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ARTICLE

Does salvage logging erase a key physical legacy of a tornado blowdown? A case study of tree tip-up mounds

Michelle Elise Spicer, Kyle F. Suess, John W. Wenzel, and Walter P. Carson

Abstract: While large-scale wind disturbances are rare, they are nonetheless powerful drivers of plant community reassembly in temperate forests worldwide. These disturbances cause the formation of tree tip-up mounds that serve as regeneration niches, but the time scale at which novel plant communities develop on mounds is unknown. Moreover, salvage logging can cause mounds to "tip back down" and could therefore erase these microsites. Here, we test three hypotheses with a replicated field experiment: (1) novel plant communities rapidly form on tip-up mounds; (2) salvaging erases these microsites; and (3) "tipped-down" tip-up mounds are novel intermediate microsites. We salvaged a random half of four 3–6 ha blowdowns created by an F1 tornado, measured 249 mounds, and censused the vegetation on 48 mounds and 48 reference plots. Plant communities on mounds had two to three fewer species, 50% less cover, and lower diversity than reference communities. However, salvaging caused modest increases in species richness and diversity on mounds and caused 40% of mounds to tip back down. The physical characteristics and vegetation of these tipped-down "inclined mounds" were more similar to vertical mounds than to reference plots. Our results suggest that salvaging may increase microsite heterogeneity across the landscape by creating novel intermediate mounds.

Key words: diversity, herbaceous regeneration, wind disturbance, salvage, inclined mound.

Résumé : Bien que les perturbations à grande échelle causées par le vent soient rares, elles sont néanmoins de puissants facteurs de réassemblage des communautés végétales dans les forêts tempérées du monde entier. Ces perturbations renversent des arbres et soulèvent des monticules de terre qui servent de niches de régénération, mais l'échelle de temps nécessaire pour que ces nouvelles communautés végétales se développent sur les monticules est inconnue. De plus, les coupes de récupération peuvent rabattre les monticules et, par conséquent, pourraient éliminer ces microsites. Dans cette étude, nous avons testé les trois hypothèses suivantes à l'aide d'un dispositif sur le terrain comportant plusieurs répétitions : (1) de nouvelles communautés végétales se forment rapidement sur les monticules, (2) la récupération élimine ces microsites, et (3) les monticules rabattus constituent de nouveaux microsites intermédiaires. Nous avons récupéré, au hasard, la moitié de quatre chablis couvrant chacun de 3 à 6 ha et provoqués par une tornade d'intensité F1. Dans ces chablis, nous avons mesuré 249 monticules et recensé la végétation sur 48 monticules et 48 placettes de référence. Les communautés de plantes établies sur les monticules comportaient deux à trois fois moins d'espèces, 50 % moins de couvert et une plus faible diversité que les communautés de référence. Cependant, la récupération a causé une augmentation modeste de la richesse et de la diversité des espèces sur les monticules et a provoqué le rabattement de 40 % des monticules. Les caractéristiques physiques et floristiques de ces monticules rabattus et inclinés ressemblaient davantage à celles des monticules verticaux qu'à celles des placettes de référence. Nos résultats indiquent que la récupération peut augmenter l'hétérogénéité des microsites dans le paysage en créant de nouveaux monticules intermédiaires. [Traduit par la Rédaction]

Mots-clés : diversité, régénération herbacée, perturbation par le vent, récupération, monticule incliné.

Introduction

Stand-replacing wind disturbances are powerful drivers of forest dynamics because they create large and highly heterogeneous patches of early successional habitat embedded within a matrix of older forest (Mitchell 2013). These blowdowns are characterized by tree tip-up mounds, which are one of the signature physical legacies left by wind disturbances (Lyford and MacLean 1966; Beatty 1984; Peterson et al. 1990; Schaetzl and Follmer 1990; Vodde et al. 2011). The mounds and corresponding pits often increase plant diversity because they create bare soil patches and unique microsites (Schaetzl et al. 1989, 1990; Simon et al. 2011). The pits and mounds also create steep gradients for an array of abiotic factors including temperature, humidity, snowfall, and soil resources (Beatty 1984; Peterson et al. 1990; Simon et al. 2011). In addition, tall elevated mounds can provide refugia from browsers, and avian frugivores often perch on these mounds, thereby dispersing seeds (Thompson 1980; Long et al. 1998). Consequently, the vegetation on mounds often differs from adjacent off-mound reference sites even decades after the disturbance, and the soil characteristics may not return to a predisturbance state for centuries (Peterson et al. 1990; Carlton and Bazzaz 1998; Ulanova 2000; Lang et al. 2009; Darabi et al. 2014). What remains unclear is whether novel plant communities will develop rapidly on mounds a few years after a blowdown.

Salvage logging commonly occurs after windthrows and has the potential to eliminate post-disturbance ecological legacies (McIver and Starr 2000; Peterson and Leach 2008; Vodde et al. 2011; Royo et al. 2016; Lindenmayer et al. 2017). Harvesting fallen trees decreases dead trees available for habitat use, scarifies the soil, and homogenizes the landscape (Lindenmayer et al. 2004; Peterson and Leach 2008; Brewer et al. 2012; Waldron et al. 2014; Thorn et al. 2018). In particular, salvage logging can reduce the abundance of intact or

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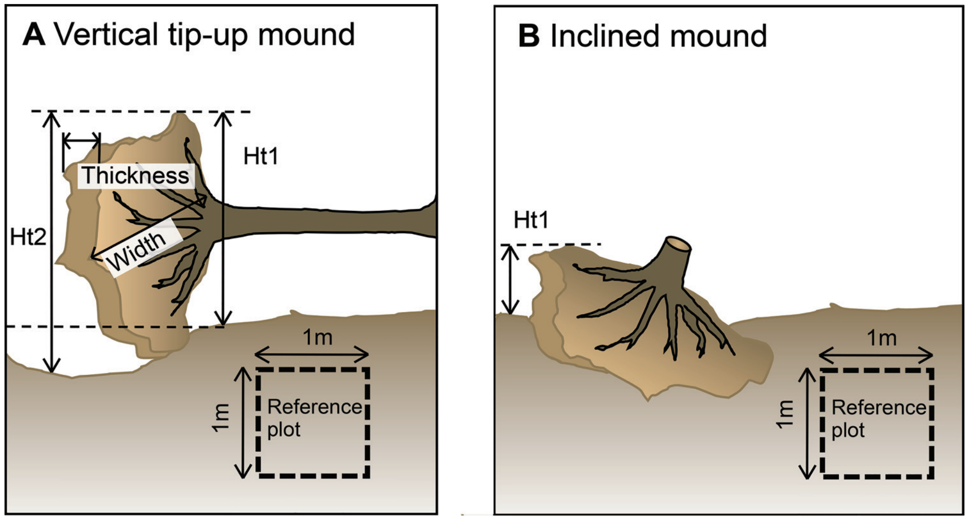
Fig. 1. (A) Measurements and depiction of a vertical tip-up mound. (B) Depiction of a “tipped down” inclined mound after salvage logging. Randomly selected adjacent reference sites are shown in both A and B. Note how inclined mounds provide a putatively unique microsite or hillock that contrasts with both a vertical mound (which occurs much closer to a 90° angle relative to the soil surface) and the adjacent reference site. [Colour online.]



vertical tip-up mounds because cutting the bole often causes the root mass and stump to fall back down into the pit (Waldron et al. 2013). Thus, salvaging has the potential to partially erase an important physical legacy left by a stand-replacement disturbance. This process may in turn reduce diversity, particularly if unique plant communities form on tip-up mounds shortly after a blowdown.

Here we test three hypotheses. (1) Novel plant communities with contrasting species composition, richness, and diversity will form on tip-up mounds rapidly after a large stand replacement disturbance. (2) Salvaging will substantially reduce the number of vertical tip-up mounds by causing the root mass to tip back down into the pit after logging and alter the physical characteristics of mounds. (3) Salvaging will create a novel habitat because “tipped-down” tip-up mounds remain elevated relative to reference areas but occur at a shallower angle (relative to the ground) versus near-vertical mounds that did not tip back down (Fig. 1). To address these hypotheses, we salvaged one-half of each of four large windthrows and quantified plant community composition and diversity on 48 tip-up mounds in both salvaged and unsalvaged areas. We also quantified how many once vertical tip-up mounds had tipped back down into the pit (hereafter referred to as “inclined mounds”) after the bole was cut and compared the vegetation on these inclined mounds with that on vertical mounds and on adjacent randomly selected reference sites off the mound (Fig. 1).

Materials and methods

Study site

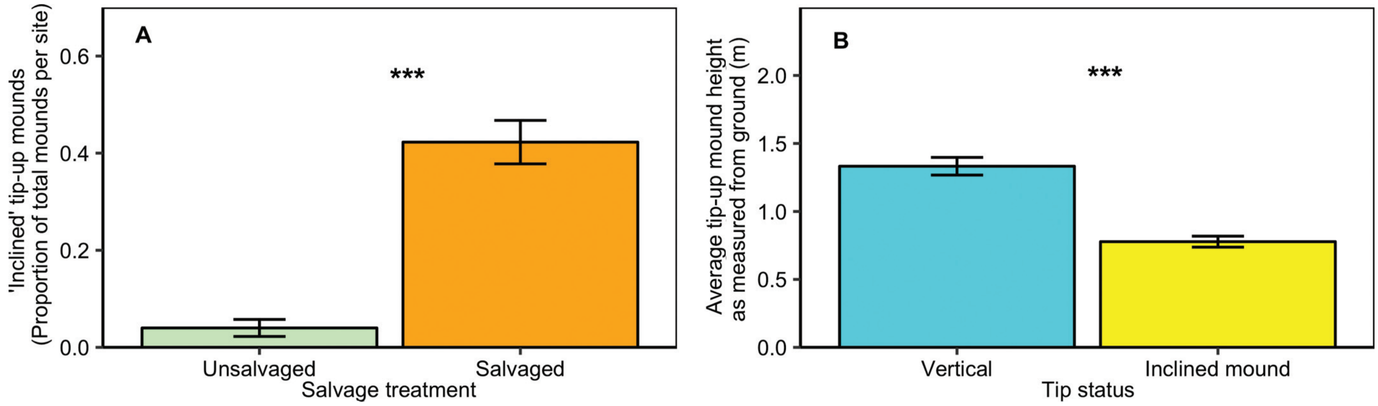
We conducted this study at four different blowdowns at the Powdermill Nature Reserve in Westmoreland County, Pennsylvania (40.16°N, –79.27°W). Annual precipitation at Powdermill is approximately 1100 mm and temperatures range from –20 to 33 °C (Murphy et al. 2015). Powdermill is 900 ha of mostly mature mixed mesophytic forest and lies on the Allegheny Plateau with slopes ranging from 8% to 35% (Murphy et al. 2015; Natural Resources Conservation Service (NRCS) 2017). The whole forest was likely cut during the 1800s and some sections of the current reserve were actively used for agriculture and mining (Murphy et al. 2015). However, portions of the study area forest have been growing back for more than 100 years and have not experienced anthropogenic disturbance since the establishment of the reserve in 1956. The canopy is dominated by red and sugar maple (*Acer rubrum* L., *Acer saccharum* Marsh., respectively), tulip poplar (*Liriodendron tulipifera* L.), and red and white oak (*Quercus rubra* L., *Quercus alba* L., respectively; Spicer unpublished data). The soils are very stony Rayne channery loams and extremely stony Laidig gravelly loams (NRCS 2017). In June of 2012, an F1 tornado with winds reaching 105 mph created four fairly large blowdowns (5.82, 4.51, 3.84, and 3.47 ha each) (National Oceanic and Atmospheric Administration (NOAA) 2012). We randomly selected one-half of each to be salvaged, while the other half served as an unsalvaged control. Salvaging occurred during the winter of 2013–2014 and used standard techniques widely applied throughout the region; this approach removed nearly all downed and standing trees at each site (~100% standing stems).

Quantifying mound density, dimensions, orientation, and vegetation

We surveyed the entire area of all four blowdowns via a systematic meander and marked the location of each tip-up mound with a handheld GPS (Garmin Montana 680t). To quantify mound dimensions, we measured the height first from the ground to the top of the mound and second from the bottom of the pit to the top of the mound (Ht1 and Ht2, respectively; Fig. 1A). We also measured the mound width and the thickness of the uprooted soil mass with a tape measure and meterstick (Fig. 1A; after Peterson et al. 1990). We determined whether each tip-up mound had tipped back down into the pit from which it originated, forming an inclined mound, or whether the mound was near vertical by observing the angle of the tree stump with respect to the ground (Fig. 1B). Tip-up mounds were considered vertical if (*i*) the root plate was near perpendicular (vertical) with respect to the ground, and therefore, the angle of the tree trunk or stump was near parallel (horizontal) to the ground, and (*ii*) there was a clear separation between the base of the tip-up mound root plate and the pit.

We quantified the vegetation on 48 (of 249) randomly selected tip-up mounds, 12 in each of the four sites, six in the salvaged area and six in the unsalvaged area. From June to July of 2015, 3 years after the tornado, we visually estimated plant cover on each tip-up mound for all species in 1 m² plots located on the top center of each selected tip-up mound (Royo et al. 2010; Nuttle et al. 2014). For comparison, we also censused a randomly selected 1 m² reference plot (off the mound) within 2 m of each tip-up mound.

Fig. 2. (A) Mean proportion of tip-up mounds that tipped back down into the pit forming inclined mounds and vertical mounds (N = 249). (B) Average height of intact vertical and tipped-down inclined mounds. Note that inclined mounds remain elevated 0.8 m above the ground. Error bars are standard error. [Colour online.]



Data analysis: physical tip-up mound characteristics and "tipping down"

We used paired t tests to determine whether the average density of tip-up mounds per hectare was different in salvaged versus unsalvaged sites. We ran the analyses with all tip-up mounds combined (vertical and inclined), as well as with the inclined mounds removed (to compare with studies in which inclined mounds are excluded, e.g., Waldron et al. 2013). To quantify the extent to which salvage logging created inclined mounds, we ran a generalized linear mixed model (GLMM) with a binomial distribution testing the effects of salvaging on the position of the tip-up mounds (binary: vertical, where the root plate is at or close to vertical relative to the soil surface, or inclined, where the stump is at a shallow angle with respect to soil surface; Fig. 1). Site differences were accounted for with random nested effects in the model.

To test whether salvage logging creates differences in tip-up mound dimensions, thereby potentially driving plant community differences (Lang et al. 2009; Waldron et al. 2014), we compared the measurements of 191 intact vertical tip-up mounds in salvaged and unsalvaged areas with a linear mixed model. We excluded inclined mounds from this analysis to avoid confounding salvaging effects and mound orientation effects. Site and salvage treatment halves were included as nested random effects in the model. Heights, width, and thickness measurements were square-root-transformed to fit Gaussian model assumptions of the linear model. We adjusted the p values for multiple tests (Bonferroni α = 0.05/4 = 0.0125). Finally, we quantified the physical differences between inclined and vertical mounds by comparing the height measurements of all mounds in the salvaged areas. We excluded unsalvaged mounds in this analysis to avoid confounding salvaging and orientation effects.

Data analysis: plant community metrics

We compared total plant cover, species richness, and the Shannon diversity index using percent cover (Magurran 1988; Oksanen et al. 2013) between tip-up mounds and nearby reference plots using GLMMs constructed with the lme4 package in R (version 3.4.1; Bates et al. 2014; R Core Team 2017). Our model included the main (fixed) effects of salvaging (salvaged or unsalvaged), microsite (tip-up mound or nearby reference plot), and microsite × salvaging interaction. We explicitly accounted for the nested split-plot experimental design using nested random effects of site, salvaging treatment (salvage logged or unsalvaged half), and pair ID (paired tip-up and off-mound reference plots) in the model (Royo et al. 2016). We performed pairwise post-hoc comparisons among the four treatment combinations with the emmeans package in R (Lenth 2016). Species richness was modeled with a Poisson distribution and log link function, and percent cover data were square-root-transformed to fit model assumptions with a Gaussian data distribution.

To evaluate whether communities were different among microsites, we used nonmetric multidimensional scaling (NMDS) with a Jaccard distance matrix, centering, and PC rotation in the vegan package in R (Oksanen et al. 2013). We evaluated the similarity of community composition using the cover of each plant species among salvaged and unsalvaged areas and on versus off tip-up mounds with the adonis permutated analysis of variance (PERMANOVA) in the vegan package. We excluded species that occurred in fewer than 5% of the plots because rare species can bias the analyses (McCune and Grace 2002; Nuttle et al. 2013; Royo et al. 2016). Data were blocked by site, and the main effects and interaction between microsite and salvaging treatment were evaluated for total cover of all species, for just tree species, and for non-tree species together (herbs, shrubs, and vines).

We followed up the overall community composition analyses with three complimentary approaches. First, we ran an indicator species analysis with the indicspecies package in R to evaluate whether some species were associated with one of the treatments based on specificity and fidelity (Dufrêne and Legendre 1997; De Cáceres 2013). Second, we ran simultaneous GLMMs on the square-root-transformed percent cover estimates of the indicator species to test whether the mean cover was different among the four treatment combinations. We interpreted the results of the GLMMs with a Bonferroni-adjusted alpha for multiple tests (α = 0.05/3 = 0.017). Finally, we tested whether tip-up mounds hosted any unique species by identifying any of the 26 species that were present on tip-up mounds but completely absent in reference plots.

We then analyzed a subset of the data from the 48 tip-up mounds used for community analyses — just from the salvaged areas — to test whether the orientation of the tip-up mound drives differences in plant community metrics. We compared the plant species richness, Shannon diversity index, and total cover among the reference plots, the inclined mounds, and the vertical tip-up mounds with GLMMs (distributions and random effects as before). We used an NMDS and a PERMANOVA on the community composition to compare inclined mound communities with reference plots and with vertical mound communities.

Results

We found a total of 249 tip-up mounds across the four blowdowns. The density of tip-up mounds did not differ significantly between salvaged and unsalvaged sites, regardless of whether or not we included inclined mounds (mean ± standard error (SE)): salvaged including inclined mounds = 14 ± 4 mounds·ha^{-1}; unsalvaged

Fig. 3. Physical characteristics of vertical tip-up mounds between salvaged and unsalvaged areas (inclined mounds are excluded, $N = 191$): (A) mean height of mounds measured from lowest point of pit to highest point of mound; (B) height from ground to highest point of mound; (C) width of mound; and (D) thickness of root plate. The cutoff for statistical significance is adjusted for multiple tests (Bonferroni $\alpha = 0.05/4 = 0.0125$). See Fig. 1 for a depiction of these measurements. [Colour online.]

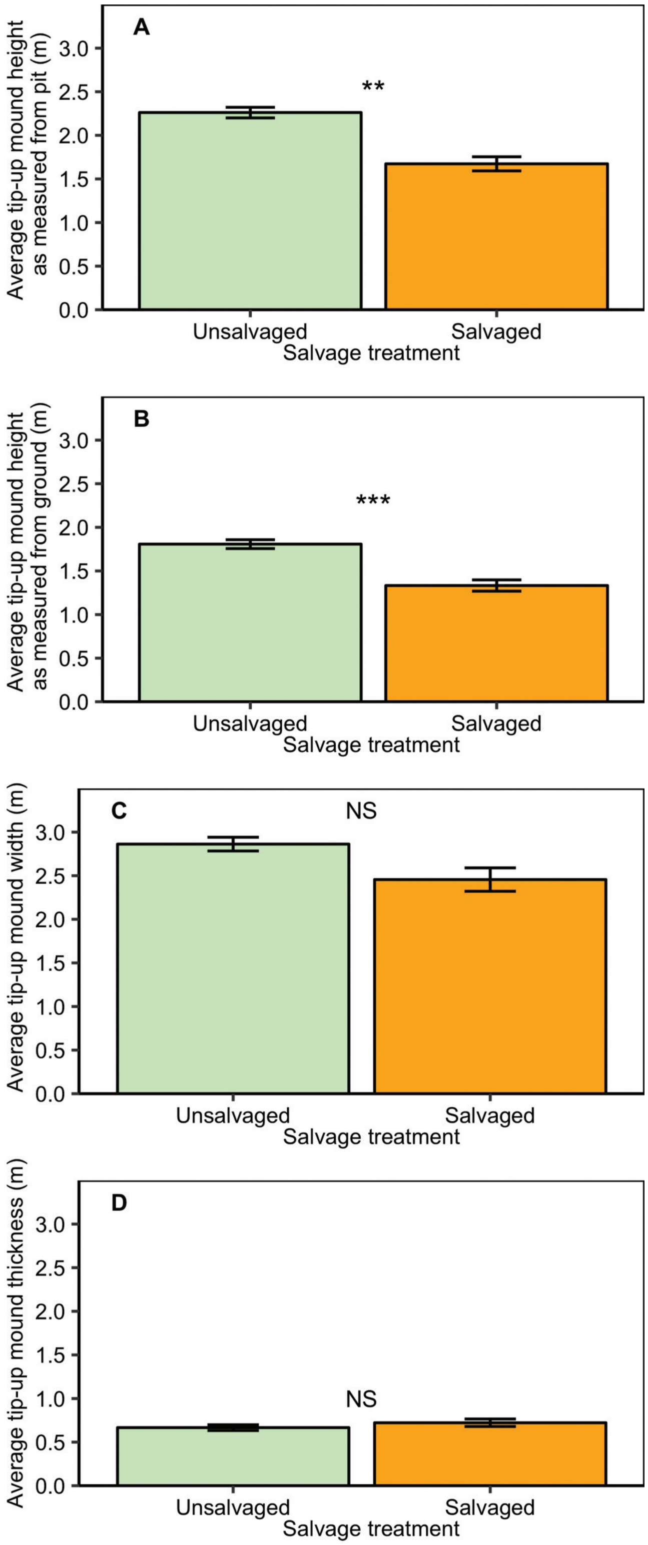
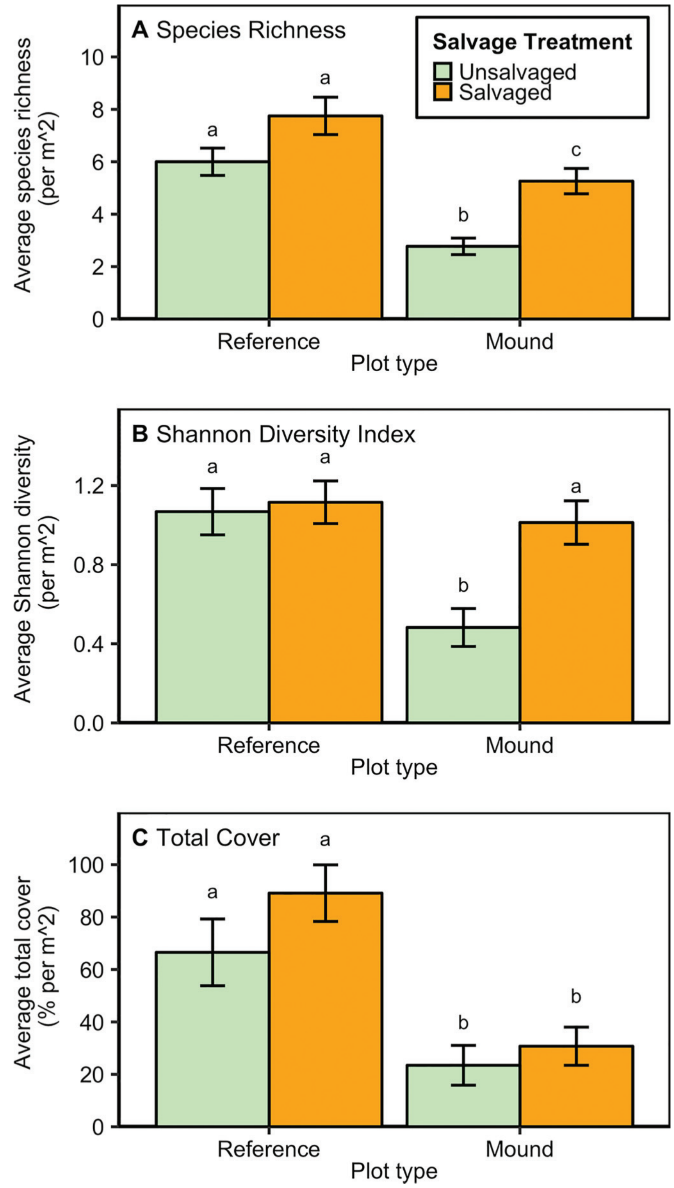


Fig. 4. Comparison of (A) species richness, (B) Shannon diversity, and (C) total cover among tip-up mounds and reference plots in salvage logged and unsalvaged areas ($N = 96$). Lowercase letters above bars indicate significant differences according to post-hoc pairwise comparisons. [Colour online.]



including inclined mounds = 13 ± 3 mounds·ha^{-1}, $p > 0.05$; salvaged excluding inclined mounds = 8 ± 4 mounds·ha^{-1}; unsalvaged excluding inclined mounds = 13 ± 3 mounds·ha^{-1}, $p > 0.05$). Fifty-two of 124 tip-up mounds tipped back down in salvaged areas (37%), forming inclined mounds, and only 5 of 125 did so in unsalvaged areas (4%; Fig. 2A; $p < 0.0001^{***}$).

Physical characteristics of tip-up mounds

Vertical tip-up mounds in salvage-logged areas were ½ m shorter than vertical tip-up mounds in unsalvaged areas, when measured both from the pit (Ht2, $p < 0.00125^{**}$; Fig. 3A) and from the ground (Ht1, $p < 0.0001^{***}$; Fig. 3B). Tip-up mounds did not differ in width or in root plate soil thickness between salvaged and unsalvaged areas (width, $p = 0.08$ NS; thickness, $p > 0.05$ NS; Figs. 3C and 3D). Inclined tip-up mounds were, on average, 0.6 m shorter than vertical tip-up mounds (when measured from the ground, $p < 0.0001^{***}$) but remained elevated as a hillock 0.8 m taller than ground level (standard error bars do not intersect height = 0 m) (Fig. 2B).

Effects of microsite and salvage logging on plant diversity and community composition

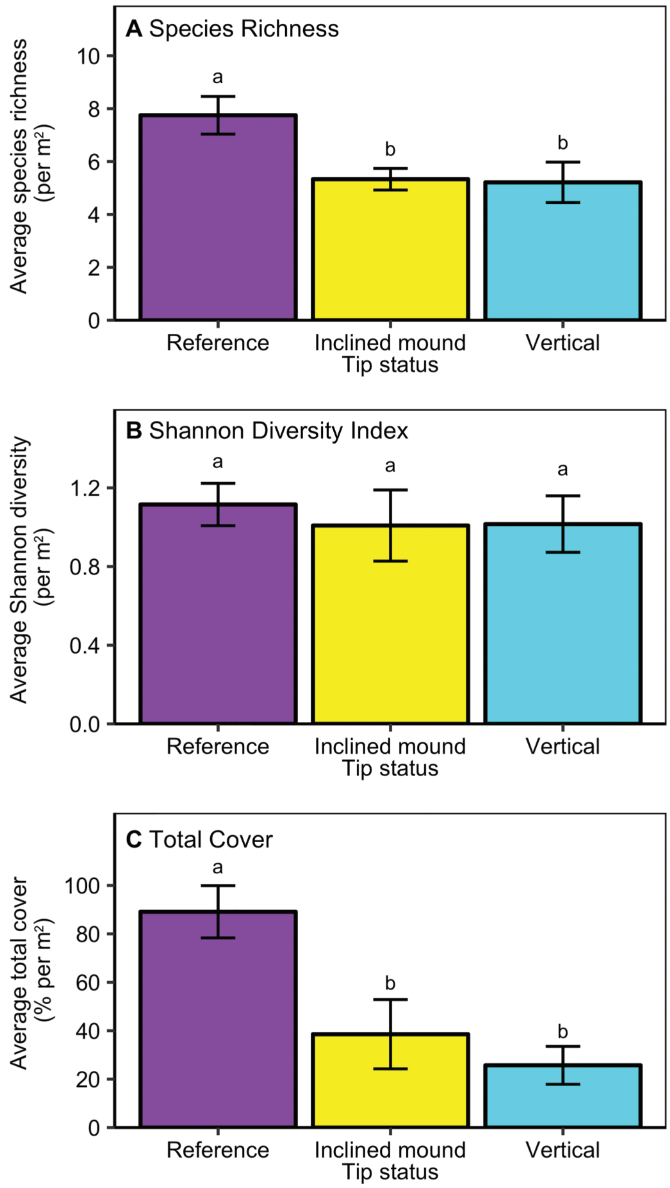
Species richness was lower on tip-up mounds (both inclined and vertical together) compared with adjacent reference plots off the mounds, but the magnitude of this difference was reduced in salvaged treatments (significant microsite by salvaging interaction; Fig. 4A; Supplemental Table S1[1]). Shannon diversity was significantly lower on tip-up mounds than in reference plots, but only in unsalvaged areas (significant microsite by salvaging interaction; Fig. 4B; Supplemental Table S1[1]). Mean total plant cover was 52% lower on tip-up mounds versus reference plots in both the salvaged and unsalvaged sites (Fig. 4C; Supplemental Table S1[1]). Overall, mounds had an impoverished flora relative to adjacent reference sites, and this was particularly true on the unsalvaged side of the blowdowns.

Salvaging caused the formation of different plant communities, and tip-up mounds had different communities compared with adjacent reference plots (both main effects $p = 0.001$; Supplemental Fig. S1A[1]). Salvaging created significantly different communities of herbs, vines, and shrubs (combined), and these communities also differed significantly between tip-up mounds and adjacent reference plots (Supplemental Fig. S1B[1]). Salvaging did not, however, significantly change tree communities, but tree communities on mounds were significantly different from reference plots (Supplemental Fig. S1C[1]).

Indicator species analyses revealed that only three species were consistently associated with one of the four treatment combinations. *Podophyllum peltatum* L. and *Rosa multiflora* Thunb. were associated with unsalvaged reference plots, and *Robinia pseudoacacia* L. was associated with salvaged tip-up mounds (Supplemental Table S2[1]). *Podophyllum peltatum* and *Rosa multiflora* were completely absent on the 48 surveyed tip-up mounds, and *Robinia pseudoacacia* cover was slightly higher (2%) in salvaged areas than in unsalvaged areas (Supplemental Table S3[1]). We found no species that occurred only on tip-up mounds.

Mean species richness was significantly higher in reference plots than on either inclined or vertical mounds, and Shannon diversity did not differ among vertical mounds, inclined mounds, or reference plots (Figs. 5A and 5B). Total plant cover was more than twofold higher in reference plots than in either vertical or inclined mounds (Fig. 5C). Community composition differed between both types of tip-up mounds and the reference plots ($p = 0.001$; Fig. 6A). Specifically, community composition differed between inclined tip-up mounds and reference plots ($p = 0.013$; Fig. 6B), but not between inclined and intact vertical tip-up mounds ($p > 0.05$; Fig. 6C). Overall, the vegetation on inclined mounds was more similar to that of vertical mounds than of the reference plots (Figs. 5A, 5C, 6B, and 6C).

Fig. 5. Comparison of (A) species richness, (B) Shannon diversity, and (C) total cover among reference plots, inclined mounds, and intact vertical mounds in salvaged sites ($N = 48$). Letters indicate significant differences according to post-hoc pairwise comparisons. [Colour online.]

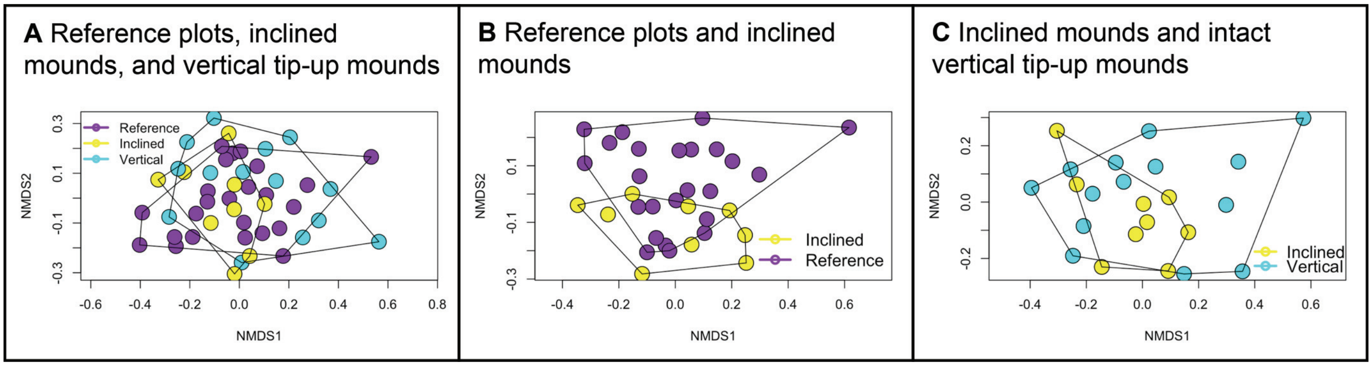


Discussion

Catastrophic windstorms create a rare opportunity for early successional species to establish within mature forests and for the plant community to reassemble on a large scale. Tip-up mounds can be regeneration hotspots because they add topographic heterogeneity to the landscape and may provide unique regeneration microsites or a refuge from herbivores (Peterson et al. 1990; Long et al. 1998; Webb 1999). We found that after 3 years, mounds were characterized by different plant communities in comparison with nearby reference sites. Mound communities were moderately impoverished and had much less total plant cover than reference plots, likely because these habitats are less stable and experience high levels of desiccation, freezing, and soil slough-off (Beatty 1984; Peterson et al. 1990; Bates et al. 2014). While the communities on mounds and reference sites were different, this was primarily because plants were less abundant on the mounds. We found no species that were unique to mounds, and indicator species analyses demonstrated that only three species showed affinity to any one of the four treatment combinations. There are two important implications of these results. First, if sharp differences in community composition do develop on mounds versus reference plots, our results suggest that these differences develop later during forest regeneration. Second, because mounds had much less cover (by as much as 60%), they will remain open for subsequent colonization much later during forest regeneration than

[1]Supplementary data are available with the article through the journal Web site at http://nrcresearchpress.com/doi/suppl/10.1139/cjfr-2018-0037.

Fig. 6. Plant community composition differences among intact vertically oriented tip-up mounds, inclined mounds that have tipped back down, and reference plots in salvaged logged sites (N = 47): (A) reference plots, inclined mounds, and vertical tip-up mounds; (B) reference plots and inclined mounds; and (C) inclined mounds and intact vertical tip-up mounds. Polygons highlight the differences between plant community compositions based on percent cover estimates. [Colour online.]



sites off mounds. This may be important if mounds stabilize over time and thus provide open habitats with bare soil for colonization and establishment well after the disturbance event.

We quantified whether salvage logging reduced the abundance of mounds on the landscape. Our results show that salvage logging does not eliminate tip-up mounds from the landscape or destroy them (cf. Cooper-Ellis et al. 1999; Waldron et al. 2013, 2014), but rather, in our case, salvaging "tips down" approximately 40% of the mounds forming inclined mounds. Thus, salvage logging potentially creates a new intermediate habitat — inclined hillocks that are not as uplifted as vertical tip-up mounds but have upturned soil and are elevated above reference areas (Fig. 2B). Salvage logging also contributed to creating shorter vertical mounds (by 0.5 m, inclined mounds were excluded), likely because salvaged areas typically have more open canopies, which expose mounds to higher light and direct precipitation, thus increasing the rates that mounds decay (see also Schaetzl and Follmer (1990) and Lang et al. (2009)). We suggest that these hillocks, although only a few years old, resemble pit-and-mound topography after several decades (Lyford and MacLean 1966; Beatty 1984; Ulanova 2000; Šamonil et al. 2009). Salvage logging may therefore accelerate post-windthrow soil development processes on tip-up mounds, but this has scarcely been tested (see mention in Lang et al. (2009) and Waldron et al. (2013)).

We evaluated not only whether plant assemblages would contrast between vertical tip-up mounds and adjacent reference sites but also whether plant assemblages would be different on the inclined mounds created by salvaging. The plant communities and species richness on inclined mounds were very similar to those on vertical mounds, which were both very different from reference plots. On one hand, the similarity of the inclined mounds to the vertical tip-up mounds may be, in part, a historic imprint of the time between the tornado and the salvaging operation (in our case, 0–2 growing seasons). Inclined mounds were, in fact, tipped up for a few months to years before the bole was salvaged and the mound was tipped back into the pit. Thus, the vegetation may still reflect this time period a few years later, bearing the legacy (and vegetation characteristics) of the vertical tip-up mound that it once was. Nonetheless, we suggest that these inclined mounds, which form a characteristic hillock, are potentially unique microsites that are physically distinct from either vertical mounds or sites off mounds. We predict that over many years, distinct plant communities will develop on these hillocks at least partly because the soil on inclined mounds will stabilize sooner than on vertical mounds yet bare soil will still be present. The rate of soil stabilization and the dynamic nature of tip-up mound topographical degradation are likely important drivers of plant community composition and species turnover over long time periods (Schaetzl and Follmer 1990; Ulanova 2000; Vodde et al. 2011; Phillips et al. 2017). However, if the reason that vertical mounds have unique vegetation is because they serve as a refuge from browsers (Long et al. 1998; Krueger and Peterson 2006), then inclined mounds are likely too short and will instead have vegetation that becomes more similar to reference plots in time. In areas where deer are over abundant, if salvaging tips down the vast majority of mounds, then salvaging may erase an important herbivore refuge across the landscape. Thus, more studies are needed to quantify the percentage of tip-up mounds that tip back down. In addition, the degree to which salvaging causes stumps to tip back down completely into the pit is not clear from other studies; in contrast to our findings, this would not create hillocks and could truly "eliminate" mounds. There are likely to be substantial variations in these processes among forest types, disturbance types (e.g., fire versus blowdown), intensity of salvaging, and scale of analysis (Bradford et al. 2012; Kramer et al. 2014; Royo et al. 2016; Lindenmayer et al. 2017; Thorn et al. 2018). Finally, we suggest that it would be fruitful to return to older salvaged sites and locate inclined mounds and compare the vegetation on these mounds with that of once vertical mounds and adjacent reference sites.

Conclusions

Here, we demonstrate that salvaging does not completely erase a signature legacy of a large-scale blowdown, specifically tip-up mounds. Rather, salvaging tips down a substantial percentage of these mounds (~40%), causing the formation of inclined mounds that create novel heterogeneity in the form of numerous hillocks. Most studies that describe tip-up mounds after salvage logging have referred to mounds that tipped back down as returning to the pre-disturbance state or as completely eliminated (Cooper-Ellis et al. 1999; Waldron et al. 2013; but see mention by Lang et al. 2009). Here, we show that this "tipping down" creates inclined mounds with physical characteristics and vegetation more similar to vertical mounds than to reference sites (Figs. 2B, 5, and 6). No species were unique to either inclined or vertical mounds; thus, mounds were a slightly impoverished subset of the vegetation found within adjacent reference sites. Our findings suggest that mounds, especially in unsalvaged sites, will remain more open microsites with patches of bare soil available for colonization for many years into the future.

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