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Abstract.

Forest harvesting can impact site quality by removing essential nutrients, exacerbating effects of historic base cation losses associated with acid deposition. We studied the 30-year trajectory of forest recovery from clearcutting (whole-tree harvest (WTH)) in a forest originally dominated by sugar maple (*Acer saccharum*). At both the watershed-scale (21.9 ha) and "detailed" plot-scale (1 m^2), a dramatic decline of sugar maple was observed, along with maintenance of American beech (*Fagus grandifolia*), and an increase in birch, mainly yellow birch (*Betula alleghenіensis*). Many of the "detailed" plots where sugar maple failed to recruit became unoccupied rather than being "won" by another species. The decline of sugar maple was most severe in the upper elevation zones of the watershed, where low base status (especially Ca) of the soils was a likely driver. The results support previous studies indicating that regeneration by sugar maple is severely compromised on base cation depleted soils. Lower survival of seedlings for sugar maple emphasized the importance of maintaining advance regeneration to favor desired species such as sugar maple. Foresters should consider that sites with low base saturation and exchangeable Ca are likely to exhibit regeneration failure for sugar maple in the long-term, even those with initial dominance by this species.

Key words: forest recovery**,** northern hardwood forest, priority effects, community assembly, management implications

Introduction

Concerns about the possible effects of repeated forest harvest on soil fertility were expressed long ago by Rennie (1957), who argued that calcium (Ca) removal by logging on base-poor silicaceous substrates could threaten Ca supply to recovering vegetation. These concerns were heightened when whole-tree harvesting (versus conventional stem-only harvesting) became a more common practice in the 1970s (Weetman and Webber 1972). Moreover, evidence of high base cation losses by leaching following forest cutting (Bormann et al. 1969) as well as chronically increased leaching resulting from acid deposition (Likens et al. 1972) raised further concerns about soil nutrient depletion. Early research summaries (Mann et al. 1988, Federer et al. 1989) concluded that despite some inadequacies of available information there was a strong basis for concluding that a Ca deficit owing to forest harvest plus acid rain effects might not be compensated by natural processes of mineral weathering, atmospheric deposition and detrital recycling on many base-poor soils.

In the northern hardwood forests of eastern North America maintenance of sugar maple (*Acer saccharum* Marsh.; ACSA) after forest harvest is a particular concern. Sugar maple supports the economically important maple syrup industry, provides particularly high quality lumber, as well as spectacular fall foliage, which is the heart of the autumn tourist trade in the northeastern United States (Caputo et al. 2016). Sugar maple re-establishment and survival are expected to be particularly problematic with respect to soil Ca depletion because of its high Ca requirement and known sensitivity to soil acidification (Long et al. 1997, Moore et al. 2000, Schaberg et al. 2006). Sugar maple is often limited by low soil Ca during regeneration (Juice et al. 2006, Sullivan et al. 2013) while its primary mature forest competitor, American beech (*Fagus grandifolia* Ehrh.; FAGR), appears to be relatively insensitive to the depletion of soil Ca

(Park and Yanai 2009, Duchesne et al. 2013). The desirability of favoring ACSA over FAGR following forest harvest is further emphasized by the effect of beech bark disease (BBD), which greatly reduces the economic value of FAGR.

The interaction between ACSA and FAGR following forest harvest has been the subject of considerable research and appears to depend upon both light availability and soil base cation supply. In understory environments FAGR is often favored over ACSA owing to its greater tolerance of low light, whereas ACSA demonstrates a greater response in canopy openings (Canham 1988, Beaudet et al. 1999). In Quebec, clearcut harvesting appeared to give ACSA an advantage over FAGR because of benefits from greater light availability (Nolet et al. 2008, 2015). In addition, New Brunswick researchers have found that sites initially dominated by ACSA are likely to regenerate into ACSA-dominated stands post-harvest (Beland and Chicoine 2013). However, Bannon et al. (2015) observed that on base-poor soils clearcutting did not favor ACSA over FAGR, suggesting an interaction with soil Ca supply. In contrast, other studies from Canada have demonstrated a high light advantage for ACSA (Nolet et al. 2008, 2015). There is a growing literature debating the efficacy of FAGR control versus Ca amendment in managing for ACSA regeneration (Nolet et al. 2015, Moore et al. 2015).

The present study at Hubbard Brook Experimental Forest (HBEF) was originally undertaken to evaluate the effects of whole-tree harvest (WTH) on soil nutrient capital and vegetation recovery at a site where detailed budgetary studies using the small-watershed approach indicated substantial depletion of soil base cations during the 20th century (Likens et al. 1994). On these experimental watersheds, including Watershed 5 (W5), the subject of this study, soil base cation pools decline significantly at higher elevations owing to thinner, more severely depleted soils (Johnson et al. 2000), creating a natural contrast in soil fertility across the landscape. Early surveys following WTH of W5 (Mou et al. 1993) indicated that ACSA, the pre-harvest dominant, exhibited moderately high abundance throughout the regenerating forest. However, on the adjacent uncut reference watershed (W6), ACSA has shown clear signs of recent decline and regeneration failure particularly at higher elevations. The application of Ca on nearby watershed (W1) in an amount calibrated to replace that lost during the 20th century, largely corrected the decline of ACSA (Juice et al. 2006, Battles et al. 2014). Surveys of tree regeneration at HBEF supported the claim that soil acidification has tipped the competitive balance between ACSA and FAGR towards the latter species (Marlow and Peart 2014, Pontius et al. 2016).

The overall objective of the present study was to evaluate the long-term effects of clearcutting (in this case, whole tree harvesting, WTH) on forest recovery in a northern hardwood watershed. The study takes advantage of two long-term (30-year) surveys of forest composition following WTH of W5 at HBEF. One set of surveys documents the overall forest composition across the complex environmental gradient in this 21.9 ha watershed at scales chosen to accommodate the shifting tree density in the growing forest; the other follows the changes of individual stems mapped at the 0.25 m^2 scale, thereby facilitating long-term observation of the outcome of competitive interactions. In conjunction with this vegetation work detailed measurements of soil chemistry were conducted using the quantitative soil pit method across the entire watershed in 1983 (pre-harvest), 1986, 1991 and 1998, providing evidence of treatment effects on soil base cation status. Moreover, a comparison with strip clearcutting on the adjacent watershed (W4; cut in 1970-1974) provides some basis for judging the possible effects of increased harvest intensity associated with WTH on long-term forest recovery.

The detailed record of repeated observations in the present study provides a robust quantification of patterns as well as limited insights into the underlying processes. In particular, we can evaluate the extent to which early establishment promotes future species dominance (Connell and Slatyer 1977, Fukima 2015). These "priority effects" were assumed to be critical to community assembly following WTH. Thus, an emphasis of the W5 study was on understanding the factors that contribute to successful plant colonization (Hughes and Fahey 1991, Mou et al. 1993). Now, 30 years post-harvest, we test this assumption by evaluating the comparative ability of the mature forest dominants, ACSA and FAGR, to hold spaces that they colonized initially. We further investigate the possible modification of any priority effects by an abiotic factor (elevation) and a biotic factor (mode of stem origin: seed, vegetative sprout, advance regeneration). Based on initial patterns of colonization by a mixture of ACSA, FAGR, yellow birch (*Betula alleghaniensis* Britt., BEAL) and a short-lived pioneer, pin cherry (*Prunus pensylvanica* L., PRPE) (Mou et al. 1993), we expected a similar long-term outcome across most of the watershed owing to priority effects. However, we also expected a combination of high leaching losses and tree nutrient sequestration to deplete soil Ca supplies, especially at the higher elevation zones of the watershed where we hypothesized that FAGR might thereby outperform ACSA. Finally, we hypothesized that these patterns of vegetation recovery would be quantitatively similar on W5 and W4, assuming that the added effects of WTH on nutrient supplies would not be sufficient to drive major differences.

Methods

Study site. The treated watershed, denoted as W5, is located in the HBEF in central New Hampshire. At the HBEF, precipitation averages 1,395 mm (std. dev. = 189 mm) per year, part of which is captured in snow pack persisting from December until April. The mean annual temperature is 5.5 °C (std. dev = 0.61°C); daily average temperatures range from -8.5°C in January to 18.8°C in July (Bailey et al. 2003). The soils are moderately well-drained Spodosols (Haplorthods) and Inceptisols (Dystrochrepts) of sandy-loam texture formed from glacial till. There is a high degree of spatial variability in the experimental watersheds with shallower, more acidic soils at higher elevations (Johnson et al. 2000). These soils exhibit a pattern common in mountainous forest landscapes throughout the Northeastern United States, with low rates of Ca supplied by weathering, and the effects of acidic deposition on soil base status intensifing with increasing elevation (Cho et al. 2012)

W5 is 21.9 ha in area and spans an elevation gradient from 488 to 762 m. Our research focused on the lower 85% of the watershed, which is dominated by species characteristic of the northern hardwood forest, namely ACSA, FAGR and BEAL. Prior to harvest, W5 was gridded into 360 cells, each 25m by 25m (**Fig. S1**). Tree composition and size structure were measured prior to harvest in 1982 and then periodically post-harvest starting in 1990 (see **Tree surveys**). Eight of the 360 cells within the northern hardwood zone were designated as intensive permanent plots to monitor the details of vegetation recovery (“**Stem origin plots”**; Hughes 1986). During the autumn and winter of 1983-1984, all trees > 2 cm diameter at breast height (DBH; 1.37 m) were cut. Stems greater than 10 cm DBH were removed except trees on the steepest terrain which were cut and dragged off the watershed.

Stem origin plots. Each of the eight stem origin plots (25 m by 25 m) was gridded into 25 5m by 5 m (25 m^2) “sections” (**Fig. S1**). Twenty-five of the 200 25 m^2 sections were randomly selected and further divided into 25 1 m^2 permanent plots for intensive study of regeneration (625 1 m^2 plots total, **Fig. S1**). In 1983 (pre-harvest), tallies were taken of all stems in the understory in the 25 m^2 sections (**Table S1**). Stem density in the then-intact forest was relatively low, making it unnecessary to survey at the 1 m^2 scale. Following the harvest, soil disturbance and all vegetation (trees, shrubs, herbs) were surveyed at 0.5 x 0.5 m scale (Hughes 1986; Mou et al. 1993). Initial post-harvest patterns were reported previously (Hughes 1986; Hughes and Fahey 1991; Mou et al. 1993). Stems in the stem origin plots were surveyed 13 times in the 30 years post-harvest: 1984-1989; 1994-1997; 2001, 2003 and 2014/2015 (**Table S1**). These detailed plots provided a record of the species and origin of all stems. The origin of each stem was assigned to one of three classes: advance regeneration, vegetative sprout, or seed; advance regeneration was defined as stems established in the understory and present prior to WTH. Sprouts were differentiated by their attachment to stumps or large roots, as well as their thicker bases and lack of cotyledon scars.

Tree surveys. The sampling strategy to monitor the tree stratum across the entire watershed varied through time to accommodate changes in tree size and stem density. Despite differences in some details, the tree surveys each year were randomly distributed across W5 and always included more than 1,300 individual tree measurements. Prior to harvest, in 1982, all trees ≥ 10 cm in diameter at breast height (1.37 m, DBH) were identified and measured in every grid cell across the entire watershed. Post-harvest, the extent of area sampled and the size of trees measured were designed to capture the variation in the tree community across W5 separately from the stem-origin permanent plots. The first post-harvest tree survey in 1990 defined the tree stratum as trees ≥ 1.5 cm DBH, and composition and abundance were assessed in 199 transects, each 1m by 25 m in area. The 1994, 1999, and 2004 surveys measured trees ≥ 1.5 cm DBH in transects on a random subset (38 in 1994; 101 in 1999 and 2004) of the 360 grid cells. In 2009 and 2014, tree surveys consisted of circular plots located in the same 101 grid cells used in 1999 and 2004, with trees sampled in two size classes; all individuals ≥ 7.5 cm DBH were measured in the 100 m^2 circular plots, while smaller trees (1.5cm ≤ DBH < 7.5 cm) were measured in a nested 30 m^2 transect.

Soil sampling. Soils were sampled before (1983) and 3 yr (1986), 8 yr (1991) and 15 yr (1998) after forest harvest, each time in July. A quantitative pit method, described in detail by Johnson et al. (1991a), was employed, with 9 to 15 pits located randomly across the three hardwood-dominated elevation zones (lower = 500-560 m; mid = 560-610 m; upper = 610-670 m). Several soil layers were separated in the field, with the focus in the present study on the densely-rooted Oa horizon and the 0-10 cm mineral soil layer. Soil samples were air-dried to constant weight and sieved through either a 5-mm (Oa horizon) or a 2-mm (mineral soil) screen. For determination of exchangeable cations, 2.5 g of air-dried soil was extracted with 50 mL of 1 M NH_4Cl for 12 h by mechanical vacuum extraction. Element concentrations in extracts were determined by ICP optical-emission spectrometry.

After the NH_4Cl extraction, samples were washed with ethanol for 1 h, then extracted with 1 M KCl for 12 h. Effective cation exchange capacity (CEC) was then determined by analyzing the KCl extract for NH_4 colorimetrically using a continuous-flow analyzer (USEPA, 1983). Percent soil base saturation was calculated as the ratio of the sum of exchangeable base cations to CEC (Johnson et al. 1991b). Effects of sampling year (1983, 1986, 1991, 1998) and elevation zone (low, mid, high) on base saturation and exchangeable Ca were evaluated with a general linear model in Minitab (version 17, Minitab, Inc., State College, PA).

Vegetation analysis. Our vegetation analysis focused on quantifying the factors determining tree establishment and persistence. For context, we provide an overview of the watershed-wide pattern of changes in forest composition. For our more specific questions regarding the drivers of change, we used generalized linear mixed models where the fixed effects included time since harvest, and the random effects accounted for spatial correlation (Bolker et al. 2009). We also conducted multinomial logistic regression (*sensu* Augustin et al. 2001) to test the factors that affected the persistence of species after establishment post-harvest. We compared model performance using an information theoretic approach (Burnham and Anderson 2002).

For each model, we calculated Akaike's information criterion (AIC), differences in AIC values relative to the model with the lowest AIC (ΔAIC), and AIC weights (w_i). Akaike weights (w_i) were calculated to normalize the strength of evidence for a given model and can be interpreted as the probability that a given model is the best Kullback–Leibler model for the data given the candidate set of models; models < 2ΔAIC have substantial empirical support (Burnham and Anderson 2002). Analyses were conducted using JMP Pro 11 for Windows (SAS Institute. Cary, NC) and the R statistical computing environment version 3.3.0 (R Core Team 2016).

Post-harvest changes in density (stems m^{-2}) of five species over time (1984-2014) were compared with a linear mixed model. To decrease the number of zero counts, stem counts were averaged from all the 1 m^2 stem origin plots surveyed in the section (i.e. seven 25 m^2 sections per elevation zone; **Table S1**). The average density per section was then log transformed to normalize the distribution of residuals. To account for spatial autocorrelation, section was included as a random effect. To account for repeated measures, year was nested within section. The fixed effects were: species (5 species), elevation zone (three classes defined as lower, mid and upper, as for soil sampling), year (as a continuous variable; 13 years) and all two and three-way interactions. The trend in stem densities over time suggested that the relationship was quadratic rather than linear; hence, the term $year^2$ was also included in the model. The best model was selected from these candidate models using ΔAIC and w_i.

We tested whether initial establishment post-harvest (1984, year 1) predicted future persistence 30 years later (2014, year 30). For each of the 1 m^2 stem origin plots, we determined the dominant species in 1984, which we refer to as the "winner" species for the plot. Dominance was defined both by stem density and stem origin. In plots showing clear dominance of one species on the basis of stem density that species was assigned as the initial "winner". In plots with similar stem densities for more than one species, the stem origins were used to determine dominance in the order: advance regeneration > sprouts > seedlings to account for size differences between stems of different origin. Using the same criteria, we assigned species dominance in 2014 for each stem origin plot. However, ties in 2014 were determined on the basis of canopy position with field checks in spring 2015; the taller species was assigned the "winner". Some plots in both time periods (1984, 2014) were recorded as ties; in these cases, plots had more than a single species assigned as "winner". With these assignments, we calculated the probability of species persistence given successful colonization (i.e. probability that the species that won the plot in 1984 also won the plot in 2014).

Our analysis focused on the species that make-up the mature northern hardwood forest namely ACSA, FAGR, and *Betula* spp. (BETU). We lumped all the birch species (BEAL; gray birch, *Betula populifolia* Marsh.; paper birch, *B. papyrifera* Marsh*.;* and mountain paper birch, *B. cordifolia* Regel) to genus level because of the difficulty of distinguishing young specimens of these species. Stem origin plots with no tree species present or only pin cherry (PRPE; a pioneer species that rarely persists in the forest past 30 years) were classified as NONE. The class of OTHER species was dominated by striped maple (*Acer pensylvanicum* L., ACPE), an understory tree species (Hibbs et al. 1980).

To account for the spatial autocorrelation in the post-harvest recruitment of ACSA and FAGR (Nelson and Wagner 2014), the distance from each plot to a common origin (location of the weir at the base of W5) was calculated. We developed the set of candidate models to evaluate using multinomial logit regression. The base model predicted plot dominance in 2014 simply as a function of plot dominance in 1984. Additional models included elevation class and distance as main effects and with interactions. For ACSA and FAGR, we used the same approach to test the probability of persistence in 2014 given the origin (seed, sprout, or advance regeneration) of the dominant stem in 1984.

Results

Prior to harvest, the northern hardwood forest on W5 (**Fig. 1**) supported on average 26.9 $m^2 ha^{-1}$ (SE = 0.39 $m^2 ha^{-1}$) of live tree basal area. Sugar maple accounted for almost half of the tree basal area (47%) followed by BETU (25%, mostly BEAL) and FAGR (20%). The forest composition varied somewhat among elevation zones (**Table 1**). Tree density increased with elevation with no detectable change in basal area. The abundance of ACSA, as measured by relative basal area, increased with elevation; BETU declined; and FAGR reached its maximum at higher elevations. Based on the watershed-scale post-harvest surveys the forest had recovered only 21% of its pre-harvest basal area by 1990, seven years post-harvest. By 2014, basal area approached pre-harvest levels (**Fig. 1A**). In contrast, ACSA was a minor component of the post-harvest forest, accounting for < 5% of the basal area (**Fig. 1B**). In 2014 the forest was dominated by BETU (59%) and FAGR (16%).

In the stem origin plots, tree density reached a maximum of 26 stems m^{-2} (SE = 1.1 stems m^{-2}) two years (1984) after harvest (**Fig. 2A**). From this peak, density declined steeply until stabilizing at approximately 3-5 stems m^{-2} after 1996. The temporal pattern in species composition observed in the watershed-scale surveys was matched by the changes observed in the stem origin plots (**Fig. 2B**). Specifically, following a transient proliferation and decline in years 1 to 4, relative density of BETU gradually increased from 1987 to 2014; FAGR remained roughly constant through time, and relative density of ACSA declined steadily after 1994. Also evident at both sampling scales was the rapid recruitment response of PRPE post-harvest followed by steady decline. PRPE was the most abundant species in 1987 (**Fig. 2B**) and accounted for the majority of the live tree basal area in 1990 (59%, **Fig. 1B**) but by 2014 PRPE comprised of only one-tenth of the trees as measured by both density (**Fig. 2B**) and basal area (**Fig. 1B**).

Despite the similarity in the overall pattern in tree density with time since harvest, there were distinct differences among species and across elevations (**Fig. 3**). There was overwhelming support (w_i =1) for the full statistical model of tree density that included a quadratic response by year and interactions among species, elevation class, and year (**Table S2**). The influence of elevation class on abundance was particularly striking for ACSA. Using the parameters from the best model of tree density, we estimated the trend in tree density after harvest for the dominant species (ACSA, FAGR, BETU) in each elevation class (**Fig. 4**). While as expected the density declined over time for all species at all elevations, the decrease in density for ACSA was greatest at upper elevation and least at lower elevation.

Both elevation class and distance from the base of the watershed influenced the probability of persistence of stems established in 1984. Both the best model (#4 in Table S3, w_i = 0.56) and the second best model (#10, w_i = 0.43) included elevation class and distance. To examine the species differences, we predicted persistence probabilities using the best model.

Overall, the probability that a plot that was won by ACSA in 1984 was still dominated by ACSA in 2014 was 0.16 (**Table 2**). In contrast, FAGR had a probability of 0.70 of retaining dominance. Sugar maple persistence was strongly related to elevation with the probability of persistence declining sharply with elevation (**Table 2**). American beech persistence also was reduced in the upper elevation class. BETU won relatively few plots in 1984 but in 2014 dominated most of the plots at the upper elevation. The coefficients for the distance term suggest spatial autocorrelation for persistence probability of ACSA and FAGR but not for BETU.

The lack of persistence in plots won by ACSA in 1984 was not entirely driven by replacement by another species. For example, of the plots won by ACSA in 1984, the probability of FAGR winning in 2014 was 0.37 while the next most common fate (probability = 0.31) was that the plot simply remained unoccupied or was temporarily held by PRPE (NONE; **Table 2**).

Immediately post-harvest, the origin of stems varied by species. Most of the BETU initiated from seed. The majority (55%) of ACSA stems also grew from seeds, with sprouting accounting for only 16% of the recruits. In contrast, 65% of the FAGR stems originated from sprouts, with only 13% beginning as seeds.

The origin of the stems establishing in 1984 was a strong predictor of persistence in 2014 for ACSA but not for FAGR. For the subset of plots won by ACSA in 1984 (n = 175), the best model (#6; **Table S4**) included only origin (w_i = 0.72). Based on predictions from the best model, stems that originated as sprouts had the highest probability of persistence in 2014 (0.32) followed by advance regeneration (0.12) and then seeds (0.03). In contrast, origin was not included in the best model (#3) for the subset of plots won by FAGR in 1984 (n = 117, **Table S5**).

Surface soil chemistry in the hardwood forest varied both across years and elevation zones (**Table 3**). In particular, exchangeable Ca in the Oa horizon differed significantly both among elevation zones and sampling years (**Table S6**), with lowest values in the upper elevation zone in post-harvest years (**Table 3**). Base saturation also was lowest in the upper elevation zone post-treatment, but the year effect was not significant. No significant year by treatment interactions were detected for either base saturation or exchangeable Ca. Although patterns for the 0-10 cm mineral soil were similar, with the lowest values post-harvest in the upper elevation zone (**Table 3**), none of the effects was statistically significant (**Table S6**).

Discussion

Recovery of the northern hardwood forest following WTH of W5 at the HBEF demonstrated sustained capacity for growth in basal area but a striking change in species composition through 30 years. Most importantly for ACSA, the dominant species prior to treatment, initially high abundance was followed by a drastic decline in relative density and basal area so that ACSA has been relegated to be a minor species in the recovering forest (**Figs 1** and **2**). Detailed observations in permanent plots indicated that the decline in abundance of ACSA was associated with a combination of biotic (competition from FAGR) and abiotic (elevation) factors.

Overall, FAGR was four times as likely as ACSA to persist as the dominant species in a location (**Table 2**). Intriguingly, ACSA was almost as likely to lose its spot to FAGR as for the spot to become unoccupied. This observation supports the hypothesis of Kardol et al. (2013) that priority effects for some species (in this case ACSA) may be weakened on infertile soils and suggests that ACSA was limited not only by competition with FAGR and BETU, but also by abiotic factors (probably low soil Ca). Elevation was the strongest modifier of priority effects, weakening these effects for both ACSA and FAGR and allowing the eventual domination of upper elevation by BETU, which came in a year after harvest (**Fig. 3**) following high seed production in 1985.

Although we cannot conclusively disentangle elevation-based climatic and soil effects in driving the performance of ACSA on W5, it is likely that the thin, base-poor soils in the upper elevations played a primary role. The elevation range of the northern hardwood forest on W5 (500-660 m) falls squarely within the climatic envelope of ACSA (Canham and Murphy 2016). Regeneration of ACSA is clearly limited by low soil Ca availability at the HBEF, as illustrated by observations from an adjacent watershed (W1), where experimental replacement of Ca lost as a result of human activity in the 20th century corrected both regeneration failure (Juice et al. 2006) and mature ACSA growth and health (Battles et al. 2014). Thus, the correspondence between poor performance of ACSA (**Fig. 2**) and low soil base saturation and exchangeable Ca concentration in surface soils in upper elevation zones (**Table 3**) is likely a causal relationship.

The finding that forest clearcutting, which increases light availability dramatically, did not favor ACSA over FAGR agrees with observations made by Bannon et al. (2015) on sites poor in base cations in Quebec. Our study lends further support for a threshold of soil base saturation or exchangeable Ca for successful ACSA regeneration (Sullivan et al. 2013). Thus, without soil amendments, efforts to remove the beech sapling layer may not lead to successful regeneration of ACSA on acidified soils. In contrast, on richer sites control of FAGR often will be necessary for the successful regeneration of ACSA following harvest (Nolet et al. 2008, 2015).

For ACSA, low survival of seedlings emphasized the importance of maintaining sprouts and advance regeneration in forest management activities. Sugar maple seedlings would draw their nutrients largely from the organic soil horizons. It is notable therefore that these low seedling survival rates coincided with significant decreases in exchangeable Ca concentrations and base saturation in Oa horizon soils, especially in mid- and upper-elevation hardwood zones (**Tables 3, S6**). Johnson et al. (1997) noted that losses of cations from upper soil horizons on W5 would lead to an advantage for growth of advance regeneration and sprouts as they have roots that penetrate to deeper soil layers. This may also be part of the mechanism explaining the greater ability of FAGR to persist in sites where it established because 65% of the initial stems were sprouts.

Widespread dieback of ACSA has been associated with nutrient stress throughout its northern range (Bal et al. 2015), and Ca limitation of ACSA regeneration, growth and health has been commonly observed on base-poor and Ca-depleted soils (Long et al. 1997; Schaberg et al. 2006; Battles et al. 2014). Further depletion of soil Ca pools and availability associated with forest harvest is likely to result in reduced abundance and growth of ACSA in post-harvest stands on acidified soils. In New England, the problems for ACSA are particularly severe at higher elevations (Juice et al. 2006, Pontius et al. 2016) primarily because of thinner, base-poor soils. Notably, ACSA often thrives near its elevation limits (ca. 800 m at Hubbard Brook) on base-rich soils (S. Bailey, personal observation). Thus, potential upward expansion of the elevation range of ACSA in a warming climate is likely to be constrained by low soil base status associated with natural edaphic patterns, limited competitive ability for mineral nutrient acquisition in conifer-dominated areas (Collin et al. 2017), and with depletion by atmospheric deposition and forest management.

The WTH treatment on W5 was motivated in part by concern that nutrient removal by the practice might represent a greater threat to soil fertility and forest recovery than conventional harvest (Weetman and Webber 1972). Long-term observations following strip clearcutting of the adjacent W4 at HBEF (Thurston et al. 1992, A. Bailey, unpublished data) indicate less extreme but qualitatively similar regeneration results as for W5. In particular, on a watershed-wide basis relative basal area of ACSA on W4 prior to harvest averaged 30% and was 8% at 30 yr post-harvest (compared with W5: 47% pre-harvest and 5% after 30 yr). Notably, ACSA had the most severely reduced abundance in the higher elevation zone of W4 similar to the pattern we observed on W5. Therefore, although the strip clearcutting on W4 resulted in less removal of base cations from the site both as timber products (only boles were removed) and in stream water (Hornbeck et al. 1986), soil nutrient depletion was apparently still sufficient to limit the success of ACSA.

Our observations raise an intriguing question: what explains the high abundance of ACSA on the naturally base-poor soils of HBEF, especially at higher elevations where its regeneration and regrowth are clearly impaired (Battles et al. 2014, **Fig. 4**)? Regional comparisons of historic and modern forest composition indicate that the abundance of ACSA greatly increased between pre-settlement (early 19th century) and modern times in mid-elevation zones of the northeastern US mountains (Siccama 1971, Vadeboncouer et al. 2013) similar to HBEF. This increase coincided with a dramatic decline in the abundance of red spruce (*Picea rubens* Sarg.) owing in part to intensive logging for this species in the 19th century. At the HBEF, historical records (C.V. Cogbill, personal communication) indicate selective logging of red spruce in the late 19th century, followed by heavy cutting of all merchantable trees between 1908-1920 and some salvage cutting following blowdown by the 1938 hurricane (van Doorn et al. 2011). This combination of disturbances appeared to strongly favor ACSA in the experimental (south-facing) watersheds, including W5. Based on the sensitivity of ACSA regeneration to low soil Ca availability (Long et al. 1997, Juice et al. 2006), one possible explanation for increase in ACSA early in the 20th century is the higher soil Ca supply at that time. Notably, atmospheric deposition of Ca was several-fold higher in the first half of the 20th century than at present (Junge and Werby 1958, Likens et al. 1998) and presumably also during pre-settlement times, as a result of rapidly increasing cement production, fossil fuel burning without emission controls, and transport of dust from more-abundant unpaved roads. Thus, we surmise that ACSA performance may have been promoted by enriched soil Ca and the decline of red spruce, and is currently strongly disfavored by soil base cation depletion and competition from FAGR.

Finally, the suggestion by several authors (Marlow and Peart 2014, Pontius et al. 2016) that the competitive relationship between ACSA and FAGR has shifted toward FAGR under the legacy of acidified soils was supported in this study and importantly, clearcutting appears to promote this disparity. Forest managers seeking to favor ACSA regrowth should retain significant advance regeneration of this species and consider soil amendments when feasible.

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Table 1. Elevational gradient in pre-harvest forest composition (A) and species distribution (B) in Watershed 5 at Hubbard Brook Experimental Forest, NH. Means and standard errors (se) reported for each elevation zone; n represents the number of tree survey plots in each zone. Species distribution reported as relative basal area.

A. Forest composition		Basal area (m^2 ha^{-1})		Density (stems ha^{-1})	
	N	mean	se	mean	se
Lower hardwood	49	27.3	0.8	425	14
Mid hardwood	67	27.3	0.8	424	13
Upper hardwood	79	26.8	0.6	518	17

B. Relative basal area	ACPE	ACSA	BETU	FAGR	PRPE
Lower hardwood	0.00	0.40	0.32	0.17	0.00
Mid hardwood	0.00	0.48	0.25	0.20	0.00
Upper hardwood	0.01	0.51	0.22	0.20	0.00

Table 2. Predicted persistence probabilities by species and by elevation class for Watershed 5 at Hubbard Brook Experimental Forest, NH. For these estimates, distance set to the mean.

		Winners in 2014				
Low		ACSA	BETU	FAGR	NONE	OTHER
Winners in 1984	ACSA	0.39	0	0.15	0.30	0.16
	BETU	0.13	0	0.26	0.41	0.20
	FAGR	0.16	0	0.50	0.23	0.11
	NONE	0	0	0	1	0
	OTHER	0.39	0	0.18	0.30	0.13
Mid		ACSA	BETU	FAGR	NONE	OTHER
Winners in 1984	ACSA	0.09	0.21	0.27	0.39	0.04
	BETU	0.01	0.54	0.20	0.22	0.02
	FAGR	0.02	0.27	0.52	0.17	0.01
	NONE	0	0.74	0	0.26	0
	OTHER	0.08	0.28	0.28	0.34	0.03
Upper		ACSA	BETU	FAGR	NONE	OTHER
Winners in 1984	ACSA	0	0.98	0.01	0.02	0
	BETU	0	0.99	0	0	0
	FAGR	0	0.98	0.01	0.01	0
	NONE	0	1	0	0	0
	OTHER	0	0.98	0.01	0.01	0
All		ACSA	BETU	FAGR	NONE	OTHER
Winners in 1984	ACSA	0.16	0.06	0.37	0.31	0.09
	BETU	0.04	0.19	0.43	0.27	0.07
	FAGR	0.04	0.08	0.70	0.14	0.03
	NONE	0	0.47	0	0.53	0
	OTHER	0.14	0.07	0.45	0.25	0.08

Table 3. Soil base saturation and exchangeable calcium concentration in three elevation zones and two soil horizons on Watershed 5 at the Hubbard Brook Experimental Forest, NH before (1983) and after (average for 1986,1991,1998) whole tree harvest. Results of general linear model for elevation and treatment effects can be found in Table S6.

Elevation Zone	**Soil depth**	**% Base saturation**		**($cmol_c$/kg) Exchangeable Ca**	
		Pre-trt	**Post-trt**	**Pre-trt**	**Post-trt**
Lower	Oa	56.6	53.1	8.43	7.41
hardwood	0-10 cm	14.0	18.0	0.89	0.96
Mid	Oa	47.3	44.6	6.78	4.83
hardwood	0-10 cm	14.4	16.9	0.79	1.02
Upper	Oa	53.7	40.4	7.89	4.61
hardwood	0-10 cm	15.7	14.4	0.98	0.89

Figure Legends

Figure 1. Shift in (**A**) total basal area and (**B**) relative basal area of most common tree species prior to and following whole tree harvest on Watershed 5 at Hubbard Brook Experimental Forest, NH. Data from tree surveys.

Figure 2. Changes in (**A**) tree density and (**B**) relative abundance of the most common tree species following whole-tree harvest on Watershed 5 at Hubbard Brook Experimental Forest, NH. Data from stem origin plots.

Figure 3. Trajectory of recovery in three elevation classes for sugar maple (ACSA), American beech (FAGR), birch species (BETU) and other species (mainly pin cherry and striped maple) for the first 30 years after whole-tree harvest on Watershed 5 at Hubbard Brook Experimental Forest, NH. Data from stem origin plots.

Figure 4. Modelled predictions of stem density change for sugar maple (ACSA), American beech (FAGR) and birch species (BETU) to illustrate species interactions with elevation class.

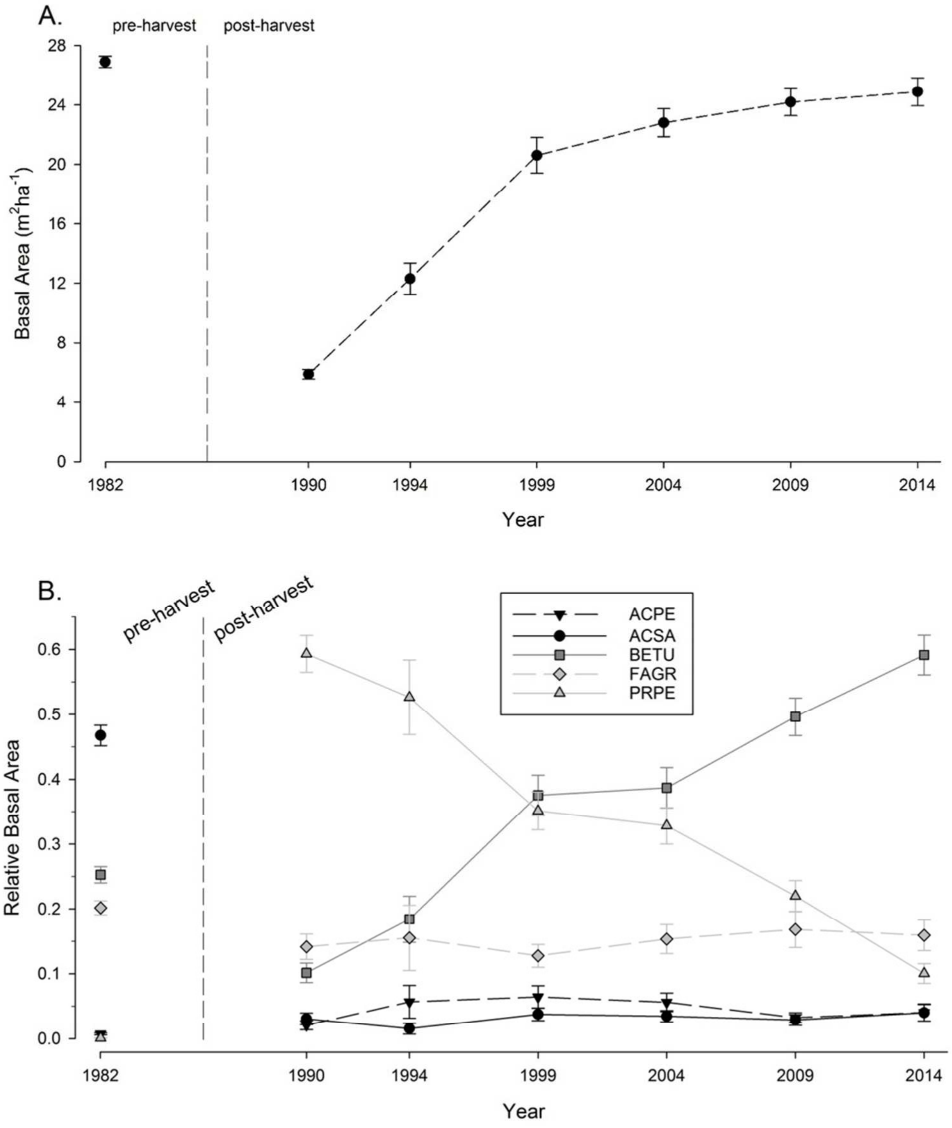

Figure 1

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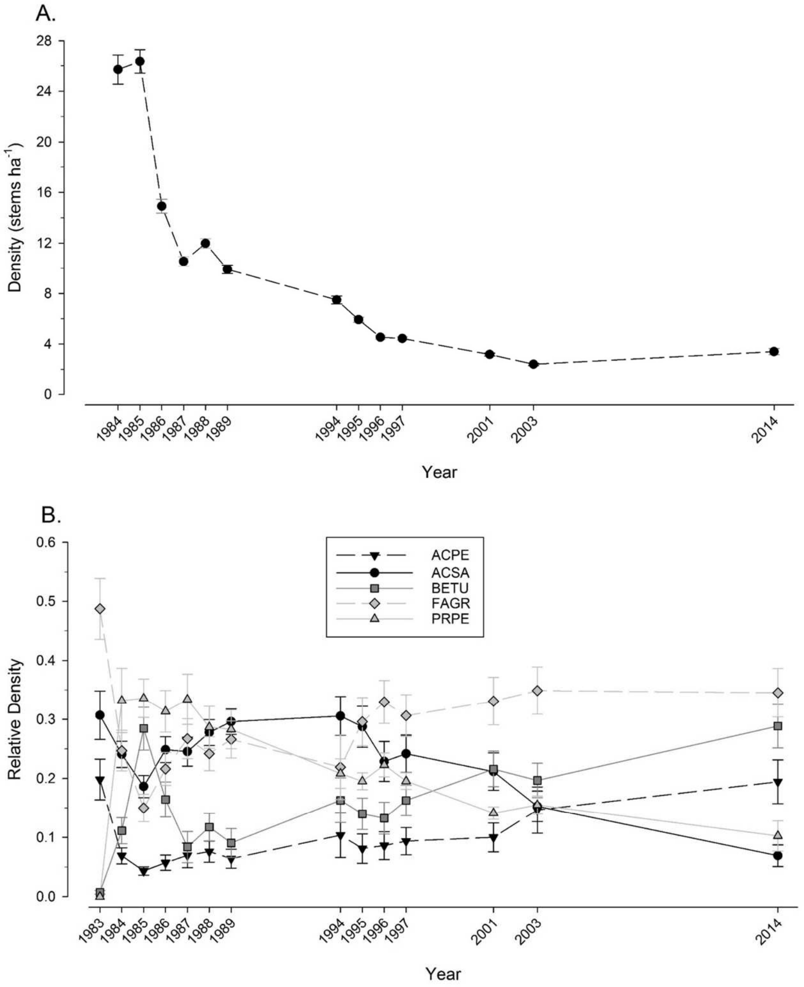

Figure 2

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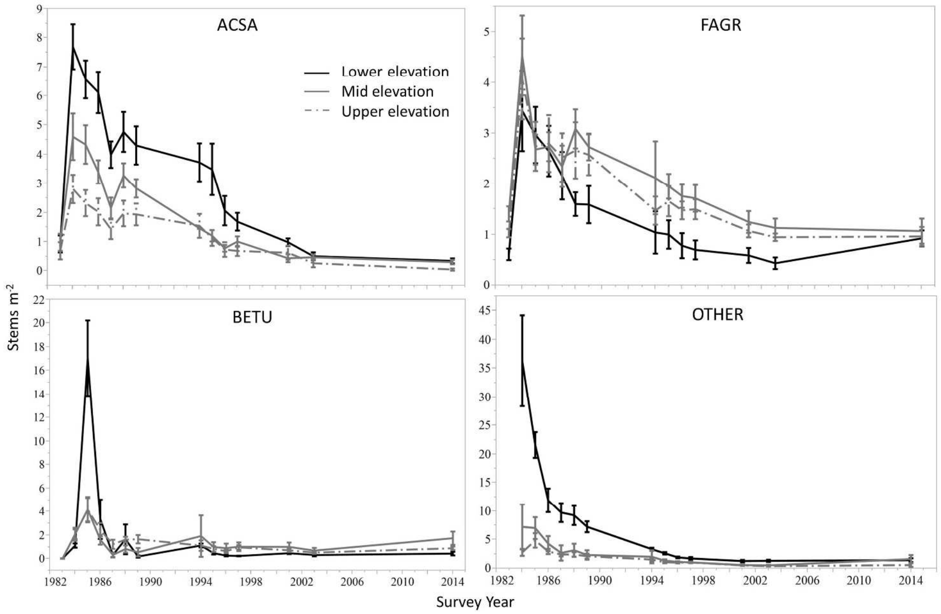

Figure 3

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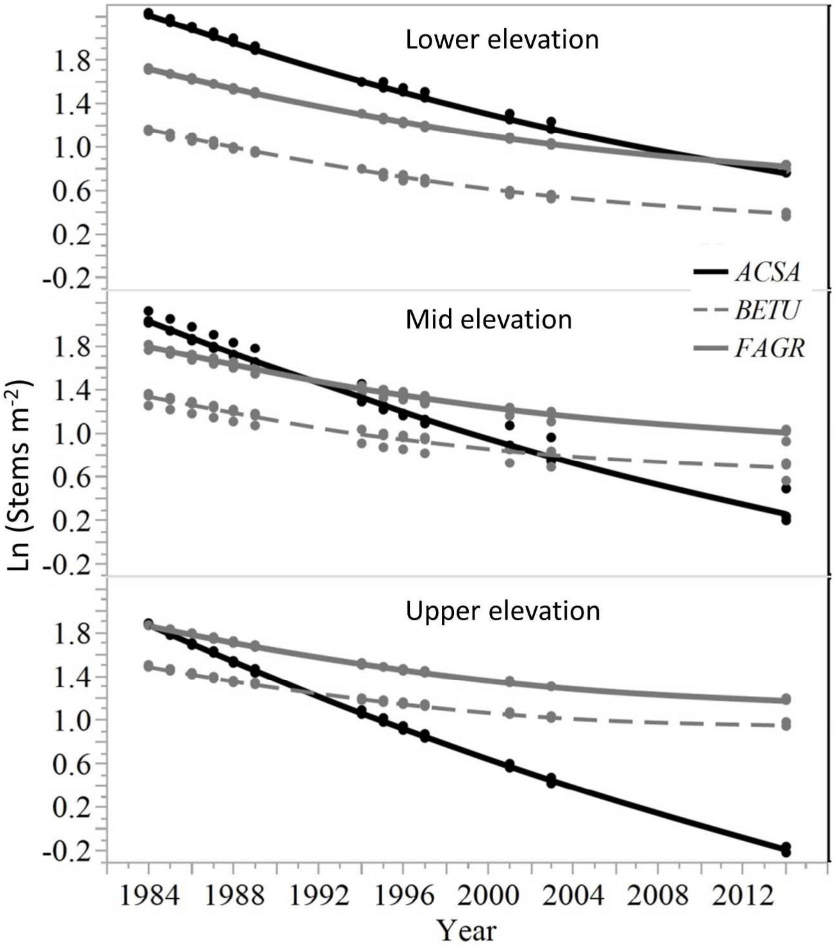

Figure 4

254x338mm (300 x 300 DPI)