



## Mounds facilitate regeneration of light-seeded and browse-sensitive tree species after moderate-severity wind disturbance

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### ABSTRACT

Using natural disturbance as a guide to management is an approach to develop resilience, maintain or restore natural processes, and sustain ecosystem goods and service. Here, we compare features of mounds resulting from tree uprooting, tree structure and composition, and browsing in recent 10–12-year-old moderate-severity wind disturbance events and reference stands in old hemlock–(*Tsuga canadensis*–) hardwood forests in Wisconsin, USA. Compared to reference stands, recent, partial blowdown stands had reduced overstory tree density and canopy heights, and more large gaps, coarse woody debris, exposed mineral soil, and newly-created mounds. Regeneration of light-seeded species was greater in blowdown stands relative to reference stands. We found an association between old mounds and overstory eastern hemlock and yellow birch, indicating mounds provide a long-term competitive advantage for these light-seeded species relative to pits and undisturbed areas. Notably, we found that the distance to the canopy was shortened by 30% for trees regenerating on young mounds in blowdown stands. In addition, light-seeded species, such as yellow birch, grew above browse height (2 m) in 10+ years on young mounds. In contrast, on flat and pit microsites, saplings were short (< 2 m) and more likely browsed. Maintaining and/or protecting naturally created mounds may facilitate regeneration of light-seeded, browse-sensitive species in mixedwood forests that evolved under infrequent, moderate-severity wind storms. Therefore, reserving a subset of uprooted trees from salvage operations could provide suitable substrate for germination and long-term development advantages, especially for light-seeded and browse-sensitive species and stands managed for high conservation values.

### 1. Introduction

Natural disturbance-based management (NDBM) posits that elements of natural disturbance can be emulated in practice. NDBM is a coarse filter approach to biological conservation and sustainability of ecosystem processes that are foundational to the many ecosystem goods and services that we expect from managed forests (Seymour and Hunter, 1999). For instance, conventional clearcut systems in Douglas fir (*Pseudotsuga menziesii* [Mirbel] Franco) of the Pacific Northwest, USA lack structural legacies such as live-tree islands. In contrast, new variable retention harvests, aimed to emulate natural disturbance, leave residual tree aggregates that provide biological refugia while the new cohort develops in an otherwise clearcut stand (Franklin et al., 2002,

Baker et al., 2016).

In some cases, NDBM emulates the range of canopy openings found after a wind disturbance (Coates and Burton, 1997). For instance, group or patch selection silvicultural systems, or partial harvests that create canopy openings in the forest matrix, are regarded as a potential NDBM approach to regenerate species less tolerant to the shady conditions of closed forests (Smith et al., 1997, Leak, 1999). This approach would suit gap specialists, such as yellow birch (*Betula alleghaniensis* Britton var. *alleghaniensis*), that can recruit into the canopy in medium to large openings that result from moderate-severity wind disturbances (Woods, 2000, Webster and Lorimer, 2005). However, recent research shows canopy gap creation does not guarantee tree regeneration; group selection openings have been associated with poor seedling survival of

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species such as yellow birch and, in some cases, total tree regeneration failures (Matonis et al., 2011, Kern et al., 2012).

Gap-based management when applied is often focused on the canopy opening that is created (Kern et al., 2017). In wind-disturbed ecosystems, residual forest ecosystems undergo many structural changes, including creation of standing dead and downed woody debris, uprooted trees, exposed mineral soil, and live tree islands in addition to canopy openings (Ulanova, 2000). Canopy gap creation has been a focus in NDBM, because it integrates well within conventional and new silvicultural systems (O'Hara, 2002, Franklin et al., 2007) and it is implemented through merchantable tree harvesting that generates timber revenue to pay for the treatment. Emulation of other processes not related to timber extraction may cost more than conventional methods and, therefore, be difficult to implement (Wagner et al., 1998, Saunders and Arseneault, 2013). Yet, the numerous cases of regeneration failures in gap-based management (e.g., Gasser et al., 2010, Matonis et al., 2011, Kern et al., 2013, Forrester et al., 2014) highlight the need for further development and a closer examination of other co-occurring edaphic, structural, and microtopographic changes from wind disturbances to emulate in NDBM.

Tree uprooting and the associated root- and soil-exhumed mounds ("mounds" hereafter) created after disturbance provide a niche for tree regeneration in otherwise continuous forest floor substrate and closed canopy conditions. In Japan, only canopy gaps with mounds caused differences in tree composition (characterized by small-seeded, wind-dispersed species) compared to canopy gaps without mounds or to undisturbed areas (Nakashizuka, 1989). In tropical forests, new mounds in or near new canopy gaps and with exposed mineral soil supported concentrations of pioneer species (Putz, 1983). Moderate-severity disturbances appear to play an important role in cohort regeneration of shade-intolerant and light-seeded species in many ecosystems (Woods, 2000, Fischer and Fischer, 2012). If mounds are a contributing factor to regeneration of these species, then mounds could be a critical aspect to developing NDBM and overcoming regeneration challenges in ecosystems with moderate-severity wind disturbances.

Past studies show a range of mechanisms or processes that make mounds unique in the tree regeneration process. Mounds may be nutrient refuges compared to pits and undisturbed forest floor, because pits and forest floor leach nutrients more quickly than mounds (Šamonil et al., 2010). In Japan, trees growing on mounds are elevated relative to competing vegetation of the same cohort (Nakashizuka, 1989). In hemlock- (*Tsuga canadensis* (L.) Carrière) hardwood forests of Pennsylvania, USA, mounds provided refugia from ungulates by elevating seedlings above browsing height (Long et al., 1998, Krueger and Peterson, 2006). Yet, the inference of mound function in tree regeneration is limited. For instance, do mounds consistently provide browse refugia for the regeneration of browse-sensitive species in other ecosystems?

Moreover, data on availability of mounds for tree regeneration is

lacking or variable for many ecosystems. For instance, in northern hardwood-conifer ecosystems of North America, reported percentages of area in mounds vary from 3% to more than 60% (Habecker et al., 1990, Tyrrell and Crow, 1994, Kabrick et al., 1997a). In some cases, tree-mound associations are conflicting in the same ecosystem type; for example, several studies mention the association of specific species (e.g., yellow birch) with mounds (Hanson and Lorimer, 2007, Lang et al., 2009), yet other studies quantify broad suitability for a range of species to regenerate on mounds (Collins and Pickett, 1982, Šamonil et al., 2016). Additional research is needed in order to achieve clear management objectives for increasing tree diversity with mound creation.

Understanding the relationships between trees and mounds will highlight the usefulness of integrating mounds into forest management. Here, we compare forest regeneration in stands having recent partial blowdown compared to nearby undisturbed forests to aid in development of NDBM for forests where moderate-severity wind events (with damage creating 30–60% canopy openness) are an important component of their disturbance regime. Our objectives were to describe (1) how wind disturbance affects stand structural and compositional conditions for regeneration and (2) how tree regeneration responds to stand conditions on and off of tip-up mounds in northern hardwood-conifer ecosystems of North America. While a study focus is tree regeneration, a novel approach to our work was that we used overstory trees, in addition to understory trees, to assess long-term competitive advantage of growing on and off mounds. In stands with recent partial blowdown, we anticipated that the lower stand density and greater canopy openness would be related to more exposed mineral soil, mounds, and tree seedlings and saplings than reference stands. We expected tree seedlings and saplings would be greater in number in blowdown stands and on mounds, especially for light-seeded species and browse-preferred species.

## 2. Methods

### 2.1. Study sites

Our example ecosystem was unmanaged, mixedwood stands of hemlock-hardwood forests. The natural disturbance regime for this ecosystem is characterized by (1) frequent, low-severity wind disturbances that create < 30% canopy openness and (2) moderate-severity disturbances that create 30–60% canopy openness resulting from blowdown events occurring once approximately every 300–390 years in mature and old-growth stands (Frelich and Lorimer, 1991a, Woods, 2000). Despite their infrequent occurrence, there is a high probability of partial stand destruction at least once in the lifespan of a cohort of its long-lived and dominant tree species, yellow birch, sugar maple (*Acer saccharum* Marshall) and eastern hemlock (Frelich and Lorimer, 1991b).

We used four study sites with stands that experienced a recent,

**Table 1**

Study sites in northern Wisconsin, USA. Blowdown stands were created by a moderate-severity wind event (see Hanson and Lorimer (2007) for disturbance details) 10–15 years prior to sampling. Reference stands were adjacent to blowdown stands, but not affected by the wind event. Mound area was estimated from transect surveys in blowdown stands.

Site (LAT/LONG)	Disturbance Year	Blowdown Area (ha) # plots	Reference Area (ha) # plots	Mound Area (%)
1, Gilman Chequamegon-Nicolet National Forest (45.15, -90.66)	2002	3.4	2.7	28.2
2, Kemp Natural Resource Station (45.50, -89.67)	2000	8.8	3.5	18.3
3, Headwater Lakes Research Natural Area (45.97, -90.00)	2001	2.1	3.6	27.0
4, Patterson Hemlocks State Natural Area (45.89, -89.96)	2000	2.4	4.0	26.3

**Table 2**  
Site properties of the research study in northern Wisconsin, USA. Habitat was noted for the first (1<sup>a</sup>) and second (2<sup>b</sup>) most representative ground-layer plant class (Kotar et al., 2002). Soils information from Web Soil Survey (Soil Survey Staff).

Site	Blowdown	Habitat type (1 <sup>a</sup> / 2 <sup>b</sup> )	Soil map unit	Soil classification	Parent material	Soil drainage
1	Reference	ATM <sup>a</sup> /ATD <sup>b</sup>	Newot sandy loam (9081C)	Coarse-loamy, mixed, superactive, frigid Alfic Haplorthods	Loamy till	Well drained
	Recent	ATM/ATD	Newot sandy loam (9081C)	Coarse-loamy, mixed, superactive, frigid Alfic Haplorthods	Loamy till	Well drained
2	Reference	ATD/ATM	Sayner loamy sand (SaD)	Sandy, mixed, frigid Entic Haplorthods	Sandy drift over stratified sandy and gravely outwash	Excessively drained
	Recent	ATD/ATM	Sayner loamy sand (SaD)	Sandy, mixed, frigid Entic Haplorthods	Sandy drift over stratified sandy and gravely outwash	Excessively drained
3	Reference	ATD/TMC <sup>c</sup>	Sayner loamy sand (SaC)	Sandy, mixed, frigid Entic Haplorthods	Sandy and gravely outwash	Excessively drained
	Recent	ATD/TMC	Karlin loamy fine sand (KsC)	Sandy, mixed, frigid Entic Haplorthods	Sandy outwash	Somewhat excessively drained
4	Reference	ATD/TMC	Padus-Pence sandy loam complex (PeC and PeB)	Coarse-loamy, mixed, superactive, frigid Alfic Haplorthods (Padus) and Sandy, isotic, frigid Typic Haplorthods (Pence)	Loamy alluvium over sand and gravely outwash	Well drained and somewhat excessively drained
	Recent	ATD/TMC	Padus-Pence sandy loam complex (PeC and PeB)	Coarse-loamy, mixed, superactive, frigid Alfic Haplorthods (Padus), Sandy, isotic, frigid Typic Haplorthods (Pence)	Loamy alluvium over sand and gravely outwash	Well drained and somewhat excessively drained

<sup>a</sup> *Acer-Tsuga/Maianthemum* (or mesic and nutrient medium to rich site).

<sup>b</sup> *Acer-Tsuga/Dryopteris* (or dry-mesic to mesic and nutrient medium site).

<sup>c</sup> *Tsuga/Maianthemum-Coptis* (or mesic to dry-mesic and nutrient medium site).

moderate-severity blowdown in northern Wisconsin, USA (Tables 1 and 2); most were previously described by Hanson and Lorimer (2007). Sites were selected upon the following criteria: (1) well-drained soils with similar habitat types (Table M2; Kotar et al., 2002), (2) mature forests with trees  $\geq 120$  years, (3) eastern hemlock-hardwood or northern hardwood forest type (or eastern hemlock or sugar maple dominated), and (4) stands with recent blowdown events dating to 10–15 years prior to sampling (Hanson and Lorimer, 2007, Randy Hoffman personal communication). The region has continental climate with approximate mean annual temperature of 5.4 °C and mean annual precipitation of 80 cm.

## 2.2. Study design

A nested complete block study design overlaid the study area such that each site represented a block ( $n = 4$ ) and each block included two *in-situ* treatments, recent blowdown and reference condition (8 stands [EUs] total). The recent blowdown included stands with recently uprooted and downed trees from wind events that occurred during the early 2000s. The reference condition included stands that were nearby the blowdown treatment with similar conditions but were not severely altered by the recent blowdown events. It is important to note that reference treatment had evidence of past wind events as indicated by the presence of pit and mound microtopography.

## 2.3. Sampling design

We sampled each stand with parallel line transects spaced  $\geq 50$  m apart and ideally 300 m long. The length and number of these transects depended on stand size, shape, and features (e.g., wetland inclusions were avoided). In recent blowdown stands, the transects were laid along the longitudinal axis of wind damage. Sample points were set every 50 m along the transects. Eight to ten sample points were established in each reference and recent blowdown stand (Table 1).

## 2.4. Data collection

At each sample point, a pair of circular, nested plots were established: understory subplots with a 2-m radius were centered within overstory plots with a 16.1-m radius. Overstory plots were used to record tree species, DBH (diameter at breast height, 1.4 m) > 11.4 cm, and microtopographic status of trees (> 50% of rootcollar area on the soil-exhumed mound, pit, or undisturbed flat) and then classed stems as alive or dead. We visually estimated canopy cover of the main plot area from plot center using 4 categories: 0– < 40%, 40– < 70%, 70– < 90%, or 90–100%. We also measured both the crown-shoulder height (widest portion of the crown; *sensu* Webster & Lorimer, 2005) and total height for the four super canopy, dominant, or co-dominant trees closest to center of each main plots.

Understory subplots were used to record tree species, height class (0.5-m classes from 0.5 to 2 m and  $\geq 2$  m), deer browse (presence/absence), microtopographic position, and substrate (floor, coarse woody debris, and soil) for all living tree saplings  $\geq 0.5$  m tall and < 11.4 cm DBH. The DBH was measured on saplings  $\geq 2$  m tall. Height was the maximum distance from root collar to terminal bud and measured perpendicular to the ground surface.

In the subplots, we also recorded cover of substrate to the nearest percent. These approximations could sum to > 100% in cases of structural layering (e.g., a log or downed crown hanging over forest floor). When mounds were identified in reference and recent blowdown stands, additional data were recorded. Mound height was measured, while age and mineral soil exposure (%) were approximated. Mound height was generally taken from the companion pit (approximately 30 cm deep in new pits and 10 cm in old pits) to the estimated peak of the companion mound. Mound age class was determined by the presence or absence of an adjacent downed log (the uprooted tree stem)

and categorized into one of two age classes: young (log visible, Mound Age 1 or 2) vs. old (log not visible, Mound Age 3 or 4 (Tyrrell and Crow, 1994)).

To estimate young and old mound frequency, four secondary transects of 300 m each were established 20 m apart at each site in the recent blowdown stands (Kabrick et al., 1997a) (Table 1). Sample points were set every 3 m, ideally resulting in 100 sample points per transect and 400 sample points per site. Actual number of sample points at sites varied due to variations in size and site conditions (e.g., wetland inclusions). At each sample point, the microtopography was recorded as a pit, mound, or flat.

### 2.5. Analysis

To test the effects of the blowdown on stand structure and composition, we used generalized linear mixed models of plot-level responses, where blowdown (recent vs. reference) was a fixed factor and site and plot within site were random factors. Models were run separately by species for those having a sufficient sample size: sugar maple, eastern hemlock, and yellow birch. We also grouped species with small, wind-blown seeds (> 100,000 seeds/kg) such as eastern hemlock, yellow birch, paper birch (*Betula papyrifera* Marshall), quaking aspen (*Populus tremuloides* Michx.), white spruce (*Picea glauca* (Moench) Voss), white cedar (*Thuja occidentalis* L.), and balsam fir (*Abies balsamea* (L.) Mill.) into a single category designated as light-seeded species. The models were run with PROC GLIMMIX with the Kenward-Rogers denominator degrees of freedom method (SAS Institute Inc. 2012). To achieve assumptions of normality and/or homoscedasticity, gamma and log-normal distributions with log and identity link functions, respectively, were used in models. Means and standard errors from the raw, untransformed data are presented for interpretation. When  $p$  was  $\leq 0.05$ , the result was considered statistically significant and, when it was between  $> 0.05$  and  $\leq 0.10$ , the result was considered as approaching statistical significance.

We also compared densities of trees found on mounds with tree densities found off of mounds. We used generalized linear mixed models of expanded plot-level density responses with treatment, mound status (stem found on or off mound [pit + flat]), and the interaction as fixed factors and site and plot within site as random factors. We used expanded densities to remove the noise of varying and low frequency of mounds (Table 1). We expanded densities by mound status (trees found on or off of mounds) and inflated each group from the current relative frequency of microtopography position (Table 1) to an equal relative frequency of 1.0 to allow for a relative comparison, regardless of microtopography availability.

## 3. Results

### 3.1. Recent moderate-severity blowdown effects

Forest stand structure and composition differed between stands disturbed and undisturbed by recent blowdown events (Table 3). Stands disturbed by the blowdown event had lower mean canopy tree ( $\geq 11.4$  cm DBH) density, basal area, canopy height, crown shoulder height, and canopy cover than reference stands. The relative basal area of overstory sugar maple was greater in reference than recent blowdown stands, while relative basal area of overstory eastern hemlock, yellow birch, and light-seeded species were similar across sites.

Presence of understory trees (> 0.5 m tall and < 11.4 cm DBH) varied among stands, where understory yellow birch, light-seeded species, and stems taller than 2 m (height range: 2–14 m) were more prevalent in recent blowdown than reference stands (Table 4). Understory trees densities in general were highly variable and were not significantly different. Relative stem densities for understory sugar maple, eastern hemlock and yellow birch in the reference stands were approximately 0.41, 0.25, and 0.02, respectively, and in the partial

**Table 3**

Comparison of structure and composition metrics (mean [standard error]) for living overstory trees (> 11.4 cm DBH) and selected species of reference and recent partial blowdown stands at four sites ( $n = 4$ ).  $F$ -value and significance level from generalized linear mixed models are **bold** when  $p \leq 0.05$ . QMD = quadratic mean diameter. BA = basal area.

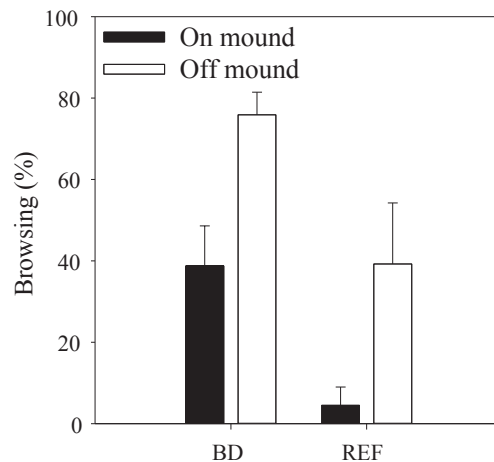
Metric	Units	Disturbance		
		Reference	Blowdown	$F$ -value
Density	no. per ha	<b>409.2 (17.0)</b>	<b>290.6 (22.3)</b>	<b>28.13</b>
QMD	cm	35.2 (0.7)	33.4 (1.2)	2.08
BA	m <sup>2</sup> /ha	<b>39.5 (1.7)</b>	<b>24.2 (1.5)</b>	<b>47.01</b>
Relative Basal Area	%			
Sugar Maple		<b>28 (3)</b>	<b>13 (12)</b>	<b>9.10</b>
Eastern Hemlock		54 (4)	55 (4)	0.43
Yellow Birch		11 (1)	11 (2)	1.95
Light-seeded Species		64 (2)	68 (11)	0.09
Height	m			
Total Canopy		<b>24.5 (0.7)</b>	<b>20.0 (1.2)</b>	<b>27.96</b>
Crown Shoulder <sup>a</sup>		<b>19.2 (0.6)</b>	<b>14.8 (0.8)</b>	<b>43.60</b>
Canopy Opening Size	m <sup>2</sup>	<b>115.2 (43.3)</b>	<b>573.6 (97.6)</b>	<b>37.49</b>
Canopy Cover	% cover	<b>91.8 (2.9)</b>	<b>43.8 (6.8)</b>	<b>22.99</b>

<sup>a</sup> Height to the widest portion of dominant and codominant tree crowns.

**Table 4**

Comparison of structure and composition density (no. per ha, mean [standard error]) for living understory trees (> 0.5 m tall and < 11.4 cm DBH) of reference and recent partial blowdown stands at four sites ( $n = 4$ ).  $F$ -value and significance level (**bold** when  $p \leq 0.05$  and *italicized* when  $p > 0.05$  and  $\leq 0.10$ ) are results of generalized linear mixed models of stem presence/absence (P/A).

Density metric	Disturbance		
	Reference	Blowdown	P/A $F$ -value
All Species, All Sizes	5196 (3923)	11,288 (2480)	0.48
Sugar Maple, All Sizes	3803 (3100)	3381 (1550)	3.39
Eastern Hemlock, All Sizes	552 (319)	577 (209)	0.57
Yellow Birch, All Sizes	<b>25 (25)</b>	<b>4116 (915)</b>	<b>19.54</b>
Light-seeded Species, All Sizes	<b>602 (349)</b>	<b>5953 (328)</b>	<b>16.66</b>
All Species, < 2 m tall	4463 (3672)	7368 (1612)	8.31
All Species, > 2 m tall	<b>732 (1612)</b>	<b>3920 (1024)</b>	<b>11.59</b>



**Fig. 1.** Presence of browsing (percent mean + standard error) on living understory trees (> 0.5 m tall and < 11.4 cm DBH) of recent partial blowdown (BD) and reference (REF) stands at four sites ( $n = 4$ ).

**Table 5**

Mean (standard error) abundance (%) of substrates and mounds in reference and recent partial blowdown stands at four sites ( $n = 4$ ).  $F$ -value and significance level (**bold** when  $p \leq 0.05$  and *italicized* when  $p > 0.05$  and  $\leq 0.10$ ) are results of generalized linear mixed models.

Metric	Disturbance		$F$ -value
	Reference	Blowdown	
Floor	<b>95.2 (0.6)</b>	<b>81.3 (4.6)</b>	<b>22.8</b>
Coarse woody debris	<b>2.8 (0.7)</b>	<b>14.1 (2.3)</b>	<b>38.7</b>
Mineral soil	<b>0 (0)</b>	<b>6.4 (2.3)</b>	<b>1156.7</b>
Young mounds	<b>1.2 (1.2)</b>	<b>4.9 (0.4)</b>	<b>1596.8</b>
Old mounds	23.7 (4.8)	18.3 (3.6)	2.2

blowdown were 0.21, 0.10, and 0.31, respectively. Presence of browsing was found more often in partial blowdown than reference stands ( $F$ -value = 19.52,  $p < 0.002$ ) and less often on mounds ( $F$ -value = 36.0,  $p < 0.001$ ) (Fig. 1).

Recent partial blowdown events affected the availability of substrates and mounds for tree regeneration (Table 5). Recent blowdown stands had more exposed mineral soil, coarse woody debris, and young mounds than reference stands. Reference stands had more available forest floor substrate than recent blowdown stands. Only old mounds had similar frequency in recent blowdown and reference stands. Height of young mounds were greater than height of old mounds ( $1.4 \pm 0.2$  m and  $0.2 \pm 0.2$  m, respectively,  $F$ -value = 29.7,  $p < 0.001$ ).

### 3.2. Tree densities expanded to available mound area

Overstory tree associations with microtopography were variable and not distinct when all species were combined (Table 6). By species, overstory eastern hemlock were more abundant on than off mounds (Fig. 2). Overstory yellow birch and light-seeded species were slightly more common on mounds as well; however, sugar maple had no significant association with microtopography.

Understory tree (> 0.5 m tall and < 11.4 cm DBH) associations with microtopography were distinct (Table 7, Fig. 3). Sugar maple was more common off than on mounds. Yellow birch was too infrequent in reference stands to test mound associations, but was more abundant on mounds in blowdown stands. There were too few observations to test eastern hemlock associations with microtopography. When examined by height class (short, 0.5 m tall to < 2.5-cm DBH; tall,  $\geq 2.5$ -cm and < 11.4-cm DBH) trends by species remained the same, except for one additional result: tall, light-seeded species were associated with mounds ( $F$ -value = 6.58,  $p$ -value = 0.043).

Browsing on understory trees was size- and microtopography-specific. Browsing was more likely off than on mounds for trees < 2 m tall for all species ( $F$ -value = 7.12,  $p$ -value = 0.034) and for light-seeded

**Table 6**

Generalized linear mixed model results of living and dead overstory trees (> 11.4 cm DBH) stem density expanded to available microtopographic area (on and off mounds) and partial blowdown (recent and reference) at four sites ( $n = 4$ ). Significance level from generalized linear mixed models is **bold** when  $p \leq 0.05$  and *italicized* when  $p > 0.05$  and  $\leq 0.10$ .

Variable	Microtopography $F$ -value	Blowdown $F$ -value	Blowdown $\times$ Microtopography $F$ -value
All species	3.42	1.17	0.38
Sugar Maple	0.30	8.50	0.13
Eastern Hemlock	<b>7.78</b>	0.18	1.09
Yellow Birch	5.12	0.08	0.00
Light-seeded Species	5.63	0.74	0.28

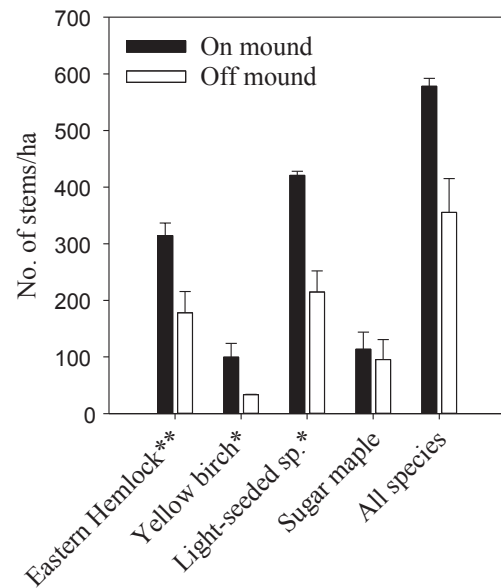


Fig. 2. Overstory eastern hemlock, yellow birch, and light-seeded species (> 11.4 cm DBH) densities expanded to available area on and off mounds at four sites ( $n = 4$ ). Asterisk indicates microtopographic status (on or off mound) was significant (\*\* =  $p < 0.05$  and \* =  $p < 0.10$ ) in generalized linear mixed models (full model results in Table 6).

species ( $F$ -value = 19.3,  $p$ -value = 0.010). Browsing patterns were not distinct for other species.

## 4. Discussion

Developing NDBM approaches requires a comprehensive examination of natural disturbance outcomes. Following a moderate-severity wind disturbance, areas of wind-thrown trees are snapped and uprooted creating canopy gaps, pit-mounds complexes, and large woody debris along with areas of relatively undisturbed low and high-light patches that create a diversity of regeneration niches for trees (Vodde et al., 2011). To evaluate the role that mounds play in forest stand dynamics, this study focused on saplings (> 0.5 m) and mature canopy trees, because mature trees and associated microtopographic features highlight potential long-term competitive advantages of species on mounds. Overstory tree species did differ in microtopographic position; a greater number of light-seeded species were found on than off of mounds. Likewise, we found that large, light-seeded, and browse-sensitive saplings were more likely on recent mounds. The role of mounds in conferring competitive advantages to select tree species, and therefore altering the trajectory of stand development and future structure and composition, has important implications for NDBM recommendations.

Mounds also provide growth advantages by acting as refugia from browse. We found browsing was more evident on seedlings off rather than on mounds. This may be due to their accessibility to browsers. In an experimental blowdown study, browsing was the major cause for death of seedlings regenerating on the forest floor, but not for seedlings regenerating on mounds (Carlton and Bazzaz, 1998). Mounds were refugia from deer for eastern hemlock for up to 18 years after a blowdown event in U.S. Alleghany old-growth hemlock-hardwood forests. These eastern hemlock seedlings were taller and browsed less often than seedlings growing on flat terrain (Long et al., 1998, Krueger and Peterson, 2006). Our study provides evidence outside of Pennsylvania that young mounds support high densities of light-seeded species that can grow above reach of browsers (> 2 m) in 13 years or less, thereby facilitating yellow birch and other browse-sensitive saplings through regeneration bottlenecks by elevating trees away from browsers.

An important finding is the reduction of the forest canopy height

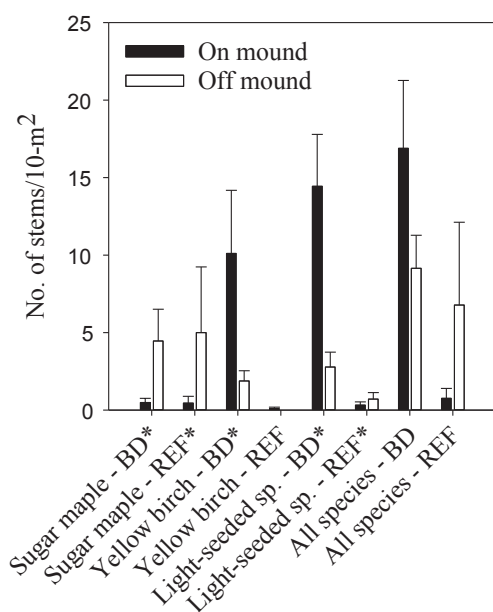
**Table 7**

Generalized linear mixed models of living understory tree (> 0.5 m tall and < 11.4 cm DBH) density expanded to available microtopographic area (on or off mounds) and partial blowdown (recent and reference) at four sites ( $n = 4$ ). Significance level from generalized linear mixed models is **bold** when  $p \leq 0.05$  and *italicized* when  $p > 0.05$  and  $\leq 0.10$ .

Variable	Microtopography	Blowdown	Blowdown $\times$ Microtopography
	F-value	F-value	F-value
All species	0.07	<b>8.37</b>	<i>4.64</i>
Sugar Maple	<b>11.24</b>	11.24	0.05
<i>Eastern Hemlock</i> <sup>a</sup>			
Yellow Birch <sup>b</sup>	<b>6.74</b>		
Light-seeded Species	0.32	0.32	<b>15.85</b>

<sup>a</sup> Observations too few for analysis.

<sup>b</sup> Model for recent blowdown stands only; observations too few in reference stands.



**Fig. 3.** Understory sugar maple, yellow birch, and light-seeded species (> 0.5 m tall and < 11.4 cm DBH) densities expanded to available area on and off mounds at four sites ( $n = 4$ ). Asterisk indicates microtopographic status (on or off mound) was significant ( $p < 0.05$ ) in generalized linear mixed models (full model results in Table 7). BD = Recent partial blowdown stands and REF = Reference stands.

after disturbance in tandem with new mound creation. Crown shoulder height (two-thirds of total canopy height), in particular, is important to tree regeneration; it is the height when trees secure a position in the main canopy (Webster and Lorimer, 2005). In other stands of hemlock-hardwoods in Wisconsin, canopy gap openings were considered filled by gap tree regeneration when a gap sapling reached crown shoulder height, or the height of the widest point of the surrounding dominant and codominant tree crowns. At that growth stage, the gap sapling crown can physically obstruct lateral crown extension of the existing dominant and codominant canopy trees and capture the gap (Cole and Lorimer, 2005). Ten years after blowdown, we found a 23% reduction in crown shoulder height compared to crown shoulder height in reference stands (Table 3). Factoring in the height of new mounds (1.4 m), a tree growing on a mound in the blowdown area would experience ~30% shorter distance to the canopy than a tree growing from pits or the ground in the reference area. Other studies in the region indicate gap capture from in-filling saplings occurs in 28–37 years (Webster and Lorimer, 2005). Assuming similar growth rates, trees established on new mounds under a lowered canopy after a moderate-severity blowdown could attain a canopy position in 20–26 years or 8–9 years sooner than a tree growing from pits or the ground in the

reference area. Moreover, others have reported that trees on mounds have faster growth rates attributable to decreased canopy cover and increased light levels (Vodde et al., 2010). The shortened distance to the canopy and potentially faster growth rates for trees regenerating on mounds is an important consideration for stand dynamics and requires additional study.

The moderate-severity blowdowns created conditions suitable for new cohort establishment and changed the density and proportions of understory trees. Yellow birch and all light-seeded species combined increased density nearly ten-fold in the recent blowdown versus reference stands. Mounds played a substantial role in this shift. Over 80 percent of young mounds contained saplings of light-seeded species. In field studies of pit-mound pairs, yellow birch was the dominant species regenerating on these substrates (Lang et al., 2009), with a greater proportion of stems on mounds than pits 14 years after a hurricane in New Hampshire (Hutnik, 1952). Follow-up studies in the same area showed long-term growing advantages for the birch species growing on mounds created by the hurricane; mature birch were still found disproportionately on than off mounds (Schoonmaker, 1992, Barker Plotkin et al., 2017). Our study provides evidence for long-term advantage for light-seeded and shade-intolerant yellow birch in western Great Lakes forests as well. Thus, mounds serve an important regeneration function in western Great Lakes hemlock-hardwood forests and in other ecosystems of functionally similar species and disturbance regimes.

The affinity of yellow birch to mounds may be attributed to a variety of factors. The 10+ years of exposed mineral soil (9% of mound surface area) provided substrate for multiple occurrences of good to excellent (2.7 years with a 1–8 year range (Tubbs, 1977)) yellow birch seed crops. Moreover, yellow birch requires warmer germination temperatures than competitors such as sugar maple (Godman, 1992) and, thus, may be more likely to germinate with the warmer soil temperature of young mounds than of pits or undisturbed forest floor (Peterson et al., 1990). Also, Carlton and Bazzaz (1998) found maximum growth of planted yellow birch on mounds, because these seedlings had adequate light and well-developed root systems that appeared capable of drawing water and nutrients from undisturbed forest floor.

In contrast to yellow birch, eastern hemlock, a light-seeded but shade-tolerant species, was associated with mounds as mature trees, but not as saplings. At other sites, mature eastern hemlock were also more likely on than off of mounds in New England old-growth forests (Barker Plotkin et al., 2017) and regenerating eastern hemlock were larger and more abundant on older mounds than on other microsites in Pennsylvania hardwood forests (Long et al., 1998). An important substrate for eastern hemlock regeneration, coarse woody debris, was present on site and in newly created mounds (i.e. dead roots), but insufficiently decayed for eastern hemlock germination and survival (Marx and Walters, 2008), which could explain the lack of association between eastern hemlock seedlings and mounds. Alternatively, the disturbances that we studied may have been too severe for favorable eastern hemlock

regeneration. Studies of old-growth eastern hemlock stands suggest frequent, low-severity disturbance maintain low light levels suitable for eastern hemlock regeneration (Webster and Lorimer, 2005). Our study may underestimate eastern hemlock recruitment if seedling establishment proceeds gradually over several decades (Abrams and Orwig, 1996), which appears to be plausible given the long-term exposed mineral soil on mounds.

We observed that the establishment of sugar maple, a large-seeded and shade-tolerant species, was more common on than off mounds and overstory sugar maples were similar on and off mounds. Beatty (1984) reported that sugar maple seedlings were more abundant in undisturbed sites than on mounds or pits in east-central New York. In contrast, findings from regional studies in Upper Michigan (Šamonil et al., 2016) and drumlin landforms in northeastern Wisconsin (Kabrick et al., 1997b) have shown that mature sugar maples were more abundant on mounds than other microsites. The differences between our findings and those of other studies appear to be related to the soil properties prior to and following pit and mound formation. For example, in the Michigan study calciphilic sugar maple appeared to be more restricted to mounds due to the increased pH and nutrient availability where soil horizon inversion created more Ca- and Mg-rich spodic horizons nearer to the surface (Šamonil et al., 2016). In the Wisconsin study, mounds reportedly provided a more favorable microenvironment for sugar maple establishment and growth because the mounds formed in a thick mantle of loess that provided well-drained soils compared to adjacent pits in the underlying dense glacial till during (Kabrick et al., 1997b). This suggests that the parent materials and soil processes resulting from tree uprooting have an important effect on soil properties and the kinds of microenvironments created and, consequently, the tree species that colonize and grow on and off of mounds.

#### 4.1. Management implications

Management practices following blowdown events usually involve salvaging the largest, most valuable stems. Severing the stem from the mound often results in mounds swinging back into the pit either by the force of gravity alone and/or through the elasticity of bent roots (Beatty and Stone, 1986) leaving an upright stump and little exposed mineral soil. Conventional salvage practices have reduced young mound density by up to 50% (Waldron et al., 2013, Fraver et al., 2017). Our study in unmanaged, old forest areas highlights the affinity of shade-intolerant and browse-sensitive species to mounds at sapling and mature stages. As such, we suggest best practices for salvage areas leave a portion of the uprooted trees unsalvaged and protected from heavy equipment traffic to maintain the newly created mound features and their potentially unique regeneration niche.

Determining the number of reserved uprooted trees will depend on management objectives. If maintaining light-seeded species is a goal, then an approach could be to assume some new mounds will be missed by operating equipment and then specifically reserve enough uprooted trees from salvage. The total mound substrate density (misses + reserves) would be aimed at the mid to upper density range of target species to regenerate on mounds. Mounds can be protected by marking areas to be avoided by equipment and/or propping mounds with harvested boles with a low-grade log or large pulpwood. On Wisconsin Board of Commissioners Lands in northeastern Wisconsin, propped, young mounds following a blowdown in 2013 have remained upright to date (2018).

Selection of reserved uprooted trees should include species with rot-resistant wood, such as long-lived conifers (e.g., eastern hemlock in this study ecosystem) to provide decayed wood substrate for future tree regeneration that depends on such germination sites (Marx and Walters, 2008). In addition, rot-resistant, long-lived conifer crowns and intertwined horizontal boles may provide physical barriers to browsers (de Chantal et al., 2009) and therefore increase browse-sensitive seedling

success on flat microtopography (van Ginkel et al., 2013). While this was not a focus of our study, we observed similar trends at our site for yellow birch.

Proximity to seed trees and canopy gaps, especially light-seeded species, is another consideration when selecting locations for reserved uprooted trees. In our study ecosystem, reserving uprooted trees near a residual yellow birch in a large gap could facilitate regeneration success. In Finland, Pasanen et al. (2016) similarly suggested creating harvest gaps over or near uprooted trees for birch regeneration.

Artificially created mounds have potential to supplement naturally created mounds. In Quebec, growth potential for birch was high on artificial mounds (Elie et al., 2009), but few studies have published on this approach for broader application. Large-scale creation of new tip-mounds could be a creative way to establish regeneration in some stands if operational costs or impacts of large equipment are not an issue (e.g., introduction of invasive species on unwashed equipment). Others have reported mounding soil for artificial regeneration on poorly drained soils (Londo and Mroz, 2001, Kabrick et al., 2005). We suggest more research on artificial mound creation to stimulate diverse tree regeneration and further develop “mound-based” management strategies in forest types where mounds influence tree regeneration.

#### 4.2. Conclusions

The conditions under which forest ecosystems develop and persist are changing (Stocker et al., 2013). As conditions change unevenly and unpredictably at local, regional, and global scales, modifying current approaches to forest management becomes necessary (Mori et al., 2013). Using natural disturbance as a guide to management is an approach to develop resilience, maintain or restore natural processes, and sustain ecosystem goods and service (Franklin et al., 2007).

Current best management practices often include retention or creation of standing and downed wood (e.g., Minnesota Forest Resources Council, 2013) and inclusion of canopy gaps (e.g., Wisconsin Department of Natural Resources, 2008). However, few consider emulating other features of uprooting, such as retention or creation of pit-mound topography. Moreover, in northern temperate, mixedwood forests, moderate-severity disturbances appear common based on studies of old-growth (Foster, 1988, Frelich and Lorimer, 1991a,b, Fraver and White, 2005), but have received less study and emulation in practice than either single-tree (mortality) gaps or extreme disturbances (Seymour et al., 2002).

Maintaining and/or protecting naturally created mounds may be the best opportunity to regenerate light-seeded, browse-sensitive species in mixedwood forests that evolved under infrequent, moderate-severity wind storms. Furthermore, mounds outlive trees, providing unique structure to forests for hundreds to thousands of years (Šamonil et al., 2013). Mound functions are complex and may change over time as the stand develops and site conditions change. While protection of young mounds in salvage areas may reduce short-term revenue recovery, the long-term ecological and economic benefits of regenerating a cohort of light-seeded species may offset initial financial concerns, especially in high conservation areas. The post-disturbance changes in forest structure, substrate conditions and light environment provided by tip-up mounds represents a unique opportunity to regenerate a diverse cohort of trees.

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analyzed data. Kern, Schwarzmann, and Kabrick wrote the manuscript. Gerndt, Boyden, and Stanovick contributed significant revisions to the manuscript.

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## Appendix A. Supplementary material

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.foreco.2018.12.040>.

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