



Post-windthrow salvage logging increases seedling and understory diversity with little impact on composition immediately after logging

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Abstract

Salvage logging after forest disturbances is a controversial but common practice, yet it remains relatively poorly studied, particularly after windstorms within deciduous forests. Here, we present results from the first growing season following salvage logging on four gaps (3.5–6 ha) created by a 2012 tornado. While salvage logging shifted the distribution of stem heights to smaller sizes, it increased woody species seedling diversity by 33% and total plant richness and diversity by 20%. Salvaging did not alter or homogenize community composition. These short-term differences in richness and diversity were partly driven by a more even distribution of seedlings among species and increased species recruitment from the seed bank after salvaging. Overall, the initial impacts of salvage operations in a mixed deciduous forest redirected forest regeneration towards a more diverse community with a wider pool of species.

Keywords Wind disturbance · Salvage logging · Diversity · Composition · Deciduous forest

Introduction

Salvage logging commonly occurs following forest disturbances to generate revenue from downed or damaged trees; nonetheless many describe the process as inimical to forest regeneration (Beschta et al. 2004; Karr et al. 2004; Lindenmayer et al. 2004; Baird 2006; DellaSala et al. 2006; Donato et al. 2006; Newton et al. 2006; Lindenmayer et al. 2017). The post-disturbance landscape, characterized by a high structural and microsite

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heterogeneity that promotes diversity (e.g., Sass et al. 2018), is often largely homogenized by the salvaging process, potentially leading to a depauperate plant community (Purdon et al. 2004; D'Amato et al. 2011; Brewer et al. 2012; Waldron et al. 2013). Furthermore, salvaging could delay or alter forest succession through the destruction of established saplings that survived the initial disturbance, creating both ecological and economic disincentives to salvaging (Donato et al. 2006).

Despite the prevalence and potential deleterious impacts of salvage logging, there is a dearth of experimental studies that rigorously assess salvaging following windstorms within deciduous forests (Royo et al. 2016; Leverkus et al. 2018a). Indeed, the majority of the literature on salvage logging follows wildfire, and it may be difficult to extend these conclusions to windstorms where, unlike fire, the understory typically remains intact (Sousa 1984; Roberts 2004; Leverkus et al. 2018a). More challenging yet, only a quarter of 90 publications reviewed by Leverkus et al. (2018a) address impacts on non-arborescent understory species, which constitute the vast majority of floristic diversity in deciduous forests (Gilliam 2007). Thus, the degree to which salvage logging is deleterious to forest regeneration, and plant community diversity more broadly, remains unclear.

Here, we present results from the first growing season after salvage logging following a windstorm in a deciduous forest of the eastern United States. Unlike many previous studies (though not all, see Royo et al. 2016), we used an experimental approach to evaluate the woody and herbaceous community response to salvage logging by randomly assigning half of four blowdowns to a salvage logging treatment. We focused on the period immediately after salvaging because that has been identified as the period when declines in species diversity and richness, and impacts on plant community composition, are the most profound (Donato et al. 2006; Royo et al. 2016). Consequently, we predicted that salvage logging would (1) reduce the abundance, richness, diversity, and average size of woody stems, (2) decrease the richness, diversity and abundance of the plant community species, and (3) alter the plant community by shifting composition towards dominance by a few species (i.e., lower beta diversity) and changing functional group abundance. There are, however, clear alternatives to these predictions. Specifically, post-windthrow salvaging could accentuate the positive impacts of a single disturbance (the original blowdown), thereby extending the establishment window for species with a broad range of shade tolerance. Moreover, even intensive salvaging does not wholly erase key structural legacies of windthrows (e.g., tree tip-up mounds, Spicer et al. 2018). Furthermore, because salvaging typically scarifies the soil, it may also promote the establishment of early successional ruderal species that colonize open or upturned soil (Kurulok and Macdonald 2007; Brewer et al. 2012; Fidej et al. 2016). Thus, under certain conditions, salvaging could promote the regeneration of a more diverse stand.

Materials and methods

Study area

This study was conducted at Powdermill Nature Reserve in southwestern Pennsylvania, USA, a 900 ha reserve of mature, second-growth mixed mesophytic forest with moderate slopes (8–35%) and shallow, rocky soil (Murphy et al. 2015; NRCS 2018). Temperatures range from -20 to 33 °C, and annual precipitation is approximately 1100 mm, with greater precipitation in summer months (Murphy et al. 2015). The overstory of this

forest is dominated by tulip-poplar (*Liriodendron tulipifera*), red maple (*Acer rubrum*), sugar maple (*Acer saccharum*), black cherry (*Prunus serotina*), American beech (*Fagus grandifolia*), red oak (*Quercus rubra*), and cucumber tree (*Magnolia acuminata*). Though we did not perform a full dendrochronological assessment, cross sections taken from salvage-harvested red oaks indicate some of these unmanaged stands are at least 150 years old. On 1 June 2012, an EF-1 tornado moved northeast across the reserve, damaging 37 ha of forest, concentrated in seven blowdowns.

Experimental design

We mapped damaged areas in the field using a handheld GPS, and selected the four largest blowdowns (3.5–6 ha) for salvage logging. Due to their oblong shape, we divided each blowdown in half along its longest axis, and randomly assigned one half to be salvaged (Fig. 1). We placed eight 36 m² plots in each half of each blowdown (4 sites × 2 treatments × 8 plots = 64 total plots). To ensure that plots covered the range of topographic conditions, the blowdowns were divided lengthwise, half of those eight plots were assigned to each end through randomly generated points (Fig. 1). No plots were placed within 10 meters of the forest or treatment edge. An intensive salvaging operation, wherein all standing live trees were harvested in addition to all downed and leaning trees, was carried out mid-summer of 2013 through early spring of 2014 (Fig. S1). While intensive, this level of salvaging is common; Leverkus et al. (2018a) found that the percentage of trees or basal area removed through salvaging typically exceeds 90%. This is especially true for small- to medium-scale disturbances, such as these blowdowns, where a greater proportion must be harvested to be profitable (L Leverkus et al. 2018a). Salvaging was carried out by a commercial operator performing a bole-only harvest (i.e., tree tops and branches left behind), with trees manually cut by chainsaws and removed using rubber-tired skidders. Note that the numbering of blowdowns in text and figures reflects both the direction the storm moved as well as the order in which salvaging was completed.

Vegetation survey

In summer 2014, we conducted a thorough vegetation survey of all 64 plots. To assess the potential for salvage logging to impact advance regeneration, we inventoried all woody stems (including shrubs) > 10 cm tall, in each of the 36 m² plots. For each stem we identified species and measured its height and basal diameter. To assess salvaging's immediate impact on community composition, we estimated species percent cover of all woody and herbaceous plants < 1 m in height within four 1 m² subplots placed in the corners of the larger 36 m² plot. Because species could overlap, total cover could exceed 100%. Finally, community richness was assessed by combining the species present in the subplots with any additional species found in a timed meander survey throughout the larger 36 m² plot. Occasionally, definitive species identifications were problematic and in these cases taxa were lumped into genera (e.g., *Carex* spp.). Hereafter we refer to results on the tree regeneration inventory by referencing "stem" and results derived from the percent cover data by "community".

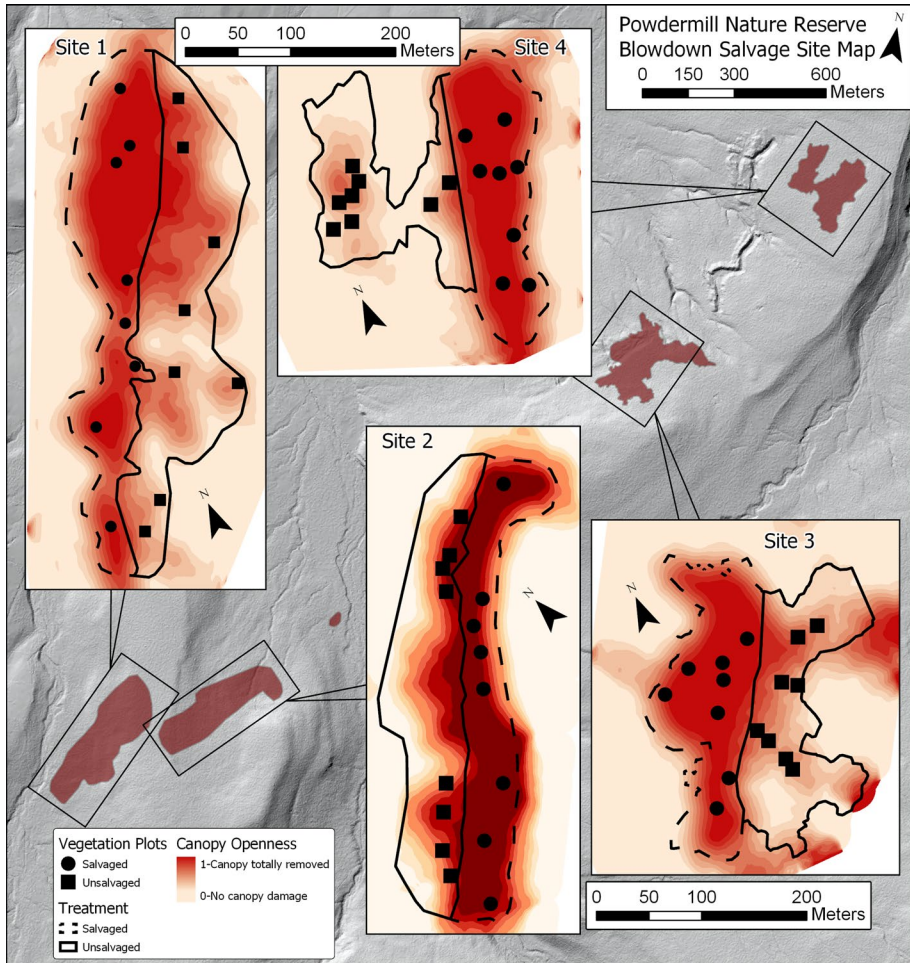


Fig. 1 Map of study area highlighting the four blowdowns included in this study with 33 vegetation sampling plots. Plot locations were distributed in the unsalvaged (solid line) and 34 salvaged (dashed extension) treatment using a stratified random approach. Our metric of canopy openness is symbolized in red, with darker shades representing more open canopy with most of 36 the salvaged area characterized by full sun. All four site callouts are at a scale of 1:4000 while 37 the background map shows topography and site orientation at a scale of 1:33,500

Post-hoc damage assessment

To assess storm and logging canopy damage, we first manually inspected the most recent publicly available pre-storm aerial imagery (National Aerial Imagery Program, 18 June 2010) to verify that all four sites were characterized by closed-canopy forest prior to the storm. Next, we collected aerial imagery over the four blowdowns in April and June 2016 using an unmanned aerial vehicle (DJI Phantom 3 Professional). We used photogrammetric processing to create high-resolution orthoimagery and a canopy height model using methods outlined in Carr and Snyder (2018) and ESRI (2010). We used the canopy height model

(with a spatial resolution of 25 cm) and corresponding imagery to delineate areas of canopy damage (Fig. 1). Because imagery was collected after logging, we estimate site-level damage by calculating the percentage of raster cells where the canopy remained intact for the unsalvaged half of the blowdown. Additionally, we created a metric of canopy openness for each plot between 0 (undamaged canopy) and 1 (canopy fully removed), based on the proportion of cells within a 15 m radius where the canopy is intact.

Analysis

We calculated stem density, Shannon–Weiner diversity (H' , hereafter diversity), and richness for each plot. We pooled percent cover data from all subplots and calculated mean total cover, richness, and diversity, as well as mean total cover by understory functional groups (forbs, shrubs, graminoids, and ferns) for each 36 m² plot. To assess the impact of salvage logging on stem and overall community richness, diversity and abundance, we constructed generalized linear mixed models using GLIMMIX (SAS Institute 2013) wherein we modeled treatment (salvaged vs. unsalvaged) as a fixed effect variable and both site and plots nested within salvage treatments as a second random effect to account for the nested nature of the experiment. Stem density data were right-skewed and overdispersed, hence these data were modeled using a gamma distribution (Bolker 2008). Cover data of the functional groups was bounded by 0 and 1 and were therefore modeled using a beta distribution (Eskelson et al. 2011). All other variables were modeled using a normal distribution.

To assess the impact of salvage logging on stem heights, we plotted the distributions of all inventoried stems in salvaged and unsalvaged plots and used a Kolmogorov–Smirnov test to determine whether salvage logging altered stem height distribution. The Kolmogorov–Smirnov compares the cumulative distribution function of two distributions to determine the maximum distance between these functions, and thus provides a nonparametric comparison of the distributions, independent of sample size (Conover 1971).

To determine if salvage logging had an impact on community composition, we analyzed the percent cover data using *vegan* and *indicspecies* packages in R (DeCaceres and Legendre 2009; Oksanen et al. 2018). Because rare species can exert large effects on multivariate analyses, we removed species present in less than five percent of plots from the community matrix (McCune and Grace 2002). To avoid pseudoreplication by treating individual plots as independent observations, we averaged species cover values to a single plot-treatment value (i.e., two values from each site, one from the salvage treatment and one from the unsalvaged control). After these steps, we calculated multivariate distances between plots using the Bray–Curtis method. To test whether salvage logging shifted the overall composition, we ran a permutational multivariate analysis of variance (PERMANOVA; Oksanen et al. 2018). Next, we assessed the homogeneity of group dispersions using the *betadisper* function (R package ‘vegan’; Oksanen et al. 2018) on the original species matrix, including rare species, to calculate the distance from each salvaged and unsalvaged plot to treatment centroid in multivariate space. This measure of multivariate dispersion is often used as a metric for beta diversity (Anderson 2006; Anderson et al. 2011; Oksanen et al. 2018). Once we obtained plot-centroid distances, we used an ANOVA to test whether these distances differed between salvaged and unsalvaged plots. For our purposes, a significant decrease in average distance-to-centroid in the salvaged plots, relative to the control plots, would indicate a reduction in beta diversity (i.e., increasingly similar plant communities). We used the entire species matrix because one way in which salvage logging could reduce beta diversity is through its impact on rare species. Lastly, we

tested for associations between species and treatments using an indicator species analysis as described by Dufrene and Legendre (1997) on the original matrix with the *multipatt* function in *indicspecies* (DeCaceres and Legendre, 2009). All composition analyses were conducted using R version 3.4.3 (R Core Team 2017; Wickham 2016).

Results

Site-level canopy loss decreased as the storm moved northeast across the study area, from about 50% at sites one and two to 23% at site four. Plot-level canopy openness was generally above 90% for salvaged plots, but varied from 14 to 92% for unsalvaged plots (Fig. 2). Salvage logging increased stem diversity by 33%, but had no effect on stem richness (Table 1, Fig. S2). Though stem density was considerably higher in unsalvaged plots, this difference was driven by a handful of plots within one site, and we found no overall significant effect of salvaging on density (Table 1, Fig. S3). Salvaging increased community diversity by approximately 20% and average community richness by nearly five species, but had no effect on total cover (Table 1). Salvaging had no significant effect on forb, shrub, or fern cover. While grass cover was low overall, graminoids were three times more abundant in salvaged plots (Table 1).

Salvaging shifted the distribution of stems towards smaller sizes (K–S test: $D=0.19$, $p < 0.001$; Fig. 3). Median stem height on salvaged plots was 26% shorter

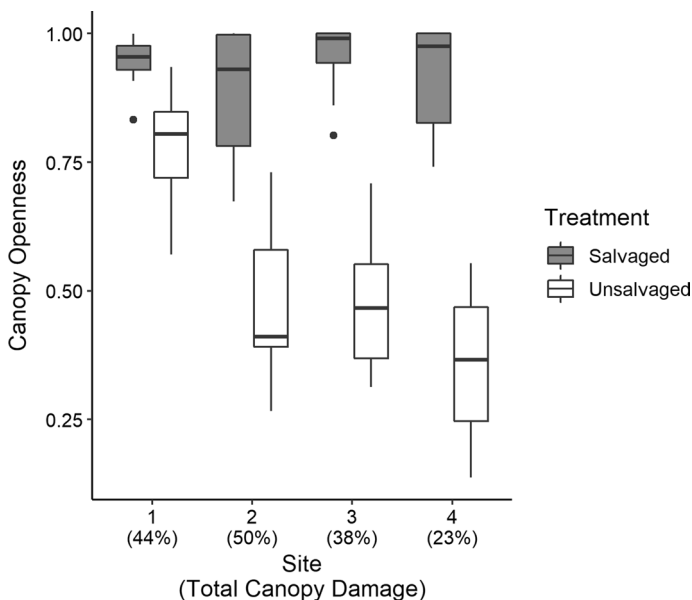


Fig. 2 Boxplots summarizing plot-level canopy openness, measured as the proportion of canopy removed within a 15-m radius of each plot following the storm and salvage logging. Black bars indicate median values, and dots indicate outliers beyond 1.5 times the interquartile range. Site-level canopy damage for the unsalvaged half of each site, estimated using remotely sensed imagery, is reported at the bottom. Though canopy openness varies both within and between sites, the canopy is consistently wide-open above salvaged plots. Site numbers reflect the direction the storm moved (from southwest to northeast), as well as the order in which logging was performed

Table 1 Results of summary response variables assessed using generalized linear mixed models, reported with variable means and standard errors (SE)

Variable	Unsalvaged		Salvaged		Results	
	Mean	SE	Mean	SE	F	<i>p</i>
Stem richness	9.4	1.4	8.8	1.4	0.61	0.450
Stem diversity	0.9	0.1	1.2	0.1	6.79	0.021
Stem density	7.7	1.8	5.6	1.2	0.57	0.462
Percent cover	47.0	2.7	47.9	3.0	0.08	0.773
Community richness ^a	22.3	1.2	26.9	1.2	9.65	0.008
Community diversity	1.9	0.1	2.3	0.1	9.28	0.009
Fern cover	11.1	2.7	11.0	2.7	0.02	0.897
Forb cover	16.4	2.7	18.1	2.8	0.42	0.526
Graminoid cover	1.2	0.3	3.3	0.8	16.55	<0.001
Shrub cover	4.2	1.3	3.1	0.6	3.20	0.096

All models were constructed with treatment (salvaged vs. unsalvaged) as a fixed effect variable and site and plots nested within salvaged treatments as random effects

^aIncludes timed meander survey

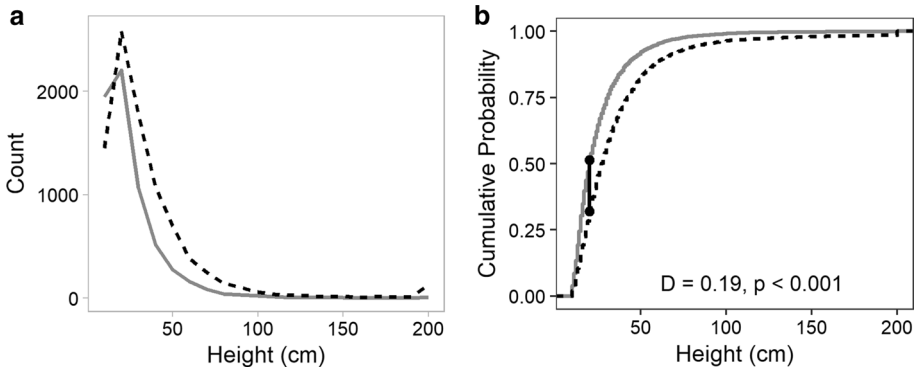


Fig. 3 Distributions of stem heights for salvaged (solid grey) and unsalvaged (dashed black) plots using data pooled from all plots. **a** Stem count by heights, binned to 10 cm groups. Only in the smallest size class (10–20 cm) are stems more abundant in salvaged plots. There are consistently fewer stems in salvaged plots for all other size classes. **b** The cumulative probability curves indicate that, regardless of count, there are proportionally more stems in smaller size classes for salvaged plots. The point of the largest difference between distributions (where the KS test statistics, *D*, is calculated) is indicated by the vertical black line

than on unsalvaged plots (20 cm vs. 27 cm). Moreover, stems > 1 m and > 2 m tall were 79% and 92% less abundant, respectively, in salvaged plots relative to unsalvaged plots. Only short stems (10–20 cm) were more abundant in salvaged areas.

Salvage logging did not alter community composition (PERMANOVA: $F = 0.306$, $R^2 = 0.059$, $p = 0.845$) nor did it significantly decrease beta diversity (Betadisper: $F = 0.401$, $p = 0.506$). Seven taxa were significantly associated with salvage logging based on our indicator species analysis, while unsalvaged plots had no associated species (Table 2).

Table 2 Results of the indicator species analysis, with species broken up by functional group

	Common name	Scientific name	Indicator value	<i>p</i>
Trees	Common serviceberry	<i>Amelanchier arborea</i>	0.255	0.016
Forbs	Enchanter's nightshade	<i>Circaea lutetiana</i>	0.247	0.003
	American burnweed	<i>Erechtites hieraciifolius</i>	0.801	0.001
	Sweetscented bedstraw	<i>Galium odoratum</i>	0.268	0.041
	Indian tobacco	<i>Lobelia inflata</i>	0.271	0.008
	Goldenrod	<i>Solidago</i> spp.	0.281	0.007
Graminoids	Grasses		0.312	0.049

All species listed were associated with the salvaged treatment, whereas the unsalvaged blowdown had no significant species associations

Discussion

Counter to our predictions, salvage logging did not impoverish vegetation assemblages. Instead, salvaging increased stem diversity and augmented overall understory community richness and diversity. Salvage logging caused these increases by promoting the recruitment of early successional species that colonize from the seed bank (e.g., *Carex* spp. and *Erechtites hieraciifolius*), and by substantially (80%+) reducing the density of tall advance regeneration present prior to salvage logging, thereby allowing increases in relative abundance of other tree species.

Salvaging may delay forest succession because it removed larger saplings, but this removal promoted tree species coexistence (Fig. S2). Specifically, the 33% increase in stem diversity in salvaged areas was driven not by heightened species recruitment, but rather the reduction in stem densities of the two most common tree species, *A. rubrum* and *L. tulipifera*. These two species dominated the regeneration layer in unsalvaged areas, but their relative abundance was reduced by 28% in salvaged areas thereby likely allowing other species (e.g., *P. serotina*, *Fraxinus americana*) to increase. Similarly, Royo et al. (2016) found post-windthrow salvage logging promoted native tree species coexistence by mitigating the dominance of taller advance regeneration. Promoting coexistence of *F. americana* and *P. serotina* is highly relevant in these forests as *F. americana* is critically endangered (Jerome et al. 2017) due to emerald ash borer (*Agrilus planipennis*; Flower et al. 2018) and *P. serotina* provides high ecological and economic value (e.g., Rose et al. 2014; Ray 2018).

While some studies have reported large reductions in seedling densities following salvaging (e.g., 71%, Donato et al. 2006), which may delay forest recovery, our findings of neutral or positive changes in stem diversity and density are not uncommon (Lain et al. 2008; Peterson and Leach 2008a, b; Nelson et al. 2008; Laing et al. 2011; Thorn et al. 2018). In our study, salvaged plots had nearly 35% more seedlings 10–20 cm tall than unsalvaged plots. Thus, while salvaging may delay how rapidly stems move into larger size classes, forgoing salvaging may come at the expense of a less diverse seedling layer.

Though there is little doubt that large disturbances precipitate changes in vegetation abundance and composition, subsequent salvage logging often has little additional impact, even when logging alters microsite diversity (Nelson et al. 2008; Peterson and Leach 2008b; Keyser et al. 2009). Salvaging often creates a substantial soil disturbance (and we observed considerable bare ground immediately after salvaging), yet total understory cover was nearly identical within the first growing season, with salvaging

causing a 20% increase in both richness and diversity (see also Rumbaitis del Rio 2006; Peterson and Leach 2008a). We expected salvaging would alter community composition and diminish beta diversity by promoting the establishment of widespread ruderal species (e.g., Brewer et al. 2012), as the same high-intensity harvest was applied across the heterogeneous blowdowns. Instead, we saw no change in composition or reduction in beta diversity; rather the disturbance associated with salvaging provided an opportunity for a somewhat wider pool of species to become established (Table 2, Royo et al. 2016). Many of the species that were significantly associated with salvaging colonize from the seed bank (e.g., *Erechtites hieraciifolius*, *Galium odoratum*, *Circaea luetiana*), suggesting the soil scarification typical of salvaging (e.g., Rumbaitis del Rio 2006; Peterson and Leach 2008a) promotes species that would otherwise remain “trapped” in the seed bank (Table 2; Peterson et al. 1990; Leckie et al. 2000; Royo and Ristau 2013; Royo et al. 2016). Moreover, all taxa identified in the indicator species analysis are native and several exhibit wide ecological amplitudes, persisting in both early-successional and mature woodlands (Morgan and Smith 1979; Ziegenhagen et al. 2003; Fridley et al. 2007).

Despite these few colonists, the observed impact of salvaging on composition was minimal. Of the 95 taxa encountered in our census, only four were found only on the salvaged side, all at extremely low abundance (Table S1). While we are well aware of the drawbacks in drawing conclusions from short-term studies, these studies provide critical information on how salvaging could potentially redirect successional trajectories by altering understory vegetation composition. In a review of post-windthrow salvaging logging, Royo et al. (2016) found approximately half of short-term studies (<5 years) reported negative impacts of salvage logging on vascular flora. For example, Rumbaitis del Rio (2006) documents a shift towards graminoid dominance after salvage logging that could inhibit conifer regeneration, and Waldron et al. (2014) found reduced seedbed heterogeneity and a loss of understory species following salvaging. While longer-term studies (>5 years) suggest these early deleterious effects are ephemeral (Royo et al. 2016), these short-term impacts nonetheless provide a mechanism by which salvaging could alter forest recovery. Though it remains unclear whether this increased diversity will persist, these findings, drawn from a well-replicated experimental framework, contrast sharply with short-term studies suggesting that salvaging redirects forest regeneration down an alternative, depauperate successional trajectory (e.g., Rumbaitis del Rio 2006; Brewer et al. 2012; Waldron et al. 2014).

The limited impacts of salvage logging observed at this site may stem, in part, from a storm event that caused moderate to low (<50%) canopy damage within relatively constrained patches (Fig. 2). In contrast, researchers have found pronounced salvage effects where overstory damage is sufficiently widespread and severe to trigger substantial and dynamic changes in the understory (Peterson and Leach 2008a; Brewer et al. 2012; Royo et al. 2016; Santoro and D’Amato 2019). Moreover, the relatively small size, narrowly oblong shape, and SW–NW directionality of the gaps may constrain seasonal light availability, and therefore the potential for dynamic changes, given shading from the surrounding intact forest and low solar light angles found in higher latitudes (Canham et al. 1990). Despite these caveats, the range of canopy disturbance size and severity in this study is representative of a majority of windthrow disturbance in temperate deciduous forests (Evans et al. 2007; Hanson and Lorimer 2007; Rich et al. 2007; Peterson 2007; Fraver et al. 2009; Leverkus et al. 2018a). Clearly, more studies are required to reconcile contrasting results regarding the short- and long-term impacts of salvaging and to elucidate how interactions between natural and anthropogenic disturbance shape subsequent responses (Leverkus et al. 2018b).

Conclusions and future directions

Salvage logging is often described as detrimental to forest regeneration, based in part on short-term studies, particularly following fire in the western United States (Beschta et al. 2004; Karr et al. 2004; Lindenmayer et al. 2004; Baird 2006; DellaSala et al. 2006; Donato et al. 2006; Newton et al. 2006). While salvage logging can have broader negative impacts on biodiversity (e.g., birds, saproxylic beetles, reviewed in Thorn et al. 2018), this study joins a growing literature that suggest the impact of salvaging on vascular flora is more complex and context-dependent (Royo et al. 2016). Recognizing this complexity, this manuscript represents the first year of a long-term experiment in which we will simultaneously test the effects of white-tailed deer exclusion and the removal of interfering recalcitrant understory vegetation (*sensu* Royo and Carson 2006), in conjunction with salvage logging, on forest regeneration.

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