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2 Long-term decline of sugar maple following forest harvest, Hubbard Brook

3 Experimental Forest, New Hampshire

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23 **Abstract.**

24 Forest harvesting can impact site quality by removing essential nutrients, exacerbating
25 effects of historic base cation losses associated with acid deposition. We studied the 30-year
26 trajectory of forest recovery from clearcutting (whole-tree harvest (WTH)) in a forest originally
27 dominated by sugar maple (*Acer saccharum*). At both the watershed-scale (21.9 ha) and
28 “detailed” plot-scale (1 m²), a dramatic decline of sugar maple was observed, along with
29 maintenance of American beech (*Fagus grandifolia*), and an increase in birch, mainly yellow
30 birch (*Betula allegheniensis*). Many of the “detailed” plots where sugar maple failed to recruit
31 became unoccupied rather than being “won” by another species. The decline of sugar maple
32 was most severe in the upper elevation zones of the watershed, where low base status (especially
33 Ca) of the soils was a likely driver. The results support previous studies indicating that
34 regeneration by sugar maple is severely compromised on base cation depleted soils. Lower
35 survival of seedlings for sugar maple emphasized the importance of maintaining advance
36 regeneration to favor desired species such as sugar maple. Foresters should consider that sites
37 with low base saturation and exchangeable Ca are likely to exhibit regeneration failure for sugar
38 maple in the long-term, even those with initial dominance by this species.

39
40 **Key words:** forest recovery, northern hardwood forest, priority effects, community assembly,
41 management implications

42 **Introduction**

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

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

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

68 The interaction between ACSA and FAGR following forest harvest has been the subject
69 of considerable research and appears to depend upon both light availability and soil base cation
70 supply. In understory environments FAGR is often favored over ACSA owing to its greater
71 tolerance of low light, whereas ACSA demonstrates a greater response in canopy openings
72 (Canham 1988, Beaudet et al. 1999). In Quebec, clearcut harvesting appeared to give ACSA an
73 advantage over FAGR because of benefits from greater light availability (Nolet et al. 2008,
74 2015). In addition, New Brunswick researchers have found that sites initially dominated by
75 ACSA are likely to regenerate into ACSA-dominated stands post-harvest (Beland and Chicoine
76 2013). However, Bannon et al. (2015) observed that on base-poor soils clearcutting did not favor
77 ACSA over FAGR, suggesting an interaction with soil Ca supply. In contrast, other studies from
78 Canada have demonstrated a high light advantage for ACSA (Nolet et al. 2008, 2015). There is a
79 growing literature debating the efficacy of FAGR control versus Ca amendment in managing for
80 ACSA regeneration (Nolet et al. 2015, Moore et al. 2015).

81 The present study at Hubbard Brook Experimental Forest (HBEF) was originally
82 undertaken to evaluate the effects of whole-tree harvest (WTH) on soil nutrient capital and
83 vegetation recovery at a site where detailed budgetary studies using the small-watershed
84 approach indicated substantial depletion of soil base cations during the 20th century (Likens et al.
85 1994). On these experimental watersheds, including Watershed 5 (W5), the subject of this study,
86 soil base cation pools decline significantly at higher elevations owing to thinner, more severely
87 depleted soils (Johnson et al. 2000), creating a natural contrast in soil fertility across the

88 landscape. Early surveys following WTH of W5 (Mou et al. 1993) indicated that ACSA, the
89 pre-harvest dominant, exhibited moderately high abundance throughout the regenerating forest.
90 However, on the adjacent uncut reference watershed (W6), ACSA has shown clear signs of
91 recent decline and regeneration failure particularly at higher elevations. The application of Ca
92 on nearby watershed (W1) in an amount calibrated to replace that lost during the 20th century,
93 largely corrected the decline of ACSA (Juice et al. 2006, Battles et al. 2014). Surveys of tree
94 regeneration at HBEF supported the claim that soil acidification has tipped the competitive
95 balance between ACSA and FAGR towards the latter species (Marlow and Peart 2014, Pontius et
96 al. 2016).

97 The overall objective of the present study was to evaluate the long-term effects of
98 clearcutting (in this case, whole tree harvesting, WTH) on forest recovery in a northern
99 hardwood watershed. The study takes advantage of two long-term (30-year) surveys of forest
100 composition following WTH of W5 at HBEF. One set of surveys documents the overall forest
101 composition across the complex environmental gradient in this 21.9 ha watershed at scales
102 chosen to accommodate the shifting tree density in the growing forest; the other follows the
103 changes of individual stems mapped at the 0.25 m² scale, thereby facilitating long-term
104 observation of the outcome of competitive interactions. In conjunction with this vegetation work
105 detailed measurements of soil chemistry were conducted using the quantitative soil pit method
106 across the entire watershed in 1983 (pre-harvest), 1986, 1991 and 1998, providing evidence of
107 treatment effects on soil base cation status. Moreover, a comparison with strip clearcutting on
108 the adjacent watershed (W4; cut in 1970-1974) provides some basis for judging the possible
109 effects of increased harvest intensity associated with WTH on long-term forest recovery.

110 The detailed record of repeated observations in the present study provides a robust
111 quantification of patterns as well as limited insights into the underlying processes. In particular,
112 we can evaluate the extent to which early establishment promotes future species dominance
113 (Connell and Slatyer 1977, Fukima 2015). These "priority effects" were assumed to be critical to
114 community assembly following WTH. Thus, an emphasis of the W5 study was on understanding
115 the factors that contribute to successful plant colonization (Hughes and Fahey 1991, Mou et al.
116 1993). Now, 30 years post-harvest, we test this assumption by evaluating the comparative ability
117 of the mature forest dominants, ACSA and FAGR, to hold spaces that they colonized initially.
118 We further investigate the possible modification of any priority effects by an abiotic factor
119 (elevation) and a biotic factor (mode of stem origin: seed, vegetative sprout, advance
120 regeneration). Based on initial patterns of colonization by a mixture of ACSA, FAGR, yellow
121 birch (*Betula allegheniensis* Britt., BEAL) and a short-lived pioneer, pin cherry (*Prunus*
122 *pensylvanica* L., PRPE) (Mou et al. 1993), we expected a similar long-term outcome across most
123 of the watershed owing to priority effects. However, we also expected a combination of high
124 leaching losses and tree nutrient sequestration to deplete soil Ca supplies, especially at the higher
125 elevation zones of the watershed where we hypothesized that FAGR might thereby outperform
126 ACSA. Finally, we hypothesized that these patterns of vegetation recovery would be
127 quantitatively similar on W5 and W4, assuming that the added effects of WTH on nutrient
128 supplies would not be sufficient to drive major differences.

129

130 **Methods**

131 **Study site.** The treated watershed, denoted as W5, is located in the HBEF in central New
132 Hampshire. At the HBEF, precipitation averages 1,395 mm (std. dev. = 189 mm) per year, part

133 of which is captured in snow pack persisting from December until April. The mean annual
134 temperature is 5.5 °C (std. dev = 0.61°C); daily average temperatures range from -8.5°C in
135 January to 18.8°C in July (Bailey et al. 2003). The soils are moderately well-drained Spodosols
136 (Haplorthods) and Inceptisols (Dystrochrepts) of sandy-loam texture formed from glacial till.
137 There is a high degree of spatial variability in the experimental watersheds with shallower, more
138 acidic soils at higher elevations (Johnson et al. 2000). These soils exhibit a pattern common in
139 mountainous forest landscapes throughout the Northeastern United States, with low rates of Ca
140 supplied by weathering, and the effects of acidic deposition on soil base status intensifying with
141 increasing elevation (Cho et al. 2012)

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

152 **Stem origin plots.** Each of the eight stem origin plots (25 m by 25 m) was gridded into
153 25 5m by 5 m (25 m²) “sections” (**Fig. S1**). Twenty-five of the 200 25 m² sections were
154 randomly selected and further divided into 25 1 m² permanent plots for intensive study of
155 regeneration (625 1 m² plots total, **Fig. S1**). In 1983 (pre-harvest), tallies were taken of all stems

156 in the understory in the 25 m² sections (**Table S1**). Stem density in the then-intact forest was
157 relatively low, making it unnecessary to survey at the 1 m² scale. Following the harvest, soil
158 disturbance and all vegetation (trees, shrubs, herbs) were surveyed at 0.5 x 0.5 m scale (Hughes
159 1986; Mou et al. 1993). Initial post-harvest patterns were reported previously (Hughes 1986;
160 Hughes and Fahey 1991; Mou et al. 1993). Stems in the stem origin plots were surveyed 13
161 times in the 30 years post-harvest: 1984-1989; 1994-1997; 2001, 2003 and 2014/2015 (**Table**
162 **S1**). These detailed plots provided a record of the species and origin of all stems. The origin of
163 each stem was assigned to one of three classes: advance regeneration, vegetative sprout, or seed;
164 advance regeneration was defined as stems established in the understory and present prior to
165 WTH. Sprouts were differentiated by their attachment to stumps or large roots, as well as their
166 thicker bases and lack of cotyledon scars.

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

179 and 2004, with trees sampled in two size classes; all individuals ≥ 7.5 cm DBH were measured in
180 the 100 m² circular plots, while smaller trees ($1.5\text{cm} \leq \text{DBH} < 7.5$ cm) were measured in a
181 nested 30 m² transect.

182 **Soil sampling.** Soils were sampled before (1983) and 3 yr (1986), 8 yr (1991) and 15 yr
183 (1998) after forest harvest, each time in July. A quantitative pit method, described in detail by
184 Johnson et al. (1991a), was employed, with 9 to 15 pits located randomly across the three
185 hardwood-dominated elevation zones (lower = 500-560 m; mid = 560-610 m; upper = 610-670
186 m). Several soil layers were separated in the field, with the focus in the present study on the
187 densely-rooted Oa horizon and the 0-10 cm mineral soil layer. Soil samples were air-dried to
188 constant weight and sieved through either a 5-mm (Oa horizon) or a 2-mm (mineral soil) screen.
189 For determination of exchangeable cations, 2.5 g of air-dried soil was extracted with 50 mL of 1
190 M NH₄Cl for 12 h by mechanical vacuum extraction. Element concentrations in extracts were
191 determined by ICP optical-emission spectrometry.

192 After the NH₄Cl extraction, samples were washed with ethanol for 1 h, then extracted
193 with 1 M KCl for 12 h. Effective cation exchange capacity (CEC) was then determined by
194 analyzing the KCl extract for NH₄ colorimetrically using a continuous-flow analyzer (USEPA,
195 1983). Percent soil base saturation was calculated as the ratio of the sum of exchangeable base
196 cations to CEC (Johnson et al. 1991b). Effects of sampling year (1983, 1986, 1991, 1998) and
197 elevation zone (low, mid, high) on base saturation and exchangeable Ca were evaluated with a
198 general linear model in Minitab (version 17, Minitab, Inc., State College, PA).

199 **Vegetation analysis.** Our vegetation analysis focused on quantifying the factors
200 determining tree establishment and persistence. For context, we provide an overview of the
201 watershed-wide pattern of changes in forest composition. For our more specific questions

202 regarding the drivers of change, we used generalized linear mixed models where the fixed effects
203 included time since harvest, and the random effects accounted for spatial correlation (Bolker et
204 al. 2009). We also conducted multinomial logistic regression (*sensu* Augustin et al. 2001) to test
205 the factors that affected the persistence of species after establishment post-harvest. We compared
206 model performance using an information theoretic approach (Burnham and Anderson 2002).

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

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

225 We tested whether initial establishment post-harvest (1984, year 1) predicted future
226 persistence 30 years later (2014, year 30). For each of the 1 m² stem origin plots, we determined
227 the dominant species in 1984, which we refer to as the "winner" species for the plot. Dominance
228 was defined both by stem density and stem origin. In plots showing clear dominance of one
229 species on the basis of stem density that species was assigned as the initial "winner". In plots
230 with similar stem densities for more than one species, the stem origins were used to determine
231 dominance in the order: advance regeneration > sprouts > seedlings to account for size
232 differences between stems of different origin. Using the same criteria, we assigned species
233 dominance in 2014 for each stem origin plot. However, ties in 2014 were determined on the
234 basis of canopy position with field checks in spring 2015; the taller species was assigned the
235 "winner". Some plots in both time periods (1984, 2014) were recorded as ties; in these cases,
236 plots had more than a single species assigned as "winner". With these assignments, we calculated
237 the probability of species persistence given successful colonization (i.e. probability that the
238 species that won the plot in 1984 also won the plot in 2014).

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

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

255

256 Results

257 Prior to harvest, the northern hardwood forest on W5 (**Fig. 1**) supported on average 26.9
258 $\text{m}^2 \text{ha}^{-1}$ ($\text{SE} = 0.39 \text{ m}^2 \text{ha}^{-1}$) of live tree basal area. Sugar maple accounted for almost half of the
259 tree basal area (47%) followed by BETU (25%, mostly BEAL) and FAGR (20%). The forest
260 composition varied somewhat among elevation zones (**Table 1**). Tree density increased with
261 elevation with no detectable change in basal area. The abundance of ACSA, as measured by
262 relative basal area, increased with elevation; BETU declined; and FAGR reached its maximum at
263 higher elevations. Based on the watershed-scale post-harvest surveys the forest had recovered
264 only 21% of its pre-harvest basal area by 1990, seven years post-harvest. By 2014, basal area
265 approached pre-harvest levels (**Fig. 1A**). In contrast, ACSA was a minor component of the post-
266 harvest forest, accounting for < 5% of the basal area (**Fig. 1B**). In 2014 the forest was dominated
267 by BETU (59%) and FAGR (16%).

268 In the stem origin plots, tree density reached a maximum of 26 stems m^{-2} ($\text{SE} = 1.1$ stems
269 m^{-2}) two years (1984) after harvest (**Fig. 2A**). From this peak, density declined steeply until

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

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

289 Both elevation class and distance from the base of the watershed influenced the
290 probability of persistence of stems established in 1984. Both the best model (#4 in Table S3, $w_i =$
291 0.56) and the second best model (#10, $w_i = 0.43$) included elevation class and distance. To
292 examine the species differences, we predicted persistence probabilities using the best model.

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

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

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

308 The origin of the stems establishing in 1984 was a strong predictor of persistence in 2014
309 for ACSA but not for FAGR. For the subset of plots won by ACSA in 1984 ($n = 175$), the best
310 model (#6; **Table S4**) included only origin ($w_1 = 0.72$). Based on predictions from the best
311 model, stems that originated as sprouts had the highest probability of persistence in 2014 (0.32)
312 followed by advance regeneration (0.12) and then seeds (0.03). In contrast, origin was not
313 included in the best model (#3) for the subset of plots won by FAGR in 1984 ($n = 117$, **Table**
314 **S5**).

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

323

324 **Discussion**

325 Recovery of the northern hardwood forest following WTH of W5 at the HBEF
326 demonstrated sustained capacity for growth in basal area but a striking change in species
327 composition through 30 years. Most importantly for ACSA, the dominant species prior to
328 treatment, initially high abundance was followed by a drastic decline in relative density and basal
329 area so that ACSA has been relegated to be a minor species in the recovering forest (**Figs 1** and
330 **2**). Detailed observations in permanent plots indicated that the decline in abundance of ACSA
331 was associated with a combination of biotic (competition from FAGR) and abiotic (elevation)
332 factors.

333 Overall, FAGR was four times as likely as ACSA to persist as the dominant species in a
334 location (**Table 2**). Intriguingly, ACSA was almost as likely to lose its spot to FAGR as for the
335 spot to become unoccupied. This observation supports the hypothesis of Kardol et al. (2013) that
336 priority effects for some species (in this case ACSA) may be weakened on infertile soils and
337 suggests that ACSA was limited not only by competition with FAGR and BETU, but also by

338 abiotic factors (probably low soil Ca). Elevation was the strongest modifier of priority effects,
339 weakening these effects for both ACSA and FAGR and allowing the eventual domination of
340 upper elevation by BETU, which came in a year after harvest (**Fig. 3**) following high seed
341 production in 1985.

342 Although we cannot conclusively disentangle elevation-based climatic and soil effects in
343 driving the performance of ACSA on W5, it is likely that the thin, base-poor soils in the upper
344 elevations played a primary role. The elevation range of the northern hardwood forest on W5
345 (500-660 m) falls squarely within the climatic envelope of ACSA (Canham and Murphy 2016).
346 Regeneration of ACSA is clearly limited by low soil Ca availability at the HBEF, as illustrated
347 by observations from an adjacent watershed (W1), where experimental replacement of Ca lost as
348 a result of human activity in the 20th century corrected both regeneration failure (Juice et al.
349 2006) and mature ACSA growth and health (Battles et al. 2014). Thus, the correspondence
350 between poor performance of ACSA (**Fig. 2**) and low soil base saturation and exchangeable Ca
351 concentration in surface soils in upper elevation zones (**Table 3**) is likely a causal relationship.

352 The finding that forest clearcutting, which increases light availability dramatically, did
353 not favor ACSA over FAGR agrees with observations made by Bannon et al. (2015) on sites
354 poor in base cations in Quebec. Our study lends further support for a threshold of soil base
355 saturation or exchangeable Ca for successful ACSA regeneration (Sullivan et al. 2013). Thus,
356 without soil amendments, efforts to remove the beech sapling layer may not lead to successful
357 regeneration of ACSA on acidified soils. In contrast, on richer sites control of FAGR often will
358 be necessary for the successful regeneration of ACSA following harvest (Nolet et al. 2008,
359 2015).

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

370 Widespread dieback of ACSA has been associated with nutrient stress throughout its
371 northern range (Bal et al. 2015), and Ca limitation of ACSA regeneration, growth and health has
372 been commonly observed on base-poor and Ca-depleted soils (Long et al. 1997; Schaberg et al.
373 2006; Battles et al. 2014). Further depletion of soil Ca pools and availability associated with
374 forest harvest is likely to result in reduced abundance and growth of ACSA in post-harvest
375 stands on acidified soils. In New England, the problems for ACSA are particularly severe at
376 higher elevations (Juice et al. 2006, Pontius et al. 2016) primarily because of thinner, base-poor
377 soils. Notably, ACSA often thrives near its elevation limits (ca. 800 m at Hubbard Brook) on
378 base-rich soils (S. Bailey, personal observation). Thus, potential upward expansion of the
379 elevation range of ACSA in a warming climate is likely to be constrained by low soil base status
380 associated with natural edaphic patterns, limited competitive ability for mineral nutrient
381 acquisition in conifer-dominated areas (Collin et al. 2017), and with depletion by atmospheric
382 deposition and forest management.

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

395 Our observations raise an intriguing question: what explains the high abundance of
396 ACSA on the naturally base-poor soils of HBEF, especially at higher elevations where its
397 regeneration and regrowth are clearly impaired (Battles et al. 2014, **Fig. 4**)? Regional
398 comparisons of historic and modern forest composition indicate that the abundance of ACSA
399 greatly increased between pre-settlement (early 19th century) and modern times in mid-elevation
400 zones of the northeastern US mountains (Siccama 1971, Vadeboncouer et al. 2013) similar to
401 HBEF. This increase coincided with a dramatic decline in the abundance of red spruce (*Picea*
402 *rubens* Sarg.) owing in part to intensive logging for this species in the 19th century. At the
403 HBEF, historical records (C.V. Cogbill, personal communication) indicate selective logging of
404 red spruce in the late 19th century, followed by heavy cutting of all merchantable trees between
405 1908-1920 and some salvage cutting following blowdown by the 1938 hurricane (van Doorn et

406 al. 2011). This combination of disturbances appeared to strongly favor ACSA in the
407 experimental (south-facing) watersheds, including W5. Based on the sensitivity of ACSA
408 regeneration to low soil Ca availability (Long et al. 1997, Juice et al. 2006), one possible
409 explanation for increase in ACSA early in the 20th century is the higher soil Ca supply at that
410 time. Notably, atmospheric deposition of Ca was several-fold higher in the first half of the 20th
411 century than at present (Junge and Werby 1958, Likens et al. 1998) and presumably also during
412 pre-settlement times, as a result of rapidly increasing cement production, fossil fuel burning
413 without emission controls, and transport of dust from more-abundant unpaved roads. Thus, we
414 surmise that ACSA performance may have been promoted by enriched soil Ca and the decline of
415 red spruce, and is currently strongly disfavored by soil base cation depletion and competition
416 from FAGR.

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

422

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433

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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	N	Basal area (m ² ha ⁻¹)		Density (stems ha ⁻¹)	
		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
<hr/>						
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
<hr/>						
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
<hr/>						
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	%		(cmol _c /kg)	
		Pre-trt	Post-trt	Pre-trt	Post-trt
Lower hardwood	Oa	56.6	53.1	8.43	7.41
	0-10 cm	14.0	18.0	0.89	0.96
Mid hardwood	Oa	47.3	44.6	6.78	4.83
	0-10 cm	14.4	16.9	0.79	1.02
Upper hardwood	Oa	53.7	40.4	7.89	4.61
	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.

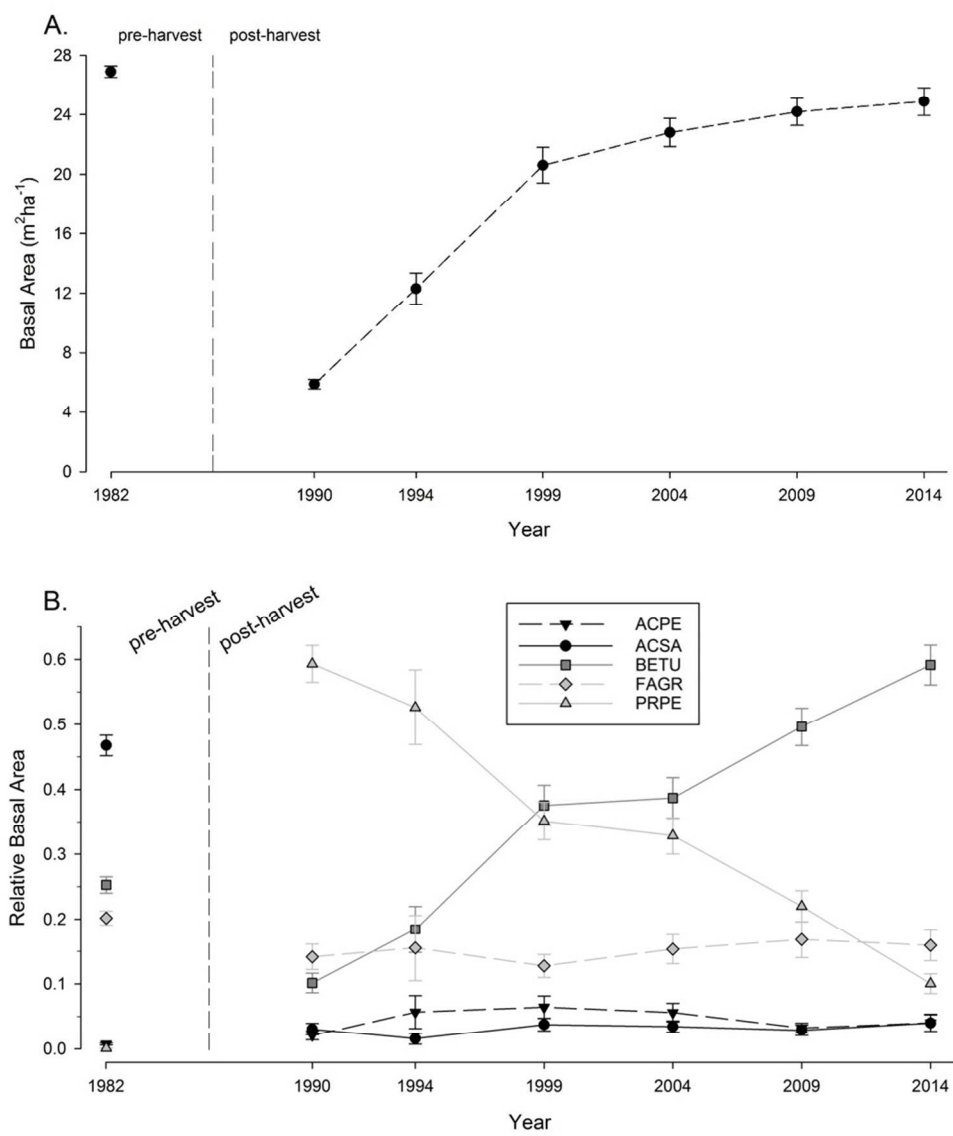


Figure 1

184x210mm (150 x 150 DPI)

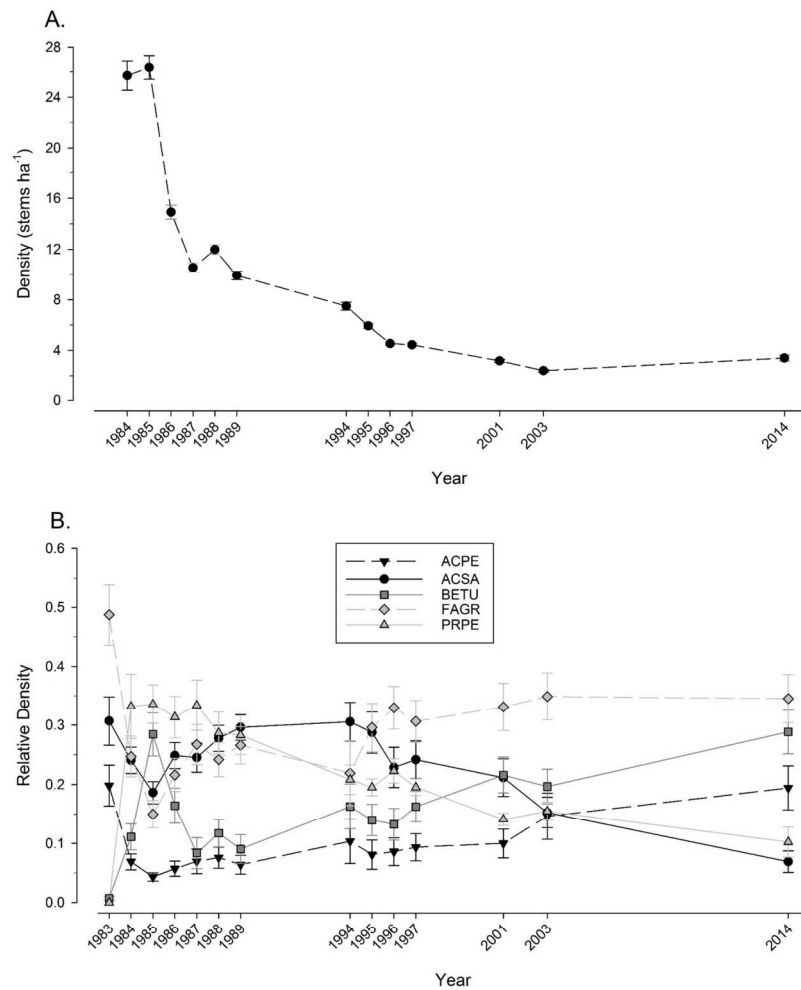


Figure 2

254x338mm (300 x 300 DPI)

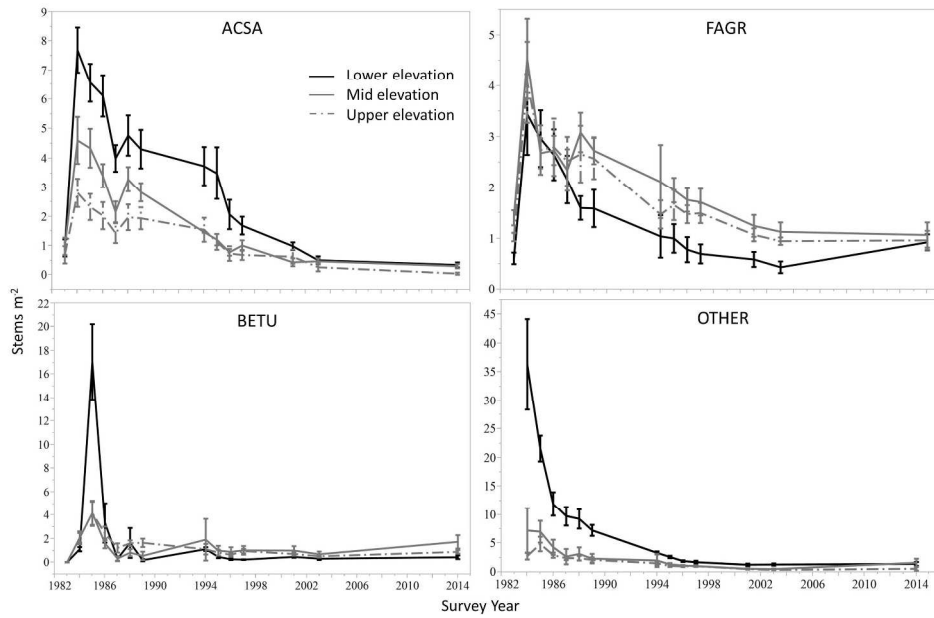


Figure 3

337x253mm (231 x 231 DPI)

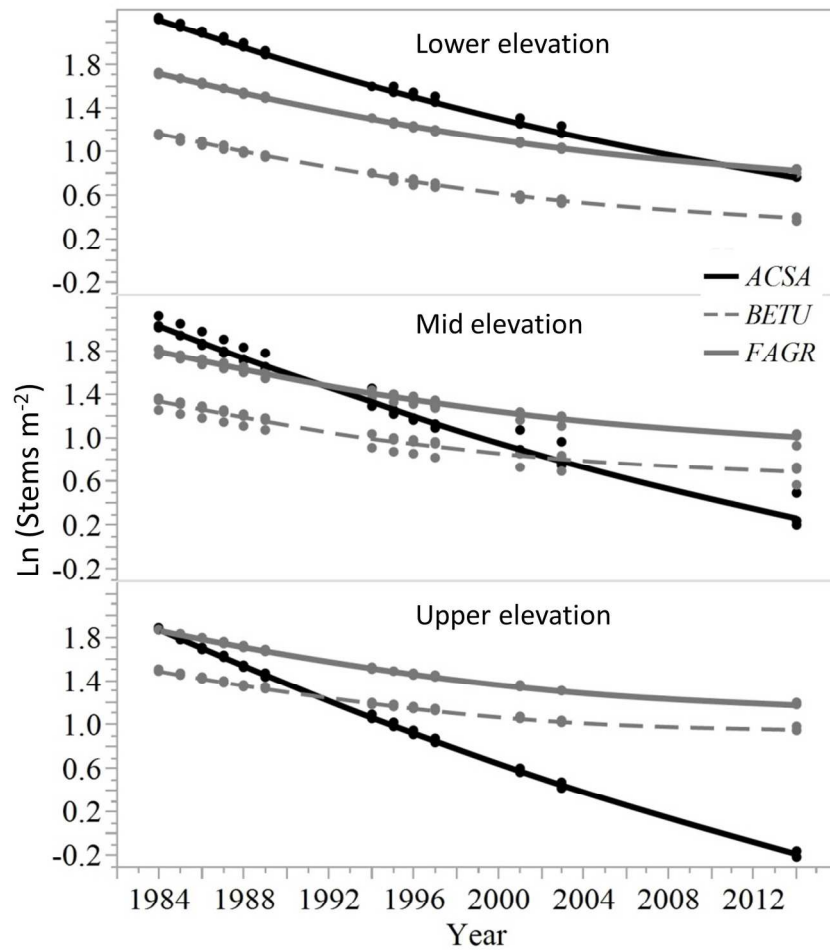


Figure 4

254x338mm (300 x 300 DPI)