

# Long-term structural and biomass dynamics of virgin *Tsuga canadensis*–*Pinus strobus* forests after hurricane disturbance

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**Abstract.** The development of old-growth forests in northeastern North America has largely been within the context of gap-scale disturbances given the rarity of stand-replacing disturbances. Using the 10-ha old-growth Harvard Tract and its associated 90-year history of measurements, including detailed surveys in 1989 and 2009, we document the long-term structural and biomass development of an old-growth *Tsuga canadensis*–*Pinus strobus* forest in southern New Hampshire, USA following a stand-replacing hurricane in 1938. Measurements of aboveground biomass pools were integrated with data from second- and old-growth *T. canadensis* forests to evaluate long-term patterns in biomass development following this disturbance. Ecosystem structure across the Tract prior to the hurricane exhibited a high degree of spatial heterogeneity with the greatest levels of live tree basal area (70–129 m<sup>2</sup>/ha) on upper west-facing slopes where *P. strobus* was dominant and intermixed with *T. canadensis*. Live-tree biomass estimates for these stratified mixtures ranged from 159 to 503 Mg/ha at the localized, plot scale (100 m<sup>2</sup>) and averaged 367 Mg/ha across these portions of the landscape approaching the upper bounds for eastern forests. Live-tree biomass 71 years after the hurricane is more uniform and lower in magnitude, with *T. canadensis* currently the dominant overstory tree species throughout much of the landscape. Despite only one living *P. strobus* stem in the 2009 plots (and fewer than five stems known across the entire 10-ha area), the detrital legacy of this species is pronounced with localized accumulations of coarse woody debris exceeding 237.7–404.2 m<sup>3</sup>/ha where this species once dominated the canopy. These patterns underscore the great sizes *P. strobus* attained in pre-European landscapes and its great decay resistance relative to its forest associates. Total aboveground biomass pools in this 71-year-old forest (255 Mg/ha) are comparable to those in modern old-growth ecosystems in the region that also lack abundant white pine. Results highlight the importance of disturbance legacies in affecting forest structural conditions over extended periods following stand-replacing events and underscore that post-disturbance salvage logging can alter ecosystem development for decades. Moreover, the dominant role of old-growth *P. strobus* in live and detrital biomass pools before and after the hurricane, respectively, demonstrate the disproportionate influence this species likely had on carbon storage at localized scales prior to the widespread, selective harvesting of large *P. strobus* across the region in the 18th and 19th centuries.

**Key words:** aboveground biomass; coarse woody debris; forest structure; hurricane; *Pinus strobus*; temperate forest ecosystems; *Tsuga canadensis*.

## INTRODUCTION

Understanding the influence of disturbance on the structure and function of forest ecosystems has long been a central element in the development of forest conservation and management approaches (Seymour et al. 2002), as well as in forest and ecosystem simulation models (Bugmann 2001, Mladenoff 2004). Old-growth systems have been used both to approximate natural disturbance patterns and processes to guide this work (Pacala et al. 1996) and serve as natural structural and compositional

benchmarks for comparison with contemporary managed forests or those developing following historic periods of intensive land use (Sarr et al. 2004). In regions where old-growth forests are relatively abundant, such as the Pacific Northwest, USA, a wide range of structures and processes can be quantified to establish upper bounds for expected patterns in natural variability (Smithwick et al. 2002); however, old-growth forests are rare for most regions of the globe, thereby limiting similar approximations. This limited abundance not only hampers efforts to describe the full range of compositional and structural conditions found in a given forest type, but also limits our ability to fully document disturbance regimes affecting these systems and associated developmental pathways (Lorimer and Frelich 1994). Given projected shifts in the frequency and

Manuscript received 13 June 2016; revised 19 October 2016; accepted 29 November 2016. Corresponding Editor: John J. Battles.

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severity of disturbance for many regions (Dale et al. 2001), this truncated understanding of disturbance presents a key knowledge gap for anticipating the impacts of novel and increasing levels of disturbance on forest developmental dynamics.

The frequency of stand-replacing disturbance is quite low for many temperate forests and correspondingly much of our understanding of structural and compositional dynamics of temperate old-growth forest systems is within the context of fine-scale and occasionally mesoscale disturbances (Hanson and Lorimer 2007, D'Amato et al. 2008, Lorimer and Halpin 2014, Pederson et al. 2014). Nevertheless, historical accounts of disturbance regimes for these regions highlight the importance of infrequent, high-severity disturbances such as hurricanes, straight-line wind events, and crown fire (Lorimer 1977, Canham and Loucks 1984). Salvage logging following these events, as well as an incomplete understanding of pre-disturbance stand conditions, has limited opportunities to document the effects of severe disturbances on natural forest development. Moreover, the very feature often used to define old-growth systems, namely the presence of old canopy trees (Hunter 1989), has restricted much of the work aimed at documenting the influence of disturbance on forest development to areas where high-severity disturbance events have been less frequent in the recent past (McGee et al. 1999, D'Amato et al. 2008). As a result, key knowledge gaps exist regarding historic, natural developmental pathways following stand-replacing disturbances for these systems and their comparability to second-growth forests developing following stand-replacing anthropogenic disturbances such as forest harvesting or agricultural clearing.

Forest structural development patterns are strongly governed by disturbance processes and associated patterns of tree mortality, both through their effects on resource availability for tree recruitment and growth (Zenner 2005, Runkle 2013) and in affecting the abundance and distribution of detrital components, namely standing dead trees and downed logs (D'Amato et al. 2008). General models describing long-term forest structural and biomass development have largely focused on time since stand-replacing disturbance as the driver of observed conditions at any given point in development with living and dead biomass often following asymptotic and u-shaped trends, respectively, over time (Bormann and Likens 1979, Harmon 2009). Nonetheless, works investigating the role of gap-scale disturbances on stand structural development have highlighted the influence of such events in generating a range of structural conditions for any given forest developmental stage resulting in deviations from these expected trends (Sturtevant et al. 1997, D'Amato et al. 2008).

One consistent finding across the large body of work examining natural forest developmental pathways is the carry-over effect of gap-scale and stand-replacing disturbances on long-term patterns of coarse woody debris abundance in early to late-successional stands (Spies et al. 1988).

The importance of these legacies in affecting ecosystem properties (e.g., heterotrophic respiration; Harmon et al. 2011), tree regeneration, and biodiversity has led to an increased emphasis on conserving these features in managed forest stands (Franklin et al. 2000), particularly in light of post-disturbance management interventions such as salvage logging that remove or reduce coarse woody debris (Schmiegelow et al. 2006). Yet, the long-term persistence and importance of these legacies is still largely unknown for most forested regions given historic salvage logging efforts and a lack of contemporary natural landscapes for documenting natural post-disturbance dynamics.

This study takes advantage of a globally unique, long-term data set from a virgin (i.e., never impacted by land use) forest in southern New England, USA to document the influence of a stand-replacing hurricane event on long-term forest structural development in mixed eastern hemlock (*Tsuga canadensis* L.)-white pine (*Pinus strobus* L.) forests. The depth of historic data collected immediately prior to and following this event and lack of post-disturbance salvage harvesting allows a rare opportunity to document the natural post-disturbance recovery of a forest type and condition that were once a predominant feature on the landscapes of northeastern North America (Whitney 1994). The primary objectives of this study were to (1) describe the spatiotemporal range in forest structural conditions immediately prior to and following a stand-replacing wind event and (2) to approximate general patterns in post-disturbance forest biomass development for hemlock-dominated systems by integrating measurements from this forest with those from other second- and old-growth hemlock systems in the region.

#### Study area

This study took place in the 10-ha Harvard Tract, which is located 11 km northwest of the town of Winchester, New Hampshire, USA within the 5400-ha Pisgah State Park (42°49' N, 72°27' W). The study area elevation ranges from 300 to 350 m above sea level and contains a north-south trending ridge. Shallow stony podzolic soils overlie bedrock of schist, granite, and gneiss (Simmons 1942). Approximately 100 cm of precipitation fall evenly throughout the year, and the growing season averages 153 d (Rosenberg 1989). The Harvard Tract is located near the southern boundary of the northern-hardwoods-hemlock-white-pine region (Westveld et al. 1956) and within the Worcester/Monadnock Plateau ecoregion (Barbour and Anderson 2003).

At the turn of the 20th century, the Tract contained one of the few remaining old-growth remnants in New England and continues to contain one of the only examples of virgin forest in the region. Our use of the term "old growth" here and throughout the manuscript refers to forests lacking any past land-use and containing at least five canopy trees per hectare >225 yr old, which exceeds 50% of the maximum longevity for species commonly encountered in these forests (McGee et al. 1999), whereas

“virgin forests” is used to refer to forests never directly impacted by human activity (Peterken 1996). Since 1905, the Harvard Tract has been the focus of extensive study, including documentation of the old-growth hemlock–white-pine forest (Branch et al. 1930, Foster 2014), the factors controlling the distribution of major forest types (Cline and Spurr 1942), and detailed disturbance histories of fire, wind, and pathogens that helped shape the vegetation over time (Henry and Swan 1974, Foster 1988, Schoonmaker 1992, Stafford 1992). Findings from this previous work demonstrated the forests on the Tract were largely uneven aged, with wind events, including downbursts and hurricanes, serving as the main form of canopy disturbance initiating cohorts in the 1630s, 1810s, 1850s, and 1920s (Foster 1988). The abundant, overstory white pine encountered on the Tract in the 1900s were postulated to have originated as a single cohort following a severe fire event in the 1660s (Henry and Swan 1974).

The great hurricane of 1938 blew down the majority of old-growth forest in the area. However, unlike the vast majority of the surrounding area, the Harvard Tract was not salvage logged and the numerous damaged and uprooted trees remained, allowing post-hurricane succession to proceed naturally (Spurr 1956). The forest is currently dominated by hemlock (*T. canadensis*) with lesser amounts of American beech (*Fagus grandifolia*), red maple (*Acer rubrum*), black birch (*Betula lenta*), and paper birch (*Betula papyrifera*). Nomenclature follows Gleason and Cronquist (1991).

## METHODS

### *Modern vegetation*

In order to assess the fine-scale spatial variation in vegetation development over time, contiguous 10 × 10 m plots located along two parallel transects (300 and 270 m long, respectively) were established across the central north-south trending ridge on the Tract in 1989. Each plot was classified by slope position (low, middle, upper) and aspect. All stems >2 cm diameter at breast height (1.37 m; dbh) were mapped, measured for dbh, and assigned a canopy class (dominant, codominant, intermediate, suppressed), a condition class (alive, moribund, dead) and microsite class (soil, rock, tip-up mound). Plots were resampled in 2009. Any trees not listed in 1989 were considered ingrowth and were measured and mapped as described. Trees listed in 1989 that could not be located were recorded as missing. Biomass of living trees was determined based on species-specific allometric equations in Jenkins et al. (2003).

### *Coarse woody debris, snags, and pre-hurricane structure*

Coarse woody debris (CWD), including downed stems with an average diameter >10 cm, and snags (standing dead trees > 10 cm dbh) were tallied and mapped to the nearest 10 cm within the plots located along the two

east-west transects described in *Methods: Modern vegetation*. Each CWD piece was identified to species or genus by comparing thin sections of samples to a reference collection and wood identification keys (Core et al. 1979). The following was recorded for each downed stem intersected by the transects: length, diameter at the base and tip, estimated breast height diameter at time of mortality (with bark thickness estimated where missing), orientation of fall, origin (tip-up, snapped, unknown), and estimated date of origin (pre-1938, 1938, post-1938, unknown). Each downed log and snag was assigned to a decay class using a five-class scheme after Sollins (1982) with emphasis placed on status of bark, structural integrity, and branches; in this scheme, class 1 represents least and class 5 most decayed. Volume of each downed CWD piece present in plots was determined for all stems in classes 1, 2, and 3 based on the formula for a conic paraboloid

$$V = \frac{L}{12} \left( 5A_b + 5A_u + 2\sqrt{A_b A_u} \right)$$

where  $V$  is volume,  $L$  is the length of the stem,  $A_b$  is area of the stem at the base, and  $A_u$  is the area of the stem at the tip (Fraver et al. 2007). For stems in decay classes 4 and 5, volume reduction factors were applied to account for the progressive vertical collapse of logs as they decay (Fraver et al. 2013). Biomass of coarse woody debris was determined based on species and decay class-specific estimates of wood density presented in Harmon et al. (2008). All CWD was resurveyed in 2009 and its status recorded (present or missing); however, log and snag dimensions were not remeasured. As such, our estimates of these structural components are likely overestimates for this time period, but provide a general gauge for the degree to which CWD pieces disappeared from the sample population between measurement periods.

Pre-hurricane live-tree structure in terms of diameter distributions and live tree density and basal area was reconstructed for each transect based on the estimated DBH of CWD pieces that originated in 1938. Live-tree reconstructions are based solely on CWD measurements from individuals that were rooted within the transects at the time of the hurricane (153 total stems). Time of origin (pre-1938, 1938, post-1938, unknown) was estimated based on stem position, decay class, and evidence of damage to adjacent stems. Reconstructions were compared to data from a similar nearby portion of the Harvard Tract collected across 14 plots in 1929 (hereafter referred to as the “1929 plots”; Branch et al. 1930). Given the higher likelihood of complete decomposition of smaller diameter trees by the 1989 sampling, comparisons of reconstructed basal areas and densities with the 1929 measurements are restricted to values derived for stems >15 cm.

### *Data analysis*

Structural attributes were summarized by each 100-m<sup>2</sup> transect segment and each transect was analyzed separately given our interest in documenting the spatial

variability in downed CWD and other structural conditions across the Tract. One-dimensional semivariogram analysis was used to assess the spatial autocorrelation of downed CWD volumes across the topographically varied transects following the methods outlined in Kuuluvainen et al. (2001). In short, semivariance in downed log volume between 10-m segments on each transect were calculated with maximum lag distances of 150 and 130 m for the 300 and 270 m transects, respectively. Theoretical semivariogram models were fitted to the resultant experimental semivariograms to illustrate general patterns in semivariance using PROC NLIN in SAS Version 9.2 (SAS Institute 2008). The directionality of downed CWD was analyzed with Rayleigh's Uniformity Test using the circular statistics macro %rayleigh\_test in SAS (Kölliker and Richner 2004).

Given the rarity of studies documenting the recovery of old-growth hemlock-white pine forests after stand-replacing disturbance, we were interested in applying these data to describe the age-related patterns in biomass development for this forest type, an approach more commonly applied in regions and forest types where stand-replacing disturbance is more frequent (Turner and Long 1975). To accomplish this, we utilized data from all measurement periods at the Harvard Tract, as well as from 16 old-growth and eight-second-growth hemlock forests in the Berkshire Region of western Massachusetts. These additional sites were chosen based on their proximity and compositional similarity to the Harvard Tract (see D'Amato et al. 2008 for site descriptions). Live-tree, standing dead, downed CWD, and total aboveground biomass for stems  $\geq 10$  cm diameter were calculated for each site and measurement period using the above-mentioned methods, and relationships between biomass development and dominant tree age were quantified using linear and nonlinear regression models. Note 13% of trees from the reconstructed, pre-hurricane live-tree structure had diameters greater than those used for developing the species-specific biomass equations we applied (Jenkins et al. 2003) and therefore these estimates should be interpreted with caution. Also, the assignment of a "stand age" is not appropriate for uneven-aged systems, such as the old-growth forest sites included in this analysis, so median dominant tree age was used as a proxy for degree of structural development (Keeton et al. 2011). For the Harvard Tract, downed CWD biomass immediately following the 1938 hurricane was based on reconstructed log dimensions for pieces originating in this event. We did not reconstruct standing dead biomass for this period given the difficulty in retrospective estimates of this highly dynamic pool. Trends in biomass development over time were examined using linear and nonlinear regression models based on functional forms used in past studies describing age-related trends in biomass development (Harmon 2009, Bradford and Kastendick 2010, Keeton et al. 2011). A set of candidate models were evaluated for each biomass pool (i.e., downed woody debris, live tree, and total aboveground

biomass pool) and included multiple functional forms for describing biomass development with age, including linear, exponential increase, exponential rise to a maximum, and negative exponential forms using PROC NLMIXED in SAS. Based on the findings of previous work, we also included models combining linear and non-linear functions to account for potential intermediate maxima and minima in live tree (Bradford and Kastendick 2010) and downed woody debris (Duvall and Grigal 1999, Harmon 2009) biomass. Models were ranked based on Akaike's information criterion ( $AIC_c$ ) and the model with the lowest  $AIC_c$  value in the set was selected for describing a given biomass pool (Burnham and Anderson 2001).

## RESULTS

### *Reconstructed pre-hurricane forest conditions*

Dominant overstory tree species prior to the 1938 hurricane based on basal area and density were *Tsuga canadensis* and *Pinus strobus*, with minor components of *Fagus grandifolia*, and *Acer*, *Quercus*, and *Betula* spp. The abundance of these species varied across the landscape with *P. strobus* dominating upper west-facing slopes (100–150 m along transects) while *T. canadensis* was more evenly distributed throughout the Tract (Fig. 1). Average pre-hurricane basal area and density ranged from 32.0 to 55.7 m<sup>2</sup>/ha and 280.8 to 322.9 stems/ha across the Tract (Table 1). As with species composition, basal area and density also varied across the landscape ranging from no or low basal area and density on steep east-facing slopes to high levels on upper west-facing slopes where *P. strobus* was dominant (Fig. 1). *T. canadensis* was found across all but the largest (>89 cm) diameter classes, whereas *P. strobus* was largely restricted to size classes >50 cm for which it was the dominant species. Hardwood species were primarily <50 cm diameter (Fig. 2). Reconstructions of 1938 conditions based on downed woody material sampled in 1989 contained a lower density of hardwood species and were generally lower in basal area and density than 1929 measurements, particularly on the more southerly transect (Figs. 1 and 2, Transect B).

### *Post-hurricane forest conditions and development*

Seventy one years after the hurricane, average stand basal area had recovered to levels similar to pre-hurricane conditions; however, the distribution of stand basal area and density across the Tract were much more uniform than pre-hurricane stands (Fig. 1). In particular, coefficients of variation (CV) for basal area ranged from 25.6% to 36.8% in 2009, compared to 68.6–90.0% in 1938. Stem densities were also more uniformly distributed in 2009 (CV = 30.7–34.8% in 2009 vs. 54.3–64.3% in 1938) and were up to four times higher than average 1938 densities (Fig. 1). *Tsuga canadensis* was the dominant overstory

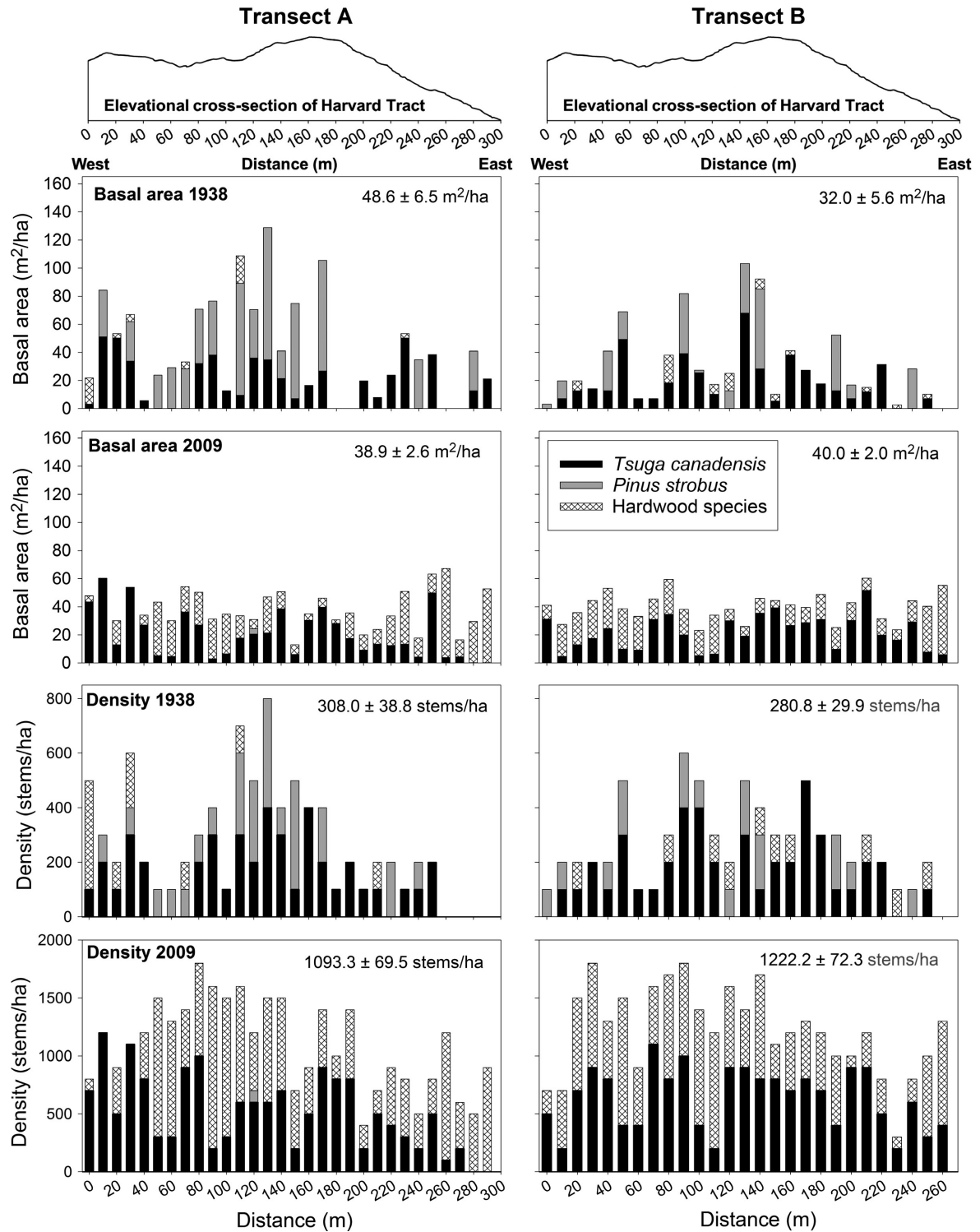


FIG. 1. Live-tree basal area and density in 1938 and 2009 along sampling transects at the old-growth Harvard Tract, New Hampshire, USA. Values for 1938 represent conditions immediately prior to the 1938 hurricane based on reconstructions using coarse woody debris present in 1989. See *Methods* for details on reconstruction. Values in upper right-hand corner of each panel represent transect-level mean  $\pm$  SE. Transects are oriented west to east.

TABLE 1. Estimates of average live-tree (a) basal area and (b) density of the old-growth *Tsuga canadensis*–*Pinus strobus* forests on the Harvard Tract prior to the 1938 hurricane.

Source	<i>Tsuga canadensis</i>	<i>Pinus strobus</i>	<i>Fagus grandifolia</i>	Other hardwoods	Total
a) Basal area (m <sup>2</sup> /ha)					
Transect A	21.3 (3.3)	25.3 (5.6)	0.9 (0.6)	1.2 (0.8)	48.6 (6.5)
Transect B	17.6 (3.3)	11.7 (3.5)	0.7 (0.5)	2.0 (0.9)	32.0 (5.6)
1929 plots	25.6 (4.4)	24.1 (6.6)	2.5 (0.6)	3.4 (1.4)	55.7 (6.3)
b) Density (stems/ha)					
Transect A	165.4 (22.8)	103.8 (24.5)	23.1 (13.9)	15.4 (7.2)	307.7 (38.8)
Transect B	173.1 (25.8)	69.2 (17.3)	11.5 (6.4)	26.9 (8.9)	280.8 (29.9)
1929 plots	192.8 (24.3)	76 (21.6)	22.8 (10.2)	31.3 (12.1)	322.9 (37.9)

Notes: Transects A and B represented reconstructed forest conditions from coarse woody debris sampled in 1989, whereas 1929 plots correspond to values from 14 plots measured on the Harvard Tract in 1929 (Branch et al. 1930). Other hardwoods include *Acer* spp., *Betula* spp., and *Quercus* spp. Standard errors are in parentheses.

tree species throughout much of the landscape following the hurricane with minor components of *F. grandifolia*, *Acer rubrum*, *Betula lenta*, and *B. papyrifera*. Only one living *P. strobus* stem was encountered across the 57 plots sampled in 2009.

Downed coarse woody debris (CWD) volume averaged 184.4 and 140.8 m<sup>3</sup>/ha for Transects A and B, respectively, in 1989, with a high degree of fine-scale variability

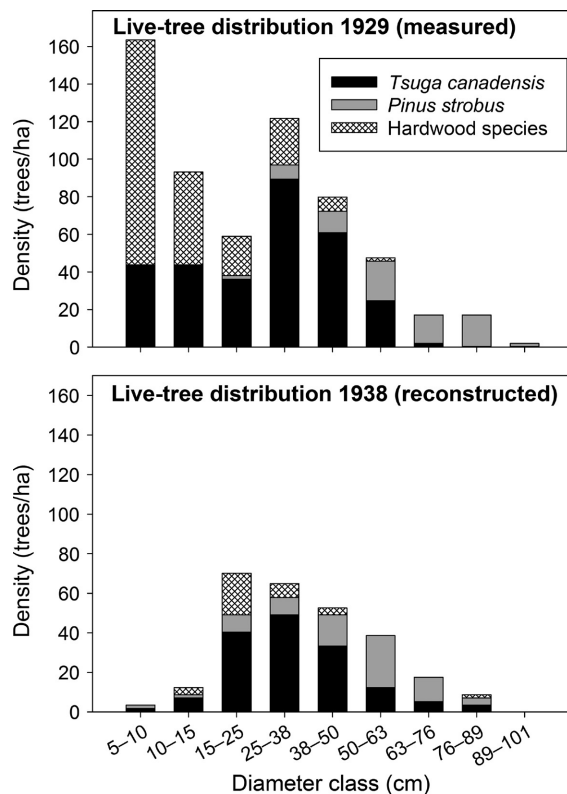


FIG. 2. Size distribution of living stems on the Harvard Tract in 1929 and 1938 (pre hurricane) based on field data collected by Branch et al. (1930) and reconstructions of pre-hurricane structure along sampling transects in 1989. Hardwood species consists primarily of *Fagus grandifolia*, and *Acer*, *Quercus*, and *Betula* spp.

across plots ranging from 8.9 to 703.5 m<sup>3</sup>/ha at the 100-m<sup>2</sup> scale (Fig. 3). The spatial distribution of total log volumes was autocorrelated up to distances of 100 m on Transect A, whereas there was no spatial pattern on Transect B (See Appendix S1: Fig. S1). Peaks in log volume along both transects were associated with portions of the landscape containing a high abundance of *P. strobus* prior to the 1938 hurricane (Figs. 1 and 3). The majority of downed CWD was in advanced decay classes (decay classes 3–5; See Appendix S2: Fig. S1) and displayed uniform orientation (Rayleigh's  $P > 0.001$ ) with mean vectors that were statistically indistinguishable between transects (mean vector = 274° and 275° for Transects A and B, respectively; modified Rayleigh's  $P > 0.8$ ; See Appendix S3: Fig. S1) and largely perpendicular to slopes in these areas. Downed CWD originating after the 1938 hurricane constituted only 5% of the total volume across the two transects in 1989. The average volume of downed CWD, based on census of pieces present in 2009, declined 28% and 2% between 1989 and 2009 for Transects A and B, respectively. This decline reflected disappearance of approximately 82% of hardwood species, 60% of *T. canadensis* and 30% of *P. strobus* CWD pieces detected in 1989.

The distribution of snags was much less continuous than downed CWD with 59.6% of plots lacking snags in 1989. Despite the low overall average snag volumes across the landscape, localized volumes were occasionally quite high (maximum values = 228.2 and 635.0 m<sup>3</sup>/ha on Transects A and B, respectively) reflecting areas with large *P. strobus* snags. Average snag volumes increased slightly from 1989 to 2009 reflecting relatively low snag fall rates (50.0% and 57.8% of snags between 1989 and 2009 on Transect A and B, respectively) and recruitment of an average of 88 new snags/ha between 1989 and 2009 across the two transects. These new snags were largely *F. grandifolia*, *T. canadensis*, *B. papyrifera*, and *A. rubrum*.

#### Post-disturbance forest biomass development

Total aboveground live-tree biomass of the Harvard Tract prior to the 1938 hurricane ranged from 22 to

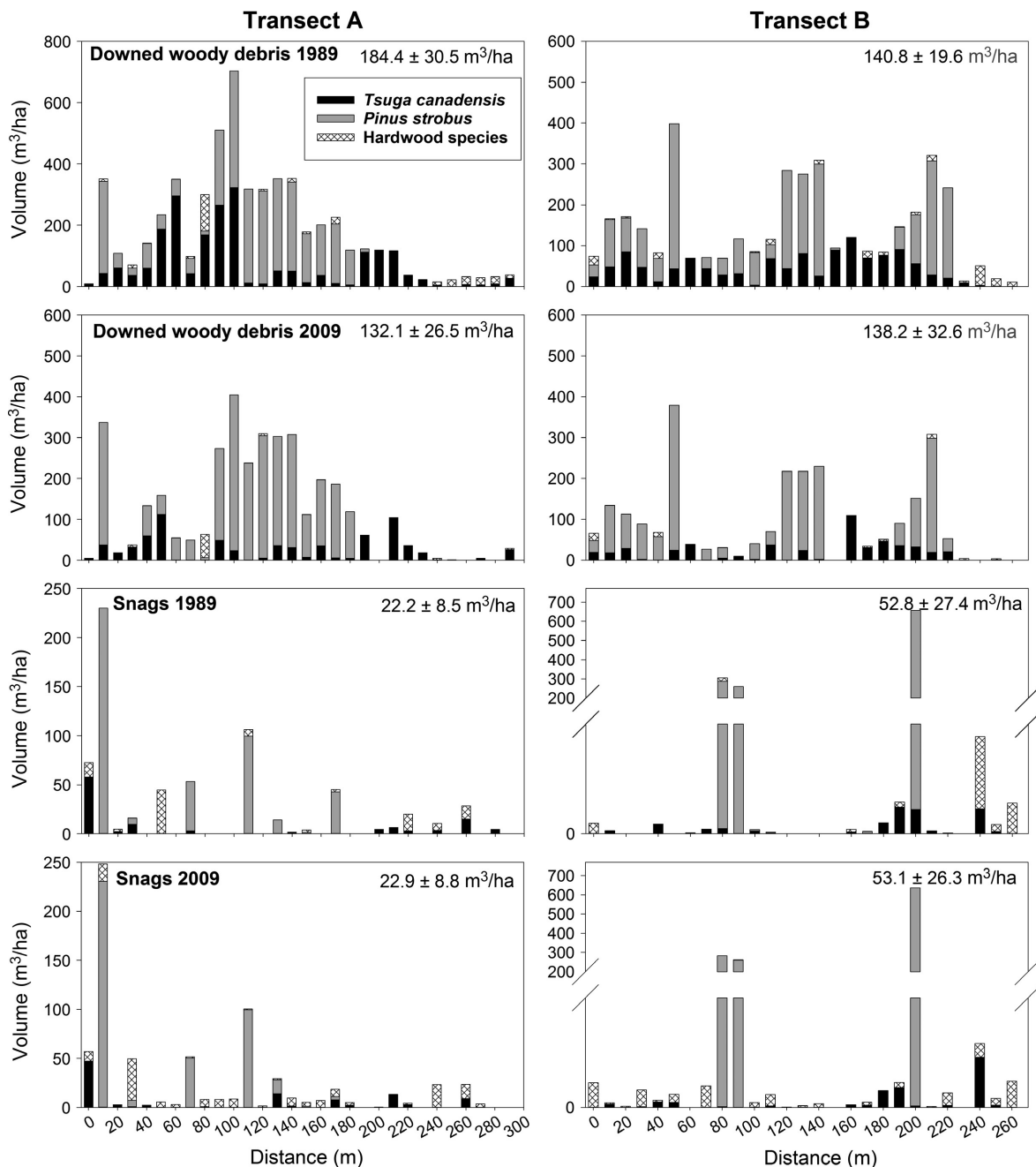


FIG. 3. Volume of downed coarse woody debris and snags across sampling transects on the Harvard Tract, New Hampshire in 1989 and 2009. Individual downed woody debris pieces were only noted as present or absent in 2009 and therefore estimates do not account for volume loss due to decay between 1989 and this period. Values in upper right-hand corner of figures represent transect-level mean  $\pm$  SE. Transects are oriented west to east.

503 Mg/ha across 100-m<sup>2</sup> plots with an overall Tract average of  $169.3 \pm 17.8 \text{ Mg/ha}$ . As with basal area, the greatest aboveground live-tree biomass values were on upper west-facing slopes where *P. strobus* was dominant, particularly on Transect A where values averaged  $367.1 \pm 73.3 \text{ Mg/ha}$  across the contiguous 500 m<sup>2</sup> between distances 100–150 m. Much of this biomass was transferred to detrital pools, namely downed CWD (Fig. 4).

When examined in combination with other *Tsuga*-dominated systems, post-disturbance patterns of CWD biomass temporal change followed a broad reverse-J-shaped trajectory best described by a combination of linear and exponential functions (Fig. 4a). Post-hurricane snag abundance was not estimated given the difficulty in reconstructing this pool; however, biomass of snags 71 years following the hurricane was over four times

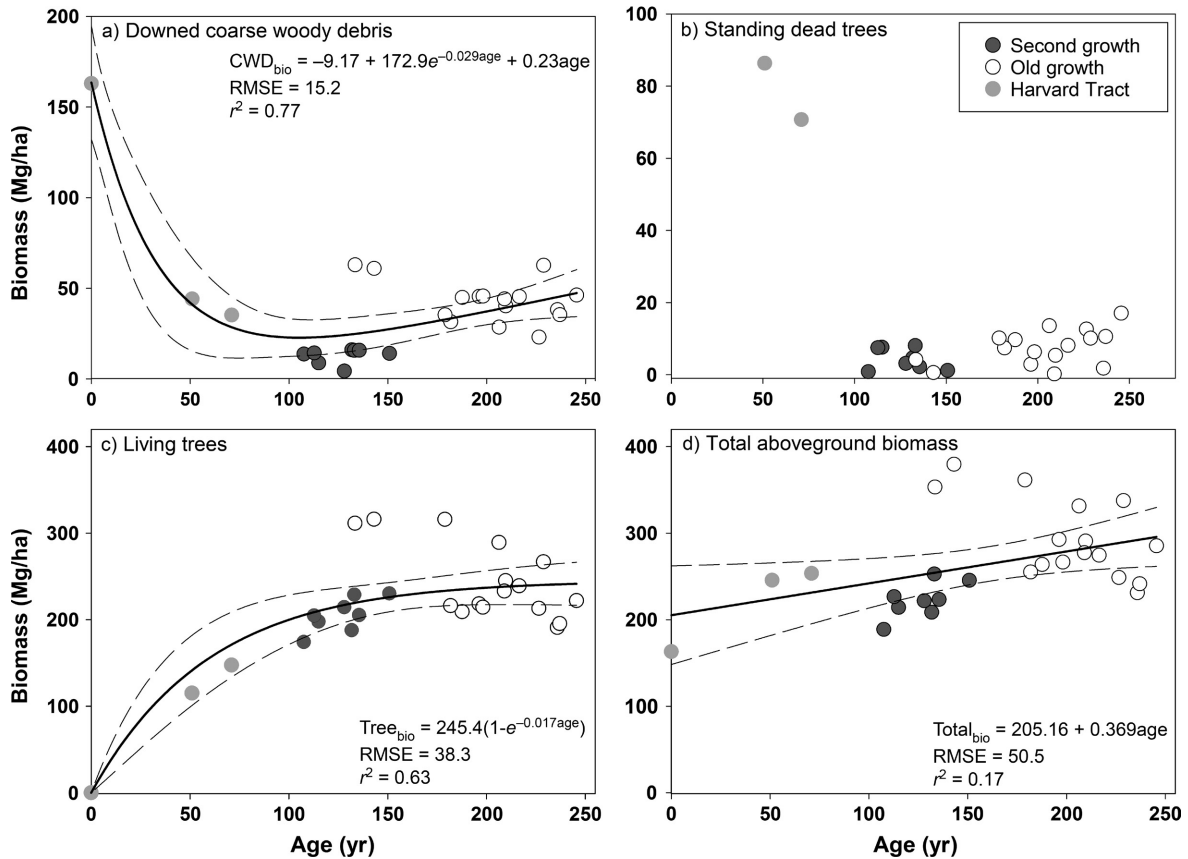


FIG. 4. Relationships between (a) downed coarse woody debris, (b) standing dead tree, (c) living tree, and (d) total aboveground biomass, including coarse woody debris, and median dominant tree age at the Harvard Tract and second-growth and old-growth *Tsuga canadensis*-dominated forest in southern New England. Values for the Harvard Tract represent the average across the two sampling transects. Snag biomass immediately following the 1938 hurricane was not estimated given the difficulty in reconstructing this dynamic pool.

greater than the highest observed value across other *Tsuga*-dominated systems in the region (Fig. 4b). Live tree and total aboveground biomass were positively related to age, with live-tree components best described by a combination of linear and exponential functions and total aboveground biomass reflecting a linear relationship with age (Fig. 4c, d).

#### DISCUSSION

Quantifying the range in old-growth forest structural conditions and dynamics has been a primary focus of ecological research for over a century providing insights on natural bounds for forest structure and functioning (Landres et al. 1999, Luyssaert et al. 2008, Fraver and Palik 2012), as well as templates and targets for forest ecosystem restoration and conservation (Foster et al. 1996, Bausch et al. 2009). This study took advantage of a unique, long-term history of research in an old-growth landscape to quantify the impacts of a stand-replacing hurricane event on long-term forest structural and biomass development. While several studies have documented the short-term impacts of similar events on

old-growth post-disturbance regeneration and live-tree dynamics (Dunn et al. 1983, Peterson and Pickett 1995), this study, to our knowledge, is the first multi-decadal examination of the impacts of stand-replacing wind on old-growth live-tree and detrital development. Reconstructions of pre-hurricane conditions highlight the tremendous range and magnitude of structural conditions and aboveground biomass historically characterizing old-growth hemlock–white-pine systems and the persistence of woody debris legacies in affecting forest structural conditions 70 years removed from this stand-scale event. These findings underscore the importance of considering the impacts of post-disturbance management treatments on deadwood legacies and associated functions.

#### *Pre-hurricane live-tree structure and aboveground biomass*

Eastern hemlock–white-pine forests were frequently identified in historical accounts as the most structurally impressive forest ecosystems in northeastern North America at the time of European settlement (Whitney 1994), particularly in terms of live tree sizes. The



exploitation of these forests in the 18th and 19th centuries limited opportunities to quantify their structural characteristics; however, findings from this and other work in remnant old-growth hemlock–white-pine systems (Abrams and Orwig 1996) substantiate these early observations. Pre-hurricane aboveground live tree biomass varied considerably across the Harvard Tract; however, the upper bounds we observed at the plot scale (503 Mg/ha) were consistent with other estimates for old-growth hemlock–white-pine forests in Pennsylvania and Great Lakes occurring at similar scales (437 and 572 Mg/ha; Crow 1978, Whitney 1994). Of note, extrapolations by Whitney (1994) based on data collected on the Harvard Tract prior to the hurricane and presented in Foster (1988) suggest an even greater upper limit for these systems (735 Mg/ha); however, this estimate should be viewed with caution since species-specific biomass equations were not used. Similarly, the relatively small plot sizes used in the present study limit our ability to generalize these results to a broader landscape condition; however, average live-tree biomass over the contiguous portion of Transect A where white pine was most abundant (367 Mg/ha; distances 110–150 m) approach maximum values reported for other old-growth forest systems in northeastern North America (Woods 2014). These maximum values reflect the complementarity in light requirements between white pine and hemlock, which allowed for greater aboveground production in portions of the landscape where they existed in stratified mixtures (Kelty 1989, Jucker et al. 2014).

Although the maximum live tree basal area, density, and biomass values observed in this and other studies are useful for establishing the “carbon carrying capacity” (sensu Keith et al. 2009) for a given forest type and region, of greater importance is the level of variability observed in these attributes across the Harvard Tract prior to the 1938 hurricane. Many areas contained low or average basal area, density, and biomass, reflecting both variation in site quality across the sampling transects (Larson et al. 2008) as well as recovery from historic gap-scale disturbances (Cline and Spurr 1942). This variability has often been overlooked by past studies due to biases in plot placement towards undisturbed, “majestic” portions of old-growth stands resulting in elevated population-level estimates of forest structure and biomass stores (Phillips et al. 2002, Woods 2014). Our use of transects bisecting the environmental and stand conditions found on the Harvard Tract allowed for a more accurate representation of fine-scale variation in these conditions, yet resulted in population-level estimates well below those from studies focused on undisturbed, old-growth conditions (Woods 2014).

Live-tree size distributions based on historic plot data from 1929 were comparable to other old-growth hemlock–white-pine forests (Abrams and Orwig 1996) with white pine found primarily in the larger diameter classes and hemlock and shade-tolerant (*Fagus grandifolia* and *Acer* spp.) and midtolerant (*Betula* and *Quercus*

spp.) hardwood species found in the small to intermediate classes. Live-tree distributions reconstructed from coarse woody debris in 1989 approximated the historic size distribution of white pine and hemlock, yet failed to capture the significant, smaller-statured hardwood component likely due to the higher wood decomposition rates for these species (Harmon et al. 1986). Estimates of the levels of live-tree basal area, density, and aboveground biomass across the Tract prior to the hurricane are likely underestimates given our inability to fully reconstruct these hardwood components.

#### *Post-hurricane forest development*

*Pinus strobus* constituted a major component of the forest prior to the 1938 hurricane; however, only a single live individual (DBH in 2009 = 21.9 cm) was encountered across the sampling transects 71 years after this event. Instead, the forest that has developed is primarily dominated by *T. canadensis*, *F. grandifolia*, *Acer rubrum*, and *Betula lenta*, many of which established as advance regeneration prior to the hurricane (Spurr 1956, Henry and Swan 1974). The lack of *P. strobus* in the forests developing following the hurricane is consistent with broader findings from the region following this event (Spurr 1956), as well as from other work examining post-blowdown development in which mortality of less tolerant overstory species results in a shift in dominance towards shade-tolerant species that existed as advance regeneration in the pre-disturbance stand (Rich et al. 2007).

The landscape-wide release of advance regeneration by the hurricane served to homogenize live-tree basal area and density conditions relative to the highly spatially variable conditions prior to this event. This historic variability largely reflected the distribution of habitats on which white pine was able to establish in response to the mixture of historic wind and fire events affecting the Tract over the past several centuries (Foster 1988, Fahey and Lorimer 2014). In particular, a large component of the white pine dominating the Harvard Tract is believed to have established following a severe fire in the 1660s that eliminated existing advance regeneration of other species and created the seedbed conditions necessary for white pine establishment across large areas of the landscape (Foster 1988). Given that wind was the agent of stand replacement in 1938, little opportunity existed for post-disturbance establishment of white pine relative to species with regeneration mechanisms (i.e., advance regeneration) adapted to recruitment following disturbance events that primarily kill overstory trees.

The average volume of downed woody debris across the Tract 71 years after the hurricane (~135 m<sup>3</sup>/ha) was similar to and slightly exceed values found in old-growth *Tsuga canadensis*-dominated systems in northeastern North America (112, 126, 135 m<sup>3</sup>/ha; Tyrrell and Crow 1994b, Ziegler 2000, D’Amato et al. 2008), with localized accumulations approaching values found in old-growth *Pseudotsuga menziesii* in the Pacific Northwest of the



FIG. 5. Downed *Pinus strobus* logs originating from the 1938 hurricane. Photo was taken in 2015. Note structural integrity of logs despite mortality event occurring over seven decades prior to this photo being taken. [Color figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

United States (Spies et al. 1988). The long-term legacy of the 1938 hurricane in terms of the size of downed woody debris pools is largely attributable to the persistence of *P. strobus* logs; the majority of which were only in intermediate stages of decay in 1989 (See Appendix S2: Fig. S1). Although hemlock and hardwood logs also contributed to long-term downed wood pools, many were in the most advanced stages of decay by 1989 (See Appendix S2: Fig. S1), with a significant proportion of these (60% and 82% for hemlock and hardwood logs, respectively) no longer detectable by 2009. The persistence of white pine logs is related to several factors, including the higher levels of extractives in the heartwood of this species relative to hemlock and hardwood species (Harmon et al. 1986), the greater size of these individuals at the time of the hurricane, and the suspension of many white pine logs above the soil surface for extended periods due to windthrow (Fig. 5). While the short-term importance of downed woody debris legacies in structural development following stand-replacing wind in hardwood-dominated temperate forests has been previously highlighted (Busing et al. 2009, Barker Plotkin et al. 2012), these legacies have been projected to only persist for a few decades (Busing et al. 2009). The findings from this study expand these estimates due in large part to the extended residence time of white pine and to a lesser degree, hemlock (Tyrrell and Crow 1994a) downed woody debris and highlight the importance of the nature of wind damage (i.e., snapping vs. uprooting) in affecting persistence of deadwood legacies.

Snags constituted a lesser component of detrital pools given the majority of stems (>66%) were uprooted by the hurricane vs. snapped (Schoonmaker 1992). The high degree of spatial variability in snag volumes across the Tract reflected fine-scale patterns of hurricane damage with greater snag volumes in lower, protected slopes where hurricane damage was less severe and soil rooting volume likely greater (Foster 1988). As with downed woody debris,

the majority of snag volume 71 years after the hurricane was composed of large white pine individuals killed or damaged by the storm. The extended longevity of these snags is in contrast to previous estimates of snag fall rates for white pine, which suggest 10-year fall rates for this species ranging from 26% to 51% (Wilson and McComb 2005, Vanderwel et al. 2006). These differences are likely due to the restricted range of stem sizes examined in previous work (<60 cm DBH) relative to the large individuals at the old-growth Harvard Tract, as snag longevity has been shown to increase with increasing diameter (Hilger et al. 2012) due to increases in the proportion of decay-resistant heartwood (Parish et al. 2010).

#### *Aboveground biomass development in Tsuga canadensis-dominated systems*

Integrating long-term post-hurricane measurements of aboveground biomass from the Harvard Tract with those from other hemlock-dominated systems revealed trends in long-term biomass development that agree with broad trends suggested for natural post-disturbance patterns (Spies et al. 1988, Harmon 2009), as well as empirical relationships developed from chronosequences in northeastern North America (Gore and Patterson 1986, Duvall and Grigal 1999, Keeton et al. 2011). These trends included a reverse-J-shaped relationship between downed woody debris biomass and canopy tree age expressed as a combination of a negative exponential function to reflect decay of post-disturbance CWD and linear function to describe accumulation of new CWD over time (Gore and Patterson 1986, Spies et al. 1988, Duvall and Grigal 1999, Harmon 2009) and strong positive relationships between live-tree and total aboveground biomass and age (Pregitzer and Euskirchen 2004, Luyssaert et al. 2008, Keeton et al. 2011). A unique aspect of this work relative to past investigations in eastern North America was our ability to describe natural patterns of biomass development over the first century following stand-replacing disturbance. Past efforts have been restricted to integrating post-logging chronosequences with old-growth estimates to infer temporal dynamics (Duvall and Grigal 1999, Keeton et al. 2011), which although effective at describing live tree biomass development, may underestimate the early contributions of large deadwood legacies to detrital biomass stocks in young, developing stands. This is particularly important in the context of forests with a white pine component given the long-term recalcitrance of white pine snags and logs demonstrated in this study. Note stand age in the context of the relationships described in this study may represent a nonlinear scale given the use of median canopy age to characterize the uneven-aged, old-growth, hemlock forests used in this work.

#### CONCLUSIONS

The Harvard Tract prior to the 1938 hurricane likely represented the upper bound of aboveground carbon

storage for forests in northeastern North America, due in large part to the large upper canopy white pines in stratified mixtures with the shade-tolerant and abundant eastern hemlock dominating lower canopy strata. White pine's unique contribution to biomass pools in these systems was not restricted to live tree components. The long-term persistence of white pine snags and downed logs more than 70 years after the 1938 hurricane highlights the unique role this species played in old-growth forests as a large and stable component of biomass. In light of the exploitive removal of old-growth white pine across the region in the 18th–19th centuries and the impending threat posed to eastern hemlock by the introduced hemlock woolly adelgid (*Adelges tsugae*), it is likely forest ecosystems of this stature will not be realized in the future. The long-term importance of deadwood legacies following the 1938 hurricane in maintaining elevated aboveground biomass stocks is an invaluable point of reference for informing future decisions regarding management following disturbance events in contemporary forests.

#### ACKNOWLEDGMENTS

This work was supported by a Charles Bullard Fellowship at Harvard University to A. W. D'Amato, the Harvard Forest Pisgah Fund, and Harvard Forest LTER (NSF-DEB-1237491). We are indebted to R. T. Fisher and A. C. Cline for their wisdom and foresight to protect the old-growth systems on the Harvard Tract prior to and following the 1938 hurricane and countless other researchers at the Harvard Forest that have continued to maintain this invaluable ecological laboratory. B. Gallagher and B. Fisher provided assistance with field work. C. Peterson and an anonymous reviewer provided valuable feedback that greatly improved an earlier version of this manuscript.

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