Ecological Applications, 18(2), 2008, pp. 407–420

LIMITED SALVAGE LOGGING EFFECTS ON FOREST REGENERATION AFTER MODERATE-SEVERITY WINDTHROW

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Abstract. Recent conceptual advances address forest response to multiple disturbances within a brief time period, providing an ideal framework for examining the consequences of natural disturbances followed by anthropogenic management activities. The combination of two or more disturbances in a short period may produce "ecological surprises," and models predict a threshold of cumulative disturbance severity above which forest composition will be drastically altered and regeneration may be impaired. Salvage logging (the harvesting of timber after natural disturbances; also called "salvaging" or "sanitary logging") is common, but there have been no tests of the manner in which salvaging after natural wind disturbance affects woody plant regeneration.

Here we present findings from three years after a moderate-severity wind disturbance in west-central Tennessee, USA. We compare two unsalvaged sites and two sites that had intermediate-intensity salvaging. Our approach demonstrates the calculation of cumulative severity measures, which combine natural windthrow severity and anthropogenic tree cutting and removal, on a plot-by-plot basis. Seedling/sapling density and species richness were not influenced by cumulative disturbance severity, but species diversity showed a marginal increase with increasing cumulative severity. The amount of compositional change (from pre-disturbance trees to post-disturbance seedlings/saplings) increased significantly with cumulative severity of disturbance but showed no evidence of thresholds within the severity range examined. Overall, few deleterious changes were evident in these sites. Moderate-severity natural disturbances followed by moderate-intensity salvaging may have little detrimental effect on forest regeneration and diversity in these systems; the ecological surprises and threshold compositional change are more likely after combinations of natural and anthropogenic disturbances that have a much greater cumulative severity.

Key words: diversity; salvage; wind disturbance; wind severity; woody plant regeneration.

Introduction

Disturbances, both natural and anthropogenic, can profoundly alter the composition, structure, successional dynamics, and ecosystem processes in forests (Lorimer and Frelich 1994, Foster et al. 1997, White and Jentsch 2001, Frelich 2002). Consequently, the realization that management actions in forests often constitute a type of anthropogenic disturbance has prompted attempts to emulate natural disturbances with the size, intensity, timing, and distribution of management activities (Perera et al. 2004, Schmiegelow et. al. 2006). The rationale is sound: forests and their component species are likely to have evolved abilities to cope with naturally occurring types, frequencies, and severities of disturbance. Yet there is concern (Beschta et al. 2004, Foster and Orwig 2006, Lindenmayer 2006) that an increasingly common management activity, salvage logging after natural disturbance, may impose a repeat disturbance (sensu Paine et al. 1998) whose cumulative severity is beyond the coping abilities of native species and ecosystems. Salvage logging ("salvaging" or "sanitary logging") is the harvesting of commercially valuable timber from naturally disturbed stands such as fire or windthrow areas. However, the consequences of salvage logging after natural disturbances remain poorly documented and controversial (Karr et al. 2004, Lindenmayer et al. 2004). Perhaps lost in the controversy over impacts of salvage logging is the excellent opportunity it provides for testing disturbance theory. Current disturbance concepts (Paine et al. 1998, Frelich 2002, Roberts 2004) propose that two disturbances in quick succession are likely to have a cumulative severity of impact above that of the single natural events to which most ecosystems are accustomed. If this cumulative severity is sufficiently high, dramatic change in forest structure and composition is likely to result, with possible detrimental consequences for reestablishment of pre-disturbance forest structure and composition, biodiversity, and ecosystem functioning (Lindenmayer et al. 2004, Lindenmayer and Noss 2006). Such reasoning applies whether the disturbances are natural or anthropogenic. Thus, a framework in which to understand

Manuscript received 10 April 2007; revised 27 August 2007; accepted 11 September 2007. Corresponding Editor: B. A. Hungate.

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impacts of salvage logging is to consider the cumulative severity of both the natural and anthropogenic disturbances. Moreover, salvage logging may also qualitatively differ from natural disturbances in that it has distinct environmental effects (McIver and Starr 2001) to which natural species and ecosystems have had little evolutionary exposure. Species and ecosystems may respond negatively to novel types (e.g., Foster et al. 1997, Foster and Orwig 2006) of disturbance, separate from the cumulative severity.

Several recent papers report on comparisons between sites with and without salvage logging after natural disturbances, mostly emphasizing the consequences of salvaging for reestablishment of forest structure and composition and long-term sustainable use. Thus far, nearly all the direct research into effects of salvaging has been in forests disturbed by wildfire (reviews in McIver and Starr 2001, Beschta et al. 2004, Lindenmayer 2006, Lindenmayer and Noss 2006). Studies following the 2002 Biscuit fire in conifer forests of Oregon, USA, showed substantial reduction in initial regeneration in the salvaged areas (Donato et al. 2006), although Newton et al. (2006) point out that these findings need to be seen in the context of management objectives; if achieving the greatest total woody seedling density was not a primary management objective, then salvage logging might remain desirable even if regeneration density is reduced. Similar reductions in abundance of regeneration and changes in successional trajectory have been documented elsewhere (Stuart et. al. 1993, van Nieuwstadt et al. 2001). Other types of consequences include effects on wildlife (Nappi et al. 2003), hydrology (Foster et al. 1997), and soil nutrients (Brais et al. 2000). It is not surprising that dramatic impacts have been found after catastrophic wildfire and salvage logging, because such fires are themselves disturbances of very high severity (Turner et al. 1998) and adding salvaging would result in an exceedingly severe cumulative impact. It is expected, therefore, that such combinations of severe disturbances would cause drastic changes in forest ecosystems. In this light, it is notable that Macdonald (2007) found that partial salvaging after moderate-intensity fires in boreal mixed-wood forests of Alberta, Canada, did not negatively affect understory vegetation richness or cover characteristics and in fact increased regeneration density of aspen.

While all of the above research has focused on salvaging after fire, wind is also a common and important agent of natural disturbance (Everham and Brokaw 1996, Webb 1999), and salvage logging is common after wind disturbance (Foster et al. 1997, Lindenmayer et al. 2004, Foster and Orwig 2006). We know of only two published studies that directly documented vegetation effects of salvaging after wind disturbance. In Elliott et al. (2002), the sample areas all had both types of disturbance and therefore the effect of salvaging could not be separated from that of the natural disturbance. In a study conducted in subalpine forests of northwestern Colorado, USA, Rumbaitis del Rio (2006) reported on effects of windthrow and salvage logging on herbaceous vegetation, but effects on woody regeneration have not yet been reported. Cover and diversity of herbaceous vegetation was reduced in salvage-logged areas, and composition was shifted towards greater graminoid dominance. She speculated that such shifts toward graminoid dominance might hinder conifer regeneration in subsequent decades. We thus conclude that the literature lacks direct comparisons of woody vegetation in salvaged vs. unsalvaged areas after wind disturbance, and we therefore have limited knowledge of how "wind plus salvage" might affect forest characteristics and woody species regeneration. In addition to the dearth of direct post-windthrow studies (but see Foster et al. [1997] for retrospective findings), most of the existing studies do not attempt to quantitatively characterize either the natural or the anthropogenic disturbance severity and restrict comparisons to categorical "salvaged vs. unsalvaged." This precludes presenting regeneration responses in the context of disturbance severity to test the recent models and hypotheses (Paine et al. 1998, Frelich 2002, Roberts 2004).

Here we test the disturbance severity hypotheses using data from three years after a moderate-severity wind disturbance in pine-hardwood stands in central Tennessee, USA, some of which were subsequently salvaged and some of which were left to regenerate naturally. To address predictions about the cumulative severity of natural and anthropogenic disturbances, we calculated "cumulative severity" indices on a per-plot basis that combine independent measures of the natural severity (number of trees fallen) and anthropogenic severity (number of trees cut and removed in the salvage operation). Analogous cumulative severity indices were calculated on the basis of basal area. We tested three hypotheses. First, we hypothesized that although moderate-severity wind damage would cause only modest effects on tree regeneration, addition of salvaging would exceed the severities to which species are adapted and result in dramatically different species composition, lowered stem density, and reduced species richness and diversity of regeneration. Second, based on Frelich (2002) and Roberts (2004), we hypothesized that the relationship between compositional change and cumulative disturbance severity would be nonlinear or exhibit a threshold. Third, we hypothesized that because species presumably are adapted to historical disturbances but have little evolutionary exposure to salvage logging, the anthropogenic component of cumulative severity would have greater influence on vegetation responses than natural severity.

Study Site

Natchez Trace State Park and Forest (NTSF; Fig. 1) is located in west-central Tennessee, USA (35° N, 88° W). The area lies within the East Gulf Coastal Plain section

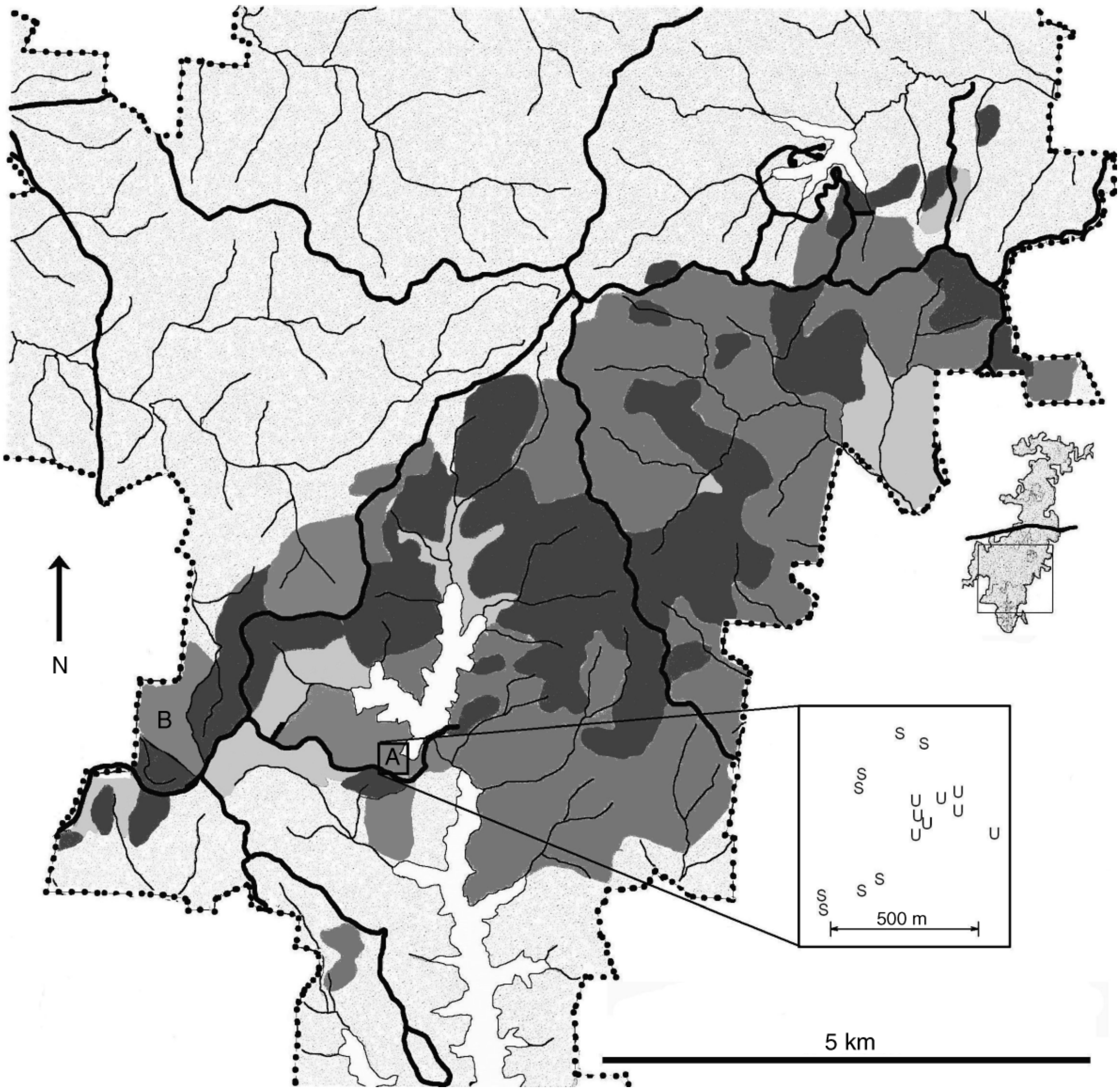

FIG. 1. Map of the southern portion of Natchez Trace State Park and Forest (NTSF), west-central Tennessee, USA. The inset shows enlarged area in context of the entire park; the heavy black line in the inset is highway I-40. The enlarged map is based on aerial reconnaissance of wind damage to NTSF. The heavy dotted line marks the park boundaries; the light stippled area is parkland. "A" and "B" mark sites; "S" and "U" refer to salvaged and unsalvaged plots, respectively. The heavy black lines are roads, and the thin black lines are streams and rivers. The white areas in the lower center are lakes. Light uniform gray indicates areas with <40% timber fallen; medium gray indicates areas with 40–80% of timber fallen; dark gray indicates areas with >80% of timber fallen.

of the Coastal Plain physiographic province (Braun 1950), and topography consists of gently rolling uplands separated by broad floodplains. Soils are derived from the McNairy sands geologic formation (Kupfer and Franklin 2000). Both of the study areas have soils in the Ruston-Lexington association, with Lexington soils on the narrow ridgetops and Ruston soils on slopes (Flowers et al. 1960). In site A, both the salvaged area and the unsalvaged area were on Ruston fine sandy loam, a somewhat excessively drained, acid soil consisting of fine sandy loam above loamy fine sand to depths >1 m. The soils in the unsalvaged part of site B are classified as intermingling of two acid, moderately well-drained to excessively drained soils, the Lexington silt loam and Ruston fine sandy loam. The Lexington silt loam consists of very friable silt loam to a depth of ~15 cm, a friable heavy silt loam from 15 to 50 cm, and below 50 cm a loose loamy sand. The Ruston fine sandy loam has a similar profile to depths of at least 1 m. Beneath the salvaged part of site B are deeply gullied soils such as Freeland silt loam (a moderately well-drained acid soil with a slight pan) and Providence silt loam (a well-drained acid soil). The climate is humid continental, with short, mild, wet winters and long, hot, dry summers and an

TABLE 1. Characteristics of 32 large sample plots in Natchez Trace State Forest, Tennessee, USA.

Plot	Latitude (°N)	Longitude (°W)	Slope (degrees)	Aspect	Elevation (m)
Site A, unsalvaged					
1	35°43′23.9″	88°17′38.5″	9	N	155
2	35°43′25.7″	88°17′42.1″	12	N	167
3	35°43′23.8″	88°17′46.3″	0		184
4	35°43′26.7″	88°17′43.8″	0		166
5	35°43′27.2″	88°17′42.1″	30	N	169
6	35°43′26.5″	88°17′46.3″	20	N	181
7	35°43′25.3″	88°17′46.1″	25	NW	177
8	35°43′24.7″	88°17′46.3″	15	N	159
Site A, salvaged					
9	35°43′31.8″	88°17′47.9″	20	S	186
10	35°43′31.0″	88°17′45.5″	0		147
11	35°43′28.2″	88°17′51.8″	20	E	170
12	35°43′27.5″	88°17′52.0″	28	S	167
13	35°43′19.0″	88°17′55.7″	25	NW	169
14	35°43′17.9″	88°17′55.5″	12	N	183
15	35°43′20.3″	88°17′49.9″	15	S	179
16	35°43′19.4″	88°17′51.7″	22	S	167
Site B, unsalvaged					
17	35°43′49.5″	88°19′23.1″	30	W	195
18	35°43′48.3″	88°19′25.5″	10	N	210
19	35°43′48.1″	88°19′26.8″	10	N	208
20	35°43′50.1″	88°19′28.2″	15	N	206
21	35°43′47.8″	88°19′29.8″	22	SW	203
22	35°43′47.4″	88°19′27.1″	5	NW	208
23	35°43′45.4″	88°19′24.6″	20	SW	197
24	35°43′47.2″	88°19′24.9″	10	E	196
Site B, salvaged					
25	35°43′29.5″	88°19′16.2″	15	W	211
26	35°43′49.3″	88°19′19.2″	20	SW	196
27	35°43′52.7″	88°19′17.3″	10	W	201
28	35°43′54.5″	88°19′18.0″	12	SW	206
29	35°43′54.4″	88°19′16.3″	5	W	207
30	35°43′48.4″	88°19′18.6″	10	NW	203
31	35°43′48.3″	88°19′15.2″	15	SW	218
32	35°43′53.9″	88°19′15.1″	5	SW	202

average growing season of 202 days. Mean annual precipitation is 1240 mm, mostly rain falling in the late winter and early spring (Flowers et al. 1960). Second-growth forests developed across the region following agricultural abandonment in the 1930s. *Quercus* spp. (oaks), *Carya* spp. (hickories), and other mixed mesophytic species, including *Pinus taeda* L. (loblolly pine), dominate the uplands (Table 1). The understory consists primarily of *Cornus florida* L. (flowering dogwood), *Nyssa sylvatica* Marsh. (blackgum), and *Sassafras albidum* (Nutt.) Nees. (sassafras).

On 5 May 1999, a downburst (straight-line windstorm) damaged ~3000 ha at NTSF (R. Ward, *personal communication*; Fig. 1). As recorded in nearby Lexington, Tennessee, the thunderstorm lasted >1.5 h with sustained wind speeds of >90 km/h and wind gusts exceeding 145 km/h (NOAA 1999). Damage was spatially quite variable, but restricted to the southern portion of NTSF. Aerial surveys within two weeks of the storm showed that categories of damage occurred in large patches of tens to a few hundred hectares (Fig. 1), whose shape and extent were strongly influenced by landscape and topography (R. Ward, *personal communication*). Nevertheless, boundaries between patches of differing levels of damage were gradual, making it difficult to characterize particular locations according to distance from patch edges. Downed trees were harvested in the damaged stands with the exception of two areas of 6 ha each, which were set aside for research purposes and left unsalvaged; we refer to these as site A and site B. Site A was unsalvaged because of difficulty of access; site B was unsalvaged because salvaging had not yet progressed to that location when we initiated our study. The storm-damaged areas were divided into harvest units on the basis of stream watersheds, with one landing area per harvest unit. Cutting was predominantly with chain saws; logs were moved to landings with motorized skidders. Quantitative characteristics of the salvage logging are presented by plot in Table 2. No concurrent treatments of vegetation or slash were conducted (R. Ward, *personal communication*).

METHODS

Forest characteristics

We sampled at NTSF in 2002, the third growing season after the wind disturbance. Sampling plots were

TABLE 2. Characteristics of salvage logging in sample plots, Natchez Trace State Forest, Tennessee, USA.

Plot	No. trees removed	Basal area removed (m^2)	dbh (cm)	Most-removed species
9	4 (5.3)	0.353 (12.0)	30.1 ± 17.0	*Quercus rubra*, *Pinus taeda*
10	5 (12.2)	0.789 (26.3)	42.9 ± 14.6	*Quercus coccinea*, *Quercus rubra*, *Quercus alba*
11	10 (25.6)	0.952 (47.0)	32.6 ± 12.7	*Quercus* sp., *Acer rubrum*, *Quercus rubra*
12	1 (2.4)	0.177 (8.7)	47.5 ± 0.0	*Quercus alba*
13	0 (0)	0.0 (0.0)		
14	5 (9.3)	0.746 (30.6)	43.2 ± 6.3	*Quercus alba*, *Quercus* sp., *Quercus falcata*
15	8 (36.4)	0.706 (51.9)	33.1 ± 5.9	*Pinus taeda*, *Quercus coccinea*
16	7 (13.7)	0.538 (26.5)	30.3 ± 8.5	*Pinus taeda*
25	10 (16.7)	1.131 (44.5)	36.3 ± 11.8	*Pinus taeda*
26	5 (8.5)	0.677 (39.1)	38.6 ± 17.0	*Pinus taeda*, *Liriodendron tulipifera*, *Quercus coccinea*
27	9 (13.8)	0.831 (29.1)	34.2 ± 2.9	*Pinus taeda*, *Liriodendron tulipifera*
28	8 (10.8)	0.769 (36.0)	34.5 ± 6.1	*Pinus taeda*
29	8 (18.2)	0.832 (35.6)	35.9 ± 6.5	*Pinus taeda*
30	7 (14.8)	0.620 (41.3)	32.4 ± 9.4	*Pinus taeda*
31	7 (14.0)	0.829 (34.2)	38.6 ± 4.7	*Pinus taeda*
32	11 (28.2)	0.932 (51.3)	31.8 ± 8.7	*Pinus taeda*, *Quercus* sp.

Notes: Plots were 30 × 30 m. Values in parentheses are percentages based on pre-disturbance number and basal area of trees in that plot. "Most-removed species" are listed in descending order, based on number of trees removed. Diameter at breast height (dbh) values are presented as means ± SD.

established within unsalvaged and adjacent salvaged portions of wind-damaged sites A and B, which were ~2.5 km apart. In each of the four site × treatment (salvaged and unsalvaged) combinations ("stands"), we established eight 30 × 30 m plots (8 plots × 4 stands = 32 plots) in a stratified random fashion. Physical characteristics of plot locations are presented in Table 1. Plot locations for unsalvaged and salvaged portions of site A are shown in Fig. 1; with a few exceptions, plots within a particular stand were at least 50 m apart. In site B, all plots were at least 100 m from the edges of the disturbance patch as defined by the aerial survey. In site A, where locations of a nearby lake and a road constrained sampling to a more restricted area, all plots were at least 50 m from either of these patch edges. Within a site, approximate distance between salvaged and unsalvaged areas was 200–500 m. Mean slopes of plots did not differ between sites A and B, but mean elevation was slightly greater in site B (204.2 ± 6.3 m [mean ± SD]) than in site A (170.4 ± 10.9 m), a significant difference (t test, $t = 10.71$, $P < 0.001$). Soils were very similar in the two sites (see *Study site*). In addition to the 32 large plots in wind-disturbed areas, we also sampled eight large (30 × 30 m) plots in undisturbed forest, for both trees (>5 cm dbh) and seedlings/saplings (<5 cm dbh).

Within the large plots, we characterized forest wind damage and used an exhaustive tree inventory of each plot to reconstruct the pre-disturbance characeristics of subcanopy and tree layers (stems > 5 cm dbh). For all trees > 5 cm dbh (diameter at breast height, measured at 1.4 m above the soil surface), we recorded species identity, dbh (at 1.4 m along the trunk for fallen trees), and damage category (standing or fallen). Species nomenclature followed the USDA Plants list (USDA and NRCS 2002). Fallen trees and snags that were obviously dead prior to 1999 were excluded from sampling. For salvaged stems, identity was assigned on the basis of bark characteristics, and basal diameter of the stump was used with an allometric regression to estimate dbh of the cut stem (Leach 2003).

We established 2 × 2 m regeneration quadrats in each of the four corners of each large plot (4 quadrats × 32 large plots = 128 regeneration quadrats), for sampling of woody stems <5 cm dbh. Destructive harvesting of hundreds of saplings was not permitted, so it was not possible to determine ages of these individuals. Note that the individuals sampled within these quadrats would of necessity be a mixture of saplings surviving from pre-disturbance, plus newly established post-windthrow recruits. Thus we were not attempting to reconstruct the pre-disturbance seedling community, but simply characterizing the new community that resulted from post-disturbance recruitment intermingled with the survivors. If increasing disturbance severity influenced regeneration, such an effect would be detectable despite the presence of numerous surviving pre-disturbance saplings. Within each quadrat, we recorded species identity, size (height for "seedlings" < 2 m tall; dbh for "saplings" > 2 m tall), damage category, and condition (intact, bent, branches broken, stem broken, uprooted) of stems < 5 cm dbh. In 2002, seedlings < 2 m tall made up 97.9% of stems < 5 cm dbh and >98% were intact.

Soil disturbance

To quantify the amount of disturbed soil at NTSF, we sampled each plot along four parallel lines 10 m apart. At 0.5-m intervals along these lines, we dropped a pin and recorded whether the substrate was intact or disturbed, and if disturbed, whether it was a pit, mound, or other disturbed soil (i.e., skid trail), yielding a total of 244 points per large plot (244 points × 32 plots = 7808 sampling points). From this inventory, we calculated the proportion of soil surface disturbed, one possible measure of natural disturbance severity. Bulk density (in grams per cubic meter) is the density of soil in place, including solids and pores, and is inversely related to the porosity or percentage of pore space. To determine whether salvaging compacted soils, two 5 cm diameter × 5 cm length intact cores were collected from the soil surface in 56 regeneration quadrats at site B, in November 2002; logistical constraints precluded a larger sample. Soils were oven dried at 50°C for five days and analyzed for bulk density using the core method. The two bulk density samples from each quadrat were averaged for analysis.

Statistical analyses

We performed initial two-way analyses of variance (ANOVA) to examine the effects of treatment (salvaged and unsalvaged; fixed effect) and site (A or B; fixed effect) on severity (e.g., percentage of basal area fallen, percentage of trees fallen, or percentage of soil disrupted), and regeneration characteristics (seedling/sapling density, richness, diversity, and compositional change). Because sites were not chosen at random from a population of secondary mixed pine/hardwood stands, we used a two-way fixed effects model with the two factors being site and treatment. Although the distance between sites (~2.5 km) presumably assured meteorologic, edaphic, and vegetation independence, all of these initial two-way ANOVAs found no significant site effect; therefore, for subsequent analyses, sites are pooled to allow examination of the severity effect via regression and ordination.

We considered four potential indicators of plot-scale severity of natural disturbance (cf. Roberts 2004): number of trees fallen, basal area of trees fallen, percentage of trees fallen, and percentage of basal area fallen. These variables were used as predictor variables in regressions of vegetation response to severity. These were chosen because as measures of natural wind disturbance severity, they also have obvious analogues as measures of extent of anthropogenic salvaging. Thus we also quantified extent of salvaging on a per-plot basis as number and percentage of trees cut and amount and percentage of basal area cut. By choosing these measures of natural severity, we facilitate calculation of a cumulative severity index by, for example, summing natural basal area fallen and basal area cut. While other variables, such as percentage of soil disruption (e.g., Roberts 2004) can indicate natural disturbance severity, in the context of both natural and anthropogenic disturbances, these alternate severity measures are less useful because they do not allow for calculating separate measures of natural and anthropogenic severity.

To test the primary hypotheses, we regressed various vegetation characteristics against cumulative severity indices that summed both natural and anthropogenic severity on a per-plot basis. Thus, in a given plot, the cumulative absolute individual severity was the sum of the number of trees fallen and the number of trees cut, and the cumulative basal area severity was the sum of the basal area fallen and the basal area cut for that plot. These cumulative severity indices are more readily comparable among plots when calculated from proportions of fallen and cut. For example, in Fig. 2a, where severity is expressed as proportions, plot 10 had 0.29 of pre-disturbance individuals fallen and 0.122 of pre-disturbance individuals cut during the salvage, for a cumulative stem-based severity of 0.412; similarly, in Fig. 2b, plot 10 had 0.32 of basal area fallen and 0.263 of basal area cut during salvage, for a cumulative basal-area-based severity of 0.583. We examined four cumulative severity variables: cumulative absolute individual severity, cumulative absolute basal area severity, cumulative percentage individual severity, and cumulative percentage basal area severity. The cumulative percentage severity indices performed somewhat better as predictors of vegetation response, so results from these predictors will be presented, although the results from the regressions on cumulative absolute severity indices were very similar. Because some response variables might be more influenced by severity calculated using basal area rather than number of stems as a measure of abundance, or vice versa, we present results of analyses using each of these approaches to severity calculations. We examined the results of first- and second-order polynomial regressions to test for nonlinearity in the relationships between vegetation response and the indices of severity; significant quadratic or cubic terms in these regressions would indicate nonlinear relationships. Negative coefficients in the linear regression equations relating response variables to the indices of severity would indicate that the response variable decreased with increasing severity.

For severity estimates from the large plots to be used as predictors, data from the four regeneration quadrats per large plot were averaged, which also normalized the data so that transforms were unnecessary. Regeneration characteristics included in analyses were seedling/sapling density, size, species richness, species diversity, and compositional change. We calculated mean (per plot) richness (S, the number of species per sample) and Shannon diversity ($H' = -\Sigma\ p_i \log(p_i)$, where p_i is the proportion of individuals found in the ith species and log is to base 10; Kent and Coker 1994) for salvaged and unsalvaged portions of the wind-disturbed forests as well as for the undisturbed forest at NTSF.

We used two different indices of compositional change between pre-disturbance trees (>5 cm dbh) and 2002 regeneration (stems < 5 cm dbh). First, to characterize qualitative change (presence/absence of species) we calculated Sørensen's index of similarity (Kent and Coker 1994); this index is based on presence/absence rather than abundance and varies between 0 and 1; it approaches 0 for samples with completely nonoverlapping species composition. Second, to characterize quantitative change that considers abundances of species, we calculated the Chao-Sørensen

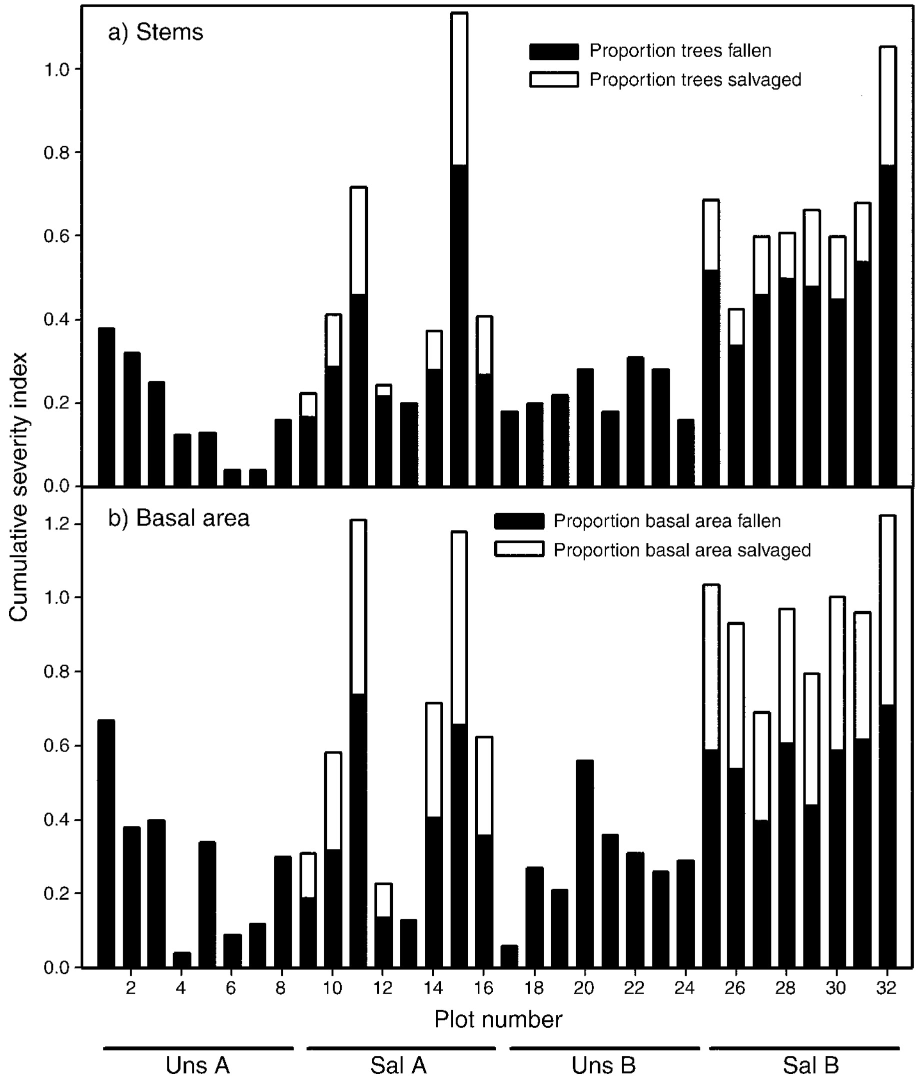

FIG. 2. Cumulative severity of disturbance in 32 salvaged (Sal) and unsalvaged (Uns) plots within four stands (2 sites × 2 treatments) in west-central Tennessee, USA. The cumulative severity index is the sum of natural and anthropogenic severity, i.e., the sum of windthrow and salvage severity, calculated either from individuals or basal area. (a) Severity based on the proportion of individuals fallen plus the proportion of individuals cut; (b) severity based on the proportion of basal area (m^2) fallen plus the proportion of basal area cut. Not all trees were cut in salvaged areas; thus some sample plots in salvaged areas had little or no cutting.

similarity (Chao et al. 2005) between pre-disturbance trees and post-disturbance seedlings/saplings. This index also varies between 0 and 1. SigmaStat version 3.01 (SPSS, Chicago, Illinois, USA) was used for regressions, and EstimateS 7.5 was used to calculate the Chao-Sørensen similarity (*available online*).[4]

Total disturbance severity is made up of both natural (windthrow) and (in areas with both windthrow and salvage logging) anthropogenic (cutting) components; each of these might be considered from an absolute or proportional perspective (e.g., absolute number of trees fallen or percentage of trees fallen); and each might utilize either individuals or basal area as a measure of abundance. Considering two possible values for three different factors yields eight possible ways to express some aspect of severity, which we will refer to as severity components. We examined the relative importance of these eight severity components to regeneration characteristics with stepwise multiple regression of response variables on severity components. We used the forward stepwise approach, with $P < 0.05$ to enter and $P > 0.055$ to remove. In all significant regressions reported below, assumptions of normality and homogeneity of variances were met.

[4] ⟨http://viceroy.eeb.uconn.edu/EstimateS⟩

We performed goodness-of-fit G tests (Sokal and Rohlf 1995) to test for significant departures from expected proportions of shade tolerance classes within tree and seedling/sapling strata of salvaged and unsalvaged areas at each location. Tree species were assigned to one of three shade-tolerance classes (tolerant, intermediate, or intolerant) based on data in Burns and Honkala (1990) and Brown and Kirkman (1990; Leach 2003). Species for which no published shade tolerance value could be found were excluded from analyses.

We used nonmetric multidimensional scaling (NMS) to characterize the trajectory of species compositional change between pre-disturbance trees and 2002 regeneration. The four regeneration quadrats within each large plot were combined for purposes of the ordinations, and ordination was performed on 64 samples (32 plots of pre-disturbance trees and the same 32 plots of post-disturbance seedlings). The NMS was performed using PC-Ord software (McCune and Mefford 1999); we used Sørensen's index to quantify dissimilarity and specified a two-axis solution.

Soil bulk density in salvaged and unsalvaged areas at site B was examined using confidence intervals, because uncertainty about independence among samples may have compromised t tests.

Results

Pre-disturbance stand characteristics indicated broad overlap in density, basal area, and richness between sites A and B. Stem density was 47.6 ± 12.5 stems/plot (mean ± SD; range 22–75) in site A and 54.8 ± 11.3 stems/plot (range 36–74) in site B. Sites A and B had per-plot basal areas of 2.15 ± 0.44 m^2 and 2.30 ± 0.54 m^2, respectively. Richness in sites A and B was 12.6 ± 2.5 species/plot (range 8–16) and 11.3 ± 2.2 species/plot (range 8–15), respectively. These reconstructions of pre-disturbance values for sites A and B correspond well to measured characteristics in eight plots in undisturbed forest: stem density of 71.6 ± 27.5 stems/plot (range 31–114); basal area of 3.02 ± 0.74 m^2 (range 1.93–4.39); and richness of 10.0 ± 3.5 species/plot (range 6–16). The means of density and basal area in the undisturbed site were strongly influenced by exceptionally high values in one of the eight plots; nevertheless, standard deviations for all three sites overlap well. In addition, species composition of the undisturbed plots, as characterized by NMS ordination, placed the undisturbed site mean midway between means for sites A and B, indicating an intermediate species composition. Together, these traits all indicate that the disturbed sites were representative of pre-disturbance stands in the area.

Disturbance severity

Pre-disturbance tree density at NTSF was 568 trees/ha and basal area was 25.1 m^2/ha. Density of standing trees was reduced by 19.9% and basal area by 27.2% in unsalvaged areas and by 40.5% and 44.7% in salvaged areas. Structural damage (losses of standing trees) was slightly greater than mortality (Leach 2003), because not all fallen trees were dead by the time of sampling. In all plots, proportional loss of basal area was greater than that of individuals; thus damage was concentrated in the larger size classes.

Natural wind disturbance severity was greater in salvaged areas than in unsalvaged areas. Two-way ANOVA of percentage basal area downed found significant effects for treatment ($F_{1,28} = 7.77$, $P = 0.009$), but not for site or the treatment × site interaction (both $P > 0.1$). Similarly, in a two-way ANOVA of percentage of trees downed, treatment was significant ($F_{1,28} = 20.63$, $P < 0.001$), as was site ($F_{1,28} = 5.35$, $P = 0.028$), but the interaction was not significant (Fig. 2). The percentage of soil surface disrupted did not vary between treatments (two-way ANOVA, $P > 0.05$ for both main effects and interaction). Bulk density of soils was higher in salvaged areas (mean = 1.25 g/cm^3, 95% CI = 1.14 and 1.36 g/cm^3) than in unsalvaged areas (mean = 1.09 g/cm^3, 95% CI = 1.00 and 1.18 g/cm^3).

Salvaging operations removed from 0% to 36% of the pre-disturbance individuals and from 0% to 52% of the pre-disturbance basal area (Table 2, Fig. 2). Only damaged or fallen trees were removed. However, not all fallen trees were of economic value, so some fallen trees remained uncut and in situ even in the plots within the salvaging areas. Therefore, extent of salvaging, while correlated with natural wind disturbance severity, did exhibit independent variation. Mean diameters of cut trees (Table 2) were substantially greater than means for the pre-disturbance plots as a whole, indicating that the largest trees were removed by the salvaging operations; similarly, in plots in which *Pinus taeda* was abundant, it was the primary focus of removal (Table 2).

Regeneration response—cumulative disturbance severity

Density of seedlings/saplings (i.e., stems <5 cm dbh) did not significantly increase or decrease with cumulative severity of disturbance, whether measured on the basis of individuals or basal area (Fig. 3), and there was no indication of nonlinearity to the relationship. Height of small stems (i.e., <2 m tall) did not vary in response to cumulative severity when measured via percentage of trees fallen and cut (data not shown), but height did exhibit a marginally significant increase with cumulative percentage basal area fallen and cut ($R^2 = 0.108$, $P = 0.06$). Quadratic and cubic terms were not significant for seedling height vs. cumulative severity. Tree regeneration species richness (Fig. 4) did not vary in relation to cumulative severity, whether measured as percentage of basal area or percentage of individuals fallen and cut, nor was there any nonlinearity in the regressions. There was a marginally significant ($R^2 = 0.10$, $P = 0.079$) increase in woody seedling Shannon diversity with cumulative severity, when measured as percentage of basal area fallen and cut (Fig. 5). Neither of the nonlinear terms were significant in the polynomial

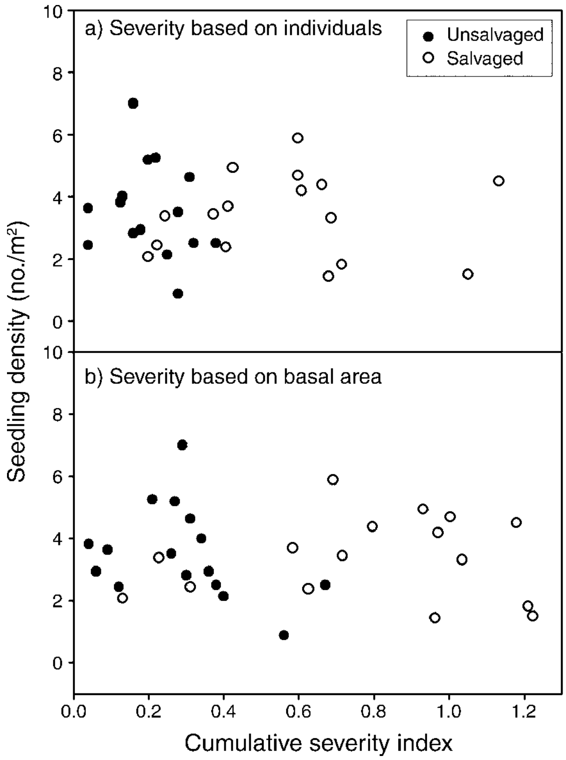

FIG. 3. Regenerating woody seedling/sapling density (four pooled 2 × 2 m quadrats per 30 × 30 m plot) in 32 plots in west-central Tennessee, USA, as a function of cumulative severity. The cumulative severity index is the sum of natural and anthropogenic severity, i.e., the sum of windthrow and salvage severity, calculated either from individuals or basal area.

regression. Unlike the other regeneration responses, woody seedling diversity also showed a significant positive relationship to cumulative absolute severity based on individuals (R^2 = 0.158, P = 0.024; data not shown), although the quadratic and cubic terms were not significant.

Compositional change between pre-disturbance trees and post-disturbance seedlings was examined both qualitatively and quantitatively. Qualitative change is described by the Sørensen index of similarity, which considers only presence/absence of species, not their abundances. The Sørensen index significantly decreased with increasing cumulative severity (Fig. 6): both the regression of similarity on cumulative percentage of density (R^2 = 0.319, P < 0.001) and cumulative percentage of basal area (R^2 = 0.232, P = 0.005) were significant. Also, both of the regressions of similarity on absolute cumulative severity were significant (absolute individuals, R^2 = 0.201, P = 0.01; absolute basal area, R^2 = 0.208, P = 0.009; data not shown). However, in all four of these regressions, the quadratic and cubic terms were nonsignificant. In contrast to the qualitative results, all of the quantitative results showed no significant relationship between the Chao-Sørensen similarity index and the measures of cumulative severity.

Pre-disturbance tree and post-disturbance seedling/sapling species composition were relatively distinct between salvaged and unsalvaged areas, as shown by the NMS ordination (Fig. 7). Although a shift in composition was apparent from pre-disturbance adults to post-disturbance regeneration, the shifts in ordination space were similar in direction within ordination space, for plots in both salvaged and unsalvaged areas, indicating that the compositional change caused by the disturbance(s) was similar for both salvaged and unsalvaged areas.

Relative importance of severity components

Stepwise multiple regression of response variables against components of severity revealed that different vegetation characteristics responded to different components. In an attempt to regress woody seedling density and woody seedling height against severity components, no predictors entered the model. Woody seedling species richness was significantly negatively related to both percentage of basal area fallen (incremental R^2 = 0.118, P = 0.043) and significantly positively related to absolute basal area cut (incremental R^2 = 0.119, P = 0.006). Woody seedling diversity (Shannon's H') increased

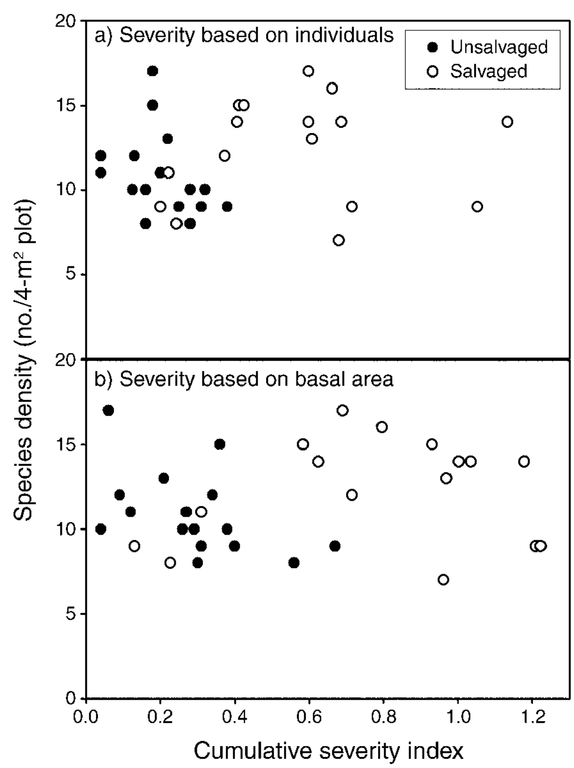

FIG. 4. Regenerating woody seedling/sapling species richness in 32 plots in west-central Tennessee, USA, as a function of cumulative severity. The cumulative severity index is the sum of natural and anthropogenic severity, i.e., the sum of windthrow and salvage severity, calculated either from individuals or basal area. Seedling/sapling richness values are from four pooled regeneration quadrats per large plot.

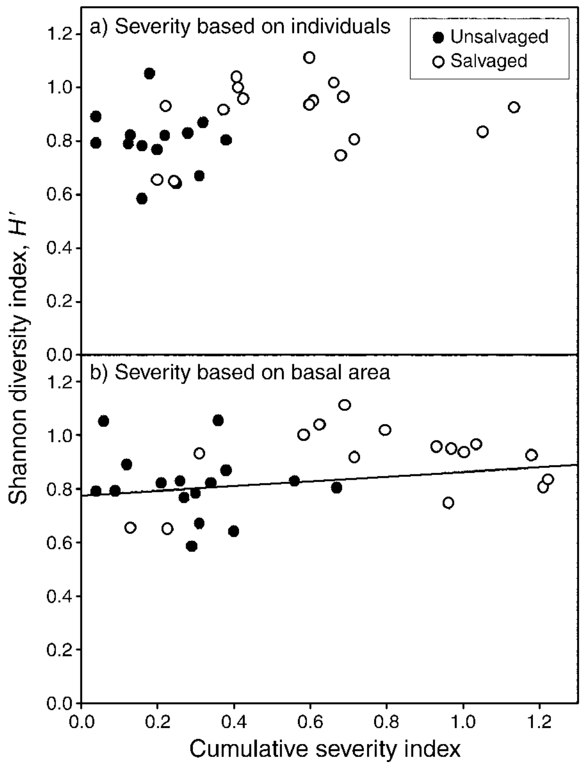

FIG. 5. Regenerating woody seedling/sapling species diversity in 32 plots in west-central Tennessee, USA, as a function of cumulative severity. The cumulative severity index is the sum of natural and anthropogenic severity, i.e., the sum of windthrow and salvage severity, calculated either from individuals or basal area. Seedling/sapling abundance values are from four pooled regeneration quadrats per large plot. Species diversity is expressed as Shannon's index, calculated with $\log_{10}$.

significantly as a function of absolute individuals cut ($R^2 = 0.225$, $P = 0.006$), but no other predictor variables were significant. Sørensen's index of similarity (pre-disturbance to post-disturbance compositional similarity) decreased significantly with percentage of individuals fallen ($R^2 = 0.312$, $P < 0.001$), but no other variables entered the model.

The Chao-Sørensen abundance-based similarity index was not significantly related to any of the severity components.

In both unsalvaged and salvaged areas, relative abundances of regeneration stems within the three shade tolerance classes were significantly different from the pre-disturbance adults (Table 3; G tests of table homogeneity, $G = 193.6$, $P < 0.001$ for unsalvaged, $G = 35.6$, $P < 0.001$ for salvaged). Prior to disturbance, shade-intolerant individuals were more common in the areas that would be salvaged than in the areas that would not be salvaged, and as expected, relative abundances of intolerant regeneration was greater in the salvaged areas than in unsalvaged areas. Regeneration stems of intermediate shade tolerance were the most abundant category in unsalvaged areas, whereas shade-intolerant stems were the most abundant category in salvaged areas (Table 3); however, the proportional increase of intolerant species (from pre-disturbance tree relative abundances to regeneration relative abundances) was similar in absolute terms for both unsalvaged and salvaged areas. Nevertheless, intolerant species such as *Quercus stellata*, *Quercus falcata*, and *Liriodendron tulipifera* were common only in the salvaged areas.

DISCUSSION

Our findings show the feasibility of quantitatively characterizing both the natural and anthropogenic components of total severity in sites that have experienced multiple disturbances from wind and salvaging. In our sites, there was substantial heterogeneity in both the natural and anthropogenic severities, which would degrade analysis of vegetation response in terms of simple categorical descriptors like "salvaged" and "unsalvaged." Instead, the combination of the natural and anthropogenic components of severity into a cumulative measure allows the examination of vegetation responses on a plot-by-plot basis and is not

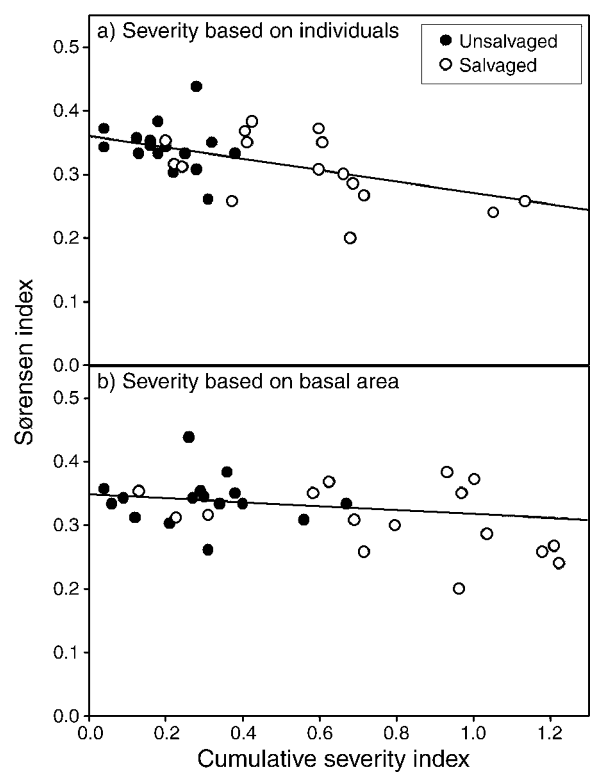

FIG. 6. Pre- to post-disturbance compositional change in 32 plots as a function of wind damage severity (proportion of trees fallen) in west-central Tennessee forests. Change is expressed as the Sørensen similarity index, based on species presence/absence among pre-disturbance trees (>5 cm dbh) and post-disturbance seedlings/saplings (<5 cm dbh). The cumulative severity index is the sum of natural and anthropogenic severity, i.e., the sum of windthrow and salvage severity, calculated either from individuals or basal area.

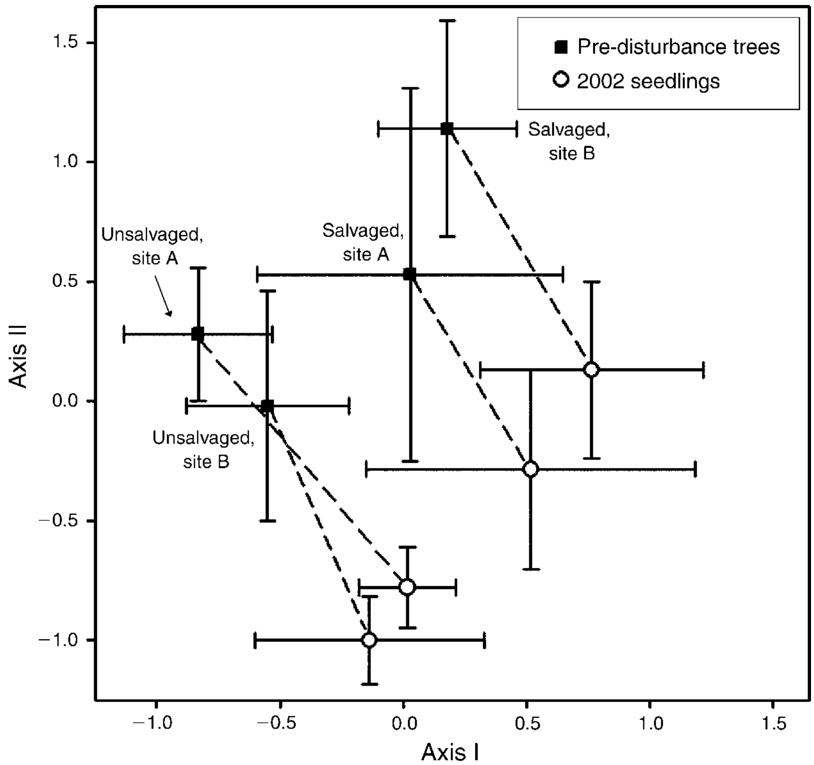

FIG. 7. Two-dimensional mean and standard deviation of plot positions in a two-axis nonmetric multidimensional scaling ordination. Each symbol represents the spread in ordination space of eight plots. Seedling data were pooled among four regeneration quadrats within each large plot.

compromised by among-plot heterogeneity of severity. By chance the natural wind disturbance severity (measured as the percentage of trees fallen or the percentage of basal area fallen) was greater in the areas that would be salvaged, probably because of a greater initial abundance of *Pinus taeda*; pines are often more vulnerable to wind damage than neighboring hardwoods (Everham and Brokaw 1996, Peterson 2007). Yet because our analyses utilized separate quantitative measures of natural and anthropogenic severity, this potential confounding of treatment with natural severity did not preclude either analysis of cumulative severity effects or separate analyses of natural and anthropogenic severity components on vegetation responses.

Notably, our two measures of the disturbance effects on soil yielded somewhat different results. The percentage of soil surface that was disrupted was not greater in salvaged areas, despite extensive sampling and contrary to expectations. In this context it is important to point out that after modest levels of salvaging the "soil disruption" component (Roberts 2004) of disturbance impact may be minimal. This is not to say that the mechanized salvage logging has no impact on the site; our data on soil bulk density is consistent with greater soil compaction as result of heavy-machinery activities in the salvaged area (Lockaby et al. 1997). However, bulk density findings were based on a much smaller sample size, and by chance more of the samples may have been taken from machine-impacted points. The general conclusion from these two site characters is that moderate-intensity salvaging may have direct influence on a rather small portion of the surface, but the affected areas can substantially differ from surrounded unaffected points.

Contrary to the reduction in regeneration reported after wildfire and salvaging in the Pacific Northwest (Donato et al. 2006), in our study sites, the salvaging produced no negative impact on seedling density, richness, or diversity. Indeed, while it is only one

TABLE 3. Frequency of stems within three shade tolerance categories in wind-damaged forest in west-central Tennessee, USA.

Category	Tolerant	Intermediate	Intolerant
Pre-disturbance trees			
Unsalvaged	412 (62.2)	137 (20.7)	113 (17.1)
Salvaged	235 (47.3)	59 (11.9)	203 (40.8)
2002 regeneration			
Unsalvaged	241 (27.2)	364 (41.0)	282 (31.8)
Salvaged	266 (31.0)	134 (15.6)	459 (53.4)

Notes: Sample area for trees was 16 plots (900 m^2) each in unsalvaged and salvaged areas. Sample area for regeneration was 64 quadrats (4 m^2) each in unsalvaged and salvaged areas. Values in parentheses are percentages.

PLATE 1. Heterogeneous conditions and abundant regeneration in a mixed oak–pine forest three years after moderate-severity wind damage and moderate-intensity salvage logging. Catastrophic disturbances followed by intensive salvaging may often produce situations like the very open, graminoid-dominated area in the left distance, but most of our study area resembled the foreground of the photograph, with abundant regeneration of *Quercus* and *Sassafras*. The findings of this study suggest that partial salvaging after moderate-severity disturbances may not have the detrimental effects of complete salvaging following catastrophic natural disturbances. Photo credit: A. D. Leach.

component of regeneration, there was a weak but marginally significant increase in woody seedling diversity with increasing cumulative severity expressed as percentage of basal area (Fig. 5). Thus we find no evidence of negative effects on density, richness, or diversity, and our results do not support our first hypothesis, although the expected patterns of compositional change were confirmed. In a related study, we did document salvaging effects on microsite richness and relative abundance (Peterson and Leach 2008). Elsewhere in the southern Appalachians, Elliott et al. (2002) reported that richness was enhanced in areas subject to hurricane damage plus salvaging, in comparison to undisturbed forest. It appears that in both their study and ours, the cumulative impact of the wind disturbance and salvaging were within the range of severities to which component species are well adapted (see Plate 1). In contrast, Rumbaitis del Rio (2006) examined the effect of windthrow and salvage logging on herbaceous vegetation in subalpine forests of northwestern Colorado and found that cover and diversity were both reduced in salvage-logged areas compared to areas with blowdown only. Although salvage intensity was not quantified in the Colorado study, the canopy cover was $<10\%$, suggesting that cumulative severity may have been substantially greater than in our study sites. If so, then the substantial negative effects on cover and diversity found by Rumbaitis del Rio (2006) are consistent with the conceptual models of Frelich (2002) and Roberts (2004). At the same time, our findings of limited deleterious effects after (presumably) lower cumulative severity also are consistent with the same models.

Despite sound rationale for expecting that salvaging may often have greater impact than the natural disturbance itself (Foster and Orwig 2006), in our stepwise multiple regressions only woody seedling species richness responded to both natural and anthropogenic measures of severity. Richness declined with increasing percentage of basal area fallen, but increased with absolute basal area cut and removed. Thus the natural and anthropogenic measures had opposing effects on woody seedling species richness, and the anthropogenic effect was positive in the range studied.

As expected, regeneration in salvaged areas contained a higher proportion of shade-intolerant individuals than in unsalvaged areas, but much of this is probably due to a greater relative abundance of intolerant species prior to the disturbance in the areas to be salvaged, as well as greater wind damage. In fact, the increase in relative abundances of intolerants (from pre-disturbance trees to post-disturbance regeneration) was greater in unsalvaged areas than in salvaged areas; consequently, salvaging did not appear to greatly impact the relative abundances of shade tolerance classes.

Also contrary to our expectations, salvaging operations resulted in only modest compositional changes from pre-disturbance trees to post-disturbance seedlings/

saplings. Sørensen similarity between the pre- and post-disturbance woody vegetation did significantly decrease with cumulative severity (Fig. 6), so our data support the well-established pattern of greater compositional change with greater severity (White and Jentsch 2001). This is consistent with the findings of Rumbaitis del Rio (2006) for herbaceous species. However, our stepwise multiple regressions showed that much of the change in composition similarity was driven by the natural disturbance severity: percentage of trees fallen entered the model, but none of the measures of salvage severity entered the model. Thus salvaging did not cause dramatically greater compositional change than the natural disturbance, providing little support for our third hypothesis. We caution that our findings are based on regeneration quadrats that by chance did not sample skid trails or loading areas, and thus known soil compaction and soil disruption effects (Lockaby et al. 1997, McIver and Starr 2001) could well have more substantial influences on vegetation regeneration elsewhere within our study sites.

None of the regressions of vegetation response vs. cumulative severity exhibited any significant nonlinearity. Consequently, our data do not show the threshold or nonlinear relationships expected under our second hypothesis. This does not contradict the existence of such thresholds, as stipulated by Frelich (2002), and in fact demonstrates the range of moderate severities for which the cusp catastrophe model predicts linear responses. The severity level at which the putative cusp threshold exists in our system remains unknown, but is clearly beyond the severity levels we sampled. A similar conclusion might be suggested for the findings of Elliott et al. (2002).

Ordination of the pre- and post-disturbance woody seedling/sapling composition at NTSF showed (Fig. 7) that trajectories of compositional change in ordination space were similar for both unsalvaged and salvaged sites; thus qualitative aspects of compositional change are consistent with quantitative measures of change captured by the Sørensen similarity indices. The presence of several shade-intolerant species (*Quercus stellata*, *Quercus falcata*, and *Liriodendron tulipifera*) only in salvaged areas cannot be firmly attributed to the salvaging, since these areas had greater natural severity and thus greater cumulative severity. Frelich (2002) points out that when component species have the ability to replace themselves in situ, moderate levels of disturbance will be unlikely to cause major changes in species composition. The wind disturbance severity in our study areas was generally less than that reported in numerous other wind-disturbance studies (Everham and Brokaw 1996, Peterson 2007), and cumulative effects may have provided insufficient canopy opening or soil disruption to encourage establishment of large numbers of shade-intolerant "pioneer" species. These findings must be interpreted carefully, however, because they present only the initial regeneration condition, three years after the natural disturbance. If the greater canopy openness, greater soil compaction, or removal of organic carbon and nutrients in salvage-logged areas (McIver and Starr 2001) influence subsequent vegetation dynamics and regeneration patterns, greater effects of the salvaging could become apparent in coming decades. Only future resampling of these study sites will confirm whether the initial limited effect of salvage logging continues into later stages of forest recovery from these combined disturbances.

Post-disturbance salvaging policy varies according to management objectives and disturbance severity (Beschta et al. 2004, Lindenmayer et al. 2004, Newton et al. 2006); the study of the consequences of salvaging provides a rational basis for making informed management decisions (Foster and Orwig 2006). We expect that impacts of salvage logging on forest structure, composition, and regeneration potential will be greater following more severe disturbances because the sum of the natural disturbance and the salvaging operation severities are likely to exceed severities to which species have evolved tolerance (Lindenmayer 2006). At the opposite extreme, natural events at the low end of the severity scale may have such limited impact that the cumulative severity becomes almost entirely comprised of the salvage logging, and such situations become difficult to differentiate from standard (non-salvage) harvesting. Regardless, consideration of severity offers a common currency for the study of both natural and anthropogenic disturbance. Thus we suggest that the impacts of salvaging after natural disturbance in forests must be considered from a context of the cumulative severity of both events; while some natural disturbances followed by modest intensity of salvaging may have little negative impact, intense salvaging after high-severity natural events (catastrophic wildfires or extreme blowdowns) may nevertheless often have detrimental consequences.

Acknowledgments

We thank Roy Ward and Chris Goetz at Natchez Trace State Forest for permission to conduct research at NTSF. Paul Stuffel provided invaluable field assistance. The work was funded by the USDA Forest Service Southern Research Station, cooperative agreement number SRS 01-CA-11330136-405; we especially thank John Stanturf for facilitating our application for the cooperative agreement.

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