Supporting Information. Anoszko, E.R., L.E. Frelich, R.L. Rich, and P.B. Reich. 2021. Wind and fire: rapid shifts in tree community composition following multiple disturbances in the southern boreal forest. Ecosphere.

Appendix S2. Additional discussion on effects of single and multiple disturbances on community types.

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

Despite the large increase in aspen and birch dominance following fire and fire combinations, both birch and aspen often exhibited surprisingly weak self-replacement rates and in many instances birch stands were more likely to succeed to aspen following fire than to birch, and vice-versa. The low rate of self-replacement could in theory be due in part to small shifts in composition in mixed stands, but on average plots classified as paper birch dominated or aspen dominated were greater than 60% dominated by their nominal species, with the other (either aspen or birch) making up less than 10% of the total stand. The low self-replacement rates of aspen and birch following wind and fire combinations suggest that these species have neutral to negative neighborhood effects whereby these species are unable to modify their local environment to favor their own regeneration over other species. In this case factors other than pre-fire composition such as seasonal timing of fire are likely more useful predictors of post-disturbance composition. One exception to the trend of low self-replacement following fire was paper birch stands affected by single fires. Most of the single fire sites we examined were burned in late-season fires that are known to favor paper birch over aspen (Anoszko 2018). Conversely aspen stands had very high self-replacement in instances of multiple fires, where the last fire for all samples was the early-season Ham Lake Fire; early season fires tend to favor aspen over paper birch even when accounting for differences in fire severity between early and late season fires (Anoszko 2018).

Because of narrow moisture and temperature requirements for aspen seedling establishment (Einspahr and Winton 1976; Perala 1990), it is possible that the large increase in aspen documented across burned areas in our study could in part be due to ample moisture following fire in the spring of 2007 when most post-fire recruitment occurred. Had the period following the 2007 Ham Lake Fire been drier, it is possible aspen might have failed to reproduce sexually and been restricted to areas where it could root sprout. Without this significant aspen seedling recruitment, overall regeneration may have been sparser and more paper birch dominated. The high severity nature of multiple combined disturbances also suggests that long-distance seed dispersal might be more important than sprouting, especially in cases of large infrequent disturbances (Turner et al. 2003) or multiple disturbances within a short period of time.

Red maple community type—Red maple was an uncommon community type prior to disturbance, but increased in abundance following the 1999 windstorm, as it was relatively wind firm (Rich et al 2007) and a well distributed minor component of advanced regeneration across a variety of stand types. Following the fires of 2006-2007 red maple increased in abundance via both basal sprouts and seedlings. Like paper birch, red maple was one of the few community types that increased in dominance across virtually all disturbance types/combinations. Although red maple is commonly thought of as a fire sensitive species, our results are similar to at least one other study of combined disturbance in the Lake States that found red maple increased in relative abundance in a clear cut followed by fire (Scheiner et al. 1988). As red maple appears both tolerant of a wide variety of disturbances and is a temperate species well adapted for a warming boreal climate (Reich et al. 2015), it appears red maple could be among the most successful species under climate change scenarios that increase both temperatures and future disturbance frequency.

Jack pine community type—Jack pine was the most common pre-disturbance stand type across areas examined in this study, however, representation of jack pine stands decreased after all disturbance types and combinations. Jack pine is typically regarded as a pyrophillic species because of its serotinous cones and its well-documented tendency to self-replace with high density regeneration following stand-replacing boreal crown fires (Ahlgren 1959, Cayford 1963, Ohmann and Grigal 1979, Heinselman 1996). However, jack pine was notably absent from regeneration following the Cavity Lake and Ham Lake Fires in areas previously wind-disturbed (in 1999) and it was present but declining in dominance in areas experiencing single or multiple fires. In many cases jack pine stands subjected to wind followed by fire failed to regenerate to jack pine and were replaced by aspen or birch. The paucity of jack pine regeneration following fire documented in this study is counter to the published literature on jack pine silvics and warrants careful examination. We hypothesize several possible explanations for why jack pine failed to regenerate following wind and fire. 1) Windstorm fueled fires may have burned with a greater intensity and duration, and/or the fallen crowns of jack pine may have placed aerially-stored seedbanks in areas of higher fire intensity and duration, either of which could have generated lethal temperatures that destroyed or consumed the serotinous cones and seeds. 2) Mortality of adult trees followed by a three to eight year period of time until fires occurred may have reduced the viability of jack pine seed such that jack pine failed to regenerate. 3) Other stochastic factors such as the seasonal timing of fire or unique fire behavior may have created seed bed conditions that placed jack pine at a competitive disadvantage.

There is no doubt that heavily wind-damaged areas of our study had greater fuel loads than those that had escaped the 1999 blowdown (Woodall and Nagel 2007) and consequently these areas tended to burn with greater intensity than non-windstorm areas, but it is unclear whether the increased intensity of post-windstorm fires alone was enough to cause mortality of jack pine seed. Serotinous jack pine cones are very tolerant of temperatures generated during forest fires and seed mortality typically occurs only when the cones themselves ignite. However, despite the increased temperature and duration of fires in windstorm fuels and proximity of fallen crowns and cones to the most intense part of the fire, field crews collecting data in the aftermath of the fire reported large numbers of open jack pine cones, indicating that windstorm fires did not always burn so hot as to consume all jack pine cones. Nonetheless, it is difficult to rule out the possibility that some jack pine seed was destroyed by fire. The consensus of forest management for jack pine is that burning slash following clear cutting does not typically lead to successful jack pine reproduction unless there are viable seed trees left after harvest, because slash fires generally destroy seeds in slash even if they otherwise produce good seedbeds (Chrosciewicz

1959, Benzie 1977, McRae 1979, Chrosciewicz 1990). In our study, the combination of wind followed by fire may have created conditions similar to a clear cut followed by a slash fire without sufficient seed trees, partially explaining the failure of jack pine to regenerate in these areas.

Viability of jack pine seed declines with age and may be partially responsible for the failure of jack pine to regenerate following the windstorm fires in our study. Beaufait (1960) in a study of jack pine seed collected from Michigan, USA, found that jack pine seed germination rates average about 76% for one-two year old cones, but that germination rates fall as low as 33% for cones five years and older. In our study, the majority of adult jack pine trees were killed in the July 4th, 1999 derecho event. The first fires in our study occurred in 2002, three years following the windstorm and the last fires in our study, which account for the large majority of area burned, occurred seven to eight years after the windstorm. Although the data are limited, there is some evidence to suggest that jack pine regeneration was more successful in areas that burned three years after the windstorm than areas that burned after eight years. Two prescribed post-windstorm fires, the 2002 Threemile Island burn and the 2002 Magnetic Lake burn, both had relatively good regeneration of jack pine; of 18 plots classified as jack pine prior to the pre-wind and fire, 10 (55%) remained jack pine post-wind and fire. This rate of self-replacement is closer to that of the single fire stands we observed where jack pine self-replaced on 43% of plots. In contrast, only 23% (n=151) of stands classified as jack pine before the windstorm remained jack pine dominated following burns in the windstorm affected portions of the Ham and Cavity Lake Fires of 2006-2007. Although differences in regeneration success between these prescribed fires and the wildfires in our study could be due to differences in fire effects, all of these fires had mean ground fire severity values close to four, indicating that there was on average, complete consumption of the litter layer and at least partial consumption of the duff layer, which is expected to yield good conditions for jack pine seed germination. This suggests that the timing of fire following windstorm may have played a role in successional outcomes due to declining jack pine seed viability with time since adult tree mortality.

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

Jack pine also declined in dominance in cases of multiple fires within a short period of time, although the reductions in jack pine were not as severe as in cases of wind+fire combinations. We observed jack pine in our study producing non-serotinous cones at three years of age although good seed crops and serotinous cones typically take >10 years to develop (Rudolf 1965). If a fire occurs before young trees develop sufficient serotinous cones there is little chance of reseeding after fire unless significant refugia of surviving jack pine are present. Even in cases where jack pine is old enough to produce sufficient serotinous cones, the re-burn fire may burn with too low of an intensity and merely girdle the trunks without generating sufficient heat to release serotinous cones. Both of these patterns were observed in our multiple fire sites where jack pine stands that originated after the 1995 Sag Corridor fire were reburned 12 years later by the Ham Lake Fire. Flame lengths were generally very low in this reburned area (<50cm) such that the few serotinous cones that existed at the time of the fire were observed to remain unopened following fire. The lack of sufficient jack pine seed source created conditions favorable for the invasion of light-seeded and long-dispersing aspen and birch. Similar regeneration failure occurred on sites experiencing wind followed by two fires where stands of jack pine which survived the windstorm had extremely low self-replacement rates after two fires (<15%). Although there have been few observations of jack pine following repeated fires, our results are similar to the observations of Eyre and LeBarron (1944), who noted that fires which occurred before jack pine can produce sufficient seed may convert jack pine stands to "a waste of brush and grass". In addition, our results are similar to those of Johnstone and Chapin (2006) who found that boreal conifer dominated stands in the Yukon and British Columbia were much more likely to succeed to aspen if fires occurred less than 25 years apart.

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

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

Balsam fir community type—Like black spruce, balsam fir is relatively wind-firm when small, but vulnerable to wind when large (Rich et. al 2007). As a shade-tolerant species, balsam fir was well established throughout pre-disturbance stands in our study. Most stands were greater than 100 years old and had already begun the demographic transition from typically monodominant stands of early-successional species to more mixed stands dominated by gap dynamics as shade-tolerant advance regeneration succeeds the initial post-fire cohort (Frelich and Reich 1995). While balsam fir was not among the most dominant community types prior to disturbance, it was a well distributed component of early-successional stand types. The 1999 windstorm greatly increased balsam fir's dominance on the landscape by selectively removing the remaining early-successional jack pine and aspen components of stands and releasing advanced regeneration of fir. Thus, the effect of the windstorm was to accelerate succession.

Unlike black spruce, balsam fir is both vulnerable to fire, and lacks fire adaptations such as serotinous cones, and is therefore wholly dependent on surviving refuge populations for reestablishment post-fire. In areas burned in single fires balsam fir dominance declined modestly following fire, but declines were steep and dramatic for areas affected by wind-fire combinations. While balsam fir was more dominant post wind alone, the increased intensity of windstorm-fueled fires left fewer unburned patches and fewer surviving trees, resulting in a loss of balsam fir seed sources. In the case of wind followed by single fires this resulted in a 78% decline in balsam fir dominance and in the case of wind followed by two fires balsam fir was practically eliminated. There was a small increase in dominance following multiple fires as balsam fir was not a community type documented in these stands pre-fire, but post fire there was a single balsam fir plot, and this result could be due to a classification error or colonization of a lightly burned plot by an adjacent unburned fir stand, neither of which represents a significant increase in fir dominance.

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

Although its bark is somewhat thicker than that of black spruce or balsam fir, cedar trees have shallow roots that are easily damaged by fire (Caulkins 1967). Like balsam fir it is largely dependent on survival in unburned refuge areas for re-establishment post fire. Similar to balsam fir, white cedar abundance declined in dominance following single fire events but was largely eliminated as a community type by multiple fires, or wind-fire combinations. The mechanism of cedar decline in cases of multiple disturbances is likely a combination of increased fire severity and less unburned area in the case of wind followed by a fire, and less unburned area in cases of repeated fires.

Appendix S2: Literature Cited

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