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# Wind and fire: Rapid shifts in tree community composition following multiple disturbances in the southern boreal forest

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**Abstract**

Under a warming climate, the southern boreal forest of North America is expected to see a doubling in fire frequency and potential for increased wind disturbance over the next century. Although boreal forests are often considered fire-adapted, projected increases in disturbance frequency will likely 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 tree 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 nonmetric 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 relative to single disturbances. We found that multiple disturbances often resulted in strong shifts toward wind-dispersed early-successional tree species, 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. Although boreal forests appear to be somewhat resilient to multiple disturbance events, multiple disturbances resulted in post-disturbance tree communities that were heavily dominated by disturbance-adapted deciduous trees at the expense of conifers. Our results demonstrate that multiple disturbances are capable of altering successional pathways relative to single disturbance events and that increasingly frequent disturbances are likely to alter boreal forest structure and composition, perhaps leading to a forest region strikingly unlike that of today.

**KEYWORDS**
Boundary Waters Canoe Area Wilderness, climate change, compound disturbances, forest fire, forest succession, Minnesota, successional pathways

# INTRODUCTION

Boreal forests comprise 33% of all forests on the Earth; they harbor enormous biodiversity, wildlife, timber, and freshwater resources, and a vast carbon sequestration pool (Kuusela, 1992; Pan et al., 2011; Schindler & Lee, 2010; Schmiegelow et al., 1997). Therefore, it is imperative that we better understand how disturbance dynamics in the boreal forest are changing and the ecological consequences of these shifting disturbance regimes (Johnstone et al., 2016). In this paper, we focus on the successional dynamics and interactions between fire and wind disturbances in the southern boreal forests of Minnesota's Boundary Waters Canoe Area Wilderness (BWCAW), a part of the central North American boreal forest that was recently highlighted as a tipping point for global climate change (Lenton et al., 2019) and thus a useful model system for southern boreal forests more generally.

The boreal forest of central North America is a fire-dominated ecosystem characterized by stand-replacing crown fires that occur at intervals ranging from 50 to 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 (Flannigan et al., 2009; Intergovernmental Panel on Climate Change, 2014; Tam et al., 2018; 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; Krawchuk et al., 2009; Le Goff et al., 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 (Diffenbaugh et al., 2013; Frelich & Reich, 2010; Peterson, 2000). Under historic disturbance regimes, single disturbance events over intermediate timescales (ca 50–100 years) were common. However, with increases in both fire and wind frequencies, multiple compounding disturbance events, such as wind followed by fire or multiple fires within a short period of time (<50 years), are predicted to become more common (Frelich & Reich, 2010; Whitman et al., 2019). Furthermore, there is also the possibility of synergistic interaction between disturbance events (Buma, 2015). More frequent windstorms often lead to increased fuel loads (Mitchell, 2013; Woodall & Nagel, 2007). Because fuel loads have a direct relationship to fire intensity (Byram, 1959), fires that follow wind disturbance often burn with greater intensity and fire severity (Cannon et al., 2014; Kulakowski & Veblen, 2007).

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 the underlying structure and dynamics of the ecosystem. This includes increased terrestrial carbon emissions. Soil carbon is the largest carbon pool in boreal forests, and increasing fire frequency and intensity along with warmer temperatures has the potential to consume more of this legacy carbon pool (Walker et al., 2019). Other disturbances including insects and windstorms have the potential to increase boreal carbon emissions as well (Bradford et al., 2012; Hicke et al., 2012). Increasingly, frequent disturbance events in the boreal forest have the potential to convert one of Earth's largest terrestrial carbon sinks to a source during the 21st century (Balshi et al., 2009; Bond-Lamberty et al., 2007; Kasischke et al., 1995; Kurz et al., 2008; Pan et al., 2011).

Succession following single fires in the central North American boreal forest, including the BWCAW, has been extensively studied (e.g., Carlson et al., 2011; Heinselman, 1973; Ohmann & Grigal, 1981). However, successional dynamics of wind disturbance (Rich et al., 2007) and the dynamics of multiple and compounding disturbances remain an area of evolving research (Brown & Johnstone, 2012; Buma, 2015; Johnstone et al., 2016; Johnstone & Chapin, 2006; Paine et al., 1998) that we address in this study.

Under historic disturbance regimes where single fires were the most common disturbances, self-replacement of fire-dependent communities dominated by jack pine (*Pinus banksiana* Lamb.), black spruce (*Picea mariana* [Mill.] Britton, Sterns & Poggenb.), red pine (*Pinus resinosa* Aiton), aspen (*Populus tremuloides* Michx.), or paper birch (*Betula papyrifera* Marshall) was common (but not ubiquitous) after severe fires (Heinselman, 1973; Heinselman, 1996; Ohmann & Grigal, 1981). Note that although seedlings of these species have very low post-fire survival, the overall populations nevertheless tend to be perpetuated due to the compatibility between physical effects of fires and their disturbance adaptation traits (at reproductive, seedling, and adult stages), known as legacy syndromes (Jõgiste et al., 2017). Legacy syndromes in BWCAW forests include serotinous cones (canopy-stored seeds) allowing seeds to survive fires in jack pine and black spruce, thick bark and tall stature allowing mature red pine trees to survive, and root survival with the ability to sprout via the root system in aspen or stump in paper birch (Frelich, 2002). Therefore, due to the match in legacy syndromes and fire effects, the pre-fire composition and post-fire composition are similar (i.e., the forest has high ecological memory) and forests are resilient to single occurrences of fire (Jõgiste et al., 2017).

This high resilience can be eroded in three ways. The first is loss of a dominant species ability to respond to disturbance in the same way as it did historically, due to changing climate and/or other ecological conditions so that additional occurrences of similar disturbances fail to perpetuate the species (e.g., single-crown fires fail to perpetuate jack pine). Some have labeled this a resilience deficit (or debt), which leads to unexpected changes in forest composition when the next disturbance occurs (Johnstone et al., 2016). The second is occurrence of a disturbance type incompatible with the disturbance adaptations (i.e., legacy syndromes) of the dominant tree species (e.g., wind rather than fire in jack pine forests). The third is occurrence of compound disturbances with very high cumulative severity that overwhelms the legacy syndrome (e.g., two fires occur in a short time so that jack pine trees are not of seed-bearing age at the time of the second fire). The following two paragraphs provide more details of the second and third ways in which resilience can be eroded.

The effects of wind as a disturbance are (for the most part, see exceptions noted below) incompatible with the legacy syndromes of the fire-adapted species mentioned above, but are compatible with legacy syndromes of several other species. Wind disturbances remove large trees of early-successional, shade-intolerant species (e.g., jack pine, red pine, and aspen) and release smaller trees of late-successional, shade-tolerant species such as black spruce, balsam fir (*Abies balsamea* [L.] Mill.), and white cedar (*Thuja occidentalis* L.), thus accelerating succession (Chen & Taylor, 2012; Frelich & Reich, 1995b; Rich et al., 2007), with white cedar becoming a potential climax community type in the BWCAW if fire is absent for 3–4 centuries (Grigal & Ohmann, 1975). Note that black spruce has both serotinous cones and shade-tolerant seedlings, which are released from suppression after windstorms. Furthermore, because of the properties of its wood, mature paper birches commonly survive windstorms (Rich et al., 2007). Thus, these two species have multiple adaptations (i.e., diversity in their legacy syndromes), which accommodate survival of both fire and wind disturbances so that they function as both early- and late-successional species (Frelich & Reich, 1995b).

Compound disturbances such as wind followed by fire or two fires within a short time span are incompatible with the legacy syndromes of most species present in the BWCAW. Such sequences of disturbance destroy canopy-stored seed banks, seedlings, and mature trees so that ecological memory of pre-disturbance composition is likely to be lost, and ecosystem resilience to disturbance is eroded (Johnstone et al., 2016; Paine et al., 1998), possibly leading to novel successional outcomes, altered ecosystem states, and disruptions in ecosystem functioning (Buma, 2015; Johnstone et al., 2016; Paine et al., 1998). 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 trees and shrubs with potential negative impacts on wildlife and herbaceous plant species of old-forest habitats (Brown & Johnstone, 2012; Johnstone & Chapin, 2006). In the BWCAW, paper birch and aspen are the only important tree species likely to survive compound disturbances and are also the species best equipped to reseed disturbed areas via long-distance seed dispersal (Frelich, 2002; Heinselman, 1973).

The cusp catastrophe theory of forest dynamics (also known as neighborhood effect theory; Frelich & Reich, 1995a, 1998, 1999; Frelich, 2002, 2016) pulls together the ecological memory, legacy, and resilience debt concepts explained above for a unified view of forest resilience to disturbance. The theory is used to predict post-disturbance successional status—alternate states dominated by early- versus late-successional species—across a gradient of cumulative disturbance severity (Figure 1). Note that cumulative severity includes additive severity of sequences of disturbances, which occur close enough in time so that little or no recovery occurs between disturbances. Low- to moderate-severity disturbances (windstorms or low-intensity surface fires) maintain dominance of, or cause accelerated succession to, late-successional species with strong overstory–understory neighborhood effects, with release of advanced regeneration or reseeding from surviving mature trees maintaining dominance post-disturbance (basin of attraction above the cusp). Moderate- to high-severity disturbances with strong disturbance-activated neighborhood effects (e.g., serotinous cones and surviving root systems) maintain dominance of early-successional species post-disturbance (below the cusp), or in the case of late-successional stands above the cusp, if cumulative disturbance severity above a certain threshold disturbance severity occurs, then the stand falls over the cusp, making a transition from late- to early-successional status referred to as a compositional catastrophe. Note that moderate-severity disturbances can maintain either alternate state (Frelich, 2002; Frelich & Reich, 1999). The cusp catastrophe theory is useful also as a conceptual framework for examining disturbance effects and vegetation responses to climate in disparate systems (Frelich & Reich, 1999; Kern et al., 2021; Scheffer et al., 2012).

A double cusp may exist across the disturbance severity gradient in the BWCAW (Frelich, 2002). Late-

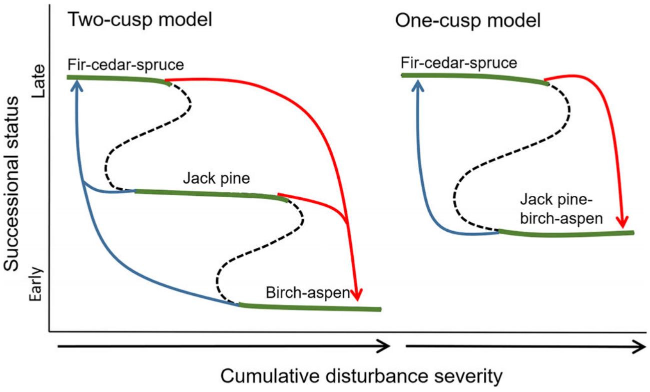

**FIGURE 1** Comparison of one- and two-cusp catastrophe models applied to Boundary Waters Canoe Area Wilderness forests. Cumulative disturbance severity is low at the start of each arrow along the *x*-axis. Note that the length of the successional gradient on the *y*-axis and severity gradient on the *x*-axis are longer for the two-cusp model. Green areas on each cusp are areas of attraction. Red arrows indicate succession when severity of a single disturbance, or cumulative severity of compound disturbances, exceeds the resilience of a forest community. Blue arrows show successional pathways when cumulative disturbance severity is low

successional forests of balsam fir, white cedar, and black spruce are on the highest level above the upper cusp (low-to-moderate cumulative disturbance severity), while jack pine forests are on the middle level between the upper and lower cusp (high cumulative severity), and paper birch and aspen forests are on the lowest level, below the lower cusp (extremely high cumulative severity; Figure 1). This prediction extends the length of the severity gradient to include extremely severe compound disturbances, while the original theory (Frelich & Reich, 1999) lumped severe and extremely severe disturbances together. It also extends the length of the successional gradient by designating birch–aspen forests as an earlier successional state than jack pine (Figure 1).

Furthermore, cusp catastrophe theory makes predictions regarding divergent or convergent post-disturbance succession in stands based on whether the late-successional species have positive neighborhood effects (divergence into separate late-successional stand types) or neutral-to-negative neighborhood effects (convergence into mixed stand types) (Frelich, 2002; Frelich & Reich, 1999). This can lead to maintenance of monodominant or mixed stands as long as low-to-moderate cumulative disturbance severity continues to occur. It can also lead to transition into late-successional stands in cases where low- to moderate-severity disturbances affect old early-successional stands with late-successional advanced regeneration—a common condition in the BWCAW (Rich, 2005).

Successional patterns can be influenced by changes in community dispersion (changes in the variability of composition) and 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). Following a disturbance, a community may have a more variable composition, that is, an increase in community dispersion, or alternatively, a disturbance may act like a filter and select against certain species leading to more homogenous post-disturbance composition. Changes in composition can also be directional in nature, independent of changes in community diversity. For example, a forest comprised of paper birch and black spruce stands could become monodominant aspen stands following disturbance, resulting in a community that has both lower dispersion and different compositions. Alternatively, a forest of aspen and fir stands could succeed to monodominant aspen stands following fire, resulting in a decline in dispersion, and a moderate shift in composition, or a monodominant fir forest could succeed to a mixed forest of aspen and birch stands, resulting in both an increase in dispersion and a shift in composition.

The objectives of this paper were to (1) determine how patterns of succession differ between single and multiple disturbances and (2) determine whether instances of multiple disturbances lead to different patterns of succession, including successional convergence where dissimilar predisturbance communities succeed to a post-disturbance community with homogenous composition relative to single disturbance events. We used a series of recent disturbance events in the BWCAW of northern Minnesota, USA, 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 wind alone, fire alone, wind followed by single fire, wind followed by two fires, and multiple (two or three) fires within a 35-year period. Using this matrix of disturbances, we sought to characterize tree community responses to disturbances ranging from windstorms and single fires to instances of combined multiple disturbances, and to address the following questions and hypotheses.

(Q1) Given that ecological filters differ between disturbance types, how do patterns of succession differ after wind and fire disturbances?

H1. We expected that post-wind regeneration will consist of mainly shade-tolerant advanced regeneration of species such as balsam fir, white cedar, and red maple (*Acer rubrum* L.). Given their dual roles as early- and late-successional species, black spruce and paper birch may also be present. Although post-wind succession will converge on late-successional species as a group, we also hypothesized that divergence will occur among late-successional species—that is, monodominant stands of the mentioned species.

H2. Single fires will not cause convergence in composition; post-fire stands will be composed of a mix of early-successional, fire-adapted species similar to the pre-fire composition, including aspen, paper birch, jack pine, black spruce, red pine, and white pine (*Pinus strobus* L.), with late-successional species occasionally present. This hypothesis also implies that single fires will maintain pre-fire composition of stands dominated by jack pine, the quintessential fire-adapted conifer species of the boreal forests in central North America.

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

H3. We expected that areas experiencing multiple disturbances (wind plus fire or 2–3 fires) would undergo successional convergence toward disturbance-adapted, early-successional species and expected that this would lead to a more homogenous landscape resulting in both decreased dispersion post-disturbance (among stands subjected to the same disturbances) and shifts in community composition.

H4. We expected that after multiple disturbances, fire-adapted conifers (jack, red, and white pines) will be replaced by the deciduous species paper birch and aspen. If this is the case, and H2 is also true, then there is evidence for the two-cusp model, as well as a rationale for separating jack pine and birch–aspen forest types into early- and very-early-successional status, respectively (Figure 1).

# METHODS

## Study area

Our research area (≈15,000 ha in the vicinity of Seagull and Saganaga Lakes) 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 Minnesota, USA. It consists of areas affected by the 1999 windstorm, various wild and prescribed fires from 1974 to 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 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). Although fire return intervals lengthened during the 20th century due to climate change and fire exclusion (Heinselman, 1996), forests within the study area have seen significant disturbance over the last 40 years. Today, within a 25-km radius of Seagull Lake, there is a unique mosaic of stands that have been variously affected by wind, single fires, wind followed by a single fire, wind followed by two fires, and stands that have been burned two or three times within a 33-year period (Table 1).

## Field methods

We used an array of 82 transects containing 1086 vegetation monitoring plots to track changes in forest composition. Six hundred and eighty-two plots were established in 2000–2001 following the 1999 windstorm (Rich, 2005), while the remaining 404 plots were established in 2011–2012 following the major fire events of 2006 and 2007. We used a stratified sampling approach with previously mapped stand ages and disturbance types to locate transects. We used Heinselman's stand-origin maps (Heinselman, 1973, 1996) and subsequent analyses of the study area (Frelich & Reich, 1995b) for pre-disturbance stand age information. We overlaid US Forest Service maps of the 1999 windstorm and fires listed in Table 1 onto Heinselman's stand-origin maps to stratify plot locations by disturbance types and combinations thereof, and to summarize pre-disturbance stand age information. 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 and 400 m. Because 80% of the BWCAW landscape is within 500 m of a lakeshore (Rich, 2005), and because there are numerous small hills superimposed on the larger-scale pattern of ridges between lakes, with slope, aspect, and stand type changing at a spatial scale of ca 20 m (Frelich & Reich, 1995b), this sampling approach provides a representative sample of the forest landscape with respect to forest type.

Plots were circular and centered at 25-m intervals along transects with the first plot on each transect originating 5 m from the lakeshore; the first plot of a lake-originating transect was semicircular. Plot centers were marked with 3/8″ steel rebar, and GPS coordinates were

**TABLE 1** Major stand-replacing disturbance events occurring within the study area from 1974 through 2007

| Disturbance | Year | Size (ha) | Description | No. 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 | 193,000 | Extreme wind event-producing straight-line winds in excess of 190 km/h | 627 |
| BWCAW fuel reduction treatments | 2002–2005 | 1500 | Prescribed fires initiated by the Superior National Forest aimed at reducing 100-h fuels and creating barriers to fire spread within portions of the BWCAW heavily impacted by the 1999 BWCA Derecho | 108 |
| Cavity Lake Fire | 2006 | 10,000 | 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 | 30,000 | 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 |

*Note:* The total number of plots was 1086, but because some disturbances overlapped spatially, some plots experienced more than one disturbance event.
Abbreviation: BWCAW, Boundary Waters Canoe Area Wilderness.

recorded using a Trimble GeoExplorer or Garmin Garmin eTrex Vista HCx. We used a nested plot design with fixed plot radii of 12.5, 5, and 3 m for a coarse-scale tree plot, fine-scale tree plot, and regeneration plot, respectively. On the coarse-scale tree plots, all live and dead trees >5 cm diameter at breast height (dbh) were counted and classified by species and size class (5–15, >15–25, and >25 cm). Across the entire coarse-scale plots, we observed percent cover for all trees that occupied at least 1% of plot area through ocular estimate. We recorded cover separately for overstory trees and regeneration, with overstory trees defined as those >2 m in height and regeneration defined as trees <2 m in height. Cover measurements could stack such that each species could 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 plots, 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 (Appendix S1: Figure S1).

In our regeneration plots, all trees from new seedlings to saplings were counted by species. We did not attempt to distinguish aspen seedlings of seed origin from those of sprout origin.

Across the entire coarse-scale plots, we also recorded the percent of plot area burned using ocular estimation, and categorical fire severity (for the most recent fire occurring from 2002 to 2007) and categorical wind severity (Table 2), after Carlson et al. (2011).

All plots established in 2000–2001 (post-wind plots; many of these subsequently burned from 2002 to 2007 and were used for the analysis of wind plus fire) were resurveyed in 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.

On the 404 new plots added in 2011–2012, we inferred past composition by surveying all live and dead trees rooted within the fine-scale tree plots, and assigning a cause of mortality for any standing snags or fallen dead trees. This was done to assess the species composition prior to the large fires of 2006 and 2007, from 4 to 6 years prior to field visits. We did not attempt to assess composition prior to the fires from 1974 to 1995. On the coarse-

**TABLE 2** Categorical disturbance severity classes

| Level | Ground fire severity classes | Categorical wind severity classes |
|---|---|---|
| 0 | Unburned | No evidence of major wind damage, all trees are still standing, or if fallen have intact boles, branches may be broken |
| 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) |
| 2 | 1%–50% of surface litter consumed | <50% of canopy trees have broken boles or have fallen, and most wind-firm species are undamaged |
| 3 | 50%–99% of surface litter consumed | >50% of canopy trees have broken boles or have fallen, and only wind-tolerant species remain in canopy (although some may suffer damage or have fallen) |
| 4 | 100% of surface litter consumed, some duff consumed | Wind damage extensive. All canopy trees have broken boles or have fallen, and sub-canopy of wind-firm species may remain intact |
| 5 | All organic litter and duff consumed | All canopy trees and most sub-canopy trees are broken or have fallen, and only standing stumps and immature trees (<5 m in height) remain |

scale plots, we recorded the number of live, dead, and fallen dead trees by species and size class.

## Data analyses

We used geospatial data on the extent of disturbances to stratify transects by disturbance types; because the 1999 windstorm was diffuse in its spatial extent, there were few, if any, plots in our study area that were completely unaffected by wind. Therefore, we used a critical threshold of quantitative wind severity as a cutoff to designate plots on which we considered wind to be an important influence. We calculated quantitative disturbance severity at the coarse-scale plot level after Peterson and Leach (2008) as the relative change in basal area pre- and post-disturbance. 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 and on-the-ground observations of charring to determine whether a plot had been burned, and by which fires.

Changes in forest composition and succession were analyzed by comparing the relativized pre-disturbance composition (measured as basal area on coarse-scale plots) with the relativized post-disturbance composition (measured using stem counts on nested regeneration plots or percent cover on coarse-scale plots; we initially ran both percent cover and regeneration stem count analyses and chose to use the latter for further analysis as described below).

Trees measured on fine-scale plots were assigned mortality causes by observation of patterns of charring and stem breakage, but at the coarse-scale level, we used species-specific logistic regression equations (Appendix S1: Table S1) to calculate the fraction of coarse plot-level basal area by species that had been killed 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 (Table 2). From these equations, we were able to calculate the fraction of an individual tree's basal area 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 total basal area of 0.5 $m^2$ on a coarse-scale plot and a 75% chance of being killed by fire, we allocated 0.375 $m^2$ of its basal area as having been killed by fire and 0.125 $m^2$ of its basal area as having been killed by wind. Individual tree basal areas by species were then aggregated at the coarse plot level to create plot-level estimates of living basal area by species before and after wind disturbance and before and after fire disturbance to estimate disturbance severity.

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 & 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 NMDS ordination in the statistical software program Pc-Ord 5 (McCune & Grace, 2002) and the VEGAN package for R (version 2.3; Oksanen et al., 2013). 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.

Successional vectors were created by running both hierarchical clustering and ordination analyses with a matrix containing three time steps of community composition. The first time step was community composition of trees in 1999, prior to the windstorm. This was reconstructed from direct observations made during fieldwork in 2000–2001. To translate size class data into diameter estimates for trees tallied in the coarse-scale plots, we used quadratic mean diameters (QMD; Curtis & Marshall, 2000) calculated from trees in fine-scale plots to estimate the diameter of trees of each species and size class on coarse-scale plots. For example, to estimate the diameter of a red maple in the 5- to 15-cm size class that had been observed in a coarse-scale plot, we calculated the QMD of red maples within this size class on fine-scale plots where we had used diameter tapes to directly measure dbh. The second time step was post-wind tree community composition in 2000–2001 as measured through direct observation during fieldwork. 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 were 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 <5 cm dbh by species on the regeneration plots. Given the high density of post-fire regeneration, with thousands of seedlings and saplings per coarse-scale plot, it was not possible to count all regeneration, and therefore, we considered the nested regeneration plots as representative samples of the coarse-scale plots. Because the first two time steps used basal area and the third time step used stem counts, a row relativization was performed to create unitless measures of proportional dominance for each species.

We considered an alternative definition of the third time step that consisted of basal area of live trees >5 cm dbh in 2011–2012, but because 65% of all plots had no surviving trees in this size category in 2011–2012, it 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 2 time steps, but relativized percent cover of the coarse-scale plots rather than regeneration stem counts for our third time step. The overall solution for ordinations using percentage cover was similar to that 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 very similar whether using cover data or nested regeneration plot data.

Nonmetric multidimensional scaling ordinations were run in the program R using the VEGAN package (Oksanen et al., 2013). We used Bray-Curtis dissimilarity (Sørensen's distance) as our distance measure and

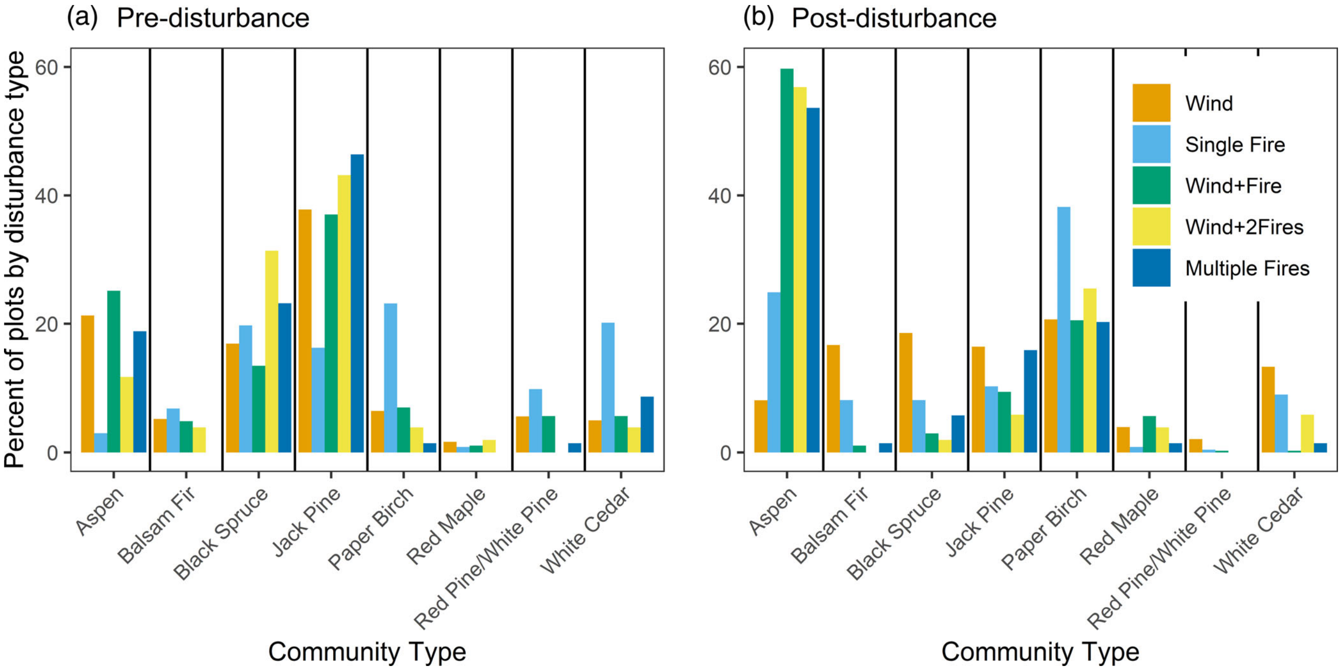

**FIGURE 2** Pre- and post-disturbance community composition by disturbance type/combination

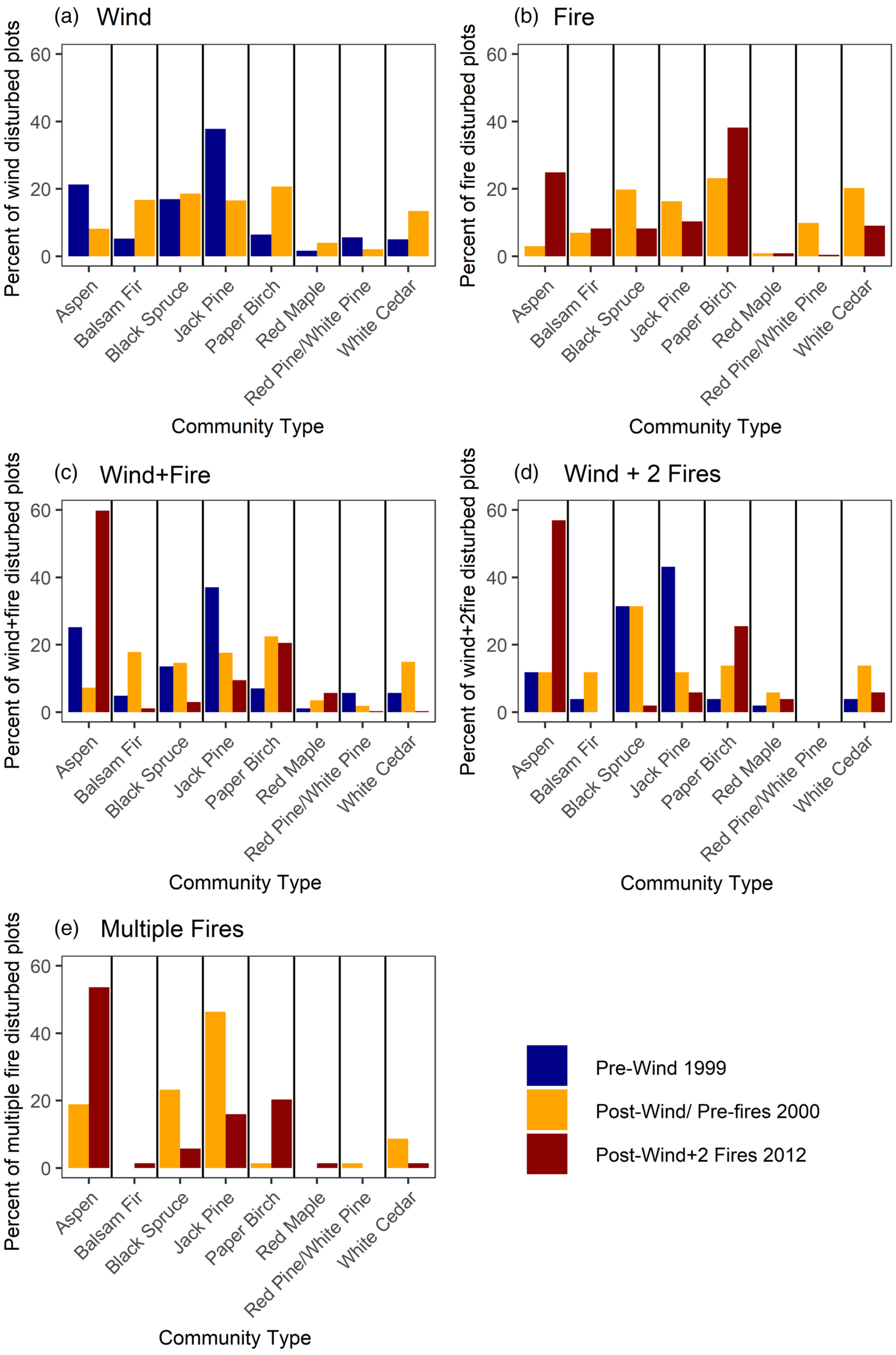

**FIGURE 3** Change in community composition by disturbance type or disturbance combination

performed 3000 runs with a three-dimensional solution resulting in a final stress of 14.6411. 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 (*Larix laricina* [Du Roi] K. Koch) and black ash (*Fraxinus nigra* Marsh). We also combined three species of *Populus* in our study into a single aspen category; the vast majority were *P. tremuloides*.

Tree community types were determined using hierarchical cluster analysis in PC-Ord 5 with a flexible beta of −0.25 (McCune & Grace, 2002). The cluster dendrogram was cut into eight 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 on the NMDS ordination output to identify community types based on species abundance. Each cluster was defined as a community type named after the most dominant one or two species in each cluster. The named species made up 47%–67% of the trees within a given community type. We identified the following eight 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 (Frelich & Reich, 1995b; Grigal & Ohmann, 1975; Heinselman, 1996; Ohmann & Ream, 1971; Rich, 2005).

We tested for changes in community dispersion pre- and post-disturbance using PERMDISP, which is a multivariate analogue of the Levene (1960) test for homogeneity of variances (criterion for statistical significance was $p \leq 0.05$). PERMDISP measures the distances of plots from the centroid in multidimensional space. We considered decreasing distances to the centroid post-disturbance as evidence of successional convergence, and increasing distances as evidence of successional divergence.

We tested for shifts in mean composition pre- and post-disturbance within disturbance types using PERMANOVA, a multivariate analogue of ANOVA that uses multivariate distance metrics (Anderson, 2001). We used Bray-Curtis dissimilarity 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. We concluded that there was statistical evidence of shifting composition in cases where the PERMANOVA $p$ value was ≤0.05.

# RESULTS

## Pre-disturbance composition

Pre-disturbance composition for the study area as a whole was roughly similar among all disturbance types/

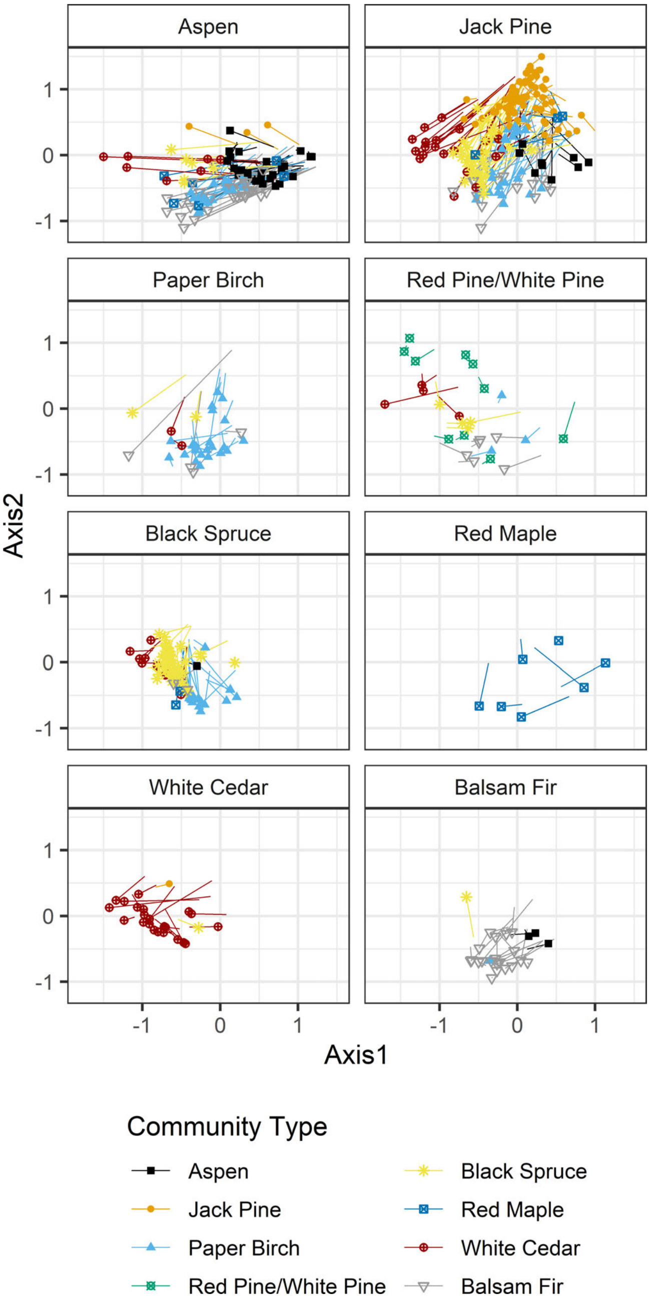

**FIGURE 4** Community transitions before and after wind disturbance sorted by pre-wind community type. Colors represent community type following disturbance. Symbols represent post-disturbance positions of plots in ordination space, and origins of vectors represent pre-disturbance positions. All panels are facets of the same overall nonmetric multidimensional scaling ordination solution

combinations and was dominated by a mix of jack pine, black spruce, and aspen, with substantial paper birch, red/white pine, white cedar, and balsam fir, while red maple was present but not abundant (Figure 2a). Areas affected by single fires had pre-disturbance community composition more dominated by paper birch and white cedar, and less dominated by aspen, than other disturbance types/combinations (Figure 2a).

## Single disturbance: stand-leveling wind

Prior to the 1999 windstorm, areas that would subsequently experience wind disturbance were composed of old stands (median age 197 years) dominated by a mix of jack pine (38% of plots), aspen (21%), and black spruce (17%) communities, with paper birch (7%), red pine/white pine (6%), balsam fir (5%), and white cedar (5%) community types also present (Figure 3a). After the 1999 windstorm, community types followed multiple successional pathways, with a net shift toward paper birch and later-successional (more shade-tolerant) community types (Figure 3a). Aspen, jack pine, and red pine/white pine community types were heavily impacted by wind disturbance; numbers of plots declined by >50% (Figure 4; Table 3). Black spruce and jack pine stands experienced significant post-storm succession to other community types, but as 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 4; Table 3). Paper birch, white cedar, red maple, and balsam fir community types all experienced no or only slight shifts in composition following the 1999 windstorm (Table 3). These community types tended to be either dominated by wind-firm species or have significant advanced regeneration with composition very similar to overstory composition so that even in areas of high wind severity, there was little change in stand composition despite changes in stand structure.

Aspen and red pine/white pine community types experienced varied successional pathways following wind disturbance, but they varied in similar ways. 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 4). 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%) (Table 3, Figure 4). In contrast to aspen and red pine/white pine stands, succession to balsam fir was a less frequent 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 some conversion of black spruce to paper birch (27%) and white cedar (11%) (Figure 4).

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

**TABLE 3** Transition table for areas experiencing wind disturbance. Transitions reflect changes in community composition 1 year after wind disturbance[a]

| | **Community type (%)** | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | **Post-wind, 2000** | | | | | | | | **Percentage of plots** | | | **No. plots ($n = 479$)** | |
| **Pre-wind 1999** | **Aspen** | **J. pine** | **P. birch** | **R-W pine** | **B. spr** | **R. map** | **W. cedar** | **B. fir** | **Pre-wind** | **Post-wind** | **Change** | **1999** | **2000** |
| 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 |
| J. 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 |
| P. 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 |
| R-W 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 |
| B. spr | 1.2 | 0.0 | 27.2 | 0.0 | 53.1 | 2.5 | 11.1 | 4.9 | 16.9 | 18.6 | 9.9 | 81 | 89 |
| R. map | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 100.0 | 0.0 | 0.0 | 1.7 | 4.0 | 137.5 | 8 | 19 |
| W. 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 |
| B. 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 |

[a] Community types: Aspen *Populus* sp., J. pine *Pinus banksiana*, R-W pine *Pinus resinosa* and *Pinus strobus*, B. spr *Picea mariana*, R. map *Acer rubrum*, W. cedar *Thuja occidentalis*, and B. fir *abies balsamea*.

paper birch (21% of plots), black spruce (19%), balsam fir (17%), jack pine (17%), and white cedar (13%) (Figure 3a). Red maple increased from 1.7% to 4.0% of the areas affected by wind (Table 3). We found 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%), and jack pine (16%) stands, with red pine/white pine (10%), balsam fir (7%), and aspen (3%) also present (Figure 3b). 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 toward aspen and birch community types, but successional pathways were multiple and divergent (Figure 5; Table 4). Post-fire composition was heavily dominated by paper birch (38% of plots) and aspen (25%), with areas of jack pine (10%), cedar (9%), black spruce (8%), balsam fir (8%), and red pine and white pine (<1%) stands also present (Figure 3b).

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%). Balsam fir, black spruce, and paper birch stands also experienced some succession to jack pine following single fires (Figure 5), which partially offset conversions of jack pine stands to aspen or birch, in terms of post-fire jack pine abundance.

While the general successional pathway for single fire stands was toward early-successional community types, some plots showed shifts in composition from early-successional to 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 4). The majority (65%) of red pine/white pine-dominated plots succeeded to aspen post-fire (Table 4). 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 5; Table 4).

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 statistically significant convergence. A PERMANOVA test indicated significant differences in centroid locations before and after fire (*F* [1, 465] = 68.94; *p* = 0.0001).

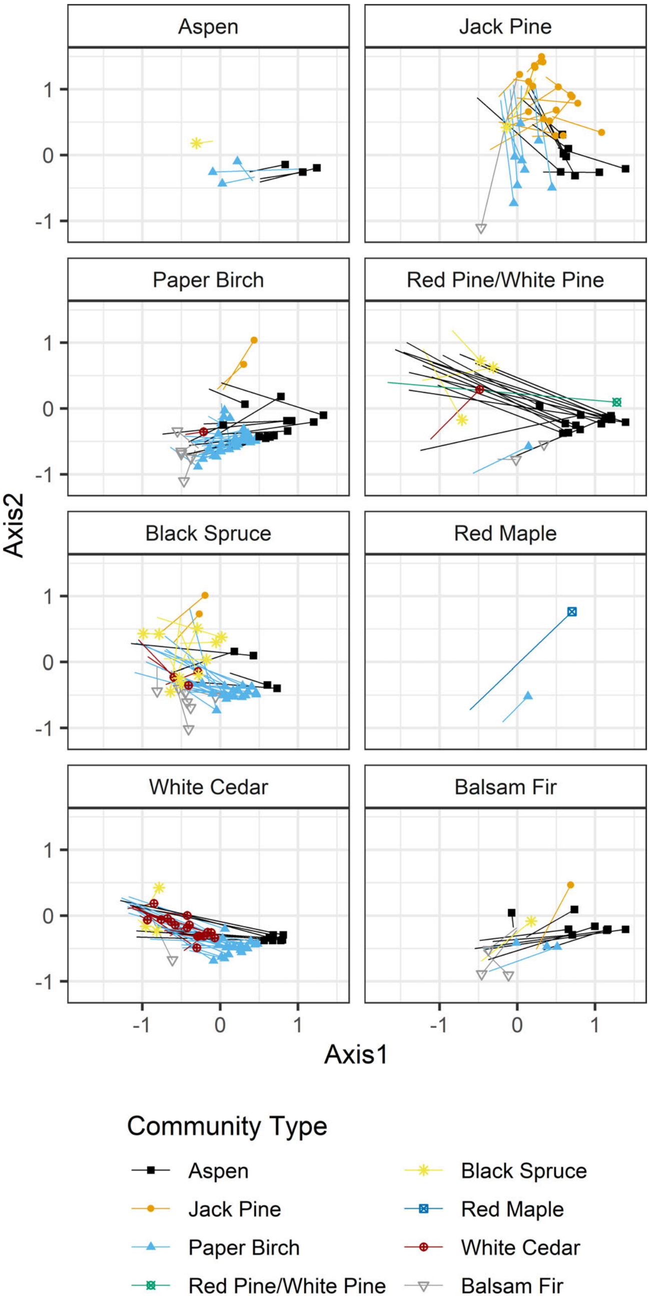

**FIGURE 5** Community transitions before and after fire for plots experiencing single fires sorted by pre-fire community type. Colors represent community type following disturbance. Symbols represent post-disturbance positions of plots in ordination space, and origins of vectors represent pre-disturbance positions. All panels are facets of the same overall nonmetric multidimensional scaling ordination solution

**TABLE 4** Transition table for areas experiencing single fires

| | **Community type (%)** | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | **Post-fire, 2012** | | | | | | | | **Percentage of plots** | | | **No. plots ($n = 233$)** | |
| **Pre-fire 2006** | **Aspen** | **J. pine** | **P. birch** | **R-W pine** | **B. spr** | **R. map** | **W. cedar** | **B. fir** | **Pre-fire** | **Post-fire** | **Change** | **2006** | **2012** |
| 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 |
| J. 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 |
| P. 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 |
| R-W 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 |
| B. spr | 8.7 | 4.3 | 43.5 | 0.0 | 21.7 | 0.0 | 6.5 | 15.2 | 19.7 | 8.2 | −58.7 | 46 | 19 |
| R. map | 0.0 | 0.0 | 50.0 | 0.0 | 0.0 | 50.0 | 0.0 | 0.0 | 0.9 | 0.9 | 0.0 | 2 | 2 |
| W. 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 |
| B. 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 |

*Note:* Community types as in Table 3.

## 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 6a), but following either the Cavity Lake Fire (2006) or the Ham Lake Fire (2007), there was strong convergent succession toward early-successional community types (Figure 6b). 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 6b).

Before the windstorm, this subset of the broader landscape was composed of older stands (median age 148 years) 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%), and 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 (15%), with aspen (7%), red maple (4%), and red pine/white pine (2%) also present (Figure 3c; Table 5). Aspen, black spruce, and jack pine 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 60% and paper birch 20% of this landscape post-wind and single fire (Table 6). 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 3c). Despite being heavily favored by the combination of wind followed by fire, neither aspen nor birch exhibited strong self-replacement following fire (Figure 6b). After fire, 52% of previously aspen plots remained aspen-dominated vs 41% succeeding to paper birch (Table 6). 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 6).

All community types except red maple, aspen, and birch declined in dominance following the combination of wind and single fire (Tables 5 and 6). 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%) and the majority of post-wind jack pine plots succeeded to either aspen (39%) or paper birch (15%) (Table 6). After both wind and fire, jack pine remained dominant on 10% of wind + single-fire plots (Figure 3c).

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-disturbance and 49% of plots post-wind (Figure 3c; Tables 5 and 6). 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 3c; Tables 5 and 6). Red maple stands were more likely to succeed to aspen than to self-replace, but some jack pine, balsam fir, and white cedar stands succeeded to red maple following fire (Figure 6b).

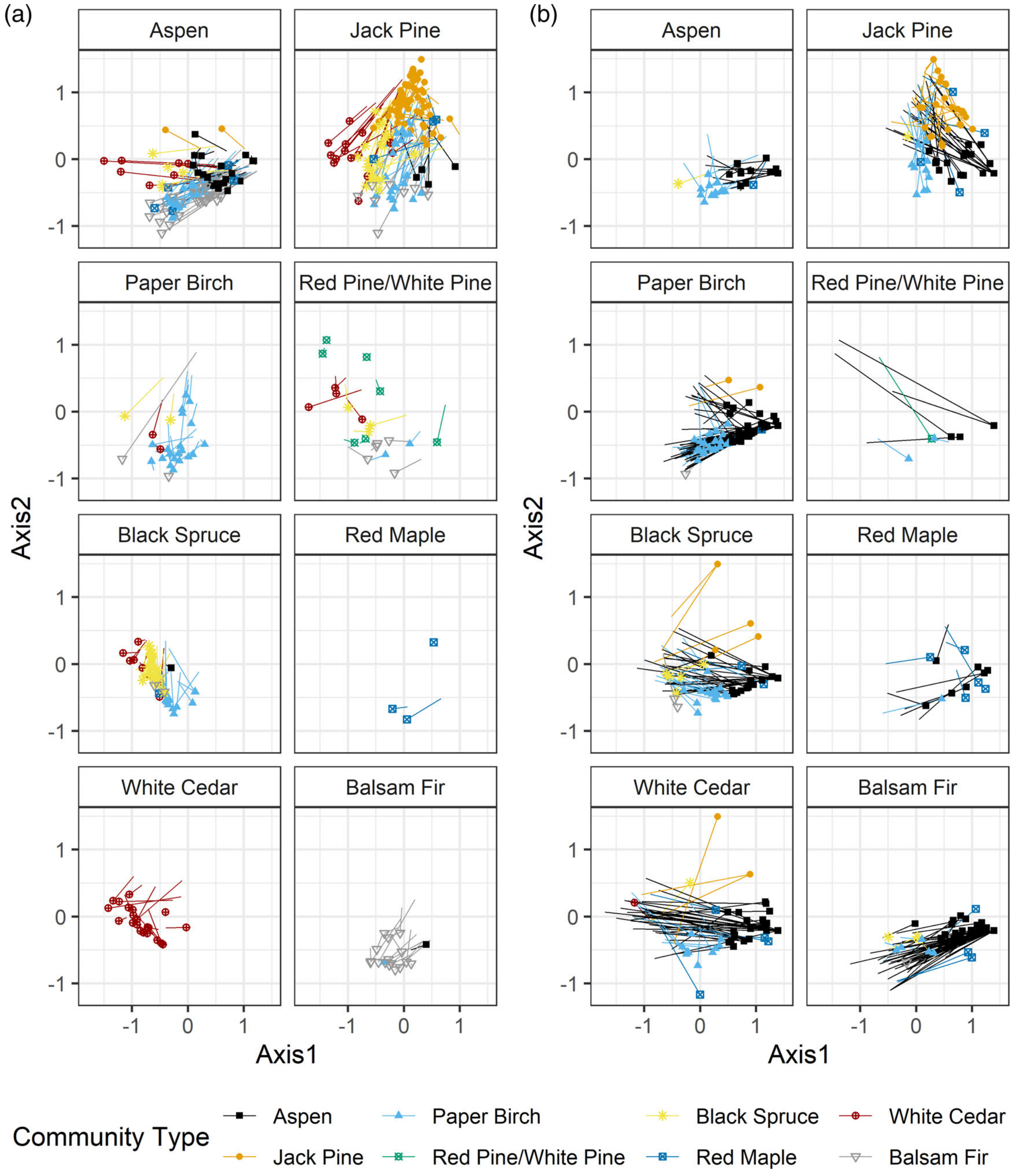

**FIGURE 6** Community transitions for plots experiencing wind followed by fire sorted by pre-disturbance community type. (a) Change in community composition following the 1999 windstorm sorted by the pre-wind community type. (b) Change in community composition after either the 2006 Cavity Lake Fire or the 2007 Ham Lake Fire sorted by the community type after the 1999 windstorm. Colors represent community type following disturbance. Symbols represent post-disturbance positions of plots in ordination space, and origins of vectors represent pre-disturbance positions. All panels are facets of the same overall nonmetric multidimensional scaling ordination solution

A PERMDISP test failed to find differences in dispersion before wind and after wind plus fire, indicating that although certain community types became rarer on the landscape, there was still a similar magnitude of variation among community types. A PERMANOVA test indicated that there were significant differences in centroid location 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 two fires

Areas subjected to wind followed by two 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 years) dominated by jack pine (43% of plots), black spruce

**TABLE 5** Transition table for areas experiencing wind followed by fire

| | Community type (%) | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Post-wind, 2000 | | | | | | | | Percentage of plots | | | No. plots ($n = 370$) | |
| Pre-wind 1999 | Aspen | J. pine | P. birch | R-W pine | B. spr | R. map | W. cedar | B. fir | Pre-wind | Post-wind | Change | 1999 | 2000 |
| 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 |
| J. pine | 2.9 | 46.0 | 17.5 | 0.0 | 14.6 | 2.2 | 10.2 | 6.6 | 37.0 | 17.6 | −52.6 | 137 | 65 |
| P. birch | 0.0 | 0.0 | 76.9 | 0.0 | 7.7 | 0.0 | 7.7 | 7.7 | 7.0 | 22.4 | 219.2 | 26 | 83 |
| R-W pine | 0.0 | 0.0 | 9.5 | 33.3 | 14.3 | 0.0 | 19.0 | 23.8 | 5.7 | 1.9 | −66.7 | 21 | 7 |
| B. spr | 2.0 | 0.0 | 28.0 | 0.0 | 48.0 | 2.0 | 14.0 | 6.0 | 13.5 | 14.6 | 8.0 | 50 | 54 |
| R. map | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 100.0 | 0.0 | 0.0 | 1.1 | 3.5 | 225.0 | 4 | 13 |
| W. 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 |
| B. 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 |

*Note:* Transitions in this table are those occurring following wind. Community types as in Table 3.

**TABLE 6** Transition table for areas experiencing wind followed by fire

| | Community type (%) | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Post-fire, 2012 | | | | | | | | Percentage of plots | | | No. plots ($n = 370$) | |
| Post-wind, pre-fire 2000 | Aspen | J. pine | P. birch | R-W pine | B. spr | R. map | W. cedar | B. fir | Post-wind pre-fire | Post-fire | Change | 2000 | 2012 |
| 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 |
| J. pine | 38.5 | 38.5 | 15.4 | 0.0 | 1.5 | 6.2 | 0.0 | 0.0 | 17.6 | 9.5 | −46.2 | 65 | 35 |
| P. birch | 66.3 | 2.4 | 27.7 | 0.0 | 0.0 | 2.4 | 0.0 | 1.2 | 22.4 | 20.5 | −8.4 | 83 | 76 |
| R-W pine | 57.1 | 0.0 | 28.6 | 14.3 | 0.0 | 0.0 | 0.0 | 0.0 | 1.9 | 0.3 | −85.7 | 7 | 1 |
| B. spr | 48.1 | 9.3 | 25.9 | 0.0 | 9.3 | 3.7 | 0.0 | 3.7 | 14.6 | 3.0 | −79.6 | 54 | 11 |
| R. map | 53.8 | 0.0 | 7.7 | 0.0 | 0.0 | 38.5 | 0.0 | 0.0 | 3.5 | 5.7 | 61.5 | 13 | 21 |
| W. cedar | 65.5 | 5.5 | 18.2 | 0.0 | 1.8 | 7.3 | 1.8 | 0.0 | 14.9 | 0.3 | −98.2 | 55 | 1 |
| B. fir | 81.8 | 0.0 | 7.6 | 0.0 | 4.5 | 4.5 | 0.0 | 1.5 | 17.8 | 1.1 | −93.9 | 66 | 4 |

*Note:* Transitions in this table are those occurring following fire. Community types as in Table 3.

**TABLE 7** Transition table for areas experiencing wind followed by 2 fires

| | Community type (%) | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Post-wind, 2000 | | | | | | | | Percentage of plots | | | No. plots ($n = 51$) | |
| Pre-wind 1999 | Aspen | J. pine | P. birch | R-W pine | B. spr | R. map | W. cedar | B. fir | Pre-wind | Post-wind | Change | 1999 | 2000 |
| 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 |
| J. pine | 18.2 | 18.2 | 4.5 | 0.0 | 27.3 | 0.0 | 22.7 | 9.1 | 43.1 | 11.8 | −72.7 | 22 | 6 |
| P. birch | 0.0 | 0.0 | 100.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 3.9 | 13.7 | 250.0 | 2 | 7 |
| R-W pine | NA | NA | NA | NA | NA | NA | NA | NA | 0.0 | 0.0 | NA | 0 | 0 |
| B. spr | 0.0 | 0.0 | 25.0 | 0.0 | 56.3 | 6.3 | 6.3 | 6.3 | 31.4 | 31.4 | 0.0 | 16 | 16 |
| R. map | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 100.0 | 0.0 | 0.0 | 2.0 | 5.9 | 200.0 | 1 | 3 |
| W. 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 |
| B. 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 |

*Note:* Transitions in this table are those occurring following wind. Community types as in Table 3.

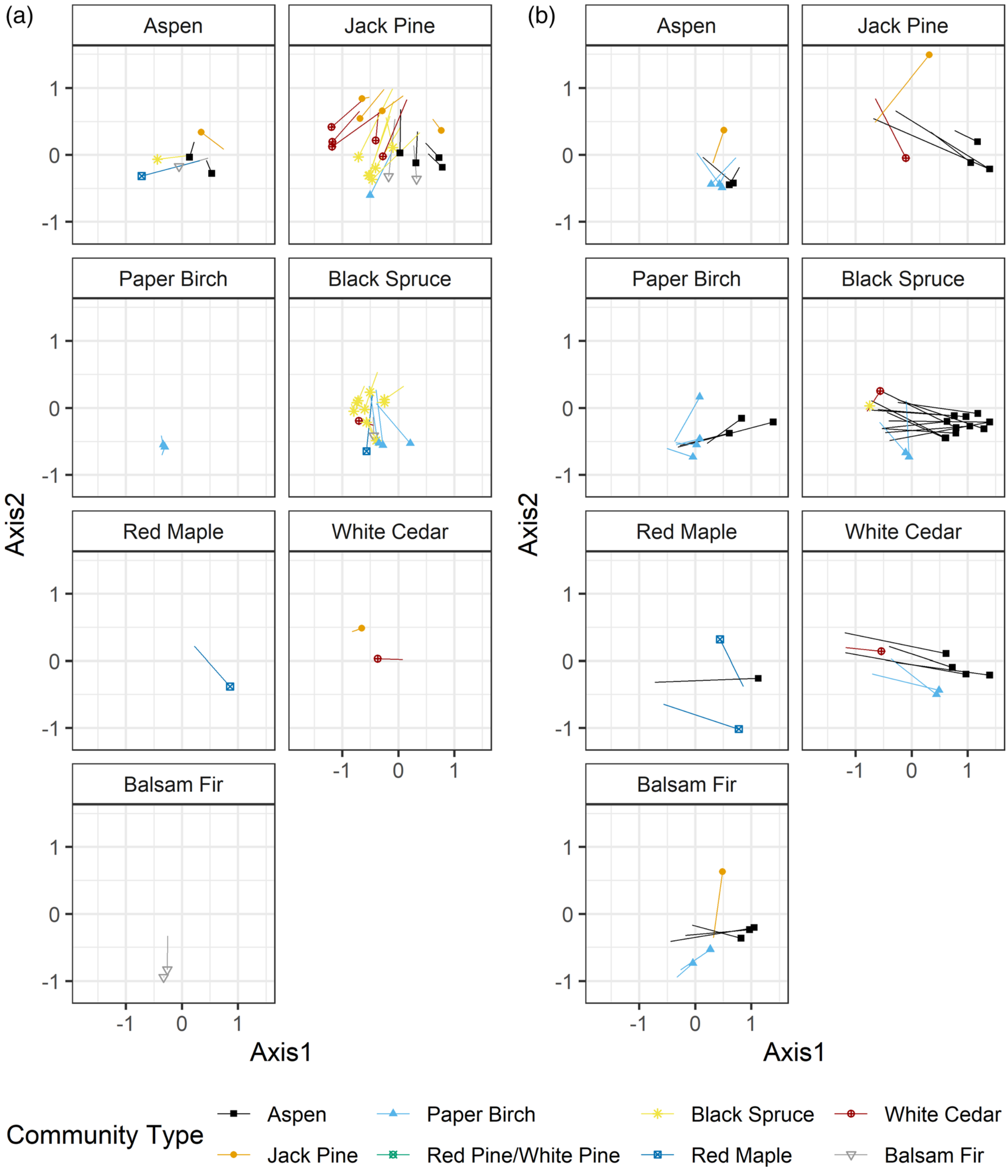

**FIGURE 7** Community transitions for plots experiencing wind followed by two fires. (a) Community transitions following the 1999 windstorm sorted by the community type prior to wind disturbance. (b) Community transitions following prescribed fires in 2002–2004 followed by the Ham Lake Fire of 2007 sorted by the community type prior to fire disturbance. Colors represent community type following disturbance. Symbols represent post-disturbance positions of plots in ordination space, and origins of vectors represent pre-disturbance positions. All panels are facets of the same overall nonmetric multidimensional scaling ordination solution

(31%), and aspen (12%), with balsam fir (4%), white cedar (4%), paper birch (4%), and red maple (2%) also present (Figure 3d, Table 7). 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 (Figures 3d and 7a). Following prescribed fires in either 2002, 2003, or 2004 and the Ham Lake Fire of 2007, there was a strong trend toward increasing aspen and birch regardless of pre-fire composition (Figure 7b; note that there were no data between the two fires). After wind and two fires, this area was dominated by aspen (57% of

**TABLE 8** Transition table for areas experiencing wind followed by 2 fires

| | **Community type (%)** | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | **Post-two fires 2012** | | | | | | | | **Percentage of plots** | | | **No. plots ($n = 51$)** | |
| **Post-wind, pre-fire 2000** | **Aspen** | **J. pine** | **P. birch** | **R-W pine** | **B. spr** | **R. map** | **W. cedar** | **B. fir** | **Post-wind pre-fire** | **Post-2 fires** | **Change** | **2000** | **2012** |
| 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 |
| J. 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 |
| P. 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 |
| R-W pine | NA | NA | NA | NA | NA | NA | NA | NA | 0.0 | 0.0 | NA | 0 | 0 |
| B. spr | 75.0 | 0.0 | 12.5 | 0.0 | 6.3 | 0.0 | 6.3 | 0.0 | 31.4 | 2.0 | −93.8 | 16 | 1 |
| R. map | 33.3 | 0.0 | 0.0 | 0.0 | 0.0 | 66.7 | 0.0 | 0.0 | 5.9 | 3.9 | −33.3 | 3 | 2 |
| W. 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 |
| B. 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 |

*Note:* Transitions in this table are those occurring following 2 fires. Community types as in Table 3.

plots) and paper birch (26%) with jack pine (6%), white cedar (6%), red maple (4%), and black spruce (2%) also present (Table 8).

Aspen stands were a minor component of this landscape prior to the 1999 wind disturbance, and declined further afterward, 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 largely failed to self-replace following repeated fires with only 17% of the residual post-wind jack pine plots remaining jack pine-dominated after two fires (Figure 7; Table 7).

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 two 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 (Table 8). Black spruce, balsam fir, and white cedar community types all increased following wind, but were greatly reduced following repeated fires (Figure 3d; Tables 7 and 8). Red maple was present on only 2% of plots for areas affected by wind and two fires prior to disturbance, but increased following wind to 6% of plots. Following two fires, there was a modest decline in red maple dominance, but sample size for this community type was very small (three plots) (Table 8).

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 two or three 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 instances of multiple disturbances, there was a successional shift toward aspen and birch following the final fire in the sequence (Figure 8). Prior to the Ham Lake Fire, this portion of the landscape was composed of mostly young jack pine (46% of plots), black spruce (23%), and aspen (19%) 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 16% of plots post-fire (Table 9; Figure 8). There was significant succession of jack pine plots to aspen (56%) and paper birch (13%) community types. Paper birch was only a minor component (1% of plots) of this landscape prior to the Ham Lake Fire, but increased significantly following the Ham Lake Fire to dominate 20% of this landscape (Table 9; Figure 3e). Many stand types including black spruce, jack pine, red/white pine, and white cedar stands succeeded to paper birch after the Ham Lake Fire. Aspen increased significantly from 19% to 54% of plots following the Ham Lake Fire (Figure 3e) through a combination of high self-replacement (85%) and succession from jack pine and black spruce stands (Figure 8; Table 9). Black spruce self-replaced on 13% of black spruce plots and largely succeeded to aspen (44%) and paper birch (25%). White cedar was a minor component of these stands pre-Ham

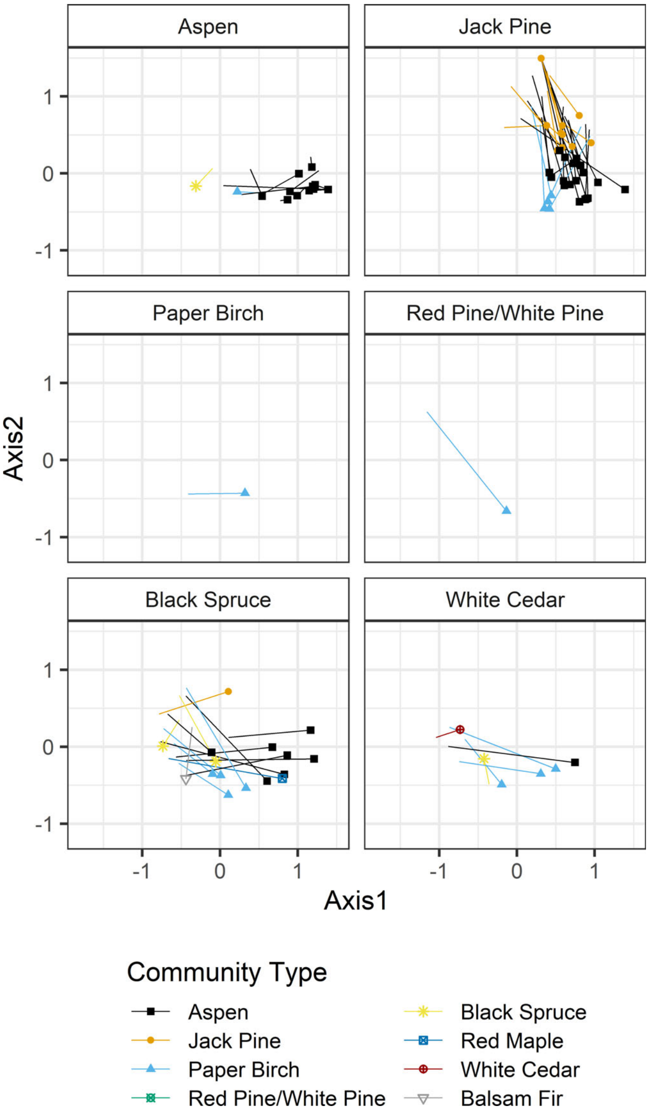

**FIGURE 8** Community transitions following the Ham Lake Fire (2007) for plots previously experiencing fires in 1995, 1974 and 1995, or 2002–2004 (but no wind disturbance). Colors represent community type following disturbance. Symbols represent post-disturbance positions of plots in ordination space, and origins of vectors represent pre-disturbance positions. All panels are facets of the same overall nonmetric multidimensional scaling ordination solution

Lake Fire (9% of plots) and declined significantly (1% of plots) post-fire (Figure 3e). 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 9).

A PERMDISP test failed to find differences in dispersion before and after the Ham Lake Fire for plots experiencing two or three 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

Our large number of plots with different disturbance histories enabled an examination of how single and multiple disturbances differed in their effects on succession and community composition. Because of the potential for reduced disturbance legacies, we expected instances of multiple disturbances to result in greater compositional change and increased successional convergence relative to single disturbances. 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 (Figure 2b) and that wind disturbance increased shade-tolerant coniferous community types and decreased aspen community types (Figures 2b and 9). In contrast, in instances of multiple disturbances many coniferous community types were greatly reduced, and aspen and birch community types increased dramatically, resulting in a landscape that was far more dominated by deciduous species post-disturbance (Figures 2b and 9). Here, we discuss the successional pathways of disturbance types and disturbance combinations and the degree to which the data support the hypotheses presented in Introduction, while additional details of discussion for each community type are given in Appendix S2.

## Wind disturbance

Although wind disturbances are locally important drivers of successional dynamics in the eastern boreal zone and maritime portions of the boreal forest where fires are less frequent (Waldron et al., 2013), stand-leveling wind disturbance has historically been a relatively rare disturbance compared with fire in the central North American boreal forest. This study presents to our knowledge the most detailed picture of windstorm dynamics in such forests published to date. The results support all of the tenets of H1. First, that post-wind forests consisted mainly of shade-tolerant advanced regeneration of balsam fir, white cedar, and red maple, with some black spruce and paper birch. Second, that wind disturbance caused succession from early-successional communities to late-successional species as a group across the landscape, but that at the stand scale, there was divergence among those late-successional community types. Furthermore, this case of accelerated and divergent succession, caused by selective weeding of the forest by wind, also supports the predictions of the cusp catastrophe and forest legacy/ecological memory theories (Frelich, 2002; Jõgiste et al., 2017; Johnstone et al., 2016).

Some early-successional species including aspen and jack pine are especially susceptible to wind disturbance (Rich et al., 2007). Aspen and jack pine both experienced high mortality during the 1999 windstorm, with mortality

**TABLE 9** Transition table for areas experiencing 2 or 3 fires

| | Community type (%) | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Post-Ham Lake Fire, 2012 | | | | | | | | Percentage of plots | | | No. plots ($n = 69$) | |
| Pre-Ham Lake Fire 2006 | Aspen | J. pine | P. birch | R-W pine | B. spr | R. map | W. cedar | B. fir | Pre-fire | Post-fire | Change | 2006 | 2012 |
| Aspen | 84.6 | 0.0 | 7.7 | 0.0 | 7.7 | 0.0 | 0.0 | 0.0 | 18.8 | 53.6 | 184.6 | 13 | 37 |
| J. pine | 56.3 | 31.3 | 12.5 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 46.4 | 15.9 | −65.6 | 32 | 11 |
| P. birch | 0.0 | 0.0 | 100.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 1.4 | 20.3 | 1300.0 | 1 | 14 |
| R-W pine | 0.0 | 0.0 | 100.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 1.4 | 0.0 | −100.0 | 1 | 0 |
| B. spr | 43.8 | 6.3 | 25.0 | 0.0 | 12.5 | 6.3 | 0.0 | 6.3 | 23.2 | 5.8 | −75.0 | 16 | 4 |
| R. map | NA | NA | NA | NA | NA | NA | NA | NA | 0.0 | 1.4 | NA | 0 | 1 |
| W. cedar | 16.7 | 0.0 | 50.0 | 0.0 | 16.7 | 0.0 | 16.7 | 0.0 | 8.7 | 1.4 | −83.3 | 6 | 1 |
| B. fir | NA | NA | NA | NA | NA | NA | NA | NA | 0.0 | 1.4 | NA | 0 | 1 |

*Note:* The 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. The 2012 time step is following the 2007 Ham Lake Fire and one of the previously mentioned fire scenarios. Community types as in Table 3.

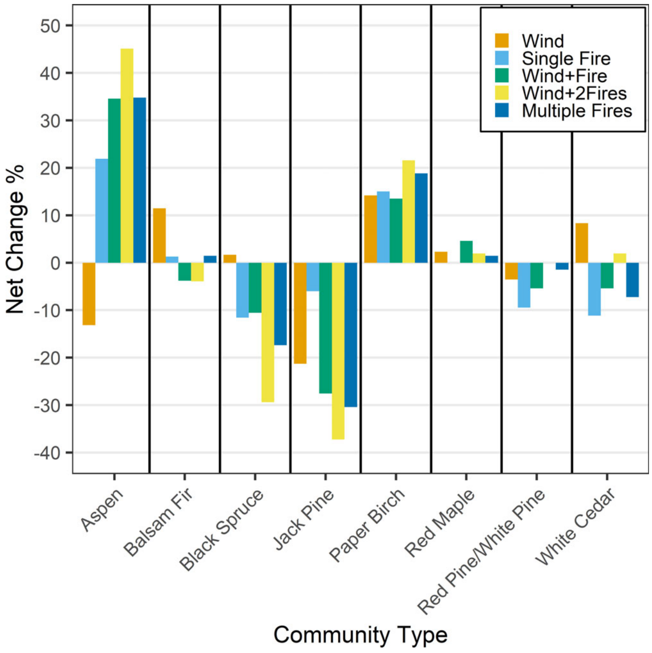

**FIGURE 9** Net change in community type dominance by disturbance type

rates for mature trees in the range of 50%–80% (Rich et al., 2007), and these community types became much less dominant post-windstorm (Figures 3a and 4). Some shade-tolerant species—red maple and white cedar—are relatively wind-firm across all size classes of trees, while advanced regeneration of black spruce and balsam fir had very low wind mortality, despite high mortality of mature individuals in the canopy (Rich et al., 2007). In many cases, shade-tolerant species were able to survive the storm as scattered mature trees, or the selective removal of early-successional species allowed shade-tolerant advanced regeneration to become the new canopy layer following wind disturbance (Rich et al., 2007). Paper birch, however, was an outlier in that it is both shade-intolerant and wind-firm, allowing it to increase in dominance, consistent with the observation by Frelich and Reich (1995b) that paper birch in the BWCAW is both an early- and a late-successional species.

Because of differences in shade tolerance and wind firmness among 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, white cedar, black spruce, and the species with ambiguous successional status, paper birch, as indicated by both the ordination and the significant PERMDISP statistic. In contrast, paper birch and white cedar community types experienced successional convergence as other community types succeeded to them (indicated by ordination in Figure 4; however, we were not able to perform a PERMDISP for this convergence). The existence of simultaneous divergence and convergence was previously noted by Frelich and Reich (1995b) and Frelich (2002).

## Single fires

Stand-replacing crown fires are the primary disturbance events shaping species composition and succession in the

North American boreal forest (Johnson, 1992); moreover, most boreal tree species are well adapted to fire (Johnson, 1992). Because of the long history of fire and concomitant fire adaptations of many boreal tree species, we expected that single fires would result in mixes or early-successional species similar to pre-fire composition, without strong successional convergence (H2). However, the results showed only a moderate level of support for this hypothesis, as some convergence did occur (as indicated by a significantly decreasing PERMDISP test) and some late-successional species were present in most post-fire stands.

The single-fire events that we examined resulted in modest successional convergence toward the early-successional forest types aspen and paper birch, which 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 (Figure 5). Natural disturbances tend to be inherently patchy, and in a landscape of broken topography with many rock outcrops and numerous lakes and low-lying wetlands, even large fires routinely leave disturbance legacies in the form of unburned islands, lakeshores, or small patches of surviving trees (Carlson et al., 2011; Heinselman, 1996). Despite increased dominance by aspen and birch, many post-fire stands had at least some black spruce, white cedar or balsam fir components (Table 4). Where ample seed sources existed, some of these species were locally dominant, ensuring the continued presence of these community types on the landscape.

Overall succession in the case of single-fire events exhibited multiple successional pathways with a general shift toward 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 (Figure 5).

This latter finding for jack pine is contrary to our expectation that jack pine would be maintained by single fires, since this is the quintessential boreal "fire pine" species with serotinous cones, low foliar moisture, and high canopy density, all characteristics that promote the types of fires that perpetuate the species (Heinselman, 1973; Mutch, 1970). Instead, the findings showed mixed results with a significant proportion of jack pine stands converting to aspen and birch, representing a substantial resilience debt that only became evident at the time of a fire. The lack of jack pine regeneration in single fires was most likely due to the seasonal timing of fire and fire effects. Ninety-five percent of jack pine stands affected by single fire were located in the Ham Lake Fire, which burned in early May when deep organic layers were still relatively moist, and as a result generally failed to expose large areas of mineral soil that are an important prerequisite for jack pine regeneration (Chrosciewicz, 1974, details in Appendix S2).

## Multiple disturbances

Changes in composition following multiple disturbances were more pronounced than those occurring following single disturbances, with strong convergence to early-successional species (H3). With few exceptions, birch and aspen were heavily favored, regardless of the pre-disturbance community type, by combinations of wind and fire or multiple fires within a short period of time (H4). Intriguingly, however, neither birch nor aspen was particularly strong at self-replacement, often shifting to each other (Figures 6–8). At the same time, multiple disturbances largely eliminated boreal conifers that had been among the most dominant pre-disturbance community types.

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 two 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 two 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 compositions, which were more like each other than to any other disturbance types or combinations. 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 differences in successional pathways between wind and fire as single disturbances, we found little difference in composition of stands that had undergone combinations of these disturbances.

Despite strong shifts toward aspen and birch community types following multiple disturbances, we failed to find significant differences in community dispersion as predicted by H3 and measured by PERMDISP. There was a significant decrease in community dispersion for single fire plots, but not for other disturbance types/combinations that we investigated. Although the results of our ordination indicated strong convergence toward aspen and birch as the dominant community types, the PERMDISP results suggested that 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 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 restricted to refuge positions such as lowlands and lakeshores where disturbance frequency and severity tend to be lower.

The results also partly support the existence of the double-cusp model of the cusp catastrophe theory of forest dynamics proposed by Frelich (2002). Some jack pine communities were perpetuated by single fires (H2), and most of those which experienced multiple disturbances were converted to birch and aspen communities (H4). Clearly, fires coming at intervals short enough so that boreal conifers do not reach seed-bearing age by the time of the second fire, or a fire coming after windthrow so that cones of boreal conifers are close to the ground where fire intensity and duration are longer, combined with lack of seed production between the time of the windstorm and fire, can lead to (1) very high cumulative disturbance severity and a longer gradient of disturbance severity as predicted by the cusp catastrophe two-cusp model (Figure 1), and (2) a much stronger filter on ecological legacies and incompatibility of boreal conifer legacy syndromes as predicted by ecological memory/legacy theory.

The evidence presented here indicated that the cumulative disturbance severity of multiple disturbances caused convergence of boreal conifer communities into birch–aspen communities, regardless of whether they started as fire-dependent jack pine or non-fire-dependent communities dominated by late-successional, shade-tolerant species after wind disturbance; these changes are not the signature of latest disturbance that occurred by itself. However, the middle level of the two-cusp model where jack pine exists is also shrinking as resilience debt diminishes the ability of the species to regenerate after single fires, and jack pine stands are likely to experience more multiple disturbances in the future. Thus, the "safe operating space" (Johnstone et al., 2016) for jack pine forests, at least in the BWCAW, appears to be shrinking for two different reasons.

## An overview of BWCAW disturbance and comparison with Heinselman's classic research

In this study, we documented dramatic shifts in community composition following both single and multiple disturbance events (Figures 2 and 9). Although the data revealed some similarities compared with classic research on fires and succession in the BWCAW with regard to community change following all single disturbance types and all disturbance combinations, we also found some important differences and characterized community responses to multiple disturbances, which were previously poorly documented (Figure 10). Single fires resulted in relatively large proportions of conifer stands converging into aspen and birch (Figure 10a, dashed arrows) in contrast to the lack of succession (Figure 10a, solid arrows) found by previous studies (Frelich & Reich, 1995b; Heinselman, 1973; Ohmann & Grigal, 1979). Wind disturbance resulted in extensive mortality of mature aspen, jack, red, and white pine, releasing shade-tolerant advanced regeneration of black spruce, balsam fir, and cedar, with a pattern of diverging successional pathways coming from the pre-disturbance community types, converging into the post-disturbance types (Figure 10b). The multiple disturbance events we observed tended to greatly reduce or eliminate coniferous community types (including both old early-successional pine forests that survived the 1999 windstorm and young, late-successional balsam fir, black spruce, and white cedar created by the windstorm) and heavily favored convergence into deciduous species capable of long-distance seed dispersal and vegetative reproduction (Figure 10c), in agreement with the very limited previous observations of multiple disturbances (Heinselman, 1973).

## CONCLUSIONS

All disturbances leave legacies in their wake whether they are material legacies such as 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), although if the disturbance type is incompatible with the disturbance-legacy syndrome of a dominant species, change in community composition can occur (Jõgiste

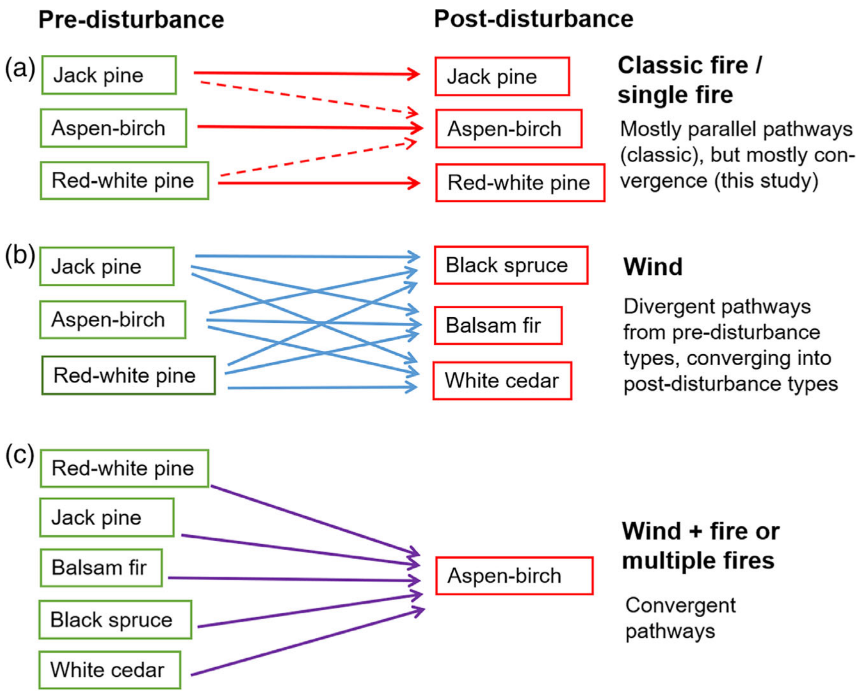

**FIGURE 10** Conceptual diagram summarizing predominant types of community change following disturbance in the Boundary Waters Canoe Area Wilderness (BWCAW). (a) Solid arrows, succession after classic studies of single fires; and dashed arrows, convergence from conifer forests to aspen and birch in the current study. (b) Divergent pathways from pre-windstorm community types and convergence into post-windstorm community types. (c) Convergent pathways after multiple disturbances, including late-successional conifer forests created by the 1999 windstorm that were later burned (wind + fire) or burned two or three times within 35 years. Note that to reduce the complexity of this figure and focus on the main findings, birch and aspen community types were merged, and the red maple community type (which occupies a very small proportion of the BWCAW) was not included

et al., 2017). This explains the answer to the first question posed in Introduction: How do patterns of succession differ after wind and fire? Single-wind disturbance causes accelerated succession to a variety of species adapted to that disturbance type via the presence of advanced regeneration associated with shade tolerance (Figure 1, blue arrows), while single fires cause or maintain dominance by early-successional species (Figure 1, red arrows).

The answer to the second question posed in Introduction: Do multiple disturbances lead to successional convergence? is yes, for complex reasons. First, 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 so that post-disturbance material legacies may include very few, if any, surviving seeds, seedlings, root systems, or mature trees of the pre-disturbance species. In such cases, loss of ecosystem resilience may lead to novel successional outcomes (Paine et al., 1998). A second reason for convergent succession after multiple disturbances is that, because of the ages for sexual maturity of many boreal conifers (20–40 years), even fire-adapted coniferous species are vulnerable to fire disturbance when young, at least until the initial cohort can produce seeds (Heinselman, 1973). A second or third fire such as those that occurred on our multiple fire sites can easily eliminate any conifer regeneration and reduce or eliminate legacies from the first disturbance. In stands affected by multiple disturbances, some community types such as jack pine or red pine and white pine were largely eliminated by the paucity of disturbance legacies. In the boreal forest, where single disturbances on rotation intervals of 50–100 years are the norm and forests tend to be dominated by serotinous conifers such as 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 boreal deciduous species.

Aspen and birch both had dramatic increases in dominance at the expense of conifers, following single-fire events, wind–fire combinations, and multiple fires within a short period of time, but increases were most dramatic in multiple disturbance areas (Figure 9). 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 are similar to those caused elsewhere 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 (Friedman & Reich, 2005; Heinselman, 1996; Stearns, 1997). These changes to the landscape outside the BWCAW have proven persistent (Friedman & Reich, 2005), and it seems likely that the conversion of pine 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 temperature and reduced soil moisture availability (Reich et al., 2015; Reich et al., 2018), and increased disturbance frequency, are likely to favor boreal deciduous species over boreal coniferous species (Johnstone & Chapin, 2006), although in ecotonal forests, more southerly temperate species such as red maple will benefit the most (Reich et al., 2015). While advanced regeneration of boreal conifer species such as black spruce and balsam fir is 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, 2012) 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, Reich et al., 2018), 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 to the direct effects of climate change than black spruce or balsam fir, but these species are still vulnerable to a warming climate. 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 Great Lakes region, 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., 1993). 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.

To successfully manage forests in the face of climate change, managers will need to consider both species potential physiological tolerances to warmer temperatures and their ability to adapt and tolerate changing disturbance regimes. Unfortunately, except for red maple, all of 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 (Fisichelli et al., 2012; Handler et al., 2014; Reich et al., 2015).

Without modulation of future disturbance regimes or meaningful reductions in $CO_2$ 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 & Reich, 2009). Boreal forests exhibit threshold responses to climate change that can transform them quickly to alternate states such as temperate forests or savannas (Scheffer et al., 2012; Toot et al., 2020), and adding novel disturbance regimes on top of climate change would only exacerbate the direct effects of climate change (Frelich & Reich, 2010; Johnstone et al., 2016).

With both fire and wind events 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 refugial populations of species that are vulnerable to multiple disturbances and to climate change itself (Stralberg et al., 2020).

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## CONFLICT OF INTEREST

The authors declare no conflict of interest.

## DATA AVAILABILITY STATEMENT

Data are available from the Data Repository for U of M: https://conservancy.umn.edu/handle/11299/219223.

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## SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

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