

Long-term influence of disturbance-generated microsites on forest structural and compositional development

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Abstract: Wind disturbance generates heterogeneous microsite structures, including downed logs, windthrow mounds, and pits. While these structures can provide opportunities for regeneration of certain tree species, the long-term influence of microsites and microsite heterogeneity on forest development has not been quantified. We used long-term measurements of a formerly old-growth *Tsuga canadensis* – *Pinus strobus* forest severely damaged by a category 3 hurricane in 1938 to quantify the impact of microsite conditions on overstory composition and structure. We asked (i) “What are the patterns in live-tree size, growth, and mortality five and seven decades after disturbance?” and (ii) “What roles do microsite heterogeneity and the presence of disturbance-generated microsites play in long-term forest development following disturbance?” We compared live-tree (>2 cm DBH) development and survival to microsite heterogeneity at the 100 m² scale. Microsite diversity was positively related to overstory species diversity and stem density and negatively related to average tree size. We propose that plots with higher microsite diversity may have experienced more severe local disturbance, which allowed more species and individuals to establish and created varied niches that allowed these individuals to coexist and generate greater stand-level diversity. These persistent relationships highlight how microsite conditions affect forest development after severe disturbances.

Key words: downed woody debris, hemlock–pine forest, heterogeneity, large, infrequent disturbance, pit-and-mound microtopography.

Résumé : Les perturbations causées par le vent produisent des structures hétérogènes de microsite, ce qui inclut des troncs d'arbre au sol de même que des monticules et des dépressions créés par les chablis. Bien que ces structures soient des occasions de régénération pour certaines espèces d'arbre, l'influence à long terme des microsites et de leur hétérogénéité sur le développement des forêts n'a pas été quantifiée. Nous avons utilisé des mesures prises sur une longue période dans une vieille forêt initialement composée de *Tsuga canadensis* et de *Pinus strobus*, qui a été fortement endommagée par un ouragan de catégorie 3 en 1938, pour quantifier l'impact des conditions de microsite sur la composition et la structure du couvert dominant. Nous voulions savoir (i) quels étaient les patrons de taille, de croissance et de mortalité des arbres 50 et 70 ans après la perturbation et (ii) quel rôle ont joué la présence et l'hétérogénéité des microsites produits par la perturbation sur le développement à long terme de la forêt à la suite de la perturbation. Nous avons analysé le développement et la survie des arbres (>2 cm de DHP) en fonction de l'hétérogénéité des microsites à une échelle de 100 m². La diversité des microsites était positivement reliée à la diversité des espèces du couvert dominant et à la densité des tiges, et elle était négativement reliée à la taille moyenne des arbres. Nous croyons que les placettes associées à une plus grande diversité de microsites peuvent avoir subi une perturbation locale plus forte, ce qui a permis l'établissement d'un plus grand nombre d'espèces et d'individus, et que la variété de niches a permis à ces individus de coexister et de produire une plus grande diversité à l'échelle du peuplement. Ces relations persistantes mettent en évidence la façon dont les conditions de microsite influencent le développement des forêts après de fortes perturbations. [Traduit par la Rédaction]

Mots-clés : débris ligneux au sol, forêt de pruche et de pin, hétérogénéité, perturbation de grande taille peu fréquente, microtopographie formée de dépressions et de monticules.

Introduction

Disturbance is a key driver of forest composition and structural dynamics, as resources are made available for species establishment or release following a disturbance event (Pickett and White 1985; Turner 2010). Distinct microsite structures are created by different disturbance agents (Foster 1988b; McRae et al. 2001), which further influences patterns of tree recruitment and forest

development (Vodde et al. 2010). Disturbance-generated microsites are directly linked to recruitment of particular tree species (Lyford and MacLean 1966) and habitat for several wildlife species (Nappi et al. 2003), and there has been an increasing emphasis on assessing the long-term influence of these disturbance-generated microsites on forest development and patterns of diversity (Roberts 2004).

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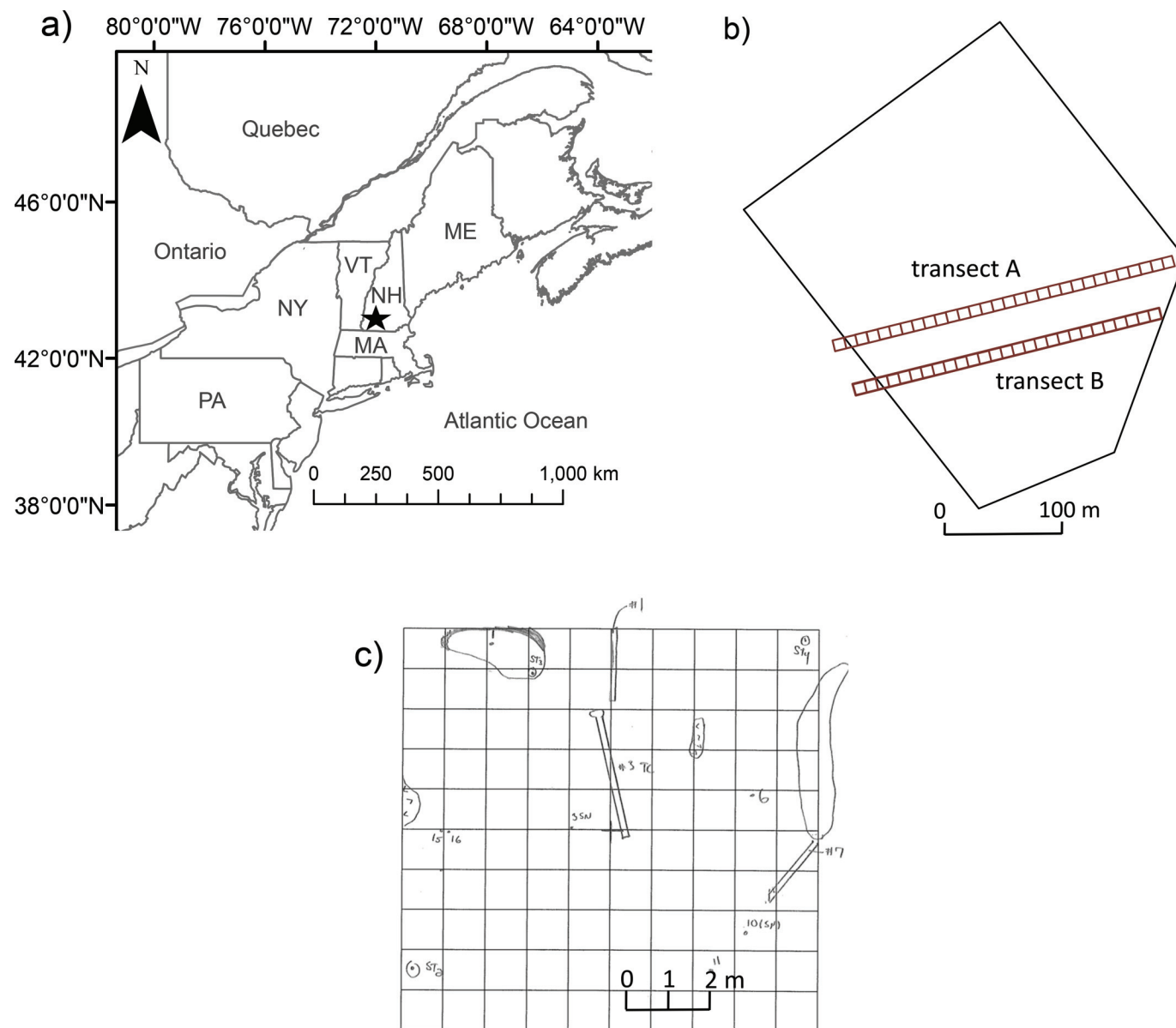
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Fig. 1. (a) The Harvard Tract is located in southwestern New Hampshire, USA. (b) In 1989, two transects running east–west were established across the Harvard Tract. Each square represents a 10×10 m plot within the transect. (c) At each 10×10 m plot, microsites and live and dead trees were mapped onto a 1×1 m grid. [Colour online.]



Windstorms, including hurricanes, downbursts, and tornadoes, are a major forest disturbance worldwide (Everham and Brokaw 1996) that leave a mosaic of surviving, uprooted, and broken trees (Prengaman et al. 2008). Pit-and-mound microtopography created by uprooting of large trees during windstorms can persist for decades to centuries (Ulanova 2000), with some age estimates exceeding 1000 years (Schaetzl and Follmer 1990). These structures influence tree establishment patterns, with trees in some systems tending to grow on mounds and avoiding pits (Lyford and MacLean 1966). Several early- and mid-successional species preferentially establish on mounds due to exposed mineral soil seedbed conditions and reduced competition from advance regeneration found in undisturbed forest floor areas (Carlton and Bazzaz 1998); others establish preferentially in pits due to higher moisture and deeper soil (Peterson and Pickett 1990). Pit-and-mound microtopography can further alter the composition of developing forests through moderation of temperature and moisture gradients on the forest floor (Peterson et al. 1990), retention of lower leaf litter, and main-

tenance of greater snow depths (Beatty 1984; Ulanova 2000). They also increase microhabitat heterogeneity, which results in a greater diversity of regeneration niches and, subsequently, higher species diversity (Jonsson and Esseen 1990).

Large volumes of downed woody material (DWM) are also often generated during windstorms from uprooting or snapping, and these structures can persist for decades (Fraver et al. 2013). In some systems, DWM supports higher seedling establishment rates than other substrates, especially larger diameter pieces in advanced stages of decay (Chečko et al. 2015). Certain tree species preferentially regenerate on DWM, particularly genera with smaller seeds such as *Picea* (Chečko et al. 2015) and *Betula* (Bolton and D'Amato 2011). The presence of DWM on a site can also moderate temperature and moisture conditions experienced by seedlings, as well as potentially protect them from herbivory, allowing higher survival of sheltered seedlings (Gray and Spies 1997).

Despite the well-documented importance of disturbance-generated microsites on seedling establishment, little is known about how

patterns and variability in such microsites affect long-term development of stand structure and composition. This study takes advantage of a unique, long-term dataset that follows the development of a formerly old-growth *Tsuga canadensis* (eastern hemlock) – *Pinus strobus* (white pine) forest between five and seven decades following a stand-replacing hurricane in the northeastern US. Specifically, we ask “What are the patterns in live-tree size distributions, mortality, and growth five and seven decades after disturbance?” and “What roles do microsite heterogeneity and the presence of different microsites play in the long-term stand development following disturbance?” To our knowledge, this study is the longest direct analysis of the effects of microsite heterogeneity on forest stand development.

Materials and methods

Field site

This study was conducted at the Harvard Tract within Pisgah State Park in southwestern New Hampshire, USA, within the Northern Hardwoods – Hemlock – White Pine ecoregion (Griffith et al. 2009; Fig. 1a). This area was historically dominated by old-growth mixed eastern hemlock and white pine forests (Cline and Spurr 1942); however, much of this forested landscape was severely impacted by a category 3 hurricane in 1938. Prior to 1938, the Harvard Tract was dominated by large (75–100 cm diameter at breast height, DBH) *Tsuga canadensis* (L.) Carrière and *Pinus strobus* L. Almost all of the mature trees at the Harvard Tract were destroyed by the 1938 hurricane (Cline and Spurr 1942), leaving only five live and 10 standing dead, large *Tsuga canadensis* and *Pinus strobus* across the 10 ha Tract in 1984 (Foster 1988a). This stand subsequently developed into the contemporary forest dominated by eastern hemlock with lesser amounts of red maple (*Acer rubrum* L.), black birch (*Betula lenta* L.), and American beech (*Fagus grandifolia* Ehrh.; D’Amato et al. 2017). The soil is podzolic, with 5–10 cm of organic material over schist, granite, and gneiss bedrock (Rosenberg 1989). A north–south trending ridge bisects the site, with elevation ranging from about 200 to 400 m a.s.l. (Cline and Spurr 1942).

Field methods

Data were collected from two east–west transects within the Harvard Tract to capture forest conditions across the topographic variability of the site. From 1985 to 1989, Schoonmaker (1992) collected detailed spatial data on live and dead trees, microsites, site topography, and downed deadwood across these transects, which were 10 m × 270 m and 10 m × 300 m and spaced 20 m apart (Fig. 1b). Each transect was divided into contiguous 10 × 10 m plots that were further subdivided into 1 × 1 m grids for recording fine-scale variability in microsite conditions (Schoonmaker 1992; Fig. 1c). Seedlings are influenced by finer scale dynamics than overstory trees, but due to this study’s focus on established trees, we analyzed dynamics at the 10 × 10 m plot level. Within each plot, species and DBH were recorded for all live trees ≥ 2 cm DBH in 1989 (Schoonmaker 1992). Trees were re-inventoried in 2009, and new trees ≥ 2 cm DBH were documented (D’Amato et al. 2017). Substrate within each 1 × 1 m grid was divided into seven categories in 1989: windthrow mounds, mounds of unknown origin, pits, logs, stumps, thin soil, and bare rock, with areal coverage of each category recorded and mapped on the grid. Area not in these categories was categorized as undisturbed ground. Bare rock was not included in our analyses because the focus of this work was on evaluating disturbance-generated substrate conditions, and the occurrence of this substrate type was directly related to topographic position (i.e., on the ridge tops).

Data manipulation

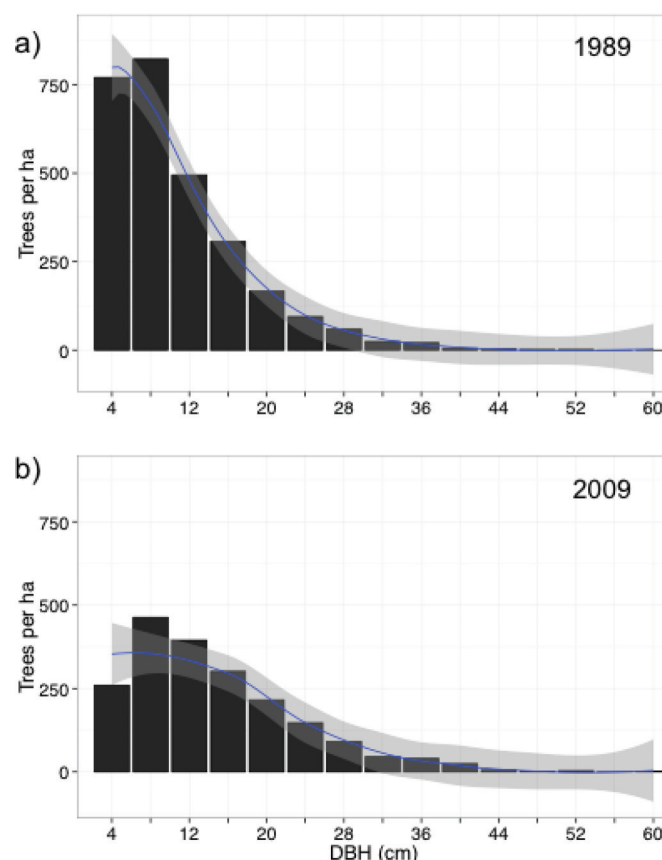
Microsite diversity, tree species diversity, and live-tree size diversity were calculated using Shannon’s diversity index (H) at the plot level (10 × 10 m), with the relatively small plot size allowing analysis of these fine-scale processes. Shannon’s diversity index

Table 1. Descriptive summary of stand structure in 1989 and 2009, 51 and 71 years following the hurricane, respectively.

Year	QMD (cm)	Basal area (m ² ·ha ⁻¹)	Density (stems·ha ⁻¹)
1989	14.0±0.6 (7.2–27.9)	36±1 (13–55)	2770±180 (300–6800)
2009	18.0±0.6 (9.8–31.7)	42±2 (16–67)	1710±100 (300–3700)

Note: Each measurement is expressed as mean ± standard error, followed by range in parentheses. QMD, quadratic mean diameter.

Fig. 2. Live-tree diameter distribution (a) 51 and (b) 71 years after hurricane disturbance (1989 and 2009, respectively) at the Harvard Tract in Pisgah State Park, New Hampshire, USA. Trees are binned in 4 cm diameter size classes. Lines and shading represent smoothed conditional means ± standard error for best approximating curve. [Colour online.]

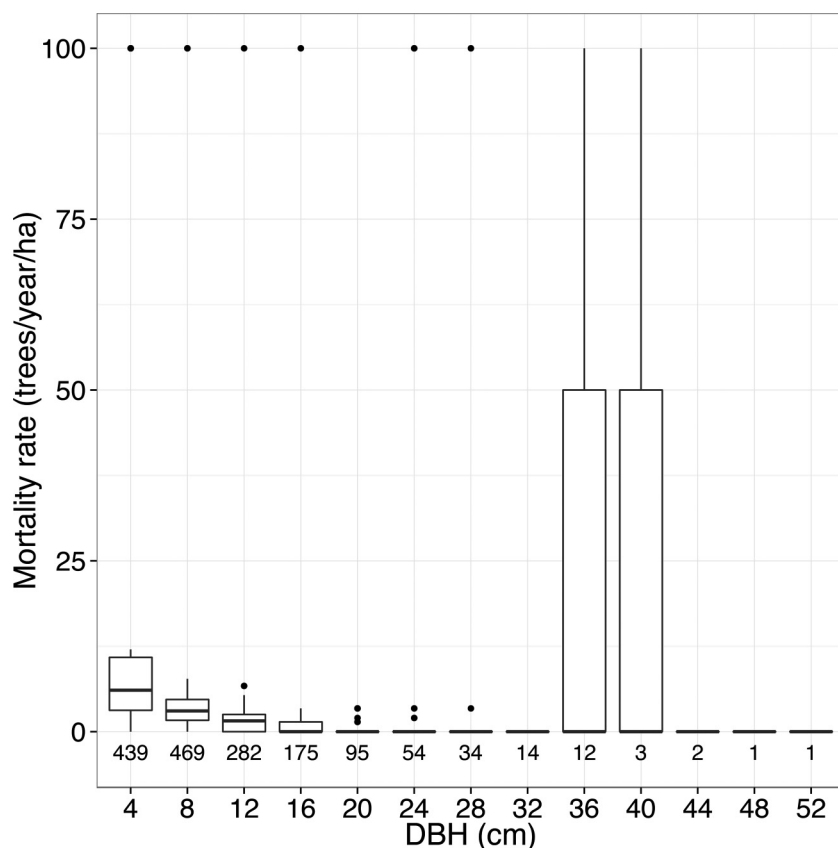


characterizes the richness and evenness of attributes such as species and structures, thereby allowing quantitative comparisons among groups, and has been used to determine alpha diversity of species, stand structure, and other metrics (Brower et al. 1998). For tree size diversity, individual trees were grouped into 4 cm bins. Tree size was calculated as quadratic mean diameter (QMD; Curtis and Marshall 2000). Live-tree biomass was calculated by applying species-specific wood density values (Harmon et al. 2008) to tree volume estimates (Honer 1967; Honer et al. 1983). Net growth increment was defined at the plot level as the total live-tree biomass gained between 1989 and 2009. Mortality rate was calculated following Sheil and May (1996) at the plot level and by diameter class using all live trees present in 1989.

Analyses

The influence of microsite H on forest structural and compositional development was examined using linear mixed-effects models in R (R Core Team 2014) with the package lme (Pinheiro

Fig. 3. Mortality rates between 1989 (51 years after the hurricane) and 2009 by diameter class. Trees are binned in 4 cm size classes. Boxes represent variability in plot-level mortality. Numbers at the base of each bar represent trees present in each size class 51 years after the hurricane.



et al. 2017). Separate models were developed predicting tree species H , tree size H , QMD, stem density, and total basal area as a function of microsite diversity, with year (1989 and 2009) and location along the transect as random effects. Location was added as a random effect to account for the influence of differences in plot characteristics such as elevation, slope, and aspect on patterns in response variables. To further analyze the potential for microsite heterogeneity to influence niche differentiation and the ability of species with different resource needs to coexist, we used linear mixed-effects models to compare the basal area of shade-tolerant, mid-tolerant, and intolerant species to plot-level microsite diversity, with year and location along the transect as random effects. Shade-intolerant species included *Betula papyrifera* Marsh., *Fraxinus americana* L., and *Prunus serotina* Ehrh.; mid-tolerant species included *Betula alleghaniensis* Britton, *Betula lenta*, *Quercus rubra* L., *Pinus strobus*, and *Ulmus americana* L.; and shade-tolerant species included *Acer rubrum*, *Acer saccharum* Marsh., *Fagus grandifolia*, *Ostrya virginiana* (Mill.) K. Koch, *Picea rubens* Sarg., and *Tsuga canadensis*. Normal distributions and Gaussian families were selected for each regression. We used ANCOVA to test for differences in the regression slopes between years. The relationships between mortality rate and microsite H and growth increment and microsite H were examined using linear mixed-effects models (R Core Team 2014; Pinheiro et al. 2017) with location as a random effect, as there was only one value for each plot across the 20 years of the study. The shape of diameter distributions were quantified following Janowiak et al. (2008) using the corrected Akaike's information criterion (AIC_c) to compare models, with the best model

determined as the simplest model within 10 ΔAIC_c units of the lowest AIC_c score.

Results

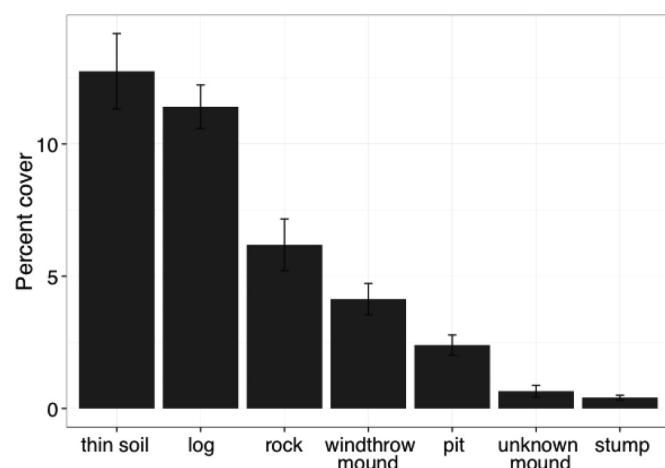
Across both transects, 1581 live trees were measured in 1989 and 974 were measured in 2009. Live-tree size and basal area increased between 1989 and 2009, and density decreased (Table 1). The diameter distribution after 51 years followed a negative exponential curve (Fig. 2a), whereas the distribution followed an increasing- q shape after 71 years, with fewer trees in the smallest size classes (Fig. 2b; Janowiak et al. 2008).

The average plot-level mortality rate ($\pm$ standard error) was 2.2 ± 0.1 trees·ha⁻¹·year⁻¹ and ranged from no mortality to 47 trees·ha⁻¹·year⁻¹. Mortality was highest for trees in the smallest size classes and descended monotonically with increasing size to the 20 cm size class, although there was high variability among plots (Fig. 3). This pattern held for both shade-tolerant and intolerant species groups (Supplementary Fig. S1¹). Growth increment averaged 2.19 ± 0.10 Mg·ha⁻¹·year⁻¹ and ranged from 0.74 to 3.90 Mg·ha⁻¹·year⁻¹ across all plots.

Over half of the ground area within the plots was undisturbed, with the seven measured substrates comprising 38% of the transect area (Fig. 4). Microsite diversity, as measured by Shannon's diversity index (H), was positively related to tree species H (slope estimate = 0.398 ± 0.093 , $t = 4.270$, $p = 0.0001$; Fig. 5a) and tree density (slope estimate = 1065 ± 309 , $t = 3.450$, $p = 0.0011$; Fig. 5b) and negatively related to QMD (slope estimate = -3.773 ± 1.239 ,

¹Supplementary data are available with the article through the journal Web site at <http://nrcresearchpress.com/doi/suppl/10.1139/cjfr-2018-0097>.

Fig. 4. Percent cover of seven microsite categories measured 51 years after the hurricane disturbance (1989) averaged over all plots and both transects. Area not in the seven listed categories was considered undisturbed ground. Note that area in rock was excluded from subsequent analyses.



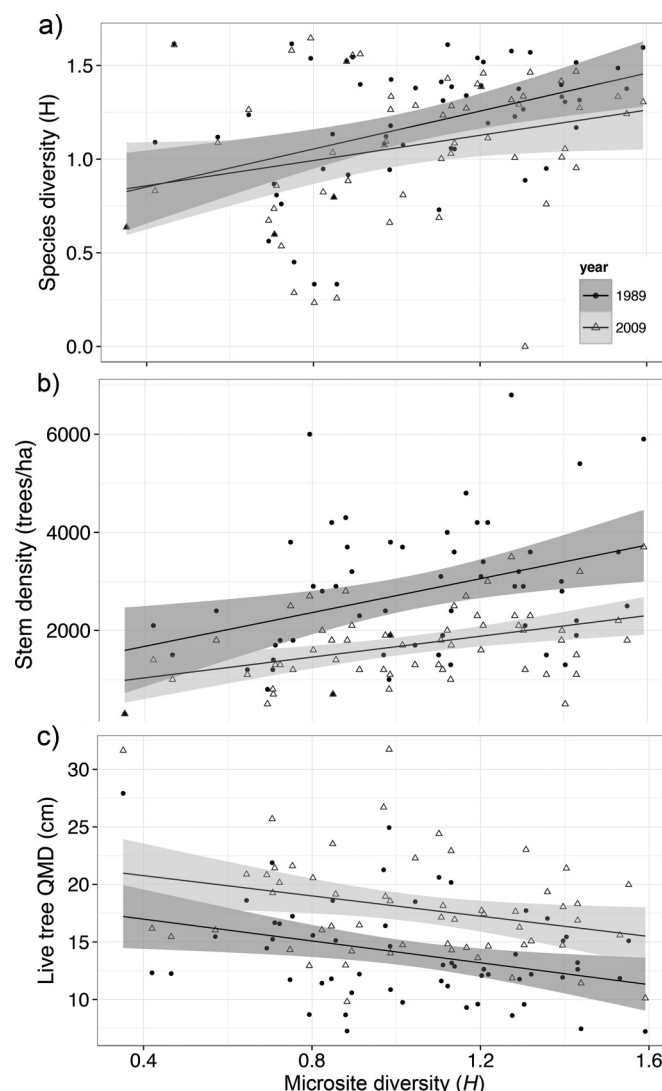
$t = -3.045$, $p = 0.0036$; Fig. 5c). The relationships between microsite diversity and overstory diversity, tree density, and QMD did not differ between years ($p > 0.05$). There was no relationship between microsite H and live-tree size H , mortality rate, basal area, or growth increment ($p > 0.05$). There was no relationship between the basal area of tolerant, mid-tolerant, and intolerant species and microsite H ($p > 0.05$); however, plots in the highest quartile of microsite diversity appeared to have a greater abundance of shade-intolerant species present in the mid-sized classes relative to plots with the lowest microsite diversity (Figs. 6a–6d).

Discussion

Microsite conditions generated by disturbances influence tree species composition of the recovering stand through differential establishment on various substrates, as well as its structural development; however, our understanding of the influence of microsites, including heterogeneity, on these processes has generally been limited to the first few years following disturbance. This study takes advantage of a long-term dataset following a formerly old-growth hemlock–pine stand that was severely damaged in the 1938 hurricane to determine the influence of microsite conditions and heterogeneity on post-disturbance stand development over seven decades. While this study covers only 20 years within the 70-year period since the hurricane, it allows us to investigate forest dynamics for a longer term following natural disturbance.

Microsite diversity had lasting impacts on species diversity, with plots containing higher microsite diversity having more diverse overstory composition five and seven decades following the hurricane, which is consistent with short-term findings from other work (Vodde et al. 2015) and long-term predictions based on niche theory (Grubb 1977). Multiple cohorts of mounds at this site contributed to the diversity of niches, with birch species, in particular, able to recruit on windthrow mounds created in 1938 and *Fagus grandifolia* and *Tsuga canadensis* growing more on mounds created prior to the hurricane (Barker Plotkin et al. 2017). Birch often colonizes windthrow mounds (Hutnik 1952; Carlton and Bazzaz 1998), which may be especially important for maintaining this early-successional species in old-growth forests that do not otherwise have a large component (Barker Plotkin et al. 2017). Other studies have demonstrated the importance of particular microsite structures in promoting coexistence of species that would otherwise disappear from a stand (Čečko et al. 2015), as

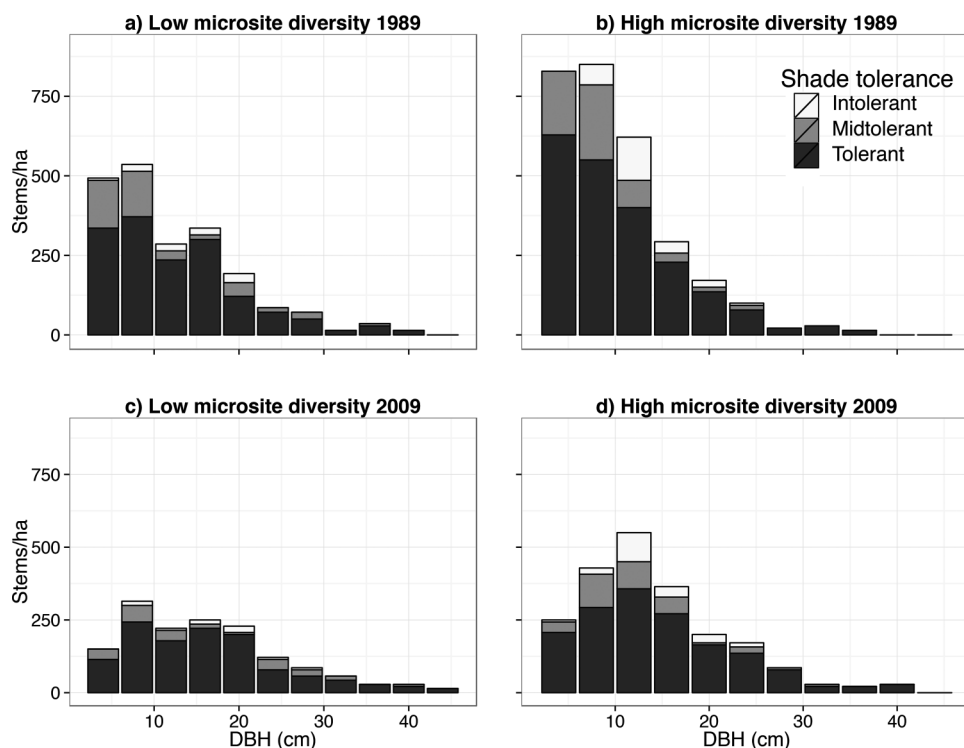
Fig. 5. (a) Tree species diversity, (b) stem density, and (c) average tree size (live-tree QMD) were related to microsite diversity (H) as measured 51 years after the 1938 hurricane (i.e., in 1989) both 51 and 71 years after the hurricane (in 1989 and 2009, respectively). Slopes do not differ between years. Grey shading indicates 95% confidence interval. QMD, quadratic mean diameter.



well as a range of microsite conditions for maintaining species diversity (von Oheimb et al. 2007; Marx and Walters 2008).

In the more microsite-diverse plots, the tree species mixture was stratified, with a smaller, tolerant understory below the more intolerant overstory. Evidence for stratification included the positive relationship between microsite diversity and stem density, the negative relationship between microsite diversity and QMD, and the persistence of mid-sized intolerant individuals in plots with high microsite diversity (Fig. 6d). Plots with lower microsite diversity had larger trees and lower stem density, which likely reflects lesser local disturbance severity, allowing higher survival of established trees and limiting available microsites for new individuals to establish. The increased species diversity in areas with higher microsite diversity was potentially due to greater local disturbance severity, allowing early- and mid-successional species to establish in this formerly old-growth forest (Fig. 6b; Barker Plotkin et al. 2017). Despite the positive relationships between microsite diversity and tree density, we did not see evidence of higher productivity in plots with more microsite

Fig. 6. Microsite diversity and diameter distribution were measured in 1989, and diameter distributions were remeasured in 2009. Plots in the highest ($n = 14$) and lowest ($n = 14$) quartiles of diversity were selected for diameter comparison. Diameter distributions from 1989 and 2009 for low (a, c) and high (b, d) microsite diversity are shown. Note the mid-sized shade-intolerant individuals present in the plots with high microsite diversity compared with those with low microsite diversity. Shade-intolerant species include *Betula papyrifera*, *Fraxinus americana*, and *Prunus serotina*; mid-tolerant species include *Betula alleghaniensis*, *B. lenta*, *Quercus rubra*, *Pinus strobus*, and *Ulmus americana*; and shade-tolerant species include *Acer rubrum*, *Acer saccharum*, *Fagus grandifolia*, *Ostrya virginiana*, *Picea rubens*, and *Tsuga canadensis*. Trees are binned in 4 cm size classes.



diversity, as has been observed in studies of other stratified mixtures (Kelty 2006). This is potentially due to greater mortality for trees established on windthrow mounds (Barker Plotkin et al. 2017) resulting in lower net biomass accumulation on these plots over the study interval (i.e., five to seven decades after the hurricane).

Regeneration mechanisms following the hurricane differed by species, with hardwoods sprouting or establishing by seed within 25 years and the hemlock and beech present as advance regeneration that was released by the hurricane, resulting in a two-aged structure (Foster 1988a). Hurricanes have diverse impacts on forest succession, depending on stand composition and developmental stage at the time of the hurricane. It is unclear what factors contributed to white pine historically dominating this site (Foster 2014); however, it is likely that the closed canopy old-growth stand prior to 1938 did not support understory conditions conducive for white pine to survive as advance regeneration. The removal of overstory trees by the hurricane largely eliminated white pine as a live tree in this forest and accelerated the successional shift from pine-hemlock to hemlock-hardwood (cf. Abrams and Nowacki 1992).

The microsite heterogeneity observed in this study could have been driven by pre-hurricane species composition and structure (Foster 1988a), with areas containing more diverse pre-hurricane overstory conditions having greater levels of post-hurricane microsite heterogeneity. For example, species and size classes of trees respond differently to wind disturbance (Foster 1988b; Canham et al. 2001) and have different rates of decay for deadwood (Harmon et al. 1986). We investigated the potential relationship between pre-hurricane overstory composition and microsite structures and heterogeneity using Schoonmaker's (1992) reconstruction

of pre-hurricane overstory composition derived from deadwood along each transect. There were no significant relationships between these reconstructions and microsite heterogeneity or the area in different microsites (Supplementary Table S1¹); however, we acknowledge the importance of the pre-hurricane forest in affecting the distribution of disturbance-mediated microsites and subsequent forest development. In particular, previous work examining forest structural development in these areas highlighted the strong linkages between areas currently containing high deadwood volumes and the historic occurrence of large, living white pine in these portions of the landscape (D'Amato et al. 2017). Other factors that were not quantified in this study, including larger topographic gradients, could also play a role in impacting forest development.

The changes in forest structure five to seven decades after the 1938 hurricane followed general post-disturbance patterns described elsewhere, with increasing average tree size, increasing basal area, and decreasing stem density over time characteristic of the stem exclusion stage of stand development (Oliver 1980). We also documented a shift in diameter distribution, from negative exponential to increasing q . The increasing- q distribution has fewer small trees and more mid-sized trees than the negative exponential distribution, which is logical as smaller trees in 1989 grew or died and were not replaced by ingrowth into those size classes (Figs. 2a and 2b). This is consistent with studies following stands after stand-replacing events (Zenner 2005; Janowiak et al. 2008). Although the stands examined in the present study were in an uneven-aged, old-growth condition prior to the 1938 hurricane (Henry and Swan 1974), the extensive damage to the overstory by the 1938 hurricane (Foster 1988a) functionally generated a two-

cohort stand through the release of advance regeneration and establishment of new seedlings.

Mortality rates varied by size class, with trees in the smallest size classes experiencing the highest mortality rates, similar to the size–mortality relationships seen in single-cohort, self-thinning temperate forests (Coomes and Allen 2007). Mortality rates for shade-tolerant trees followed a descending monotonic relationship with diameter, similar to patterns found by Lorimer et al. (2001); however, intolerant species also followed this pattern, which is potentially due to their representation being low relative to the *Fagus grandifolia*, *Tsuga canadensis*, and *Acer rubrum* that dominated after the 1938 hurricane (Figs. 6a and 6b). In addition, work examining mortality patterns on different microsites at this site demonstrated that mortality over this period was higher on mounds than on non-mound structures, where intolerant and mid-tolerant species largely recruited after the 1938 hurricane (Barker Plotkin et al. 2017). While these mortality patterns reflect a snapshot of forest development, we do not know how these dynamics may have been different in the first 50 years since the hurricane.

This study expands our understanding of the long-term development of temperate forest ecosystems following stand-replacing windstorms and it emphasizes the lingering influence of microsite structures and diversity on forest structure and composition. Certain structures, for example, windthrow mounds, play a critical role in the maintenance of small-seeded, less shade tolerant tree species in these forests due to favorable seedbed conditions and an absence of established advance regeneration, as has been observed with other short-term examinations. Moreover, the diversity of microsites, as influenced by pre-disturbance forest conditions, disturbance type, and other factors, has a strong influence on long-term patterns in species diversity, stand density, and average tree size for decades following severe disturbance.

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