

# Evaluating the ecological impacts of salvage logging: can natural and anthropogenic disturbances promote coexistence?

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**Abstract.** Salvage logging following windthrow is common throughout forests worldwide even though the practice is often considered inimical to forest recovery. Because salvaging removes trees, crushes seedlings, and compacts soils, many warn this practice may delay succession, suppress diversity, and alter composition. Here, over 8 yr following windthrow, we experimentally evaluate how salvaging affects tree succession across 11 gaps in Eastern deciduous forests of Pennsylvania, wherein each gap was divided into salvaged and control (unsalvaged) halves. Our gaps vary in size and windthrow severity, and we explicitly account for this variation as well as variation in soil disturbance (i.e., scarification) resulting from salvaging so that our results would be generalizable. Salvage logging had modest and ephemeral impacts on tree succession. Seedling richness and density declined similarly over time in both salvaged and unsalvaged areas as individuals grew into saplings. The primary impact of salvaging on succession occurred where salvaging scarified soils. Here, salvaging caused 41 to 82% declines in sapling abundance, richness, and diversity, but these differences largely disappeared within 5 yr. Additionally, we documented interactions between windthrow severity and scarification. Specifically, low-severity windthrow and scarification combined reinforced dominance by shade-tolerant and browse-tolerant species (*Acer pensylvanicum*, *Fagus grandifolia*). In contrast, high windthrow severity and scarification together reduced the density of a fast-growing pioneer tree (*Prunus pensylvanica*) and non-tree vegetation cover by 75% and 26%, respectively. This reduction enhanced the recruitment of two mid-successional tree species, *Acer rubrum* and *Prunus serotina*, by 2 and 3-fold, respectively. Thus, our findings demonstrate that salvaging creates novel microsites and mitigates competing vegetation, thereby enhancing establishment of important hardwoods and promoting tree species coexistence. Our results, coupled with an assessment of 27 published post-windthrow salvage studies, suggest short-term studies may overestimate the impact of salvaging on regeneration. We conclude that the ecological costs and benefits of salvaging depend upon the variation in canopy and soil disturbance severity as well as the timescale at which effects are evaluated. Thus, our findings are inconsistent with the view that salvaging inexorably undermines plant diversity; rather we suggest salvaging can promote tree species coexistence within various contexts.

**Key words:** disturbance severity; diversity; salvage; tree regeneration; wind disturbance.

## INTRODUCTION

Salvage logging in forests following major disturbances has received intense scrutiny and debate because salvaging may inhibit forest recovery and undermine many of the benefits to biodiversity that accrue following disturbance (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). Specifically, many warn that salvaging reduces or even eliminates key biological and structural legacies generated by natural disturbances,

in particular a wide assortment of unique regeneration microsites (Foster et al. 1997, Cooper-Ellis et al. 1999, Purdon et al. 2004, D'Amato et al. 2011, Brewer et al. 2012, Waldron et al. 2013). These legacies create a highly patchy landscape that may be the basis for tree species coexistence via niche partitioning (Grubb 1977, Ricklefs 1977, Denslow 1987). If so, then salvage logging may homogenize the post-disturbance landscape leading to depauperate successional pathways (Lindenmayer et al. 2008). Yet, despite these concerns, salvage logging remains a widespread response to forest disturbance (e.g., fire, wind, insect outbreaks, ice damage) across hundreds of thousands of hectares yearly throughout forests of North America and elsewhere (Haymond et al. 1996, American Lands Alliance 2003, Schelhaas et al. 2003, Nappi et al. 2004, Lindenmayer et al. 2008).

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To date, the vast majority of studies evaluating the influence of post-disturbance salvage logging have focused on the post-fire salvaging of drier forests (reviewed by McIver and Starr 2000, Lindenmayer and Noss 2006). While much of this work emphasizes changes to structural and physical attributes (e.g., organic matter, coarse woody debris and snags, fuel loads; Fraver et al. 2011, Waldron et al. 2013), a small number of studies have found that salvage logging can be harmful because it diminishes seedling recruitment by as much as an order of magnitude and reduces species abundance and richness (Purdon et al. 2004, Donato et al. 2006, Greene et al. 2006). Indeed, salvage logging can have striking impacts. For example, Donato et al. (2006) reported that post-fire salvaging reduced conifer seedling abundance by 71% relative to unsalvaged areas. The degree to which these changes were deleterious, however, was unclear because the study lasted only a year (e.g., Baird 2006, Newton et al. 2006). To date, the evidence that post-fire salvage is inimical to forest recovery remains unclear and contradictory due, in part, to the short-term duration of the studies (i.e., < 3 yr) and because most studies did not account for the degree of disturbance severity (McIver and Starr 2000, Lindenmayer and Noss 2006, Lindenmayer et al. 2008). Furthermore, Lindenmayer and Noss (2006) concluded that the impacts of salvage logging remain poorly documented partly because much of the past research was conducted on an *ad hoc* basis, was typically short-term, had little to no replication, or surprisingly lacked unsalvaged control areas entirely (see also Lindenmayer and Ough 2006, Palik and Kastendick 2009 for similar critiques).

Because the bulk of past studies of salvaging have occurred following fire, it is problematic to draw conclusions about post-windthrow salvage effects using post-fire salvage studies because wildfires often exert very different impacts on the biotic and abiotic features of forests compared to windthrow (reviewed by Sousa 1984, Roberts 2004). Moreover, although a growing number of post-windthrow papers do exist (Table 1), with few exceptions the same critiques levied at post-fire salvage studies often apply to post-windthrow research. Thus, rigorous new studies and syntheses of existing studies are critical because wind is often the predominant disturbance regime within temperate forests (e.g., Everham and Brokaw 1996, Schulte and Mladenoff 2005) affecting hundreds of thousands, if not millions, of hectares yearly, the bulk of which are ultimately salvaged (Foster et al. 1997, Schelhaas et al. 2003, Lindenmayer et al. 2008). For example, in the US within 9 months of Hurricane Hugo, land managers salvaged nearly 11 000 000 m<sup>3</sup> of timber (Haymond et al. 1996) and in Europe they logged approximately 75 000 000 m<sup>3</sup> of timber within 18 months after Storm Gudrun (Sondell 2006). Even in years and regions lacking these large-scale storm events, salvaging smaller blowdowns often represents a major portion of the total timber harvest. For example, on the Allegheny National Forest (ANF) of Pennsylvania, salvage logging

accounted for 32% of the area harvested in the period between 2003 and 2012 (A. Hille, *pers comm*). Given the ubiquity of salvaging and the dearth of information of its effects, current management decisions regarding salvaging are often based on short-term economic, public safety, and fire hazard considerations without explicit consideration of the longer-term ecological impacts (Foster and Orwig 2006, but see Angst and Volz 2002 for a post-windthrow salvage harvesting decision-support tool). Consequently, there exists an urgent need to address the current knowledge gap on post-windthrow salvage logging.

Here we explore the degree to which salvage logging delays forest recovery and alters successional trajectories of woody species over eight growing seasons following windthrow by experimentally salvaging multiple gaps and applying salvage treatments to only half of each gap. We took advantage of a large storm event in 2003 that created numerous canopy gaps across a 500 000 ha region. The canopy gaps varied substantially in two critical disturbance metrics: gap size (area) and windthrow severity. Here, we emphasize disturbance severity (e.g., percent loss from pre-disturbance conditions in basal area; Pickett and White 1985, Roberts 2004) because it allows us to examine vegetation responses across the heterogeneous disturbance conditions that occur within- and among gaps (Frelich and Reich 1999, Frelich 2002, Roberts 2004, Peterson et al. 2013). We hone in on interactions that may be common between natural disturbance severity and salvaging. For example, Peterson and Leach (2008a) argued that salvaging impacts on understory plant diversity and abundance may be more detrimental in more severely disturbed patches because salvaging would directly impact areas where increases in understory species richness, abundance and diversity would be most pronounced and dynamic (Runkle 1981, Brokaw 1985, Clebsch and Busing 1989, Peterson et al. 1990, reviewed by Denslow 1987, McCarthy 2001). By deploying our experiment across numerous gaps with heterogeneously disturbed canopies we can rigorously evaluate whether salvage impacts change along a disturbance severity gradient.

We predict salvage logging will (1) delay succession by decreasing seedling and sapling abundance (i.e., density, basal area) and richness, (2) suppress seedling and sapling layer diversity ( $H'$ ), and (3) alter to patterns of species composition when compared to unsalvaged wind-disturbed areas. However, these predictions may depend entirely on interactions between salvage logging and natural disturbance severity. Past studies in eastern deciduous forests suggest that interactions among disturbance are pervasive, drive dynamics, and can be difficult to predict *a priori* (Paine et al. 1998, Royo et al. 2010a). Nevertheless, we predict salvaging impacts on seedling and sapling abundance, richness, diversity, and composition may be negligible and short-lived in less severely disturbed patches where established shade-tolerant individuals (i.e., advance regeneration) or species with

TABLE 1. Published studies of post-wind disturbance salvage effects on species richness (S), density (N), various measures of diversity (D), and composition (Comp) of plant communities from multiple forest types in forests of North America, Europe, and Asia. Citations in bold represent studies that evaluated salvage effect on herbaceous (i.e., non-woody) vegetation composition or diversity. We report the forest type and location of the study, the treatments employed, and replication at the scale of the disturbed patch (Nb), and whether treatments were blocked, the duration of the study, and whether measures of canopy (C) or soil (S) disturbance severity were used as covariates.

Location	Treatments <sup>a</sup>			Blocked by site	Duration (yr) <sup>c</sup>			Effects <sup>e</sup>				
	Control	Salvage	N <sup>b</sup>		Post-storm	Post-salvage	Severity <sup>d</sup>	S	N	D	Comp	Citation
N. Hardwoods; U.S.	Y	Y	11	Y	8	5	C, S	=	=	=	*	<i>This study</i>
Sub-Boreal Pine; U.S.	Y	Y	12	N	10	7-10		=	=	=	*	1
Subalpine Spruce-Fir-Pine-Aspen; U.S.	Y	Y	10	N	5	3	S	-	-	-	*	2
<i>Populus</i> ; U.S.	Y	Y	10	N	12	11	C		+, =		*	3
Spruce; Italy	N	Y	3	Y	19-20	17-18	S				*	4
Spruce; Switzerland	Y	Y	3	Y	10	10	C, S		+		*	5, 6
Fir-Beech-Spruce; Switzerland	Y	Y	90	N	10 & 20	?			+, =		=	7
Hemlock-N. Hardwoods; U.S.	Y	Y	2	N	27	25		+	+, =		*	8
Eastern Black Spruce; Quebec	Y	Y	6	N	4	2-4	C, S		-		*	9
Norway Spruce; Estonia	Y	Y	4	N	3-4	?	C, S		+		*	10
Aspen; Canada	Y	Y	5	N	2-3	1-2			+, -		*	11, 12
Mixed Hardwoods; U.S.	Y	Y	2	Y	3	2	C, S		=	+, =	=	13, 14
Mixed Hardwoods; U.S.	Y	Y	5	Y	2	1	C, S		=, -		*	15, 16
Spruce-Jack Pine; U.S.	Y	Y	P	N	2	1		+	+		*	17
Spruce; Slovakia	Y	Y	P	N	3-4	2-3	S		=, -		*	18
Spruce; Germany	Y	Y	P	N	25	?			+, -		*	19, 20
Bottomland Hardwoods; U.S.	Y	Y	P	N	3	3	S		+, =		*	21
Oak; U.S.	Y	Y	P	N	2	2			+		*	22
<i>Chamaecyparis thuyoides</i> ; U.S.	Y	Y	3	N	4-5	1-4			+		*	23
Mixed Hardwoods; U.S.	Y	Y	*	N	*	*						24
<i>A. sachalinensis</i> plantation; Japan	Y	Y	P	N	5	1	C, S	+	-	+		25
Pine-Hardwoods; U.S.	Y	Y	P	N	6	5						26
Mixed Hardwoods; U.S.	N	Y	P	N	4	3						27

<sup>a</sup>Treatments: Control = disturbed, no Salvage; Salvaged = disturbed and salvaged.  
<sup>b</sup>Replication: Number of disturbed sites/patches. P refers to studies that are pseudoreplicated. Studies may have additional treatment units.  
<sup>c</sup>Duration: Number of growing seasons (years) post storm and/or post salvage.  
<sup>d</sup>Severity: Summarizes whether study reports significant overall effect of salvage logging on species richness (S), abundance (N), diversity (D), or compositional shifts (Comp) relative to control (unsalvaged) plots. Symbols represent increases (+), decreases (-), no significant change (=) and altered species composition (\*).  
<sup>e</sup>Effects: Indicates whether study reports significant overall effect of salvage logging on species richness (S), abundance (N), diversity (D), or compositional shifts (Comp) relative to control (unsalvaged) plots. Symbols represent increases (+), decreases (-), no significant change (=) and altered species composition (\*).  
 1. D'Amato et al. (2011) All salvaged areas were subject to wildfire 5 to 8 yr post-salvage; 2. Rumbaitis del Rio (2006); 3. Palik and Kastendick (2009) Canopy disturbance measured, but not included as covariate in vegetation response; 4. Boitero et al. (2013) Summarized results from wind disturbed Parrot site. Soil disturbance refers to coarse woody debris piles; 5. Schönenberger (2002); 6. Wohlgemuth et al. (2002) A 4<sup>th</sup> site lacked salvage logging. Canopy and soil disturbance categorizations are (±); 7. Kramer et al. (2014) 24 sites from a 1990 storm & 66 sites from a 1999 storm; 8. Lang et al. (2009); 9. Waldron et al. (2014); 10. Ilisson et al. (2007) Average diversity (H') and evenness (E<sub>j</sub>) were lower in salvaged areas, but no statistical test presented; 11. Man et al. (2013); 12. Schafer et al. (2014); 13. Peterson and Leach (2008a); 14. Peterson and Leach (2008b); 15. Brewer et al. (2012); 16. Cannon and Brewer (2013); 17. Lain et al. (2008); 18. Jonašová et al. (2010); 19. Fischer et al. (2002); 20. Fischer and Fischer (2012); 21. Nelson et al. (2008) Evaluated herbaceous abundance, but not composition or diversity; 22. White et al. (2014); 23. Laing et al. (2011) Variation in timing of salvage and surveys; 24. Spurr (1956) Descriptive results of regeneration surveys following disturbance and salvaging; 25. Morimoto et al. (2011); 26. Fail (1999) Abundance measures are herbaceous NPP, and sapling height & diameter; 27. Elliott et al. (2002).

aggressive vegetative reproduction often dominate following windthrow (Webb and Scanga 2001, Dietze and Clark 2008). In contrast, in more severely disturbed areas, salvage logging effects on seedling and sapling abundance, richness, and diversity may be more detrimental and long-lasting. Alternatively, if salvage logging reduces the abundance of advance regeneration (Wohlgemuth et al. 2002, Jonášová et al. 2010, Waldron et al. 2014), salvaging may enhance opportunities for recruitment of less shade-tolerant species, particularly in more severely disturbed patches, thereby increasing richness and altering the species composition of the regenerating tree community.

## METHODS

### *Study site and gap selection*

Gaps were distributed throughout the Allegheny National Forest (ANF) in northwestern Pennsylvania. The ANF covers ~208 000 ha and lies within the Hemlock-Northern Hardwoods forest type. The vast majority of forested area in the region is comprised of second-growth forests established following extensive clearcutting in the early part of the 20<sup>th</sup> century. Major tree species are red maple (*Acer rubrum* L.), sugar maple (*Acer saccharum* Marsh.), black cherry (*Prunus serotina* Ehrh.), and American beech (*Fagus grandifolia* Ehrh.), with somewhat lesser abundances of hemlock (*Tsuga canadensis* L.), birches (*Betula alleghaniensis* Britt., *Betula lenta* L.), and white ash (*Fraxinus americana* L.) (Marquis 1975). Understory vegetation is dominated by striped maple (*Acer pensylvanicum* L.), beech (mostly root sprouts) in the shrub layer, and a variety of mesic forest ferns (e.g., *Demstaedia punctilobula* (Michx.) Moore and *Thelypteris noveboracensis* (L.) Nieuwl.) in the herb layer (Royo et al. 2010b).

In July 2003, a windstorm damaged over 5000 ha across a 150 km swath. Ground and aerial reconnaissance immediately thereafter revealed that 30% of gaps were under 1 ha and 60% were less than 3 ha (median: 2.18 ha; mean 4.78 ha; Evans et al. 2007). From the >200 gaps created within the Allegheny National Forest, we randomly selected 11 gaps along a gap size gradient that reflected the range of gap size created by the storm. Individual gaps varied in size from 0.05 to 4.0 ha. We excluded gaps near heavily-trafficked roads and selected gaps that occurred in mature second growth without a recent history of natural or anthropogenic disturbance. Sites were distributed throughout three counties (Elk, McKean, and Warren, Pennsylvania) and cover a gradient spanning a 24 km E–W and 9.2 km N–S. Soils across study sites were mostly sandstones and siltstones in the Buchanan, Brinkerton, Cookport, and Hazelton series. Gap size was positively correlated to disturbance severity measures ( $R^2 = 0.38$ ) and average disturbance severity across gaps ranged from 28 to 85% of basal area lost and within any one gap, disturbance severity was

spatially variable ranging from 0 to 100% (see Peterson et al. 2013 and Appendix S1 for more details on sites).

### *Salvaging*

We randomly selected half of each of the nine larger ( $\geq 0.1$  ha) gaps to be salvaged leaving the other half as an unsalvaged control. Division of gaps was along slope, aspect, or both so as to control for potential differences in these gradients. Gaps at the low end of the size gradient (0.05 ha) were too small to split into halves. Hence, we randomly selected two additional 0.05 ha gaps and randomly assigned salvaging to one of them. Thus, our design contains a total of 10 blocks. Nine of these blocks were individual blowdowns and the tenth block consists of two 0.05 gaps. All salvage logging operations were conducted by commercial loggers in accordance to specifications set by Allegheny National Forest, National Environmental Policy Act (NEPA) decision for these harvests. The operations salvaged dead and downed trees and harvested strongly leaning trees which were expected to die and also posed a safety hazard. Standing trees were left on site as were most snags, unless they posed a safety hazard. Per ANF guidelines (USDA Forest Service 2007), harvesting utilized stem-only methods (i.e., leaving tree tops, branches, and foliage on site) using rubber-tired skidders on planned skid trails during winter 2006/07.

### *Vegetation sampling*

Within each gap, we established permanent vegetation monitoring plots along stratified random transects in summer 2004. The number of and distance between transects and survey points along transects increased as gap size increased (range: 7 to 16 points; total  $n = 135$  points; see Peterson et al. 2013 for more details). We monitored seedling ( $\leq 2$  m) densities, by species, in 1 m<sup>2</sup> plots centered on each survey point in 2004, 2006, 2007, 2008, 2010, and 2011. We censused sapling ( $> 2$  m,  $< 10$  cm dbh) density and diameter at breast height (dbh) for all individuals in larger, 5 m radius (78.5 m<sup>2</sup>) plots centered on each seedling plot in census years. Additionally, we assessed total percent cover for all non-tree species (i.e., ferns, shrubs, graminoids, herbs, mosses) combined. Species nomenclature follows USDA Plants Database (USDA NRCS 2012).

### *Quantifying disturbance severity*

While our work spans an important gradient in gap sizes, it also spans a significant gradient in windthrow disturbance severity, which typically explains much of the variation in forest response following disturbance (reviewed by Frelich and Reich 1999). Thus, we carefully characterized windthrow severity; specifically, we tallied all trees ( $\geq 10$  cm dbh) within 7.5 m of each survey point for species, size (diameter at 1.4 m, or dbh), status (live or dead), and type of damage (intact, crown damaged,

bent, leaning, trunk snapped, or uprooted) in 2004. Our metric of windthrow severity was the proportion of basal area loss from the canopy (i.e., trunks snapped or trees uprooted; Roberts 2004).

Additionally, conceptual models of forest vegetation responses to disturbance stress the need to explicitly consider the degree to which the understory (i.e., existing vegetation and soil properties) is disturbed (Oliver and Larson 1996, Roberts 2004). Indeed, existing evidence demonstrates that mechanized timber harvesting operations and associated effects (e.g., logging equipment traffic, skid trails, log landings) often injure or kill established vegetation and disturb the forest floor by scarifying the soil surface (e.g., Zenner et al. 2006). As it is impossible to determine where salvage harvesting operations would disturb the soil surface *a priori*, we visually quantified the presence or absence of salvage-generated soil disturbance within each 5 m radius sapling plot immediately following the salvage operations. Here, as in other studies and for the sake of brevity, we define soil disturbances created by salvage logging as passive scarification (hereafter scarification; Nyland 2002).

#### Statistical analysis

We examined the effect of salvage logging and windthrow severity on seedling density and sapling abundance (density and basal area), richness, and diversity using repeated-measures analyses of covariance on a hierarchically randomized complete block design. Practical limitations in salvage harvesting operability and execution resulted in an unbalanced and non-orthogonal array of salvage-generated soil disturbance. Control plots lacked any scarification ( $n = 58$ ), whereas plots on salvaged halves contained a mix of plots with ( $n = 50$ ) and without ( $n = 27$ ) scarification. Thus, we assigned plots to three different salvage treatment categories: Control (unsalvaged, no soil disturbance), Salvage without scarification and Salvage with scarification. Creating these three categories *post-hoc* and using a hierarchical repeated measures model allows us to easily isolate and test differences in the scarification effect (i.e., salvage+scarification vs. control) as well as the overall salvage effect (i.e., average of all salvaged plots [i.e., with and without scarification] vs. control).

Because our hypotheses make explicit predictions regarding the effect of windthrow disturbance severity and its interaction with salvaging, we modeled plot-level windthrow severity (i.e., proportion of basal area loss) as a continuous covariate (Milliken and Johnson 2002, Littell et al. 2006). This procedure first required testing the homogeneity of slopes assumption. If the full model revealed a nonsignificant ( $P > 0.05$ ) covariate  $\times$  main effects interaction, the interaction term was removed resulting in an equal slopes model testing only the main effects and the covariate. However, in cases where the equal slope assumption was not met (i.e., significant covariate  $\times$  main effects), treatment differences were

tested at three levels of the windthrow severity covariate as different statistical significances will be observed depending on where the test is conducted along the covariate (Milliken and Johnson 2002, Littell et al. 2006). For our models we chose to test these responses at average windthrow severity (59% basal area loss), as well as the 20<sup>th</sup> (16% loss) and 80<sup>th</sup> (98% loss) representing low- and high-disturbance severity, respectively. We felt these three levels adequately address differences in the unequal slopes model and are biologically relevant.

Because our primary interest was whether responses varied between the control and the overall salvaged halves or between the control and either type of salvaged conditions (i.e., scarified or undisturbed) within each census period, we utilized *a priori* contrasts using least squares means to isolate these comparisons only following a significant year  $\times$  treatment (equal slopes model) or year  $\times$  covariate  $\times$  plot (treatment) interaction (unequal slopes model) in the overall analysis. We utilized Holm's sequential Bonferroni correction to minimize the Type I error rate (Holm 1979). Within the 2 size classes, response variables were: total stem density (stems  $\text{ha}^{-1}$ ), sapling basal area ( $\text{m}^2 \text{ha}^{-1}$ ), species richness ( $S$ ), Shannon diversity ( $H' = -\sum_i p_i \log(p_i)$ ), where  $p_i$  represents the relative stem density of  $i^{\text{th}}$  species; Magurran 1988), and total non-tree cover. Because average sapling densities changed by 2 orders of magnitude over time and density is known to affect estimates of diversity (Gotelli and Colwell 2001), we calculated expected species richness (i.e., rarefaction) in each plot for a sample size of 25 individuals.

All tests were conducted using generalized linear mixed models (Proc Glimmix; SAS Institute Inc. 2011) as these allow the modeling of longitudinal data with random effects and unbalanced designs (Cnaan et al. 1997). We modeled year, treatment, and year  $\times$  treatment as fixed effects. Because we randomly selected study sites from throughout the gradient in gap sizes created by the 2003 storm event, we modeled blocks (i.e., gaps) as a random effect. We included plots  $\times$  treatment (block) as a second random effect to account for the hierarchical nature of the design (Milliken 2006). The inclusion of these random effects is valid and valuable when the sample plausibly represents a larger population because it allows broader, more generalized inference (Littell et al. 2006). Year was the repeated measures in the model and the covariance structure between census periods was modelled using either the autoregressive order (AR(1)) or the autoregressive heterogeneous order (ARH(1)) covariance structure when the Levene's test of the residuals for the year effect was significant. We examined homoscedascity and normality of the residuals within each treatment and across time using boxplots and Levene's test. We added a group = "treatment" option in the random statement to adjust the model if the Levene's test showed a significant treatment effect (Moser 2004). All models were run with the Kenward-Rogers denominator degrees of freedom method. Analyses on stem density were

right-skewed and were best modeled using a gamma distribution with log link function and total non-tree percent cover was modeled using a beta distribution with a logit link function (Bolker 2008). Richness and diversity were modeled using a normal distribution and an identity link function.

To examine whether species composition differed across treatments, windthrow severity gradient, and their interaction, we ran distance-based redundancy analyses (dbRDA) using Bray-Curtis dissimilarity metric on both immediately pre-salvage (2006) and final post-treatment (2011) sapling importance values ( $IV = \frac{p_d + p_{ba}}{2}$ , where  $p_d$  and  $p_{ba}$  represent relative stem density and basal area of each species; Brown and Curtis 1952). We chose this metric as it integrates over 2 measures of abundance and thus more accurately measures dominance in a community, particularly by dampening the influence of a few large trees (i.e., basal area) or many small trees (density). dbRDA is a constrained ordination technique that is flexible with regards to distance measures, avoids problems associated with the assumptions of linear responses to environmental gradients, and is recommended for analyses that include continuous gradients and require tests of significance for interaction terms (Legendre and Anderson 1999). Analyses were performed on species matrices that culled species present on < 5% of plots because rare species exert unduly large influence in multivariate analyses and distort interpretation (McCune and Grace 2002). Significance of model terms was assessed using permutational tests of significance with 999 permutations. Species dominance values were transformed using the  $\log_e(x) + 1$  for  $x > 0$ , as suggested by Anderson et al. (2006), in order to reduce the influence of abundant species while simultaneously allowing for zeros (i.e., absences). To account for the paired nature of the design, we utilized gap as blocking factor using the *strata* option in *vegan* package R version 3.1.2 (Oksanen et al. 2015) so that randomizations were constrained within each block. Species associations to the constraining variables of treatment windthrow severity were visualized using dbRDA biplots. Community composition analyses were run using the *capscale* and *anova* functions in the *vegan* package.

## RESULTS

### *General patterns*

The windstorm caused a major loss of basal area (59%  $\pm$  2.6) across all gaps; however, within any individual gap windthrow severity was highly heterogeneous among individual sample points (range: 0 to 100% loss; Appendix S1). Salvage logging disturbed soils throughout ~65% (50/77 sample plots) of each salvaged site beyond that created by the windthrow alone. In 2011, we measured 2023 seedlings and 9230 saplings in plots representing a total area of 135 m<sup>2</sup> and 10 598 m<sup>2</sup>, respectively. Ninety percent of the seedling and sapling layer was composed

of seven tree species (27 total species, Fig. 1). The remainder of the community was largely comprised of small trees and shrubs, including *Aralia spinosa* L., *Carpinus caroliniana* Walter, *Ostrya virginiana* (Mill.) K. Koch, and *Amelanchier arborea* (Michx. F.) Fernald. Finally, although we present seedling data, we focus our attention on saplings because seedling dynamics were highly transient due to rapid recruitment into or out of seedling size classes (see below). Moreover, it is the sapling layer that ultimately determines future forest composition (Pacala et al. 1996).

### *Salvage logging impacts were short term even when coupled with soil disturbance*

In general, salvage logging (i.e., both scarified and non-scarified areas) caused short-term reductions in both species richness and the density of seedlings and saplings, and this was exacerbated in areas where salvage operations scarified the ground layer. Through 8 yr of succession across all treatments, both seedling species richness and diversity declined by 24% ( $S$ : 3.34 vs. 2.54;  $H'$ : 0.84 vs. 0.64) due to mortality and recruitment into the sapling size class (Table 2; Fig. 2). Seedling density dynamics varied across the windthrow severity gradient (year  $\times$  severity  $\times$  treatment interaction): at low windthrow severity, seedling densities remained stable or increased while at higher windthrow severities seedling densities declined by as much as 70% (Table 2). In areas of high windthrow severity, scarification created by salvaging reduced seedling densities by 44% relative to control areas immediately following salvaging, but this effect was not significant following Holm adjustment for multiple comparisons.

Sapling diversity ( $H'$ ) quadrupled and sapling species richness increased 2 to 3 fold, depending on the intensity of windthrow severity, during the first 8 yr of forest regeneration. In general, salvaging reduced sapling richness by 25%, but only in the 2 yr following salvaging (control vs. average salvage response: Holm-adjusted  $P$ -value = 0.09 in 2008 and 2009; Table 3, Fig. 3). Sapling density and basal area increased 1 to 2 orders of magnitude over the eight years, respectively, as seedlings recruited into the sapling size class (Table 3, Fig. 3B and C). Overall, salvaging significantly reduced sapling basal area by 60–70% in the first two years following salvaging but this effect was only observed at high windthrow severity (Fig. 3C). Similarly, salvage logging reduced sapling densities in the year following salvaging (Holm-adjusted  $P$ -value = 0.057), but only at high windthrow severities.

### *Consequences of scarification and variation in windthrow severity*

The most pronounced and longest-lasting salvaging impacts on vegetation were observed only where salvage operations scarified soils and even then, impacts were

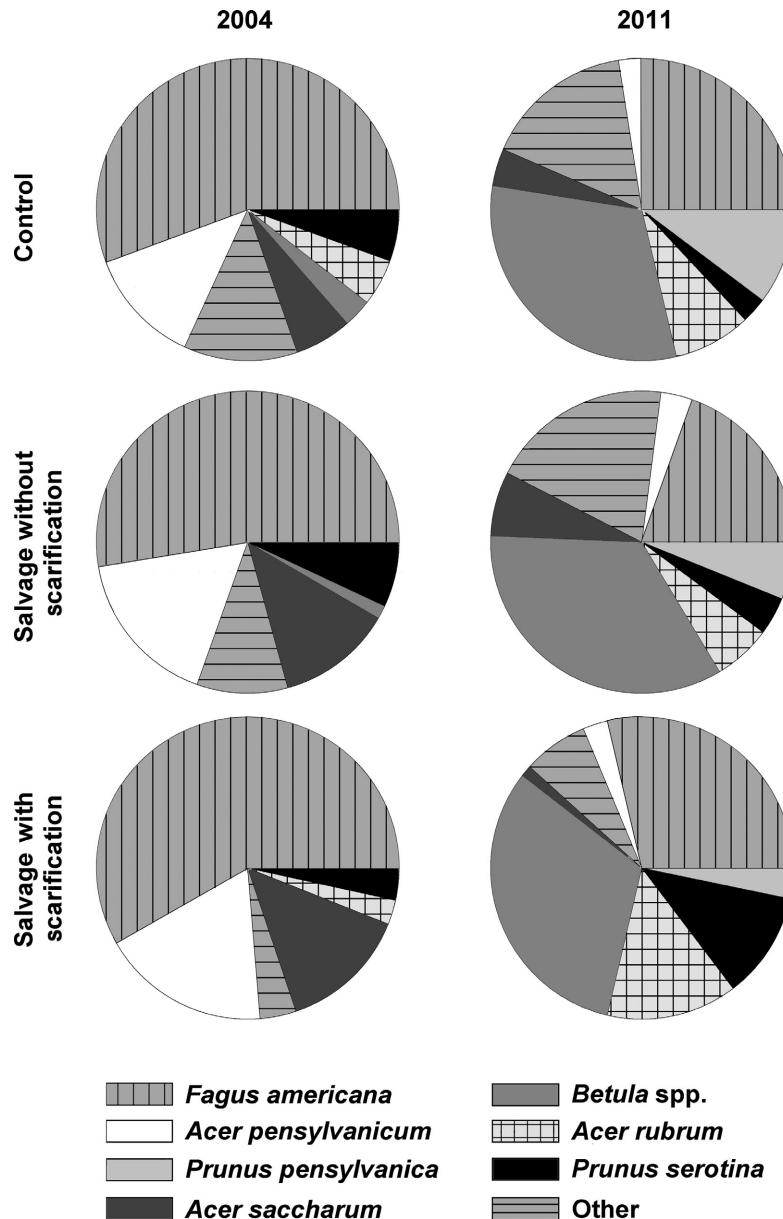


FIG. 1. Mean relative dominance of the sapling layer (> 2 m, < 10 cm dbh) for the seven most common tree species and all other canopy and subcanopy tree species combined in salvaged areas with scarification, salvaged areas without scarification, and controls at the onset of the study (2004) and 5 yr post-salvaging (2011).

typically restricted to the areas that experienced average to high windthrow severities ( $\geq 59\%$  BA loss). In these areas, salvage-generated scarification initially reduced sapling richness and diversity by 63% and 48%, respectively, although this impact persisted for only 2 yr following salvage logging (Table 3; Fig. 3A). Increasing windthrow severity augmented sapling basal area and stem densities. By 2011, sapling densities in areas with high windthrow severity were 27% and 50% greater than areas with moderate and low disturbance severity, respectively (Fig. 3B). Similarly, sapling basal areas in

areas with high windthrow severity were 20% and 37% greater than moderate and low disturbance severity areas, respectively (Fig. 3C). Where high windthrow severity and scarification co-occurred, sapling densities and basal area were initially suppressed by 77% and 82%, respectively, relative to control plots, reductions persisted until the end of the study (Table 3, Fig. 3B and C). Finally, non-tree cover increased significantly with increasing windthrow severity (covariate:  $F_{1,84} = 9.43$ ,  $P < 0.0029$ ). Scarification initially reduced non-tree cover by as much as 26% relative to control plots (year

TABLE 2. Results of repeated measure analyses of covariance on seedling richness, density (stems  $m^{-2}$ ), and diversity ( $H'$ ). Seedling richness and diversity were modeled using equal slopes ANCOVA (non-significant covariate  $\times$  main effects; see Fig. 2). Seedling density was modeled using unequal slopes ANCOVA (significant covariate  $\times$  main effects); therefore, treatment effects on stem density (stems  $m^{-2}$ ; LSM  $\pm$  1 SE) were tested at three levels of the windthrow severity covariate.

	Seedling richness			Seedling density (stems $m^{-2}$ )			Seedling diversity ( $H'$ )		
Year	$F_{5,250} = 9.91; P < 0.0001$			$F_{5,274.5} = 4.21; P = 0.0011$			$F_{5,230.7} = 4.80; P = 0.0003$		
Treatment	$F_{2,192.2} = 0.14; P = 0.8691$			$F_{2,93.1} = 0.80; P = 0.4540$			$F_{2,125} = 0.94; P = 0.3935$		
Y $\times$ Trt.	$F_{10,331.5} = 0.77; P = 0.6623$			$F_{10,249.3} = 1.27; P = 0.2449$			$F_{10,305.9} = 0.71; P = 0.7128$		
Severity	$F_{1,129} = 3.58; P = 0.0607$			–			$F_{1,125.2} = 1.30; P = 0.2555$		
Y $\times$ Sev $\times$ Plot (Trt)	–			$F_{144,374.2} = 1.62; P = 0.0002$			–		

	Low severity			Average severity			High severity		
Year	Sal+Scar	Sal–Scar	Control	Sal+Scar	Sal–Scar	Control	Sal+Scar	Sal–Scar	Control
2004	16.1 $\pm$ 5.7	17.6 $\pm$ 6.7	15.8 $\pm$ 5.1	20.0 $\pm$ 4.3	17.4 $\pm$ 5.0	18.0 $\pm$ 4.0	24.3 $\pm$ 7.7	17.1 $\pm$ 7.1	20.2 $\pm$ 7.2
2006	14.6 $\pm$ 5.2	17.8 $\pm$ 6.8	9.4 $\pm$ 3.1	12.7 $\pm$ 2.9	12.9 $\pm$ 3.7	11.9 $\pm$ 2.7	11.2 $\pm$ 3.5	9.8 $\pm$ 4.1	14.4 $\pm$ 5.1
2007	15.5 $\pm$ 5.5	23.6 $\pm$ 9.0	15.5 $\pm$ 5.0	9.8 $\pm$ 2.2	13.2 $\pm$ 3.8	13.4 $\pm$ 3.0	6.6 $\pm$ 2.1	8.0 $\pm$ 3.3	11.8 $\pm$ 4.2
2008	17.6 $\pm$ 6.2	15.6 $\pm$ 5.2	8.9 $\pm$ 2.9	7.4 $\pm$ 1.7	9.7 $\pm$ 2.9	8.6 $\pm$ 1.9	3.5 $\pm$ 1.1	6.4 $\pm$ 2.7	8.3 $\pm$ 3.0
2010	28.9 $\pm$ 10.2	20.6 $\pm$ 7.8	15.7 $\pm$ 5.1	12.2 $\pm$ 2.8	11.9 $\pm$ 3.4	7.7 $\pm$ 1.7	5.7 $\pm$ 1.8	7.3 $\pm$ 3.0	4.1 $\pm$ 1.5
2011	20.9 $\pm$ 7.9	20.7 $\pm$ 8.2	12.9 $\pm$ 4.2	11.8 $\pm$ 2.8	11.2 $\pm$ 3.2	10.6 $\pm$ 2.4	7.2 $\pm$ 2.3	6.6 $\pm$ 2.7	8.9 $\pm$ 3.2

$\times$  treatment:  $F_{10,530.1} = 4.46, P < 0.0001$ ; Fig. 4) but then it recovered and ultimately exceeded control plots by approximately 38%.

Together, salvage logging and greater wind disturbance severity, caused sapling communities to diverge from understories dominated by shade-tolerant and browse-tolerant species in unsalvaged areas experiencing low disturbance severity (dbRDA<sub>Trt $\times$ Sev</sub>:  $F_{2,109} = 2.84, P = 0.004$ ; Fig. 1 and Appendix S3). Species composition immediately prior to salvage operations was similar across all study plots (dbRDA<sub>Trt $\times$ Sev</sub>:  $F_{2,113} = 1.56, P = 0.106$ ). By 2011, 5-years post salvage, severe windthrow combined with scarification led to a sapling layer that contrasted in species composition with plots that had less severe windthrow and no soil disturbances (i.e., control plots and salvage-logged without soil disturbance). At the beginning of the study, three shade-tolerant and browse-tolerant species, striped maple, sugar maple, and American beech, dominated the sapling layer with beech comprising >50% of the community (Fig. 1). Increasing windthrow severity reduced the relative abundance of these species by 50% and increased by an order of magnitude the relative abundance of shade-intolerant and intermediately-tolerant species, particularly the birches (Fig. 1; Appendices S2 and S3). Although beech was co-dominant along the entire windthrow severity gradient (Appendix S2: Table S1, Appendix S3: Fig. S1A), these three shade-tolerant and browse-tolerant species in general dominated at the low end of the windthrow severity gradient particularly in areas where salvaging did not cause scarification (i.e., sugar maple and striped maple; Appendix S3: Fig. S1B). Among the intermediately-tolerant species, birch became co-dominant throughout the windthrow severity gradient irrespective of salvage-generated soil

disturbance (Appendix S3: Fig. S1C). However, moderate to high windthrow severity ( $\geq 59\%$  BA loss) and scarification together caused a 2-to 3-fold increase in the recruitment of other intermediately-tolerant species (e.g., black cherry and red maple), relative to areas without soil disturbance (i.e., control plots and salvage plots without scarification; Fig. 1 and Appendix S3: Figs. S1D and S1E). In contrast, the short-lived and shade-intolerant pin cherry (*P. pensylvanica*) was 2 to 3 times more abundant in areas without soil disturbance, particularly where windthrow severity was high (Fig. 1 and Appendix S3: Fig. S1F).

## DISCUSSION

Salvage logging has come under scrutiny because it may severely delay forest recovery and compromise biodiversity. Our results from a robust experiment deployed across multiple gaps spanning a broad disturbance severity gradient demonstrate that, on average, salvage logging effects on the rate and trajectory of sapling tree regeneration and diversity are modest and for the most part disappear in less than a decade. Moreover, the combination of moderate- to high severity windthrow and scarification created by salvaging enhanced the establishment of intermediately shade-tolerant species (e.g., black cherry, red maple) that were relatively uncommon in areas with high severity blowdown alone, thus likely promoting coexistence. It is important to note that this dynamic occurred where overbrowsing has been occurring for many decades (Carson et al. 2014), a condition that is typical of much of the eastern deciduous forest biome (Waller and Alverson 1997, Rooney 2001, Russell et al. 2001, Côte et al. 2004, Royo et al. 2010b, Nuttle et al. 2013) as well as other forested regions worldwide (e.g.,

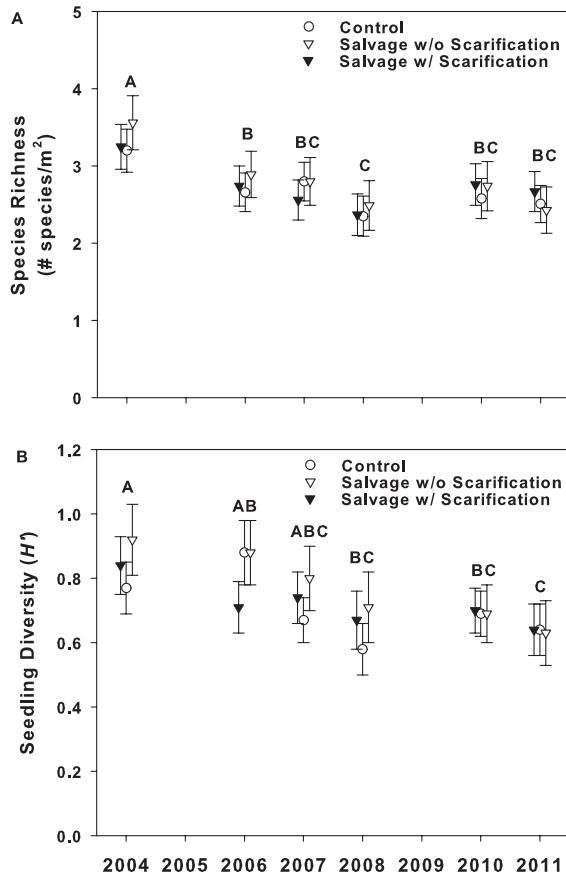


FIG. 2. Change in mean seedling (< 2 m) (A) richness and (B) diversity ( $H'$ ) over time in the three treatments following the July 2003 windstorm and salvage logging in winter 2006/07. Analysis of covariance model detected only significant differences in overall means over time. Superscripts denote significant differences among sample periods following Holm correction. See Table 2.

Coomes et al. 2003). In these regions overbrowsing typically creates a dense, depauperate, and recalcitrant layer of advance regeneration (*sensu* Royo and Carson 2006) composed of species that are not just highly shade-tolerant *but also* highly browse-tolerant (Krueger et al. 2009). Placed within this context, our findings suggest that it took the combination of windthrow and scarification to disrupt this recalcitrant layer and allow less shade-tolerant as well as browse-sensitive species into the sapling size class. Overall and counter to our expectations, salvaging and scarification together promoted the coexistence of tree species that spanned the gradient of both shade and browse tolerance while causing only short-term declines in woody species diversity that essentially disappeared by the end of the study. The forest that regenerated with salvaging and scarification more closely resembled the species composition typical of a second-growth northern hardwoods forest of this region where both black cherry and red maple were typically quite

abundant (Marquis 1975, Horsley et al. 2003, Royo et al. 2010b).

#### *Salvaging effects are ephemeral*

Considered in its entirety, salvage logging (i.e., both scarified and non-scarified areas) did not have long-term detrimental effects on the regenerating tree community but rather promoted a more heterogeneous regenerating woody species' community. Over eight growing seasons, seedling richness and abundance declined as individuals grew into the sapling size class and salvaging did little to change these dynamics. Furthermore, although salvaging caused immediate declines in sapling richness, diversity, and abundance relative to unsalvaged controls, these differences largely disappeared within 5 yr. Indeed, our study is noteworthy because we report on vegetation trajectories over five growing seasons post-salvage and 8 yr post-storm. To our knowledge, fewer than half of existing post-windthrow salvage studies report effects on similar timescales, and none of these found a long-term negative impact on the richness, abundance, or diversity of the regeneration (Table 1). In fact, a recent study by Kramer et al. (2014) examining regeneration patterns in 90 windthrow gaps in Swiss alpine forests found salvaging did not reduce advance regeneration and enhanced seedling recruitment 10 and 20 yr post-salvage. In contrast, 50% of shorter-term studies (i.e., < 5 growing seasons post-salvage) report salvaging negatively impacts richness, abundance, or diversity of the regeneration layer. Collectively, these findings demonstrate that although the regenerating woody plant community is negatively affected immediately following salvaging, forests can recover relatively rapidly via sprouting by pre-established species (e.g., *Populus* spp.; Lang et al. 2009, Palik and Kastendick 2009), recruitment from seed bank (e.g., pin cherry), and germination of newly dispersed seed (e.g., birches).

Our results strongly suggest that it is not the act of salvaging (i.e., removing logs) *per se* that alters tree regeneration patterns, but rather the physical disturbance to the site. Notably, the most pronounced and longer-lasting impacts of salvaging occurred where logging disrupted the forest floor (e.g., run over by logging equipment, skid trails, log landings) and where canopy disturbance was most severe. Indeed, our work combined with recent studies in North American and European forests suggests that salvaging creates communities distinct from unsalvaged areas where salvaging disturbance removes vegetation and disturbs soils (Rumbaitis del Rio 2006, Jonášová et al. 2010, Brewer et al. 2012, Fischer and Fischer 2012, Cannon and Brewer 2013). This is consistent with the 3-axis perspective on disturbance severity advocated by Roberts (2004, 2007) who urges consideration of soil disturbance as an axis of severity independent of canopy or shrub layer disruption. It is important to point out, however, that while salvage

TABLE 3. Results of repeated measure analyses of covariance sapling richness, basal area, stem density, and diversity ( $H'$ ). Sapling richness, basal area, and density were best modeled with unequal slopes ANCOVA model (significant covariate  $\times$  main effects; see Fig. 3). Sapling diversity was best modeled using equal slopes ANCOVA; therefore treatment effects on diversity ( $H'$ ; LSM  $\pm$  1 SE) at the mean disturbance severity covariate level are reported below. Asterisks (\*) denote treatments that differ from control within a given year following Holm corrections.

	Saplings richness <sup>†</sup>	Sapling basal area (m <sup>2</sup> ha <sup>-1</sup> )	Sapling density (stems ha <sup>-1</sup> )	Sapling diversity ( $H'$ )
Year	$F_{5,264.1} = 4.15; P = 0.0012$	$F_{5,424.4} = 1.97; P = 0.0824$	$F_{5,518.2} = 4.85; P = 0.0002$	$F_{5,275.2} = 35.55; P < 0.0001$
Treatment	$F_{2,113} = 0.43; P = 0.6532$	$F_{2,54.93} = 2.15; P = 0.1262$	$F_{2,120.9} = 0.75; P = 0.4739$	$F_{2,128.3} = 2.96; P = 0.0556$
Y $\times$ Trt.	$F_{10,331.4} = 1.65; P = 0.0916$	$F_{10,375} = 1.59; P = 0.1075$	$F_{10,526.6} = 1.82; P = 0.0544$	$F_{10,348.1} = 2.19; P = 0.0180$
Severity	—	—	—	$F_{1,158.7} = 0.98; P = 0.3232$
Y $\times$ Sev $\times$ Plot (Trt)	$F_{144,468.8} = 1.37; P = 0.0079$	$F_{144,390.1} = 4.32; P < 0.0001$	$F_{144,535.5} = 2.16; P < 0.0001$	—

Sapling diversity ( $H'$ ) at average severity			
Year	Sal+Scar	Sal-Scar	Con
2004	0.19 $\pm$ 0.11	0.20 $\pm$ 0.12	0.15 $\pm$ 0.11
2006	0.29 $\pm$ 0.11	0.25 $\pm$ 0.12	0.27 $\pm$ 0.11
2007	0.28 $\pm$ 0.12*	0.44 $\pm$ 0.13	0.54 $\pm$ 0.11
2008	0.40 $\pm$ 0.11*	0.60 $\pm$ 0.12	0.62 $\pm$ 0.11
2010	0.64 $\pm$ 0.11	0.63 $\pm$ 0.12	0.75 $\pm$ 0.11
2011	0.67 $\pm$ 0.12	0.72 $\pm$ 0.12	0.83 $\pm$ 0.11

<sup>†</sup>Richness analyses based on rarefied species richness utilizing a sample of 25 individuals from each subplot. Analyses on Shannon are based on stem density as abundance measure.

logging often creates large areas with soil disturbance (e.g., % bare soil: 24.6% to 65% of area; Rumbaitis del Rio 2006, Peterson and Leach 2008a, Brewer et al. 2012, Cannon and Brewer 2013, this study), a substantial portion of the area typically remains undisturbed. In these areas, seedling and sapling communities are indistinguishable from windblown controls, thus tempering the effect of salvage logging across the entire site. Indeed, Peterson and Leach (2008a) likely found little detrimental effects of salvaging because of the absence of skid trails or machine disturbance in their sampling quadrats. Similarly, Kramer et al. (2014) found no differences between salvaged and unsalvaged gaps because of careful logging operations that limited disturbance to existing vegetation and soils. In contrast, where more intensive salvaging practices remove much of the biological and structural legacies (e.g., silvicultural scarification, milling or piling of slash), detrimental impacts on tree regeneration appear more pronounced (e.g., Morimoto et al. 2011, Bottero et al. 2013).

#### *Salvaging and windthrow severity interactions enhance species coexistence*

Our results demonstrate that wind disturbance alone largely fails to promote tree coexistence in forests dominated by shade-tolerant and browse-tolerant sapling cohorts and a recalcitrant non-tree vegetation layer (Royo and Carson 2006, Dietze and Clark 2008, Nuttle et al. 2013, Plotkin et al. 2013). Beyond the recruitment

of sub-canopy tree species and the short-lived, shade-intolerant pin cherry (Burns and Honkala 1990), the sapling cohort in areas lacking scarification remained dominated by beech advance regeneration and newly recruited birch (see Kramer et al. 2014 for similar results in European beech forests). Yellow and black birch were the only long-lived canopy tree species that vigorously recruited across all conditions and ultimately became co-dominant with beech (Fig. 1). Birches often proliferate following disturbance (Carlton and Bazzaz 1998, Fischer et al. 2002, Plotkin et al. 2013). Moreover, Krueger et al. (2009) found the birches had the highest absolute growth rate of the regenerating seedlings, particularly when protected from herbivory, at these sites. The paucity in new recruitment of additional species capable of forming the future canopy (e.g., red maple and black cherry) is particularly troubling because across much of its North American range, beech dies before recruiting into larger size classes due to beech bark disease (Houston 1994). Hence, future forest diversity in disturbed patches in the absence of scarification may collapse to near monodominance of a birch canopy with a beech thicket understory (Runkle 2007). In sharp contrast, increasing canopy windthrow severity combined with scarification resulting from salvage logging enhanced the establishment of hardwood species of high economic value and promoted species coexistence. Similarly, Willis et al. (2015) demonstrated interactions between canopy openness and scarification were critically important for tree establishment and

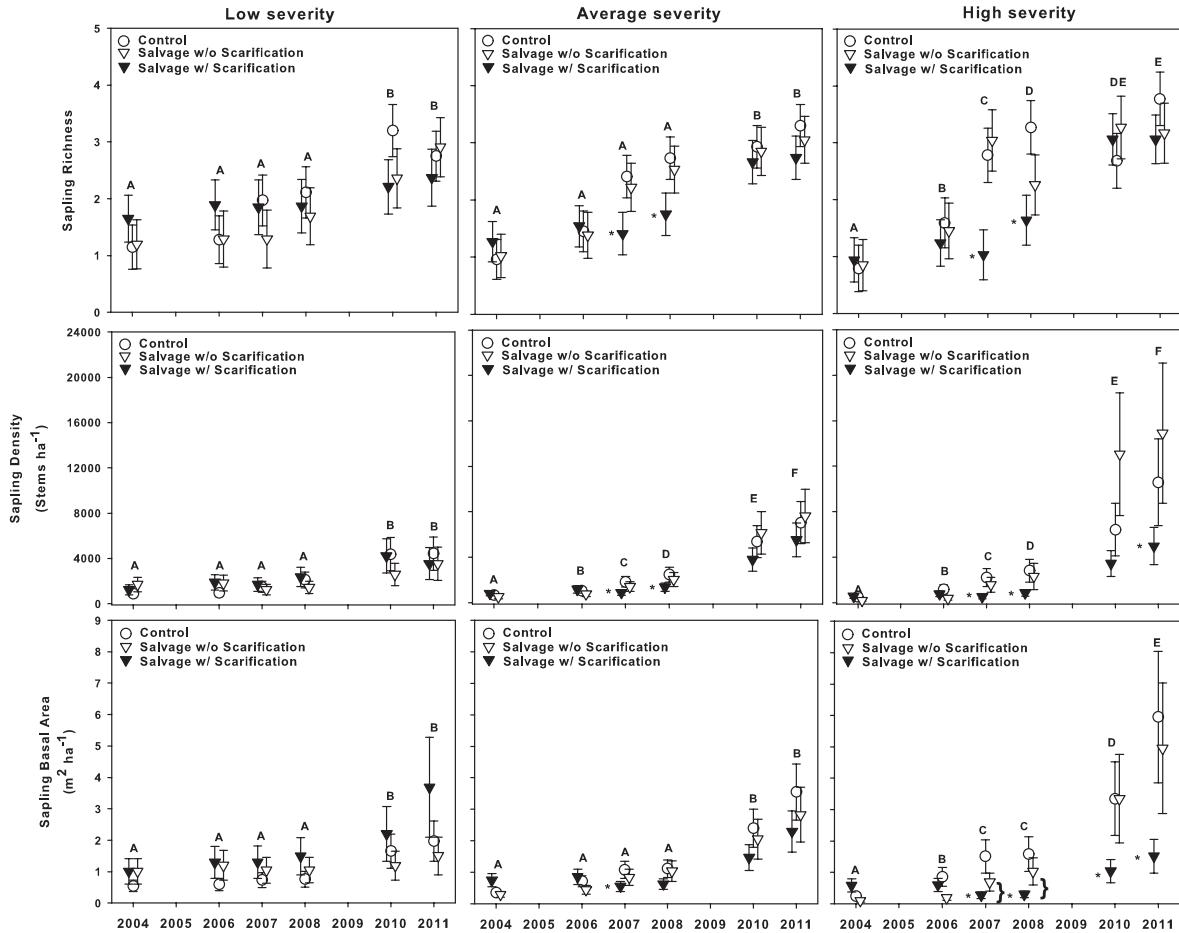


FIG. 3. Change in mean sapling (> 2 m, < 10 cm dbh) (A) richness, (B) density, and (C) basal area over time at three levels of the disturbance severity covariate following the July 2003 windstorm and salvage logging in winter 2006/07. Low (16% BA lost), Average (59% BA lost), and High (98% BA lost). Superscripts denote significant differences among sample periods, asterisks (\*) denote a significant treatment between a salvage treatment and control plots within a given year, and brackets (}) denote when the overall salvage effect is different from control. All tests employed a Holm correction. See Table 3.

coexistence in harvest gaps. These results suggest that a historical disturbance regime (i.e., windthrow) can promote coexistence, but only in combination with additional disturbances to the understory vegetation and soil (here, scarification caused by salvaging; see also Oliver and Larson 1996, Roberts 2004, 2007).

Our findings suggest scarification promotes tree coexistence through at least two mechanisms: the creation of novel establishment microsites and a reduction of interspecific and apparent competition from a dense layer of recalcitrant vegetation composed of both trees and herbaceous species (Royo and Carson 2006, 2008, Carson et al. 2014). Salvaging, and its concomitant scarification, creates unique microsites that enhance the abundance of less shade-tolerant species (Schönenberger 2002, Wohlgemuth et al. 2002, Nelson et al. 2008, Peterson and Leach 2008b, Cannon and Brewer 2013) and even a globally imperiled tree species (*Chamaecyparis thyoides*; Laing et al. 2011). Salvaging also temporarily

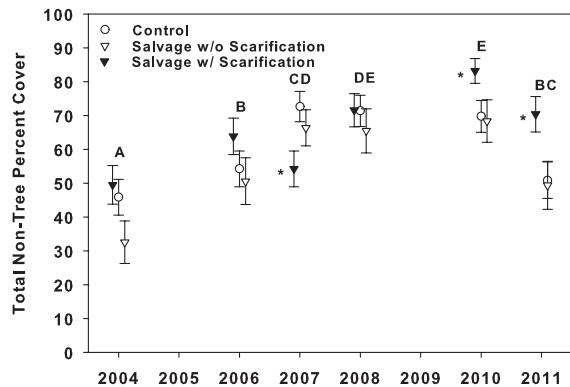


FIG. 4. Change in mean total non-tree percent cover over time following the July 2003 windstorm and salvage logging in winter 2006/07. Superscripts denote significant differences among sample periods and asterisks (\*) denote a significant treatment between a salvage treatment and control plots within a given year following Holm correction.

the abundance of herbaceous and woody species that proliferate immediately following the windthrow (see also Rumbaitis del Rio 2006, Brewer et al. 2012) and are known to strongly limit tree seedling richness and density (Krueger and Peterson 2009). Thus, salvage logging may provide enhanced establishment and growth opportunities for less shade-tolerant tree species.

#### *The domain of generality and caveats of this study*

Debate over salvage logging impacts has caused a recent proliferation on studies examining the effects of this common, yet often controversial, practice. We identified 27 papers from 22 additional study areas that studied plant community responses to post-windthrow salvage logging; most of which were published in the last 6 yr (Table 1). These studies vary considerably with respects to experimental design and sampling effort and several are limited in their inference by the same deficiencies in design identified by McIver and Starr (2000), Lindenmayer and Ough (2006) in their assessments of post-fire salvage studies. Because natural disturbances are unpredictable, unsurprisingly most studies (including ours) lack pre-storm vegetation community data. Thus, very few studies can assess the rate of recovery of plant communities following disturbance and salvaging to their pre-disturbance state (but see Brewer et al. 2012). A few studies confound salvage logging with post-windthrow wildfire or lack adequate controls (e.g., windthrow without salvage) altogether. Nearly half the existing studies do not replicate their design across multiple gaps and even for replicated studies, only a minority of these control for potential inter-site variation by blocking salvage and unsalvaged within gaps. Notably, only six of 27 studies explicitly considered the effect of variation in both overstory and understory disturbance severity. In order to build on these previous studies, we suggest that future studies must consider the variation within and interaction between these overstory and understory disturbance severity. Finally, as noted above, empirical studies to date indicate the overall effects of post-windthrow salvaging on tree richness and abundance are short-lived; therefore, studies of short duration (< 5 yr) likely overestimate the negative impact of salvage logging on tree successional dynamics and may well overlook whether scarification can promote coexistence. Although our study circumvents these limitations, our results *suggest* a general synthesis, specifically that salvaging has only short-term impacts on forest regeneration (< 5 yr) and can promote coexistence by reducing the dominance of preexisting woody or herbaceous layers and by creating novel soil microsites, thereby promoting establishment of relatively small-seeded and less shade-tolerant species. Nonetheless, the number of long-term studies remains too few and a lack of methodological standardization among studies precludes more definitive conclusions.

We want to be careful to place our conclusions within their proper context. Our results apply primarily to the impact of salvage logging on woody species' regeneration across a gap size and severity gradient that spanned from less than a hectare to 4 ha. This range of canopy disturbance size and severity represents by far the most common type of windthrow in the eastern deciduous forest (Canham and Loucks 1984, Schulte and Mladenoff 2005, Evans et al. 2007, Hanson and Lorimer 2007, Rich et al. 2007, Fraver et al. 2009). Nonetheless, it is not clear the degree to which our results will scale up and apply to much less common but extremely large-scale windthrows (e.g., Peterson and Pickett 1995, Turner et al. 1998, Peterson 2000). In addition, while salvaging had little impact on the abundance of non-woody (i.e., herbaceous) species, we did not evaluate species-specific responses and thus we do not know whether salvaging altered the species composition or diversity of this group. We acknowledge this limits our ability to generalize to effects on the broader plant community as herbaceous species account for a large fraction of total plant species richness (Royo et al. 2010*b*). Nevertheless, only 10 of the 27 studies in Table 1 evaluated the species composition or diversity of this group. These studies suggest impacts on herbaceous communities may be more lasting (e.g., Rumbaitis del Rio 2006, Brewer et al. 2012). Moreover, we did not evaluate whether salvaging caused important changes to faunal assemblages, soils, and stand structural attributes (Rumbaitis del Rio 2006, Lain et al. 2008, Man et al. 2013, Waldron et al. 2013). Finally, we did not explore potential interactions between disturbances and browsing (e.g., Royo et al. 2010*a*, Nuttle et al. 2013). For example, salvaging removes downed logs and crowns that may provide refugia from deer browsing (Grisez 1960, de Chantal and Granström 2007, but see Krueger and Peterson 2009 for study documenting no refugia effect). These caveats are important and should be the focus of future well-designed experimental studies.

#### *Management implications in a world where salvaging is nearly ubiquitous*

Our findings are particularly important when one considers the frequency and severity of wind disturbance in forests and the ubiquity of post-windthrow salvage. Globally, wind disturbance affects hundreds of thousands, if not millions, of forested hectares yearly (Schelhaas et al. 2003, Lindenmayer et al. 2008) and is often the predominant disturbance in mesic forests of tropical, temperate, and boreal regions (Everham and Brokaw 1996, Stueve et al. 2011). Despite being controversial, salvage logging typically occurs after disturbance (Haymond et al. 1996, Schelhaas et al. 2003, Lindenmayer et al. 2008).

Our experiment demonstrated that salvage logging increases establishment of intermediately-tolerant

species and likely enhances coexistence, particularly at the high end of the windthrow severity gradient when associated with disturbed soil patches. In the absence of soil disturbance, the impact of salvaging was limited and short-lived. Our results suggest managers should explicitly consider windthrow disturbance severity, the advance regeneration layer composition, and harvest disturbance intensity during their salvage operations planning. Indeed, the literature suggests carefully planned, partial salvaging (e.g., limiting soil disturbance, leaving residual trees) can mitigate impacts on forest recovery in post-windthrow (Peterson and Leach 2008a, Man et al. 2013, White et al. 2014, this study) and post-fire systems (Macdonald 2007). In contrast, where salvage practices are more intense (e.g., harvesting live trees, soil tilling, milling or piling of slash) impacts may be more pronounced and long-lasting (Jonášová et al. 2010, Morimoto et al. 2011, Bottero et al. 2013, Waldron et al. 2014).

If the existing tree regeneration suits their management goals and recalcitrant layers are not established, then minimizing scarification is important so as to not delay forest recovery. Indeed, our results show sapling richness and densities in scarified areas are diminished for 2 yr following salvaging. Moreover, in areas experiencing high windthrow severity, sapling basal area remained at approximately one-fourth that of control areas even 5 yr post-salvage. However, in forests similar to ours where the advance regeneration layer is both depauperate (often due to overbrowsing), fairly dense, and of low-value, scarification will likely promote tree species coexistence, enhance woody species' diversity, mitigate the impact of beech bark disease, and have the added benefit of promoting the establishment of high-value hardwood species.

Our management conclusions regarding salvaging apply to salvage logging that was conducted ~3 growing seasons after the storm, so our results may be less applicable to salvage harvests that occur immediately after the disturbance. Indeed, our finding that most effects were observed on saplings, rather than seedlings, suggests the delay allowed for ingrowth into the sapling layer in advance of the salvage harvest. To our knowledge, no one has evaluated how the timing of salvaging following a windstorm impacts forest recovery (but see Fraser et al. 2004 for effects of delayed post-fire salvage impacts on forest recovery). Nevertheless, delays are the norm on public lands where the National Environmental Policy Act of 1969 (NEPA; 42 U.S.C. §§4321–4370) mandates the evaluation of potential environmental impacts, including periods for public comment and potential judiciary appeals (Prestemon et al. 2006). Although the timing of salvage logging in our study remains within the range of previous studies (0 to 4 yr; Rumbaitis del Rio 2006, Lang et al. 2009, D'Amato et al. 2011, Laing et al. 2011, Morimoto et al. 2011), the degree to which salvaging can be timed to mitigate deleterious impacts warrants further study.

Regardless, our findings highlight the importance of considering cumulative effect of both natural and anthropogenic disturbance on tree successional trajectories (Peterson and Leach 2008a) and challenge the view that salvage logging operations will inexorably disrupt tree diversity and successional dynamics. Under certain scenarios, salvage logging may represent a “tax on ecological recovery” (*sensu* Franklin 2005), for example, where natural disturbance causes extensive structural changes to both the overstory and understory (e.g., fires). Nevertheless, we suggest that in forest understories dominated by few shade-tolerant and browse-tolerant tree species (now widespread throughout the eastern U.S.), salvaging yields dividends including enhanced recruitment of underrepresented and potentially important tree species.

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