Historic forest composition and structure across an old-growth landscape in New Hampshire, USA[1]

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Abstract. Old-growth forests often represent an important natural benchmark for evaluating the effects of management and changing environmental conditions on forest and ecological dynamics. In regions with a history of extensive land use, such as New England, there is limited opportunity to develop such information, given that only a few old-growth forests remain scattered across a finite portion of the landscape. This study takes advantage of a unique historic data set collected across 250 ha of old-growth forest, within a larger area (2,000 ha), in southern New Hampshire in 1929–30, to characterize natural forest composition, live-tree size distributions, recruitment history, and aboveground biomass conditions across six common regional forest types. Forest composition ranged from areas dominated by *Pinus strobus* L. and *Tsuga canadensis* (L.) Carrière to mixed hardwood forests composed of *Fagus grandifolia* Ehrh., *Betula lenta* L., and *Betula papyrifera* Marshall, and *Acer saccharum* Marshall. Across forest types, smaller diameter classes were composed primarily of shade-tolerant species, namely *T. canadensis* and *F. grandifolia*, whereas larger size classes consisted of *P. strobus* and *T. canadensis*, with the largest size class composed of *P. strobus* exclusively. Age data collected from these forests reflected largely multicohort conditions, with the largest peaks in recruitment documented between the mid-1600s and mid-1700s. Biomass values were positively correlated with stem density, and stratified forests containing high densities of smaller diameter *T. canadensis* in both the understory and midstory as well as *P. strobus* in the overstory tended to have the highest basal area and a greater number of trees within the largest diameter classes ($\geq$ 89 cm). Forests with high basal area densities of large *P. strobus* ($\geq$ 51 cm) had the greatest biomass values. In these sites, understory *T. canadensis* stem density was relatively high, likely suggesting that the stratification of both species accounted for the high biomass values; however, the presence of large-diameter *P. strobus* was most important to generating those high biomass totals. The wide range of composition and structure observed across this landscape likely reflects the historic importance of variability in disturbance processes and site conditions in maintaining a mosaic of forest compositional and structural conditions and may serve as a reference for restoration and conservation activities in areas heavily affected by past land use. Moreover, the disproportionate influence of *P. strobus* on aboveground biomass conditions in areas in which it historically predominated highlights the unique potential of this species for use in regional mitigation strategies.

Key words: aboveground biomass, forest structure, northern hardwood forests, *Pinus strobus*, size distributions, *Tsuga canadensis*

An understanding of the ecological dynamics of forested landscapes unaffected by human activities has been a central component to the development of forest conservation and management strategies for more than a century (Griffith *et al*. 1930,

Lorimer and Frelich 1994, Seymour *et al*. 2002, D'Amato and Palik *et al*. 2017). Much of our knowledge about pre-European settlement forest dynamics comes from old-growth forests, with numerous investigations highlighting the range in forest structural and compositional conditions characterizing those forests, as well as the role of biophysical conditions and disturbance processes in generating those patterns (Hough and Forbes 1943, Woods 2000). In recent decades, knowledge of forest processes has been used to guide forest management that incorporates variability and management targets approximating the natural long-term spatiotemporal dynamics of a given forest system (Bauhus *et al*. 2009). Additionally, retrospective analyses of old-growth forests have been central to comparisons of structural development with and without human intervention (Foster *et al*.1996), allowing for modification of current

management regimes when old-growth conditions are a desired management outcome.

A primary area of emphasis in studies of old-growth forests has been forest structure, given the importance of structural attributes in regulating key ecosystem processes (Spies 1998) and the need for reference conditions for informing ecological forestry approaches (Franklin *et al.* 2007). A characteristic of particular focus has been the size distributions of trees, as described by diameter distributions, because of their relationship with past forest dynamics and overall habitat conditions (Goff and West 1975; Leak 1996; Westphal *et al* 2006). Uneven-aged, old-growth forests are generally characterized by multicohort age structures, and early works have predicted diameter distributions to follow a reverse-J or negative exponential distribution in reflection of that condition (Meyer 1952, De Liocourt 1898). Since that early work, numerous studies have documented alternate distribution forms in old-growth systems, included rotated sigmoid structures, and have related those differences to the influence of historic disturbance patterns, scales of measurement, and forest compositional conditions (Leak 1964, Schmelz and Lindsey 1965, Goodburn and Lorimer 1999, Zenner 2005, Janowiak *et al* 2008).

The role and importance of old-growth forests in terrestrial carbon cycles has become increasingly recognized as concerns have grown over rising atmospheric CO_2 concentrations and temperatures. Research in old-growth landscapes in the western United States has demonstrated the disproportionate contribution of forests to terrestrial carbon stocks because of the large amounts of live-tree biomass relative to secondary forests (Luyssaert *et al.* 2008, Lutz *et al.* 2012). Similarly, analyses of historic data sets of pre-European settlement vegetation in the Upper Midwest region of the United States indicate that historic levels of carbon storage were much greater than modern levels because of a higher abundance of old-growth landscapes containing much larger trees (Rhemtulla *et al.* 2009). Other studies indicate the potential for increased carbon storage as secondary forests age during recovery from past land use (*e.g.*, Woodall *et al.* 2015); however, little information exists for estimating that potential given the lack of intact old-growth forests in regions with a history of extensive land use, such as New England, USA.

This study takes advantage of a unique historical data set to reconstruct the composition and structure of forests across an old-growth forest landscape in southern New England in the early 20th century. Although this region has been greatly altered by human and natural disturbance since their collection, this data set provides an opportunity to describe the variability in structural and live-tree biomass conditions that existed historically, to serve as a potential reference for current conservation and management efforts. The specific objective for this research was to characterize the composition, live-tree size structures, recruitment history, and aboveground biomass conditions for the six common forest types (hemlock, hemlock-hardwood, hardwood, pine, pine-hemlock, and pine-hemlock-hardwood) that covered this landscape in the 1920s before extensive human disturbance, as characterized by Branch *et al* (1930).

Methods. Study Area. The study area occupies approximately 2,000 ha within Pisgah State Park, Winchester, NH (42°49′N, 72°27′W), and data were collected from 250 ha. Soils are composed of prominently shallow podzolic series overlying schist, granite, and gneiss bedrock (D'Amato, Orwig *et al.* 2017). Pisgah State Park is located at the convergence of the northern hardwoods-hemlock-white pine– and transition hardwood-white pine-hemlock–dominated forests (see Westveld 1956 for a detailed description).

Study Methods. This study used an extensive survey of forest conditions led by several graduate students at Harvard Forest in the late 1920s under the supervision of Dr. Richard T. Fisher (Branch *et al.* 1930). The survey consisted of 101, square, 0.04-ha plots, distributed throughout Pisgah State Park across old-growth (74 plots; 73%) and recently harvested forests (27 plots; 27%). Harvested plots were commercially clear-cut 9 mo before sampling, and cut stumps were measured and tallied to reconstruct live-tree conditions. Within each plot, species and diameter at breast height (dbh) was recorded for all trees; the dbh was recorded in 12.7-cm (5-in.) diameter classes for all stems ≥ 25 cm, with all trees ≤ 24.9 cm lumped into a single class, with the minimum stem size falling between 0 and 5 cm. Each site was assigned to 1 of 20 forest types based on the composition of the dominant canopy species in the surrounding area (Branch *et al.*, 1930). Of the 20 forest types
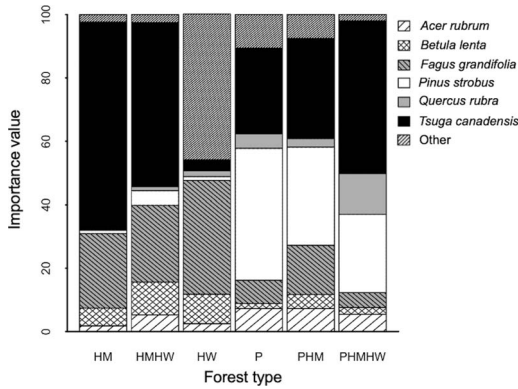
Fig. 1. Importance values (IV) of each species found within each forest type at Pisgah State Forest, NH, in 1929, where HM = hemlock, HMHW = hemlock-hardwood, HW = hardwood, P = pine, PHM = pine-hemlock, and PHMHW = pine-hemlock-hardwood forest types, IV = (*Relative basal area* + *Relative stems ha^{-1}*)/2.

identified by Branch *et al*. (1930), we focused on the six most ubiquitous: hemlock (16 plots; 22%), hemlock-hardwood (8 plots; 11%), hardwood (8 plots; 11%), pine (12 plots; 16%), pine-hemlock (7 plots 9%), and pine-hemlock-hardwood (4 plots; 5%), given the limited sample sizes for the other forest types (see Appendix for a complete list of forest types identified by Branch *et al*. [1930]). Hemlock and hemlock-hardwood sites contained mostly *Fagus grandifolia* Ehrh. and *Tsuga canadensis* (L.) Carrière. The hardwood forest types contained primarily *F. grandifolia*, *Acer saccharum* Marshall, and *Fraxinus americana* L. Pine, pine-hemlock, and pine-hemlock-hardwood forest types consisted mainly of *Pinus strobus* L. and *T. canadensis*, with smaller amounts of *Quercus rubra* L. and *F. grandifolia* (Fig. 1). This study builds on previous work that applied these historic data collections to generate landscape-wide age and diameter distributions to interpret the influence of topographic setting on historic forest conditions (Foster 1988). The focus of the present study was to use these data to characterize the range of structural and compositional conditions found across this old-growth landscape and to expand those measurements to estimate historic levels of aboveground biomass in these areas.

For each old-growth forest type we calculated basal area (m^2 ha^{-1}); stem density in trees (ha^{-1}); species importance values (IV), based on relative basal area and relative stem density (Curtis and McIntosh 1951); and aboveground biomass values.

Tree recruitment distributions were constructed for each forest type using data collected from 137 stumps sampled across the 27 logged sites with these forest-type groupings. No further analyses were conducted on the logged sites. Ring counts were made in the field by laying strips of paper radially on each stump and marking every tenth ring (Branch *et al*. 1930). Wood samples were not cross-dated; therefore, establishment dates should be interpreted as approximations. Additionally, it is likely that nonmerchantable individuals were not removed during those clearcuts, so reconstructed age structures may be biased toward those species and individuals harvested. Similarly, the age estimates collected from these sites may reflect a bias toward species for which ring counts were easily obtained in the field. Average year of establishment was calculated for trees within each forest type in an attempt to identify common establishment dates across forest types. No age data were collected from the 74 old-growth sites.

Data Analysis. The shape of live-tree diameter distributions was determined following the approach outlined by Janowiak *et al*. (2008), as adapted from Leak (1996). In short, diameter class (dbh), dbh^2, and dbh^3 were regressed (using the 'glm' function in R) against the base-10 logarithms of the values of trees per hectare for each 12.7-cm class to approximate common distribution forms documented in old-growth and managed forests (negative exponential, increasing-q, rotated sigmoid, concave, and unimodal, following Janowiak *et al*. 2008). The model with the lowest corrected Akaike information criterion (AIC$_c$) score for a given forest type was selected as the best-approximating model. The shape of the distribution was then determined based on interpretation of parameter direction (positive or negative) and the significance of the coefficients (Table 1; Janowiak *et al*. 2008). R-squared values between actual and predicted base-10 logarithms of the values of trees per hectare were calculated using the 'cor.test' function in R (Table 1). The diameter classes used in this work were limited to the broad classes established by Branch *et al*. (1930), which may have limited our ability to detect patterns more apparent if finer-scale demarcations of size classes were used.

Biomass values for each of the six cover types were calculated using the species-specific equations in Jenkins *et al*. (2004). A one-way ANOVA and Dunnett's test were used to examine the influence of forest type on aboveground biomass.

Table 1. Distribution shape and signs (+ or −) of significant coefficients in best-approximating polynomial-regression models used to determine diameter-distribution shape (based on smallest AIC_c).

Forest type	dbh	dbh²	dbh³	AIC_c	r^2	Shape
Hemlock	−	ns	ns	1.04	0.95	NE
Hemlock-hardwood	−	ns	ns	−4.75	0.97	NE
Hardwood	−	ns	−	−41.12	0.999	RS
Pine	−	ns	−	−2.75	0.98	RS
Pine-hemlock	−	ns	ns	5.03	0.83	NE
Pine-hemlock-hardwood	−	+	ns	−5.64	0.99	CO

Abbreviations: dbh = diameter at breast height, AIC_c = corrected Akaike information criterion, ns = not significant, NE = negative exponential, RS = rotated sigmoid distribution, CO = concave.

Additionally, the relationship between above-ground biomass and forest density was examined using linear regressions. Regressions were run using plot-level biomass values, based on all measured trees and on those derived from trees ≥ 51 cm only to evaluate the influence of large-tree biomass on population-level values. All statistical analyses were run in the programming environment R version 3.4.1 (R Core Team 2017).

Results. LIVE-TREE STAND ATTRIBUTES. *Hemlock.* Hemlock forests averaged 58.81 m² ha⁻¹ of basal area and were dominated by *T. canadensis*, with lesser amounts of *F. grandifolia* (Fig. 1; Table 2). Age data were only collected for *T. canadensis* throughout this forest type, and the mean year of establishment for this species was 1620 (Fig. 2A; Table 3). Several *T. canadensis* individuals were older than 320 yr at the time of harvesting (*i.e.*, established before 1610; Fig. 2A). Live-tree distribution was best approximated by a negative exponential distribution (Table 1) with *F. grandifolia* being the most dominant in the smallest size class and *T. canadensis* being most dominant throughout all other size classes (Fig. 3A; Table 3).

Hemlock-Hardwood. Hemlock-hardwood forests averaged 46.63 m² ha⁻¹ of basal area. *Tsuga canadensis* was the dominant species in this forest type, with *F. grandifolia* a significant component, particularly in the smaller size classes; other species were low in abundance (Fig. 1; Table 2). The mean year of establishment of the trees was 1729, with a large number of *T. canadensis* established between 1640 and 1670 (Fig. 2B). Live-tree distribution was best approximated by a negative exponential distribution (Table 1). *Fagus grandifolia* was the dominant in size classes < 64 cm, whereas *P. strobus* and *Betula lenta* L. were the most abundant species in size classes ≥ 76 cm, with *P. strobus* in the largest size class (Fig. 3B; Table 3).

Hardwood. Hardwood forests averaged 49.9 m² ha⁻¹ of basal area and were dominated by *F. grandifolia* with lesser amounts of other hardwood species, including *A. saccharum*, *Acer pensylvanicum* L., and *B. papyrifera* (Fig. 1; Table 2). The mean year of establishment of trees within this forest type was 1717, with a large number of *Castanea dentata* (Marshall) Borkh. (under "other") and *F. grandifolia* established in the mid-1700s (Fig. 2C). Live-tree distribution for this forest type was best approximated by a rotated sigmoid distribution (Table 1), with *F. grandifolia* being the dominant species in the smallest size

Table 2. Basal area densities of each species within a forest type (m² ha⁻¹).

Forest type	ACRU	BELE	FAGR	PIST	QURU	TSCA	Other
Hemlock	0.87	3.1	3.99	1.05	0.19	48.5	1.1
Hemlock-hardwood	3.4	5.77	10.13	3.32	0.70	22.68	0.63
Hardwood	1.19	4.64	10.85	0.98	1.09	0.58	30.58
Pine	2.61	0.34	1.66	46.57	3.28	14.11	5.14
Pine-hemlock	1.92	0.54	2.17	33.96	0.59	22.50	1.66
Pine-hemlock-hardwood	2.6	1.1	1.83	19.89	7.92	23.9	0.54

Abbreviations: ACRU = red maple, *Acer rubrum* L.; BELE = sweet birch, *Betula lenta* L.; FAGR = American beech, *Fagus grandifolia* Ehrh.; PIST = eastern white pine, *Pinus strobus* L.; QURU = northern red oak, *Quercus rubra* L.; TSCA = eastern hemlock, *Tsuga canadensis* (L.) Carrière.
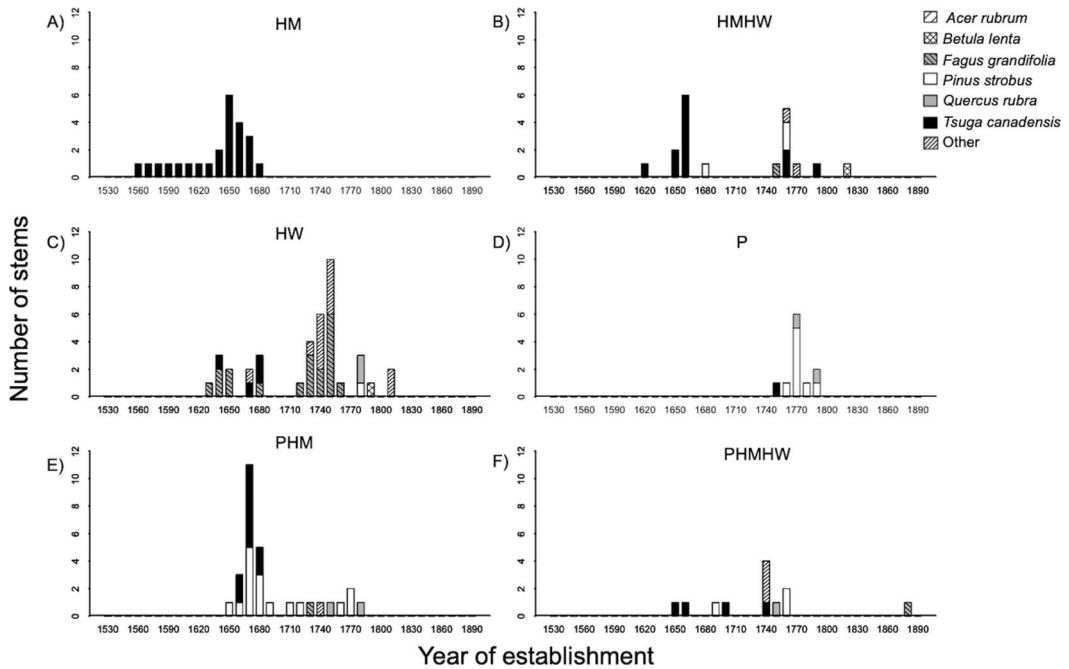
FIG. 2. Age distribution determined from 27 logged sites for the following forest types (A) hemlock (*n* = 26), (B) hemlock-hardwood (*n* = 19), (C) hardwood (*n* = 39), (D) pine (*n* = 11), (E) pine-hemlock (*n* = 30), and (F) pine-hemlock-hardwood (*n* = 12) forest types (n = the number of individuals measured at each site). Age data were collected by Branch *et al.* (1930) by laying strips of paper radially on each stump and marking every tenth ring. Ages displayed are grouped in 10-year intervals (e.g. trees shown to be established in 1750 contain all trees established between 1750 and 1759). *n* = number of stems.

class, and various other hardwood species dominating between 25 and 64 cm. *Pinus strobus* was the only species with diameters ≥ 64 cm (Fig. 3C; Table 3).

Pine. Pine forests averaged 73.71 m² ha⁻¹ of basal area and were dominated by *P. strobus*, with lesser amounts of *T. canadensis* (Fig. 1; Table 2). The mean year of establishment was 1773, with most *P. strobus* trees established between 1770 and 1780 (Figure 2D). Live-tree distribution was best approximated by a rotated sigmoid distribution (Table 1),

with *T. canadensis* being most abundant in the smallest two size classes, and *P. strobus* dominating all size classes ≥ 38 cm (Fig. 3D; Table 3).

Pine-Hemlock. Pine-hemlock forests averaged 63.3 m² ha⁻¹ of basal area and were dominated by *T. canadensis* in terms of density; however, *P. strobus* dominated the largest diameter classes. *Fagus grandifolia* was found in lesser amounts but was among the more-prevalent species (Fig. 1; Table 2). The mean year of establishment of trees within this forest type was 1708, with cohorts of *P. strobus* and

Table 3. Stem densities per species with each forest type (no. of trees ha⁻¹).

Forest type	ACRU	BELE	FAGR	PIST	QURU	TSCA	Other
Hemlock	14	39	266	2	2	319	22
Hemlock-hardwood	22	56	176	6	6	364	25
Hardwood	22	77	417	3	12	49	259
Pine	107	27	122	196	45	344	138
Pine-hemlock	42	46	155	134	21	251	74
Pine-hemlock-hardwood	92	35	92	219	170	805	42

Abbreviations: ACRU = red maple, *Acer rubrum* L.; BELE = sweet birch, *Betula lenta* L.; FAGR = American beech, *Fagus grandifolia* Ehrh.; PIST = eastern white pine, *Pinus strobus* L.; QURU = northern red oak, *Quercus rubra* L.; TSCA = eastern hemlock, *Tsuga canadensis* (L.) Casrrière.
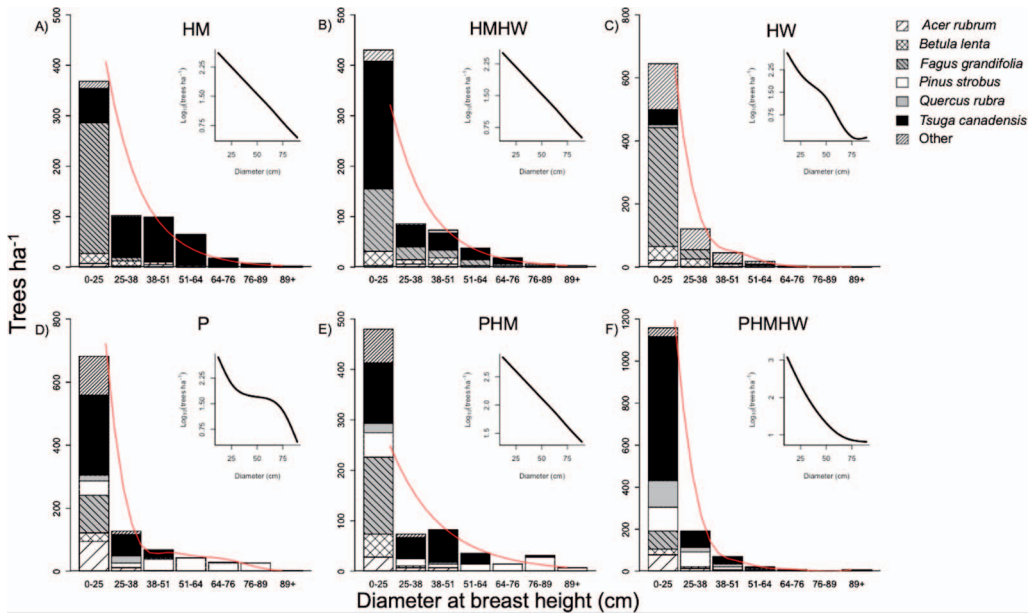
FIG. 3. Diameter distributions grouped by species for (A) hemlock, (B) hemlock- hardwood, (C) hardwood, (D) pine, (E) pine-hemlock, and (F) pine-hemlock-hardwood forest types. Diameter-class bins reflect size classes used by Branch *et al.* (1930) for tallying trees. All individuals within the largest size class for each forest type are *Pinus strobus*. Trend line represents best-approximating curve form based on criteria outlined by Janowiak *et al.* (2008). Curves in the top right corner of each diameter distribution represent the predicted $\log_{10}$ value for trees per hectare, regressed against diameter (see Table 1).

T. canadensis establishing between 1650 and 1690 (Fig. 2E). Live-tree distribution for this forest type was best approximated by a negative-exponential distribution (Table 1), with *T. canadensis*, *F. grandifolia*, and *B. lenta* most common in the smaller diameter classes (< 51cm) and *P. strobus* found across all size classes (Fig. 3E; Table 3).

Pine-Hemlock-Hardwood. Pine-hemlock-hardwood forests averaged 57.78 m^2 ha^{-1} of basal area and were dominated by *T. canadensis*, with lesser amounts of *P. strobus* and *Q. rubra* (Fig. 1; Table 2). The mean year of establishment for this forest type was 1730, with several *T. canadensis* and *P. strobus* established between 1650 and 1700 (Fig. 2F). Live-tree distribution for this forest was best approximated with a concave distribution (Table 1), with *T. canadensis*, *F. grandifolia*, and *Q. rubra* most common in the smaller-diameter classes (< 51 cm), and *P. strobus* found across most classes in low abundance, including the largest diameter class (Fig. 3F; Table 3).

Biomass. Overall, there was a significant difference in average biomass conditions across forest types ($F_{5,49} = 4.68$, $P = 0.001$). Hemlock

forest biomass values were significantly lower than hardwood forests and were marginally and insignificantly lower than hemlock-hardwood forests (Fig. 4; $P = 0.028$ and $P = 0.069$, respectively). These trends could be expected, given the relatively low biomass of hemlock forests and the high range in variation for biomass values associated with each forest type (Fig. 4). Pine forests had the greatest range and the largest plot-level biomass value (705 Mg ha^{-1}), whereas hardwood forests had the highest average biomass value across plots (202 Mg ha^{-1}). There was a positive, significant relationship between aboveground biomass and live-tree stem density (Fig. 5A; $P = 0.002$, $r^2 = 0.15$) and large-tree (≥ 51 cm dbh) stem density (Fig. 5B; $P < 0.001$, $r^2 = 0.51$) across forest types. Given *P. strobus* often occupied the larger-diameter class in the forest types in which it occurred, there was a strong positive relationship between large *P. strobus* density and total aboveground biomass in those areas (Fig. 5C; $P < 0.001$, $r^2 = 0.96$).

Discussion. Land use has had a central role in the vegetation dynamics of most landscapes
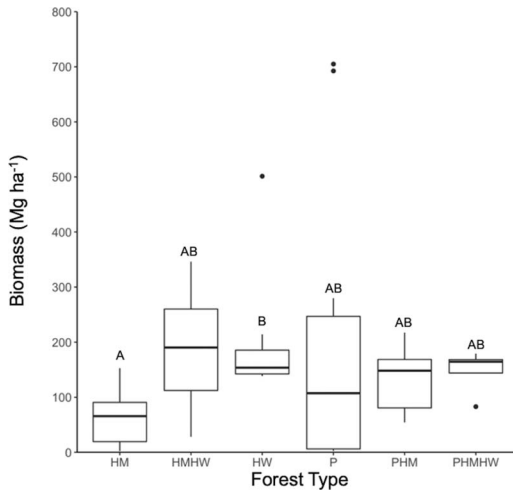
Fig. 4. Biomass values for most common old-growth forest types in Pisgah State Park in 1929 (HM = hemlock, HMHW = hemlock-hardwood, HW = hardwood, P = pine, PHM = pine-hemlock, and PHMHW = pine-hemlock-hardwood). Values within the boxes represent the interquartile range (IQR) of the data, and the black line represents the median. The whiskers of each plot represent the fifth and ninety-fifth percentile of the data, and black dots are outliers that fall outside the fifth and ninety-fifth percentile of the data. Different letters above data represent significant differences between groups as determined by a Dunnett's test.

encompassed by eastern deciduous forest in North America. Despite that, an understanding of natural forest conditions remains a critical element for guiding sustainable forest-management strategies and for informing modeling efforts as the contemporary forests occupying modern landscapes mature. This understanding of natural forest dynamics was what led early ecologists, such as Richard Fisher, to the area now encompassed by Pisgah State Park and generated the unique data collections applied in the present study (Fisher 1933). Most contemporary old-growth stands often occupy inaccessible or low–timber-value portions of the landscape that escaped past land use (Stahle and Chaney 1994, Therrell and Stahle 1998, D'Amato *et al*. 2006) and may not fully represent the full range of conditions found in forests before European settlement (Lorimer and White 2003). As such, the Pisgah forests have been an important focus of numerous studies regarding old-growth New England forests, considering its anomalously wide range in old-growth forest conditions (Foster 2014). Despite the relatively coarse nature of the
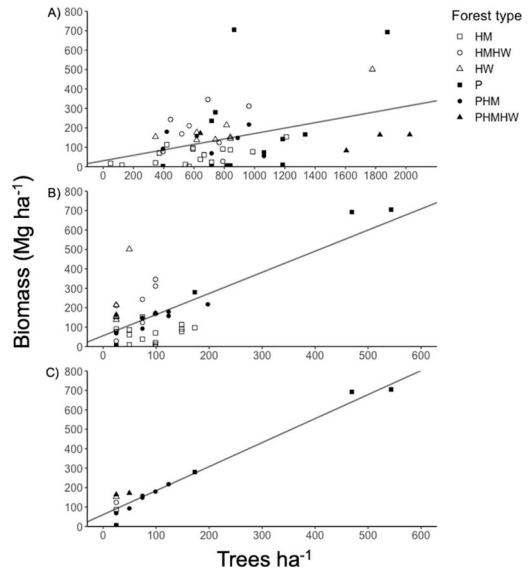

Fig. 5. Relationship between aboveground biomass and tree density across primary forest types in Pisgah State Park in 1929, and the black line represents the best-approximating linear model. Note trend lines are meant for describing general relationships and are not meant to serve as predictive models for aboveground biomass. HM = hemlock, HMHW = hemlock-hardwood, HW = hardwood, P = pine, PHM = pine-hemlock, and PHMHW = pine-hemlock-hardwood forest types. To illustrate the influence of large stems on these values, (A) represents biomass-density relationships for all forest types ($r^2 = 0.15$, $P = 0.002$), (B) density is based on only measured stems $\geq$ 51 cm diameter at breast height (dbh; $r^2 = 0.51$, $P < 0.001$), and (C) density only includes *Pinus strobus* stems $\geq$ 51 cm dbh ($r^2 = 0.96$, $P < 0.001$). The data from part c only consist of sites with a *P. strobus* component.

historic data used in this study, they provide a novel opportunity to illustrate the range in composition and structure for several old-growth forest types across a natural landscape, something not afforded by extant New England forests. Results highlight the great range in composition and live-tree structural conditions characterizing these forests, including aboveground biomass values that approach the maximum reported for forests in eastern North America (Whitney 1994, Keith *et al*. 2009).

Species Composition. *Pinus strobus* and *T. canadensis* co-occurred across several old-growth forest types in the Harvard Tract of Pisgah State Park, a 10-ha portion of the study area purchased by Harvard University in the late 1920s to protect

one of the few remaining old-growth areas in this landscape at that time. This area was heavily affected by the 1938 hurricane and was protected from subsequent salvage logging activities; however, *P. strobus* has largely been lost as a canopy species as a result (D'Amato, Orwig *et al.* 2017). Branch *et al.* (1930) noted little *P. strobus* regeneration, with the highly shade-tolerant *F. grandifolia* and *T. canadensis* dominating subcanopy layers. Age data collected by Branch *et al.* (1930) suggests that many *P. strobus* and *T. canadensis* trees established within the same decade, presumably after moderate to severe canopy disturbance. Similar trends were observed in old-growth stands in Pennsylvania, USA, where *P. strobus* developed above similarly aged and suppressed *T. canadensis* until subsequent canopy disturbance released *T. canadensis* into overstory positions (Abrams and Orwig 1996).

In the hardwood forest type, *F. grandifolia* was the dominant species, which is consistent with descriptions of pre-European settlement forest composition for northern hardwood forests in the region (Siccama 1971, Lorimer 1977, McGee *et al.* 1999, Cogbill 2000, Thompson *et al.* 2013). Specifically, *F. grandifolia* was most prevalent in the smallest size class, a trend that has been observed in other old-growth northern hardwood forests (McGee *et al.* 1999; Orwig *et al.* 2001). The abundance of *B. lenta* in these areas also aligns with pre-European settlement surveys for southern New England, which indicated this species as one of the most common *Betula* species on the landscape (Cogbill *et al.* 2002).

BASAL AREA AND STEM DENSITY. Values for basal area across old-growth forest types in Pisgah State Park were comparable to those quantified for other regions of the eastern United States. In particular, old-growth forests examined in this study had basal area values of 46.63–73.71 m² ha⁻¹ across forest types, which are slightly higher than the median value reported in a broad synthesis of temperate old-growth forest structure across North America (44.4 m² ha⁻¹; Burrascano *et al.* 2013). Additionally, the mean basal area value for old-growth hardwood forests in this study (49.9 m² ha⁻¹) was higher than those found in Adirondack State Park, NY, perhaps because of the loss of the large overstory beech from these latter areas in the 1970s from beech bark disease (33.7 m² ha⁻¹; McGee *et al.* 1999, McGee 2000). Values found for other forest types were consistent with studies of comparable old-growth

forests in the region. The mean basal area value in hemlock forests (58.81 m² ha⁻¹) was within the range of those found in numerous studies examining these forests in eastern USA, although on the higher end (44 m² ha⁻¹ [D'Amato and Orwig 2008]; 24–61 m² ha⁻¹ [Ziegler 2000]; and 47.8–52.7 m² ha⁻¹ [Busing *et al.* 1998]). Because basal-area values were calculated based on the average dbh for each size class, estimates of basal area may be inflated given the greater detection probabilities for stems in the lower versus upper portions of a given size class when using fixed-area plots (Avery and Burkhardt 2002).

There are few extant old-growth *P. strobus*–dominated forests; however, basal area values from old-growth stands in Cook Forest, PA (78.6 m² ha⁻¹ [Abrams and Orwig 1996]) were greater than those found in Pisgah State Forest in the 1920s (57.78–73.71 m² ha⁻¹ for forest types with a dominant *P. strobus* component). That difference may reflect a longer growing season length and greater soil fertility at the Cook Forest, which allows for greater tree sizes at that location relative to that at Pisgah State Park. Additionally, old-growth forests in Cook Forest contained many *T. canadensis* trees > 80 cm in diameter, whereas, in Pisgah State Park, the largest size class was solely dominated by *P. strobus* (Abrams and Orwig 1996). Overall, forest types with a *P. strobus* component tended to have the highest basal areas because of the stratified stands developing in those areas. This is consistent with other work that has demonstrated the unique contribution of *P. strobus* in old-growth stands in terms of increasing live-tree basal area (Roovers and Shifley 2003, Bebber *et al.* 2004).

BIOMASS CONDITIONS. As with basal area, average biomass values in the forests examined fell within the range reported for other old-growth forests in the eastern United States (220–260 Mg ha⁻¹; Brown *et al.* 1997, Keeton *et al.* 2011, Burrascano *et al.* 2013). Beyond average conditions, individual plots had biomass values that approached the maximum values reported elsewhere for old-growth forests in northeastern North America (Keith *et al.* 2009, Woods 2014, D'Amato, Orwig *et al.* 2017), particularly those with a *P. strobus* and *T. canadensis* component. That likely reflects complementarity in light requirements between the two species, which resulted in greater biomass values because of species packing in different canopy strata. In particular, *P. strobus*

often grows at a faster rate than *T. canadensis*; however, *T. canadensis* is able to thrive underneath a *P. strobus* canopy because of its shade tolerance (Kelty 1989, Jucker *et al.* 2014, D'Amato et. al. 2017). There was also a considerable range in aboveground biomass conditions within a given forest type, with lower values likely corresponding to areas experiencing recent disturbance or containing lower-quality site conditions.

Luyssaert *et al.* (2008) found that increased stem density was associated with decreased biomass accumulation, presumably because of the lower abundance of large trees in stands with more stems. We found the opposite trend in the present study, a trend that can be ascribed to the stratified nature of the forests examined with many shade-tolerant species (*e.g.*, *T. canadensis* and *F. grandifolia*) additively increasing biomass beneath larger, upper canopy *T. canadensis*, *P. strobus*, and hardwood species (Kelty 1989, Jucker *et al.* 2014, D'Amato et. al. 2017). Nevertheless, we found that biomass values were primarily driven by the number of large *P. strobus* stems, regardless of stem density in the smaller size classes. Areas with large trees, specifically large *P. strobus*, generally had the greatest biomass values, which is consistent with previous work demonstrating the disproportionate influence of large-diameter trees in affecting biomass values in old-growth forests (Luyssaert *et al.* 2008, Rhemtulla *et al.* 2009, Stephenson *et al.* 2014, Lutz *et al.* 2018). The considerable variation in biomass values within a given forest type likely reflects historic disturbances and differences in growing conditions across the landscape, as well as the small plot sizes used in this work.

RECRUITMENT HISTORY. The age data examined in this study are coarse in nature and lack the sample sizes necessary for detailed reconstructions of stand history; however, several general trends that are consistent with prior studies at this site and across eastern North America are worth noting. Similar patterns in canopy-age structure have been observed across forests in the eastern United States, in which pulses in establishment occurred in the mid-1600s as well as the mid-1700s, presumably because of increased disturbance, drought, and frost events documented during those periods, leading to an increased potential for establishment (Pederson *et al.* 2014; Trouet *et al.* 2017). Studies of old-growth forests across western Massachusetts documented synchronous recruitment peaks and canopy distur-

bance events during the 1780s and 1790s and ascribed those patterns to the 1788 hurricane (D'Amato and Orwig 2008). A recent synthesis of dendroecological data across central New England and New York documented a similar peak in age structure during the 1780s and 1790s (Pederson *et al.* 2017). Given the coarse nature of the dendrochronological data in the present study, it is unclear how closely the recruitment events at Pisgah State Park align with those documented elsewhere during that period. Nonetheless, the overall recruitment patterns at Pisgah do suggest that the regional-scale disturbance pulses affecting historic forest conditions, documented in other portions of the northeast region, may have also affected the stands sampled in the present study. These and other disturbance events were likely a key factor in generating the wide range of forest compositional and structural conditions described across this landscape.

Pinus strobus was found in multiple age classes in all but one forest type in which it was documented. That trend was also noted in northeast Wisconsin and the upper peninsula of Michigan, in which more than one age class of *P. strobus* was a common occurrence across old-growth forests (Fahey and Lorimer 2014). Multicohort recruitment of *P. strobus* was also noted in the southern Appalachians and western Pennsylvania (Abrams *et al.* 1995; Abrams and Orwig 1996). Although the dominance of *P. strobus* in old-growth areas has often been ascribed to stand-replacing fires, it may also highlight the ability of this species to recruit over time in these forests, particularly when disturbance processes, such as windthrow and low severity fire, interact with edaphic conditions, such as the shallow soils in ridgetop portions of Pisgah State Park, to provide favorable sites for establishment (Fahey and Lorimer 2014). Similarly, *Q. rubra*, a species often associated with larger canopy openings and fire, was documented in several of the forest types examined, suggesting a similar potential interplay between site conditions and disturbance processes in supporting its historic recruitment in this landscape.

SIZE DISTRIBUTIONS. Live-tree size distributions are often reflective of past disturbance history, site conditions, and the silvical characteristics of constituent species (Leak 1964, Schmelz and Lindsey 1965, Goodburn and Lorimer 1999, Zenner 2005, Janowiak *et al.* 2008). Negative exponential distributions have often been attributed to forests dominated by shade-tolerant species

that experience frequent, fine-scale disturbance (Leak 1964, D'Amato and Orwig 2008), whereas departures from that form reflect more-moderate canopy disturbance and admixtures of species of varying tolerances (Schmelz and Lindsey 1965, Goff and West 1975, Zenner 2005). These trends are generally reflected in the best-approximating curve forms for describing live-tree distributions; however, the level of precision on diameter classes was comparatively low in the present study in comparison to similar studies, limiting our ability to fully detect the influence of past dynamics. In particular, forest types dominated by the very shade-tolerant *T. canadensis* (hemlock, pine-hemlock, and hemlock-hardwood) had distributions best represented by negative exponential distributions. In contrast, pine and hardwood forest types were best described by rotated sigmoid distributions, whereas pine-hemlock-hardwood expressed concave distributions. The tendency toward rotated sigmoid distribution curve forms in cover types containing *P. strobus* likely reflects the combined distributions of upper-canopy *P. strobus* with the descending monotonic distributions of the subordinate, shade-tolerant species in those stands (*e.g.*, Fig. 3D). A similar dynamic was observed in old-growth *Pseudotsuga menziesii* (Mirb.) Franco × *Tsuga heterophylla* (Raf.) Sarg. forests in the Pacific Northwest, USA, in which the combination of emergent *P. menziesii* with abundant *T. heterophylla* in the lower-canopy strata resulted in rotated sigmoid forms (Zenner 2005).

Conclusions. The historic data used in this study provided an opportunity to further describe the structure and composition of old-growth forests in southern New England. Average structural conditions, such as biomass, basal area, and stem density, documented across this landscape were similar to site-level studies from the region; however, the range in conditions characterizing these forests is equally noteworthy. Although shade-tolerant species, namely *T. canadensis* and *F. grandifolia*, dominated many of these areas, less-tolerant species, often associated with larger canopy disturbances, such as *P. strobus* and *Q. rubra*, were also a significant component of many of the forests examined. These findings highlight the importance of historic disturbance processes in maintaining a range of compositional conditions across the landscape and the resultant effects on forest structure and biomass stocks. Specifically, forest types that contained high densi-

ties of *P. strobus* in the larger-diameter classes tended to have higher biomass values, reflecting the importance of this species in affecting localized aboveground carbon stocks. This finding is particularly important in the context of emerging management objectives around increasing forest-carbon benefits, because strategies for encouraging stratified mixed-species forests that contain upper canopy *P. strobus* may provide the greatest potential for maximizing on-site carbon stores, particularly if larger-diameter individuals are retained on site.

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Appendix

Forest type	Dominant species
Beech-birch-maple (2 plots)	*Acer saccharum, Betula lenta, Fagus grandifolia Fraxinus americana, Ostrya virginiana*
Black birch-beech-hemlock (1 plot)	*Acer pensylvanicum, Betula lenta, Fagus grandifolia, Picea rubens, Tsuga canadensis*
Chestnut-oak-beech (1 plot)	*Acer pensylvanicum, Betula lenta, Betula papyrifera, Castanea dentata* (standing/downed dead), *Fagus grandifolia, Tsuga canadensis*
Hardwood (8 plots)	*Acer pensylvanicum, Acer rubrum, Acer saccharum, Betula lenta, Betula papyrifera, Fagus grandifolia, Fagus americana, Pinus strobus, Quercus rubra, Tsuga canadensis*
Hemlock (16 plots)	*Acer pensylvanicum, Acer rubrum, Acer saccharum, Betula alleghaniensis, Betula lenta, Betula papyrifera, Castanea dentata* (standing/downed dead), *Fagus grandifolia, Picea rubens, Pinus strobus, Quercus rubra, Tsuga canadensis*
Hemlock-hardwood (8 plots)	*Acer pensylvanicum, Acer rubrum, Acer saccharum, Betula alleghaniensis, Betula lenta, Fagus grandifolia, Pinus strobus, Prunus serotina, Quercus rubra, Tsuga canadensis*
Hemlock-oak (1 plot)	*Acer rubrum, Fagus grandifolia, Quercus rubra, Tsuga canadensis*
Hemlock-oak-pine (2 plots)	*Acer rubrum, Betula lenta, Pinus strobus, Quercus rubra, Tsuga canadensis*
Hemlock-spruce (1 plot)	*Betula lenta, Picea rubens, Tsuga canadensis*
Hole in pine-hemlock (1 plot)	*Acer rubrum, Fagus grandifolia, Pinus strobus, Tsuga canadensis*
Oak-paper birch-maple (1 plot)	*Acer rubrum, Betula lenta, Betula papyrifera, Fagus grandifolia, Quercus rubra, Tsuga canadensis*
Opening in pine-hemlock (1 plot)	*Fagus grandifolia, Tsuga canadensis*
Oak ridge (3 plots)	*Acer pensylvanicum, Acer rubrum, Acer saccharum, Betula lenta, Betula papyrifera, Fagus grandifolia, Fagus americana, Ostrya virginiana, Pinus strobus, Quercus rubra, Tsuga canadensis*
Pine-hemlock (7 plots)	*Acer pensylvanicum, Acer rubrum, Betula alleghaniensis, Betula lenta, Betula papyrifera, Fagus grandifolia, Picea rubens, Pinus strobus, Quercus rubra, Tsuga canadensis*
Pine-hardwood (2 plots)	*Acer pensylvanicum, Acer rubrum, Betula lenta, Betula papyrifera, Picea rubens, Pinus strobus, Quercus rubra, Tsuga canadensis*
Pine (12 plots)	*Acer rubrum, Betula lenta, Betula papyrifera, Fagus grandifolia, Picea rubens, Pinus strobus, Populus spp., Prunus pensylvanica, Quercus alba, Quercus rubra, Tsuga canadensis*
Pine-hemlock-hardwood (4 plots)	*Acer pensylvanicum, Acer rubrum, Betula lenta, Betula papyrifera, Fagus grandifolia, Pinus strobus, Quercus rubra, Tsuga canadensis*
Pine-oak (1 plot)	*Acer rubrum, Betula lenta, Betula papyrifera, Pinus strobus, Quercus rubra, Tsuga canadensis*
Pine-oak-hardwood (1 plot)	*Acer rubrum, Betula lenta, Betula papyrifera, Fagus grandifolia Pinus strobus, Quercus rubra, Tsuga canadensis*
Red oak ridge (1 plot)	*Acer rubrum, Betula lenta, Betula papyrifera, Picea rubens, Pinus strobus, Quercus rubra, Tsuga canadensis*