



## Microtopography and ecology of pit-mound structures in second-growth versus old-growth forests



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### ABSTRACT

Pit and mound microtopography is an important structural component of most forests, influencing soil processes and habitat diversity. These features have diminished greatly in northeastern U.S. forests since European settlement, as a result of the history of repeated logging, land-clearance followed by reforestation, and the smaller size of trees (and therefore windthrow features) comprising the prevailing second-growth forests. Despite the potential importance of this region-wide shift in forest microtopography on ecosystem structure and function, the differences in pit and mound size, distribution, and longevity between second-growth and old-growth forests are unexplored. Likewise, although many studies demonstrate that mounds and/or pits are hotspots for tree regeneration there is scant information about whether location on a mound or pit affects tree survival and growth beyond the seedling stage, or whether microtopographic regeneration patterns differ in old-growth and second-growth forests.

We compare a simulated hurricane experiment initiated in 1990 in second-growth forest (the pulldown) and an old-growth forest that was blown down by a hurricane in 1938 (Pisgah) to examine differences in pit-mound microtopography and ecology between second-growth and old-growth forest. At Pisgah, fewer, larger mounds comprised a similar areal coverage as at the pulldown. Repeated measurements of individual pit-mound structures in the pulldown revealed that pit infill proceeded more rapidly than mound erosion. Mound area increased but height decreased over time as soil from the mound tops eroded and spread around the mound base. Although 40% of mounds in the pulldown were > 1 m tall immediately after the manipulation (maximum of 2.9 m), after 25 years, maximum mound height was 0.9 m. In contrast, 11% of mounds at Pisgah remained > 1 m tall in 1989, 50 years after blowdown. At both sites, trees, especially *Betula* spp., were disproportionately found on mounds. Fewer trees than expected grew in pits at Pisgah. Tree mortality was somewhat higher on mounds and pits than on other substrates. As a mechanism to increase stand-level tree diversity, windthrow may be more critical in old-growth forests, in which niches for early-mid successional species are few, than in second-growth forest, in which early-mid successional species already comprise the majority of the trees. Pit-mound structures are a diminished component of second-growth forest, and silvicultural techniques designed to restore old-growth characteristics could include measures to preserve and enhance pit-mound features, and to cultivate large-diameter trees that will eventually create the large, long-lasting pit-mounds of the future.

### 1. Introduction

Trees build the basic structure of forested ecosystems. This is obvious for the canopy, with its variation in vertical stratification (Oliver, 1980; DeGraaf and Yamasaki, 2001) and horizontal spatial patterning (Franklin et al., 2002; Ishii et al., 2004). Trees also structure the forest floor in important ways. A subtle, but critical example is the pit-mound structures formed by the uprooting of trees. Pits and mounds are

microtopographic features with a spatial extent that varies from a single treefall to dispersed large patches formed from multiple uproots across a landscape or even a large region that may persist for centuries following a tornado or hurricane (Foster et al., 1998). Longevity of pit-mound structures varies with climate, site, and soil conditions from less than a decade in some tropical regions (Putz, 1983) to centuries on sandy soils in cold temperate forest (Schaetzl and Follmer, 1990). In temperate forests, visible pit and mound topography may affect

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15–50% of the forest floor (Stephens, 1956; Lyford and MacLean, 1966; Sobhani et al., 2014). The forest process of uprooting and erosion mixes the soil and initiates new episodes of soil formation (Veneman et al., 1984; Lenart et al., 2010), alters ecosystem processes such as soil respiration (Miliken & Bowden, 1996; Kooch et al., 2015), and diversifies microhabitats for tree regeneration and ground-layer plants (Lyford and MacLean, 1966; Carlton and Bazzaz, 1998b; von Oheimb et al., 2007) as well as many other organisms.

Tree diameter is a strong predictor of pit-mound size (Sobhani et al., 2014) so as tree size increases through forest development, pit-mound size and longevity should correspondingly increase, analogous to the relationship between forest development stage, tree size, and canopy gap size (cf. Dahir and Lorimer, 1996). The history of land-use in much of the northeastern U.S. left a lasting imprint on the structure and function of the now re-forested landscape (Foster and Aber, 2004). Forest clearing in the 18<sup>th</sup> and 19<sup>th</sup> centuries followed by plowing or grazing eliminated mound and pit topography in areas converted to agriculture. Across the rest of the region the remaining forests were cut intensively and repeatedly, replacing the old-growth forests with smaller trees in second-growth stands that resulted in a progressive reduction in the frequency of production and size of mounds and pits. A major hurricane in 1938 initiated pits and mounds across the region, from southern Connecticut to northern Vermont, but with structures that may be much less robust in stature and longevity, and therefore quantitatively different in function with those from old-growth forests. The dramatic reduction in the size, abundance and landscape distribution of mounds and pits is a significant legacy of land use.

The implications of land use history and forest development on pit-mound size, distribution, and longevity are unexplored. Likewise, despite many studies demonstrating that mounds and/or pits are hotspots for tree regeneration (e.g., Hutnik, 1952; Lyford and MacLean, 1966; Peterson and Pickett, 1990), there is scant long-term data concerning the survival of trees established on mounds or pits (Carlton and Bazzaz, 1998a), or whether microtopographic patterns of regeneration differ in old-growth versus second-growth forest.

Here, we compare a designed and natural experiment to examine differences in pit-mound microtopography and ecology between second-growth and old-growth forest. Repeated pit-mound measurements and tree regeneration data are available from a simulated hurricane experiment (the “pulldown”) initiated in 1990, and located in a second-growth forest in central New England (Cooper-Ellis et al., 1999; Barker Plotkin et al., 2013). The nearby 300+ -year-old old-growth Harvard Pisgah Tract (“Pisgah”) was blown down by the 1938 hurricane (Cline and Spurr, 1942) but left intact, and therefore retains impressive downed wood and pit-mound structures (Henry and Swan, 1974; Foster, 1988a; D’Amato et al., 2017). Fifty years after the hurricane, an intensive study and historical reconstruction of the site and its vegetation (Schoonmaker, 1992) included an inventory of mound sizes and tree regeneration on the mounds, pits, and other substrates. Through a comparative study of the designed pulldown experiment and the old-growth Pisgah stand, we test the following specific hypotheses:

- (1) Within a site, the forest floor area covered by pit-mound structures produced by an uprooting event decreases over time, as mounds erode and pits fill.
- (2) Following severe wind disturbance, old-growth forests, as represented by Pisgah, have fewer, taller, mounds than second-growth forests, as represented by the pulldown. This is primarily a function of the fewer, larger trees in old-growth versus second-growth forests.
- (3) Tree diameter is a strong predictor of mound and pit area (cf. Sobhani et al., 2014), forming a relationship that does not vary by tree species. Alternately, varying root structures may lead to diameter-area relationships that vary by species. Robust prediction of mound-pit area for a wide range of forest sizes and types informs better prediction of the microtopographic consequences of

uprooting events.

- (4) Mounds persist longer than pits. We expect pits to fill with litter and soil from adjacent mounds, whereas mound erosion may be slowed by vegetation rooted on mounds.
- (5) As found in earlier studies for tree seedlings (e.g. Carlton and Bazzaz, 1998a), we expect mounds to persist as favorable sites for trees as they develop from seedlings to small trees, especially for early-to-mid successional species. Conversely, we expect tree recruitment in pits to be low to absent.
- (6) Trees on mounds continue to benefit from the elevated position and light levels experienced as seedlings, and are thus larger and grow more quickly than those on adjacent intact sites. However, because of continued mound erosion, these trees have a higher mortality rate than those on adjacent intact sites.

The two sites differ in dominant tree species before disturbance and today, and the measurements of each site were taken at different intervals following disturbance. However, the comparison provides the opportunity to bring together intensive measurements from a second-growth and an old-growth forest to yield insights into the dynamics and importance of pit-mound structures that would not be available if each site was presented alone. In particular, the comparison can generate an understanding of the structural differences of the forest floor between old-growth and second-growth forests that can inform silvicultural techniques designed to enhance late-successional characteristics (Franklin et al., 2002; Keeton, 2006; Bauhus et al., 2009) and allow scientists, landowners, and managers to anticipate some of the changes that current forests will undergo with ongoing development.

## 2. Materials and methods

### 2.1. The simulated hurricane experiment

The pulldown experiment is located on a gentle (5°) northwest slope at the Harvard Forest in central Massachusetts (42.49° N, 72.20° W, 300–315 m a.s.l.; Fig. 1a) on well-drained to moderately well-drained stony loams derived from glacial till overlying schist bedrock. The site was most likely a cleared pasture during the 1800s; the current *Quercus rubra*-*Acer rubrum* (red oak-red maple) forest developed following a clearcut in 1915. The study area is surrounded by similar forest. The climate is cool temperate (July mean 20° C, January mean −7° C); 1100 mm average precipitation is distributed evenly throughout the year.

Details about the experiment can be found in Barker Plotkin et al. (2013). In brief, a 0.8 ha experimental site (50 × 160 m, the “pulldown”) and 0.6 ha (50 × 120 m) control site were oriented approximately east to west and separated by a 30 m forest buffer. During peak hurricane season in early October 1990, 276 trees were toppled in a northwesterly direction of natural treefall (Boose et al., 2001), using a winch and steel cable attached ca. 6 m up the bole of each tree in an effort to simulate the damage to similar stands in the 1938 hurricane (Foster, 1988b). Force was applied by the winch only until the stem snapped or roots failed and the mass of the crown brought down the tree. Stems were not pulled beyond their initial point of repose. The winch was positioned off the study site so that all plant and soil disturbance resulted from uprooting or bole breakage, plus damage to 325 trees hit by the toppled trees (Cooper-Ellis et al., 1999). The manipulation effectively simulated the effects of a hurricane in terms of overstory damage, damage to intermediate and understory vegetation, and physical structure. Eighty percent of the canopy trees, and two-thirds of all trees > 5 cm diameter at breast height (dbh), were damaged directly or indirectly by the manipulation. Uprooting, which creates pit-mound structures, affected both trees pulled down and indirectly damaged trees, and was the most common form of damage (40% of the trees were uprooted; Cooper-Ellis et al., 1999; Fig. 1c).

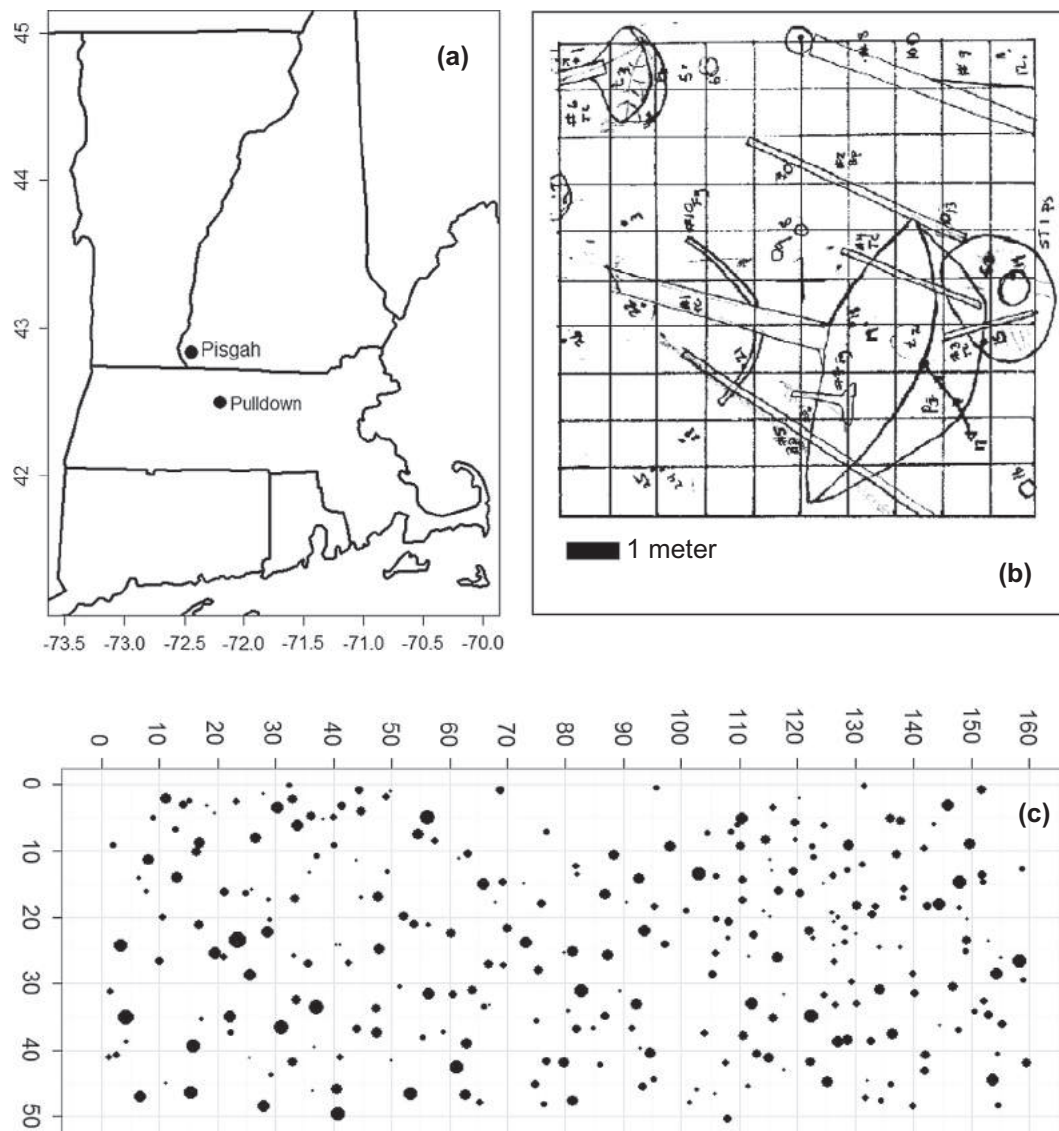


Fig. 1. Study site locations in New England, USA (a). Example map of one 10 m × 10 m plot ( $n = 57$ ) at the Harvard Pisgah Tract (b); all mound-pit structures immediately after the pulldown manipulation (grid units are m), scaled by total area of the pit-mound (c).

## 2.2. The Harvard Pisgah Tract

The 10 ha Pisgah site is located 42 km northwest of the pulldown and lies within the 5400 ha Pisgah State Park in southwestern New Hampshire (42.83 °N, 72.44 °W; Fig. 1a). Climate and elevation are similar to the pulldown site; soils are similar but tend to be shallower and the site contains a north–south trending ridge.

The Pisgah site was purchased and protected as an old-growth forest in 1926 by Harvard University and so is a rare example of New England forest that has not been directly impacted by humans. Studies at this forest began in 1905, so we know much about the old-growth *Tsuga canadensis* – *Pinus strobus* (hemlock-white pine) forest (Branch et al., 1930; Cline and Spurr, 1942; Henry and Swan, 1974; Foster, 1988a; D'Amato et al., 2017). The great hurricane of 1938 blew down the majority of old-growth stands in the area. However, unlike most of the surrounding area, Pisgah was not salvage logged so massive uprooted trees remained and their pit-mound structures were left undisturbed (Foster et al., 2014).

## 2.3. Measurements of pit and mound structures

In the pulldown, all pit-mound complexes ( $n = 277$ ) were measured

immediately after the manipulation. Of these, 100 were chosen for re-measurement in 2005 and 2015 (Plate 1); these represent 25 randomly chosen pit-mounds from each of the four most common genera in the study plot that were uprooted (*A. rubrum*, *Q. rubra*, *Betula* spp., *Fraxinus americana*). Although a few of the mounds included more than one uprooted tree, all 100 re-measured pit/mounds were associated with a single tree.

We measured mound and pit width (dimension perpendicular to the uprooted tree stem), thickness (dimension parallel to the uprooted tree stem), and height (or depth for pits). In 2005 and 2015, we recorded mound width at the greatest extent of visibly disturbed soil. Pit width was measured as the greatest extent that a depression of the soil through the leaf litter was discernable. Thickness of the mound was measured from the top of the root mat on the bole side, to a point on the pit side where the slope of the mound inflected into the pit, near the elevation of the surrounding ground level. Pit thickness was measured from the same point of inflection where the mound thickness was measured to the outside edge at a point where the pit edge was visible or could be felt under the leaf litter. We did not remove accumulated leaf litter when measuring pit depth, though we did compress loose litter with the measuring stick.

We determined the area of pits and mounds by calculating the area





**Plate 1.** Examples of pit-mound structures at the pulldown (years 0, 15, 25) and Pisgah (year 78).

of an ellipse (Peterson & Pickett, 1990):

$$A = \pi ab, \quad (1)$$

where  $A$  is the area of an ellipse,  $a$  is one-half the mound or pit width and  $b$  is one-half the mound or pit thickness.

To calculate mound or pit volume, we used an equation that approximates half of an ellipsoid (Norman et al., 1995):

$$V = [2\pi(a/2)(b/2)(c)]/3, \text{ which can be rewritten as } V = (\pi abc)/6, \quad (2)$$

where  $V$  is the volume of half of an ellipsoid,  $a$  = mound or pit width;  $b$  = mound or pit thickness;  $c$  = mound height or pit depth.

At Pisgah, 50 years after the 1938 Hurricane, two parallel transects (300 and 270 m long, respectively) of contiguous 10 m × 10 m plots ( $n = 57$ ) were established across the north–south ridge (Schoonmaker, 1992). Detailed field measurements were made by subdividing each plot into four 5 × 5 m subplots, and locating microtopographic features and stem locations to the nearest 0.1 m. These features were transferred to a 10 × 10 cm map for each plot in the field (Fig. 1b). Mounds were additionally classified into three height classes: large (> 1.0 m tall), medium (0.5–1.0 m tall) and small (< 0.5 m tall). Field maps were digitized into a GIS and areas calculated.

Since the Pisgah study did not include measurements of mound or pit volume, in 2016 we measured the dimensions of 30 of the largest pit-mound structures at Pisgah and calculated their area and volume using Eqs. (1) and (2), simply to illustrate the size the largest of these structures attained at this old-growth site (Plate 1).

#### 2.4. Tree regeneration

We focused our tree regeneration analysis on stems that survived into the tree stage (defined here as  $\geq 5$  cm dbh). At the pulldown, we used data from a recruitment survey in which the species, diameter, and microsite position for all stems that grew into the 5 cm dbh class after the manipulation were recorded in 2003, 2006, 2010, and 2015. In 2010, these recruits were mapped and tagged, and their growth and survival was assessed in 2015. The number of substrate categories varied somewhat from year to year; to make consistent categories across years, and to have an adequate sample size, substrates were combined into “Mound” (includes mound top, mound, and mound base), “Pit” (includes pit, and pit edge), and “Other” (includes undisturbed ground, stump, rock, and tree base).

At Pisgah, all tree stems  $\geq 2$  cm dbh within the two transects were mapped, diameters measured, and microsite type recorded in 1989. Survival and growth of these trees was assessed 20 years later, in 2009. The subset of stems  $\geq 5$  cm dbh in 1989 was used for analysis, to match the diameter minimum used in the pulldown. Substrate categories were combined into the same three classes as in the pulldown: “Mound” (includes three height classes of mound), “Pit” (includes two size classes of pit), and “Other” (includes ground, thin soil, rock, stump, and log), plus a “Pre-1938 Mound” category. Pre-1938 mounds were identified by the condition of their associated stems and their stems’ position relative to 1938-generated downed wood (Schoonmaker, 1992).

#### 2.5. Analyses

All analyses were conducted in R version 3.3.1 (R Core Team, 2016). Tree diameter as a predictor of mound or pit area was evaluated for the pulldown experiment with linear regression (lm function) using log–log transformed data as in Sobhani et al. (2014). We used ANCOVA to explore whether genus (*Acer*, *Quercus*, *Fraxinus*, *Betula*, *Pinus*) modified this relationship.

The number of live stems recruited into the pulldown experiment in 2006 and 2015 (the years nearest in time to the pit-mound physical re-measurements) or tallied along the Pisgah transects in 1989 was related to microsite using chi-square analysis. Whether certain microsite classes (mound, pit, other) were utilized more or less than expected was assessed overall, and for major species at each site. These relationships were visualized using a ‘distribution index’ (modified from Huenneke and Sharitz, 1986):

$$DI = \log(a_i/b_j), \quad (3)$$

where  $a$  is the percent of stems of species  $i$  on microsite  $j$ , and  $b$  is the percent of the study area covered by microsite  $j$ . Where more stems

occur than would be expected based on microsite area  $DI > 0$ , where fewer stems occur than expected  $DI < 0$ , and where the percentage of stems on a microsite matches the microsite abundance  $DI = 0$ .

To assess survival from 2010 to 2015 at the pulldown, or from 1989 to 2009 at Pisgah, annual average mortality rates were calculated as:

$$M = 1 - (S/N_0)^{(1/y)} \tag{4}$$

where  $S$  is the number of survivors,  $N_0$  is the original number of stems, and  $y$  is the number of years between samples (Runkle, 2000). Whether mortality rate differed by substrate versus overall was evaluated using chi-square analysis.

### 3. Results

#### 3.1. The pulldown pit-mound population and comparison with Pisgah

Immediately after the pulldown, the 277 pit-mound structures ( $346 \text{ ha}^{-1}$ ) covered 8.3% of the forest floor (Fig. 1c). Overall pit-mound area declined to 7.7% of the pulldown plot surface area by 2015. However, pit area declined (from 4.4% of the forest floor in 1990, to 2.9% in 2015), whereas mound area increased from 3.9% in 1990 to a peak of 5.3% in 2005, followed by a decline to 4.8% in 2015. Mound area increased as soil from the mound tops eroded and spread around the mound base. Pit and mound topography covered only slightly less surface area at Pisgah after 50 years (6.7%) than at the pulldown experiment after 25 years. At Pisgah, like the pulldown, pits comprised less coverage (2.4%) than did mounds (4.3%, plus an additional 0.6% of pre-1938 mounds). Fewer, larger pit-mound structures comprised this areal coverage at Pisgah ( $190 \text{ ha}^{-1}$  at year 50), compared to  $294 \text{ ha}^{-1}$  at year 25 in the pulldown.

The mean diameter of the trees in the pulldown experiment overall was 15.2 cm in 1990 (range 5.0–58.6 cm); the mean diameter of trees that created a mound was 22.7 cm. Diameter of the uprooted tree strongly predicted mound area ( $F_{1,275} = 451.4, P < 0.001$ ) and pit area

( $F_{1,262} = 198.4, P < 0.001$ ), and very closely fit the diameter-area relationships reported by Sobhani et al. (2014, Fig. 2a,b). Tree genus was also a significant predictor of mound (but not pit) area (effect of  $\ln dbh - F_{1,251} = 204.9, P < 0.001$ ; species -  $F_{4,251} = 4.1, P \leq 0.003$ ;  $\ln dbh \times \text{species} - F_{4,251} = 0.4, P = 0.78$ ) but the absolute differences were small (Fig. 2c).

#### 3.2. Pit and mound erosion over 25 years

At the pulldown, initial mound volume ranged from 0.006 to 4.59  $\text{m}^3$  (mean = 0.81  $\text{m}^3$ ). By year 25, maximum mound volume was 3.0  $\text{m}^3$  (mean = 0.47  $\text{m}^3$ ), a mean volume loss of 42% over 25 years (Fig. 3a). Pit infill was more rapid than mound erosion (Fig. 3b). By year 25, pits had filled in an average of 77%. Because of the faster infill rate and smaller initial size, pits disappeared more rapidly than mounds. By year 25, 19% of the pits were no longer visible, as were 12% of the mounds.

The height structure of the mounds at the pulldown changed rapidly over 25 years, and taller mounds tended to erode more than shorter mounds (Fig. 3c). Initially, nearly 40% of the mounds were > 1.0 m in height. After 15 years, only 10% of the mounds were > 1.0 m tall. By year 25, the maximum mound height was 0.9 m and 69% of the mounds were < 0.5 m in height. In contrast, after 50 years at Pisgah, there remained 21 mounds  $\text{ha}^{-1}$  (11%) that were still > 1.0 m tall (Fig. 4). Three of the 30 large pit-mounds measured in 2016 exceeded 2 m in height.

#### 3.3. Tree species recruitment on pits and mounds

At both sites, trees preferentially grew on mounds (Table 1). In the pulldown, trees recruited in pits (including pit edges) only slightly less than expected (Fig. 5a), but at Pisgah, very few trees were found in pits (Fig. 5b). The Pisgah transect data distinguished mounds created by the 1938 Hurricane from older cohorts of mounds. The pre-1938 mounds

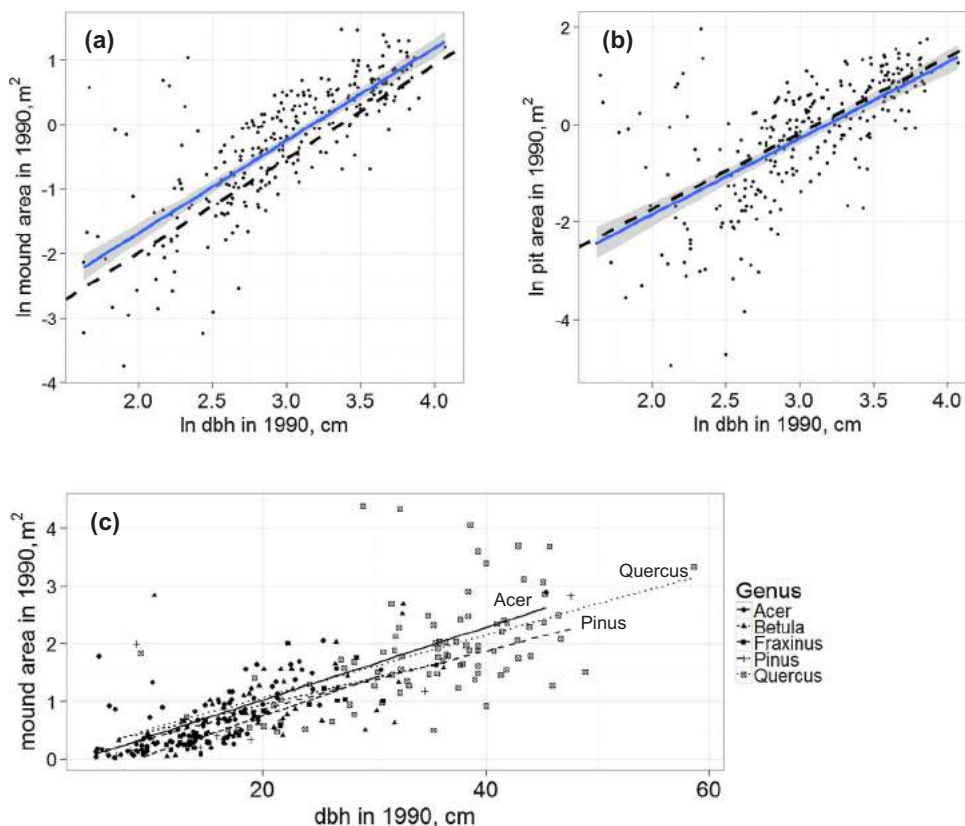


Fig. 2. Mound (a) and pit (b) area as a function of tree diameter at the pulldown. The solid lines are linear fits of  $\ln(\text{dbh})$  vs.  $\ln(\text{mound or pit area})$ ; the shaded area indicates the 95% confidence interval. The dashed lines show the  $\text{dbh}$ -area relationship from a regional synthesis by Sobhani et al. (2014). Species group (c) altered this relationship to some extent (species group and species group \*  $\text{dbh}$  was  $< 0.05$  for all combinations except the  $\text{dbh} \times \text{Acer}$  interaction) for mound area, but not pit area. Note that diameter and mound area are not transformed in panel c, to illustrate that the absolute magnitude of differences among species is fairly small.

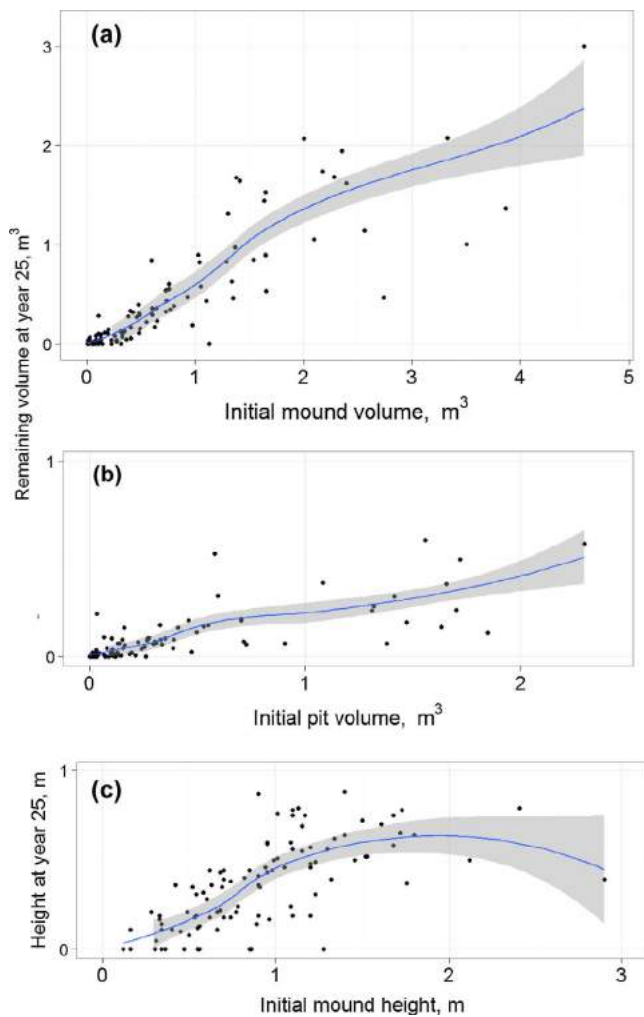


Fig. 3. Volume loss of mounds (a) & pits (b) at the pulldown. Loess curves are shown to help visualize the patterns; the shaded area is the confidence interval. On average, mounds lost 42% of their volume over 25 years, while pit infill averaged 77% after 25 years. Mounds lost more height (c) than volume, and taller mounds appear to have eroded more than shorter mounds.

supported even more trees per unit area than those originating in 1938.

Although *Betula lenta* grew on all substrates in the pulldown, it was disproportionately found on mounds (Table 1). The sample size of other major species (*A. rubrum*, *B. alleghaniensis*, *B. papyrifera*, *Prunus*

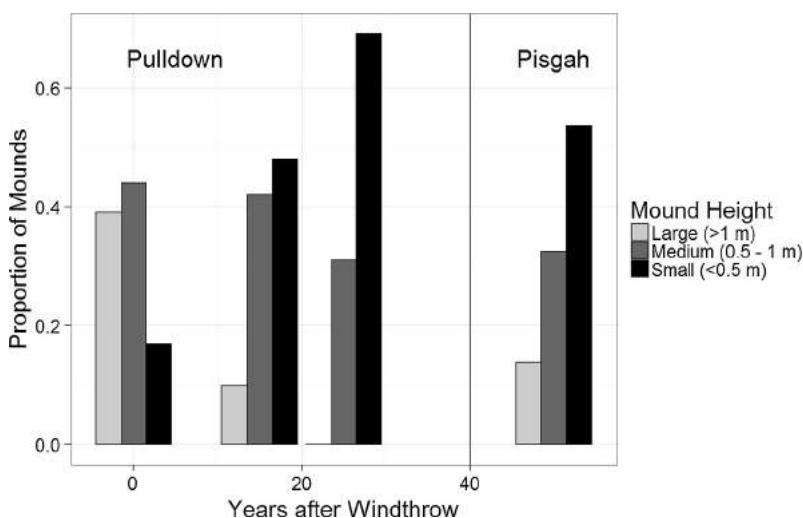


Fig. 4. Height class distribution of mounds at the Hurricane Pulldown Experiment (years 0, 15, 25) and the Pisgah Tract (year 50). Size classes are by height: large is > 1.0 m tall; medium is 0.5–1.0 m tall; small is < 0.5 m tall.

Table 1

Chi-square analysis for tree species distribution among microsites at the pulldown and Pisgah. Microsites for the pulldown include mound, pit, and other. At the pulldown, only *Betula lenta* had a sufficient sample size to analyze separately. Microsites for Pisgah overall include mound, pre-1938 mound, pit, and other. For the species-specific analyses at Pisgah, pre-1938 mound and mound were combined to generate an adequate sample size.

Site/species	$\chi^2$	df	p-value
Pulldown, overall (2006)	103.5	2	< 0.001
Pulldown, overall (2015)	71.5	2	< 0.001
<i>Betula lenta</i> (2015)	43.2	2	< 0.001
Pisgah, overall (1989)	566.7	3	< 0.001
<i>Acer rubrum</i>	3.1	2	0.217
<i>Betula lenta</i>	562.9	2	< 0.001
<i>Betula papyrifera</i>	324.7	2	< 0.001
<i>Fagus grandifolia</i>	30.3	2	< 0.001
<i>Tsuga canadensis</i>	21.2	2	< 0.001

*serotina*/*P. pensylvanica*) on pits and mounds was not large enough to permit strong inference about their distributions, although the available data hinted that early successional *B. papyrifera* and *Prunus* may be more likely to grow on mounds than other microsites. At Pisgah, the larger number of stems allowed stronger inference. Chi-square analysis showed that four of the five major species were disproportionately found on mounds (Table 1), and this was a particularly strong finding for mid-successional *B. lenta* and early-successional *B. papyrifera*. *Fagus grandifolia* and *T. canadensis* rarely grew in pits. *A. rubrum*, however, showed no preferred location by microsite (Fig. 5c). Although pre-1938 mounds covered a very small percent of the surface area of the Pisgah transects (0.6%) and therefore expected and observed numbers by species were too low to make strong inference, the data suggest larger-than-expected numbers of late-successional *F. grandifolia* and *T. canadensis* on pre-1938 mounds.

### 3.4. Growth and survival of trees on pits and mounds

In the pulldown, neither mean tree diameter nor mean diameter growth from 2010 to 2015 differed notably among trees growing on mounds, pits and other substrates (Table 2). Mortality rate of recruits found on pits and mounds (4.4% and 4.2%, respectively) was higher than the overall mortality rate (2.7%) during this five-year period; however, a chi-square test comparing the observed versus the expected number of deaths failed to reject the null hypothesis that mortality was the same across substrates ( $\chi^2 = 3.94$ ;  $p = 0.14$ ).

A similar assessment over 20 years (1989–2009) at the Pisgah transects showed higher annual mortality rate on mounds and pits



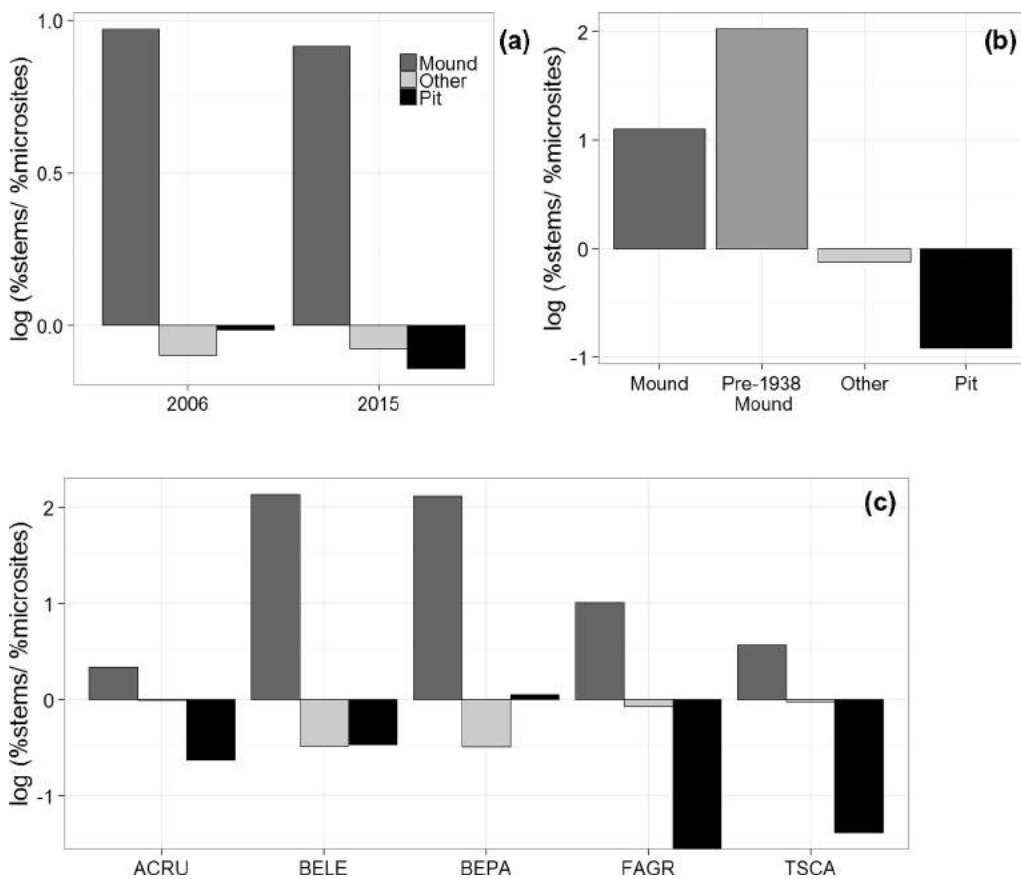


Fig. 5. Visualization of expected versus observed substrate utilization using a distribution index: values > 0 indicate more stems than expected; values < 0 indicate fewer stems than expected. This is shown for all tree recruits in the pulldown in 2006 and 2015 (a), all trees ≥ 5 cm dbh in 1989 at Pisgah (b), and for the five most common tree species at Pisgah in 1989 (c). ACRU = *Acer rubrum*; BELE = *Betula lenta*; BEPA = *B. papyrifera*; FAGR = *Fagus grandifolia*; TSCA = *Tsuga canadensis*.

(3.0% and 2.7%, respectively) than the overall mortality rate (1.9%). A chi-square test comparing the observed versus the expected number of deaths supported the hypothesis that mortality was higher on pits and mounds compared to other substrates ( $X^2 = 13.58$ ;  $p = 0.004$ ). Comparison of mean tree diameter by substrate at Pisgah is confounded by the fact that stems on mounds and pits mainly recruited after the 1938 hurricane, whereas stems on pre-1938 mounds and other microsites may pre-date the hurricane. Whether because of age or substrate, the data suggest larger stems and faster growth on pre-1938 mounds, and smaller stems and slower growth in pits (Table 2).

#### 4. Discussion

The pulldown and Pisgah studies at Harvard Forest offer an uncommon opportunity to explore the main objectives of this paper: (1)

examine the implications of forest history and structure on pit-mound size, distribution, and longevity, and (2) assess how trees utilize the pit-mound microsites in terms of regeneration, growth, and survival, and how this differs in old-growth versus second-growth forest. Although the two studies were not designed as a comparison, with care we can draw insights about how an important feature of old-growth forests – pit and mound microtopography – differs in structure and function in the second-growth forests of the northeastern U.S.

##### 4.1. Pit-mound dynamics in old-growth and second-growth forest

Through repeated measurements of 100 pit-mound structures 0, 15 and 25 years after uprooting, this study adds to our understanding of pit-mound size structure, erosion, and longevity. The amount of forest floor affected by the manipulation in the second-growth pulldown

Table 2

Size, growth and mortality of trees ≥ 5 cm DBH at the pulldown (2010–2015) and Pisgah (1989–2009). The pulldown sample includes only trees that were < 5 cm DBH prior to or germinated after the manipulation, whereas the Pisgah sample includes all stems ≥ 5 cm DBH.

Pulldown						
Substrate	Mean DBH 2015 (cm)	Mean growth 2010–2015 (cm)	N 2010	N died, 2010–2015	Expected dead	Annual mortality rate (%)
Mound	9.8	0.8	89	17	11	4.2
Pit	10.2	0.8	20	4	3	4.4
Other	9.7	0.8	600	71	78	2.5
Pisgah						
Substrate	Mean DBH 2009 (cm)	Mean growth 1989–2009 (cm)	N 1989	N died, 1989–2009	Expected dead	Annual mortality rate (%)
Mound	14.5	2.2	161	74	51	3.0
Old mound	17.7	3.0	57	20	18	2.1
Pit	9.9	1.7	12	5	4	2.6
Other	16.1	2.6	1022	295	322	1.7

(8.3%) was in the range of what other studies have found from a single uprooting event in northeastern U.S. forests (Stephens, 1956; Sobhani et al., 2014). Over 25 years the combined pit-mound surface area declined very little, but mounds and pits exhibited opposing trajectories. Mounds spread out as they eroded, whereas pits shrank as they filled in over time. Mound height declined rapidly; by year 25 mounds that had previously reached a maximum of 2.9 m tall were all less than 1 m in height. If mound height and volume erosion continues at the same rate as in the first 25 years, mound longevity would be less than expected based on past studies (e.g. Stephens, 1956). We will monitor these pit-mounds and expect height erosion to slow later in mound development, as shown by Small (1997).

The pit-mounds in the old-growth forest at Pisgah, 50 years after the 1938 hurricane, covered a similar amount of area as those in the pulldown 25 years after treatment. At Pisgah, the lasting prominence of these microtopographic structures in terms of mound height and pit depth is likely a simple function of the very large trees (some > 75 cm dbh) blown down (D'Amato et al., 2017). Since tree diameter is a strong predictor of pit-mound size, and tree size is inversely related to stand density (Oliver and Larson, 1996), the smaller trees uprooted in second-growth forest produce more, smaller pit-mound structures that exhibit shorter persistence on the landscape. Although the pulldown data suggested that tall mounds eroded proportionately more rapidly than small mounds, very large mounds will simply take longer to disappear.

In addition to differences in tree size between the two sites, erosion rate may differ due to the presence of large old-growth *P. strobus* at Pisgah. The heartwood of old-growth *P. strobus* is extremely decay resistant (D'Amato et al., 2017) and in similar fashion the root plates of uprooted *P. strobus* were still intact on many of the large mounds at Pisgah (Plate 1), even after more than 75 years. The persistence of these immense root structures clearly plays a critical role in maintaining mound structure and size over the decades. The extreme decay resistance of white pine roots has been noted previously (cf. Henry Thoreau (Foster, 1999), Beatty and Stone 1986), but we know of no studies that have explicitly compared longevity or ecological function of pit-mounds generated by different species. Despite variation in root structure among sites and species, Sobhani et al. (2014) found that tree diameter alone predicted mound or pit area across 10 sites that included a variety of hardwoods and conifers. We, too, detected no difference in the relationship between tree diameter and mound or pit size for the few *P. strobus* in the pulldown versus the hardwoods, but we would expect species-specific differences to manifest over time given differential decay rates of roots and boles. This would be particularly true in an old-growth forest composed of old trees with decay resistant heartwood. The set of 100 pit-mounds we tracked in the pulldown did not include *P. strobus*.

Other estimates of pit-mound longevity vary widely: Putz (1983) estimated pit-mound longevity of only about 10 years in one tropical forest, resulting in < 0.1% of the ground surface covered by recognizable pits and mounds. At the other extreme, Stephens (1956) and Samonil et al. (2013) used multiple lines of evidence to date individual pit-mound structures to hundreds and thousands of years old in temperate forests. Evidence from many temperate forests (summarized in Schaeztl and Follmer, 1990) supports mound longevity of 300–500+ years, suggesting that erosion is a non-linear process over longer time periods than the 25 year span examined in this study. Even after mounds and pits erode to the point that they are no longer apparent on the forest floor they can exert persistent effects on soil development and turnover (Stephens, 1956; Veneman et al., 1984; Lenart et al., 2010) and forest vegetation dynamics.

#### 4.2. Ecological role of pit-mound structures in tree recruitment, growth, and survival

After wind disturbance, disruption of the forest floor layer is largely limited to where trees uproot, unless there is subsequent salvage

logging. Despite 80% canopy damage in the simulated hurricane experiment, and > 90% destruction of large trees at Pisgah in 1938, these disturbances affected less than 10% of the forest floor. For many ground layer species, including tree seedlings, the presence of exposed mineral soil and local disruption of understory vegetation exerts a strong influence on their establishment (Peterson and Campbell, 1993; Roberts, 2004), so the forest floor affected by uprooting serves as a focal area for change following wind disturbance.

Mounds offered a favorable microsite for early and mid-successional tree species to colonize following wind disturbance at both sites. In contrast to some studies (e.g. Peterson and Pickett, 1990; Vodde et al., 2015), pits were unfavorable sites for tree regeneration, especially at Pisgah. Only *A. rubrum*, which has a broad ecological niche (Abrams, 1998), did not discriminate among microsites.

At both Pisgah and the pulldown, mounds were particularly important for *Betula* regeneration, as documented in other studies (Hutnik, 1952; Henry and Swan, 1974; Carlton and Bazzaz, 1998a). We confirmed that *Betula* stems that recruited into the small tree ( $\geq 5$  cm dbh) size class were disproportionately located on mound microsites after 25 (pulldown) and 50 (Pisgah) years. At the pulldown, mounds were less critical for *B. lenta* because there was abundant *B. lenta* advance regeneration at this site prior to the disturbance (Barker Plotkin et al., 2013). At Pisgah, more than 40% of the early-successional *B. papyrifera* and mid-successional *B. lenta* stems were located on mounds, although mounds comprised less than 5% of the plot area. This finding corroborates other studies noting a strong association between mounds and pioneer species (e.g., Peterson and Carson, 1996). As a mechanism to increase stand-level tree diversity, windthrow may be more critical in old-growth forests, in which niches for early-mid successional species are few, than in second-growth forest, in which early-mid successional species already comprise the majority of the trees.

At Pisgah, pre-1938 mounds covered a small portion of the forest floor. These sites were even more highly favorable microsites for tree regeneration than mounds created in 1938. Although the sample size of trees growing on pre-1938 mounds was small, the data available suggest that late-successional trees (*F. grandifolia*, *T. canadensis*) disproportionately grew on this substrate, perhaps because a more developed litter layer overlaying these raised substrates favors these species. The presence of multiple cohorts of mounds adds niche diversity to forests over time.

Unlike Lyford and MacLean (1966), who found larger trees on mounds than on intact microsites, we found no strong difference in tree size or growth rate of stems among substrates. However, mortality rate for trees growing on mounds at Pisgah was higher than on the ground due to structural failure of perched root systems. We observed trees fallen from mounds at both sites. At Pisgah, many of the *Betula* stems growing on mounds have complex, perched root systems (Plate 2).

The boles of uprooted trees may be another substrate favored for regeneration. These 'nurse logs' are documented in North America (Pacific Northwest, Harmon et al., 1986; northern hemlock-hardwood forests of the Upper Midwest, Marx and Walters, 2008), and Asian cool and subalpine zones (e.g. Takahashi et al., 2000) but did not play a role at the sites in this study. At the pulldown, we observed very few tree seedlings (and no saplings or tree recruits) on downed boles. This could be a function of the species and early stage of decay of the logs at this site. Yet, Schoonmaker (1992) found that the downed logs at Pisgah, including many well-decayed *T. canadensis*, supported fewer trees than would be expected given the area they occupied.

The size structure of mounds in old-growth versus second-growth forest may affect their ecological function. Taller mounds may provide protection to tree regeneration that shorter mounds (typically generated by younger forest) cannot. For example, Krueger and Peterson (2006) found that *T. canadensis* seedlings growing on mounds were protected from browsing. Typical browsing height for white-tailed deer (*Odocoileus virginianus*) is 1.8 m (Frerker et al., 2013), so mounds less than this height would provide limited browsing protection. Similarly,





**Plate 2.** *Betula lenta* stems are often seen precariously perched on mounds, as seen in this photo from the Pisgah site in 2009, 71 years after the hurricane.

Nakashizuka (1989) found that tree regeneration was concentrated on mounds in forests with a thick understory of dwarf bamboo (*Sasa kurilensis*). The bamboo layer can be up to 2 m tall (Nakashizuka, 1988), so taller mounds would provide greater competitive advantage.

## 5. Conclusions

Not only has the agricultural legacy of New England erased many of the pit-mound features of the forest, but the smaller size of trees in the modern forest limits the size and longevity of new pit-mound structures. The main difference between old-growth and second-growth pit-mound structures is size, and by extension, persistence. At the Pisgah site, the supercanopy (in life) and relatively decay-resistant (in death) *P. strobus* may also contribute to exceptional size and persistence of the pit-mound structures there. The ecological functions of pit-mound microtopography appear to be similar in second-growth and old-growth forest, at least in terms of tree establishment and growth. Yet, the early-successional habitat that pit-mounds provide is more important to niche diversity in old-growth than in second-growth forest.

Silvicultural techniques designed to enhance late-successional attributes (Franklin et al., 2002; Keeton, 2006; Bauhus et al., 2009) already emphasize promoting large-diameter dead wood and limiting salvage harvest. Additional actions to preserve pit-mound microtopography could include avoiding driving machinery over uproot mounds, as salvage logging after windstorms can destroy pit and mound features (Waldron et al., 2013, but see Peterson and Leach, 2008). In addition, the active creation of pit-and-mound conditions by pulling down trees with harvesting equipment may be an option for restoring these structures to second-growth forests. Only by allowing some forests to develop large-stemmed trees will correspondingly large pit-mound structures be replenished.

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## References

- Abrams, M.D., 1998. The red maple paradox. *Bioscience* 48, 355–364.
- Barker Plotkin, A., Foster, D.R., Carlson, J., Magill, A.H., 2013. Survivors, not invaders, control forest development following simulated hurricane. *Ecology* 94, 414–423.
- Bauhus, J., Puettmann, K., Messier, C., 2009. Silviculture for old-growth attributes. *For. Ecol. Manage.* 258, 525–537.
- Beatty, S.W., Stone, E.L., 1984. The variety of soil microsites created by tree falls. *Can. J. For. Res.* 16, 539–548.
- Boose, E.R., Chamberlin, K.E., Foster, D.R., 2001. Landscape and regional impacts of hurricanes in New England. *Ecol. Monogr.* 71, 27–48.
- Branch, W.C., Daley, R.K., Lotti, T., 1930. Life history of the climax forest on the Pisgah Tract, Winchester. Harvard University, New Hampshire.
- Carlton, G.C., Bazzaz, F.A., 1998a. Regeneration of three sympatric birch species on experimental hurricane blowdown microsites. *Ecol. Monogr.* 68, 99–120.
- Carlton, G.C., Bazzaz, F.A., 1998b. Resource congruence and forest regeneration following an experimental hurricane blowdown. *Ecology* 79, 1305–1319.
- Cline, A.C., Spurr, S.H., 1942. The virgin upland forest of central New England: a study of old growth stands in the Pisgah mountain section of southwestern New Hampshire. Harvard Forest, Bulletin No, pp. 21.
- Cooper-Ellis, S., Foster, D.R., Carlton, G., Lezberg, A.L., 1999. Forest response to catastrophic wind: results from an experimental hurricane. *Ecology* 80, 2683–2696.
- Dahir, S.E., Lorimer, C.G., 1996. Variation in canopy gap formation among developmental stages of northern hardwood stands. *Can. J. For. Res.* 26, 1875–1892.
- D'Amato, A.W., Orwig, D.A., Foster, D.R., Barker Plotkin, A., Schoonmaker, P.K., Wagner, M.R., 2017. Long-term structural and biomass dynamics of virgin *Tsuga canadensis*-*Pinus strobus* forests after hurricane disturbance. *Ecology* 98 (3), 721–733.
- DeGraaf, R.M., Yamasaki, M., 2001. New England wildlife: Habitat, natural history and distribution. Univ. Press of New England, Hanover, NH, pp. 482.
- Foster, D.R., 1988a. Disturbance history, community organization and vegetation dynamics of the old-growth Pisgah Forest, southwestern New Hampshire, U.S.A. *J. Ecol.* 76, 105–134.
- Foster, D.R., 1988b. Species and stand response to catastrophic wind in central New England, USA. *J. Ecol.* 76, 135–151.
- Foster, D.R., 1999. Thoreau's Country: Journey Through a Transformed Landscape. Harvard University Press, Cambridge, MA.
- Foster, D.R., Aber, J.D., 2004. Forests in Time: The Environmental Consequences of 1000 Years of Change in New England. Yale University Press, New Haven, CT.
- Foster, D.R., Baiser, B., Barker Plotkin, A., D'Amato, A.W., Ellison, A.M., Orwig, D.A., Oswald, W.W., Thompson, J.R., 2014. Hemlock: A Forest Giant on the Edge. Yale University Press, Yale University.
- Foster, D.R., Knight, D., Franklin, J.F., 1998. Landscape patterns and legacies resulting from large infrequent disturbances. *Ecosystems* 1, 497–510.
- Franklin, J.F., Spies, T.A., Van Pelt, R., Carey, A.B., Thornburgh, D.A., Berg, D.R., Lindenmayer, D.B., Harmon, M.E., Keeton, W.S., Shaw, D.C., Bible, K., Chen, J., 2002. Disturbances and structural development of natural forest ecosystems with silvicultural implications, using Douglas-fir forests as an example. *For. Ecol. Manage.* 155 (2002), 399–423.
- Frerker, K., Sonnier, G., Waller, D.M., 2013. Browsing rates and ratios provide reliable indices of ungulate impacts on forest plant communities. *For. Ecol. Manage.* 291, 55–64.
- Harmon, M.E., Franklin, J.F., Swanson, F.J., Sollins, P., Gregory, S.V., Lattin, J.D., Anderson, N.H., Cline, S.P., Aumen, N.G., Sedell Jr., J.R., Lienkaemper, G.W., Cromack, K., Cummins, K.W., 1986. Ecology of coarse woody debris in temperate ecosystems. *Adv. Ecol. Res.* 15, 133–302.
- Henry, J.D., Swan, J.M.A., 1974. Reconstructing forest history from live and dead plant material – an approach to the study of forest succession in southwest New Hampshire. *Ecology* 55, 772–783.
- Huenneke, L.F., Sharitz, R.R., 1986. Microsite abundance and distribution of woody seedlings in a South Carolina cypress-tupelo swamp. *Am. Midl. Nat.* 115, 328–335.
- Hutnick, R.J., 1952. Reproduction on windfalls in a northern hardwood stand. *J. Forest.* 50, 693–694.
- Ishii, H.T., Tanabe, S., Hiura, T., 2004. Exploring the Relationships Among Canopy Structure, Stand Productivity, and Biodiversity of Temperate Forest Ecosystems. *Forest Science* 50, 342–355.
- Keeton, W.S., 2006. Managing for late-successional/old-growth characteristics in northern hardwood-conifer forests. *For. Ecol. Manage.* 235, 129–142.

- Kooh, Y., Darabi, S.M., Hosseini, S.M., 2015. Effects of pits and mounds following windthrow events on soil features and greenhouse gas fluxes in a temperate forest. *Pedosphere* 25, 853–867.
- Krueger, L., Peterson, C.J., 2006. Effects of white-tailed deer on *Tsuga canadensis* regeneration: evidence of microsites as refugia from browsing. *Am. Midl. Nat.* 156, 353–362.
- Lenart, M.T., Falk, D.A., Scatena, F.N., Osterkamp, W.R., 2010. Estimating soil turnover rate from tree uprooting during hurricanes in Puerto Rico. *For. Ecol. Manage.* 259, 1076–1084.
- Lyford, W.H. and D.W. MacLean. 1966. Mound and pit microrelief in relation to soil disturbance and tree distribution in New Brunswick, Canada. *Harvard Forest Paper No. 15*, Petersham, MA.
- Marx, L., Walters, M.B., 2008. Survival of tree seedlings on different species of decaying wood maintains tree distribution in Michigan hemlock-hardwood forests. *J. Ecol.* 96, 505–513.
- Millikin, C.S., Bowden, R.D., 1996. Soil respiration in pits and mounds following an experimental hurricane. *Soil Sci. Soc. Am. J.* 60, 1951–1953.
- Nakashizuka, T., 1988. Regeneration of beech (*Fagus crenata*) after the simultaneous death of undergrowing dwarf bamboo (*Sasa kurilensis*). *Ecol. Res.* 3, 21–35.
- Nakashizuka, T., 1989. Role of uprooting in composition and dynamics of an old-growth forest in Japan. *Ecology* 70, 1273–1278.
- Norman, S.A., Schatzl, R.J., Small, T.W., 1995. Effects of slope angle on mass movement by tree uprooting. *Geomorphology* 14, 19–27.
- Oliver, C.D., 1980. Even-aged development of mixed-species stands. *J. Forest.* 78, 201–203.
- Oliver, C.D., Larson, B.C., 1996. *Forest Stand Dynamics*, Update Edition. John Wiley & Sonspp. 520.
- Peterson, C.J., Campbell, J.E., 1993. Microsite differences and temporal change in plant communities of treefall pits and mounds in an old-growth forest. *Bull. Torrey Bot. Club* 120, 451–460.
- Peterson, C.J., Carson, W.P., 1996. Generalizing forest regeneration models: the dependence of propagule availability on disturbance history and stand size. *Can. J. For. Res.* 26, 45–52.
- Peterson, C.J., Leach, A.D., 2008. Salvage logging after windthrow alters microsite diversity, abundance and environment, but not vegetation. *Forestry* 81, 361–376.
- Peterson, C.J., Pickett, S.T.A., 1990. Microsite and elevational influences on early forest regeneration after catastrophic windthrow. *J. Veg. Sci.* 1, 657–662.
- Putz, F.E., 1983. Treefall pits and mounds, buried seeds, and the importance of soil disturbance to pioneer trees on Barro Colorado Island, Panama. *Ecology* 64, 1069–1074.
- R Core Team (2016). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org/>.
- Roberts, M.R., 2004. Response of the herbaceous layer to natural disturbance in North American forests. *Can. J. Bot.* 82, 1273–1283.
- Runkle, J.R., 2000. Canopy tree turnover in old-growth mesic forests of eastern North America. *Ecology* 81, 554–567.
- Samonil, P., Schatzl, R.J., Valtera, M., Golias, V., Baldrian, P., Vasickova, I., Adam, D., Janik, D., Hort, L., 2013. Crossdating of disturbances by tree uprooting: can tree-throw microtopography persist for 6000 years? *For. Ecol. Manage.* 307, 123–135.
- Schatzl, R.J., Follmer, L.R., 1990. Longevity of tree-throw microtopography: implications for mass wasting. *Geomorphology* 3, 113–123.
- Schoonmaker, P.K., 1992. *Long-term vegetation dynamics in southwestern New Hampshire*. Thesis, Harvard University.
- Small, T.W., 1997. The Goodlett-Denny mound: a glimpse at 45 years of Pennsylvania tree-throw mound evolution with implications for mass wasting. *Geomorphology* 18, 305–313.
- Sobhani, V.M., Barrett, M., Peterson, C.J., 2014. Robust prediction of treefall pit and mound sizes from tree size across 10 forest blowdowns in eastern North America. *Ecosystems* 17, 837–850.
- Stephens, E.P., 1956. The uprooting of trees: a forest process. *Proc. Soil Sci. Soc. Am.* 20, 113–116.
- Takahashi, M., Sakai, Y., Ootomo, R., Shiozaki, M., 2000. Establishment of tree seedlings and water-soluble nutrients in coarse woody debris in an old-growth *Picea-Abies* forest in Hokkaido, northern Japan. *Can. J. For. Res.* 30, 1148–1155.
- Veneman, P.L.M., Jacke, P.V., Bodine, S.M., 1984. Soil formation as affected by pit and mound microrelief in Massachusetts, USA. *Geoderma* 33, 89–99.
- Vodde, F., Jogiste, K., Engelhart, J., Frelich, L.E., Moser, W.K., Sims, A., Metslaid, M., 2015. Impact of wind-induced microsites and disturbance severity on tree regeneration patterns: results from the first post-storm decade. *For. Ecol. Manage.* 348, 174–185.
- Von Oheimb, G., Friedel, A., Bertsch, A., Hardtle, W., 2007. The effects of windthrow on plant species richness in a Central European beech forest. *Plant Ecol.* 191, 47–65.
- Waldron, K., Ruel, J.-C., Gauthier, S., 2013. Forest structural attributes after windthrow and consequences of salvage logging. *For. Ecol. Manage.* 289, 28–37.