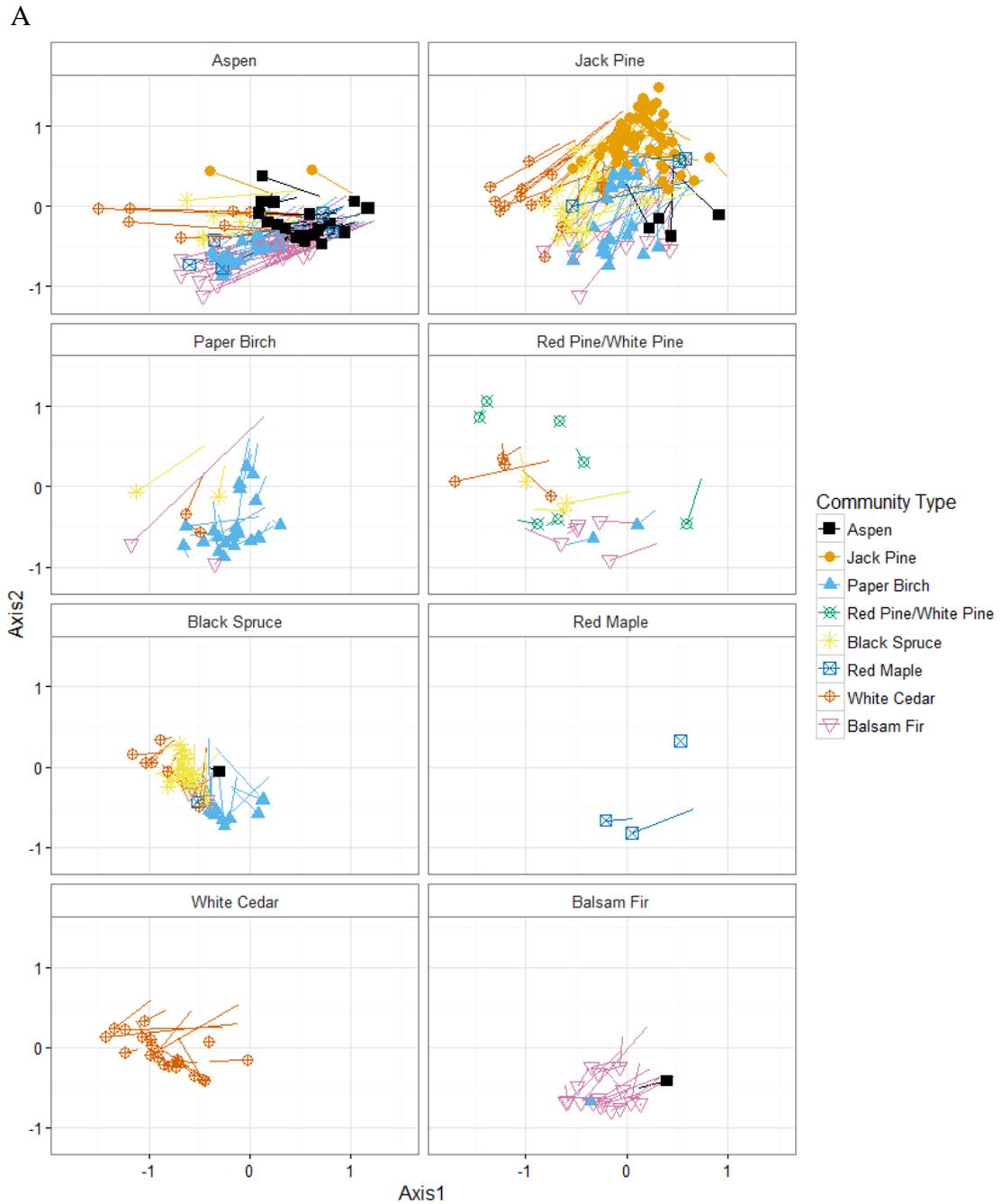
B
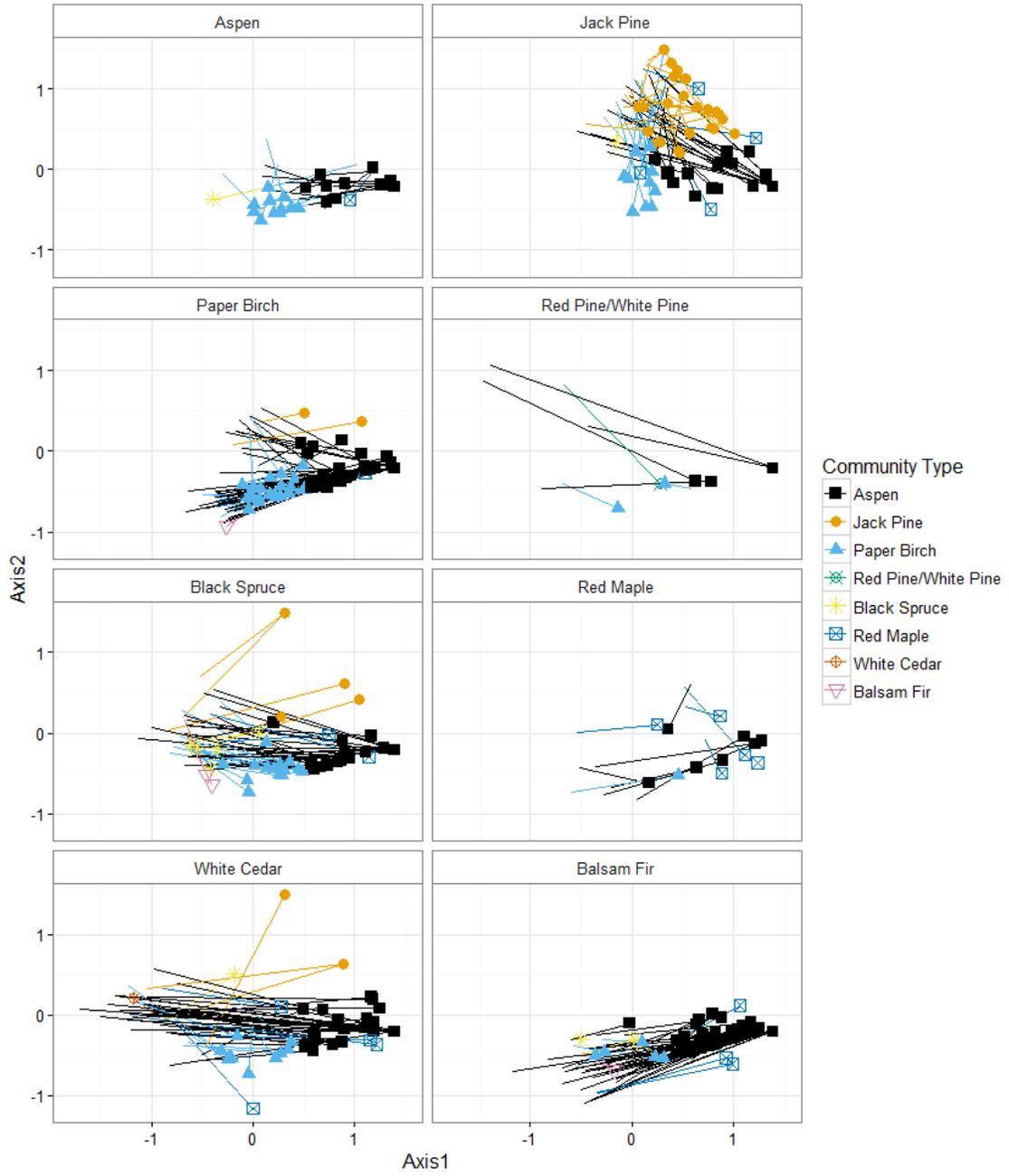
Figure 3-6. Community transitions for plots experiencing wind followed by 2 fires. A) Community transitions following the 1999 windstorm sorted by the community type prior to wind disturbance. B) Community transitions following prescribed fires in 2002-04 followed by the Ham Lake Fire of 2007 sorted by the community type prior to fire disturbance. Colors represent community type following disturbance. All panels are facets of the same overall ordination solution.

B

Aspen

Jack Pine

Paper Birch

Black Spruce

Red Maple

White Cedar

Balsam Fir

Axis2

Axis1

Community Type
- Aspen
- Jack Pine
- Paper Birch
- Red Pine/White Pine
- Black Spruce
- Red Maple
- White Cedar
- Balsam Fir
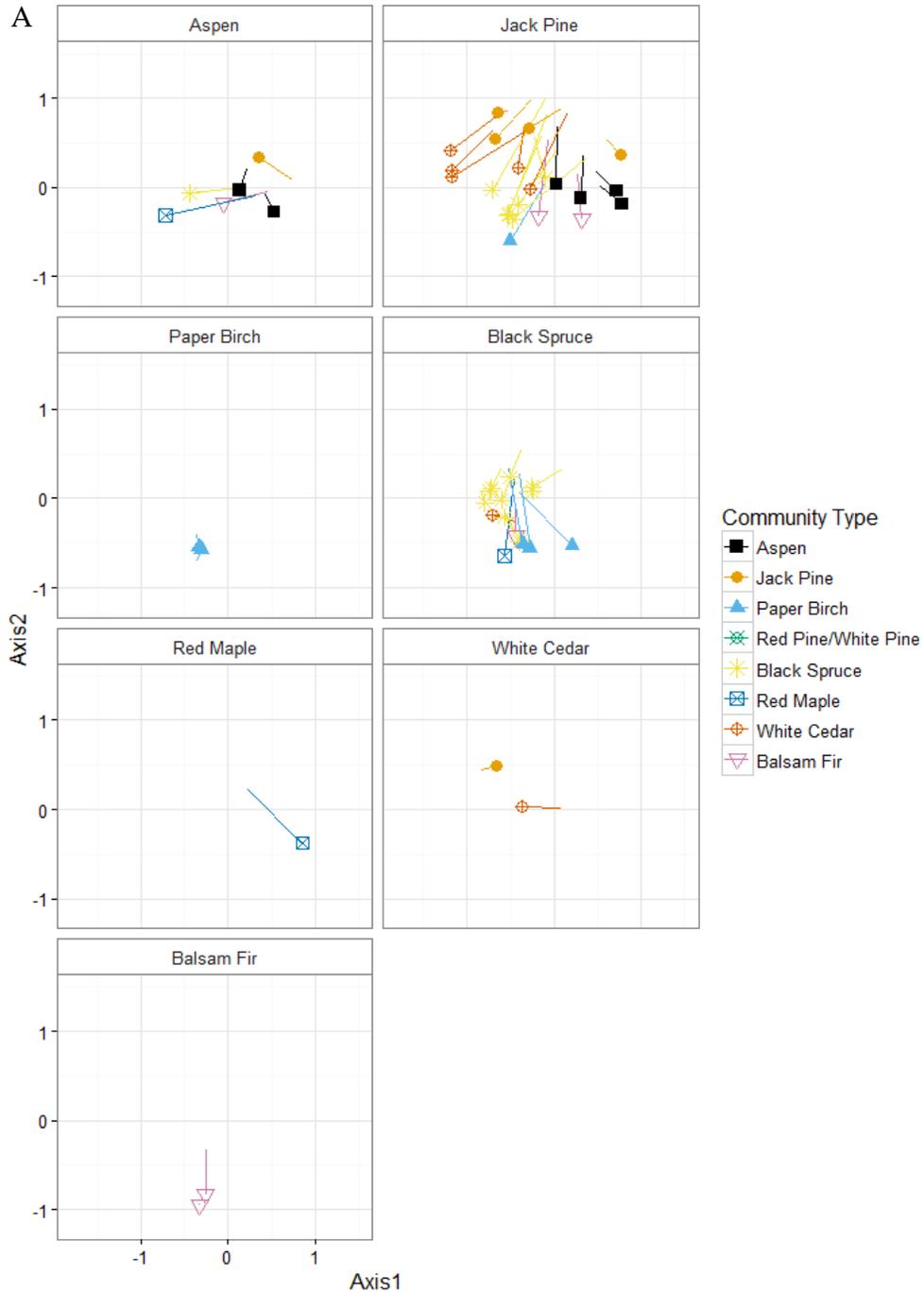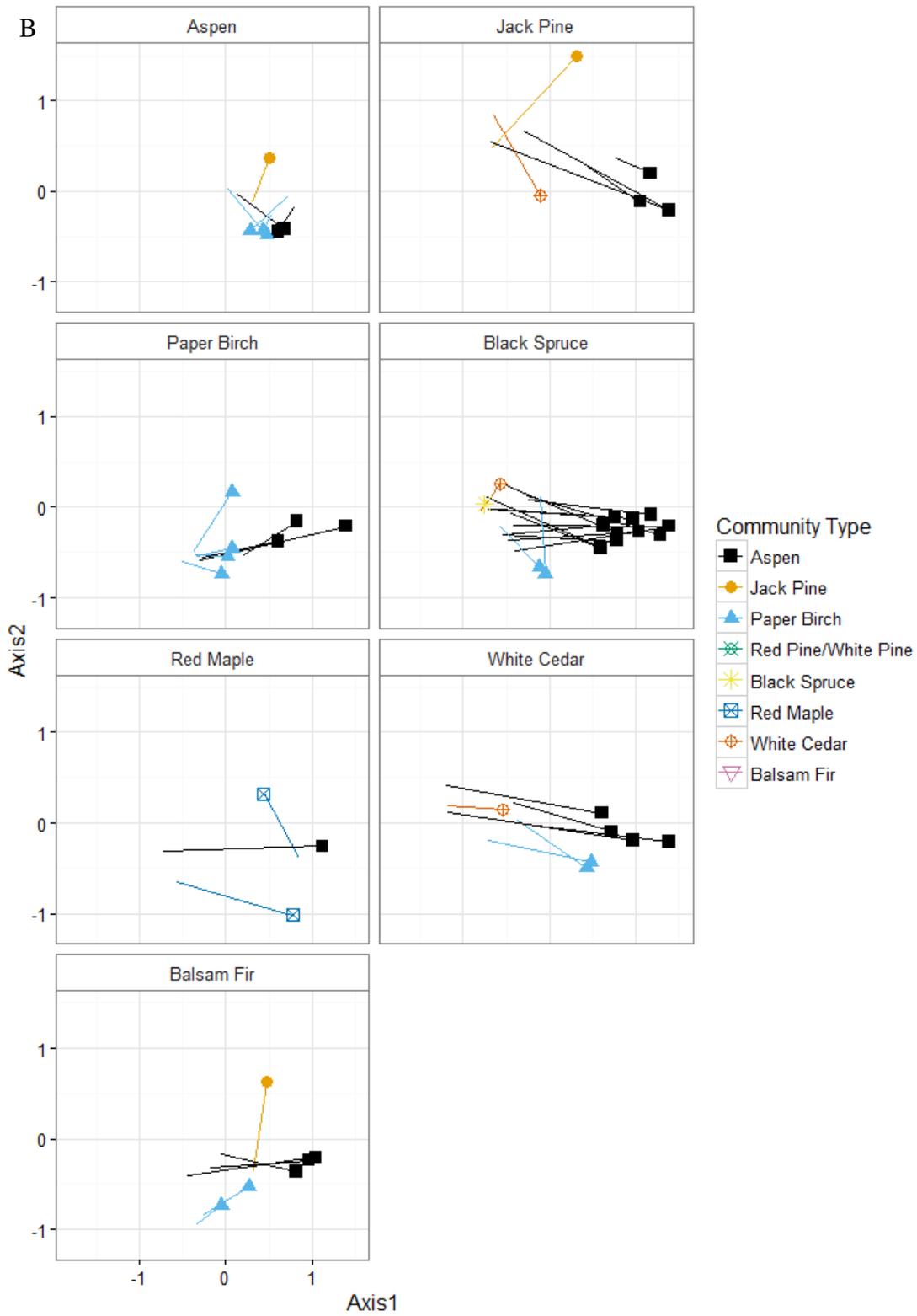
Figure 3-7. Community transitions following the Ham Lake Fire (2007) for plots previously experiencing fires in 1995, 1974 and 1995 or 2002-2004 (but no wind disturbance). Colors represent community type following disturbance. All panels are facets of the same overall ordination solution.
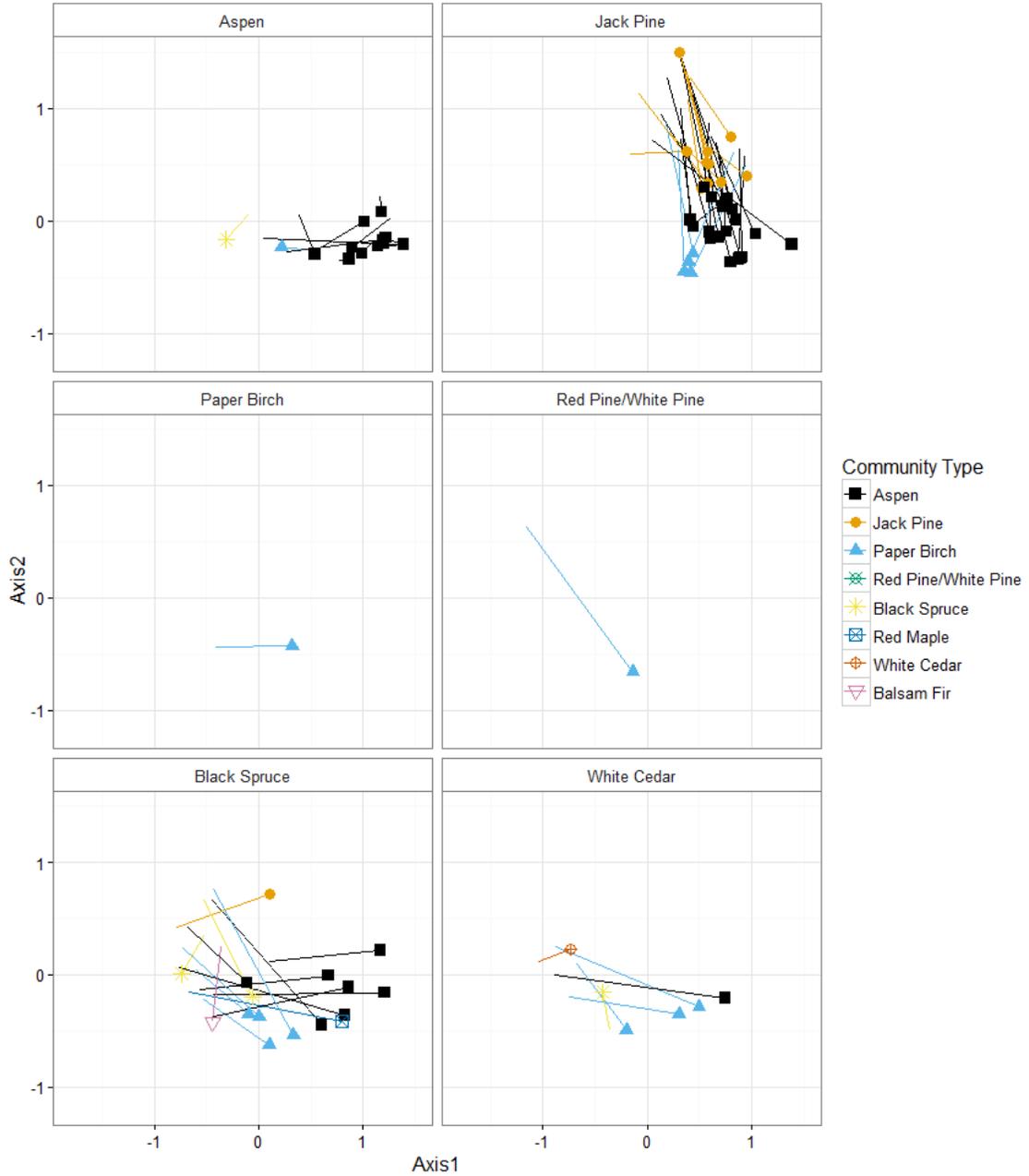
Figure 3-8. Net change in community type dominance by disturbance type.
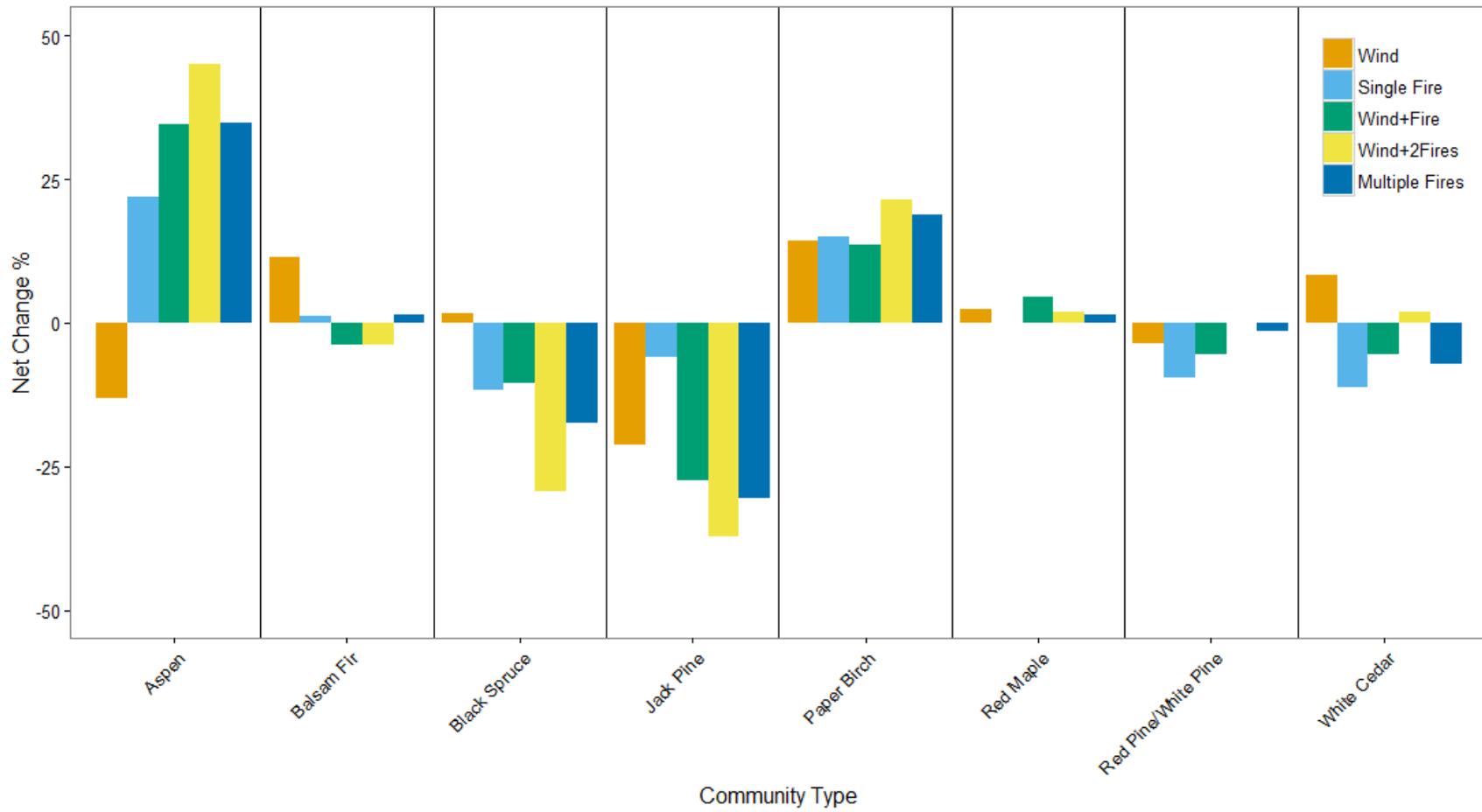
Bibliography

Ahlgren, C. E. 1959. Some effects of fire on forest reproduction in northeastern Minnesota. J. Forestry 57: 194-200

Ahlgren, C. E. 1976. Regeneration of red pine and white pine following wildfire and logging in northeastern Minnesota. Journal of Forestry 74:135-140.

Anderson, M. J. 2001. A new method for non-parametric multivariate analysis of variance. Austral Ecology 26:32-46.

Balshi, M. S., A. D. McGuire, P. Duffy, M. Flannigan, D. W. Kicklighter, and J. Melillo. 2009. Vulnerability of carbon storage in North American boreal forests to wildfires during the 21st century. Global Change Biology 15:1491-1510.

Beaufait, W. R. 1960. Some effects of high temperatures on the cones and seeds of jack pine. Forest Science 6:194-198.

Benzie, J. W. 1977. Manager's handbook for jack pine in the north central states. General Technical Report NC-32. St. Paul, MN: U.S. Dept. of Agriculture, Forest Service, North Central Forest Experiment Station

Beverly, J. L., and D. L. Martell. 2005. Characterizing extreme fire and weather events in the Boreal Shield ecozone of Ontario. Agricultural and Forest Meteorology 133:5-16.

Brown, C. D., & Johnstone, J. F. (2012). Once burned, twice shy: Repeat fires reduce seed availability and alter substrate constraints on Picea mariana regeneration. Forest Ecology and Management, 266: 34-41.

Buckman, R. E. 1964. Effects of prescribed burning on hazel in Minnesota. Ecology 45:626-629.

Buma, B., and C. Wessman. 2011. Disturbance interactions can impact resilience mechanisms of forests. Ecosphere 2(5):art64.

Carlson, D. J., P. B. Reich, and L. E. Frelich. 2011. Fine-scale heterogeneity in overstory composition contributes to heterogeneity of wildfire severity in southern boreal forest. Journal of Forest Research 16:203-214.

Caulkins, H. L., Jr. 1967. The ecology and reproduction of northern white-cedar. Masters Thesis. University of Michigan School of Natural Resources, Ann Arbor. 70 p.

Cayford, J. 1963. Some factors influencing jack pine regeneration after fire in southeastern Manitoba. Government of Canada, Department of Forestry, Forest Research Laboratory, Winnipeg, Manitoba. Department of Forestry Publication 1016. 16 p.

Chen, H. Y., and A. R. Taylor. 2012. A test of ecological succession hypotheses using 55-year time-series data for 361 boreal forest stands. Global Ecology and Biogeography 21:441-454.

Chrosciewicz, Z. 1959. Controlled burning experiments on jack pine sites. Government of Canada, Department of Northern Affairs and National Resources, Forestry Branch, Ontario Region, Ottawa, Ontario. Forest Research Division Technical Note 72. 19 p.

Chrosciewicz, Z. 1974. Evaluation of fire-produced seedbeds for jack pine regeneration in central Ontario. Canadian Journal of Forest Research 4:455-457.

Chrosciewicz, Z. 1986. Foliar moisture content variations in four coniferous tree species of central Alberta. Canadian Journal of Forest Research 16:157-162.Fauria, M. M., and E. A. Johnson. 2008. Climate and wildfires in the North American boreal forest. Philosophical Transactions of the Royal Society B-Biological Sciences 363:2317-2329.

Chrosciewicz, Z. 1990. Site conditions for jack pine seeding. The Forestry Chronicle 66:579-584.

Clements, F. E. 1916. Plant succession: an analysis of the development of vegetation. Carnegie Institution of Washington,.

Collins, S. L., and S. M. Glenn. 1997. Intermediate disturbance and its relationship to within-and between-patch dynamics. New Zealand Journal of Ecology 21:103-110.

Connell, J. H. 1978. Diversity in tropical rain forests and coral reefs. Science 199:1302.

Cowles, H. C. 1899. The ecological relations of the vegetation on the sand dunes of Lake Michigan. University of Chicago,.

Curtis, J. T. 1959. The vegetation of Wisconsin. Madison, WI: The University of Wisconsin Press. 657 p.

D'Amato, A. W., Fraver, S., Palik, B. J., Bradford, J. B., & Patty, L. (2011). Singular and interactive effects of blowdown, salvage logging, and wildfire in

sub-boreal pine systems. Forest Ecology and Management, 262(11), 2070–2078.

Dávalos, A., Nuzzo, V., & Blossey, B. (2015). Single and interactive effects of deer and earthworms on non-native plants. Forest Ecology and Management, 351, 28–35.

Dovčiak, M., P. B. Reich, and L. E. Frelich. 2003. Seed rain, safe sites, competing vegetation, and soil resources spatially structure white pine regeneration and recruitment. Canadian Journal of Forest Research 33:1892-1904.

Diffenbaugh, N. S., M. Scherer, and R. J. Trapp. 2013. Robust increases in severe thunderstorm environments in response to greenhouse forcing. Proceedings of the National Academy of Sciences of the United States of America 110:16361-16366.

Dumbrell, A. J., E. J. Clark, G. A. Frost, T. E. Randell, J. W. Pitchford, and J. K. Hill. 2008. Changes in species diversity following habitat disturbance are dependent on spatial scale: theoretical and empirical evidence. Journal of Applied Ecology 45:1531-1539.

DNR, M. 1996. Ecological Classification System (ECS) for Minnesota. State of Minnesota, Department of Natural Resources, Division of Forestry, Resource Assessment Program, Grand Rapids, Minnesota.

Einspahr D.W. and Winton L.L. 1976. Genetics of quaking aspen. USDA Forest Service Research Paper WO-25. USDA, Washington, DC, USA.

Eyre, F. H., and R. K. LeBarron. 1944. Management of jack pine stands in the Lake States. U.S. Department of Agriculture, Forest Service, Lake States Forest Experiment Station. Technical Bulletin 863.

Fauria, M. M., and E. A. Johnson. 2008. Climate and wildfires in the North American boreal forest. Philosophical Transactions of the Royal Society B-Biological Sciences 363:2317-2329.

Fisichelli, N. A., Frelich, L. E., Reich, P. B., & Eisenhauer, N. (2013). Linking direct and indirect pathways mediating earthworms, deer, and understory composition in Great Lakes forests. Biological Invasions, 15(5), 1057–1066.

Fisichelli, N., Frelich, L. E., & Reich, P. B. (2012). Sapling growth responses to warmer temperatures 'cooled' by browse pressure. Global Change Biology, 18(11), 3455–3463.

Fites, A. 2007. Fire behavior and effects, suppression, and fuel treatments on the Ham Lake and Cavity Lake fires. Superior National Forest, Eastern Region, USDA Forest Service.

Flannigan, M. D., K. A. Logan, B. D. Amiro, W. R. Skinner, and B. Stocks. 2005. Future area burned in Canada. Climatic Change 72:1-16.

Flannigan, M., B. Stocks, M. Turetsky, and M. Wotton. 2009. Impacts of climate change on fire activity and fire management in the circumboreal forest. Global Change Biology 15:549-560.

Fowells, H. A., comp. 1965. Silvics of forest trees of the United States. U.S. Department of Agriculture, Agriculture Handbook 271. Washington, DC. 762.

Fox, J. W. 2013. The intermediate disturbance hypothesis should be abandoned. Trends in ecology & evolution 28:86-92.

Fraver, S., Jain, T., Bradford, J. B., D'amato, A. W., Kastendick, D., Palik, B., Shinneman, D., Stanovick, J. (2011). The efficacy of salvage logging in reducing subsequent fire severity in conifer-dominated forests of Minnesota, USA. Ecological Applications, 21(6), 1895–1901.

Friedman, S. K., and P. B. Reich. 2005. Regional legacies of logging: departure from presettlement forest conditions in northern Minnesota. Ecological Applications 15:726-744.

Frelich, L. E., and P. B. Reich. 1995. Spatial Patterns and Succession in a Minnesota Southern-Boreal Forest. Ecological Monographs 65:325-346

Frelich, L. E., and P. B. Reich. 1999. Minireviews: neighborhood effects, disturbance severity, and community stability in forests. Ecosystems 2:151-166.

Frelich, L. E., and P. B. Reich. 2009. Wilderness conservation in an era of global warming and invasive species: a case study from Minnesota's Boundary Waters Canoe Area Wilderness. Natural Areas Journal 29:385-393.

Frelich, L. E., and P. B. Reich. 2010. Will environmental changes reinforce the impact of global warming on the prairie-forest border of central North America? Frontiers in Ecology and the Environment 8:371-378.

Gleason, H. A. 1926. The individualistic concept of the plant association. Bulletin of the Torrey Botanical Club :7-26.

Greene, D., and E. Johnson. 1999. Modelling recruitment of *Populus tremuloides*, *Pinus banksiana*, and *Picea mariana* following fire in the mixedwood boreal forest. Canadian Journal of Forest Research 29:462-473.

Greene, D. F., J. Noël, Y. Bergeron, M. Rousseau, and S. Gauthier. 2004. Recruitment of *Picea mariana, Pinus banksiana*, and *Populus tremuloides* across a burn severity gradient following wildfire in the southern boreal forest of Quebec. Canadian Journal of Forest Research 34:1845-1857.

Grigal, D., and L. F. Ohmann. 1975. Classification, description, and dynamics of upland plant communities within a Minnesota wilderness area. Ecological Monographs: 389-407.

Grime, J. P. 1973. Competitive exclusion in herbaceous vegetation. Nature, UK 242:344-347.

Haeussler, S., Bedford, L., Leduc, A., Bergeron, Y., & Kranabetter, J. M. (2002). Silvicultural disturbance severity and plant communities of the southern Canadian boreal forest. Silva Fennica, 36(1), 307–327.Hall, A. R., A. D. Miller, H. C. Leggett, S. H. Roxburgh, A. Buckling, and K. Shea. 2012. Diversity-disturbance relationships: frequency and intensity interact. Biology letters 8:768-771.

Handler, S., M. Duveneck, LIverson, E. Peters, R. Scheller, K. Wythers, L. Brandt, P. Butler, M. Janowiak, P.D. Shannon, C. Swanston, K. Barrett, R. Kolka, C. McQuiston, B. Palik, P. Reich, C. Turner, M. White, C. Adams, A. D'Amato, S. Hagell, P. Johnson, R. Johnson, M. Larson, S. Matthews, R. Montgomery, S. Olson, M. Peters, A. Prasad, J. Rajala, J. Daley, M. Davenport, M. Emery, D. Fehringer, C. Hoving, G. Johnson, L. Johnson, D. Neitzel, A. Rissman, C. Rittenhouse, R. Ziel. 2014. Minnesota forest ecosystem vulnerability assessment and synthesis: a report from the Northwoods Climate Change Response Framework project. Gen. Tech. Rep. NRS-133. Newtown Square, PA; U.S. Department of Agriculture, Forest Service, Northern Research Station. 228 p.

Harrington, M. G. 1987. Ponderosa pine mortality from spring, summer, and fall crown scorching. Western Journal of Applied Forestry 2:14-16.

Hart, S. A., and H. Y. Chen. 2008. Fire, logging, and overstory affect understory abundance, diversity, and composition in boreal forest. Ecological Monographs 78:123-140.

Heinselman, M. L. 1973. Fire in the virgin forests of the Boundary Waters Canoe Area, Minnesota. Quaternary Research 3:329.

Heinselman, M. 1996. The boundary waters wilderness ecosystem. University of Minnesota Press.

Houseman, G. R., Mittelbach, G. G., Reynolds, H. L., & Gross, K. L. (2008). Perturbations alter community convergence, divergence, and formation of multiple community states. Ecology, 89(8), 2172–2180.

Howe, H. F. 1994. Response of early-and late-flowering plants to fire season in experimental prairies. Ecological Applications 4:121-133.

Hughes, A. R., J. E. Byrnes, D. L. Kimbro, and J. J. Stachowicz. 2007. Reciprocal relationships and potential feedbacks between biodiversity and disturbance. Ecology Letters 10:849-864.

Intergovernmental Panel on Climate Change. 2014. Climate Change 2013: The Physical Science Basis: Working Group I Contribution to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press.

Jameson, J.S. 1961. Observations on factors influencing jack pine reproduction in Saskatchewan. Government of Canada, Department of Forestry, Forest Research Laboratory, Winnipeg, Manitoba. Forest Research Division Technical Note 97. 24 p.

Jayen, K., A. Leduc, and Y. Bergeron. 2006. Effect of fire severity on regeneration success in the boreal forest of northwest Quebec, Canada. Ecoscience 13:143-151.

Johnson, E. A., 1992. Fire and vegetation dynamics: studies from the North American boreal forest. Cambridge University Press.

Johnson, E., K. Miyanishi, and S. Bridge. 2001. Wildfire regime in the boreal forest and the idea of suppression and fuel buildup. Conservation Biology 15:1554-1557.

Johnson, L. B., & Kipfmueller, K. F. (2016). A fire history derived from Pinus resinosa Ait. for the Islands of Eastern Lac La Croix, Minnesota, USA. Ecological Applications, 26(4), 1030–1046.

Johnstone, J. F., and F. S. Chapin. 2006. Fire interval effects on successional trajectory in boreal forests of northwest Canada. Ecosystems 9:268-277.

Johnstone, J. F., T. N. Hollingsworth, F. S. Chapin, and M. C. Mack. 2010. Changes in fire regime break the legacy lock on successional trajectories in Alaskan boreal forest. Global Change Biology 16:1281-1295.

Jones, E. A., D. D. Reed, G. D. Mroz, H. O. Liechty, and P. J. Cattelino. 1993. Climate stress as a precursor to forest decline: paper birch in northern Michigan, 1985-1990. Canadian Journal of Forest Research 23:229-233.

Kasischke, E. S., N. L. Christensen, and B. J. Stocks. 1995. Fire, Global Warming, and the Carbon Balance of Boreal Forests. Ecological Applications 5:437-451.

Kasischke, E. S., and J. F. Johnstone. 2005. Variation in postfire organic layer thickness in a black spruce forest complex in interior Alaska and its effects on soil temperature and moisture. Canadian Journal of Forest Research 35:2164-2177.

Kasischke, E. S., and M. R. Turetsky. 2006. Recent changes in the fire regime across the North American boreal region—spatial and temporal patterns of burning across Canada and Alaska. Geophysical Research Letters 33:.

Kauffman, J. B., & Martin, R. E. (1990). Sprouting shrub response to different seasons and fuel consumption levels of prescribed fire in Sierra Nevada mixed conifer ecosystems. Forest Science, 36(3), 748–764.

Knapp, E. E., B. L. Estes, and C. N. Skinner. 2009. Ecological effects of prescribed fire season: a literature review and synthesis for managers. :.

Krawchuk, M. A., S. G. Cumming, and M. D. Flannigan. 2009. Predicted changes in fire weather suggest increases in lightning fire initiation and future area burned in the mixedwood boreal forest. Climatic Change 92:83-97.

Kurkowski, T. A., D. H. Mann, T. S. Rupp, and D. L. Verbyla. 2008. Relative importance of different secondary successional pathways in an Alaskan boreal forest. Canadian Journal of Forest Research 38:1911-1923.

Kurz, W. A., G. Stinson, G. J. Rampley, C. C. Dymond, and E. T. Neilson. 2008. Risk of natural disturbances makes future contribution of Canada's forests to the global carbon cycle highly uncertain. Proceedings of the National Academy of Sciences of the United States of America 105:1551-1555.

Le Goff, H., M. D. Flannigan, and Y. Bergeron. 2009. Potential changes in monthly fire risk in the eastern Canadian boreal forest under future climate change. Canadian journal of forest research 39:2369-2380

Levene, H. 1960. Robust tests for equality of variances1. Contributions to probability and statistics: Essays in honor of Harold Hotelling 2:278-292.

Liang, J., M. Zhou, P. C. Tobin, A. D. McGuire, and P. B. Reich. 2015. Biodiversity influences plant productivity through niche-efficiency.

Proceedings of the National Academy of Sciences of the United States of America 112:5738-5743.

Limberger, R., and S. A. Wickham. 2012. Disturbance and diversity at two spatial scales. Oecologia 168:785-795.

Lyon, L.J. and P.F. Stickney. 1976. Early vegetal succession following large northern Rocky Mountain wildfires. In 'Proceedings of the Montana tall timbers fire ecology conference and fire and land management symposium' No. 14. 8–10 October, Missoula, MT. pp. 355–375.

Mackey, R. L., and D. J. Currie. 2001. The diversity-disturbance relationship: is it generally strong and peaked? Ecology 82:3479-3492.

McArdle, B. H., and M. J. Anderson. 2001. Fitting multivariate models to community data: a comment on distance-based redundancy analysis. Ecology 82:290-297.

McCune, B. & Grace, J.B. (with Urban, D.L.) 2002. Analysis of ecological communities. Mjm Software Design, Gleneden Beach, OR, US.

McRae, D.J. 1979. Prescribed burning in jack pine logging slash: A review. Canadian Forestry Service, Great Lakes Forest Research Centre, Sault Ste. Marie, ON. Information Report O-X-289. 57 p.

Miller, A. D., S. H. Roxburgh, and K. Shea. 2011. How frequency and intensity shape diversity-disturbance relationships. Proceedings of the National Academy of Sciences of the United States of America 108:5643-5648.

Michaelian, M., E. H. Hogg, R. J. Hall, and E. Arsenault. 2011. Massive mortality of aspen following severe drought along the southern edge of the Canadian boreal forest. Global Change Biology 17:2084-2094.

Mitchell, S. 2012. Wind as a natural disturbance agent in forests: a synthesis. Forestry :cps058.

Ohmann, L. F., and R. R. Ream. 1971. Virgin Plant Communities of the Boundary Waters Canoe Area. USDA Forest Service. North Central Forest Experiment Station. Research Paper NC-63.

Ohmann, L. F., and D. F. Grigal. 1979. Early revegetation and nutrient dynamics following the 1971 Little Sioux forest fire in northeastern Minnesota. Forest Science 25:a0001-z0001.

Ohmann, L. F., and D. F. Grigal. 1981. Contrasting vegetation responses following two forest fires in northeastern Minnesota. American Midland Naturalist :54-64.

Oksanen, J., F. G. Blanchet, R. Kindt, P. Legendre, P. R. Minchin, R. O'Hara, G. L. Simpson, P. Solymos, M. H. H. Stevens, and H. Wagner. 2013. Package 'vegan'. Community ecology package, version 2.

Paine, R. T., M. J. Tegner, and E. A. Johnson. 1998. Compounded perturbations yield ecological surprises. Ecosystems 1:535-545.

Pan, Y., R. A. Birdsey, J. Fang, R. Houghton, P. E. Kauppi, W. A. Kurz, O. L. Phillips, A. Shvidenko, S. L. Lewis, J. G. Canadell, P. Ciais, R. B. Jackson, S. W. Pacala, A. D. McGuire, S. Piao, A. Rautiainen, S. Sitch, and D. Hayes. 2011. A Large and Persistent Carbon Sink in the World's Forests RID A-1523-2011 RID E-9419-2010. Science 333:988-993.

Peng, C., Z. Ma, X. Lei, Q. Zhu, H. Chen, W. Wang, S. Liu, W. Li, X. Fang, and X. Zhou. 2011. A drought-induced pervasive increase in tree mortality across Canada's boreal forests. Nature climate change 1:467-471.

Perala D. A. 1990. Populus tremuloides Michx. Quaking aspen. In Silvics of North America. Volume 2, Hardwoods, ed. R.M. Burns and B.H. Honkala. 555-569. USDA Forest Service Agricultural Handbook 654. Washington DC: USDA Forest Service.

Peterson, C. J. 2000. Catastrophic wind damage to North American forests and the potential impact of climate change. Science of the Total Environment 262:287-311.

Peterson, C. J., and A. D. Leach. 2008. Limited salvage logging effects on forest regeneration after moderate-severity windthrow. Ecological Applications 18:407-420.

Peterson, D. L., & Ryan, K. C. (1986). Modeling postfire conifer mortality for long-range planning. Environmental Management, 10(6), 797–808.

Peterson, D. W., and P. B. Reich. 2008. Fire frequency and tree canopy structure influence plant species diversity in a forest-grassland ecotone. Plant Ecology 194:5-16.

Platt, W. J., Evans, G. W., & Davis, M. M. (1988). Effects of fire season on flowering of forbs and shrubs in longleaf pine forests. Oecologia, 76(3), 353–363.

Purdon, M., S. Biais, and Y. Bergeron. 2004. Initial response of understorey vegetation to fire severity and salvage-logging in the southern boreal forest of Québec. Applied Vegetation Science 7:49-60.

Reich, P. B., P. Bakken, D. Carlson, L. E. Frelich, S. K. Friedman, and D. F. Grigal. 2001. Influence of logging, fire, and forest type on biodiversity and productivity in southern boreal forests. Ecology 82:2731-2748.

Reich, P. B., L. E. Frelich, R. A. Voldseth, P. Bakken, and E. C. Adair. 2012. Understorey diversity in southern boreal forests is regulated by productivity and its indirect impacts on resource availability and heterogeneity. Journal of Ecology 100:539-545.

Reich, P. B., K. M. Sendall, K. Rice, R. L. Rich, A. Stefanski, S. E. Hobbie, and R. A. Montgomery. 2015. Geographic range predicts photosynthetic and growth response to warming in co-occurring tree species. Nature Climate Change 5:148-152.

Ryan, K. C. 2002. Dynamic interactions between forest structure and fire behavior in boreal ecosystems. Silva Fennica 36:13-39.

Rich, R.L. 2005. Large wind disturbance in the Boundary Waters Canoe Area Wilderness. Forest dynamics and devel-opment changes associated with the July 4th 1999 blowdown. PhD dissertation, University of Minnesota, USA

Rich, R. L., L. E. Frelich, and P. B. Reich. 2007. Wind-throw mortality in the southern boreal forest: effects of species, diameter and stand age. Journal of Ecology 95:1261-1273.

Rich, R. L., L. Frelich, P. B. Reich, and M. E. Bauer. 2010. Detecting wind disturbance severity and canopy heterogeneity in boreal forest by coupling high-spatial resolution satellite imagery and field data. Remote Sensing of Environment 114:299-308.

Roxburgh, S. H., K. Shea, and J. B. Wilson. 2004. The intermediate disturbance hypothesis: Patch dynamics and mechanisms of species coexistence. Ecology 85:359-371.

Rudolf, Paul.1965. Jack pine (*Pinus banksiana* Lamb.). In Silvics of forest trees of the United States. p. 338-354. H. A. Fowells, comp. U.S. Department of Agriculture, Agriculture Handbook 2 7 1. Washington, DC.

Russell, M. B., Woodall, C. W., Potter, K. M., Walters, B. F., Domke, G. M., & Oswalt, C. M. (2017). Interactions between white-tailed deer density and the composition of forest understories in the northern United States. Forest Ecology and Management, 384, 26–33.

Scheiner, S. M. 1988. Tree density and modes of tree recruitment in a Michigan pine hardwood forest after clear cutting and burning. Canadian Field-Naturalist 102:634.

Schwilk, D., J. Keeley, and W. Bond. 1997. The intermediate disturbance hypothesis does not explain fire and diversity pattern in fynbos. Plant Ecology 132:77-84.

Sousa, W. P. 1984. The role of disturbance in natural communities. Annual Review of Ecology and Systematics :353-391.

Stearns, F. W. 1997. History of the Lake States Forests: Natural and human impacts. In: Vasievich, J. Michael; Webster, Henry H., eds. Lake States Regional Forest Resources Assessment: Technical Papers. Gen. Tech. Rep. NC-189. St. Paul, MN: U.S. Department of Agriculture, Forest Service, North Central Forest Experiment Station: 8-29.

Turner, M. G., Romme, W. H., Gardner, R. H., & Hargrove, W. W. (1997). Effects of Fire Size and Pattern on Early Succession in Yellowstone National Park. Ecological Monographs, 67(4), 411–433.

Turner, M., W. Baker, C. Peterson, and R. Peet. 1998. Factors influencing succession: Lessons from large, infrequent natural disturbances. Ecosystems 1:511-523.

Turner, M. G., W. H. Romme, R. A. Reed, and G. A. Tuskan. 2003. Post-fire aspen seedling recruitment across the Yellowstone (USA) landscape. Landscape Ecology 18:127-140.

USDA Forest Service. 2001. Final environmental impact statement for the Boundary Waters Wilderness fuel treatment. Eastern Region, Milwaukee, WI: Superior National Forest.

USDA Forest Service. 2003. Common stand exam field guide. Natural Resource Manager, Washington, DC.

Van Bellen, S., M. Garneau, and Y. Bergeron. 2010. Impact of climate change on forest fire severity and consequences for carbon stocks in boreal Quebec, Canada: a synthesis. Fire Ecology 6:16-44.

Volney, W. J. A., and R. A. Fleming. 2000. Climate change and impacts of boreal forest insects. Agriculture, Ecosystems & Environment 82:283-294.

White, P. S., & Pickett, S. (1985). Natural disturbance and patch dynamics. In *Academic Press*.

Woodall, C. W., and L. M. Nagel. 2007. Downed woody fuel loading dynamics of a large-scale blowdown in northern Minnesota, USA. Forest Ecology and Management 247:194-199.

Wotton, B. M., C. A. Nock, and M. D. Flannigan. 2010. Forest fire occurrence and climate change in Canada. International Journal of Wildland Fire 19:253-271.

Appendix 1

Wind was determined to be the mortality agent if a tree was dead and there was no evidence of fire and the tree had fallen or the bole had broken and had a decay class of at least 2 according to CSE protocol. Trees with a mortality class of 1 that had fallen or broken were recorded as having a mortality agent of "other" so as to exclude them from mortality estimates for the 1999 blowdown. In areas where we saw evidence of wind followed by fire, mortality was recorded as wind if a tree's bole was broken and the standing broken end was charred or the fallen bole was charred on the bottom side, or if a tip up mound existed that showed charring on roots that would have been below ground prior to wind throw but were subsequently exposed to fire. In these areas we recorded a tree as having fire mortality if it was standing dead with intact branches and an unbroken bole and had visible charring on the lower portion of the bole or around the root crown and was of decay class 1or 2 (indicating it was less than 10 years since mortality).

Trees that were standing dead with a broken bole could be recorded as either wind or fire depending on the species, decay class and the presence or absence of charring on the break. For example, the boles of some trees including aspen and birch tend to break quite easily following fire mortality, whereas pines tend to remain standing for a long time following fire events. In the cases of aspen and birch, a bole break on a standing dead tree was not determined to be evidence of wind mortality unless the portion above the break was charred (indicating it fell

prior to occurrence of fire), or very decayed (indicating that more than 10 years had passed since it died). Standing dead pines with bole breaks were recorded as having wind caused mortality if the bark had burned more completely than other standing dead unbroken individuals of the same size, indicating that they were not living at the time of the fire. Mortality was recorded as other if a tree was standing dead and severely decayed, but without any charring, or if it showed clear signs of animal or insect damage. Trees marked as having a mortality agent of "other" were uncommon and made up <3% of the total trees in the study and were excluded from estimates of disturbance related basal area loss.

When the mortality of an individual tree was in doubt, it was assigned a mortality cause based on the relative disturbance severities of the coarse scale plot and a priori knowledge of tree species susceptibility to wind throw and fire mortality. In the cases of fallen trees, we also looked for charring of the entire bole as opposed to charring only on the lower portion of the fallen bole which would indicate a tree bole fell as a result of fire mortality rather than wind mortality. For example, a fallen, severely-charred cedar would be unlikely to have been killed by wind as cedars are amongst the most wind-firm species in the study area (Rich et al. 2007). Similarly, a 5cm diameter balsam fir that had fallen over with burned roots would not be recorded as having wind mortality because small balsam fir are unlikely to be damaged by wind, but do uproot easily after fire. In some cases, determining the species of a tree that had been badly burned or decayed was difficult, but we were normally able to find some remnants of bark

or a distinctive branching structure or wood structure that would aid identification. In a few rare cases, a tree was so badly decayed or burned that positive identification was impossible and it was recorded as being an unknown species and excluded from further analysis.

We used logistic regression of the form logit(p)= $\beta 0$ + $\beta 1$ * (W) + $\beta 2$ * (DBH) + $\beta 3$ * (DownDead) to determine mortality agents for dead trees in our coarse scale plots. In this model p is the probability of a tree being killed by fire where p = 1 means that a tree has a 100% likelihood of having fire for a mortality cause and p = 0 means that a tree has a 0% chance of having fire as a mortality cause (and therefore is assumed to have been killed by wind). W is the categorical wind severity of the coarse plot on a 0-5 scale, DBH is the diameter at breast height in cm and DownDead is a binary variable set = 0 if the tree is fallen and dead, or 1 if the tree is dead and standing. We used mortality data from fine scale plots where we recorded mortality causes for all individual trees encountered to parameterize our models. Because tree species show differential susceptibility to wind we parameterized the model 7 times using data for individual species or species that show similar susceptibility to wind (Appendix Table 1).

All models showed good fit with p values for chi square tests <0.000. We then used our models to predict the likelihood of fire mortality by tree species, diameter, wind severity, and standing dead vs down and dead for all dead trees

in coarse scale plots. We then used these probabilities to determine the proportion of basal area that had been killed by wind vs fire in coarse scale. For example, for a 19.4 cm birch that is down and dead and is found in a plot with wind severity of 2, the log odds are 1.999 and the probability of being killed by fire = 0.69. In this case, for plot level basal area calculations we assumed that 0.69* 1178 cm2 (the basal area of the tree) = 812.82 cm2 was killed by fire and the remainder was killed by wind.

Appendix. Table 1. Logistic regression models to predict tree mortality agents for coarse scale trees in plots where pre-disturbance measurements of live basal area were unavailable. These models were parameterized using data from the fine scale plots and were used to predict the probability that a dead tree in coarse scale was killed by either wind or fire.

	Intercept	Categorical wind Severity	DBH in cm	DownDead (0= fallen dead, 1= standing dead)
	β_0	β_1	β_2	β_3
Tree Species				
Balsam Fir	8.0867	-0.9361	-0.1694	1.2765
Birch	5.3255	-0.8796	-0.1183	2.365
Jack Pine	3.6655	-0.9661	-0.0599	0.9912
Black spruce, white spruce and tamarack	5.8219	-0.7995	-0.1634	0.2454
Red Pine and White Pine	3.8535	-2.0758	-0.0589	2.5841
Aspen (bigtooth, quaking, and balsam poplar)	3.8304	-1.2205	-0.0569	1.0483
Cedar, red maple and black ash	7.0317	-1.5628	-0.0868	20.9929

Appendix Table 2. Regression analysis summary table.

Model	Equation	r^2	P value	n
# Diversity vs. fire and wind severity for plots experiencing fire				
Shannon's true div. vs. wind severity (as proportional change in basal area from 1999-2000)	$y = 3.3225 + 1.6711x - 2.5005x^2$	0.02988	<0.0001	729
Species richness vs. wind severity (as proportional change in basal area from 1999-2000)	$y = 5.7709 + 1.2770x - 3.6087x^2$	0.08441	<0.0001	729
Shannon's true div. vs. fire severity (as proportional change in basal area from 2000-2012)	$y = 1.484 + 7.147x - 5.322x^2$	0.01801	0.0005	729
Species richness vs. fire severity (as proportional change in basal area from 2000-2012)	$y = 2.642 + 11.457x - 8.823x^2$	0.02336	<0.0001	729
## Diversity vs. fire severity and % of plot area burned for partially burned plots				
Shannon's true div. vs. fire severity (as proportional change in basal area from 2000-2012)	$y = 2.4498 + 1.7967x$	0.07547	0.0036	98
Species richness vs. fire severity (as proportional change in basal area from 2000-2012)	$y = 4.5643 + 2.4501x$	0.06907	0.0052	98
Shannon's true div. vs. % of plot area burned	$y = 2.7993 + 0.0186x$	0.1806	0.0003	98
Species richness vs. % of plot area burned	$y = 4.8793 + 0.0309x$	0.2609	<0.0001	98

Appendix Figure 1. Decision tree for determining mortality agent for trees in plots where the extent of previous wind disturbance was unknown.

Decision tree for identifying the mortality agent of dead trees within fine scale plots