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**70 years of forest growth and community dynamics in an
undisturbed northern hardwood forest**

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Abstract: Long-term forest inventories provide a unique opportunity to quantify changes in forest structure and evaluate how changes compare to current stand development models. An examination of a 70-year record at the Bartlett Experimental Forest, NH indicated that while species abundances have primarily changed as expected under natural succession, some unexpected results were also detected. This included a significant decline in sugar maple (*Acer saccharum*) abundance driven by reduced regeneration, and increases in red spruce (*Picea rubens*) at the expense of sympatric balsam fir (*Abies balsamea*) and hardwoods at upper elevations. In contrast with accepted stand development models, biomass continues to accrue on these mid- to late-successional forests. Importantly, biomass accumulated at even greater rates in recent decades compared to historical norms. These results support evidence that the anthropogenic influences of a changing climate and the legacy of acid deposition may be altering stand dynamics in northeastern forests.

Key words: competition, regeneration, succession, forest inventory, forest dynamics, Bartlett Experimental Forest.

Introduction

Natural succession in upland forest ecosystems is primarily driven by shade tolerance, longevity and growth rates (Filip 1960). Models of ecosystem development based on these successional pathways have been well described across forests of the northeastern United States (US) (e.g., Bormann and Likens 1979; Leak 1991; Fahey 1998; Nicholson et al. 1979; Schwarz et al. 2001; Canham et al. 2005; Allison et al. 2003). Conventional wisdom holds that biomass accumulates in forests rapidly after disturbance, peaks near canopy closure, then declines to

constant or decreasing rate of biomass accumulation (Borman and Likens 1979, Keeton et al. 2011, Foster and D'Amato 2014). This decline in biomass accumulation has been explained by reductions in net primary productivity (Ryan et al. 2004), increasing mortality (Coomes et al. 2012), or some combination of the two (Acker et al. 2002, Wirth 2009).

Some studies continue to support this conventional model of biomass accumulation for certain forest types, including mature mixed-forests (Keeton et al 2011), northern hardwood forests (van Doorn et al. 2011, Battles 2014), and even-aged *Pinus banksiana* and *Acer saccharum* stands (Foster and D'Amato). Others studies report continued biomass accumulation in: older, low-productivity forests of *Fraxinus nigra*, *Quercus rubra* and *Thuja occidentalis* (Foster et al. 2014), *Quercus* dominated forests (Eisen and Barker-Plotkin 2015), and old growth northern mixed hardwood conifers (Keeton et al 2011).

Studies of changing forest growth and biomass accumulation *rates* from across the globe are also mixed (Boisvenue and Running 2006). Some temperate forests report increased growth rates (Salzer et al. 2009), some unchanged (Siccama et al. 2007; van Doorn et al. 2011) and some decreasing (Silva et al. 2010). Others report unexpected shifts in species composition (van Doorn et al. 2011) and distribution (Chen et al. 2011; Hamann and Wang 2006). However, individual species vary greatly in their rates of change, suggesting that changes in forest structure over time depend on multiple life history traits, their tolerance for external drivers of change, and the predominant limiting factors at play in the region studied (Chen et al. 2011).

Several recent publications have studied changes in species composition and growth in northeastern forests. At both the Hubbard Brook Experimental Forest (HBEF) (van Doorn et al. 2011) and the Bowl Research Natural Area (Martin and Bailey 1999) in the White Mountains of New Hampshire (NH), 10- to 20-year surveys showed increases in red spruce (*Picea rubens*

Sarg.) and sugar maple (*Acer saccharum* Marsh.) basal area. However, results differed between the sites for yellow birch (*Betula alleghaniensis* Britt.) (decreasing at HBEF and increasing at the Bowl) and paper birch (*Betula papyrifera* Marsh.) (decreasing only at HBEF). van Doorn et al. (2011) also reported that live tree biomass was both lower than expected, and no longer aggrading at HBEF.

These studies highlight recent changes in species demographics, biomass accumulation rates and forest dynamics. However, accurately quantifying meaningful, long-term changes requires a dataset spanning a sufficient time period to capture forest structure before and during changes in environmental conditions, with repeated measurements to control for inherent differences due to site characteristics, and on stands with known disturbance history. To this end, we present the analysis of a unique long-term dataset from the Bartlett Experimental Forest (BEF) in the White Mountains, NH. By isolating a subset of unmanaged inventory plots with mid- to late-successional forest characteristics and minimal evidence of disturbance, and comparing measurements spanning 70 years, we examined changes in long-term species composition and biomass accumulation, and compared these to expected successional patterns.

We hypothesized that over the 70-year record as mid-successional stands transition to late, and late-successional stands transition to old growth, there should be continued increases in shade tolerant climax species (e.g., sugar maple, American beech (*Fagus grandifolia* Ehrh.) and eastern hemlock (*Tsuga canadensis* (L.) Carr)), with continued decreases in early successional species (e.g., paper birch) and steady levels of mid-successional species common in forests dominated by small gap dynamics (e.g., yellow birch and red maple (*Acer rubrum* L.)). With recent cores indicating a mean stand age of over 170 years old, we hypothesize biomass accumulation should have leveled off in this forest following widely accepted biomass

accumulation models, wherein a rapid increase in aboveground biomass peaks at approximately 170 years after disturbance, followed by declining and then steady state biomass dynamics in older stands (Bormann and Likens 1979). However, investigations into current biomass dynamics have yielded contrasting results. Because many of these studies rely on short inventory intervals or stand age as a proxy for repeated inventories it is unclear what pattern might be evident if a longer time period was evaluated for stands with repeated inventories. In contrast to these approaches, here we present a comprehensive 70-year record of forest dynamics. Controlling for the influence of land use and disturbance histories, our objectives are to: 1) examine changes in species composition over the 70 year inventory record, and 2) quantify changes in biomass accumulation rates between early and more recent inventory intervals. By controlling for the influence of land use and disturbance histories, this analysis focuses on changes resulting from natural succession and steady state gap dynamics that dominate in mid- to late-successional stands. Considering how changes witnessed over this 70 year record differ from widely accepted models of stand development highlights the potential role of anthropogenic drivers in changing stand dynamics.

Materials and methods

Study area

The Bartlett Experimental Forest established in 1931, is a 2,342 ha parcel within the White Mountain National Forest, NH (44°2'39"N, 71°9'56"W) (Fig. 1). Forests at the BEF are characteristic of the northern hardwood forest complex, which spans much of the northeastern U.S. and southeastern Canada. The wide range of topographic and soil characteristics at the BEF is also representative of the four million hectares of northern hardwood forests found across the

region (USDA 2008). Consequently, results from the BEF have historically been used to answer questions about ecological structure, function, and process for a much larger regional area. Over the 70-year data record, the most common species have consistently included American beech, sugar maple, yellow birch and eastern hemlock. Red spruce and balsam fir (*Abies balsamea* (L.) Mill.) dominate the upper slopes. Repeated surveys on 212 permanent plots, tracking more than 30,000 trees over 70 years provides a uniquely comprehensive approach to examine stand development over time in mature and old-growth stands. These plots cover a range of common northern forest species assemblages, from pure hemlock and sugar maple to mixed spruce/fir/birch, maple/beech and hemlock/pine across an elevational range from 210 m in the lower forest to 915 m at the summits.

Data collection

The BEF has 500 0.1 hectare permanent inventory plots, marked with cedar post corner stakes. Plots are distributed across the landscape in a N-S/ E-W grid, spaced at 200 m by 100 m intervals. Since its establishment, four complete forest inventories have been completed: 1931-1932 (henceforth referred to as '31), 1939-1940 (referred to as '39), 1991-1992 (referred to as '91) and 2001-2003 (referred to as '01). On each plot, all stems with a diameter at breast height (DBH, 1.4 m above ground level) greater than 4 cm were tallied into 2.54 cm size classes.

Because the BEF is an actively managed forest and because two known severe disturbance events (the 1938 hurricane and the 1998 ice storm) occurred during the span of these inventories, a subset of plots was selected from the full inventory to omit the influence of forest management activities and stand-replacing disturbance. This directed the focus of the analysis to

natural succession and small gap dynamics that are typical of mid- to late-successional forests across the broader landscape and limited the influence of land use or disturbance history. Criteria to select study plots included: 1) no management activities since BEF establishment in 1931, 2) a minimum initial stocking level in the '31 inventory of $10 \text{ m}^2 \text{ ha}^{-1}$, and 3) no significant reduction in aboveground live biomass over the inventory record.

The resulting dataset included 212 inventory plots ranging from 236 m to 833 m in elevation, with each of the target study species present on 69-189 plots (Table 1). Seventy-nine plots from our subset are from management compartments with documented old growth characteristics, 58 of which were already at stocking levels consistent with old growth northern hardwood stands in 1931 (ca $30 \text{ m}^2 \text{ ha}^{-1}$) (Martin and Bailey 1999). By the '01 inventory, 154 were at or exceeded those levels. By limiting our analyses to this subset of mid- to late-successional forests, we limit the influence of past land use history and catastrophic disturbance (i.e., ice storm, hurricane) to focus more on changes resulting from natural succession and steady state gap dynamics that dominate in mid- to late-successional stands.

At each plot and in each inventory, total basal area and stem density were extracted for species that occurred on at least 50 plots and covered at least a 500 m elevational range. This included American beech, sugar maple, red maple, eastern hemlock, yellow birch, paper birch, red spruce and balsam fir (Table 1). Replication of species was sparse above 700 m and results there should be interpreted with caution. Total aboveground live biomass for each plot was calculated using species-specific allometric equations (Jenkins et al. 2003).

Following methods described by Curtis and McIntosh (1951), we also calculated species' relative importance value (RIV) at each plot by summing its proportionate density (percent of total stem count) and proportional basal area (percent total basal area), and expressing this sum

as a percent of the sum of all species RIV's at that plot. While basal area acts as a surrogate for productivity (growth) and could be compared to similar assessments of changing species biomass (van Doorn et al. 2011), the RIV provides a more nuanced assessment of species dominance that results from competition within a plot. Because stand density is included with basal area in the RIV calculation, it represents a more holistic approximation of how growth, recruitment and mortality work together to affect changes in biomass.

Statistical analyses

To identify any significant changes in the various stand demographic metrics (basal area, stem density, RIV and biomass) between survey intervals ('31 and '01) we used a Wilcoxon Signed Rank matched-pairs test. The Wilcoxon test was chosen because responses were not normally distributed for species with low sample size, and also to ensure conservative assessments where sample size was high. To determine if changes in RIV differed by elevation, tests were repeated on three distinct elevation classes determined by the 25th and 75th elevation percentiles (low 236- 317 m, mid 318- 556 m and high 557- 833 m) across plots. Because some of the more notable changes occurred at the upper elevations, a comparison of the dominant upper elevational species (red spruce, balsam fir and yellow birch) was repeated on a subset of 18 plots above 650 m where all three species were co-located. This allowed us to examine how differences in site or environmental conditions influenced species competitive dynamics.

To assess how *overall* community structure changed over time at the BEF, we also conducted a Permutational Analysis of Variance (PERMANOVA) using PRIMER-E 7.0, PERMANOVA+ (Anderson 2001; Anderson et al. 2008). This nonparametric multivariate approach allowed us to concurrently assess differences in total biomass, stem density, mean

DBH and RIV by tree species, survey interval, and elevation class along with their interactions. Means were considered statistically different when $P \leq 0.05$. When significant effects were found, subsequent pair-wise comparisons were assessed. Means ($\pm$ SE) are reported below.

Results

Total aboveground biomass

Over the 70-year survey interval, average total aboveground live biomass increased from 156 ($\pm$ 3.88) to 254 ($\pm$ 4.19) Mg ha⁻¹. In the 10 years between the last two survey intervals alone, biomass increased 36 ($\pm$ 1.89) Mg ha⁻¹ indicating that these now late-successional stands continued to aggrade carbon (C). On average, plots increased by 4.51 ($\pm$ 0.25) Mg ha⁻¹ yr⁻¹ over the '91-'01 survey interval, compared to 2.38 ($\pm$ 0.14) Mg ha⁻¹ yr⁻¹ between the '31 and '39 inventories ($P < 0.001$).

Changes in species demographics

American beech and yellow birch were the largest contributors to basal area in the '31 survey, but eastern hemlock growth outpaced all other species to reach levels matching beech by '01 (Table 2). Similarly, significant increases in red maple basal area quickly outpaced yellow birch.

While total biomass continued to increase across all plots, this trend was not consistent across species. Between the '31 and '01 inventories, forest-wide live basal area increased significantly for 5 of the 8 species included in our analysis (Fig. 2). In contrast, RIV increased significantly for only American beech and eastern hemlock, signifying both increased

regeneration and growth of existing individuals for these two late successional species. Sugar maple recorded significant increases in basal area but declines in RIV, suggesting continued growth of mature stems but limited regeneration (Fig. 2). Forest-wide trends for sugar maple also differ over time, with long-term gains in total basal area (Table 2), but near stagnation between the most recent survey intervals ('91-'01). This was likely driven by significant reductions in sugar maple sapling ingrowth and insufficient growth of survivors to balance mortality in the most recent survey intervals (Table 3). While yellow birch recorded a significant decrease in RIV, the only species to significantly decline in both basal area and RIV during this long-term study period was paper birch (Fig. 2).

Elevational trends

Several species experienced significant changes in basal area and relative importance that occurred primarily at upper elevations (Fig. 3). For example, changes in balsam fir and red spruce RIV remained relatively stable at mid-lower elevations, but above 600 m balsam fir experienced slight reductions in RIV while red spruce experienced significant increases in all but the highest elevations (Fig. 3). Similarly, the most severe decreases in paper birch occurred at upper elevations. Declines in yellow birch RIV over the long-term were present forest-wide, but were most pronounced at lower elevations (Fig. 3).

Regeneration and mortality

Typical of a maturing forest with minimal disturbance, the number of large stems (greater than 25.4cm DBH) increased for all species except balsam fir and sugar maple, with significant declines in mature stems for paper birch (Table 3). Similarly, decreases in regeneration

(captured as count of stems less than 5.1 cm DBH), were common for all species except American beech. Reductions in mean sugar maple sapling counts were significant across all elevations (from 20 stems ha⁻¹ in '31 to 8 stems ha⁻¹ in '91), but were most notable at upper elevations where sugar maple saplings were absent by the 2001 survey (from 3 stems ha⁻¹ in '31 to 0 stems ha⁻¹ in '01). Mortality of mid-range and mature sugar maple size classes were also significantly higher at upper elevations by the most recent survey.

Multivariate results

Results of the PERMANOVA that considered multiple structural metrics for each species indicated that there were significant differences in overall community structure and composition over the 70-year survey interval. Across the full range of elevations, significant increases in overall abundance were reported for American beech ($P = 0.01$), eastern hemlock ($P = 0.001$), red maple ($P = 0.001$) and red spruce ($P = 0.001$). Significant decreases were reported for yellow birch ($P = 0.001$). The significance of the *species x elevation* interaction term reinforced univariate results indicating that significant changes between interval periods varied by elevational class for many species. This included increases in red spruce primarily at upper elevations ($P = 0.003$), increases in balsam fir only at low elevations ($P = 0.011$) and decreases in red maple ($P < 0.045$) and yellow birch ($P < 0.001$) at low and mid-elevations only. Interestingly, sugar maple only reported a marginally significant decrease at mid-elevations ($P = 0.05$), with no significant forest-wide changes in the multivariate assessment. This is likely because its decrease in stem density and RIV were offset by increases in biomass and basal area for existing mature stems.

Discussion

Biomass

The selection of sub-plots for this study ensured that all stands included were mid- to late-successional stands at the time of the first survey. A mean stand age of 170 years was sufficient to place stands included in this analysis beyond the inflection point of modeled net primary productivity (Bormann and Likens 1979). As such, we hypothesized that productivity in the first survey (biomass accumulation rates from '31 to '39) should be significantly higher than more recent biomass accumulation rates from the second survey (from '91 to '01). In contrast to the widely accepted model of peaks in biomass near canopy closure, we not only found continued biomass aggradation in mature and old growth stands, but also a significant increase in biomass accumulation *rates* for the '91 to '01 survey interval in comparison to the '31 to '39 interval.

These results also differ from the nearby Hubbard Brook Experimental Forest study, where comparisons of 1995 to 2005 surveys indicated that forest biomass remained constant (van Doorn et al. 2011, Battles et al. 2014). van Doorn et al. (2011) suggest that biomass at HBEF may be depressed by novel stressors including acid deposition and beech bark disease, but these stressors are also present at the BEF. Climate and soil characteristics are also similar at the two forests. It is more likely that differences in results arise because of differences in disturbance history and stand age. The Hubbard Brook study included all plots within the survey, capturing impacts of the region wide 1998 ice storm that our subset of undisturbed BEF plots filtered out. Further, the subset of plots used in this study were specifically selected to include only mature stands to minimize the impact of land use history on changes in biomass accumulation rates.

Contrary to past assumptions, this maturity may help explain the divergence between biomass stability at HBEF and accretion at BEF. Recent evidence suggests that older forests may capture and store more C than current models suggest (Gunn et al. 2014). This could explain the continued biomass increase on mid- to late-successional stands at the BEF, where the mean tree size ranged between 17 and 22 cm DBH for the dominant species included in this study, with individuals up to 90 cm on some plots. At the BEF, the shift to these larger tree sizes was particularly evident in sugar maple, red maple, paper birch and yellow birch, where more than 40 percent of all stems were larger than 20 cm DBH by the 2001 inventory. These results are also consistent with recent studies across the region that show continued aggradation of biomass on a variety of forest types (Foster et al 2015). Foster et al. attributed this continued aggradation of biomass to the ingrowth of more shade tolerant cohorts, especially if these trees grow to a larger stature. In addition to continued increases in stand biomass, our results indicate that the *rate* of biomass accumulation is significantly higher in recent decades compared to previous growth. This is consistent with mounting evidence of increased forest productivity across temperate North America, Northern Europe, most of Central Europe, some parts of Southern Europe, and Japan (Boisvenue and Running 2006). Numerous reports have suggested that recent increases in precipitation and air temperatures (Myneni et al. 1997; Salzer et al. 2009), atmospheric CO₂ (Peters et al. 2013), or a combination of the two (without (McMahon et al. 2010b) or with (Zhang et al. 2012) the assistance of a nitrogen (N) fertilization effect from pollutant N deposition), may have stimulated tree growth. Conversely, there has been a 59% reduction in SO₄²⁻ deposition and a 22% reduction in NO₃⁻ deposition between initiation of the US Clean Air Standards in 1970 and 2014 (Lehmann et al. 2015). Specific to NO₃⁻, some

speculate that forest productivity may begin to decline as inputs are reduced (Templer et al. 2012).

Perhaps more pertinent, pollutant inputs of S and N are the primary components of acid deposition (Driscoll et al. 2001), and because acid deposition has been linked to the decline of sensitive tree species like red spruce and sugar maple (e.g., Schaberg et al. 2001; Halman et al. 2013; Battles et al. 2014), reductions in pollutant loading could instigate a rebound in health and productivity within impacted forests. Indeed, some improvement in soil nutrition with reduced pollution loading has been documented in northeastern US forests (Lawrence et al. 2012). However, to date, no documented improvements in tree productivity have been verified relative to these changes in soil status.

While insufficient concurrent ancillary data make it impossible to directly link this increase in biomass accumulation rate to anthropogenic drivers, it is possible that numerous recent anthropogenic factors (e.g., changes in climate, atmospheric CO₂, and pollutant inputs) could alone or in combination be altering forest productivity. Further mechanistic analyses are needed to tease apart possible independent and interactive effects of the many fundamental environmental changes on forest health and productivity.

Changes in species assemblages

In the mid- to late-succession stands included in this study, we expected to see steady or increasing proportions of shade tolerant, long-lived species such as eastern hemlock, American beech and sugar maple, with red spruce and balsam fir dominating upper elevations (Bormann et al. 1970) and yellow birch recruiting heavily in openings created by mesoscale disturbance (Filip 1960). Most of the changes in species composition reported here match this expectation. The

increase in all eastern hemlock abundance metrics over time (Table 3) indicates that these forests are approaching their late-successional state. Significant increases in red maple also follow trends witnessed across eastern forests. Abrams (1998) summarized a wide range of studies documenting a dramatic rise in red maple abundance across the eastern US. In part, this was attributed to reductions in oak and pine dominated systems (Abrams 1998), which are not common at the BEF. However, it is likely that red maple’s physiological, morphological and growth characteristics of both early and late successional species, with less water, nutrient and light requirements, higher genetic diversity, and greater reproductive capacity than many other mid- to late-successional species allow red maple to outcompete many co-occurring species (Abrams 1998). Trends at BEF suggest that this may be a longer-term, natural dynamic in northern forests.

Reductions in an early successional species such as paper birch were also expected for the maturing forests in this study because disturbance is needed to promote their regeneration. However, the widespread loss of paper birch basal area (Table 2), stem density (Table 3) and RIV (Figure 2), suggest that other processes may be at work. Previous studies in the region found the majority of paper birch decline was restricted to 715-900 m in elevation, and was influenced by a combination of ice storm damage and low Ca-availability (Halman et al. 2011). Our current data suggest that paper birch decline may extend to lower elevations than previously thought (Fig. 3). The PERMANOVA pairwise tests revealed that it was the lower and mid-elevations that experienced the most significant reductions in paper birch. This is similar to recent work at HBEF, which notes the near extirpation of paper birch from elevations similar to those found at BEF (Battles et al. 2014). Regardless of tree nutrition, paper birch show lower wound closure capacities and greater pathogen susceptibilities than co-occurring hardwoods

following disturbances like ice storms (Shortle et al. 2003). Although we avoided areas at BEF with losses in basal area resulting from the 1998 ice storm, the ice loading of trees there was far-ranging. If any species was likely to be pushed into decline from low-to-intermediate crown damage and wounding following the 1998 ice storm, it would have been paper birch.

The pattern of increased dominance of American beech also matches expected successional trajectories. However, the magnitude of this increased dominance, with the largest short-term gain in basal area at over $0.13 \text{ m}^2 \text{ ha}^{-1} \text{ yr}^{-1}$ (Table 2), is somewhat unexpected considering the long history of beech bark disease (BBD) complex. BBD, first noted in BEF in the 1930's, was responsible for high tree mortality initially, followed by the development of an "aftermath forest" (e.g., a high density of small, root-sprouted saplings) (Leak 2006). This type of forest can continue to accrue basal area from high sapling densities. Our data demonstrate the common sprouting response on beech with a long-term increase in sapling counts. However, this is coincident with a significant increase in large individuals (Table 3). This suggests that many individuals established as a result of the initial BBD killing front have survived and grown to maturity without suffering a second incidence of BBD-induced mortality. The beech stands included in this study have a mean DBH of approximately 13cm, with some stems surpassing 75cm. While this size structure has remained stable across the full survey, the most dramatic gains in basal area occurred quite recently (1991-2001; Table 2). This is similar to recent work in the region that has found an increase in American beech radial growth since 1999 at HBEF (Halman et al. 2015), suggesting that while BBD is still prevalent at the BEF, it is not limiting the increase in American beech productivity or the incidence of large stems.

While overall sugar maple basal area has risen over the full survey period, the rate of sugar maple basal area accumulation has slowed significantly in the most recent survey interval

compared to the long-term accumulation rate (Table 2). This is consistent with recent evidence of unexpected negative growth trends in the last several decades, regardless of age, diameter or soil fertility (Bishop et al. 2015). The recent decline of sugar maple RIV was primarily driven by a reduction in sugar maple recruitment across the forest. The mean number of stems per plot has decreased consistently over the survey interval, indicating that the marginal increases in basal area can be almost entirely attributed to continued growth of mature stems. A closer examination limited to saplings only found a long-term downward trend in number of sugar maple saplings forest-wide, but with the most dramatic decreases at upper elevations where by 2001 no sugar maple saplings were present on any survey plots (Table 3).

Similar reductions in hardwood regeneration in the central Appalachians have largely been attributed to high herbivory levels – primarily by deer (Côté et al. 2004). However, herbivory pressure in northern NH is thought to be low with estimates of less than 15 deer per square mile in the Bartlett area. This is well below levels typically expected to induce negative ecological impacts (Côté et al. 2004).

Studies from New York and New Hampshire have confirmed that sugar maple reproduction has been greatly impaired due to acidic deposition (Cleavitt et al. 2011; Halman et al. 2013; Sullivan et al. 2013). Experimental Ca additions suggest that soil acidification and Ca depletion is shifting the competitive balance in the seedling stage toward beech (Marlow and Peart 2014). Other studies have found that the increase in beech sprouts that typically results from BBD further reduces sugar maple seedling survival (Beaudet et al. 1999; Hane 2003). This combination of nutritional stress and elevated competition from increased beech dominance from prolific sprouting that followed the initial BBD wave of mortality may be responsible for the dramatic reduction in sugar maple regeneration witnessed across the forest.

The reduction in yellow birch RIV (Fig 3) and multivariate abundance metrics was also influenced by the significant decrease in regeneration for the species (Table 3). Yellow birch requires some degree of soil disturbance to effectively regenerate (Burns and Honkala 1990), and the lack of major disturbance at low- and mid-elevations may have reduced the species' recruitment ability. Because we specifically excluded plots that were likely disturbed by the 1938 hurricane or the 1998 ice storm (catastrophic disturbances that reduced standing biomass), our data may under-estimate yellow birch regeneration for areas impacted by these broad-scale events. While the long-term trend of reduced basal area for the species compliments recent work at HBEF (van Doorn et al 2011), the short-term increase in yellow birch basal area at BEF (Table 2) runs counter to previous findings. Although this trend is present at most locations throughout BEF, it appears that yellow birch at upper elevations have increased biomass over the most recent survey interval (Fig. 3), primarily attributed to the increase in the growth of existing, mature trees (Table 3). This suggests that changes in yellow birch biomass may differ across elevations and locations, and as such should only be extrapolated to the landscape-scale with caution.

Surprising results include the significant increase in red spruce dominance at upper elevations (Fig. 3). Historically, red spruce decline has been well documented across the region and attributed to the impact of acid deposition that increases foliar vulnerability to winter freezing injury and mortality (Schaberg et al. 2001; Halman et al. 2008). Reductions in red spruce basal area and RIV above 700 m (Fig. 3) may reflect this legacy of decline. In contrast, the increase in red spruce basal area and RIV between approximately 600 and 700 m could represent an alternate trend – a resurgence in red spruce survival and productivity. New evidence suggests that red spruce has recently experienced significant increases in radial growth

404 across the region (Kosiba et al. 2013; Engel et al. 2016). An increase in red spruce biomass was
405 also detected in recent inventory data from HBEF (van Doorn et al. 2011). Furthermore, remote
406 sensing data shows an expansion of spruce-fir forests to lower elevations over the past several
407 decades (Foster and D'Amato 2015)

408 While the direct cause of this resurgence in red spruce is currently unknown, there are
409 several likely scenarios. Since the enactment of the 1970 Clean Air Act, rates of nitrate and
410 sulfate deposition have decreased dramatically across the region, which could instigate a rebound
411 in the health and productivity of sensitive species like red spruce within impacted forests.
412 Furthermore, the milder winter temperatures noted in recent years (Groffman et al. 2012) has
413 likely reduced an inciting factor for red spruce decline – foliar freezing injury. It is also possible
414 that a warming climate has begun to offer red spruce a competitive advantage over its high
415 elevation counterpart balsam fir. Red spruce has the ability to become photosynthetically active
416 and gain C under favorable conditions in winter – a trait not present in sympatric balsam fir
417 (Schaberg et al. 1998).

418

419 **Conclusions**

420 The BEF continues to aggrade biomass 70 years after monitoring began, with *the highest*
421 *rates in recent decades*. This indicates that not only do these mid- to late-successional forests
422 continue to aggrade C, but that forest productivity has increased significantly over time.
423 Considering the mixed findings of biomass aggradation studies across the region, this study, and
424 others like it, are required in order to more accurately characterize regional patterns and
425 variability.

Species demographics in the forest have shifted following expected successional patterns with eastern hemlock and American beech dominating and paper birch decreasing in abundance. However, the potential threat of hemlock woolly adelgid (*Adelges tsugae*: Annan) may limit the long-term viability of eastern hemlock in the region. At upper elevations, red spruce has become the dominant species over balsam fir and paper birch, despite decades of acid deposition-associated spruce decline. Recent combinations of reduced acid deposition inputs and warming winters may have increased red spruce's competitive advantage over sympatric species. Although mature sugar maple and yellow birch are not in apparent decline at BEF, they have experienced long-term decreases in regeneration, while American beech has dramatically increased in number of saplings. Acidified soils have likely hindered the ability of the former species to reproduce while enabling more acid-tolerant, sprout prolific American beech to thrive. These results add to the growing body of literature that suggests the lack of sugar maple regeneration is a regional concern.

While many have questioned the feasibility of scaling up trends from intensive sites to broader regions, findings from the BEF have historically been considered representative and used to inform forest management across the region. Trends for the relatively undisturbed plots that we evaluated indicate that forest composition and growth may not match the patterns that land managers have used to guide management decisions for decades. It is likely that changing environmental conditions are altering the competitive relationships among tree species, with potential changes in climax forest composition and structure across the region. Of particular concern is the decrease in sugar maple regeneration, which may require targeted management if the species is desired as a component of future forests, particularly those with a heavy beech component. Our data also suggest that, in the absence of natural disturbance, silvicultural

harvests may be required to regenerate disturbance-dependent species such as paper and yellow birch. It will be important to continue to monitor forest reproduction rates and biomass accumulation in the northeast amid a changing climate, especially as forests approach maturity.

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Table 1. The number of plots where each species is present in the first (1931) and last (2001) full BEF inventories.

Species	1931 Survey	2001 Survey
BE	179	185
BF	82	69
EH	158	172
PB	158	97
RM	172	159
RS	177	157
SM	155	144
YB	189	186

Note: Species abbreviations are as follows: BE (American beech), BF (balsam fir), EH (eastern hemlock), PB (paper birch), RM (red maple), RS (red spruce), SM (sugar maple), and YB (yellow birch).

Table 2. Mean basal area to compare long-term changes (1931-1991) in species demographics to more recent short-term changes (1991-2001).

Species	Mean basal area (m ² ha ⁻¹)				Mean Yearly Long-Term Change (1931-1991)	Mean Yearly Short-Term Change (1991-2001)
	1931	1939	1991	2001		
BE	9.1	9.4	11.0	12.8	0.04	0.13 *
BF	1.8	1.8	2.5	2.4	0.00	0.00
EH	5.2	6.0	13.8	15.1	0.10	0.09
PB	5.0	5.1	4.7	4.9	-0.02	-0.02
RM	5.2	6.0	9.9	10.5	0.04	0.03
RS	7.4	7.3	9.8	10.6	0.01	0.00
SM	6.1	6.3	8.0	8.0	0.02	-0.02 *
YB	5.4	5.6	5.2	5.7	0.00	0.03 *

Note: Species abbreviations are as follows: BE (American beech), BF (balsam fir), EH (eastern hemlock), PB (paper birch), RM (red maple), RS (red spruce), SM (sugar maple), and YB (yellow birch). Asterisks denote significant differences ($P < 0.05$) in the rate of change between long- and short-term intervals.

Table 3. Mean density (stems ha⁻¹) and standard error of the difference of saplings (< 5.1 cm DBH), mid-range size classes and mature trees (> 25.4 cm DBH) by species across the full forest (top) and upper elevations (> 650 m) only (bottom).

Forest-wide stems									
	saplings			mid-range size classes			mature stems		
	1931 mean density	2001 mean density	<i>stderr</i> <i>dif</i>	1931 mean density	2001 mean density	<i>stderr</i> <i>dif</i>	1931 mean density	2001 mean density	<i>stderr</i> <i>dif</i>
BE	120	134	10	34	37	2 *	11	13	1 *
BF	22	18	5	8	7	1	1	1	0
EH	63	50	5 *	19	31	1 *	5	10	1 *
PB	13	1	3 *	14	4	2 *	7	5	1 *
RM	50	5	7 *	23	12	2 *	8	10	1 *
RS	86	38	8 *	30	20	2 *	5	7	1 *
SM	20	8	2 *	13	9	1 *	7	6	0
YB	34	7	3 *	23	12	1 *	9	11	1 *

Upper-elevation stems									
	saplings			mid-range size classes			mature stems		
	1931 mean density	2001 mean density	<i>stderr</i> <i>dif</i>	1931 mean density	2001 mean density	<i>stderr</i> <i>dif</i>	1931 mean density	2001 mean density	<i>stderr</i> <i>dif</i>
BE	58	140	26 *	25	27	5	9	11	2
BF	117	45	33 *	33	23	6 *	3	5	2
EH	4	2	3	5	4	1	2	3	1 *
PB	35	3	21	37	7	8 *	13	7	2 *
RM	13	4	4 *	17	8	2 *	9	8	1
RS	266	129	51 *	83	46	10 *	16	20	4
SM	3	0	2	9	3	2 *	8	5	1 *
YB	31	11	12	19	14	3 *	8	10	2

Note: Species abbreviations are as follows: BE (American beech), BF (balsam fir), EH (eastern hemlock), PB (paper birch), RM (red maple), RS (red spruce), SM (sugar maple), and YB (yellow birch). Asterisks denote significant ($P < 0.05$) differences between surveys.

Fig. 1. Study and plot locations. 212 long-term inventory plots at the Bartlett Experimental Forest were selected for their mid- to late-successional status and lack of severe disturbance over the 70-year study period. These plots covered a range of species compositions, elevations, slopes and aspects. General forest assemblages are distinguished to exemplify the diversity of stands included in this study.

Fig. 2. Forest-wide changes in species demographics. Across all study plots, basal area increased significantly over the 70-year study period for all species except paper birch, yellow birch and balsam fir. Relative Importance Value (RIV) only increased significantly for American beech and eastern hemlock, reflecting their increased dominance on the forest. In contrast, RIV decreased significantly for paper birch, yellow birch, and sugar maple. Asterisks indicate a significant difference between the 1931 and 2001 surveys ($P < 0.05$).

Fig. 3. Smoothed curves of the changes in species abundance between 1931 and 2001 quantified as basal area (top) and Relative Importance Value (RIV: bottom) and for all eight species across an elevational gradient.

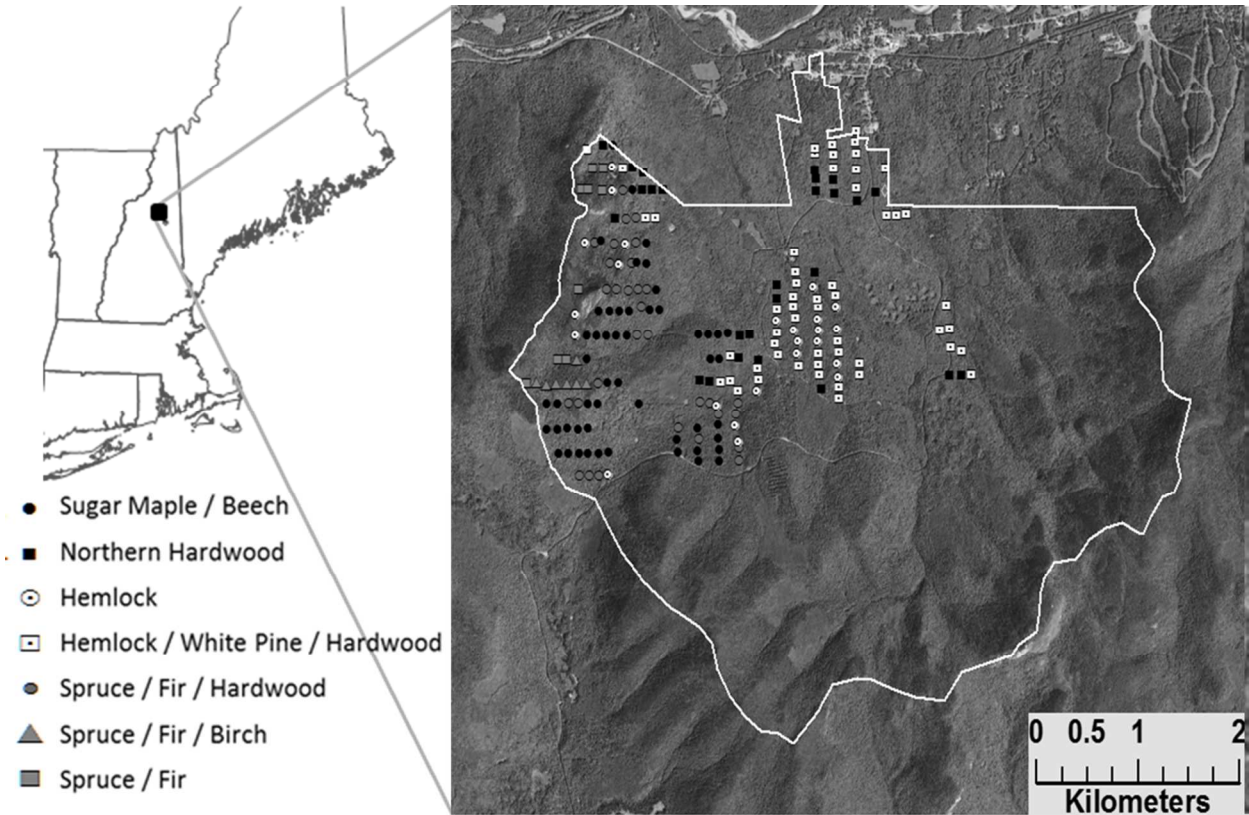
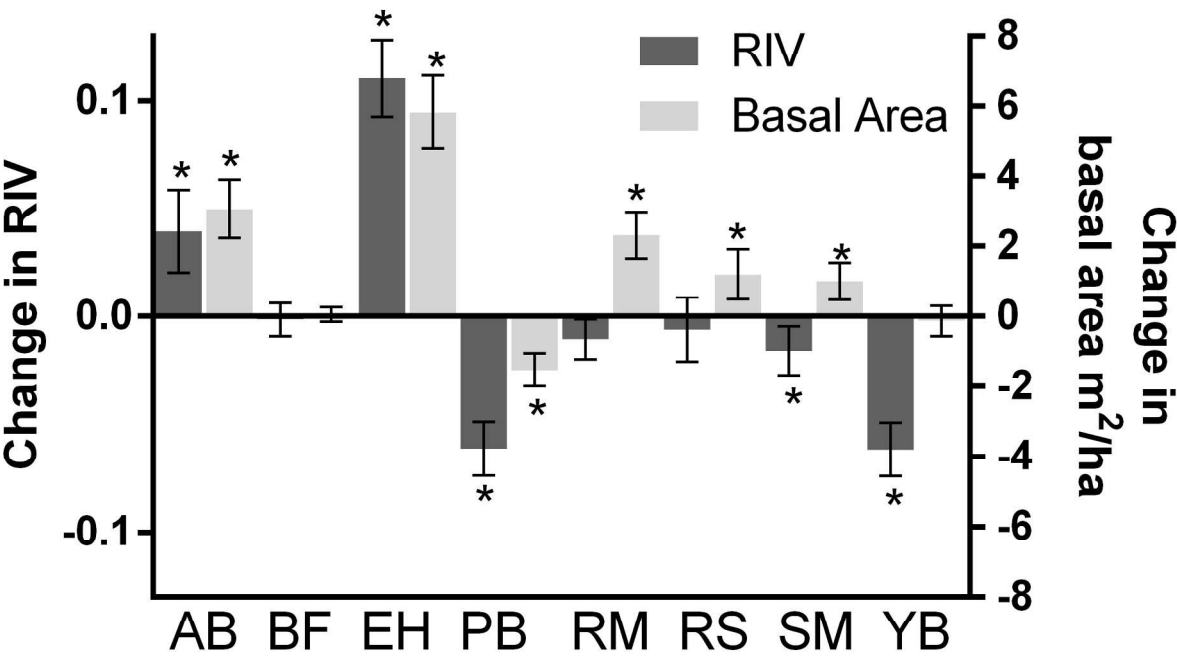


Fig. 1



Note: Species abbreviations are as follows: AB (American beech), BF (balsam fir), EH (eastern hemlock), PB (paper birch), RM (red maple), RS (red spruce), SM (sugar maple), and YB (yellow birch).

Fig. 2.

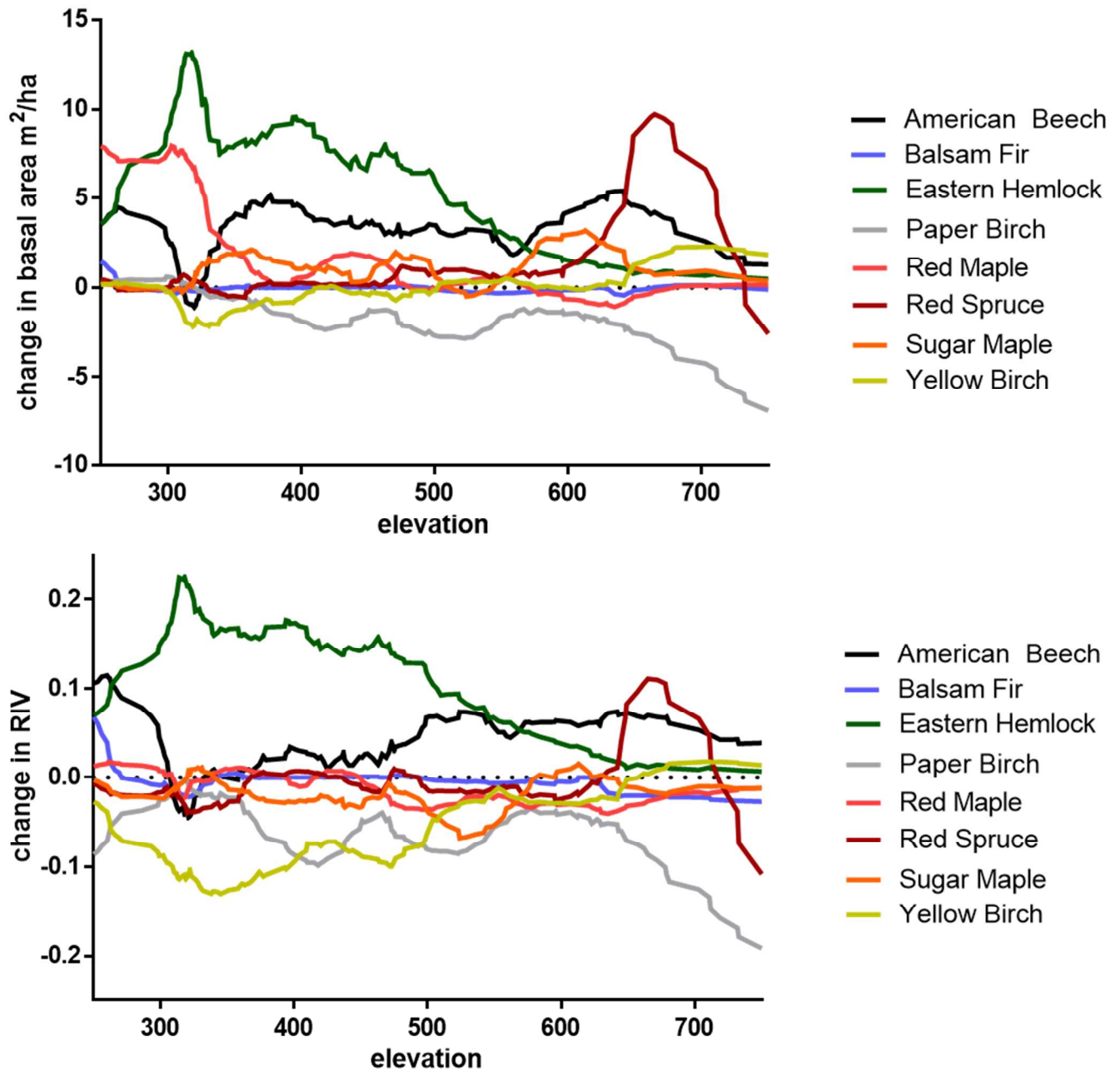


Fig. 3.