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Building a foundation: land-use history and dendrochronology reveal temporal dynamics of a *Tsuga canadensis* (Pinaceae) forest

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ABSTRACT. We used historical documents, stand mapping, and new methods of dendrochronological analysis to reconstruct 250 years of land-use history of the Simes Tract in Petersham, Massachusetts. These data were then used to interpret the origin of the current forest stand structure of the experimental plots of the Harvard Forest Hemlock Removal Experiment within the Simes Tract, an experiment that examines the effects on forest ecology of the ongoing decline of *Tsuga canadensis*. Data from tree cores revealed that the trees in the experimental plots were < 150 years old. These trees have established continually since the 1870s, with recruitment pulses following successive episodes of land division and re-aggregation, logging, irruptions of pathogens and pests, two moderate droughts, and the 1938 hurricane. Our new method of dendrochronological analysis used generalized additive models and focused on year-to-year dynamics to highlight associations between fine scale changes in tree growth, and both episodic (pulse) and longer-term environmental and biotic drivers. *Tsuga canadensis*, hypothesized to be a foundation species in this system, achieved its current dominance at the Simes Tract by responding rapidly, both positively and uniformly across age classes, in the 1920s to three concomitant environmental changes that occurred in the preceding two decades: loss of *Castanea dentata* to the chestnut blight; selective logging; and a ≈7-year drought. In contrast, *Betula lenta, Quercus rubra, Acer rubrum,* and *Pinus strobus* have declined in importance since the early 1900s in stands otherwise dominated by *T. canadensis*. *Acer rubrum* and *P. strobus* were selectively harvested or severely damaged by the 1938 hurricane, the peak of *Betula lenta* establishment followed the 1938 hurricane, and *Q. rubra* growth was impacted by the severe1981 gypsy moth outbreak. Together, the data illustrate the contingent nature of the establishment dynamics of a foundation species in a New England forest and suggest a more nuanced approach to the role of *T. canadensis* as a foundation species.

Key Words: dendrochronology, foundation species, general additive model, Harvard Forest, land-use history, Massachusetts, *Tsuga canadensis*

Foundation species are taxa that exert disproportionate control on species composition and ecosystem structure and function (Dayton 1972; Ellison et al. 2005a). In forests, foundation species are trees that often are long-lived, dominant in numbers and biomass, are associated with unique assemblages of other plants and animals, and that modulate energy and nutrient cycling in ways that contrast sharply with processes mediated by congeners or co-occurring species (reviewed in Ellison et al. 2005a; Ellison and Baiser 2014). In eastern North America, a substantial body of evidence now supports the hypothesis that eastern hemlock, *Tsuga canadensis* (L.) Carr. (Pinaceae), is a foundation species (Ellison et al. 2014; Orwig et al. 2013).

This long-lived conifer ranges over ≈ 10,000 km^2 from Georgia north into southern Canada and west into Michigan and Wisconsin (Figure 1). Across its range, *T. canadensis* accounts for ≈ 2×10^8 m^3 of harvestable volume, and in many regions, *T. canadensis* can comprise > 50% of the total basal area in a given stand (Rogers 1980; Smith et al. 2009). The dark understory beneath its dense canopy hosts unique assemblages of birds, arthropods, and salamanders (Dilling et al. 2007; Ellison et al. 2005b; Mallis and Rieske 2011; Mathewson 2009; Rohr et al. 2009; Sackett et al. 2011; Tingley et al. 2002), and the streams associated with *T. canadensis* forests support specialist communities of aquatic invertebrates and fish (Siderhurst et al. 2010; Snyder et al. 2002).

The needles of *T. canadensis* are acidic and slow to decompose (Cobb et al. 2006) and organic matter accumulates rapidly beneath *T. canadensis* canopies (Aber and Melillo 1991). Soils beneath this canopy are cool and nutrient-poor; both nutrient cycling (Jenkins et al. 1999; Orwig et al. 2008, 2013; Stadler et al. 2005) and carbon flux (Ford et al. 2012; Hadley et al. 2008; Lovett et al. 2006; Nuckolls et al. 2009; Savage and Davidson 2001) are slower in *T. canadensis* stands than in stands dominated by hardwoods or other conifers.

From southern Vermont, New Hampshire, and Maine south to Georgia, *T. canadensis* is dying from infestations by a nonnative insect, the hemlock woolly adelgid (*Adelges tsugae* Annand). This adelgid was introduced to the United States from Japan in the early 1950s. Since its initial introduction near Richmond, Virginia, *A. tsugae* has spread primarily northeast and southwest, but it crossed over to the western side of the Appalachian Mountains sometime in the late 1990s or early 2000s (Fitzpatrick et al. 2010, 2012; Morin et al. 2009). *Tsuga canadensis* has little, if any, resistance to the hemlock woolly adelgid (Ingwell and Preisser 2011) and rarely recovers from chronic infestations (McClure 1995; Orwig et al. 2012). In many infested stands, more than 90% of *T. canadensis* dies within 10 years of the establishment in the stands of the adelgid (Eschtruth et al. 2006; Knoepp et al. 2011; Orwig et al. 2002).

Most of the data on the responses of *T. canadensis*-dominated systems to infestation by the adelgid has come from observational studies of stands either as they are declining or after *T. canadensis* has died (e.g., Eschtruth et al. 2006; Ford et al. 2012; Krapfl et al. 2011; Orwig et al. 2002, 2008, 2012; Small et al. 2005), but four manipulative experiments have examined forest dynamics in response to *T. canadensis* decline (Brooks 2001; Ellison et al. 2010; Nuckolls et al. 2009; Yorks et al. 2003). The authors of all of the experimental studies were aware that the areas where they were studying *T. canadensis* stands had a history of selective logging or other allogenic disturbances (sensu Oliver and Stephens 1977) within 50–100 years of the establishment of their experiments (Brooks 2001; Elliott et al. 1999; Foster et al. 1992; Kudish 1985). However, the influences of land-use history and forest succession on the observed responses to their experimental manipulations have not been quantified because plot-specific land-use history has not been known in detail for any of the experimental sites. Without accounting for land-use history, researchers are likely to draw erroneous conclusions about the role of *T. canadensis* or other forest foundation species in controlling forest dynamics (Foster et al. 1998).

In this paper, we describe the land-use history and pre-manipulation stand structure of the experimental plots at the Harvard Forest Hemlock Removal Experiment (HF-HeRE: Ellison et al. 2010). We used a combination of historical documents, archival records, stand mapping, and analysis of tree growth from increment core samples (dendrochronology), including a new method for visualizing and modeling dendrochronological data, to infer nearly 250 years of forest dynamics at the experimental site. The proximal aim of this study was to reconstruct the establishment, stand history, and growth dynamics of trees at the Simes Tract by combining dendrochronological data and information on land-use history and environmental disturbance from a variety of sources. After standardizing data for tree size using relative growth rate, we developed and used a new method for visualizing and modeling dendrochronological data to help interpret the effects of tree age (cf. Ogle et al. 2000; Rohner et al. 2013; Ryan et al. 1994) and a variety of historical events on tree growth at the Simes Tract since the late 1800s. We used these analyses to ask how contemporary stand structure has been influenced by past logging, episodic drought, the 1938 Great Hurricane, and repeated influx of nonnative insects and pathogens that have impacted one or more tree species in this forest.

MATERIALS AND METHODS

Site description and experimental context. HF-HeRE is located within the 121-ha Simes Tract (42.47^{o}–42.48^{o} N, 72.22^{o}–72.21^{o} W; elevation 215–300 m a.s.l.) at the Harvard Forest Long Term Ecological Research Site in Petersham, MA, USA (Ellison et al. 2010; Figures 1, 2). The complete design of HF-HeRE is described by Ellison et al. (2010); only salient details are repeated here. The experimental site includes eight plots grouped into two blocks of four plots (Figures 1, 2), each consisting of three “hemlock” plots dominated (in 2003) by *T. canadensis* and one “hardwood” plot of mixed hardwoods. The “valley” block (plots 1–3 and 8) is in undulating terrain bordered on its northern edge by a *Sphagnum*-dominated wetland. The “ridge” block (plots 4–7) is on a forested ridge, approximately 0.5 km northwest of the valley block. Plots 4–8 are each 90 × 90 m (0.81 ha). Plots 1 and 3 are 85 × 90 m (0.76 ha), and plot 2 is 85 × 85 m (0.72 ha) in size; the small differences in size of the latter three plots resulted from topographic constraints and the regulatory requirement to avoid disturbance to a nearby vernal pool. The soils are predominantly coarse-loamy, mixed, active, mesic Typic Dystrudepts in the Charlton Series that are derived from glacial till (USDA n.d.). Across the eight HF-HeRE study plots, the soil pH ranges from 3.0–3.4 in the organic layer and from 3.5–4.0 in the mineral layer; soil C:N ratios range from 26–33 (Orwig et al. 2013).

Two canopy-manipulation treatments were applied in 2005 to one *T. canadensis*-dominated plot in each block: (1) girdling to kill trees standing in place, or (2) harvesting of standing *T. canadensis* along with cutting of merchantable hardwoods and *P. strobus* (Ellison et al. 2010). However, the focus of this paper is on stand structure and land-use history prior to application of the treatments.

Land-use history. The history of human activities at the Simes Tract was compiled from deeds; records of witness trees, land, and timber sales; maps of varying detail produced at irregular intervals for forest inventories, tax assessments, and the white pine blister rust (*Cronartium ribicola* J. C. Fisch) eradication campaign of the early 1900s; timber inventories and harvests; salvage assessments following the 1938 “Great Hurricane;” reconstruction of the soil seed bank (Farnsworth et al. 2012; Sullivan and Ellison 2006); and other records from the

Harvard Forest Archives, as detailed below. Additional historical interpretation was based on a reconnaissance of field sites in 2004 that included identification and assessments of stone walls, foundations, wells, and a former house site, along with excavation of artifacts from cellar holes and refuse dumps.

Environmental data and disturbance history. Temperature and precipitation data for the period spanning the dendrochronological records were obtained from the U.S. National Climatic Data Center (http://www.ncdc.noaa.gov/cdo-web/) for Amherst, MA (42.38° N, 72.53° W), the closest station (ca. 30 km SW of the Simes Tract) for which daily temperature and precipitation data were available from the late 1800s to the present; parallel climatic data were available for the Harvard Forest since 1964 (Boose 2001; Boose and Gould 1999). Instrumental records of the summer Palmer Drought Severity Index (PDSI; Cook et al. 1999; Palmer 1965) were obtained from Cook and Krusic (2004); the closest PDSI grid-point to the Harvard Forest (and the only one in Massachusetts) is at 42.5° N, 72.5°W, in Leverett, MA, ca. 25 km west of the Simes Tract. Data on the effects of the “Great Hurricane” of 21 September 1938 on the region were summarized in Foster and Boose (1992); site-specific data were derived from the Consulting Forestry File 1950-17 in the Harvard Forest archive.

Biotic changes that affected the Simes Tract and the surrounding region included the establishment of chestnut blight (*Cryphonectria parasitica* (Murrill) Barr, white-pine blister rust and subsequent logging, gypsy-moth (*Lymantria dispar dispar* (L.)) outbreaks, and human population growth. The first occurrence in Petersham of chestnut blight was reconstructed by Bradshaw and Miller (1988). Efforts to control white-pine blister rust in the area was spearheaded by the Harvard Forest (Fisher and Cline 1944, Maloy 1997); subsequent logging throughout Petersham, including at the Simes Tract, was documented by Worcester County

Land-use Planning Project (1938). Data on timing and duration of gypsy-moth outbreaks were based on observations of Baker and Cline (1936) and Bess et al. (1947), and historical reconstructions by Allstadt et al. (2013), Mass GIS (1997), and Muzika and Liebhold (1999). Human population trends in Petersham were derived from the US Census Bureau online database (http://www.census.gov) and Harvard Forest Document Archive 1980-13 (http://hfarchives.fas.harvard.edu:8080/exist/rest/db/harvard-forest/apps/archives/views/view-item.xq?id=1292).

Stand structure. In each of the eight experimental plots, every tree ≥ 5 cm diameter at breast height (DBH, measured 1.3 m above ground level) was labeled in 2003−2004 with a numbered, aluminum tag. Each tree was identified to species [nomenclature follows Haines (2011)], measured (DBH to nearest mm), determined to be alive or dead, and if alive, its crown class (dominant, co-dominant, intermediate, or suppressed; all sensu Smith et al. 1997) was recorded. Locations of individual trees and their elevations relative to a fixed point in each plot were mapped in 2003 and 2004 using stadia rods and a Topcon AT-GS auto-level (Forestry Suppliers, Inc., Jacksonville, MS).

Dendrochronology. Stratified random sampling was used to select trees to core in each plot. Trees measured during the stand mapping and growing in the central 30 × 30 m area of each plot were grouped into five size classes: 11–20, 21–30, 31–40, 41–50 and ≥51 cm DBH. At least one tree (from any species) was sampled at random from each size class; the total number of trees selected for each species and from each size class was proportional to both the relative abundance of each species and the frequency of individuals in a given size class relative to the total number of stems in the plot. Dead trees and trees < 10cm DBH were not sampled, whereas trees judged to be sufficiently decayed so as to make the sample unreadable were replaced with an alternate of the same species and size class where available. In total, 232 trees were sampled across the eight plots (Table 1).

Cores were collected using an increment borer in July 2004 and between October and December 2005. A single core was collected from each tree, and trees were cored as close to the ground as possible to more accurately determine tree age. Samples were rough-sanded using a random-orbit palm sander, then hand-sanded with sand paper (ISO 400, 600, or 1200 grit) as needed to reveal the rings. Rings on each tree core were counted under a binocular microscope and annual radial growth was measured to the nearest 0.01 mm with a Velmex tree-ring measuring system (Velmex, Inc., Bloomfield, NY) and Measure J2X software (VoorTech Consulting, Holderness, NH). Cores were visually checked for similarity within and among plots and species; years that appeared to be outliers were checked, verified, and corrected if needed. Every core was independently checked by a second investigator for ring curvature, which indicates proximity to the pith. These checks illustrated that 15% of the cores reached the pith of the tree and 69% were within 1−3 years of the pith (Table 1). Thus, 84% of all cores could be dated accurately to within three years of the pith, and the remaining cores were dated graphically using a pith locator (Applequist 1958).

Data analysis and data availability. All graphics and analyses were done using the R software system (R Development Core Team 2008), version 3.0.1 (release date 16 May 2013). Visualizations of stand structure included scatterplots of tree locations coupled to histograms of tree size to provide a sense of both species-specific and overall stand size-structure, and contour plots of the distribution of each of the dominant genera (*Tsuga, Betula, Quercus, Acer,* and *Pinus*). The spatial distribution of the stems in each of these genera were tested for departure from complete spatial randomness (CSR) assuming an underlying homogeneous spatial Poisson process (Ripley 1977). We used the `Kest` and `envelope` functions in the `spatstat` library (Baddeley and Turner 2005) of R to generate point-wise 99th-percentile simulation envelopes that specify the critical points for statistical significance based on a Monte Carlo test (Ripley 2004). Values of Ripley's *K* that fall outside the simulation envelope at a specified distance imply significant clustering ($K \gg$ simulation envelope) or dispersion ($K \ll$ simulation envelope) of stems at the given distance.

Visualizations and comparisons of environmental and dendrochronological data were based on time series of temperature, PDSI, and annual growth (ring widths) of individual trees. As a measure of annual growth of an individual tree, we used the relative change in its basal area from one year to the next ($r\mathrm{BAI}_n$ in $\mathrm{mm}^2 \cdot \mathrm{mm}^{-2} \cdot \mathrm{yr}^{-1}$) for each year in which it was alive:

$$r\mathrm{BAI}_n = \frac{\pi r_n^2 - \pi r_{n-1}^2}{\pi r_{n-1}^2}, \qquad \text{(Equation 1)}$$

where r_n is the radius of the tree (in mm) in year *n*. By adjusting for (dividing by) size at year n–1, a relative measure of growth rate such as $r\mathrm{BAI}_n$ allows for more straightforward comparisons of growth increments to be made among different size classes (e.g., Paine et al. 2012). As relative growth rate (i.e., $r\mathrm{BAI}_n$) approaches zero, virtually all carbon gain from photosynthesis in a given year is allocated to respiration. In contrast, note that $r\mathrm{BAI}_n$ is similar to the percent growth change used by Nowacki and Abrams (1997), although we used annual change, not decadal-mean change. However, it is not the same as the absolute basal area increment (BAI: growth rate in $\mathrm{mm}^2 \cdot \mathrm{yr}^{-1}$) used by, for example, Rubino and McCarthy (2000) or Johnson and Abrams (2009). Biondi and Qeadan (2008) suggested an alternative approach – the C-method – to standardizing changes in basal area caused by changes in both stem size and tree age in open-grown, shade-intolerant species. But because we were interested specifically in effects of tree age and environmental effects of particular years (see below), and of both shade-tolerant and shade-intolerant species in a closed-canopy forest, we did not use their C-method here.

Initial exploration of relationships between tree relative growth rate and environmental variables were done on 10-year moving averages of annual $r\mathrm{BAI}_n$ values; we used the `rollapply` function in the `zoo` library (Zeileis and Grothendieck 2005) of R to compute moving averages of environmental variables and the annual tree-ring data.

These initial analyses suggested a strong, monotonically increasing relationship between tree size and tree age. We thus used two different generalized additive models (GAMs) to estimate how growth changed as trees aged. Generalized additive models are an extension of generalized linear models (GLMs) in which the linear predictor of the GLM is specified as a smooth function of the predictor variable or variables (Wood 2006). Unlike in a GLM, where the exact parametric form of the smoothing function [denoted $s(\cdot)$] is specified in advance, in a GAM, the form of the function itself is estimated.

In our first GAM, we modeled $r\mathrm{BAI}_n$ as varying only with the age of the tree:

$$r\mathrm{BAI}_n = \textsc{Year} + s(\textsc{Age}). \qquad \text{(Equation 2)}$$

In this model, $r\mathrm{BAI}_n$ is a constant function of YEAR, which can be thought of as a proxy for a suite of both measured and unmeasured environmental variables in a given calendar year. By assuming a constant function for YEAR, this model implies that there are “good” and “bad” calendar years for growth, and these years would be equally “good” or “bad” for trees of any age (see also Ryan et al. 1994). We used a cubic smoothing spline with three degrees of freedom as our function $s(\textsc{Age})$ in Equation 2. Splines are piecewise polynomial functions used to fit non-linear data; see Wood (2006) for additional details.

Our first GAM (Equation 2) modeled the effect of a given calendar YEAR as being the same for every tree regardless of its AGE. However, young trees, for example, may experience the environmental conditions of a particular year differently from older ones. Thus, to account for age-specific variability in responses to the year of growth, we used a two-dimensional (a.k.a. thin-plate) smoothing spline (Wood 2006) to model the data as:

$$r\mathrm{BAI}_n = s(\mathrm{Year}, \mathrm{Age}). \qquad \text{(Equation 3)}$$

This model (Equation 3) was more general and allowed us to model the growth of each tree for the entire range of years in which it was alive.

Both types of GAM were fit for each species separately. Model fits are reported as the percent of deviance explained relative to the null model (i.e., an "intercept only" model). We used Akaike's Information Criterion (AIC) to compare the fits of the two models (Equations 2 and 3) for each species (Burnham and Anderson 2002); a higher deviance explained and a lower AIC suggests a better-fitting model. GAMs were run using the `gam` function (default settings) in R's `mgcv` library (Wood 2006); AIC comparisons were run using the `aic` function in R's `stats` library.

All raw data and associated R code for visualization and analysis are available from the Harvard Forest Data Archive (http://harvardforest.fas.harvard.edu/data-archive), datasets HF086 (dendrochronology) and HF126 (overstory vegetation). Deeds, maps, and other historical records used are stored in the Harvard Forest Document Archives and are available digitally: White Pine Blister Rust control map for Block 31 – southwest Petersham (Worcester County Land Use Planning Project 1938); Consulting Forestry File 1950-17 (http://hfarchives.fas.harvard.edu:8080/exist/rest/db/harvard-forest/apps/archives/views/view-item.xq?id=782); Stand Records for Harvard Forest Simes Lot, 1971-2006, HF1971-21 (http://pds.lib.harvard.edu/pds/view/6504291?&id=6504291); Massachusetts witness tree data, HF1993–05 (http://hfarchives.fas.harvard.edu:8080/exist/rest/db/harvard-forest/apps/archives/views/view-item.xq?id=1800); and Simes Tract deeds and timber sales, HFAdm-137 (http://hfarchives.fas.harvard.edu:8080/exist/rest/db/harvard-forest/apps/archives/views/view-item.xq?id=8576).

RESULTS

Land-use history. The ≈ 121-ha Simes Tract (Figures 1, 2), is named for Olive Simes, who bequeathed the property to Harvard University in 1970. Stone walls, barbed wire, foundations, and remnants of an old mill are scattered throughout the tract, and provided initial evidence that the majority of the land had been cleared one or more times since the settlement of Petersham (as Voluntown) in 1730.

The modern-day Simes Tract consists of four parcels accumulated by Olive Simes over her lifetime (Figure 2; Appendix). The southern half of the Simes Tract (which includes the valley block of HF-HeRE) was made up of three of these parcels, whereas the northern half of the Simes Tract (which includes the ridge block of HF-HeRE) was what remained of a larger parcel subdivided by Olive Simes in 1947 (Figure 2). Both halves of the Simes Tract represent remnants of two large farmsteads amassed in the 1780s – Joseph Gleason’s > 500-acre (≈ 200 ha) farm to the north, Samuel Chamberlain’s nearly 300-acre (≈ 120 ha) farm, woodlot, and cider mill to the south. However, the subsequent ownership patterns (Appendix) and land-use histories of these two parts of the modern-day Simes Tract were very different.

Joseph Gleason’s farm spanned both sides of the “road to New Salem,” Petersham’s present-day West Street. Gleason accumulated his acreage in the late 1700s, and sold 260 acres

(≈ 105 ha)—a portion of which is now the northern part of the Simes Tract—to his son in 1806. In the deed transfers of 1806, 1826, and 1830 (Appendix), this parcel is referred to as "the farm on which I live," and included at least two adjacent lots, a house, and a barn. However, the 1830 forest inventory map of Massachusetts (Hall et al. 2002) showed that most of this parcel was forested as of that year (Figure 2). The parcel was sold intact six times between 1859 and 1941 (Appendix); Olive Simes, who purchased it in 1941, subdivided it and sold the northern ≈ 50 acres (≈ 20 ha) along West Street in 1947 (Appendix). The remainder was bequeathed to Harvard Forest in 1970.

In the south, Samuel Chamberlain's farm lay on both sides of the "road to Dana"—now known as Dugway Road (Figures 1, 2)—and included a house and barn, extensive pasture land, small wood lots, and a cider mill (Coolidge 1948). The extensive stone walls throughout Chamberlain's farm (Figure 2) suggest that this southern portion of the Simes Tract was much more intensively managed than was the Gleason's farm to the north. Deeds (Appendix) not only describe repeated land transfers among Chamberlain's heirs and neighbors throughout the 1820s and 1830s, but also explicitly reserved water rights for the mill, harvesting rights for the apples, rights-of-way for moving livestock, and requirements that owners and abutters maintain fence-lines. By the late 1830s, the original Chamberlain farm had been subdivided into at least six parcels, ranging in size from 1–100 acres (≈ 0.4–40 ha), at which point Jonathan Towne Jr. began purchasing the pieces and reassembling it. By the mid-1800s, most of the original farm had been re-aggregated into a single large parcel. However, the timber rights were sold in 1880, cutting was completed by 1883 (diagonal hatched area in Figure 2), and the farm was again subdivided by his sons. The farmhouse burned in 1928 (Coolidge 1948); the cellar-hole is still visible at the south end of the Simes Tract.

In 1929 and 1934, Olive Simes acquired the pieces of what by the 1920s was known as the Towne Farm, the remnants of Chamberlain's farm north of Dugway Road. By then, it was covered with well-established second-growth forest that was surveyed, mapped, and organized into timber-management compartments by Harvard Forest Assistant Director A. C. Cline. His assessment of Simes's land in 1930 (in a letter to Olive Simes dated 12 February 1930; in Stand Records for Harvard Forest Simes Lot) was that the "Williams Lot" (a.k.a. the "Sprout lot" on the northeast corner of the Chamberlain farm that was subdivided by Jonathan Towne *fils* in 1880) was "covered with an inferior growth in which gray birch predominates ... [along with] a mixed growth of hardwood (both cordwood and prospective saw-timber), pine and hemlock of decidedly better quality, and of older age than the growth on the central and eastern portions." The difference in quality may have been due to less intensive harvest of the southern parts in the 1880s.

Two compartments (19 and 25) were thinned in the spring of 1932 (vertical hatched areas of Figure 2), yielding the equivalent of 329.5 cords (1195 m^3) of small saw-logs and cordwood (Report of 3 April 1932 and letter of 13 April 1932 from A. C. Cline to Francis B. Parsons, Esq., of Petersham, representing Olive Simes, both in Stand Records for Harvard Forest Simes Lot). The intent of this thinning was to release *P. strobus* for future returns; sales of timber rights in 1880 suggest that *P. strobus* also had been the focus of that decade's logging by the Towne family. The adjacent compartment 24 was used for a skid road, and some trees and limbs were cut for access to compartment 25. On March 28, 1932, during the logging operation, a severe storm occurred that damaged many of the trees slated for harvest.

The forest on the entire present-day Simes Tract was reassessed by Harvard Forest Economist E. M. Gould in the early 1970s, after Olive Simes had died and her estate was being settled (Gould 1971–1973). A 1971 rapid assessment based on aerial photos suggested that over half of the tract (72 ha) was in 40–60 year-old merchantable softwoods (conifers, mostly *P. strobus*, but with some *T. canadensis*), about one-third of the tract (43 ha) was in 20-40 year-old merchantable softwoods and hardwoods (mostly *Q. rubra*, some *Acer* spp.), and the remaining 10 ha was in young timber with no merchantable value. Gould completed a more detailed resource analysis in the summer of 1973; the tract was by then considered to be ≈ 70% stocked with primarily softwoods and a mixture of hardwood and softwoods.

In 1979–1980, a 4-acre (≈ 1.6 ha) parcel just east of the old Chamberlain homestead was thinned to promote growth of *A. saccharum* (Gould 1979; Figure 2). A more detailed inventory of the entire tract was done in 1980 to provide a new baseline for logging and future economic return (Kernan 1980). That inventory summarized stand structure in terms of the amount of roundwood (for cordwood); saw-timber for oak, mixed hardwoods, hemlock-hardwoods, and white pine-oak; swamp hardwoods (predominantly red maple); and white pine-hardwoods. Across the entire tract in 1980, *T. canadensis* accounted for 16% of the roundwood (443 of 2738 total cords, or 1606 of 9924 m^3) and 19% of the saw-timber (170,000 of 887,000 board feet, or 401 of 2083 m^3). Despite Kernan's suggestion that "at least some part of this fairly large volume could be profitably sold," no cutting was done in the tract until HF-HeRE treatments were applied in 2005.

Overall, by 1980, a mixture of hemlock and hardwoods dominated two surveyed compartments, accounting for just over 34 ha of the Simes Tract, the majority of which was in "poorly formed" (i.e., not merchantable) condition (Kernan 1980). In 2003, plots 1–6 of HF-HeRE were sited within these two surveyed compartments. Within these six plots, *T. canadensis* accounted for 50–69% of the basal area and 55–70% of the stem density in the hemlock-dominated plots (Ellison et al. 2010). In contrast, in the two hardwood-control plots (plots 7 and 8 of Figure 2), *T. canadensis* comprised < 10% of the basal area and stem density. The only other species in the HF-HeRE plots that accounted for > 10% of the basal area were *A. rubrum*, *A. saccharum* (only in hardwood-control plot 8), *Betula lenta*, *Quercus rubra*, and *Pinus strobus* (Table 3). In 2005, the Harvard Forest Woods Crew cut the two logged-treatment plots (plots 2 and 4 of Figure 2): approximately two-thirds of the basal area in these two plots was removed, including all *T. canadensis* > 20 cm DBH, most of the low quality *Acer* and *Betula* spp., and 50% of the basal area of *P. strobus*, *Q. alba*, and *Q. rubra*. The total yield from the 1.53 ha logged plots was 39,000 board feet (92 m^3) of logs for saw-timber, 47 cords (170 m^3) of firewood, and 113 (U.S.) tons (102 tonnes) of softwood pulp (Wisnewski and Barker Plotkin 2006).

Environmental data. Continuous environmental data relevant to the Simes Tract were available for just over 100 years (Figure 3): 1897–present (Amherst) and 1964–present (Harvard Forest). The 1897–2003 average annual temperature at Amherst was 8.9 °C; during the period of overlap, Harvard Forest averaged 1.7 °C cooler. Inter-annual variability in temperatures at Harvard Forest closely paralleled that seen in the Amherst data (Figure 3); when the two time series overlapped (1964–2003), the inter-site correlation (r) = 0.67 ($p = 2\times10^{-6}$), so it appeared reasonable to use the longer, Amherst, record as a temperature proxy for Harvard Forest. Similarly, average annual precipitation was nearly equal at the two sites: 1084 mm at Amherst and 1095 mm at Harvard Forest [inter-site correlation (r) = 0.82 ($p = 1\times10^{-10}$)]. On average, the region was neither overly wet nor overly dry (average PDSI from 1897−2003 = −0.1), but multi-year “moderate-drought” periods (i.e., $-2.00 \leq \text{PDSI} \leq -2.99$: Palmer 1965) occurred from 1907−1914 and 1962−1966. During these years, the population of Petersham declined from just over 1000 people in the 1880s to its low of 642 in 1930 and then increased again to 1180 people in 2000 (Figure 3). Note that the largest population in Petersham was recorded in the 1840 census (1775 people), after which it declined in every census until 1940.

In addition to the continual land-use changes described above, several major region-wide (i.e., throughout much of New England) disturbance events affected the tract during in the 1900s. From 1910 to 1915, co-incident with the 1907−1914 drought, chestnut blight swept through the region. We found no records of either the historical abundance of American chestnut (*Castanea dentata*) across the Simes Tract or the exact timing of the occurrence there of the blight. Although *Castanea dentata* accounted for 9% of the witness tree records for Petersham (Wallace and Foster 1993), this species was never mentioned as a witness tree in any of the Simes Tract deeds listed in the Appendix (the four witness trees mentioned included two “elms,” one “white oak,” and one “birch”). However, three understory *C. dentata* individuals are still growing in the plots (one in plot 2 and two in plot 7), and scattered dead *C. dentata* poles still can be found in plots on the ridge. Archival records indicate that the blight was present within Harvard Forest’s Prospect Hill Tract by 1910–1911 (C. B. Fall cited in Smith 1948; Kittredge 1913, Paillet 2002), and was considered widespread at Harvard Forest by 1912 (D. R. Foster, pers. comm. cited in Bradshaw and Miller 1988).

Chestnut blight was followed by white-pine blister rust, and extensive control efforts in Petersham between 1917 and 1944 were coordinated by Harvard Forest scientists (Fisher and Cline 1944). Although little logging of pine occurred during the blister-rust eradication campaign, tens of thousands of *Ribes* individuals were manually removed (Fisher and Cline 1944). In addition, between 1925 and 1932, much of the northern half of the Simes Tract, identified as either “Hardwood–Scattered Pine < 1” diameter” or “Hardwood–Hemlock” was “cut” or “partially cut”, respectively (Worcester County Land Use Planning Project 1938).

The largest disturbance to affect the Simes Tract was the hurricane of 21 September 1938. Detailed records of damage to the forest by the hurricane were made only for the southern half of the Tract. There, the pines released by the 1932 logging and co-incident storm, along with other larger trees (mostly hardwoods), were blown down by the 1938 hurricane (Table 2). On 18 February 1939, A. C. Cline wrote to Olive Simes that "the hurricane resulted in the complete blowdown of all of the larger timber, including at least nine-tenths of the area supporting stands which a lumberman would consider merchantable and a good logging chance. No stand completely escaped." The inspection report suggested that most of the trees were uprooted but that many of the better trees were snapped and broken 8–10 feet (2–3 meters) above the ground; remnant decaying boles are still visible today (Ellison and Barker Plotkin 2009).

Finally, extensive outbreaks of gypsy moth caterpillars occurred at various times during the last century. Gypsy moths were first targeted for control in Petersham in 1909 (Town of Petersham 1909), and relatively small outbreaks that caused at least localized deforestation were noted in 1935, 1944, and 1945 (Baker and Cline 1936, Bess et al. 1947). During the 1935 outbreak, Baker and Cline (1935) found nearly 100% defoliation of *Q. rubra, P. strobus,* and *B. populifolia* Marsh. around Dugway Road, at the south end of the Simes Tract. The largest outbreak, which affected at least an order of magnitude more area throughout New England than any previous one, occurred in 1981 (Allstadt et al. 2013). Impacts of the 1981 outbreak affected tree growth throughout New England (Muzika and Liebhold 1999). A smaller gypsy moth outbreak, comparable in scale to those of the 1940s and 1950s, occurred across New England in the early 1990s (Allstadt et al. 2013).

Stand structure. Across the eight plots in 2003–2004, 23 species had stems ≥ 5 cm DBH (Table 3). Of these, 12 species in five genera—*Tsuga, Betula, Quercus, Acer,* and *Pinus*—

accounted for 98% of the 6959 individual stems measured (Table 3). Overall diameter distributions had characteristic “reverse-J”, or right-skewed, shapes with many small trees and few large ones; larger trees were more abundant in the hemlock plots than the hardwood plots (Figure 4). In all genera in the hemlock plots, and in all genera other than *Betula* and *Quercus* in the hardwood plots, the diameter distributions were significantly more right-skewed in the valley plots than the ridge plots (Figure 4). In both blocks, *Tsuga, Acer,* and *Pinus* were dominated by individuals in the smallest diameter classes whereas *Betula* and *Quercus* had more individuals in intermediate-size diameter classes than in the smallest diameter classes (Figure 4).

Although *T. canadensis* accounted for > 60% of the stems and basal area in the six hemlock plots (Table 3), the spatial arrangement of these stems was approximately spatially uniform only in plots on the ridge (Figure 5, Table 4). In the valley, *T. canadensis* stems were more clustered in the relatively low-elevation portions of the plots (Figure 5, Table 4). The other four dominant genera also had clustered spatial distribution in the valley plots: *Quercus, Acer,* and *P. strobus* clustered in higher sections of the plot, whereas *Betula* dominated where the other four genera were less dense. In the ridge plots dominated by hemlock (plots 4−6), *T. canadensis, Q. rubra, A. rubrum,* and *P. strobus* were approximately spatially uniformly distributed in at least two-thirds of the plots, whereas *B. lenta* had clumped distributions (Figure 5, Table 4).

All genera showed some degree of spatial clustering in the two hardwood plots (Plots 7−8; Figure 6, Table 4). In the valley hardwood plot (8), *T. canadensis* (and *Acer* spp.) again clustered in the lower, eastern part of the plot, whereas the other hardwoods and *P. strobus* clustered in the higher, western or southern parts of the plot. In contrast, in the ridge hardwood plot (7), *T. canadensis* clustered in the eastern, higher part of the plot, and the hardwoods and *P. strobus* clustered in the lower parts of the plot (Figure 6, Table 4).

In both blocks, the distance at which clustering is observed begins for many of the genera at 5–7 m (Table 4). That is, a relatively small “window” (e.g., a circle with diameter of 5−7 m) moved across the plot captures clusters of trees growing close together (< 5 m apart).

Dendrochronology. In 2005, the *T. canadensis* trees in the central 30 × 30m areas of the six hemlock-dominated plots were predominantly 45–65 years old, having recruited in the two decades following the 1938 hurricane (Figure 7A, 7B). The oldest trees, approaching 140 years old, were the hemlocks in the valley block (Figure 7A). The ridge plots also had an older cohort of hemlocks that was not harvested during the 1920s and 1930s (Figure 7B). In the hemlock-dominated plots on both the ridge and in the valley plots, no sampled *P. strobus* were more than 100 years old. The few hardwoods in these hemlock plots span most of the age classes. In these plots, the *Quercus* spp. all established before the 1938 hurricane. *Acer* and *Betula* spp. were of intermediate size classes and had a varied age structure; recruitment of these genera peaked in the 1930s and 1940s, most noticeably on the ridge. In contrast, the sampled trees in the two hardwood-dominated plots were all young and dominated by birch species that established in the 1940s (Figures 7C, 7D). In these two plots, only one large tree, a 95-year-old *P. strobus* on the ridge, pre-dated the 1938 hurricane (Figure 7D). The relationship between tree age and tree diameter in three of the four areas was monotonically increasing (Figures 7A, C, D), but was more hump-shaped on the ridge (Figure 7B). This latter pattern reflects the co-occurrence of many small but old, and large bug young *T. canadensis* individuals in these plots (Figure 7B).

Species-specific relative growth responses to environmental changes and episodic disturbances were similar in the hemlock and hardwood plots, but varied with block (Figure 8). *Tsuga canadensis* provided the longest dendrochronological record in both blocks. In the valley block, relative growth rate of *T. canadensis* increased steadily in the late 1800s and early 1900s, reaching a maximum of 10–50 $mm^2 \cdot mm^{-2} \cdot yr^{-1}$, and appeared to be little affected by any disturbances before 1938. There was only modest evidence of increased relative growth of these hemlocks after the 1938 hurricane, and then a pronounced, steady decline in relative growth rate beginning in the 1950s (Figure 8, top left). In contrast, hemlocks on the ridge showed a dramatic increase in relative growth rate following both the 1907–1914 drought. Relative growth rate of these trees declined steadily beginning in the mid-1920s and was unaffected by the 1938 hurricane, but did show a short-lived increase following the 1981 gypsy moth outbreak (Figure 8, top right).

Although as a group they are substantially younger than the hemlocks, *P. strobus* and the three common hardwoods appeared to be more responsive to episodic environmental perturbations than the hemlocks (Figure 8). In both blocks, *P. strobus* relative growth rate declined after both droughts and the 1938 hurricane.

Relative growth rates of *Betula lenta* and *A. rubrum* declined during the early 20th-century drought and recovered rapidly thereafter; *Q. rubra* responded less strongly to this drought, and none of the hardwoods appeared to be strongly affected by the drought in the early 1960s. Relative growth rates of both *Q. rubra* and *B. lenta* declined during the 1981 gypsy-moth outbreak but recovered rapidly thereafter. By 2005, all trees were growing relatively slowly.

Models of annual tree growth. General additive models fit to the $r\mathrm{BAI}_n$ data (Figures 9 and 10) buttressed the conclusions drawn from observations of decadal patterns (Figure 8), but provided some additional insights into patterns of tree growth and effects of acute environmental perturbations.

The first model (Equation 2) fit annual tree relative growth rate as a function of tree AGE, but included an effect of YEAR that was considered to be independent of tree AGE (recall that using relative growth rate – $r\mathrm{BAI}_n$ – implicitly adjusts the data for tree size). This model suggested that *T. canadensis*, *B. lenta*, *A. rubrum,* and *P. strobus* all showed similar age-dependent patterns of relative growth (Figure 9, left column): $r\mathrm{BAI}_n$ declined rapidly following initial establishment, then increased in ≈40−70-year old trees, and then declined again. *Quercus rubra*, however, showed a more monotonic decline in relative growth rate. Estimation of the YEAR effect suggested that for each species, there were good and bad years (Figure 9, right column), but recall that Equation 2 estimated the YEAR effect independently of tree age. This model suggested that growth of all species responded strongly and positively to the end of the 1907−1914 drought and the concurrent elimination of *C. dentata*. The effect of the 1938 hurricane was not especially pronounced using this model, although both *A. rubrum* and *P. strobus* had somewhat better growth years in 1939 and 1940 than in 1938. The effect of the gypsy-moth outbreak was clearly apparent in a strong negative growth signal for *Q. rubra* and a strong positive growth signal for *P. strobus*. Finally, although there was an overall negative effect of tree age on growth of *Q. rubra*, in general, most years since 1918 (other than 1981 and perhaps 2000) have been good growth years for *Q. rubra*.

The second model (Equation 3) removed the assumption that the effect of YEAR was independent of AGE. The results of this model showed more clearly that what appeared as "good" and "bad" years in Figure 9 were not always good (or bad) years for all individuals of a given species. For *T. canadensis*, most individuals had similar relative growth patterns (Figure 10, top left) and the mid-1920s were high relative growth years for most individuals (red area in contour plot of Figure 10, top right). In contrast, only older *B. lenta* and *A. rubrum* trees were released in the 1920s, and only younger individuals exhibited increased growth in the 1940s−1960s (Figure 10, second row and bottom row). Younger *Q. rubra* grew more rapidly following the 1938 hurricane and all age classes grew slowly after the 1981 gypsy moth outbreak, but only younger trees resumed rapid growth after that (Figure 10, middle row). Finally, both young and old *P. strobus* grew rapidly following the 1938 hurricane, but intermediate-aged trees grew more slowly.

For all five species, the model that estimated changes in $r\mathrm{BAI}_n$ as a function of both Age and Year (Equation 3) fit the relative growth data significantly better than the model that estimated changes in $r\mathrm{BAI}_n$ as a function of Age only (Equation 2; Table 5). Deviance accounted for by the former, better-fitting model ranged from 25% (*T. canadensis* and *A. rubrum*) to 45% (*B. lenta*) (Table 5).

DISCUSSION

Our overriding goal with this study was to understand how establishment, stand structure, and growth dynamics of forest tree species led to the dominance of a foundation forest species—*Tsuga canadensis*—that controls population and community dynamics of associated species and key forest ecosystem processes (e.g., Ellison and Baiser 2014; Ellison et al. 2010, 2014; Orwig et al. 2013). Our interpretation of the importance of *T. canadensis* in contemporary forests has come from a range of observational and experimental studies where it is has dominated the stand in terms of abundance and biomass, but where it now is declining and dying (or has already died) due to infestation by the hemlock woolly adelgid (e.g., Brooks 2001; Ellison et al. 2010; Eschtruth et al. 2006; Ford et al. 2012; Krapfl et al. 2011; Nuckolls et al. 2009; Orwig et al. 2002, 2008, 2012; Small et al. 2005; Yorks et al. 2003). However, there can be long phases in forest stands when *T. canadensis* has few, large individuals or many suppressed stems in the understory, and thus plays only a minor role in overall forest dynamics, and so it is unclear whether current (or recent) conditions (i.e., *T. canadensis* as a foundation species) are one-time or transient (in forest time) phenomena or illustrate more general long-term patterns and trends.

Oliver and Stephens (1977) and Foster et al. (1998) showed convincingly that a deeper understanding of contemporary forest dynamics can be achieved when data on recent and historical land use are incorporated into analyses of data and their interpretation. Perhaps nowhere in North America is the history of environmental change and land use as well documented as it is in New England (e.g., Foster and Aber 2004; Foster and Zebryk 1993; Fuller et al. 1998; Kelty 1986; McLachlan et al. 2000). Throughout this region, there has been a long history of human activity and use overlain on the background variability and conditions before, for example, the arrival of pests and pathogens or other environmental (or experimental) perturbations, and which are as dynamic as those that come after such “disturbances.” Prior to the data presented here, however, detailed information on land-use history was unavailable for any of the experimental sites where effects of loss of *T. canadensis* have been studied.

Land-use history of the Simes Tract in the regional context. The historical uses of the Simes Tract (Figure 2; Table 2; Appendix) contrast strongly with that reported previously for many forested sites now dominated by *T. canadensis* in central New England: the hemlock woodlot studied by Foster et al. (1992) and Foster and Zebryk (1993) and four sites at Harvard Forest reconstructed by McLachlan et al. (2000). The hemlock woodlot was, as early as 1830, an isolated woodland within an agricultural landscape (Foster et al. 1992); it was part of the earliest land divisions of Petersham (Coolidge 1948) and was maintained as a woodlot as the surrounding parcels were aggregated into a larger landholding in the late 1800s and early 1900s (Foster et al. 1992; Foster and Zebryk 1993). The sites studied by McLachlan et al. (2000) were considered to be some of the oldest and least disturbed sites on the Prospect Hill and Slab City

Tracts (see Figure 1 for locations of these tracts), as well as within the least disturbed forest blocks in Petersham.

In contrast, the Chamberlain/Towne and Gleason Farms, portions of which now form the Simes Tract (Figure 2), were part of the third and fourth (last) divisions of land that were parceled out 30–50 years after Petersham was first settled (Coolidge 1948). At one extreme, the Gleason Farm was amassed quickly and then remained virtually intact from the time Petersham was parceled out through its purchase by Olive Simes (Appendix). At the other, the Chamberlain Farm was subdivided, sold, resold, re-aggregated, and re-divided more than two dozen times before it passed into the Simes family in the 1920s (Appendix). These ownership patterns differ from the regional pattern of modest subdivision following settlement followed by aggregation into large holdings in the late 1800s described by Foster (1992), coincident with the decline in Petersham's population (Figure 3).

Both the Chamberlain and Gleason Farms were used heavily. They were on the main roads to the towns of Dana and New Salem, respectively (Figures 1, 2) and had houses, barns, fences for keeping livestock in, cart roads to move them to market, orchards, and a cider mill that figured prominently in deed transactions for nearly 100 years. Although substantial portions of the tract were listed as "forested" in the 1830 Massachusetts forest survey (Figure 2; Hall et al. 2002), not a single tree that we cored was older than 145 years (in 2005), and most were much younger (Figure 7). Much of the northern half of the Simes Tract was partially logged between 1925 and 1932, and the better timber of the southern half was logged first in the 1880s and again in 1932. Even though two of our experimental plots (2 and 3) straddle the boundary of the two historic farmsteads (Figure 2), there is no obvious difference in either side of the plot related to these different farms. Rather, it appears that effects on stand dynamics of the logging in the late

19th and early 20th centuries and the 1938 hurricane have overshadowed the effects of earlier land-use.

The spatial patterning (or lack thereof) of trees on the ridge and in the valley may reflect both topography and this history of logging. In the valley, most of the genera exhibit significant departures from uniform spatial patterns, but the clusters do not match directly with topography (Table 4, Figures 5–6). For example, *T. canadensis* in plot 1 is much denser in the northwest corner of the plot, within and near a forested wetland, but in plot 2, it is clustered in the southwest, on relatively higher and drier ground. On the ridge, the five dominant genera are spatially uniformly distributed in just over half of the plots (Figures 5–6; Table 4). We observed thati in both blocks, trees were growing quite close together (the distance at which clustering was observed began for many of the genera at 5–7 m; Table 4). Because inter-tree competition and self-thinning should lead to greater interplant distance and more regular spacing, the data on clustering and interplant distances (Table 4) suggest that little self-thinning has yet occurred in these plots. In combination, these results suggest that on the ridge, either site conditions in these plots are relatively uniform or, as a consequence of repeated episodes of logging and other disturbances, these relatively young trees have not yet been subject to environmental filtering or self-thinning that would result in tighter spatial linkages between trees and fine-scale environmental conditions.

The age structure at the Simes Tract in 2005 was similar to that described by Oliver and Stephens (1977) from a 0.36-ha sample of *T. canadensis* in Compartment VI of Harvard Forest's Tom Swamp Tract. At Tom Swamp, most trees were 40−80 years old in the early 1950s; similarly at the Simes Tract, most were 40−80 years old in 2005. Stands at both Tom Swamp and the Simes Tract also had right-skewed diameter distributions with only a few *T. canadensis* individuals exceeding 60 cm DBH (Figures 4, 7; Oliver and Stephens 1977). And similar to the Simes Tract, the Tom Swamp plot was repeatedly logged, salvaged after wind-throws and hurricanes, and defoliated by gypsy moths (Oliver and Stephens 1977). The west-facing Tom Swamp compartment was less affected by the 1938 hurricane (Oliver and Stephens 1977) than was the Simes Tract (Table 2), but both appear to be representative of forest stands whose current composition reflects “allogenic influences” (Oliver and Stephens 1977). In sum, the Simes Tract, like much of the southern New England landscape, reflects not only large-scale infrequent disturbances including hurricanes and irruptions of herbivorous insects and pathogens but also (unlike the more thoroughly studied older *T. canadensis*-dominated stands in Central Massachusetts) centuries of substantial anthropogenic use.

Dendrochronological patterns, environmental changes, and episodic disturbances. The contemporary forests of the Simes Tract reflect well the general equability of the regional climate over the last 150 years, and relative growth rate ($r\mathrm{BAI}_n$) of all five common species of trees generally ranged from 1–10 $\mathrm{mm}^2 \cdot \mathrm{mm}^{-2} \cdot \mathrm{yr}^{-1}$ (Figure 8). Annual mean, minimum, and maximum temperatures since the late 1800s were relatively constant until the early 1960s; warming since 1964 has been more pronounced in the Petersham record than the Amherst record (Figure 3). Of all the taxa examined in detail, only *A. rubrum* showed a strong positive increase in relative growth in the last decade, most notably in the hemlock-dominated plots (4−6) on the ridge (Figure 8). This pattern is further illustrated by the positive “spike” in the effect of YEAR on *A. rubrum* growth observed in the last decade, an effect that is not seen for the other four dominant species (Figure 9).

Droughts have been infrequent, and even the two apparent multi-year droughts in the climatic record [1907−1914 and 1962−1966 (Figure 3)] were only “moderate” (multi-year PDSI

< 3; Palmer 1965). We note that the PDSI was first developed for semi-arid and dry sub-humid regions (Palmer 1965) and its effects on tree growth in more temperate or uniformly wet areas has not been examined often. When PDSI has been used in studies of temperate forests, moderate droughts (–2 ≤ PDSI < –3) have been associated with changes in growth of *Quercus* species (Copenheaver et al. 2011; Orwig and Abrams 1997; Pederson et al. 2012; Speer et al. 2010; Wycoff and Bowers 2010), *Carya glabra* Miller (Orwig and Abrams 1997), *Liriodendron tulipifera* L. (Orwig and Abrams 1997; Pederson et al. 2012), and *Fraxinus quadrangulata* Michx. (Pederson et al. 2012). We similarly observed that declines in *Quercus* relative growth corresponded with drought events (Figure 9): on the ridge following the 1907–1914 drought, and in the valley following the 1960s drought (Figure 8). This is one signal that might be used to differentiate the negative effect of drought from the positive effect that would have been expected when *C. dentata* was killed by chestnut blight. However, because the drought ended just as chestnut blight was at its peak, the rebound in growth seen on the ridge in the 1920s probably reflects both improved weather conditions and reduced competition from the now-dead *C. dentata*.

In contrast, *T. canadensis* relative growth trajectories changed little following either of these short-term droughts (Figure 8). Pederson et al. (2012) found a similar lack of association between *T. canadensis* growth and PDSI, even though this species is considered to be quite drought-sensitive (Godman and Lancaster 1990). However, the short-term precipitation changes during both the early 20th-century and the early 1960s drought (Figure 3) are similar in magnitude to the centuries-long drought observed during, and correlated with, the region-wide die-off of *T. canadensis ca*. 5500 years ago (Marsicek et al. 2013).

The most noticeable periods of increased relative growth were the years following the chestnut blight (1910–1915) and the logging of 1925–1932 (Figures 8–10). This may also reflect reduced competition from understory shrubs removed during the campaign to eradicate white-pine blister rust. On the drier ridge, *Tsuga canadensis*, *Q. rubra* and *A. rubrum* all exhibited increased $r\text{BAI}_n$ after the chestnut blight, and *P. strobus* in both blocks grew rapidly after the logging. Only *P. strobus* showed pronounced increases in relative growth rate following the 1938 hurricane. Most of the other trees on the Simes Tract would have been small and young at the time; the larger trees had been thinned out in 1932 (Figure 2) with the express goal of increasing growth of understory *P. strobus*; the few remaining large *P. strobus* and hardwoods were damaged or destroyed by the hurricane (Table 2).

The last episodic disturbance was the large gypsy moth outbreak of 1981. On the ridge, this outbreak strongly and negatively affected relative growth of *Q. rubra* while growth of *T. canadensis* concomitantly increased (Figures 8–9). Growth of *Q. rubra* was similarly depressed in the hardwood plot in the valley (Figure 8), where *B. lenta* and *P. strobus* showed concomitant growth increases. The smaller gypsy moth outbreaks of 1935, 1944, 1945, and 1991 (Allstadt et al. 2013; Baker and Cline 1936, Bess et al. 1947) had no perceptible effects on long-term (decadally-averaged) tree growth at the Simes Tract (Figures 9–10).

Tsuga canadensis is generally considered a slow growing, shade-tolerant, late successional species, but it retains its ability to grow after decades of suppression in the understory and can respond quickly to multiple, small disturbances (Marshall 1927). At the Simes Tract, *T. canadensis* responded rapidly and uniformly to the various environmental changes (see also Marshall 1927; Orwig and Abrams 1999). For example, *T. canadensis* on the ridge had the largest increase in relative growth rate after the drought and chestnut blight (1910–

1915) and the logging of 1925–1932 (Figure 8, top row); some large individuals (> 65 cm DBH) were only 60–115 years old (Figure 7). Joint modeling of age- and year-effects (Equation 3) revealed more clearly that all age classes of *T. canadensis* responded positively to the openings created by these disturbances (Figure 10). In contrast, all of the other common species showed age-specific growth responses in particular years and to different disturbances (Figure 10; Table 5).

Overall, our joint model that included both age- and year-effects accounted for 25–45% of the variance in growth of each species. Comparable modeling studies are few, but all suggest that including individual tree effects (as in Equation 3, Figure 10) improve the fit of the model to the available data. Ryan et al. (1994), using a mixed linear model, were able to account for only 20% of the variance in growth (specific volume increments from tree rings) of *Acer saccharum*. Most of this explained variance (60%) was attributable to differences among individual trees (as we illustrate for our data in Figure 10), and the remaining was attributed to a combination of precipitation and temperature. In contrast, Lapointe-Garant et al. (2010) were able to account for 76% of the variance in growth (absolute ring width) of *Populus tremuloides* Michx. using a mixed model to separate out effects of climate, soil, and insects while accounting for differences among individual trees. Like Ryan et al. (1994), the majority (54%) of the explained variance was accounted for by differences among trees. The remaining variance was due to climate (20%), soils (16%) and insects (6%). Other age-based models reported only root mean-square errors (Rohner et al. 2013) or Bayesian posterior prediction intervals, (Ogle et al. 2000), which Ceclie et al. (2013) point out are not directly comparable either with our results or with those of Ryan et al. (1994) or Lapointe-Garante et al. (2010).

Conclusions. The idea that *T. canadensis* is a foundation species – a species that controls abundance and dynamics of associated species and modulates key ecosystem processes (Dayton 1972; Ellison et al. 2005a) – implies that the dominance of *T. canadensis* is as long-lasting as the foundation of a building (Ellison and Baiser 2014). Foresters and vegetation scientists recognize the dominance (or at least co-dominance) of *T. canadensis* in a range of late successional vegetation types. In fact, *Tsuga canadensis* is considered to be the dominant component of more forest associations than any other tree species (FGDC 2013): 14 and sub-dominant component of 8 (of a total of 68) associations in the Northern Hardwood – Hemlock – White Pine Forest Group (T163) of the Eastern North American Cool Temperate Forest Division (1.B.2.NA) of the U.S. National Vegetation Classification (FGDC 2008; Jennings et al. 2009). Over the last 150 years, repeated abiotic and biotic disturbances (Figure 3) may have accelerated the transition from early-successional woodlands to late-successional hemlock forests at the Simes Tract and elsewhere in south-central New England. Because *Tsuga canadensis* can respond rapidly and positively to canopy-opening disturbances and some environmental changes and it can quickly come to dominate a site like the Simes Tract within only a few decades. This flexibility may in part help explain why so much of New England's old-growth forests are dominated by *T. canadensis* (D'Amato and Orwig 2008; D'Amato et al. 2009).

Nonetheless, the dominance of *T. canadensis* varies through time, and hence its role as a foundation species in our forests likely changes through time as well. *Tsuga canadensis* declined rapidly throughout its range *ca*. 5500 years ago and it took nearly 1000 years for *T. canadensis* to attain its pre-decline levels of abundance in the pollen record (Foster et al. 2006; Marsicek et al. 2013). Paleoecological data combined with historical records illustrate clearly that *T. canadensis,* while once widespread, may not have dominated forest stands in either the centuries prior to

European colonization nor during the 1700s‒late 1800s to the extent that it does today (e.g., Fuller et al. 1998). Deeper layers of the soil seed bank in the HF-HeRE plots have a preponderance of graminoids and ruderal species (Farnsworth et al. 2012; Sullivan and Ellison 2006) that likely reflect the past agricultural uses of the Simes Tract.

We conclude from this site-specific, but detailed case study that the foundation that *T. canadensis* creates in this south-central New England forests developed at a particular time, as a result of specific historical events and decisions by individual people, and while strong, is impermanent. The responses of co-occurring species and ecosystem dynamics to its loss from these forests likewise results from the unique temporal confluence of *T. canadensis* dominance overlain on historical patterns of land use and environmental change. Although *T. canadensis* recovered its dominance relatively rapidly from disturbances in the last 150 years, it will take at least another 150 years to determine whether it will rebound – in a rapidly changing climate – from its current decline caused by the hemlock woolly adelgid (Foster 2014).

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Table 1. Species cored for dendrochronological analysis in the Harvard Forest Hemlock Removal Experiment. The species are ordered by relative abundance, and the numbers of the plots from which they were sampled match plot numbers illustrated in Figures 1 and 2. The last column gives the percent of the cores sampled that reached ≤ 3 years of the pith of the tree.

Species	**Sample size**	**Plots**	**≤ 3 years of pith (%)**
Tsuga canadensis (L.) Carr.	121	1–7	82
Acer rubrum L.	32	1–8	93
Betula lenta L.	31	2, 4, 5–8	77
Quercus rubra L.	16	2, 3, 5–8	79
Pinus strobus L.	13	1–3, 6, 7	88
Betula alleghaniensis Britt.	5	1, 6, 8	100
Betula papyrifera Marsh.	5	5–7	100
Quercus alba L.	4	1, 3	80
Acer saccharum Marsh.	2	8	100
Fraxinus americana L.	1	6	100
Ostrya virginiana (P. Mill.) K. Koch	1	3	100
Quercus velutina Lam.	1	7	100

Table 2: Damage to the Simes Tract from the 1938 Hurricane based on visits to all stands and detailed assessments of older stands with merchantable timber (Raymond 1938). These older stands included compartments 27, 30, and 32 of Figure 2, in which plots 1–3 of the Harvard Forest Hemlock Removal Experiment are located. Area per compartment is in acres (1 acre = 0.405 hectare) and Volume is in thousands of board feet (MBF; one board foot = 0.002 m^3).

Compartment	**Classification***	**Area**	**% trees left standing**	**Volume down per acre**	**Total volume down**
9	Hm/Cd	2.5	50–75	10	25
16	Pine	4	25–50	15	60
22	Pine-Hm-Hdwd	1.5	0–10	15	22
25	Pine	30	0–10	25	750
27	Pine-Hm-Hdwd	2	25–50	10	20
30	Pine-Hm	10	50–75	8	80
32	Pine-Hm-Hdwd	9	50–75	8	72
33	Pine	10	25–50	10	100
33	Hardwood	10	25–50	1	10
35	Hardwood	15.4	50–75	1	15

*Cd: Cordwood; Hdwd: Hardwood; Hm: Hemlock.

Table 3: Density (trees/ha), basal area (m^2/ha), and importance value (= sum of relative density and relative basal area) in the six hemlock plots and the two hardwood plots of the Harvard Forest Hemlock Removal Experiment of the five dominant genera (*Tsuga, Quercus, Pinus, Betula*, and *Acer*). Individual species within these genera (in grey). All "Other" woody taxa (*Carpinus caroliniana* Walt., *Castanea dentata* (Marsh.) Borkh., *Carya glabra* (P. Mill.) Sweet, *Carya ovata* (P. Mill.) K. Koch, *Fagus grandifolia* Ehrh., *Fraxinus americana* L., *Fraxinus nigra* Marsh., *Hamamelis virginiana* L., *Ostrya virginiana* (P. Mill.) K. Koch, *Prunus serotina* Ehrh., and *Sorbus americana* Marsh.) were pooled. For each taxon, values given are average densities of live trees in the two blocks pooled (first row) and in parentheses, the average densities in, respectively, the valley and the ridge blocks. Genera and species within genera are ordered by importance value in the Hemlock plots.

	Hemlock plots			**Hardwood plots**		
	Density	**Basal area**	**Importance Value**	**Density**	**Basal area**	**Importance Value**
Tsuga canadensis	672	30.69	126	64	1.98	12
	(764, 579)	(30.33, 31.05)	(129, 123)	(27, 101)	(0.83, 3.13)	(5, 20)
Betula	130	4.42	21	289	7.9	53
	(82, 178)	(2.11, 6.73)	(11, 32)	(346, 231)	(9.05, 6.75)	(61, 45)
B. lenta	98	3.42	16	237	6.16	42
	(53, 143)	(1.76, 5.07)	(8, 25)	(280, 193)	(7.08, 5.23)	(49, 37)

	Hemlock plots			Hardwood plots		
	Density	Basal area	Importance Value	Density	Basal area	Importance Value
B. alleghaniensis	20	0.41	3	32	0.88	6
	(27, 13)	(0.31, 0.51)	(3, 2)	(62, 1)	(1.75, 0.01)	(11, 0)
B. papyrifera	12	0.6	2	20	0.84	5
	(2, 22)	(0.03, 1.16)	(0, 5)	(4, 36)	(0.18, 1.49)	(1, 8)
B. populifolia	—	—	—	1	0.04	0
	—	—	—	(1, 1)	(0.04, 0.03)	(0, 0)
Quercus	72	5.72	18	151	8.79	42
	(99, 44)	(6.39, 5.05)	(22, 15)	(196, 105)	(11.23, 6.35)	(55, 30)
Q. rubra	52	4.36	14	135	8.12	38
	(71, 33)	(4.77, 3.95)	(16, 11)	(184, 85)	(10.80, 5.44)	(53, 25)
Q. alba	19	1.35	4	7	0.23	1
	(26, 11)	(1.59, 1.10)	(6, 3)	(4, 9)	(0.08, 0.38)	(1, 2)
Q. bicolor	1	0.02	0	—	—	—
	(1, 0)	(0.04, 0.00)	(0, 0)	—	—	—

	Hemlock plots			**Hardwood plots**		
	Density	**Basal area**	**Importance Value**	**Density**	**Basal area**	**Importance Value**
Q. velutina	—	—	—	10	0.44	2
	—	—	—	(9, 11)	(0.36, 0.52)	(2, 3)
Acer	102	3.43	17	353	6.62	55
	(110, 94)	(2.48, 4.38)	(15, 19)	(477, 228)	(7.05, 6.18)	(66, 43)
A. rubrum	103	3.43	17	242	4.96	39
	(111, 94)	(2.48, 4.38)	(15, 19)	(256, 227)	(3.85, 6.06)	(36, 43)
A. saccharum	—	—	—	111	1.66	16
	—	—	—	(221, 1)	(3.20, 0.11)	(30, 0)
Pinus strobus	56	5.00	15	114	6.74	33
	(90, 22)	(6.22, 3.77)	(21, 10)	(47, 180)	(0.97, 12.50)	(9, 58)
Other	2	0.50	3	5	0.63	5
	(3, 1)	(0.41, 0.58)	(3, 2)	(4, 5)	(0.55, 0.70)	(4, 6)

Table 4: Departure from complete spatial randomness (CSR) in the spatial distributions of the dominant genera in the eight plots of the Harvard Forest Hemlock Removal Experiment. Plots 1−6 are hemlock-dominated plots, and plots 7−8 are hardwood-dominated plots (see Figures 4−5 and Table 3). For each genus, we indicate either the location (by compass quadrant) in the plot where the highest density of plants occurs or CSR if the species is distributed randomly in space; followed by interplant distance (maximum = 22.5 meters) at which significant clustering ($p = 0.01$, Ripley's *K* test) of stems was observed (or NA for CSR).

		Genus				
Block	**Plot**	***Tsuga***	***Betula***	***Quercus***	***Acer***	***Pinus***
Valley	**1**	NW; > 15 m	NW; > 3 m	E; > 6 m	NE; > 5 m	CSR; NA
	2	SW; > 10 m	SE; 12−16 m	SE; > 7 m	SE; > 20 m	E; > 5 m
	3	NE; > 7 m	NW; > 4 m	Center; > 7 m	N; 8−12 m	E; 12−21 m
	8	E; 0−5 m	NW; > 6 m	S; > 7 m	NE; > 12 m	SW; > 8 m
Ridge	**4**	CSR; NA	NW; > 5 m	SE; 17−18 m	CSR; NA	CSR; NA
	5	CSR; NA	SW; > 8 m	CSR; NA	CSR; NA	CSR; NA
	6	SW; > 17 m	S; > 3 m	CSR; NA	CSR; NA	NE; > 5 m
	7	E; > 2 m	Center; > 5 m	S; > 10 m	W; > 7 m	NW; > 7 m

Table 5: Comparison of fits of general additive models (GAMS) shown in Figures 9 and 10. For each species, values given are the percent deviance explained by the model relative to a null (intercept-only) model and the AIC value. The “better” of the models explains a higher percentage of the deviance and has a lower AIC value.

	BAI$_n$ = YEAR + s(AGE)		**BAI$_n$ = s(YEAR, AGE)**	
	Deviance	**AIC**	**Deviance**	**AIC**
Tsuga canadensis	24.5	65388	24.9	65106
Betula lenta	37.9	13176	45.3	12728
Quercus rubra	33.3	7989	41.7	7671
Acer rubrum	25.8	13156	26.0	12968
Pinus strobus	29.7	7227	39.4	6930

Appendix: Deeds used to reconstruct ownership and land-use history of the Simes Tract. Year is the year of the transaction, not necessarily the year the deed was recorded. Book and Page numbers refer to page numbers in the Recorded Land Books (1731 – present) at the Worcester District Registry of Deeds, available online at http://www.worcesterdeeds.com/. When no Book and Page is given, transmission was made in a will.

1. Deed transmission of Joseph Gleason's Farm

Year	**Book**	**Page**	**Grantor**	**Grantee**
1765	54	502	I. Gleason	J. Gleason
1766	54	503	Sanderson	J. Gleason
1779	86	279	Bradshaw	J. Gleason
1791	113	528	Bradshaw	J. Gleason
1792	118	278	Messinger	J. Gleason
1792	119	194	Stone	J. Gleason
1806	190	11	J. Gleason	C. Gleason
1826	253	48	C. Gleason	Brooks Jr.
1830	276	402	Brooks Jr.	I. Ayers
1859	608	457	I. Ayers	G. Ayers
1897	1552	517	G. Ayers	Johnson
1921	2249	188	Johnson	Recikauskewitz
1941	2805	331	Recikauskewitz	Recos
1941	2842	226	Recos	Morrison

Year	Book	Page	Grantor	Grantee
1941	2885	242	Morrison	O. Simes
1947	3086	156	O. Simes	Recos
1970	—	—	O. Simes	Harvard University

2. Deed transmission of Samuel Chamberlain's Farm (a.k.a the Towne Farm *ca.* 1880 and the "Simes and Williams Lots" of 1930).

Year	Book	Page	Grantor	Grantee
1785	113	30	Goodnow	Ward
1788	105	647	Goodnow	S. Chamberlain
1795	241	15	Ward	S. Chamberlain
1826	274	465	S. Chamberlain Jr.	A. Chamberlain
1827	254	484	S. Chamberlain Jr.	E. Chamberlain
1828	271	635	S. Chamberlain Jr.	Williams
1829	269	280	E. Chamberlain	Brooks
1831	281	79	E. Chamberlain	Rogers
1833	296	298	Rogers	J. Towne Jr.
1834	302	293	S. Chamberlain Jr.	Bond
1834	302	294	A. Chamberlain	J. Towne Jr.
1835	307	489	J. Towne Jr.	Bond
1835	307	490	Bond	J. Towne Jr.

Year	Book	Page	Grantor	Grantee
1835	307	484	Rogers	J. Towne Jr.
1836	314	282	Bond	R. Towne
1836	320	131	J. Towne Jr.	Carter
1836	320	132	R. Towne	J. Towne Jr.
1836	325	186	J. Towne Jr.	Bond
1837	325	187	J. Towne Jr.	Williams
1838	338	281	Bond	Witt
1839	346	304	Brooks	Ayers
1839	346	304	Ayers	J. Towne Jr.
1839	385	435	J. Towne Jr.	Ayers
1839	346	307	J. Towne Jr.	Witt
1869	785	205	J. Towne Jr.	Foster
1869	785	207	Foster	J. Towne
1880	—	—	J. Towne Jr.	J. Towne
1880	1068	166	J. Towne	Williams
1880	1068	166	J. Towne	Williams
1880	1083	178	Williams	Moore
1884	1195	219	W. J. Towne	E. Towne
1891	1363	609	E. Towne	W. Simes
1929	2508	39	W. Simes	O. Simes
1929	1193	529	E. Towne	H. Carter
1934	2519	348	Williams	O. Simes

Year	**Book**	**Page**	**Grantor**	**Grantee**
1934	2519	348	E. Towne	O. Simes
1970	—	—	O. Simes	Harvard University

3. Timber sales from the Towne Farm

Year	**Book**	**Page**	**Grantor**	**Grantee**
1880	1068	164	J. Towne and Barrows	N. Doubleday
1880	1068	165	E. Towne	J. Towne
1883	1135	468	A. Doubleday	R. Doubleday
1883	1157	364	A. Doubleday	R. Doubleday
1883	1157	365	R. Doubleday	G. Ayers
1883	1157	366	G. Ayers	R. Doubleday

Figure Legends

Figure 1. Location of the Simes Tract and the Harvard Forest Hemlock Removal Experiment in Petersham, Massachusetts, USA. The regional map shows the basal area of *T. canadensis* at a 1 km^2 resolution. The inset shows the location of Harvard Forest tracts in Petersham; the Simes Tract is labeled, and the locations of the experimental plots are indicated with black dots.

Figure 2. Historical context and use of the Simes Tract. The figure shows mapped stone walls, the cart path by the cider mill, major roads, and town boundaries prior to the disincorporation in April 1938 of the towns of Dana, Enfield, Greenwich, and Prescott to build the Quabbin Reservoir; the primary property divisions (the Gleason Farm in the north half of the tract and the Chamberlain, then Towne, Farm in the south half of the tract); area identified as “forested” based on the 1830 statewide forest survey (Hall et al. 2002); areas logged in the 1920s; areas logged between 1930 and 1980; and the Harvard Forest Hemlock Removal Experimental plots (established 2003). The experimental plots and assigned canopy manipulation treatments are overlain on this map: plots 1, 2, 3, and 8 make up the valley block; plots 4–7 make up the ridge block. In 2005, the canopy manipulation treatments – hemlock control (He), girdled (G), logged (L), and hardwood control (Hw) – were each applied to one of the ≈ 90 × 90 m plots within each block.

Figure 3. Environmental history in and around Petersham, MA, 1897–2003. Top to bottom: Population of Petersham; Mean annual temperature (°C: thin lines), 10-year running mean temperature (thick lines), and average annual minimum and maximum temperatures (shaded areas) in Amherst, MA (black lines, grey shading) and Petersham (blue lines, mauve shading);

Mean annual precipitation (mm: thin lines) and 10-year running mean precipitation (thick lines) in Amherst (dark yellow) and Petersham (dark green); Summer (July-August) Palmer Drought Severity Index (PDSI) (thin red line) and 5-year running mean PDSI (dark red line) for Pelham, MA. Timing of the four major region-wide forest disturbances and the 1925–1932 logging are indicated with shading and arrows.

Figure 4. Frequency distributions (number of stems/ha) in 10-cm increments of basal area of all stems ≥ 5-cm DBH (top row) and those of the five most abundant genera in the six hemlock plots (left column) and two hardwood plots (right column) of the Harvard Forest Hemlock Removal Experiment. The light and dark grey bars are the number of stems/ha in each diameter class in the plots in the valley or ridge block, respectively asterisks before the genus name (or "All") indicate the shape of the diameter distributions differed significantly ($P < 0.001$; Kolmogorov-Smirnov test) between the ridge and valley plots. The black line is the overall diameter distribution (plots pooled across the two blocks).

Figure 5. Maps of the hemlock plots in the valley (left column) and ridge (right column). In each column, plots are arrayed from north (top) to south (bottom); hence the valley plots (left) are ordered (top to bottom) 1 to 3, whereas the ridge plots (right) are ordered (top to bottom) 6 to 4. Relative topographic relief in each plot is shown in gray-scale, from white (relatively high elevation) to 40% gray (mean elevation) to 80% gray (relatively low elevation) contours. Genera are identified by different colors (key stripe at bottom of plot); for emphasis, the most common genera also are plotted with different symbols: squares for *Tsuga*, triangles for *Betula*, large filled circles for *Acer*, small filled circles for *Pinus* and *Quercus*, and small diamonds for all

other genera. The central rectangle in each plot map is the 30 × 30-m area from which trees were sampled for dendrochronological analysis.

Figure 6. Maps of the hardwood plots in the valley (plot 8: left) and ridge (plot 7: right). Relative topographic relief in each plot is shown using pink (relatively high elevation) to white (mean elevation) to blue (relatively low elevation) contours. Genera are identified by different colors (key stripe at bottom of plot) and symbols (as in Figure 5). The central rectangle in each plot map is the 30 × 30-m area from which trees were sampled for dendrochronological analysis.

Figure 7. Relationships between tree age (relative to 2005) and tree diameter of the five dominant genera (*Tsuga*, *Acer*, *Betula, Quercus*, *Pinus*; color-coded as in Figures 6 and 7) in the central 30 × 30-m areas of the hemlock (top row) and hardwood (bottom row) plots in the valley (left column) and ridge (right column) blocks. Marginal histograms show age (top and bottom) and diameter (left and right) distributions. Dark lines in each panel are the local regression (loess) relationship between tree age and diameter for all species pooled; shaded area is the 95% confidence interval. Years shown above the *x*-axis are endpoints of observed recruitment (as of 2005) and the 1938 hurricane.

Figure 8: Relative basal area growth ($r\mathrm{BAI}_n$ in $\mathrm{mm}^2 \cdot \mathrm{mm}^{-2} \cdot \mathrm{yr}^{-1}$) of *Tsuga canadensis*, *Betula lenta*, *Quercus rubrum*, *Acer rubra,* and *Pinus strobus* sampled in the central 30 × 30-m areas of plots in the valley (left column) and ridge (right column) blocks. Each light line represents the relative growth trajectory of an individual tree in the six hemlock (light grey) or hardwood (light blue) plots; corresponding thick lines are the average decadal (10-year moving average) relative

basal area growth in these plots. Pink shading and black vertical lines denote, from left to right in each column, the four major region-wide forest disturbances and the episode of logging across the Tract: 1910–1915 drought and chestnut blight, 1925–1932 logging, 1938 hurricane, 1962–1966 drought, and the 1981 gypsy moth outbreak.

Figure 9: General additive models (Equation 2) fit to relative growth in basal area ($r\text{BAI}_n$) of *Tsuga canadensis, Betula lenta, Quercus rubra, Acer rubrum,* and *Pinus strobus* sampled at the Simes Tract. To maximize power of these models, we pooled individuals among plots and blocks. These models assumed that there was a common effect of year regardless of tree age (right column) but that tree growth varied with individual age of the tree (left column: solid line is the estimated age effect and the dotted lines are at two standard errors of the estimate – an approximate 95% confidence interval). On the five plots in the right column, the shading and vertical dotted grey lines denote, from left to right, the major region-wide forest disturbances and the episode of logging across the Tract: 1907–1914 drought; 1910–1915 chestnut blight; 1925–1932 logging; 1938 hurricane; and the 1981 gypsy moth outbreak.

Figure 10: Line plots (left) of observed annual relative growth in basal area ($r\text{BAI}_n$) for individual trees and the corresponding contour plots (right) predicted by the two-dimensional smoothing spline model (Equation 3) for *Tsuga canadensis, Betula lenta, Quercus rubra, Acer rubrum* and *Pinus strobus* sampled at the Simes Tract. The model (results in right column) assumes that the effect of year on growth varies with tree age. To maximize power of these models, we pooled individuals among plots and blocks. In each of the line plots of the raw data (left), the trees are ordered left-to-right from oldest to youngest; age of a tree increases up the

diagonal line, and color indicates annual $r\mathrm{BAI}_n$ ($\mathrm{mm}^2 \cdot \mathrm{mm}^{-2} \cdot \mathrm{yr}^{-1}$) from 0 (yellow) to 100 (dark red). On all plots, the pink vertical shading and black vertical lines denote, from left to right, the major region-wide forest disturbances and the episode of logging across the Tract: 1907–1914 drought; 1910–1915 chestnut blight; 1925–1932 logging; 1938 hurricane; and the 1981 gypsy moth outbreak.

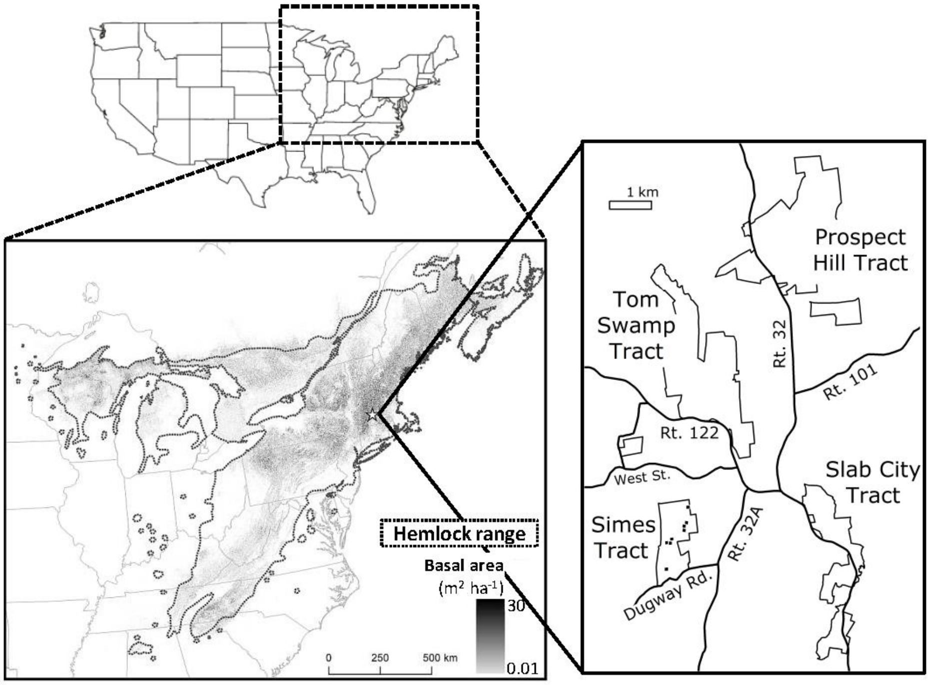
1 km
Prospect Hill Tract
Tom Swamp Tract
Rt. 32
Rt. 101
Rt. 122
West St.
Slab City Tract
Simes Tract
Rt. 32A
Dugway Rd.
Hemlock range
Basal area
(m^2 ha^{-1})
30
0.01
0
250
500 km

Figure 1

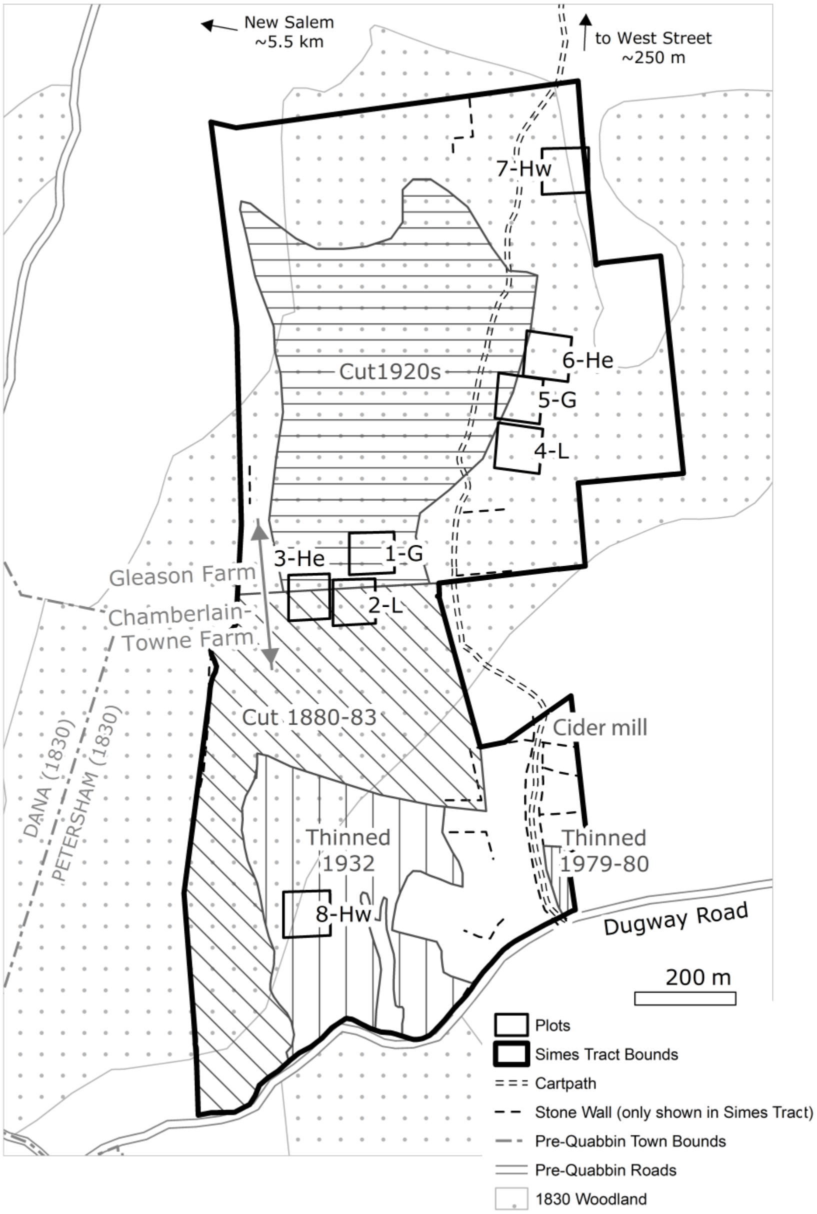
New Salem
~5.5 km
to West Street
~250 m
7-Hw
Cut1920s
6-He
5-G
4-L
3-He
1-G
Gleason Farm
Chamberlain-
Towne Farm
2-L
Cut 1880-83
Cider mill
DANA (1830)
PETERSHAM (1830)
Thinned
1932
Thinned
1979-80
8-Hw
Dugway Road
200 m
Plots
Simes Tract Bounds
Cartpath
Stone Wall (only shown in Simes Tract)
Pre-Quabbin Town Bounds
Pre-Quabbin Roads
1830 Woodland

Figure 2

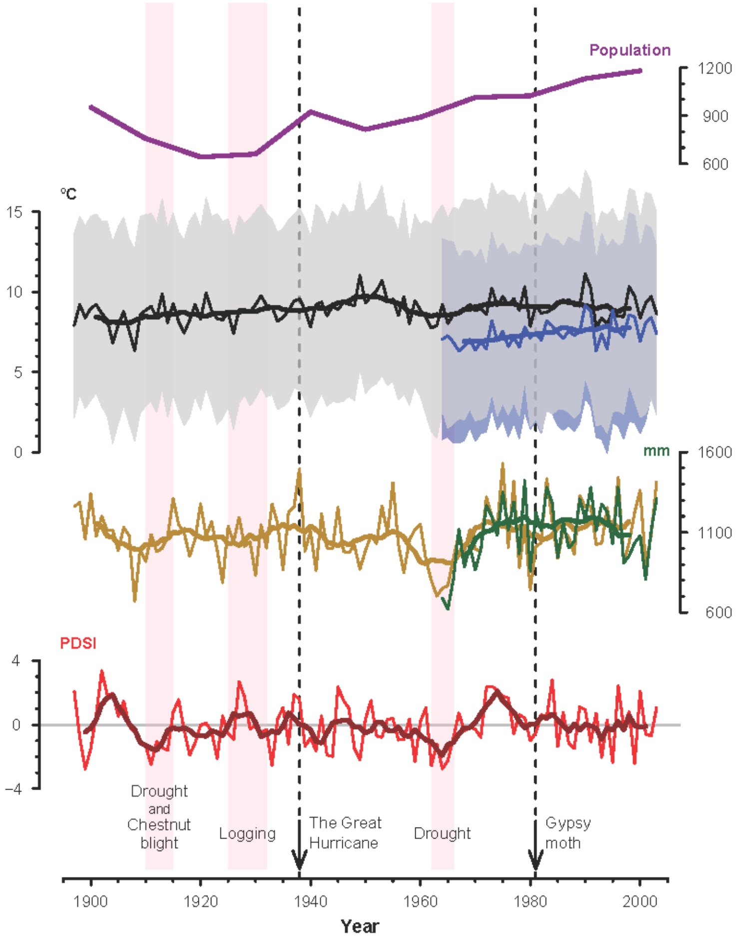
Population
1200
900
600
°C
15
10
5
0
mm
1600
1100
600
PDSI
4
0
−4
Drought and Chestnut blight
Logging
The Great Hurricane
Drought
Gypsy moth
1900
1920
1940
1960
1980
2000
Year

Figure 3

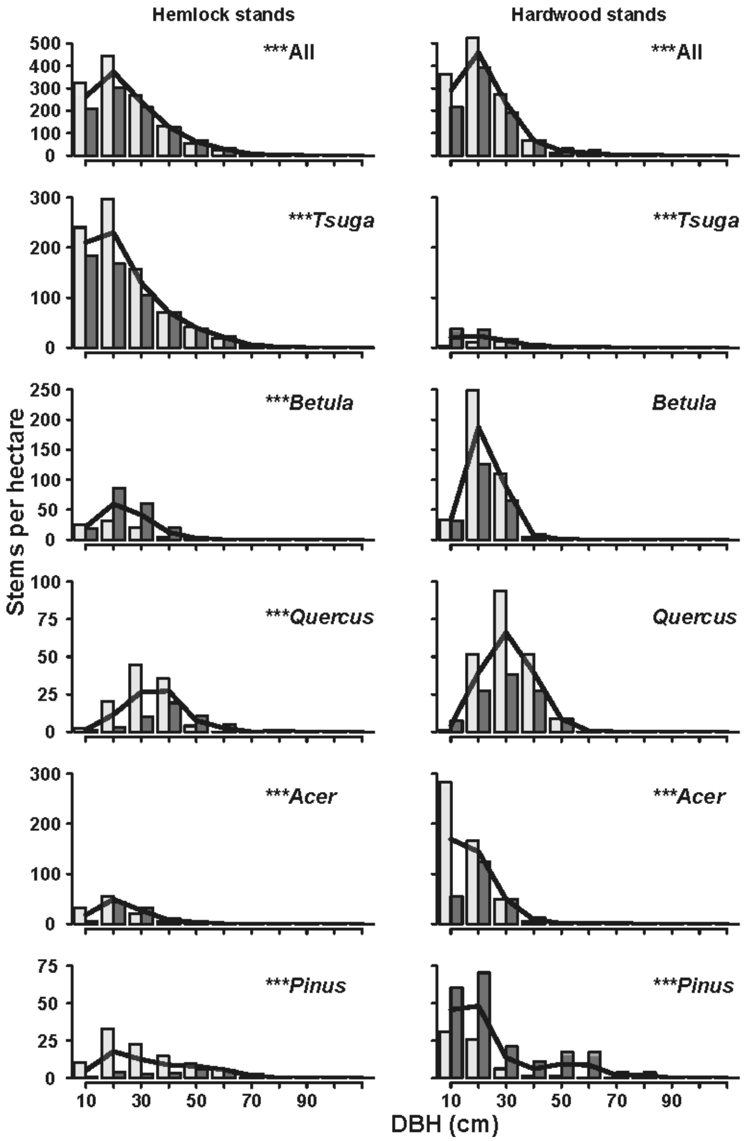
Hemlock stands
Hardwood stands
***All
***Tsuga
***Betula
Betula
***Quercus
Quercus
***Acer
***Pinus
Stems per hectare
0
100
200
300
400
500
0
50
100
150
200
250
0
25
50
75
100
10
30
50
70
90
DBH (cm)

Figure 4

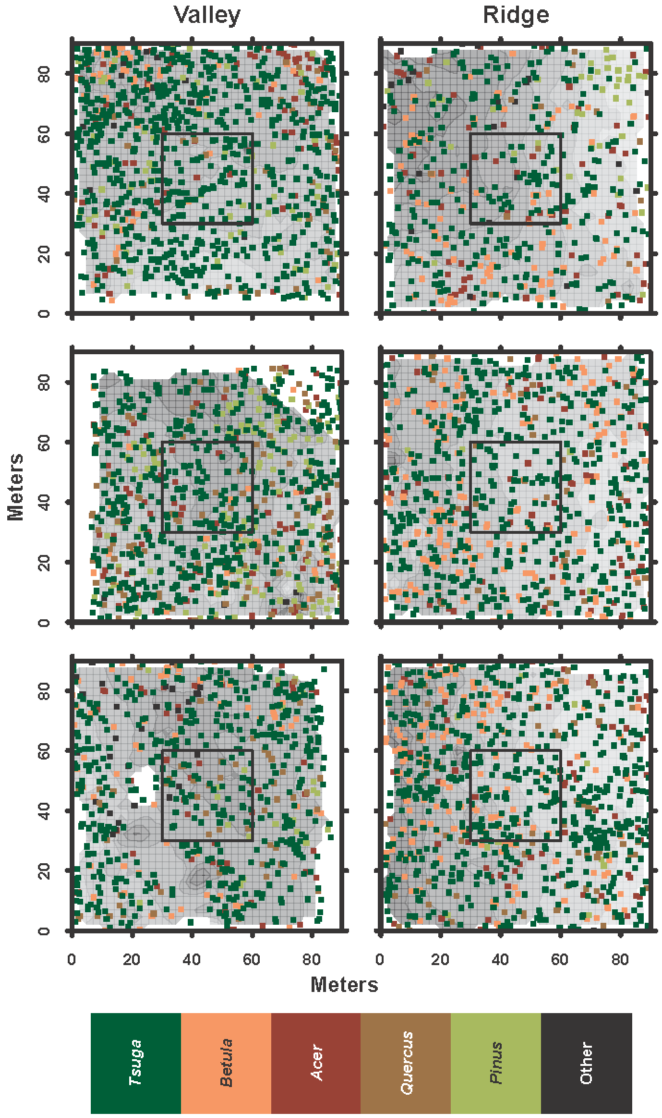
Valley
Ridge
Meters
0
20
40
60
80
Meters
0
20
40
60
80
Tsuga
Betula
Acer
Quercus
Pinus
Other

Figure 5

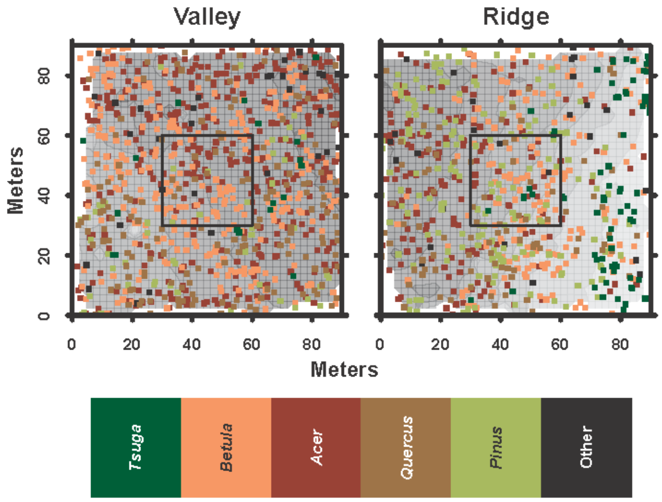
Valley
Ridge
Meters
0
20
40
60
80
Meters
0
20
40
60
80
0
20
40
60
80
Tsuga
Betula
Acer
Quercus
Pinus
Other

Figure 6

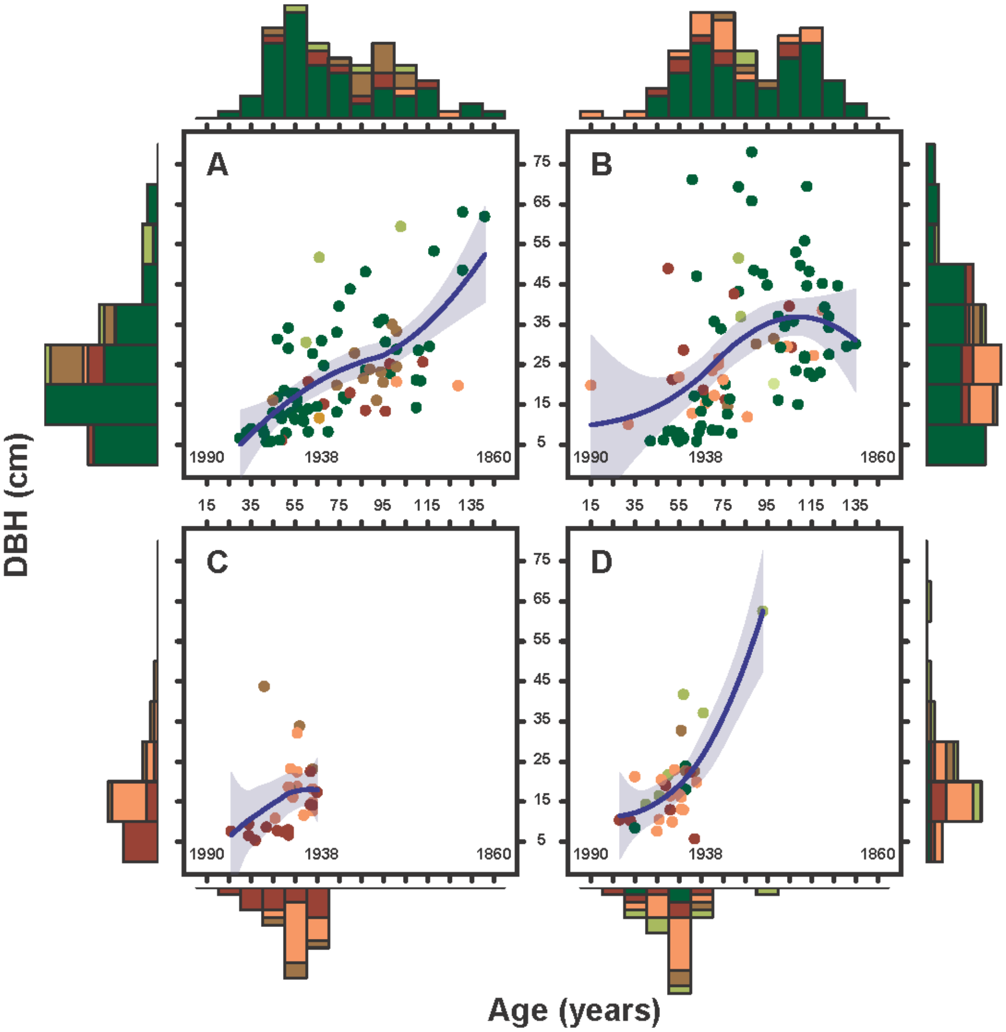
A
B
C
D
DBH (cm)
Age (years)
1990
1938
1860
15
35
55
75
95
115
135
5
15
25
35
45
55
65
75

Figure 7

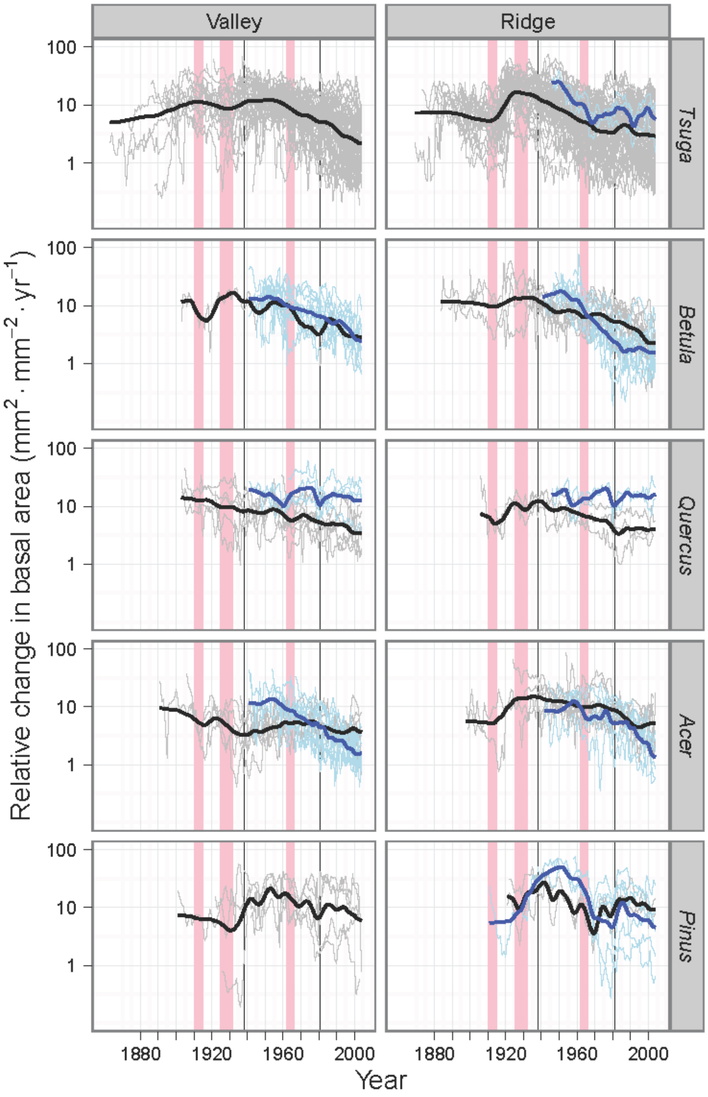
Valley
Ridge
Tsuga
Betula
Quercus
Acer
Pinus
100
10
1
Relative change in basal area (mm^2 · mm^{-2} · yr^{-1})
1880
1920
1960
2000
Year

Figure 8

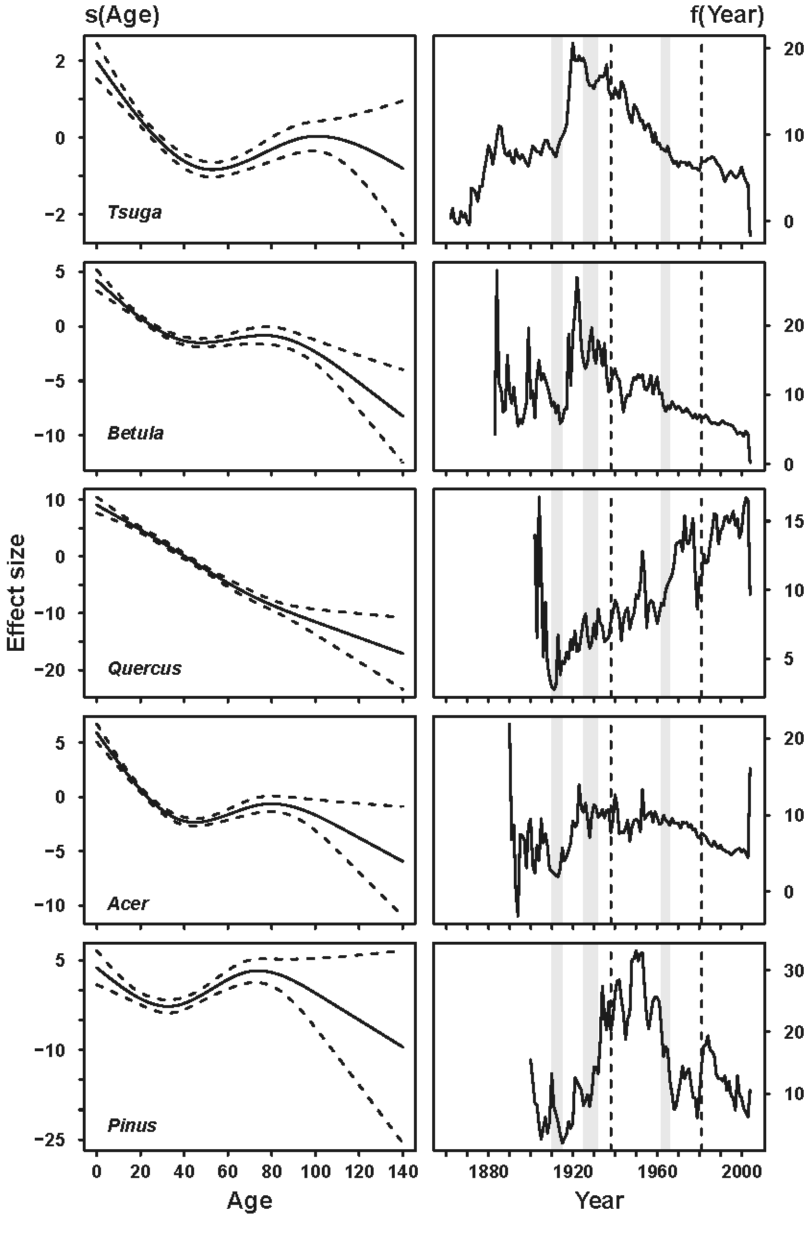
s(Age)
f(Year)
Effect size
Tsuga
Betula
Quercus
Acer
Pinus
Age
Year
0
20
40
60
80
100
120
140
1880
1920
1960
2000

Figure 9

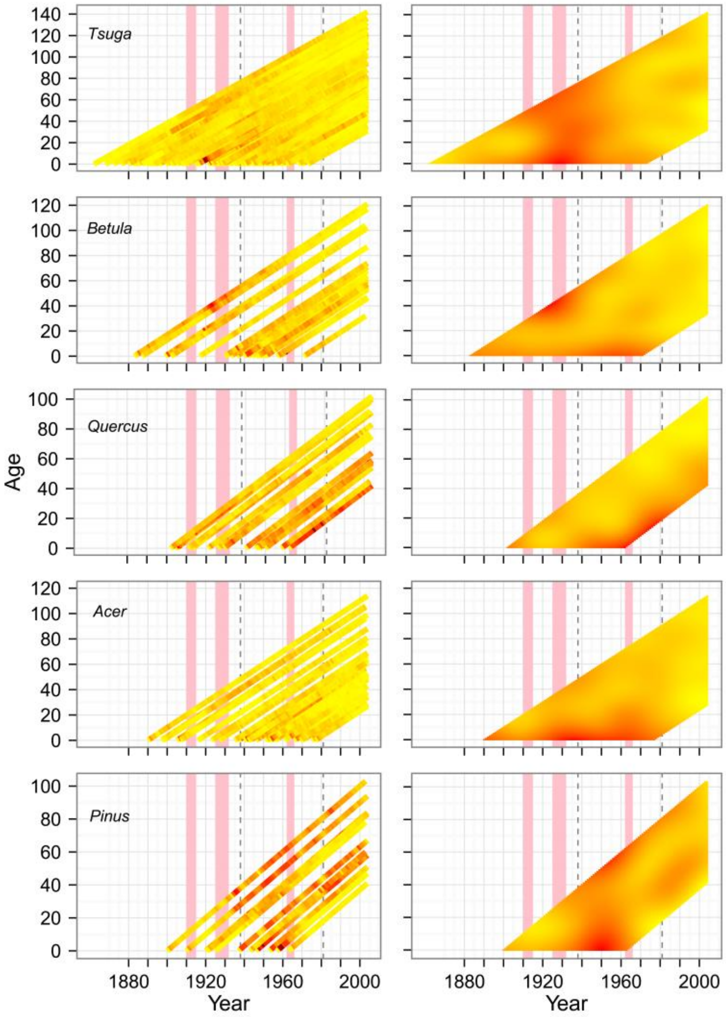
Tsuga
Betula
Quercus
Acer
Pinus
Age
Year
1880
1920
1960
2000
0
20
40
60
80
100
120
140

Figure 10