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Eight decades of compositional change in a managed northern hardwood landscape

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ABSTRACT

We analyzed over 8 decades of change in forest composition (represented by species proportion of basal area) and size class from more than 400 permanent plots located on the Bartlett Experimental Forest in the White Mountains of New Hampshire. These data represent one of the longest-term landscape-scale records of forest change based on permanent plots in North America. We analyzed the plots based on elevation class, land type indicating assumed successional direction (grouped into coniferous and deciduous), and inventory period within managed and unmanaged portions of the forest. An ongoing shift from small- to large-diameter stems is clear across all species, in response to the overall aging of the forest following exploitative harvesting in the 19th century. Major compositional changes include a continuing decline in shade-intolerant species (paper birch and aspen), along with the mid-tolerant yellow birch. An increase in red maple abundance through the early 1990s has leveled off or reversed. Among shade-tolerant species, increases in beech and red spruce were largely consistent with assumed land type on unmanaged plots, but heavy marking against diseased beech on managed plots restricted increase of that species. Sugar maple declined in abundance except where silvicultural intervention helped maintain it. By contrast, eastern hemlock showed a continuing expansion at all elevations below 600 m. The data continue to show little or no evidence of upward migration of species, despite evidence of recent regional change in climate. However, the BEF is poised for substantial changes when emerald ash borer and hemlock woolly adelgid, both of which are known to infest nearby areas, do arrive.

1. Introduction

Forests of eastern North America are continuously changing following centuries of human land use, beginning with aboriginal influences during the pre-European period (Abrams and Nowacki, 2020), but accelerating with agricultural and industrial use following European settlement and the industrial revolution (e.g., Foster and Aber, 2004). They have also been subject to multiple novel, external forcings. These include changes in physical climate (e.g., Rustad et al., 2012; Swanston et al., 2018), chemical climate (e.g., Driscoll et al., 2001; Lawrence et al., 2015), and an accelerating number of invasive insect and plant agents (e.g., Dukes et al., 2009; Kosiba et al., 2018).

However, long-term records of this decadal scale forest change at the landscape scale are relatively rare. For example, design changes in, and data limitations of, the U.S. national forest inventory complicate attempts to track change over multiple decades (Bechtold and Patterson, 2005). In the northeastern United States, only a handful of published studies track forest vegetation composition over multiple decades using permanent plots, and most of those encompass timespans of 50 years or less (e.g., Hibbs, 1983; Whitney, 1984; Mabry and Korsgren, 1998; Martin and Bailey, 1999). For example, Hibbs (1983) documents 40 years of vegetation response to a 1938 hurricane at the Harvard Forest, using 11 plots that had been heavily disturbed. The same plots, augmented by 3 others, were studied by Mabry and Korsgren (1998) who documented a decline in shade-intolerant species in the understory. Whitney's (1984) study utilized a larger sample size, representing 152 of the plots originally established by Lutz (1930) in the hemlock-dominated Heart's Content old-growth area. However, that study area was relatively small (50 ha), and disturbed areas were excluded from analysis. Martin and Bailey (1999) report change from The Bowl, an old-growth site in New

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Hampshire, using a large number ($n = 218$) of very small (0.01 ha) plots, over a 20-year period. Over that time scale, species composition was relatively stable but basal area increased slightly. Many of the longer-term records also focus on "undisturbed" or old-growth forests (e.g., Ward et al., 1999), with notable exceptions being Allen and Seaboyer (2017) and Rogers et al. (2018, 2021), both of which report on approximately 60-year records. The study of Allen and Seaboyer (2017) is notable for encompassing a 585-ha study area, with 45 permanent plots, allowing some landscape-scale inferences about management influence within a pine-hemlock-maple (*Pinus-Tsuga-Acer*) forest landscape. Rogers et al. (2018, 2021) present longer-term analyses focusing on specific silvicultural studies.

One of the longest-term records in the region is that arising from the Bartlett Experimental Forest, located in the White Mountains of New Hampshire. In 1931–1932, the Bartlett Experimental Forest was gridded with a systematic network of permanent fixed-area plots. These plots have been maintained and remeasured at irregular periods through the present day. These data, or subsets thereof, have been analyzed for a variety of purposes over the past several decades (e.g., Jensen, 1941a; Filip et al., 1960; Leak, 1961a, 1961b, 1987; Hoover, 2011). The most recent published characterizations of compositional change are those of Leak and Smith (1996), which analyzed change through the 1991–1992 inventory, and an update based on a 2002–2003 remeasurement that examined broad elevational patterns (Leak and Yamasaki, 2010). These data represent an extraordinary opportunity to analyze long-term change in both managed and unmanaged forest stands, especially that change that follows from the expansive exploitative harvesting practice that predominated throughout the 19th and early 20th centuries.

A remeasurement of the plot network was completed again in 2015–2017. The purpose of this manuscript is threefold:

1) To update the description of compositional change, expressed in terms of percent basal area by species, extending the record to over eight decades;
2) To re-examine questions about control of management, elevation, and site on compositional change that were previously analyzed by Leak and Smith (1996), bringing to bear both the extended record and recent innovations in statistical methodologies;
3) To re-interpret observed change in light of new developments in our understanding of existing external forcings since the analysis by Leak and Smith (1996), along with emergent threats that have risen to prominence since their analysis was completed.

This paper provides an initial overview of major trends in composition, to provide context for future work that will analyze more refined questions, and to set the stage for other researchers who may use the data from this long-term study to address questions of their own.

2. Methods

2.1. Study site description

The study was conducted on the Bartlett Experimental Forest (BEF; 44°03′ N, 71°17′ W) (Fig. 1). At the time of plot establishment, the forested compartments of the BEF comprised 1,042 ha, with an additional 10 ha in roads, for a total of 1,052 ha. Although subsequent additions have enlarged the BEF, this study focuses on the original area. The terrain of the BEF is generally north-facing but irregular and mountainous, with elevations ranging from 200 m in the Saco River valley to 820 m at the peaks of the Bartlett Haystacks. The Bear Notch Road, following the bed of the Bartlett and Albany Railroad (a 19th century logging railroad; Belcher, 1980; Gove, 2001) from Bear Notch to the valley floor, passes along the southern edge of the original BEF acreage before turning north just inside its eastern border (Fig. 1a).

The BEF, along with much of the surrounding region, was subject to intensive land use and exploitive timber harvesting prior to the acquisition of land by the fledgling U.S.D.A. Forest Service and the establishment of the White Mountain National Forest in 1918 (Leak and Yamasaki, 2010). Much of the area below 350 m elevation was cleared

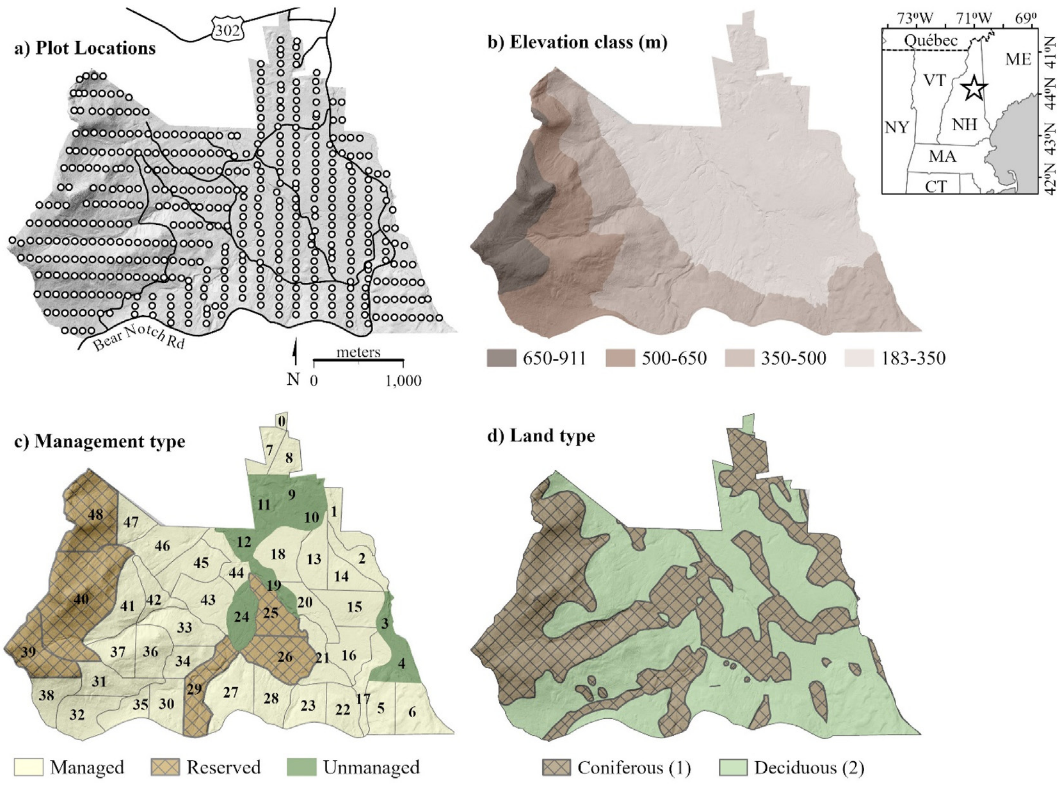

Fig. 1. Location, plot layout, land types, management types, and elevation classes on the Bartlett Experimental Forest.

for railroad fuel in the late 19th century, with nearly all trees removed and stumps left more or less intact, but most of this land was never used for agriculture. A very small area in the valley floor did experience brief agricultural use. At the same time, some conifer-dominated stands were not completely felled. As a result, most stands at low elevations are now less than 130 years old, even if subsequent management has not resulted in stand replacement. At mid-elevations up to 500 m, partial harvesting (essentially high-grading to remove large and valuable stems) was widespread, such that many of these stands have irregular age distributions and include individual trees in excess of 200 years old, presumably those that were left behind as not worth removing, and released from competition (Leak and Smith, 1996). Documentation of specific dates and extent of harvest events is not available for the pre-1918 period, and no systematic survey of legacies was conducted prior to the 1931–1932 survey (described below). Soils at low- to mid-elevations are typically shallow fine tills, with pockets of outwash along drainages. Stands at these elevations are most often comprised of northern hardwoods including paper birch (*Betula papyrifera*), yellow birch (*Betula alleghaniensis*), red maple (*Acer rubrum*), and American beech (*Fagus grandifolia*), with white ash (*Fraxinus americana*) and sugar maple (*Acer saccharum*) most abundant on nutrient-enriched sites. Aspen (*Populus tremuloides* and *P. grandidentata*) may be found in recently-disturbed areas but declining over the course of several decades, along with pin cherry (*Prunus pensylvanica*), which persists for only 20–30 years. Hemlock (*Tsuga canadensis*), red spruce (*Picea rubens*), and balsam fir (*Abies balsamea*) are common conifers, with eastern white pine (*Pinus strobus*) occurring in pockets at low elevations. Very light harvesting of the best available stems may have continued above 500 m, where the fine tills give way to bedrock-controlled soils with stands dominated by balsam fir and red spruce (Leak and Yamasaki, 2010). Stands at the highest elevations have seen little if any timber harvest but they are subject to disturbance by wind, including minor windstorms, down-bursts, and fir waves at high elevations, along with occasional ice storms. Stands across the BEF were impacted by a major hurricane in 1938 (Jensen, 1941b).

2.2. *Inventory plots*

The original plots were laid out in 1931–1932 on a rectangular grid (5 × 10 chains, or approximately 100 m × 200 m), with the orientation of the grid changing on the western slopes approaching the Haystacks, and again on the eastern slopes rising up from the Bear Notch Road in order to better account for variation across elevation. A total of 444 plots were laid out in the original inventory; of those, 422 were remeasured in all of the inventory years reported here, and form the basis for our analysis. Nearly all plots were 0.10 ha (0.25 ac) square. Six 0.04 ha (0.10 ac) plots are part of this inventory, 2 in spruce-fir in the high elevation zone, and 4 in the low elevation zone (Fig. 1a; Leak et al., 2017). Plot corners were monumented and boundary trees facing the interior of the plot scribed to facilitate exact relocation of the plot boundaries; the corner which fell on the intersection of cruise lines was designated as the primary corner to enable consistent relocation. Corner monuments have been maintained since the original establishment and were supplemented with buried survey magnets during the 2015–2017 remeasurement. Beginning at the initial inventory and continuing through 2002–2003, all tree stems over 3.81 cm (1.5 inches) were tallied by 2.54 cm (1 inch) diameter classes. During the 2015–2017 inventory, the complete tally was restricted to trees over 11.43 cm (4.5 inches) DBH (i.e., those in the 12.54 cm (5 inch) diameter class and larger); smaller trees were tallied on subplots. For consistency across inventories, the analysis in this paper uses only trees in the 12.54 cm and larger classes irrespective of inventory year.

During the 2015–2017 remeasurement, the primary corner for all inventory plots was located using a Trimble GPS unit equipped with a Trimble Hurricane Antenna. Continuously Operating Reference Station (CORS) data from the National Geodetic Survey and Trimble Pathfinder software were used to obtain approximately 1–2 m horizontal precision after differential corrections.

2.3. *Elevation class*

The White Mountain National Forest, in concert with other partners, collected airborne LiDAR data during spring 2018 for the area including the Bartlett Experimental Forest. Data were collected at a nominal pulse spacing of 0.7 m during the leaf-free, snow-free late spring season. Raw data were subsequently classified by the contractor and used to produce a 1-m resolution Digital Elevation Model (DEM). Plot locations for the BEF permanent plots were used to extract mean elevation for each plot, which was then collapsed into four elevation classes consistent with those used by Leak and Smith (1996) and reflecting the major ecological and land use divisions at the BEF: 200–350, 350–500, 500–650, and 650–820 m (Fig. 1b). We acknowledge that reducing elevation from a continuous variable to four discrete classes may obscure subtle signals that are not the focus of this specific analysis. This was done to simplify the analysis and presentation of results, and to facilitate comparison with the previous work by Leak and Smith (1996).

2.4. *Management type*

The BEF has been divided into multiple compartments, each reasonably homogenous in composition, soils, elevation, and aspect, and assigned to different treatments under a long-term study plan (Leak et al., 2017). Some compartments are reserved from silvicultural management, while a few have as yet seen no entry. The overall distribution of major silvicultural treatments prior to the 2015 inventory is summarized in Table 1. Consistent with the work of Leak and Smith (1996), we separated plots for this analysis into two broad categories: managed and unmanaged, allowing different categorization of plots within each compartment based on their individual history as reflected in maps, study plans, and other documents (Fig. 1c). The unmanaged category includes plots in reserved compartments. It also includes those areas that were cut during the exploitive period (1885–1893) but that have not seen any subsequent silvicultural treatments, despite being in compartments assigned to management activities. Due to variation in the boundaries of past management practices applied at BEF, 14 plots within unmanaged compartments were reassigned to the managed category based on documentary or other evidence. A combination of written notes, stand operational maps, study plans, and historical aerial imagery was used to confirm past management history.

2.5. *Land type*

Land types were defined for this study based on the habitat mapping concepts of Leak (1982), who aimed for a biophysical land type system labeled with the assumed late-successional forest cover associated with each type. Leak (1982) defined types in terms of their likely successional climax or endpoint based on a combination of geomorphology, soil

Table 1
Areas of major silvicultural treatments on the Bartlett Experimental Forest prior to the 2015 inventory.

Cutting methods	Area (ha)	Percent	Period
Selection, partial cutting (including thinning and diameter-limit cuts)	364	35	1951–2015
Group selection	98	9	1937–2015
Clearcut, large patches, strips	60	6	1934–2015
Shelterwood	56	5	1984–2015
Unmanaged or uncommitted	219	20	1890–2015
Reserved	246	24	1890–2015
Total	1042	100	

texture, and water availability (Fig. 1d). The overarching goals of the system were both ecological and management-oriented. As Leak (1982, p. 1) described it, “Habitats, thus defined, reflect productivity in terms of species combinations and growth rates, as well as certain management limitations such as windthrow and machine operability.” Habitat units were mapped using a combination of aerial imagery and topography by Leak (1982) and evaluated in the field using 1,050 randomly selected point locations across the BEF. For this study, an original hard copy of the 1982 habitat map was digitized with a flatbed scanner and georeferenced using a 1st order polynomial (affine) transformation consisting of 4 control points (4.31 m RMSE). The twelve (12) habitat types in the original map were later grouped into two overall land types: deciduous and coniferous, based on the descriptions provided by Leak and Smith (1996). We note that these land types reflect the anticipated late-developmental composition of forests, rather than the actual composition on the ground, at the time of the 1982 assessment. A total of 51 inventory plots were identified within the RMSE of georeferenced land type polygon boundaries. Therefore, 2015–2017 inventory plot ground photos (taken facing the interior of the plot from each of the four plot corners) were visually interpreted, leading to reassignment of land type for 28 of those 51 plots.

2.6. Statistical analysis

The focus of this analysis, following Leak and Smith (1996) and Leak and Yamasaki (2010), is on composition and relative abundance. Therefore, for each plot and year, we computed proportion of basal area by species using standard approaches for fixed-area plot inventory (see, e.g., Kershaw et al., 2016).

The resulting data are compositional data, with species abundance represented as a fraction, and many entries with values of 0 especially for less-common species. As such, no simple transformation would lead the data to satisfy the assumptions of normality common to older, more traditional statistical approaches. We employed generalized linear mixed models with a zero-inflated beta distribution to test hypotheses about species change, with the specific goal of evaluating which factors (time, elevation, land type) had a stronger association with species' relative abundances than could be explained away by sampling variability. Models were fit and evaluated using the *glmmTMB* package (Brooks et al., 2017) in R (R Development Core Team, 2020). Within these models, the beta distribution (which is bounded between 0 and 1, and commonly used to model fractions and proportions) enables direct modeling of species relative abundance without transformation, while the zero-inflation submodel addresses the probability that a species will be entirely absent on a given plot in any given year. The repeated-measures nature of the data set was addressed by incorporating plot identity as a random effect. Separate models were fit for each species, except trembling and bigtooth aspen which were combined for analysis due to their low abundance and ecological similarity. Models used year (or inventory period), land type, and elevation class alone and in combination as fixed effects, mirroring the hypothesis tests (but not the statistical technique) of Leak and Smith (1996). Specifically, to test for overall shifts in species composition in the landscape, we fit a model of the form

$$p_{\mathrm{BA}} = f(\mathrm{Inventory})$$

where p_{BA} is the basal area of a species (either in total, or for a given size class) as a proportion of the total plot basal area (all species and size classes combined). Size classes were defined as pole (12.7–26.7 cm DBH classes), sawtimber (26.8–44.4 cm DBH classes), and large sawtimber (44.5 cm DBH class and larger). For this simplest model, Inventory (the inventory period treated as a categorical variable) was the sole fixed effect in both the beta regression and logistic zero-inflation model components.

To test for the presence of more complex patterns of compositional change, we fit models of the form

$$p_{\mathrm{BA}} = f(\mathrm{Landtype}, \mathrm{Elevation}, \mathrm{Inventory}, \mathrm{Landtype} \times \mathrm{Inventory}, \\ \mathrm{Elevation} \times \mathrm{Inventory})$$

Because exploratory analysis (and the previous results of Leak and Smith, 1996) indicated a clear influence of management on compositional trends, these models were fit separately for managed and unmanaged plots. We share the opinion of Wasserstein and Lazar (2016), among many other authors, that null hypothesis statistical testing has been and continues to be over-used, and we do not view a sharp *p*-value cutoff as determinative of ecological importance. We do believe that the assessment of signal versus noise in the data should reflect the most important characteristics of the data (such as error distribution), and that motivates our approach. We use a nominal $\alpha = 0.05$ criterion here, to simplify the presentation of results, but we also caution that especially for rare species, the sampling intensity might not suffice for meaningful change to cross the threshold for “statistical significance.” Since the goal of statistical analysis here is to test whether the observed results could be the result of sampling variation, we focus on observed values and not on the coefficients of the models that were used to evaluate those observations.

3. Results

The distribution of plots by elevation, land type, and management type is shown in Table 2. This distribution differs slightly from that reported by Leak and Smith (1996), in part due to the use of updated sources of elevation data and more precise georeferencing, plot-by-plot scrutiny of land type when plots were close to boundaries on the original map, and changes in management history during the past 25 years.

Proportion of basal area by species and size class is shown for each inventory period in Tables 3 and 4 for managed and unmanaged plots, respectively. The rarest species (together comprising 4.1% or less of total basal area in managed plots, and 1.9% or less of total basal area in unmanaged plots) are not shown. Rare conifers included eastern white pine (*Pinus strobus*), red pine (*Pinus resinosa*), and the exotic Scots pine (*Pinus sylvestris*) which we believe to have been planted experimentally in the early years of the BEF. Rare hardwoods – or at least those rarely reaching measurable size for this study – included saskatoon (*Amelanchier* sp.), white and red alder (*Alnus rhombifolia* and *A. rubra*), black birch (*Betula lenta*), black walnut (*Juglans nigra*), ironwood (*Ostrya virginiana*), black cherry (*Prunus serotina*), American mountain ash (*Sorbus americana*), basswood (*Tilia americana*), and American elm (*Ulmus americana*). Examining forest-wide changes, all common species showed statistically significant change over time for proportion of basal area in total, and for at least one size class, on managed plots (Table 3). The same held true for nearly all species on unmanaged plots (Table 4). The exceptions were white ash, which showed change among size classes that was larger than could be explained by sampling variability (a decline in pole-sized stems but an increase in the larger size classes), but inconsistent change in proportion of basal area in total, and balsam fir which showed a modest decline that was not statistically significant but paralleled its decline within managed plots.

Table 2
Number of plots by elevation class, management class, and deciduous and coniferous land types on the Bartlett Experimental Forest. The original inventory included a total of 444 plots, of which 422 have been remeasured across all five inventory periods reported here.

Elevation class	Managed plots		Unmanaged plots		Total
	Deciduous	Coniferous	Deciduous	Coniferous	
I (200–350 m)	92	56	41	31	220
II (350–500 m)	67	19	14	17	117
III (500–650 m)	29	19	8	9	65
IV (650–820 m)	0	1	1	18	20
All	188	95	64	75	422

Table 3

Percent of basal area by species, tree sizes and inventory year for managed plots on the Bartlett Experimental Forest. Significance of year in a zero-inflated beta regression model for each size class and for all trees combined is indicated (* for $p < 0.05$).

Species	Pole					Saw					Large					Pole	Saw	Large	All
	1931	1939	1991	2002	2017	1931	1939	1991	2002	2017	1931	1939	1991	2002	2017				
BE	10.58	10.30	9.14	8.98	9.11	15.07	14.13	13.02	12.64	12.63	7.12	8.00	4.66	5.18	5.78	*	*	*	*
YB	9.29	8.14	3.20	2.99	2.08	5.04	5.19	5.02	4.79	4.16	2.23	2.59	1.26	1.15	1.19	*	*	*	*
SM	4.34	3.73	2.36	2.18	1.80	4.30	4.14	4.83	4.70	3.83	2.69	2.92	4.82	4.94	5.47	*	*	*	*
RM	7.51	7.51	4.37	3.75	2.54	2.99	4.01	8.78	8.63	7.69	0.84	0.78	3.14	3.56	4.94	*	*	*	*
PB	4.95	4.22	1.31	1.35	1.18	2.38	2.99	2.51	1.75	1.19	0.43	0.57	0.22	0.19	0.15	*	*	*	*
WA	1.59	1.41	0.63	0.58	0.51	1.09	1.52	1.47	1.43	1.32	0.16	0.13	1.58	1.58	1.65	*	*	*	*
ASP	1.14	0.57	0.15	0.24	0.07	0.25	0.20	0.12	0.27	0.25	0.00	0.00	0.11	0.11	0.13	*	–	–	*
EH	3.41	3.48	8.40	8.87	8.35	3.78	4.38	6.15	6.99	9.94	0.75	0.99	4.05	5.42	6.86	*	*	*	*
RS	3.66	3.40	2.28	1.99	1.64	1.52	1.69	1.74	1.67	1.78	0.11	0.14	0.28	0.20	0.37	*	–	*	*
BF	0.57	0.46	0.31	0.22	0.17	0.15	0.10	0.03	0.03	0.03	0.03	0.00	0.00	0.00	0.00	*	–	–	*

Species codes: BE = American beech, YB = yellow birch, SM = sugar maple, RM = red maple, PB = paper birch, WA = white ash, ASP = trembling and bigtooth aspen, EH = eastern hemlock, RS = red spruce, BF = balsam fir. Same as below.

Table 4

Percent of basal area by species, tree sizes and inventory year for unmanaged plots on the Bartlett Experimental Forest. Significance of year in a zero-inflated beta regression model for each size class and for all trees combined is indicated (* for $p < 0.05$).

Species	Pole					Saw					Large					Pole	Saw	Large	All
	1931	1939	1991	2002	2017	1931	1939	1991	2002	2017	1931	1939	1991	2002	2017				
BE	7.68	7.39	6.80	7.00	7.38	8.28	8.42	7.29	7.00	6.66	2.36	2.69	2.11	2.22	2.12	*	*	*	*
YB	7.40	6.73	2.70	2.62	2.20	6.18	6.03	5.08	5.12	4.55	1.93	2.55	1.71	1.78	2.08	*	–	–	*
SM	3.85	2.95	1.10	0.87	0.66	3.23	2.98	3.57	3.12	2.25	2.26	2.58	2.43	2.52	2.98	*	*	–	*
RM	9.40	9.57	5.93	5.29	4.02	3.97	5.02	9.49	10.27	9.16	1.27	1.51	4.01	4.05	4.51	*	*	*	*
PB	7.47	7.11	1.87	1.41	0.76	4.81	4.54	3.27	2.52	1.58	0.75	1.10	1.02	0.68	0.30	*	*	*	*
WA	1.41	1.39	0.27	0.21	0.12	0.67	0.95	1.60	1.29	1.14	0.16	0.17	1.08	1.29	1.27	*	*	*	–
ASP	3.55	2.27	0.26	0.14	0.05	0.20	0.21	0.63	0.68	0.56	0.00	0.00	0.21	0.32	0.28	*	–	–	*
EH	4.45	4.63	7.80	8.11	7.83	4.74	5.36	7.56	8.74	11.53	0.46	0.80	6.49	7.48	9.77	*	*	*	*
RS	7.42	6.87	5.77	5.12	4.60	3.36	3.88	5.82	6.20	6.86	0.11	0.15	1.23	1.11	1.93	*	*	*	*
BF	1.33	1.07	1.03	1.01	0.76	0.09	0.06	0.05	0.08	0.15	0.00	0.00	0.00	0.00	0.00	–	–	–	–

The most striking change, across both managed and unmanaged plots, is a steep decline in paper birch and aspen over the 85-year period. Both are very shade-intolerant species, requiring large openings for successful regeneration. Aspen and paper birch that arose from clearing of lower elevation forests during the 1885–1893 period are reaching maximum ages now. Hence, those species are senescing except on those sites where they are being regenerated through management. Yellow birch, a mid-tolerant, also declined on both managed and unmanaged plots. Taken together, these three species declined from 25.7% of basal area in the 1931–1932 inventory, to 10.4% in the 2015–2017 inventory, on managed plots; the corresponding decline on unmanaged plots was from 32.3% to 12.4%. Although some stand-initiating harvests do occur at Bartlett, the landscape-level shift away from the widespread heavy removals of the late 19th century has had a clear impact. The common beneficiary seems to have been eastern hemlock, with a substantial increase from 7.9% to 25.1% of basal area on managed plots, and 9.7%–29.1% on unmanaged plots. Although it might be tempting to associate the increase in hemlock with reallocation of growing space following partial harvests (e.g., those that discriminate against beech or other shade-tolerants), the consistency of the increase across managed and unmanaged plots argues against such an interpretation. Other species were not as consistent between managed and unmanaged plots: red maple and white ash increased on managed plots, but those species held relatively steady on unmanaged plots. On unmanaged plots, red spruce increased while sugar maple decreased; on managed plots, red spruce declined steadily while sugar maple remained relatively stable. Despite differences in overall compositional change, some structural attributes were evident across most species and across both managed and unmanaged plots. In general, the proportion of basal area in pole-sized stems declined dramatically on both managed and unmanaged plots, while larger stems increased.

Taking land type and elevation into account reveals more subtle patterns within both the managed and unmanaged areas. For all species, inventory period, land type and/or its interaction with time, and elevation and/or its interaction with time were statistically significant predictors of change, both in managed areas (Table 5) and unmanaged areas (Table 6). These statistical results substantiate the importance of location to interpretation of the temporal trends. Fig. 2 depicts the trends for the three most common shade-tolerant conifers: red spruce, balsam fir, and eastern hemlock. The increase in eastern hemlock is pronounced across all land types on managed plots below 650 m, though perhaps not quite as strong on deciduous land types between 500 and 650 m; it can also be seen on unmanaged plots of both land types below 650 m, though it is less evident on hardwood land types above 350 m and conifer land types above 500 m, where hemlock has always been less abundant. Hemlock has remained absent or nearly so above 650 m. By contrast, red spruce is increasing steadily on unmanaged plots of both land types above 500 m; its performance in managed plots is not consistent. Balsam fir fluctuates but it remains a minor component in both land types at all elevations, irrespective of management.

Considering the shade-tolerant hardwoods, American beech and sugar maple, different patterns emerge (Fig. 3). Beech is stable to declining in its proportional basal area on both land types below 500 m, but increasing on deciduous land types above 500 m, when plots are managed. By contrast, it is increasing or stable on deciduous land types, and decreasing or stable on coniferous land types, on unmanaged plots. This suggests that heavy discrimination against beech during timber marking has had an influence on beech abundance, especially at low to middle elevations, where harvesting has been more intensive. Sugar maple, on the other hand, managed slight increases only on managed plots between 350 and 650 m; elsewhere, it declined, in some cases dramatically. This might be unexpected for a species often considered as a climax species in northern hardwood forests.

Among the mid-tolerant (yellow birch, red maple, and white ash; Fig. 4), yellow birch appears to be in continuing decline on most land types and elevations, irrespective of management. The exception is at the highest elevation class, where it shows a slight increase, perhaps due to more frequent wind disturbance on higher elevation sites with more wind exposure and shallower soils. Red maple, which had shown strong increases by the 1991–1992 inventory in many portions of the BEF, has shown slight declines in the subsequent inventories, suggesting a peak in relative abundance that is passing. White ash has remained a minor component, with slight increases on deciduous land types at middle elevations under management but inconsistent performance elsewhere (see Fig. 5).

For the intolerant paper birch and aspen, the results are qualitatively consistent across elevations, land types, and management: despite very small, localized increases following the 1938 hurricane, the overwhelming story is one of decline. Even within the managed portion of the BEF, the limited amount of even-aged regeneration harvesting has not been sufficient to maintain the relative abundance of these species on the landscape.

4. Discussion

The additional 25 years of data since the report by Leak and Smith (1996) have confirmed and corroborated trends that were apparent in the first 60 years of record, but they have also shown some nuance in others. For example, the forest-wide increase in abundance of eastern hemlock can be seen to be a continuing process, rather than a simple shift between conditions in the 1930's and the early 1990's. The same can be said of the declines in aspen, paper birch, and yellow birch at most elevations. By contrast, the dramatic increase in red maple abundance seems to be subsiding. At the landscape scale, not all the changes observed in the last 85 years are unidirectional.

Shade tolerance is a critical functional trait for tree species and can be an important driver of successional trends (Valladares and Niinemets, 2008), but shade tolerance alone does not explain the spatial pattern of forest development observed at the BEF. It is evident that as the forest landscape has aged, and as the heavy harvesting of the 19th century and the hurricane of 1938 have receded into the past, opportunities for regeneration and growth of shade-intolerants such as paper birch and aspen are not keeping pace with losses due to mortality. Some of the observed patterns among the more shade-tolerant species do conform to expectations. For example, in the absence of management, beech is increasing on the land types designated as likely to trend toward deciduous species, but it is stable or decreasing on those designated as likely to move toward conifers. This confirms the general development pattern laid out by Leak (1982). However, the dramatic and continuing increase in relative abundance of hemlock, across most elevations, both land types (including those expected to develop toward deciduous trees), and without respect to management, is a striking change impacting much of the landscape. Analysis of the data from Allen and Seaboyer (2017), reporting on an oak-pine dominated landscape, also indicates an increase in proportion of hemlock basal area from 20% to 29% over a 56-year period. By contrast, Rogers et al. (2018) report little or no change in proportion of hemlock basal area on most treatments in a conifer-dominated setting at the Penobscot Experimental Forest.

The resilience of beech at the landscape scale is evident, and points to its likely dominance especially on deciduous land types, despite the prevalence of beech scale (*Cryptococcus fagisuga*) and beech bark disease (caused by *Neonectria faginata* and *N. ditissima*). Studies at Bartlett indicated that by the late 1950s, 70%–90% of beech had contracted the disease (Bjorkbom, 1959; Filip, 1978), and impacts on mortality were evident locally and regionally within three decades (Twery and Patterson, 1984). Mortality from beech bark disease can be sufficient to cause carbon reversal in old-growth forests (Gunn et al., 2014). Nonetheless, beech is increasing on suitable land types in the absence of management, and even aggressive marking against beech has only contained rather than reduced its abundance.

While the hurricane of 1938 caused mortality on the order of 10% of stems across the BEF, and greater levels at higher elevations (Leak et al.,

Table 5

Percent of basal area by species, elevation class (Elv), inventory period or year (Yr), and deciduous (D) or coniferous (C) land type (LT) for managed plots on the Bartlett Experimental Forest. Significance of factors and interactions in a zero-inflated beta regression model is indicated (* for $p < 0.05$).

Species	Elevation class I (200–350 m)										Elevation class II (350–500 m)									
	1931		1939		1991		2002		2017		1931		1939		1991		2002		2017	
	D	C	D	C	D	C	D	C	D	C	D	C	D	C	D	C	D	C	D	C
BE	30.7	17.2	30.8	17.0	28.1	10.3	29.3	11.0	31.6	11.1	48.7	28.2	48.5	29.2	40.0	21.1	38.2	19.5	36.1	17.3
YB	18.1	12.2	17.1	11.2	9.8	5.8	8.7	5.8	7.6	5.0	19.4	20.0	18.3	19.5	11.4	13.6	11.5	11.6	9.2	7.9
SM	8.6	4.7	8.2	3.1	8.1	4.0	7.8	4.5	7.4	3.3	14.0	9.6	13.6	9.6	18.4	10.3	18.7	8.9	18.8	8.6
RM	14.3	20.2	16.0	21.4	22.6	25.8	21.9	24.1	21.0	23.5	3.6	15.3	4.6	12.8	6.7	10.9	6.9	11.7	7.1	8.7
PB	9.5	9.2	9.8	9.3	6.3	4.5	5.0	3.3	3.2	1.9	5.4	6.0	5.5	5.8	2.9	0.9	3.1	0.6	3.5	1.2
WA	4.8	4.5	5.4	4.6	5.8	4.9	5.3	4.8	4.9	4.5	1.2	1.1	1.2	1.0	2.8	0.8	3.0	0.6	3.5	0.5
ASP	3.1	2.6	1.5	1.5	0.8	0.3	1.5	0.3	1.0	0.2	0.1	0.0	0.1	0.0	0.3	0.0	0.2	0.0	0.3	0.0
EH	8.5	13.9	9.0	15.6	16.1	26.2	17.6	29.4	20.9	34.8	5.0	12.5	6.0	14.3	14.7	36.8	16.5	41.7	20.0	50.4
RS	1.9	6.3	1.6	6.3	0.9	6.8	0.9	6.4	0.9	6.0	2.3	6.8	2.0	7.4	0.7	4.9	0.6	5.0	0.6	5.1
BF	0.1	2.2	0.1	1.7	0.1	1.1	0.1	0.8	0.1	0.4	0.0	0.1	0.0	0.1	0.0	0.0	0.0	0.1	0.0	0.0

Species	**Elevation class III (500–650 m)**										LT	Elv	Yr	LT/Yr	Elv/Yr
	1931		1939		1991		2002		2017						
	D	C	D	C	D	C	D	C	D	C					
BE	37.5	20.0	36.5	20.4	40.2	21.1	41.9	20.5	45.1	21.7	*	*	*	*	*
YB	13.8	11.6	15.1	12.4	9.5	10.1	8.5	10.2	7.3	8.8	–	–	*	*	*
SM	24.1	9.6	23.6	11.7	29.8	12.3	31.4	11.9	27.1	11.3	*	*	*	*	*
RM	6.5	9.1	6.9	8.7	4.6	8.9	3.9	9.6	3.5	8.3	*	*	*	*	*
PB	6.0	10.8	5.6	9.4	1.2	3.6	0.2	2.2	0.5	1.9	–	*	*	*	*
WA	0.6	2.4	0.7	1.7	0.0	1.1	0.0	0.4	0.1	0.4	–	*	*	*	*
ASP	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.2	0.0	0.0	*	*	*	*	*
EH	2.6	5.4	2.6	5.3	5.9	16.4	7.4	20.8	10.1	23.6	*	*	*	*	*
RS	4.9	25.5	5.2	25.8	4.2	22.2	3.1	20.5	3.4	19.9	*	–	*	*	*
BF	0.6	3.2	0.5	2.1	0.0	0.2	0.1	0.2	0.1	0.9	*	–	*	*	*

Table 6

Percent of basal area by species, elevation class (Elv), inventory period or year (Yr), and deciduous (D) or coniferous (C) land type (LT) for unmanaged plots on the Bartlett Experimental Forest. Significance of factors and interactions in a zero-inflated beta regression model is indicated (* for $p < 0.05$).

Species	Elevation class I (200–350 m)										Elevation class II (350–500 m)									
	1931		1939		1991		2002		2017		1931		1939		1991		2002		2017	
	D	C	D	C	D	C	D	C	D	C	D	C	D	C	D	C	D	C	D	C
BE	18.0	15.2	18.3	13.2	15.4	9.4	15.6	10.1	15.9	8.9	26.6	21.7	29.4	21.6	31.8	14.8	33.0	14.2	32.6	12.1
YB	12.4	17.5	12.1	16.0	7.3	7.0	7.3	6.3	7.1	6.1	24.2	15.5	24.2	16.0	16.2	6.3	15.2	9.1	12.6	7.0
SM	2.6	2.5	2.6	2.7	3.3	2.2	2.9	2.4	2.6	2.9	30.4	5.6	29.5	5.5	24.5	4.4	24.9	4.2	23.8	4.3
RM	22.1	21.3	25.4	23.9	30.8	28.1	30.2	28.1	28.8	23.5	3.1	7.2	3.4	7.0	5.0	9.0	4.5	8.8	5.8	7.3
PB	14.9	4.6	17.6	5.2	10.6	1.9	9.0	1.6	5.5	1.0	5.4	22.4	4.1	18.5	3.2	8.1	1.3	3.4	1.0	1.6
WA	3.2	4.6	3.4	5.0	3.4	5.6	2.8	5.3	3.1	4.0	2.5	0.8	2.6	0.8	4.6	0.6	4.8	0.6	5.1	0.7
ASP	13.5	3.2	8.1	2.1	3.4	0.5	3.5	0.4	2.8	0.3	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
EH	9.9	18.9	9.5	20.0	19.6	34.0	21.8	35.9	27.0	42.0	3.5	16.9	4.1	20.2	11.9	44.4	13.8	48.1	16.5	56.5
RS	1.8	8.7	1.5	8.8	3.3	7.9	3.4	7.0	3.6	8.5	1.2	9.2	1.1	9.7	0.3	11.3	0.3	10.6	0.2	9.8
BF	0.3	2.3	0.3	1.7	0.8	1.2	0.7	1.2	0.4	0.9	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0

Species	**Elevation class III (500–650 m)**										**Elevation class IV** (650-800 m)										LT	Elv	Yr	LT/Yr	Elv/Yr
	1931		1939		1991		2002		2017		1931		1939		1991		2002		2017						
	D	C	D	C	D	C	D	C	D	C	D	C	D	C	D	C	D	C	D	C					
BE	29.2	20.7	31.8	23.1	39.1	19.2	44.4	16.7	50.4	15.5	14.7	10.9	16.0	11.6	17.8	11.9	22.8	10.0	25.1	10.3	*	*	*	*	*
YB	18.0	17.2	20.1	18.3	15.6	14.4	17.2	14.6	15.2	11.6	16.2	9.4	13.5	9.8	14.2	12.8	20.6	12.7	25.4	13.6	–	–	*	*	*
SM	37.7	0.7	34.6	0.4	31.9	1.4	28.9	0.8	20.1	1.2	15.4	9.0	18.4	8.7	20.9	7.8	20.4	6.6	7.5	3.8	*	*	–	*	*
RM	6.0	19.7	5.7	14.1	4.1	10.7	2.9	11.7	3.9	9.9	4.7	10.4	5.4	9.8	4.3	8.3	5.0	7.9	9.1	7.7	–	*	*	*	*
PB	6.0	15.0	4.4	12.8	2.5	6.7	0.3	4.8	0.0	3.6	44.1	21.8	34.3	20.9	24.5	5.7	11.7	5.3	9.9	2.1	–	–	*	*	*
WA	0.5	0.0	0.5	0.0	0.7	0.0	0.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	–	–	*	*	*
ASP	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	–	*	*	*	*
EH	0.1	3.2	0.2	3.9	1.1	8.5	1.6	10.0	2.4	13.6	0.0	1.3	0.0	1.5	0.8	3.0	1.0	3.2	2.3	4.1	–	*	*	*	*
RS	2.2	21.9	2.4	25.9	4.6	36.8	3.9	39.6	6.6	41.6	2.8	32.3	9.9	33.6	16.5	45.3	17.8	49.3	18.8	53.7	*	*	*	*	*
BF	0.1	1.1	0.2	1.0	0.0	0.6	0.0	0.7	0.0	1.2	1.3	4.0	1.9	3.4	1.1	3.7	0.4	4.3	0.5	4.3	*	*	–	*	*

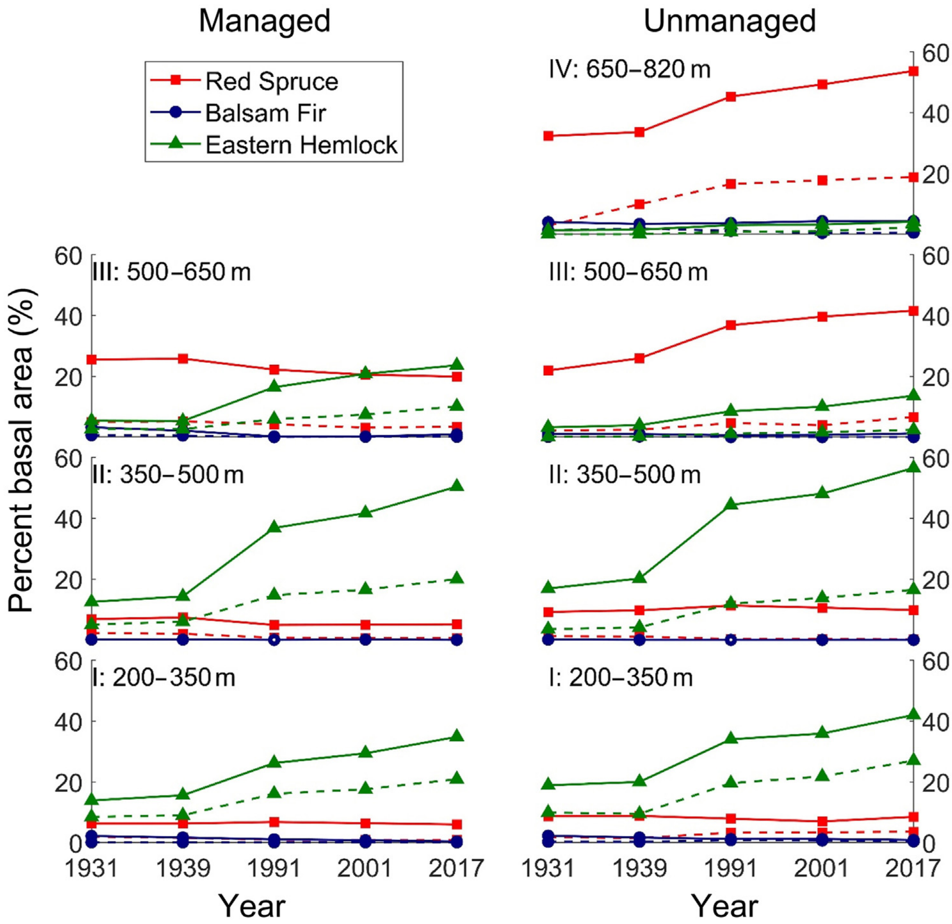

Fig. 2. Change in percent basal area of shade-tolerant conifer species on managed and unmanaged plots on the Bartlett Experimental Forest. Solid lines represent species change on conifer land types; dotted lines represent change on deciduous land types. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

1994), there is little evidence for a dramatic impact on forest composition. Likewise, a major regional ice storm in 1998 (Irland, 1998) does not seem to be associated with any sudden shifts in tree species composition, which one might hypothesize to be evident between the 1991–1992 and 2002–2003 inventories. Rhoads et al. (2002) noted heavy damage above elevations of 600 m at the nearby Hubbard Brook Experimental Forest, with greatest impacts on large trees and especially on diseased beech. At the BEF, Anderson et al. (2011) mapped ice storm damage with LiDAR and found greater volume losses in stands exceeding the average canopy height of the forest. Despite this, there is no noticeable uptick in the abundance of shade-intolerant species, indicating these species require more intense disturbance than even severe ice damage in order to regenerate. Likewise, while there may have been an increase in mortality of beech or other susceptible species, there are no obvious, sudden reductions attributable to disturbance during that period. We note that Hocking et al. (2013), in an examination of salamander responses to the ice storm at Bartlett, did not find that even heavy damage created appreciable early-successional habitat. Further analysis of the spatial pattern of ice storm damage is beyond the scope of this study; however, we note that localized variation is being averaged over, and could be worthy of further exploration. In an oak-beech forest well to the south of Bartlett, Covey et al. (2015) found that downed wood abundance by species following the 2008 ice storm was highly-correlated with pre-storm basal area of the species, suggesting that differential damage across species may not have been dramatic; however, they argued that partial disturbance would facilitate the growth of understory shade-tolerant species. We also speculate that the impacts of partial disturbances such as the 1998 ice storm may be less immediate and direct but more subtle, for example accelerating existing shifts to more shade-tolerant species through release of growing space from the overstory.

Forest health issues do not appear to be having a major impact on forest composition at the BEF at this time, but we hypothesize that may not be true by the next inventory cycle. White ash has been a valuable timber species, and the results of this study show that management has been associated with a modest increase in its relative abundance (Fig. 4). However, ash is currently threatened across its entire range by the emerald ash borer (*Agrilus planipennis*) (Herms and McCullough, 2014). Emerald ash borer was detected in New Hampshire in 2013, and there are known infestations approximately 15 km from the BEF (UNH Cooperative Extension, 2021a). Given the potential for rapid dispersal of emerald ash borer (Muirhead et al., 2006; Yemshanov et al., 2012), and the heavy mortality typical of most infestations (Knight et al., 2013), a dramatic reduction or even elimination of ash from the BEF seems probable in the not-too-distant future. Beech leaf disease, associated with the nematode *Litylenchus crenatae mccannii*, is a more recent concern. As of this writing, it has not been detected in the White Mountains or elsewhere in New Hampshire, but it has been observed in southern New England and in coastal areas of Maine (Maine Forest Service, 2022). Although modes of spread and stand-level effects remain poorly characterized, the potential for beech leaf disease to impact the BEF is significant.

The substantial increase in relative abundance of hemlock at the BEF also raises forest health concerns, as hemlock is potentially threatened by the hemlock woolly adelgid (*Adelges tsugae*). The adelgid has been present in New Hampshire since 2000, and it has also been recorded in towns within 15–20 km of the BEF (UNH Cooperative Extension, 2021b).

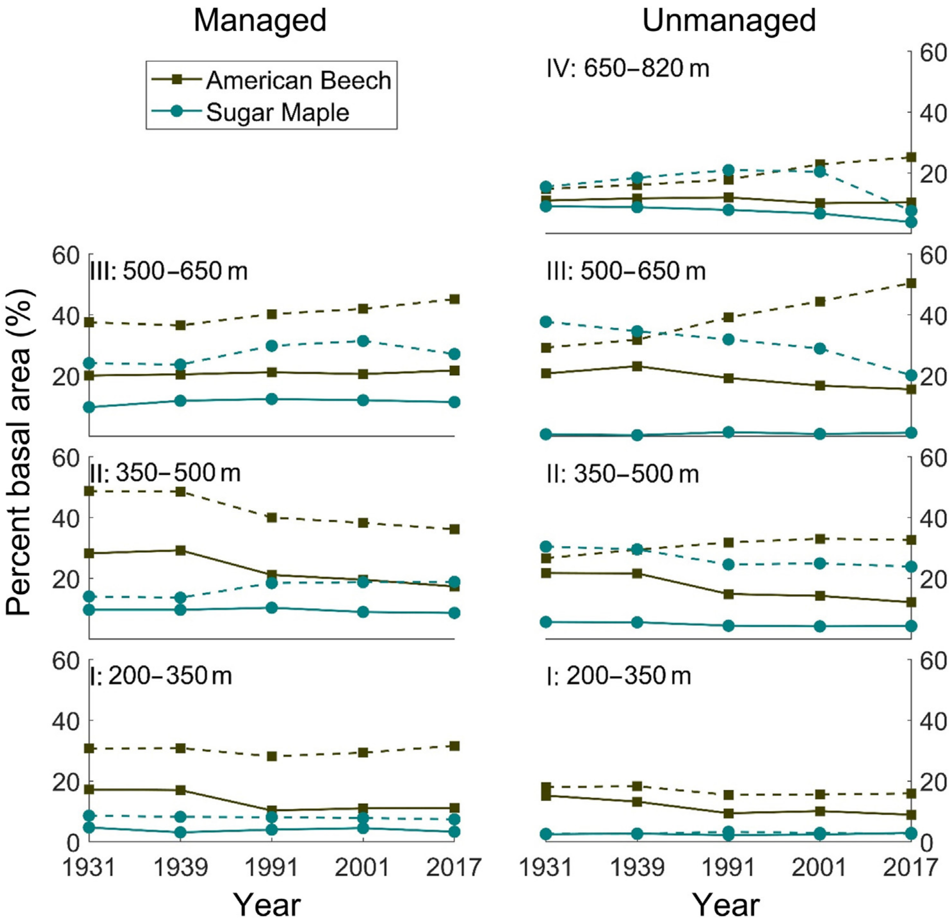

Fig. 3. Change in percent basal area of shade-tolerant hardwood species on managed and unmanaged plots on the Bartlett Experimental Forest. Solid lines represent species change on conifer land types; dotted lines represent change on deciduous land types. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

In southern portions of the range of eastern hemlock, adelgid infestation has been associated with heavy mortality (Vose et al., 2013), and there are significant concerns about its ecosystem impacts (Ellison et al., 2018). Cold temperatures at the northern edge of the current range of the adelgid may limit both its spread and its impacts (e.g., Fitzpatrick et al., 2012). Hemlock is not currently considered a primary timber species, though hemlock is used in timber frame structures, pulp, and has traditional medicinal usages as well. However, it has significant structural value for wildlife habitat. Intact stands of mature hemlock moderate both winter temperatures and snow depth conditions (Lishawa et al., 2007), two factors important in describing winter deer habitat in Vermont and New Hampshire (Reay et al., 1990; Bennett, 2010). Upwards of 160 vertebrate species use the hemlock type across New England (DeGraaf et al., 2006); and around 13 percent of these species have a strong association with the hemlock type (Yamasaki, 2018; Yamasaki et al., 2000). At the BEF, hemlock is associated with high diversity and abundance of truffles which are an important component of the mammalian food web, with implications for seed dispersers (Stephens et al., 2017). Given the substantial and increasing abundance of hemlock at all but the highest elevations, the potential for significant impacts from the adelgid must be of concern.

Finally, we note that at the time of the analysis by Leak and Smith (1996), a combination of shorter meteorological records and lack of appropriate statistical techniques led to a lack of clarity about the magnitude and direction of regional climatic change. The evidence for trends in the observational record is now much stronger (e.g., Hayhoe et al., 2007; Huntington et al., 2009). In general, the region around the BEF has experienced a warmer and wetter overall climate over the last century, but with considerable interannual variability. With that said, there is less evidence for a simple response of forest composition, such as elevational migration, to that variability. Changes in the location of the ecotone between northern hardwood and spruce-fir dominated forests would seem to be a reasonable outcome of climatic warming (Cogbill and White, 1991). Previous analyses of the understory by Leak (2009) and of the overstory by Leak and Yamasaki (2010) found no discernible sign of such changes, and the extended record here provides no indication of an upwardly-receding spruce-fir line or high-elevation hemlock encroachment. Other authors (e.g., Wason et al., 2017) have suggested that contemporary changes in physical and chemical climate may have more of an impact on forest growth than on composition; further examination of the long-term record at the BEF is needed to tease out such impacts. Simulation studies suggest that shifts in composition due to future climate change may occur over the next three centuries (Wang et al., 2017). From a compositional perspective, and bearing in mind the temporal and spatial scales considered here, our results are more consistent with successional change following land use and disturbance as major drivers, rather than climatic change (Nowacki and Abrams, 2015).

5. Conclusions

The composition of forests at the BEF shows continuous and ongoing change over an eight-decade period. Overall, there is a continued shift from small-diameter to large-diameter trees. Despite the allocation of portions of the forest to studies of single-cohort or large-patch silviculture, the proportion of shade-intolerant species (paper birch and aspen), and one mid-tolerant associated with moderate gap sizes (yellow birch),

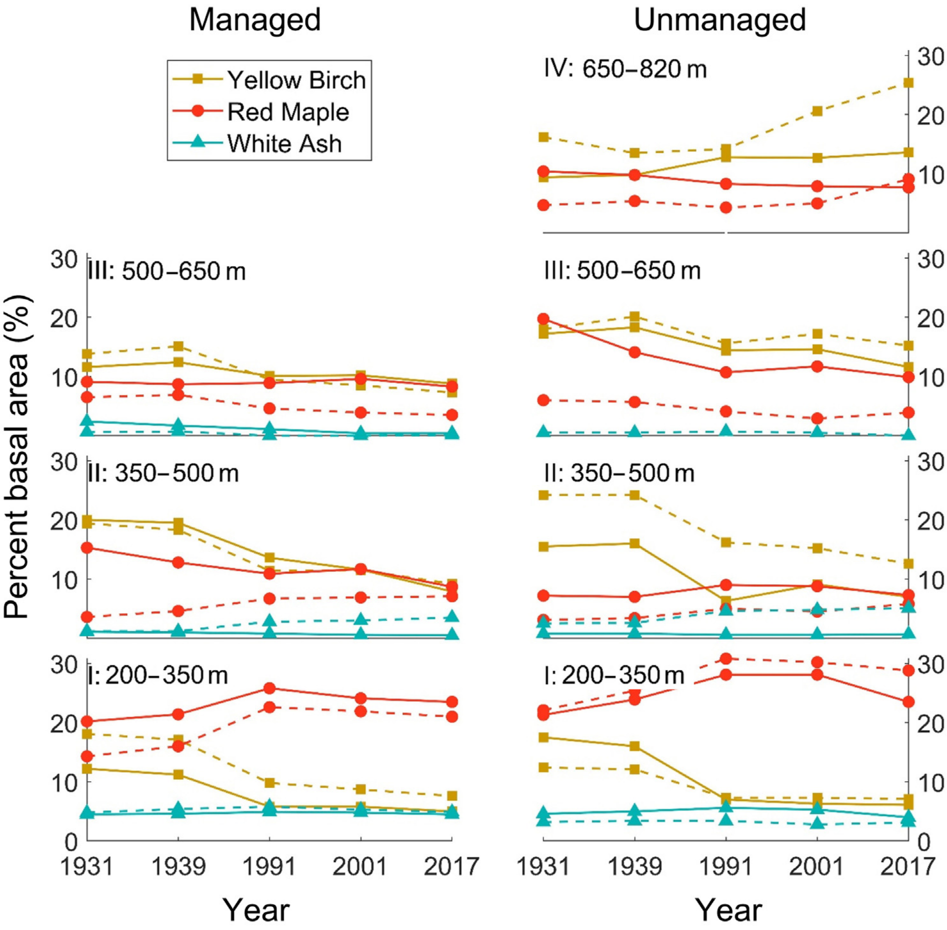

Fig. 4. Change in percent basal area of mid-tolerant hardwood species on managed and unmanaged plots on the Bartlett Experimental Forest. Solid lines represent species change on conifer land types; dotted lines represent change on deciduous land types.

have declined and continue to decline across the landscape. Between the 1938 hurricane and the 1991–1992 remeasurement, the proportion of red maple increased substantially, but that increase appears to have plateaued. Among the shade-tolerants, sugar maple is declining in many areas, beech and red spruce appear to be partitioning the landscape in a manner consistent with the site classification system of Leak (1982), and hemlock has emerged as a dominant component of the forest below 600 m elevation. A major hurricane in 1938, and a regional ice storm in 1998, did not lead to dramatic, immediate shifts in composition. Management, at the scope and intensity practiced at the BEF, has moderated some changes (for example, maintaining sugar maple while mitigating against the increase in beech) but its effect is secondary to the progression of overall forest development. Climate change and forest health have not yet made obvious impacts on compositional change, but they may do so in the near future. Long-term monitoring provides unique opportunities to benchmark such future changes.

The data available at the Bartlett Experimental Forest are unique in the northeastern United States and quite rare across North America. These data are useful for assessing the long-term impacts of management, as shown by the limitation of beech's expansion on managed sites, and for evaluating long-term trends in forest maturation across the eastern forest region. Inferences drawn from this data can provide the foundation for ecologically-informed, proactive forest management in a region where human uses of forests are many and diverse. Future research should look to expand on our findings to better understand the causes and outcomes from the broad patterns we have identified here.

Data availability

Data from this study are available at Belair, Ethan P.; Fraser, Olivia; Leak, William B.; Yamasaki, Mariko; Ducey, Mark J. (2023) Bartlett Experimental Forest permanent cruise plot data. 2nd Edition. Fort Collins, CO: Forest Service Research Data Archive. https://doi.org/10.2737/RDS-2017-0036-2.

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Authors’ contributions

Mark Ducey: conceptualization, methodology, formal analysis, writing-original draft, supervision, project administration, funding acquisition; Olivia Fraser: conceptualization, software, formal analysis, data curation, writing-review and editing, visualization; Mariko Yamasaki: conceptualization, methodology, investigation, writing-review and editing, project administration, funding acquisition; Ethan Belair:

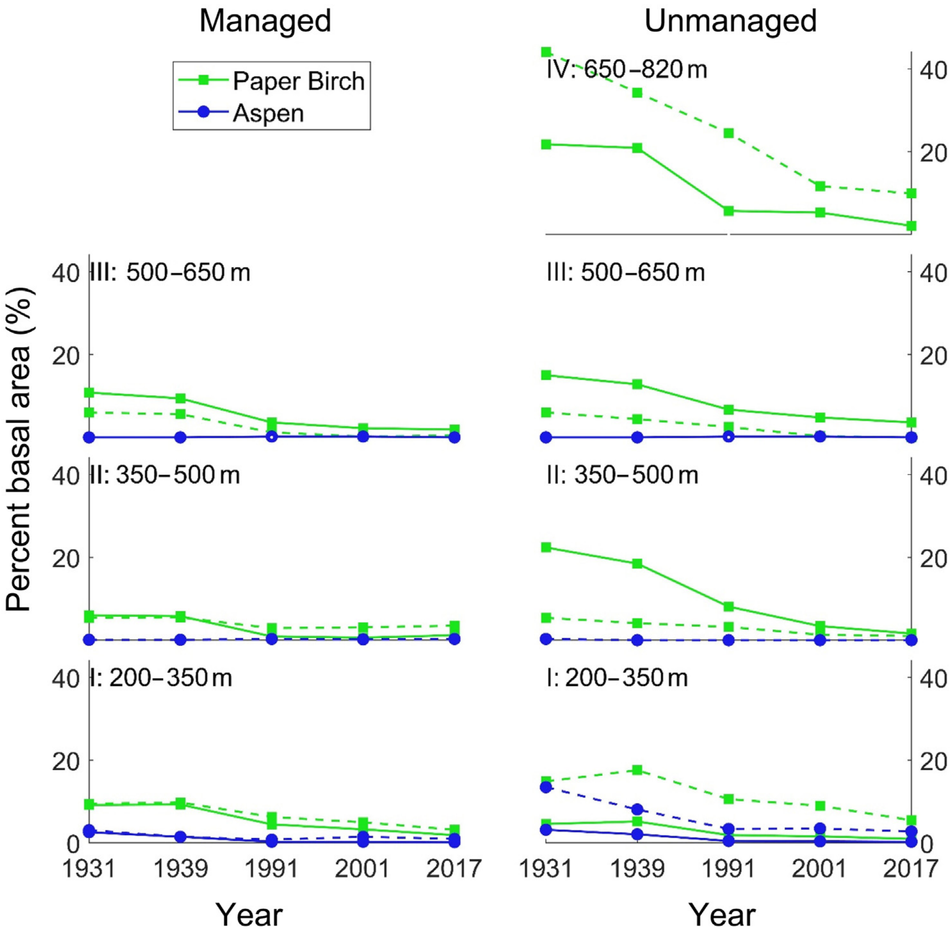

Fig. 5. Change in percent basal area of shade-intolerant hardwood species on managed and unmanaged plots on the Bartlett Experimental Forest. Solid lines represent species change on conifer land types; dotted lines represent change on deciduous land types. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

conceptualization, validation, investigation, data curation, writing-review and editing, supervision, project administration; William Leak: conceptualization, methodology, investigation, data curation, writing – review and editing, project administration.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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References

Abrams, M.D., Nowacki, G.J., 2020. Native American imprint in palaeoecology. Nat. Sustain. 3, 896–897. https://doi.org/10.1038/s41893-020-0578-6.

Allen, B.P., Seaboyer, I.V., 2017. Fifty-six years of forest development following the 1938 hurricane in Hillsborough, New Hampshire, USA. Forests 8, 225. https://doi.org/10.3390/f8070225, 2017.

Anderson, J.E., Ducey, M.J., Fast, A., Martin, M.E., Lepine, L., Smith, M.-L., Lee, T.D., Dubayah, R.O., Hofton, M.A., Hyde, P., Peterson, B., Blair, J.B., 2011. Use of lidar and hyperspectral sensors to assess selected spatial, compositional, and structural patterns with recent and repeat disturbance and the abundance of sugar maple (*Acer saccharum* Marsh.) in a temperate mixed hardwood and conifer forest. J. Appl. Remote Sens. 5, 053504. https://doi.org/10.1117/1.3554639.

Bechtold, W.A., Patterson, P.L., 2005. The Enhanced Forest Inventory and Analysis Program – National Sampling Design and Estimation Procedures. Gen. Tech. Rep. SRS-80. U.S. Department of Agriculture, Forest Service, Southern Research Station, Asheville, NC.

Belcher, C.F., 1980. Logging Railroads of the White Mountains. Appalachian Mountain Club, Boston.

Bennett, K.P., 2010. Chapter 6.9. Deer Wintering Areas. Good Forestry in the Granite State: Recommended Voluntary Forest Management Practices for New Hampshire, second ed. Univ. of New Hampshire Cooperative Extension, Durham, NH.

Bjorkbom, J.C., 1959. Office Report – 1958 Beech Scale Spraying. Unpublished report on file at the USFS Northern Research Station lab, Durham, NH.

Brooks, M.E., Kristensen, K., van Benthem, K.J., Magnusson, A., Berg, C.W., Nielsen, A., Skaug, H.J., Maechler, M., Bolker, B.M., 2017. glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. R J 9 (2), 378–400.

Cogbill, C.V., White, P.S., 1991. The latitude-elevation relationship for spruce-fir forest and treeline along the Appalachian mountain chain. Vegetatio 94 (2), 153–175.

Covey, K.R., Barrett, A.L., Ashton, M.S., 2015. Ice storms as a successional pathway for *Fagus grandifolia* advancement in *Quercus rubra* dominated forests of southern New England. Can. J. For. Res. 45, 1628–1635.

DeGraaf, R.M., Yamasaki, M., Leak, W.B., Lester, A.M., 2006. Technical Guide to Forest Wildlife Habitat Management in New England. Univ. of Vermont Press, Burlington, VT.

Driscoll, C.T., Lawrence, G.B., Bulger, A.J., Butler, T.J., Cronan, C.S., Eagar, C., Lambert, K.F., Likens, G.E., Stoddard, J.L., Weathers, K.C., 2001. Acidic deposition in the northeastern United States: sources and inputs, ecosystem effects, and management strategies. Bioscience 51 (3), 180–198.

Dukes, J.S., Pontius, J., Orwig, D., Garnas, J.R., Rodgers, V.L., Brazee, N., Cooke, B., Theoharides, K.A., Stange, E.E., Harrington, R., Ehrenfeld, J., Gurevitch, J., Lerdau, M., Stinson, K., Wick, R., Ayres, M., 2009. Responses of insect pests, pathogens, and invasive plant species to climate change in the forests of northeastern North America: what can we predict? Can. J. For. Res. 39 (2), 231–248.

Ellison, A.M., Orwig, D.A., Fitzpatrick, M.C., Preisser, E.L., 2018. The past, present, and future of the hemlock woolly adelgid (*Adelges tsugae*) and its ecological interactions with eastern hemlock (*Tsuga canadensis*) forests. Insects 9 (4), 172.

Filip, S.M., 1978. Impact of Beech Bark Disease on Uneven-Aged Management of a Northern Hardwood Forest (1952–1976). Gen. Tech. Rep. GTR NE-45. U.S. Department of Agriculture, Forest Service, Northeastern Forest Experiment Station, Broomall, PA.

Filip, S.M., Marquis, D.A., Leak, W.B., 1960. Development of Old-Growth Northern Hardwoods on the Bartlett Experimental Forest—a 22-year Record. U.S. Department of Agriculture, Forest Service, Northeastern Forest Experiment Station, Upper Darby, PA. Station Pap. 135.

Fitzpatrick, M.C., Preisser, E.L., Porter, A., Elkinton, J., Ellison, A.M., 2012. Modeling range dynamics in heterogeneous landscapes: invasion of the hemlock woolly adelgid in eastern North America. Ecol. Appl. 22, 472–486.

Forest Service, Maine, 2022. Beech Leaf Disease in Maine. https://www.maine.gov/dacf/mfs/forest_health/invasive_threats/beech_leaf_disease.htm. (Accessed 29 May 2023).

Foster, D.R., Aber, J.D., 2004. Forests in Time: the Environmental Consequences of 1,000 Years of Change in New England. Yale University Press, USA.

Gove, B., 2001. Logging Railroads of the Saco River Valley. Bondcliff Books, Littleton, NH.

Gunn, J.S., Ducey, M.J., Whitman, A.A., 2014. Late-successional and old-growth forest carbon temporal dynamics in the Northern Forest (Northeastern USA). For. Ecol. Manag. 312, 40–46.

Hayhoe, K., Wake, C.P., Huntington, T.G., Luo, L., Schwartz, M.D., Sheffield, J., Wood, E., Anderson, B., Bradbury, J., DeGaetano, A., Troy, T.J., 2007. Past and future changes in climate and hydrological indicators in the US Northeast. Clim. Dynam. 28 (4), 381–407.

Herms, D.A., McCullough, D.G., 2014. Emerald ash borer invasion of North America: history, biology, ecology, impacts, and management. Annu. Rev. Entomol. 59, 13–30.

Hibbs, D.E., 1983. Forty years of forest succession in central New England. Ecology 64, 1394–1401.

Hocking, D.J., Babbitt, K.J., Yamasaki, M., 2013. Comparison of silvicultural and natural disturbance effects on terrestrial salamanders in northern hardwood forests. Biol. Conserv. 167, 194–202.

Hoover, C.M., 2011. Assessing seven decades of carbon accumulation in two U.S. northern hardwood forests. Forests 2, 730–740. https://doi.org/10.3390/f2030730.

Huntington, T.G., Richardson, A.D., McGuire, K.J., Hayhoe, K., 2009. Climate and hydrological changes in the northeastern United States: recent trends and implications for forested and aquatic ecosystems. Can. J. For. Res. 39 (2), 199–212.

Irland, L.C., 1998. Ice storm 1998 and the forests of the Northeast: a preliminary assessment. J. For. 96 (9), 32–40.

Jensen, V.S., 1941a. Eight Years Growth in Hardwood Stands on the Bartlett Experimental Forest. Station Tech. Note 43. U.S. Department of Agriculture, Forest Service, Northeastern Forest Experiment Station, Upper Darby, PA.

Jensen, V.S., 1941b. Hurricane Damage on the Bartlett Experimental Forest. Office Report. U.S. Department of Agriculture, Forest Service, Upper Darby, PA. Northeastern Forest Experiment Station. 15 pages. [Report on file at the U.S. Forest Service, Northern Research Station, Office in Durham, N.H.].

Kershaw Jr., J.A., Ducey, M.J., Beers, T.W., Husch, B., 2016. Forest Mensuration, fifth ed. Wiley, New York.

Knight, K.S., Brown, J.P., Long, R.P., 2013. Factors affecting the survival of ash (*Fraxinus* spp.) trees infested by emerald ash borer (*Agrilus planipennis*). Biol. Invasions 15 (2), 371–383.

Kosiba, A.M., Meigs, G.W., Duncan, J.A., Pontius, J.A., Keeton, W.S., Tait, E.R., 2018. Spatiotemporal patterns of forest damage and disturbance in the northeastern United States: 2000–2016. For. Ecol. Manag. 430, 94–104.

Lawrence, G.B., Hazlett, P.W., Fernandez, I.J., Ouimet, R., Bailey, S.W., Shortle, W.C., Smith, K.T., Antidormi, M.R., 2015. Declining acidic deposition begins reversal of forest-soil acidification in the northeastern US and eastern Canada. Environ. Sci. Technol. 49, 13103–13111.

Leak, W.B., 1961a. Development of Second Growth Northern Hardwoods on the Bartlett Experimental Forest—a 25-year Record. Stn. Pap. 155. U.S. Department of Agriculture, Forest Service, Northeastern Forest Experiment Station, Upper Darby, PA.

Leak, W.B., 1961b. Yellow Birch Grows Better in Mixed-Wood Stands than in Northern Hardwood Old-Growth Stands. Res. Note NE-122. U.S. Department of Agriculture, Forest Service, Northeastern Forest Experiment Station, Upper Darby, PA.

Leak, W.B., 1982. Habitat Mapping and Interpretation in New England. Res. Paper NE-496. U.S. Department of Agriculture, Forest Service, Northeastern Forest Experiment Station, Broomall, PA.

Leak, W.B., 1987. Fifty years of compositional change in deciduous and coniferous forests in New Hampshire. Can. J. For. Res. 17, 388–393.

Leak, W.B., 2009. Seventy years of understory development by elevation class in a New Hampshire mixed forest: management implications. NJAF (North. J. Appl. For.) 26 (4), 164–166.

Leak, W.B., Smith, M.L., 1996. Sixty years of management and natural disturbance in a New England forested landscape. For. Ecol. Manag. 81, 63–73.

Leak, W.B., Yamasaki, M., 2010. Seventy-year Record of Changes in the Composition of Overstory Species by Elevation on the Bartlett Experimental Forest. Res. Pap. NRS-13. U.S. Department of Agriculture, Forest Service, Northern Research Station, Newtown Square, PA.

Leak, W.B., Yamasaki, M., Smith, M.-L., Funk, D.T., 1994. Selection criteria for forested natural areas in New England, USA. Nat. Area J. 14, 300–305.

Leak, W.B., Yamasaki, M., Belair, E.P., Knapp, R.A., Brissette, J.C., 2017. Bartlett Experimental Forest Permanent Cruise Plot Data. Forest Service Research Data Archive, Fort Collins, CO.

Lishawa, S.C., Bergdahl, D.R., Costa, S.D., 2007. Winter conditions in eastern hemlock and mixed-hardwood deer wintering areas in Vermont. Can. J. For. Res. 37, 697–703.

Lutz, H.J., 1930. The vegetation of Heart's Content, a virgin forest in northwestern Pennsylvania. Ecology 11, 1–29.

Mabry, C., Korsgren, T., 1998. A permanent plot study of vegetation and vegetation-site factors fifty years following disturbance in central New England, USA. Ecoscience 5, 232–240.

Martin, C.W., Bailey, A.S., 1999. Twenty years of change in a northern hardwood forest. For. Ecol. Manag. 123 (2–3), 253–260.

Muirhead, J.R., Leung, B., van Overdijk, C., Kelly, D.W., Nandakumar, K., Marchant, K.R., MacIsaac, H.J., 2006. Modelling local and long-distance dispersal of invasive emerald ash borer *Agrilus planipennis* (Coleoptera) in North America. Divers. Distrib. 12 (1), 71–79.

Nowacki, G.J., Abrams, M.D., 2015. Is climate an important driver of post-European vegetation change in the Eastern United States? Global Change Biol. 21 (1), 314–334.

R Development Core Team, 2020. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

Reay, R.S., Blodgett, D.W., Burns, B.S., Weber, S.J., Frey, T., 1990. Management Guide for Deer Wintering Areas in Vermont. VT Dept. Forests, Parks, and Recreation and VT Dept. of Fish and Wildlife, Waterbury, VT.

Rhoads, A.G., Hamburg, S.P., Fahey, T.J., Siccama, T.G., Hane, E.N., Battles, J., Cogbill, C., Randall, J., Wilson, G., 2002. Effects of an intense ice storm on the structure of a northern hardwood forest. Can. J. For. Res. 32 (10), 1763–1775.

Rogers, N.S., Kenefic, L.S., Crandall, M.S., Seymour, R.S., Sendak, P.E., 2018. Sixty years of silviculture in a northern conifer forest in Maine, USA. Forest Sci 64, 102–111.

Rogers, N.S., D'Amato, A.W., Leak, W.B., 2021. Long-term evolution of composition and structure after repeated group selection over eight decades. Can. J. For. Res. 51 (7), 1080–1091.

Rustad, L., Campbell, J., Dukes, J.S., Huntington, T., Lambert, K.F., Mohan, J., Rodenhouse, N., 2012. Changing Climate, Changing Forests: the Impacts of Climate Change on Forests of the Northeastern United States and Eastern Canada. Gen. Tech. Rep. NRS-99. US Department of Agriculture, Forest Service, Northern Research Station, Newtown Square, PA.

Stephens, R.B., Remick, T.J., Ducey, M.J., Rowe, R.J., 2017. Drivers of truffle biomass, community composition, and richness among forest types in the northeastern US. Fungal Ecol. 29, 30–41.

Swanston, C., Brandt, L.A., Janowiak, M.K., Handler, S.D., Butler-Leopold, P., Iverson, L., Thompson III, F.R., Ontl, T.A., Shannon, P.D., 2018. Vulnerability of forests of the Midwest and Northeast United States to climate change. Clim. Change 146 (1), 103–116.

Twery, M.J., Patterson III, W.A., 1984. Variations in beech bark disease and its effects on species composition and structure of northern hardwood stands in central New England. Can. J. For. Res. 14 (4), 565–574.

UNH Cooperative Extension, 2021a. NHBugs: Emerald Ash Borer. https://www.nhbugs.org/damaging-insects-diseases/emerald-ash-borer. (Accessed 28 September 2021).

UNH Cooperative Extension, 2021b. NHBugs: Hemlock Woolly Adelgid. https://www.nhbugs.org/damaging-insects-diseases/hemlock-woolly-adelgid. (Accessed 28 September 2021).

Valladares, F., Niinemets, U., 2008. Shade tolerance, a key plant feature of complex nature and consequences. Annu. Rev. Ecol. Evol. Syst. 39, 237–257.

Vose, J.M., Wear, D.N., Mayfield III, A.E., Nelson, C.D., 2013. Hemlock woolly adelgid in the southern Appalachians: control strategies, ecological impacts, and potential management responses. For. Ecol. Manag. 291, 209–219.

Wang, W.J., He, H.S., Thompson, F.R., Fraser, J.S., Dijak, W.D., 2017. Changes in forest biomass and tree species distribution under climate change in the northeastern United States. Landsc. Ecol. 32 (7), 1399–1413.

Ward, J.S., Anagnostakis, S.L., Ferrandino, F.J., 1999. Seventy years of stand dynamics in Connecticut hardwood forests - the Old-Series plots (1927–1997). The Connecticut Experiment Station Bulletin 959. http://www.caes.state.ct.us/Bulletins/1990s/1999/b959.pdf. (Accessed 28 September 2021).

Wason, J.W., Dovciak, M., Beier, C.M., Battles, J.J., 2017. Tree growth is more sensitive than species distributions to recent changes in climate and acidic deposition in the northeastern United States. J. Appl. Ecol. 54 (6), 1648–1657.

Wasserstein, R.L., Lazar, N.A., 2016. The ASA's statement on p-values: context, process, and purpose. Am. Statist. 70, 129–133.

Whitney, G.G., 1984. Fifty years of change in the arboreal vegetation of Heart's Content, an old-growth hemlock-white pine-northern hardwood stand. Ecology 65, 403–408.

Yamasaki, M., 2018. Wildlife Habitat Values of Eastern Hemlock Stands in New Hampshire. Timber Crier. New Hampshire Timberland Owners Association, Concord, New Hampshire, pp. 36–38.

Yamasaki, M., DeGraaf, R.M., Lanier, J.W., 2000. Wildlife habitat associations in eastern hemlock – birds, smaller mammals and forest carnivores. In: McManus, K.A., Shields, K.S., Souto, D.R. (Eds.), Proceedings: Symposium on Sustainable Management of Hemlock Ecosystems in Eastern North America. Gen. Tech. Rep. NE-267. USDA Forest Service, Northeastern Research Station.

Yemshanov, D., Koch, F.H., Barry Lyons, D., Ducey, M., Koehler, K., 2012. A dominance-based approach to map risks of ecological invasions in the presence of severe uncertainty. Divers. Distrib. 18 (1), 33–46.