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Singular and interactive effects of blowdown, salvage logging, and wildfire in sub-boreal pine systems

Anthony W. D'Amato[a,*], Shawn Fraver[b], Brian J. Palik[b], John B. Bradford[c], Laura Patty[a]

[a] Department of Forest Resources, University of Minnesota, St. Paul, MN 55108, USA
[b] USDA, Forest Service, Northern Research Station, Grand Rapids, MN 55744, USA
[c] US Geological Survey, Southwest Biological Center, Flagstaff, AZ 86001, USA

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ABSTRACT

The role of disturbance in structuring vegetation is widely recognized; however, we are only beginning to understand the effects of multiple interacting disturbances on ecosystem recovery and development. Of particular interest is the impact of post-disturbance management interventions, particularly in light of the global controversy surrounding the effects of salvage logging on forest ecosystem recovery. Studies of salvage logging impacts have focused on the effects of post-disturbance salvage logging within the context of a single natural disturbance event. There have been no formal evaluations of how these effects may differ when followed in short sequence by a second, high severity natural disturbance. To evaluate the impact of this management practice within the context of multiple disturbances, we examined the structural and woody plant community responses of sub-boreal *Pinus banksiana* systems to a rapid sequence of disturbances. Specifically, we compared responses to Blowdown (B), Fire (F), Blowdown–Fire, and Blowdown–Salvage–Fire (BSF) and compared these to undisturbed control (C) stands. Comparisons between BF and BSF indicated that the primary effect of salvage logging was a decrease in the abundance of structural legacies, such as downed woody debris and snags. Both of these compound disturbance sequences (BF and BSF), resulted in similar woody plant communities, largely dominated by *Populus tremuloides*; however, there was greater homogeneity in community composition in salvage logged areas. Areas experiencing solely fire (F stands) were dominated by *P. banksiana* regeneration, and blowdown areas (B stands) were largely characterized by regeneration from shade tolerant conifer species. Our results suggest that salvage logging impacts on woody plant communities are diminished when followed by a second high severity disturbance; however, impacts on structural legacies persist. Provisions for the retention of snags, downed logs, and surviving trees as part of salvage logging operations will minimize these structural impacts and may allow for greater ecosystem recovery following these disturbance combinations.

1. Introduction

Disturbances strongly influence ecosystem structural and successional development, as well as patterns of resource availability, effecting changes at both the site and landscape levels. Traditionally, research has focused on the effects of single disturbances or disturbance types, generating an important body of theory, concepts, and empirical data (e.g., Watt, 1947; Heinselman, 1973; Pickett and White, 1985; Turner et al., 1993; Attiwill, 1994), and producing metrics with which to characterize disturbance regimes (White et al., 1999). Recently, interest has shifted towards the effects of multiple interacting disturbances, such as windthrow, wildfire, and insect outbreaks (Paine et al., 1998; White et al., 1999; Bigler et al., 2005; Kulakowski and Veblen, 2007; Palik and Kastendick, 2009). This work suggests that multiple disturbances may interact synergistically, generating novel ecosystem responses and shifts not readily predicted from knowledge of single disturbances (Paine et al., 1998). Given that this is an emerging field of research, much remains unknown regarding the effects of these interactions (Lindenmayer et al., 2010).

One management activity increasingly being examined within the context of interactive disturbance effects is salvage logging (Lindenmayer et al., 2004), which is the removal of trees from forest stands affected by natural disturbance so as to recover economic value. Because salvage logging typically closely follows natural disturbance in time, the cumulative severity of these disturbances (sensu Peterson and Leach, 2008a) may create novel conditions for a given ecosystem (Paine et al., 1998). For example, several studies have suggested that post-fire salvage logging

* Corresponding author. Address: Department of Forest Resources, University of Minnesota, 115 Green Hall, 1530 Cleveland Avenue North, St. Paul, MN 55108, USA. Tel.: +1 612 625 3733; fax: +1 612 625 5212.

E-mail addresses: damato@umn.edu (A.W. D'Amato), sfraver@fs.fed.us (S. Fraver), bpalik@fs.fed.us (B.J. Palik), jbbradford@usgs.gov (J.B. Bradford), dunn0224@umn.edu (L. Patty).

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creates conditions quite different from those found after fire alone, resulting in increased susceptibility to subsequent disturbances (Donato et al., 2006; Thompson et al., 2007), shifts in tree regeneration and successional trajectories (Greene et al., 2006), and general declines in native biodiversity (Lindenmayer and Ough, 2006). In contrast, the impacts of salvage logging have been minimal following moderate severity blowdown due to the lower cumulative disturbance severity experienced by salvaged sites in these systems relative to those in which this practice is applied following more severe natural disturbances, such as fire (Peterson and Leach, 2008a; Lang et al., 2009). Given the considerable debate worldwide regarding salvage logging (Dellasala et al., 2006; Lindenmayer, 2006), a better understanding of the conditions under which this management practice may compromise long-term ecosystem integrity is needed.

Salvage logging typically occurs shortly (weeks to years) after a given natural disturbance. As such, it well represents the situation highlighted by Paine et al. (1998), in which multiple disturbances occurring within rapid succession, relative to a community's recovery time, may shift the community to a dramatically changed state that may persist more or less indefinitely. In some cases within fire-prone ecosystems, salvaged areas experience wildfires within years to decades following salvage logging, further compounding these disturbance effects (e.g., Hansen, 1983; Thompson et al., 2007). Nonetheless, all of the work examining salvage logging impacts to date has focused on this management practice within the context of a single natural disturbance event, leaving key knowledge gaps regarding how these effects may differ when salvage logging is then in turn followed by an additional major natural disturbance. This issue has particular relevance given the predicted increases in disturbance frequency and intensity in response to climate change (Dale et al., 2001; Flannigan et al., 2009).

A recent sequence of disturbances in northern Minnesota, USA, provide an ideal setting for examining how multiple disturbances, including blowdown, salvage logging, and wildfire occurring in rapid succession may affect ecosystem recovery. Specifically, in 1999 a severe windstorm affected over 200,000 ha of the Superior National Forest. Following the storm, the US Forest Service conducted salvage logging within a portion of the affected landscape to reduce fuel loads. Despite these efforts, in the spring of 2007, a wildfire burned *ca.* 14,700 ha throughout this same landscape (Fig. 1). Because these events created a patchwork of various disturbance combinations (blowdown, salvage logging, and wildfire and undisturbed controls; see Table 1), this landscape provides a unique opportunity to evaluate the effects of these disturbances individually and in combination. Using this framework, the objectives of this study were (1) to characterize the singular and interactive effects of wind and fire on post-disturbance structure (living and dead trees, coarse woody debris), regeneration and woody plant communities in jack pine (*Pinus banksiana* [Ait.] Sudw) forests; and (2) to determine if the juxtaposition of salvage logging between two natural disturbances (wind and fire) results in different successional trajectories and structural conditions than observed following the combination of wind and fire.

2. Methods

2.1. Study area

The study area is located in northeastern Minnesota, USA, along the southern edge of the North American boreal forest ecotone within the Superior National Forest (Fig. 1). Glacial activity has largely shaped the landscape resulting in rolling topography and mostly shallow soils over a substrate of Precambrian bedrock (Heinselman, 1973). The area exhibits a continental climate of cold winters and short summers, with a mean temperature of 2 °C and mean July and January temperatures of 17 and −8 °C, respectively. Mean annual precipitation for the area is approximately 68 cm.

On 4 July 1999, a massive storm produced straight-line winds affecting over 200,000 ha of the Superior National Forest (Woodall and Nagel, 2007). Following the storm, the US Forest Service began a sequence of salvage logging operations to reduce fuel loads within a portion of the Superior National Forest known as the Gunflint Corridor (Gilmore et al., 2003). Salvage logging occurred in the areas examined in this study between the fall of 1999 and fall of 2002. These areas were subsequently burned by a wildfire in the spring of 2007 (Fig. 1). To assess the effects of these interacting disturbances, we focused on mature *P. banksiana* communities, because of their regional ecological significance and abundance. In particular, *P. banksiana* forests covered over 490,000 ha in northern Minnesota in the 1930s; however, the extent of this system has been greatly reduced (114,000 ha in 2009; estimate from USDA Forest Service Forest Inventory and Analysis database) due to fire suppression and other land-use practices during the past century (Radeloff et al., 1999). As such, there is an urgent need to understand how natural and anthropogenic disturbances impact the regeneration dynamics in these systems.

2.2. Experimental design and vegetation measurements

In 2009, six study sites were established within each of our five treatment types: Blowdown–Salvage–Fire (BSF), Blowdown–Fire (BF), Fire (F), Blowdown (B), and Control (C), for a total of 30 sites (Table 1). Eight of these sites were chosen due to preexisting (post-1999 blowdown) data from another study (Gilmore et al., 2003), whereas the remaining 22 sites were selected using GIS to identify all potential sites for each treatment, followed by random selection within treatment combinations. Our analyses assume sites were fairly similar in structure and composition prior to the 1999 blowdown. Data from Johnson (2004), as well as archived US Forest Service GIS inventories (from 1976 to 1994), were available for a subset of sites within treatment types BSF, BF, F, and B. These data show a narrow range of stand origin dates (1903–1915), and similar basal areas (BSF at 29.6 m^2/ha, $N = 3$ sites; BF at 27.6, $N = 5$; F at 28.7, $N = 5$; and B at 29.8, $N = 4$). Post-disturbance (2009) data for the treatment type C (control) show a higher mean basal area of 34.3 m^2/ha, which might be expected given the later sampling date. Pre-disturbance deadwood pools were similar across plots with pre-existing data; however, our presented trends related to disturbance treatments and this structural attribute should be interpreted with caution given the lack of pre-disturbance deadwood data for most of our plots. Assessments of fire severity based on crown scorch and tree mortality across burned treatments (i.e., BSF, BF, and F) indicated that fire severity were similar across these treatments (Fraver et al., 2011). All blowdown and salvage logged areas burned in the 2007 fire, so we lack an unburned control for salvage logging. There was no prior management of any stands prior to these disturbances.

The heavily disturbed landscape at the west end of the Gunflint Corridor required that we search further afield to locate undisturbed controls (Fig. 1). Thus, by necessity, control sites are more dispersed than those of other treatments. However, given their pre-disturbance similarity in structure to the disturbed sites, we do not believe their dispersed locations had any meaningful influence on our findings.

Depending on site size, 6–10 200-m^2 circular plots were established at each site at 40-m intervals on a grid pattern originating from a randomly chosen starting point. Within each 200-m^2 plot, all standing living and dead trees (diameter at breast height [dbh] $\geqslant$10 cm) were recorded by species and diameter. Saplings (stems of tree species $\geqslant$2.5 cm and <10 cm dbh) within each plot

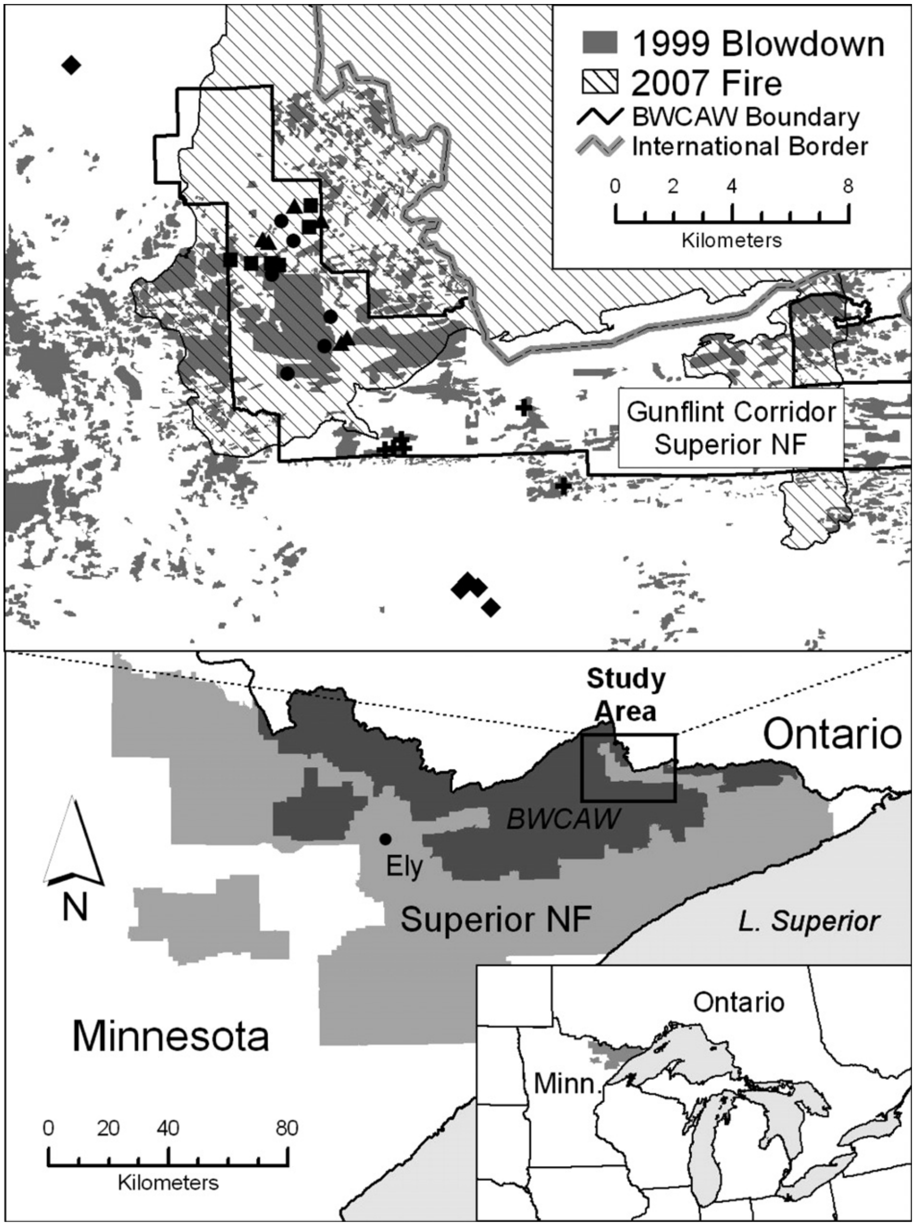

Fig. 1. Location of study sites and disturbance areas in *Pinus banksiana* forests of northeastern Minnesota, USA. ■ = Blowdown–Salvage–Fire, ● = Blowdown–Fire, ▲ = Fire, ✚ = Blowdown, ♦ = Control. One site 22 km to the east of the study area shown above was excluded for convenience of presentation.

Table 1
Disturbance combinations (i.e., treatments) examined in the Superior National Forest, northern Minnesota, USA.

Treatment	Blowdown (1999)	Salvage logging (1999–2002)	Wildfire (2007)
Blowdown–Salvage–Fire (BSF)	X	X	X
Blowdown–Fire (BF)	X	–	X
Fire (F)	–	–	X
Blowdown (B)	X	–	–
Control (C)	–	–	–

were tallied by species. Stems of shrubs and tree seedlings (stems smaller than our sapling class) were tallied by species within one 10-m^2 circular plot located within the center of each 200-m^2 plot. Additional tree seedling data were collected from 10-m^2 plots located equidistant between each large plot for a total of 14–20 seedling plots in each site.

In order to characterize the volume of coarse woody debris on each plot, we used the planar intersect method outlined by Brown (1974). For this purpose, we established one 32-m transect passing through the center of each 200-m^2 plot and positioned by random azimuth. For each piece of downed woody debris >7.6 cm in diameter intercepted by this transect, we recorded diameter and decay class, using a five class system, with class 1 being least and class 5 most decayed (Sollins, 1982). Volumes of pieces in decay classes 4 and 5 were multiplied by cross-sectional height–width ratios (0.82 and 0.42, respectively, Fraver and Palik, in press) to account for their collapse during decay.

2.3. Statistical analyses

The effect of each disturbance on stand structure (e.g., density and basal area of living and dead trees, volume of coarse woody debris, shrub density) and the densities of regeneration (seedlings and saplings) for common tree species were examined using separate mixed-model analyses of variance (ANOVA) in which disturbance type was treated as a fixed effect and site as a random effect. The effects of disturbance on average species richness (number of species per plot) and diversity (Shannon–Wiener index, H') of shrub species and tree regeneration were examined using the same procedure. In cases in which significant disturbance effects were detected, post-hoc Tukey's honest significant difference tests were used for pairwise comparisons between disturbance types. Prior to ANOVA, data distributions were checked for normality and homogeneity of variances and transformed using natural logarithmic or square–root transformations as necessary. ANOVAs were conducted using SAS version 9.2 (SAS Institute Inc.). A P-value of 0.05 or less was defined as statistically significant.

Multivariate tests for differences in the composition of shrub and tree regeneration between disturbance treatments were conducted using multi-response permutation procedures (MRPP) in PC-ORD version 5.0 (McCune and Mefford, 2006). MRPP is a non-parametric, randomization-based multivariate test of differences between groups that compares the plots within *a priori* groups to a random allocation of plots (McCune and Grace, 2002). Sørensen's index was used to calculate average within-group distances for MRPP. Indicator species analysis (Dufrêne and Legendre, 1997) was used to describe how well certain shrub and tree species differentiated between each disturbance combination.

Non-metric multidimensional scaling (NMS) was used to examine the variation in shrub and tree regeneration community composition (i.e., shrub and tree species) among disturbance treatments. NMS was performed using PC-ORD (McCune and Mefford, 2006), and optimal dimensionality for the ordination was based on the number of dimensions with the lowest stress (i.e., smallest departure from monotonicity in the relationship between distance in original space and distance in reduced ordination space, McCune and Grace, 2002). Dissimilarity was assessed by Sørensen's index. For this study, the minimum stress configuration included two axes (final stress = 12.65, instability <0.00001).

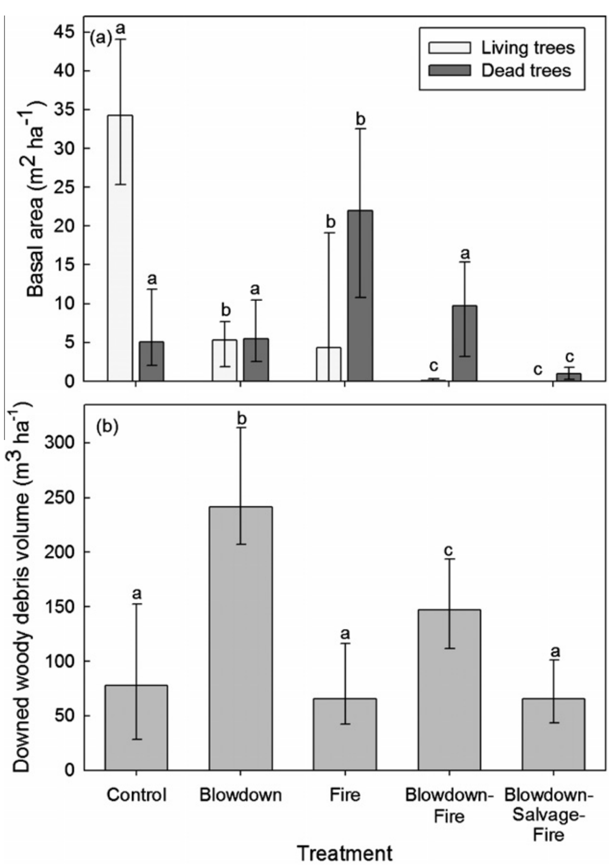

Fig. 2. (a) Tree basal area, (b) density of living and dead trees (⩾10 cm DBH), and (c) volume of downed coarse woody debris associated with Blowdown–Salvage–Fire (BSF), Blowdown–Fire (BF), Fire (F), Blowdown (B) and Control (C) treatments. Error bars represent 5th and 95th percentiles, and values with different letters are significantly different at $P < 0.05$.

3. Results

3.1. Disturbance effects on stand structure

The disturbance combination experienced by a given treatment strongly influenced the post-disturbance abundance of live and dead trees and downed woody debris (Fig. 2). As expected, the Control (C) treatment had the highest live-tree basal areas and densities, whereas no living trees remained within the Blowdown–Salvage–Fire (BSF) and Blowdown–Fire (BF) treatments (Fig. 2a and b). Sites experiencing solely Fire (F) had significantly greater densities and basal areas of standing dead trees than all other treatments (Fig. 2a and b). In contrast, the greatest volumes of downed woody debris were found within the Blowdown (B) treatment, where volumes were significantly greater than those found in all other disturbance combinations (Fig. 2c).

Disturbance combination significantly affected post-disturbance densities of tree seedlings, saplings and shrubs (Fig. 3). In particular, total seedling and shrub densities were greatest within the treatments experiencing fire (i.e., BSF, BF and F; Fig. 3a and c). In contrast, sapling densities were highest within the B and C treatments (Fig. 3b). The comparatively low sapling densities and high seedling densities within the BSF, BF and F treatments is the result of pre-existing saplings being killed by fire and insufficient time (sampling occurred 2 years post-fire) for newly established seedlings to reach sapling size (Fig. 3b).

3.2. Disturbance effects on tree regeneration and shrub communities

Post-disturbance composition of tree seedling and sapling communities differed significantly among disturbance combinations (Fig. 4). Overall, densities of disturbance-dependent, shade-intolerant species were greatest within the BSF, BF and F treatments compared to the B and C treatments (Fig. 4). For example, *Populus tremuloides* Michx. seedling densities were greatest within the BSF, BF and F treatments with little to no regeneration of this species within the B and C treatments (Fig. 4a). Similarly, *Pinus banksiana* seedling densities were greatest within the F treatment, followed by the BF and BSF treatments (Fig. 4a). In contrast, seedling densities for the shade-tolerant *Abies balsamea* (L.) Mill. were greatest in the B and C treatments, with few seedlings of this species in the other treatments (Fig. 4a). Seedlings of *Acer rubrum* L. were found at low densities across all treatments (10–20 seedlings hectare^{-1}) except the BF treatment, where this species averaged 1210 seedlings per hectare (range 0–5625; Fig. 4a).

As mentioned above, overall sapling densities were quite low within the BSF, BF and F treatments (owing to fire-induced mortality) relative to the B and C treatments, resulting in pronounced differences in sapling species composition between these two treatment groups (Fig. 4b). Species making up the sapling layers of the B and C treatments were largely shade-tolerant conifers, including *A. balsamea*, *Thuja occidentalis* L. and *Picea mariana* (Mill.) B.S.P. (Fig. 4b), which commonly establish as advance regeneration in these systems. In addition, sapling densities of *Betula papyrifera* Marsh. and *P. banksiana* (both shade intolerant) were also higher

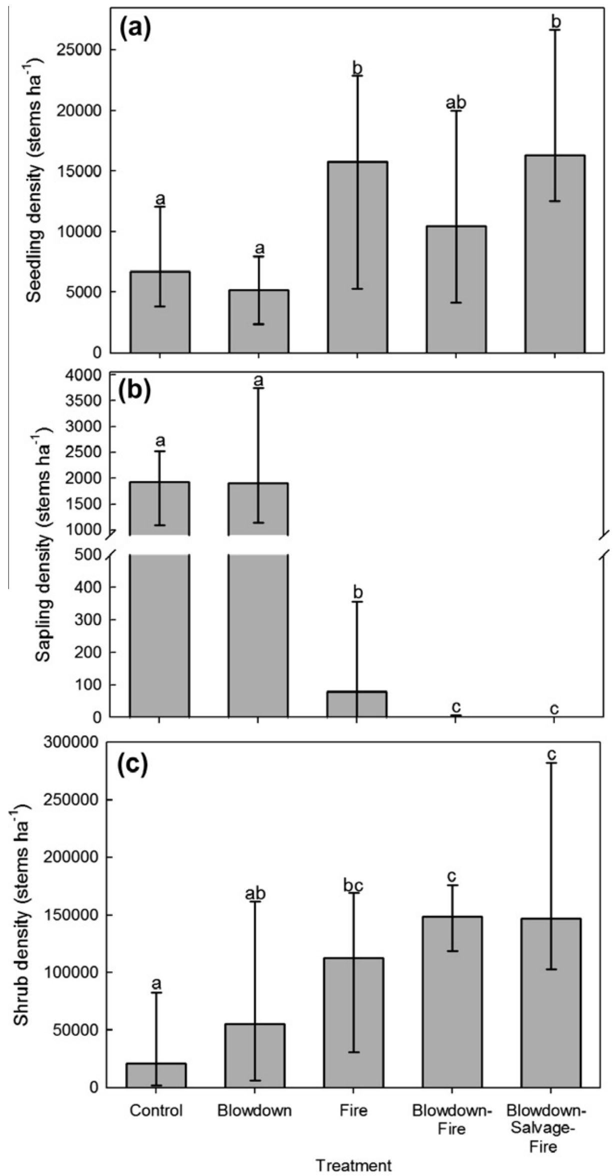

Fig. 3. Average total (a) seedling, (b) sapling and (c) shrub densities within Blowdown–Salvage–Fire (BSF), Blowdown–Fire (BF), Fire (F), Blowdown (B) and Control (C) treatments. Error bars represent 5th and 95th percentiles, and values with different letters are significantly different at $P < 0.05$.

within the B and C treatments relative to the other treatments. Of these species, the C treatment had significantly greater densities of *P. banksiana* than the B treatment (Fig. 4b).

Overall, the post-disturbance composition of shrub and tree regeneration (both seedlings and saplings) communities was distinct between treatments (MRPP A = 0.19, $P < 0.05$). Pairwise comparisons of species composition between treatments indicated that the BSF treatment differed from all others (Table 2). There was no difference in composition between the BF and F treatments or B and C treatments, respectively; however, composition significantly differed between these treatment pairs (Table 2). Within-community dissimilarity, an inverse measure of how similar sites within treatments are to each other based on species composition, showed the BSF sites to have the lowest dissimilarity (i.e., highest site-to-site similarity), followed by the C, BF, B and F treatments (Table 2). This result is also evident in the NMS ordination of these same data, where the BSF sites form a tight cluster, largely distinct from others (Fig. 5). Several species were identified as significant indicators (per Indicator Species Analysis; $P < 0.05$), driving the distinction between disturbance combinations. Specifically, *Alnus rugosa* (L.) Moench, *P. tremuloides*, *Rosa* spp. and *Salix* spp. characterized the BSF treatment, whereas *Acer rubrum* and *Diervilla lonicera* Mill. were indicators for the BF treatment, and *P. banksiana* was an indicator for the F treatment. Indicators for the B and C treatments were *P. mariana* and *A. balsamea* and *T. occidentalis*, respectively. The diversity of woody species did not differ between treatments ($P = 0.098$); however, woody species richness was significantly lower in the C treatment compared to the remaining treatments, which did not differ from each other (Table 2).

4. Discussion

The role of disturbance in structuring vegetation and influencing community dynamics is widely recognized; however, we are just beginning to understand the effects of multiple interacting disturbances on community recovery and development (Paine et al., 1998; Lindenmayer et al., 2010). Of growing international interest is the extent to which management interventions following natural disturbance shape post-disturbance communities, particularly given the controversies associated with salvage logging following disturbance (Dellasala et al., 2006). This study represents, to our knowledge, the first examination of the impacts of salvage logging on community composition and successional trajectories when juxtaposed between two natural disturbances (blowdown and wildfire). Our findings suggest that salvage logging impacts within this context are largely restricted to structural changes, as there were very few differences in the composition of tree seedling and shrub communities between areas experiencing blowdown followed by wildfire (BF treatment) and those in which salvage logging occurred between these two disturbance events (BSF treatment). Nonetheless, these structural differences may have a lasting influence on ecosystem recovery and biodiversity (Lindenmayer and Noss, 2006; Macdonald, 2007; Palik and Kastendick, 2009) and should be considered when evaluating post-disturbance management decisions in fire-prone ecosystems.

The concept of cumulative disturbance severity (sensu Peterson and Leach, 2008a), which assesses the combined effects of multiple disturbances on community structure, is useful for estimating the relative severity of disturbance combinations in this study. Although we did not have data on the amount of material removed during salvage logging to fully calculate cumulative severity, as presented in Peterson and Leach (2008a), the collective patterns in living and dead tree basal area serve as a useful surrogate for comparing relative severity observed across disturbance combinations (Fig. 2). Based on these measures, cumulative severity decreased in the order Blowdown–Salvage–Fire > Blowdown–Fire > Fire > Blowdown > Control. The impacts of these differences in cumulative severity on ecosystem structure, woody species composition and successional trajectories are discussed within the following sections.

4.1. Disturbance effects on ecosystem structure

Major disturbances, such as those examined in this study, play a central role in forest structural development through the creation of long-lasting biological legacies, including logs, snags and surviving trees (Spies, 1998; Tinker and Knight, 2000; Franklin et al., 2007). The distribution of these structural legacies across our treatments was largely a function of disturbance type and associated cumulative severity. Sites experiencing solely fire had the greatest abundance of snags, whereas downed woody debris pools in these sites were similar to those in the controls. These patterns are consistent with those found in post-fire *P. banksiana* forests of northwestern

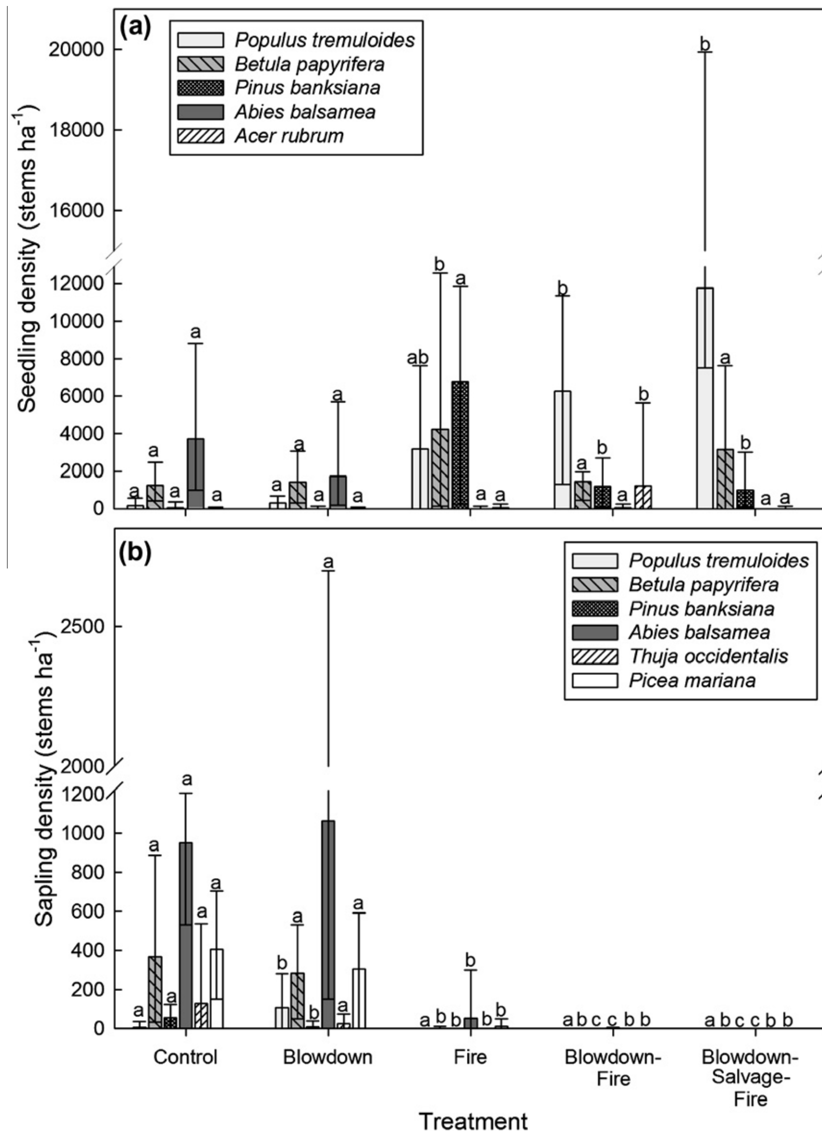

Fig. 4. Average (a) seedling and (b) sapling densities and associated 5th and 95th percentile values, by species, for common tree species occurring within the Blowdown–Salvage–Fire (BSF), Blowdown–Fire (BF), Fire (F), Blowdown (B) and Control (C) treatments. Values for a given species with different letters are significantly different at $P < 0.05$.

Table 2
Woody species richness and diversity within disturbance treatments. Values represent means with 5th and 95th percentiles in parentheses, and values with different letters are significantly different at $P < 0.05$.

Treatment	Species richness[a]	Species diversity[b]	Community dissimilarity[c]
Blowdown–Salvage–Fire (BSF)	16.17 (11, 19)[a]	2.17 (2.04, 2.29)[a]	0.462 (0.212, 0.712)[a]
Blowdown–Fire (BF)	15.80 (13, 20)[ab]	1.91 (1.23, 2.15)[a]	0.677 (0.626, 0.707)[b]
Fire (F)	17.17 (15, 19)[a]	2.00 (1.74, 2.19)[a]	0.710 (0.460, 0.888)[b]
Blowdown (B)	16.17 (10, 22)[a]	1.66 (0.89, 2.42)[a]	0.685 (0.560, 0.833)[c]
Control (C)	10.50 (8, 16)[b]	1.68 (1.11, 1.94)[a]	0.626 (0.248, 0.876)[c]

[a] # of species/plot.
[b] Shannon–Wiener index of diversity (H').
[c] Sørensen's index of dissimilarity; letters indicate significant differences based on multi-response permutation procedures (MRPP).

Quebec (Brais et al., 2005) and reflect a relatively low level of combustion of pre-fire downed woody debris and widespread snag creation due to mortality of canopy trees (cf. Tinker and Knight, 2000). In contrast, in sites experiencing solely blowdown, much of the pre-disturbance standing volume was converted to downed woody debris pools, resulting in debris volumes over four times those found in control sites (Fig. 2). By comparison, the lower downed woody debris volumes in sites experiencing a combination of blowdown and wildfire suggest that a portion of these downed logs was subsequently consumed by fire (Stephens et al., 2009).

Salvage logging strongly influenced post-fire forest structure, resulting in a lower abundance of standing dead trees and downed woody debris. These findings are not surprising given that the general objective of this practice is to remove much of this material;

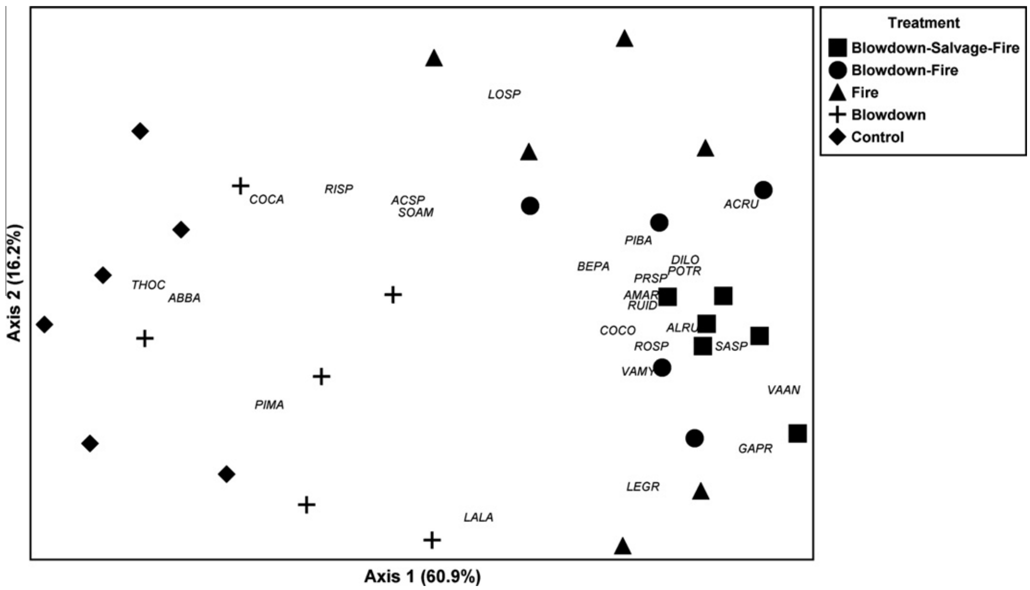

Fig. 5. Non-metric multidimensional scaling (NMS) ordination of woody species composition across disturbance treatments. Species locations in ordination space are based on weighted averaging and codes are defined in Appendix A (available online). See Appendix B (available online) for species correlations with NMS axes 1 and 2.

however, the ecological implications of these reductions should not be overlooked. For example, several studies have demonstrated the benefits of retaining structural legacies, such as snags and downed logs, for ameliorating extreme post-salvage environmental conditions on the forest floor, thus enhancing vegetation recovery (Macdonald, 2007; Palik and Kastendick, 2009). Moreover, the loss of these habitat features, particularly standing dead trees, from salvage logged areas has been suggested as a primary mechanism for the declines in biodiversity observed following the application of this management practice (Lindenmayer and Ough, 2006; Lain et al., 2008; Cahall and Hayes, 2009). Although we did not explicitly examine microenvironmental conditions or populations of deadwood-wood dependent organisms, these and other ecosystem properties are likely to be dramatically impacted by the lower abundance of deadwood legacies in salvaged areas (Spies, 1998; Lindenmayer et al., 2008). Moreover, the lower abundance of these legacies may also affect long-term forest successional dynamics, as the establishment of several tree genera in these systems is linked to downed woody debris (e.g., *Betula*, *Picea*, and *Thuja*) (Cornett et al., 2001; Caspersen and Saprunoff, 2005; Marx and Walters, 2008).

4.2. Disturbance effects on woody plant communities

Although there was little evidence that the juxtaposition of salvage logging between blowdown and fire altered tree regeneration over that observed following the combination of blowdown and fire (see Section 4.3 below), salvage logging did tend to homogenize the post-fire woody plant communities. That is, site-to-site variability in these communities was lowest in the Blowdown–Salvage–Fire treatment (Table 2), which was also reflected in the tight clustering of these sites in ordination space (Fig. 5). These patterns are consistent with the findings of Purdon et al. (2004) who documented a general homogenization of understory vegetation within burned areas experiencing salvage logging relative to areas solely experiencing high-severity fires. Possible explanations for these patterns include a reduction in microsite variability and higher soil temperatures due to the removal of downed logs by salvage logging (Purdon et al., 2004; Peterson and Leach, 2008b), as well as greater mortality and greater damage to reproductive tissues stemming from the higher cumulative disturbance severity within salvaged sites (Lindenmayer and Ough, 2006). To this end, work comparing fire severity between the salvaged and unsalvaged areas used in this study suggest that fire damage to upper soil layers was greater on sites experiencing salvage logging (Fraver et al., 2011). This greater cumulative severity likely favored those species with reproductive tissues in deeper soil horizons (e.g., *P. tremuloides* and *Alnus rugosa*; Rowe, 1983; Brown and DeByle, 1987; Frey et al., 2003) or with seed stored on site in soil seedbanks (e.g., *Salix* spp.; Whittle et al., 1997).

Consistent with the findings of several other studies, we did not observe lower woody species richness, diversity, or cover (as measured by woody plant density) in areas experiencing salvage logging relative to other disturbance types (Peterson and Leach, 2008a; Lang et al., 2009). Overall, woody species richness and diversity and shrub densities were generally greater in disturbed sites relative to undisturbed controls (Fig 3, Table 2), a pattern consistent with the findings of other work examining vegetation dynamics following wildfire and windthrow in *P. banksiana* communities (Lain et al., 2008; Smirnova et al., 2008). The lack of differences between disturbance types, despite the considerable gradient in cumulative disturbance severity from Blowdown to Blowdown–Salvage–Fire treatments, suggests that the reproductive mechanisms of woody species in these systems are adapted to even the high cumulative disturbance severity experienced within Blowdown–Salvage–Fire treatments (Rowe, 1983; Roberts, 2004).

4.3. Disturbance effects on successional trajectories

Despite the general similarities in tree seedling composition present within the burned treatments (BSF, BF and F), the differential abundance of a given species and hence future successional trajectories varied as a function of cumulative disturbance severity. Post-disturbance regeneration within Fire treatments were consistent with the patterns observed following high-severity crown fires in *P. banksiana* systems in other portions of the upper Great Lakes region and indicated future dominance by *P. banksiana* and to a lesser extent by *P. tremuloides* and *B. papyrifera* (Heinselman, 1981; Greene et al., 2004; Jayen et al., 2006). In contrast, the treatments experiencing compound disturbances (i.e., Blowdown–Salvage–Fire and Blowdown–Fire) were largely dominated by *P. tremuloides*, a finding consistent with Frelich's (2002) predictions regarding the impacts of high cumulative disturbance severities on the successional trajectory of sub-boreal *P. banksiana* systems. The dominance of *P. tremuloides* within these areas likely reflected the rapid sequence in which these disturbances occurred following the initial blowdown disturbance (cf. Paine et al., 1998). As a consequence, the vegetatively reproducing *P. tremuloides* was favored over *P. banksiana*, which had not reached sexual maturity by the time of the 2007 Fire. The greater, yet highly variable abundance of *Acer rubrum* regeneration in the BF treatments was likely due to seed dispersed from a few surviving adult *A. rubrum* stems encountered near a few of our sites (Fraver, personal observation). Collectively, the differences between the BSF, BF, and F treatments in regeneration patterns underscore the ability of multiple, interacting disturbance events to alter successional trajectories relative to a single disturbance event.

The dominance of shade-tolerant tree seedlings and saplings in sites solely experiencing blowdown is consistent with the findings of other work examining regeneration patterns after the 1999 blowdown in northern Minnesota (Rich et al., 2007). Moreover, these patterns are consistent with those found globally in systems where mortality of shade-intolerant canopy species produces a shift towards shade-tolerant species that existed as pre-disturbance advance regeneration (e.g., Spurr, 1956; Astrup et al., 2008; Ilisson and Chen, 2009). Although we lacked an unburned control for salvage logging, findings from other studies examining post-blowdown salvage logging suggests these treatments would have increased the abundance of early successional tree species, particularly *P. tremuloides*, relative to areas experiencing solely blowdown (Lain et al., 2008; Lang et al., 2009; Palik and Kastendick, 2009).

It is important to note that regeneration communities within Blowdown treatments were sampled 10 years post-disturbance versus the 2 years post-disturbance for the burned treatments. Nevertheless, other studies examining regeneration patterns 2 years following the 1999 blowdown within another portion of the Superior National Forest documented a similar pattern to those we documented for Blowdown treatments in this study (Rich et al., 2007; Lain et al., 2008). As such, the differences we detected in regeneration communities between these areas and burned treatments likely represent differential disturbance effects as opposed to successional effects.

5. Conclusions and management implications

The general similarities we documented in successional trajectories between sites experiencing blowdown followed by wildfire and those in which salvage logging occurred between these two disturbances suggest that salvage logging impacts on regeneration are diminished when followed by a second major disturbance. Overall, the primary impact of salvage logging on woody plant communities within this context was a homogenization of woody plant composition. More broadly, the trend towards greater *Populus* dominance within the sites experiencing multiple disturbance events, relative to those solely experiencing fire suggest that these compound disturbances may generate strong community differences relative to burned stands later in succession. Nonetheless, our findings should be interpreted with caution, as they represent woody plant communities only 2 years post-fire and may not reflect long-term community dynamics.

While post-blowdown salvage logging clearly reduces fuel loads (a consideration in fire-prone areas), it also has long-lasting impacts on the structure of post-fire communities, including a reduction in snags and downed woody debris. Given the importance of these structural legacies in aiding ecosystem recovery following disturbance, the retention of these features during post-disturbance management should receive greater consideration. Currently, very few regions have formal guidelines for retaining post-disturbance structural legacies, despite the demonstrated benefits of these features in ameliorating salvage logging impacts on vegetation communities (e.g., Macdonald, 2007). Planning and guideline development pertaining to the retention of post-disturbance legacies should strive to create a mosaic of salvaged and unsalvaged areas, thereby reducing fire spread through the landscape while also emulating the historic spatial variation in disturbance severity experienced by these systems. Of additional importance within the context of sub-boreal and boreal *P. banksiana* systems is the retention of living trees and cone-bearing slash as seed sources for post-disturbance establishment of *P. banksiana*. The documented low abundance of this *P. banksiana* relative to *Populus* within areas experiencing compound disturbances highlights the possible need for the use of direct seeding or planting if management objectives include the maintenance of this ecologically important forest type within areas experiencing these compound disturbance sequences.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.foreco.2011.09.003.

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