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Disruption of the competitive balance between foundational tree species by interacting stressors in a temperate deciduous forest

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Abstract

1. The complex effects of global environmental changes on ecosystems result from the interaction of multiple stressors, their direct impacts on species and their indirect impacts on species interactions. Air pollution (and resulting depletion of soil base cations) and biotic invasion (e.g. beech bark disease [BBD] complex) are two stressors that are affecting the foundational tree species of northern hardwood forests, sugar maple and American beech, in northeastern North America.
2. At the Hubbard Brook Experimental Forest in New Hampshire, a watershed-scale calcium (Ca) addition in 1999 restored soil Ca that had been lost as a result of acid deposition in a maple-beech forest that was severely affected by BBD beginning in the 1970s. We present historic data from the reference watershed for BBD progression, 20 years of comparative forest data from the treated and reference watersheds, and tree demographic rates for the most recent decade. We hypothesized that mitigation of soil acidification on the treated watershed in the presence of BBD would favour improved performance of sugar maple, a species that is particularly sensitive to base cation depletion.
3. We observed significant responses of seed production, seedling bank composition, sapling survival and recruitment, and tree mortality and growth to the restoration of soil Ca, indicating that acid rain depletion of soil base cations has influenced demographic rates of maple and beech. Overall, the reduced performance of sugar maple on acidified soils may indirectly favour the persistence of diseased beech trees and a greater abundance of beech vegetative sprouts, effectively promoting the chronic presence of severe BBD in the population.
4. *Synthesis.* The shifting conditions created by global change have altered long-term demographic rates and may thereby impact competitive interactions in the current centre of these species ranges and have more profound implications for species persistence and migration potential than previously anticipated.

KEYWORDS

Acer saccharum, competition, *Fagus grandifolia*, long-term data, northern hardwood forest

1 | INTRODUCTION

A suite of global changes—climate, atmospheric CO₂ concentration, N deposition, soil acidification, invasive species, land use—is altering the distribution and abundance of plant species including forest trees (McDowell et al., 2020). The response of forest communities to these changes is difficult to predict, in part because multiple stressors may interact in complex ways to affect the different stages in the tree life cycle (Seidl et al., 2017). For example, species distribution models might be expected to capture climate change effects on the distribution and abundance of tree species, but they cannot address the fine-scale processes like interspecific competition that influence plant distributions (Zhu et al., 2014). To address the challenge of predicting tree species responses to global change, we need to quantify the drivers of change, the species-specific tree responses as well as the responses of interspecific interactions to these drivers. Furthermore, tree vital rates—recruitment, mortality and growth—all respond jointly to the drivers of change (Clark et al., 2012), and these vital rates are determined by physiological and allocational responses across the life-history stages of forest trees. Therefore, broad surveys and long-term experimental manipulations that quantify changes in plant abundance and vital rates are needed to understand forest ecosystem dynamics in a changing world.

Among the most prominent global change agents affecting northern temperate forests are soil acidification and invasive species (Meng et al., 2019; Schmitz & Simberloff, 1997). Anthropogenic emissions of precursor gases have resulted in acid deposition that has resulted in leaching of base cations; the resulting soil acidification has profound consequences for the health of both aquatic and terrestrial ecosystems (Reuss & Johnson, 2012). At the same time, international travel and trade have spurred the introduction of numerous invasive species. In northern forests, invasive insects and fungal pathogens continue to exert severe effects on native tree species; in eastern North America notable examples include *Castanea dentata* (Marshall) Borkh., *Ulmus americana* L., *Tsuga canadensis* (L.) Carrière, *Fraxinus* spp. and *Fagus grandifolia* Ehrh. (Lovett et al., 2016). In the present study, we evaluated how these two drivers mediate the fate of the two foundational tree species (sensu Ellison et al., 2005) of northern hardwood forests, sugar maple (*Acer saccharum* Marsh.) and American beech (*F. grandifolia* Ehrh.).

Forests dominated by sugar maple and American beech are widely distributed in eastern North America (Dyer, 2006; Williams, 1936). Sugar maple has suffered a variety of decline episodes throughout its range (Houston, 1999), and a growing consensus from northeastern North America attributes many of these declines to depletion of soil base cations resulting from acid deposition (e.g. Horsley et al., 2000; Juice et al., 2006; Ouimet & Camiré, 1995; Sullivan et al., 2013). Sugar maple appears to be particularly sensitive on soils with base saturation in upper mineral (B_s) horizon below a threshold (about 17%) where toxic inorganic Al is mobilized (Lawrence et al., 2018; Sullivan et al., 2013). American beech is subject to the beech bark disease (BBD) complex associated with an invasive beech scale insect (*Cryptococcus fagisuga* Lindinger) and

fungal pathogens (*Neonectria faginata* (M.L. Lohman, A.M.J. Watson & Ayers) Castl. & Rossman and *N. ditissima* (Tul. & C. Tul.) Samuels & Rossman) that decrease growth and increase mortality of mature trees (Cale et al., 2017). The implication of these stresses for the future distribution and abundance of these two species will depend upon competitive outcomes and demographic responses at critical life-history stages. For example, Duchesne and Ouimet (2009) suggested that increased beech abundance on soils with low base saturation may be associated with decline of sugar maple. Based on a survey across the Adirondack Mountains of New York, Lawrence et al. (2018) argued that higher abundance of beech on soils with low base saturation may reflect the decline of sugar maple rather than a direct beech response to acid soil. They also suggested that BBD may reduce the ability of beech to compete with sugar maple for crown space on soils with higher base saturation. The ability of sugar maple to compete with beech in occupying canopy gaps appears to depend in part upon high soil base saturation (Bannon et al., 2015; Kobe, 1996; Pontius et al., 2016).

We quantified responses of sugar maple and American beech populations to an experimental addition of calcium (Ca) designed to restore soil base saturation at the Hubbard Brook Experimental Forest, NH, USA (Likens & Bormann, 1995). This long-term experiment provided a basis for evaluating how two global change drivers—soil acidification and invasive pest mediated disease—interact to determine the trajectory of these foundational tree species. Our overarching hypothesis was that mitigation of soil acidification would favour sugar maple over American beech, which is suffering from the stress of BBD. We also hypothesized that the various stages of each tree's life history would exhibit concordant responses to experimental restoration of soil base saturation, thereby tipping the long-term balance of the competitive interaction towards sugar maple. Finally, we hypothesized that the improved performance of sugar maple resulting from relaxing stresses associated with soil acidification would exacerbate the impact of BBD through both decreases in growth and increases in mortality of beech trees. This long-term, detailed case study illustrates what has been identified as the primary challenge for predicting forest response to global change: 'how the abiotic and biotic context alters the direction and magnitude of effects on interspecific interactions' (Tylianakis et al., 2008).

2 | MATERIALS AND METHODS

2.1 | Site description

The Hubbard Brook Experimental Forest (HBEF) is located in north-central New Hampshire, USA (43°56'N, 71°45'W). The overstorey vegetation is dominated by northern hardwoods: sugar maple, American beech and yellow birch (*Betula alleghaniensis* Britt.), which together comprise 90% of the tree basal area (van Doorn et al., 2011; Table S1). Detailed descriptions of soils, hydrology, topography and vegetation of the HBEF are presented in Likens and Bormann (1995). The climate is humid continental with short, cool summers and long,

cold winters. Annual precipitation averages 140 cm; mean annual temperature is 5.5°C; and daily temperatures average from -8.5°C in January to 18.8°C in July (Bailey et al., 2003). On the south-facing watersheds, soils are predominantly acidic Spodosols derived from base-poor glacial till.

This research was conducted in the experimental watersheds on a south-facing slope (Figure S1). Watershed 6 (hereafter REF, 13.23 ha in size and 549–792 m in elevation) serves as the biogeochemical reference watershed and has been systematically monitored since 1963. The long-term record from this watershed demonstrated how decades of atmospheric inputs of strong acids can result in marked depletion of labile pools of Ca from the Hubbard Brook ecosystem (Likens et al., 1996). The Ca addition was applied to Watershed 1 (hereafter CAL, 11.8 ha in size and 488–747 m in elevation) in 1999. By the start of the Ca addition study, BBD was widespread in both REF and CAL having been first documented in REF in 1977 (Figure S2).

These two watersheds were carefully paired in terms of elevation, topography, soils and disturbance history. The entire REF watershed is divided into 208, 25 by 25 m square plots (0.0625 ha, slope corrected) and CAL is divided into 200 plots (Figure S1). The few plots in the watersheds dominated by conifer trees (18 plots in REF and 19 plots in CAL) were excluded from the analysis (Figure S1). The Ca silicate mineral, wollastonite, was applied to CAL by helicopter in October 1999 with a uniform delivery rate of 1,028 kg Ca/ha (Peters et al., 2004). This treatment was explicitly designed to gradually replace the amount of Ca that was lost from the Hubbard Brook forest as a result of human activity during the 20th century (Likens et al., 1996) and thereby to reverse the likely effects of anthropogenic soil Ca depletion on forest ecosystem dynamics (Battles et al., 2014). The pool of exchangeable Ca increased significantly after treatment, peaking in the O horizons by 2002 and in the upper mineral soil by 2006 (Johnson et al., 2014). Exchangeable Ca in the upper soil horizons remains elevated to the present time (Driscoll, 2019).

2.2 | Analytical framework

Our synthesis leverages a diverse collection of long-term datasets that quantify the treatment effect on the population abundances and the vital rates of sugar maple and American beech. Most of our records span the period prior to the Ca addition and continues for the next two decades (Table S2). Our primary goal was to evaluate the impact of the treatment on the dynamics of the two species.

For many of our response variables, we were able to control for differences between the REF and CAL using a before-after-control-impact (BACI) design. In these instances, our analyses focus on the effect of the treatment over time (i.e. the interactive effect; Stewart-Oaten et al., 1986). For other variables, we had no pre-treatment measurements and thus relied on a control-impact (CI) design. This design assumes that any differences between treatment and reference watersheds were due to the Ca addition. This assumption risks the potential of confounding treatment effect with

other unmeasured differences. Using simulation models, Christie et al. (2019) estimate that relative accuracy of estimating the true effect is three to four times higher for BACI designs compared to CI designs. Given this difference in inferential reliability, we note the design framework for our major response variables in Table S3.

Additionally, we modelled the effects for each species individually to maintain a consistent statistical approach across our varied datasets. For this parallel analysis, we primarily relied on linear mixed-effects models (LME) to account for the repeated measures over time and the within-group correlation present in our data (Pinheiro & Bates, 2006). Specifically, we modelled the nested spatial structure (i.e. plots in watershed) of our measurements. When our data included observations that followed non-normal distributions (e.g. counts best described by a Poisson distribution), we used generalized linear mixed models (GLMMs) to match our statistics to the data (Bolker et al., 2009; Table S3). Given the challenge of precisely calculating p-values from mixed effects models (Luke, 2017), we estimated the confidence intervals for the coefficients of the fixed effects and defined statistically meaningful results as those where the 95% confidence interval did not include zero (Bates et al., 2014).

The main exception to our reliance on frequentist methods pertains to tree recruitment and mortality. We applied a Bayesian analytical framework to account for the nonlinear functional forms of these vital rates and the heterogeneity among subpopulations (Kohyama et al., 2018). We evaluated statistical relevance for results from these Bayesian models using 95% credibility intervals of the posterior distributions. To fit GLMMs, we used the `GLMMTMB` (Brooks, 2020) package for the R software environment (ver.3.4.3, R Core Team, 2017). We also conducted the Bayesian analysis in R using the package `R2JAGS` (Su & Yajima, 2015). Other analyses were completed with JMP Pro (ver. 14.0 statistical software, SAS Institute Inc.).

2.3 | Seed production

We measured seed production using collectors (0.1 m² catch area; $N = 12$ per plot) distributed in six plots (three per watershed; Cleavitt & Fahey, 2017; Fahey et al., 2005). Seed fall was estimated annually for a 20-year period (1998–2018) from sorted and counted seeds. A seed production year includes three collections: late August, early November and also early May of the following year. For the seed production data with many zero counts, the effects of treatment and time on seed production (seeds/m²) were analysed with a zero-inflated Poisson regression with seed collector nested within watershed as random effects (Table S3). Time was scaled to years since first measurement.

2.4 | Seedling abundance

Seedling densities were quantified over 20 years in a stratified random set of permanent 1 m² plots per watershed (CAL: 90; REF: 92;

Figure S1). All stems shorter than breast height and less than 2 cm in diameter (DBH, breast height = 1.37 m) were catalogued by species and censused annually for the first 10 years (1998–2008) and again in 2010 and 2018. Because of the small size of these plots, they best captured the small stems under 50 cm in height, particularly first year germinants. Change in seedling density (for stems $\leq$ 50 cm in height) over time was compared using zero-inflated Poisson regression with treatment and time as fixed effects and seedling plot within watershed as random effects (Table S3).

2.5 | Seedling bank composition in 2018

The understorey layer is complex and includes groups of stems with distinctly different chances of survival and recruitment to the sapling size class. Because the 1 m² plots did not effectively quantify the larger stem classes, in May–June 2018 we quantified the abundance of stems in the seedling bank (*sensu* Marks & Gardescu, 1998) for larger forest plots that contained seedling plots (90 CAL and 92 REF). Specifically, we positioned a 20 m long by 2-m wide transect (i.e. area = 40 m²) on the diagonal from the NW plot corner and inventoried all woody tree stems $>$ 5 cm tall and $<$ 2 cm DBH. Since the seedling bank is defined as a persistent understorey, we excluded germinants from the 2018 census because of the low survivorship of these first-year stems (Cleavitt et al., 2008, 2011). All stems were tallied by species, origin (seedling, sprout, unknown) and size class. The five size classes were: (1) 5.0–14.9 cm tall; (2) 15.0–29.9 cm; (3) 30.0–49.9 cm; (4) 50.0–99.9 cm; and (5) $\geq$ 1 m tall and $<$ 2 cm in DBH. We used the frequency of occurrence defined by the fraction of plots with at least one stem in the size class to quantify differences in size distribution between watersheds.

Differences in seedling bank density and relative density were examined with LMEs with treatment as the fixed effect and plot within watershed as the random effect. Stem size distributions were analysed by ordinal logistic regression where size class is the dependent variable and treatment is the independent variable. In addition, for American beech we analysed differences in stem origin (seedling, sprout) by treatment using an LME with the plot in watershed as a random variable (Table S3).

2.6 | Sapling abundance

Saplings (2.0 to 9.9 cm DBH) were sampled in a 3-m wide transect along the 25 m long southern edge of each plot (i.e. area = 75 m²) on the same 5-year schedule as trees (Table S2; see below). Tree saplings were measured at breast height and assessed as either live or dead. All beech saplings were also assessed for BBD (see Section 2.10). We analysed trends in live sapling density (stems/ha) as a function of time and treatment of the four census periods covering 20 years with plot nested in watershed as a random effect (Table S3).

2.7 | Tree abundance

At 5-year intervals, we measured all standing trees $\geq$ 10 cm DBH in every plot (0.0625 ha) and assessed them as alive or dead. During the 2002 census on REF and the 2006 census on CAL, we tagged all trees $\geq$ 10 cm diameter and tracked the fate of every standing tree through subsequent inventories (Table S2). In later inventories, we also measured and tagged trees that reached 10 cm DBH during the 5-year interval. These trees are termed 'recruits' because they recruited into the size class of tagged trees. The relevance of 10 cm size as the threshold for defining trees has been documented at the global scale by Crowther et al. (2015). To examine treatment effects on tree abundance, we calculated the plot-level basal area (m²/ha) by species for each census. Basal area was modelled with an LME where treatment and time were the fixed effects and plot nested in watershed was a random effect (Table S3).

2.8 | Tree recruitment and mortality

We used observed counts of newly tagged trees and of tree deaths to estimate rates of annual recruitment and mortality. To minimize the bias in vital rates due to heterogeneity among subpopulations (i.e. changing-frequency bias), we applied the individual-based Bayesian analysis described in Kohyama et al. (2018). Specifically, for sugar maple and beech, the probability of recruitment and survival was adjusted by stem size. To account for the impacts of the elevational gradient on vital rates (Bormann et al., 1970), we divided individuals into three elevation bands and then treated each elevation band as a subpopulation in the model (Kohyama et al., 2018).

Vital rate results are based on the posterior distributions of recruitment and mortality obtained using Markov chain Monte Carlo (MCMC) simulations with uninformed priors. For details on the recruitment and mortality functions, see S1 in Kohyama et al. (2018). MCMC analysis included four chains of 2,000 iterations. We discarded the first 1,000 steps as burn-in. Convergence and stationarity of the Markov chains were assessed by inspection of trace plots and the calculation of the Gelman and Rubin diagnostic (Korner-Nievergelt et al., 2015). Per-capita vital rates are reported as medians with 95% credibility intervals. Annual recruitment was calculated as the final density-based estimate (*sensu* Kohyama et al., 2018). Median values with non-overlapping credibility intervals were interpreted as being statistically different. Our Bayesian models of recruitment and mortality were well-mixed with solid evidence of convergence among the chains in the trace plots. The Gelman and Rubin diagnostic was $<$ 1.07 in all cases.

2.9 | Tree growth

Tree growth was calculated as the relative basal area increment (rBAI):

$$rBAI = \frac{BA_{t_1} - BA_{t_0}}{BA_{t_0}} / \Delta t \times 100, \quad (1)$$

where $rBAI$ is measured in %/year; BA_{t_0} is the basal area of tree at the initial measurement t_0 (time 0); BA_{t_1} is the basal area of the tree at the next measurement interval, t_1 (time 1); and Δt is the time in years between the measurements ($t_1 - t_0$). Comparison of growth for tagged trees of sugar maple and beech that survived the 5-year census periods (2006/2007–2011/2012) and (2011/2012–2016/2017) were included in an LME examining $rBAI$ for the two census times. In the model, treatment and plot covariates (total plot basal area and basal area of other tree species) were the fixed effects. The random variables were census interval and plot nested within watershed (Table S3). Plot covariates were included to account for the competitive effect reflected by greater basal area and the effect of non-target tree species (mostly yellow birch; Table S1). Census variation was included as a random effect in the model.

2.10 | Beech bark disease progression

The earliest observations of BBD on REF were from 1965 and 1977 and only indicated the proportion of stems with the scale insect present or with canopy decline (Figure S2; Table S2). In 1998 and 2002, a subsample of beech trees was rated for the presence of severe cankers (Rhoads et al., 2002). Beginning with the 2011/2012 inventories, BBD was rated for all beech trees with severe cankers on both CAL and REF (Table S2). To better capture gradients in disease presence, we extended the rating system in the 2016/2017 census to a 5-point scale (similar to Rhoads et al., 2002): 0—no scales or cankers; 1—scale present but no signs of fungal infection;

2—fungal cankers present but not widespread (cankers discrete and not more than four around the bole of the tree); 3—fungal cankers present and widespread (cankers often touching and more than three around the stem of the tree); 4—fungal canker coalesced and the outline of the tree disfigured. We defined the ratings of 3 and 4 as equivalent to represent the 'severe' BBD assessment used in earlier surveys. The effect of BBD on tree growth was examined using an LME with treatment and BBD rating as fixed effects and plot nested within watershed included as random effects (Table S3). Few trees had a BBD rating of 0; therefore, for the growth analysis we lumped trees in categories 0 and 1.

The impact of BBD includes canopy dieback (Cale et al., 2017; Garnas et al., 2011). As part of the tagged tree census, we rated the vigour of tree canopies as healthy, dying (canopy more than 50% leafless) or dead. This vigour assessment allowed us to examine the fate of beech trees rated as dying starting with the 2006/2007 census (Table S2). Trees were scored as: recovered, unrecovered but still alive and dead. Finally, we quantified disease progression by comparing BBD ratings across three size (age) classes of trees in the two watersheds: saplings (2.0–9.9 cm DBH), recruits (reaching 10 cm in past 5 years) and originally tagged larger trees.

3 | RESULTS

3.1 | Seed production

Pre-treatment seed production of sugar maple and American beech was higher on REF than CAL (Figure 1). This pattern held for the first two mast years post-treatment (2002 and 2006) but the gap in seed production appeared to be narrowed in each successive mast year.

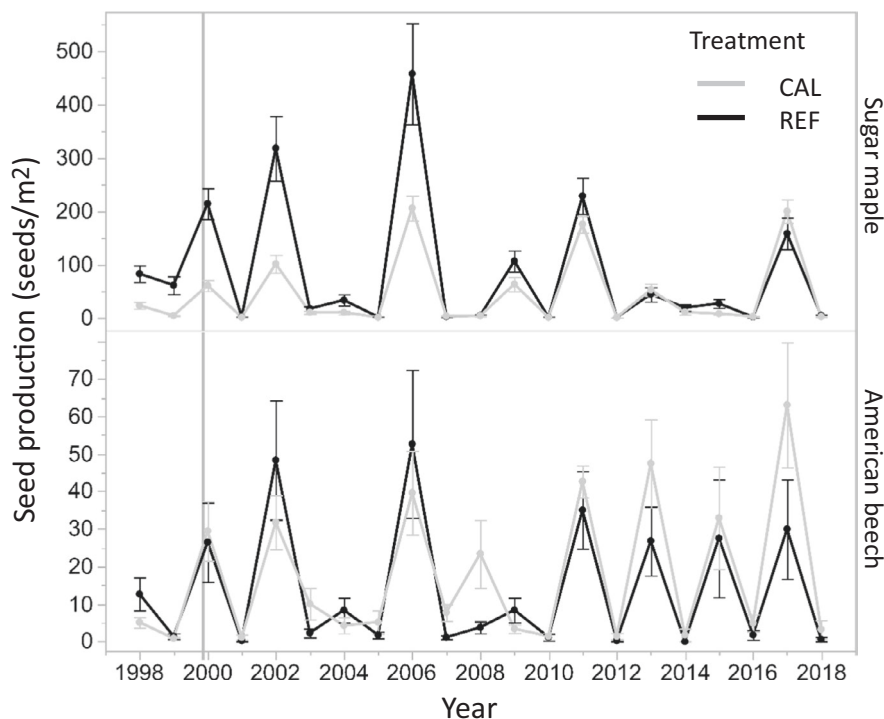


FIGURE 1 Mean annual seed production over 20 years for sugar maple and American beech on treated (CAL: calcium addition) and reference (REF) watersheds at Hubbard Brook Experimental Forest, NH, USA. Production reported as mean seed density ($\pm$ SE). Sugar maple mast years were 2002, 2006, 2011 and 2017 and American beech were 2002, 2006, 2011, 2013 and 2017. The gray vertical line indicates the calcium addition in October 1999

In the most recent mast year (2017), seed production was higher for both species on CAL, 30% higher for sugar maple and 110% higher for American beech (Figure 1). This reversal in seed production trends was supported by a significant year by treatment interaction term (Table S4).

3.2 | Seedling abundance

Seedling abundance of all species was greater on CAL, largely reflecting the regeneration of sugar maple (Figure 2; Table S5). Sugar maple seedling density (stems <50 cm in height) increased significantly on CAL over the 20 years since Ca addition (Figure 2). Pre-treatment maple seedling densities were twice as high on CAL and markedly increased in the year following each of the three large mast years: six times higher in 2003, eight times higher in 2007 and 4.5 times higher in 2018 (Figure 2; significant treatment and interaction terms, Table S5). The density of American beech seedlings varied less over time than sugar maple with only small differences between treatments (Figure 2; Table S5).

3.3 | Seedling bank composition

The density of all tree stems in the seedling bank in 2018 (19 years after treatment) was greater in CAL than REF (Figure 3a), and beech was more abundant than sugar maple in both watersheds (Figure 3b). In terms of relative abundance, the treatment had the opposite effects on the two species: the relative density of sugar maple was significantly greater in CAL than REF while the relative

density of beech was significantly less (Figure 3b; Table S6A). Beech was more frequent than maple in all size classes in both watersheds (Figure 3c); it displayed a more uniform size distribution, and there were no treatment differences in the size distribution (Table S6B). In contrast, the frequency of sugar maple stems decreased with increasing size class in both watersheds (Figure 3c) and maple was significantly more frequent on CAL in all size classes (Table S6B). In terms of beech stem origin, beech sprouts were more abundant than seedlings in both watersheds; however, beech stems of seed origin were more abundant in CAL (mean $\pm$ 1 SE: 4.06 ± 0.49 seedlings/m²) than REF (2.98 ± 0.42), while sprouts were fewer (CAL: 14.4 ± 1.30 ; REF: 20.5 ± 1.47 ; Table S6C; significant interaction) resulting in the seedling to sprout ratio on CAL (1:3.5) being half that on REF (1:7).

3.4 | Sapling abundance

The overall density of the sapling layer for all tree species decreased over time with a greater decrease in CAL (Figure 4; Table S7). Sugar maple was a minor component of the sapling layer, and its density declined over time in both watersheds (i.e. no treatment effect). Beech dominated the sapling layer of both watersheds, and beech sapling density changed more on REF than CAL over time (Figure 4; Table S7).

3.5 | Tree abundance

The trends in the basal area of all trees significantly diverged over time in the two watersheds (Figure 5; Table S8). At the beginning

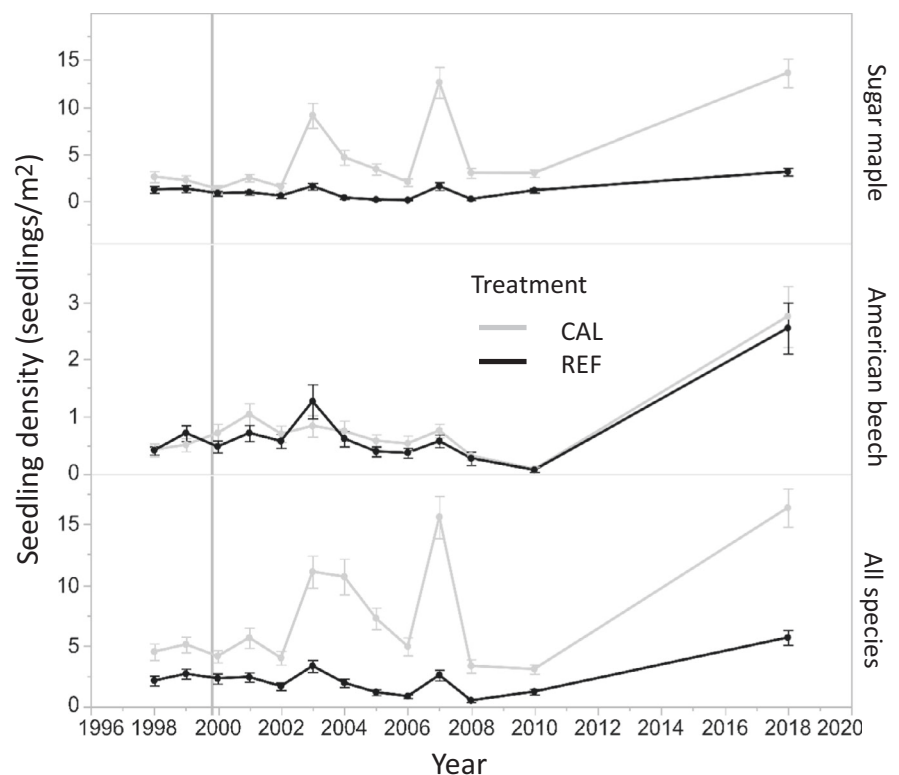


FIGURE 2 Seedling abundance over 20 years for sugar maple, American beech and all tree species on treated (CAL: calcium addition) and reference (REF) watersheds at Hubbard Brook Experimental Forest, NH, USA. Seedlings defined as stems <50 cm in height. Abundance reported as mean density $\pm$ SE. The gray vertical line indicates the calcium addition in October 1999

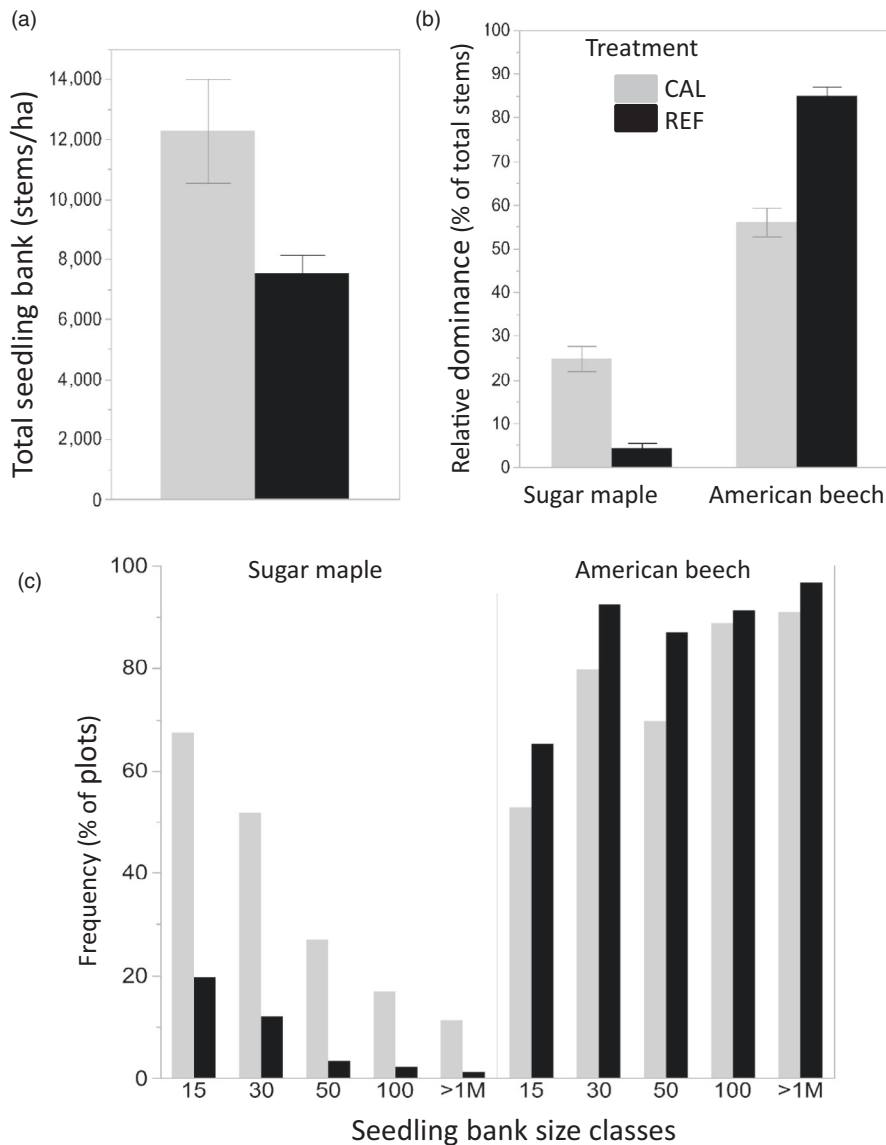


FIGURE 3 Seedling bank abundance in 2018 on treated (CAL: calcium addition) and reference (REF) watersheds at Hubbard Brook Experimental Forest, NH, USA: Seedling bank defined as stems >5 cm in height and <2 cm in diameter at breast height (breast height = 1.37 m). (a) Stem densities (mean $\pm$ SE) for all tree species; (b) Relative dominance of sugar maple and American beech stems in the seedling bank and (c). Frequency of stems in five size classes (15:5–15 cm in height; 30:15.1–30 cm in height; 50:30.1–50 cm in height; 100:50.1–100 cm in height and >1 m: >1 m in height and <2 cm in diameter)

of the experiment (1996/1997), the basal area on CAL was only 3.5% greater than REF; 20 years later the difference had grown to 11.4%. The treatment effect on the abundance of sugar maple and beech resulted in increasing differences between watersheds over time (Figure 5; Table S8). In particular, pre-treatment (1996/1997) sugar maple basal area was 4.8% greater on CAL than REF, and by 2016/2017, the difference had nearly doubled to 9.5%. In contrast, beech basal area was 16.7% lower on CAL than REF pre-treatment and this difference increased to 24% less abundant by 2016/2017.

3.6 | Tree recruitment and mortality

Across all species, per capita tree recruitment (i.e. new trees ≥ 10 cm DBH) was significantly higher in REF than CAL for both census intervals (Table 1). For example, in the latest census interval, there were 20 recruits $\text{ha}^{-1} \text{year}^{-1}$ in REF compared to 13 recruits $\text{ha}^{-1} \text{year}^{-1}$ in CAL. Beech recruitment was the main driver of this trend; not only were there more beech trees in REF (380 trees/ha in 2016) than CAL

(235 trees/ha in 2017) but also the per capita rate of recruitment of beech was significantly higher (Table 1). Recruitment of beech was nearly three times higher on REF than CAL while there was no difference in sugar maple recruitment between watersheds.

Median per capita mortality rates ranged from 1.6% to 2.0%/year for all trees in both watersheds during the last 10 years with no differences between treatments (Table 2). However, tree mortality increased in the most recent census. Sugar maple mortality was significantly lower on CAL than REF overall, and this difference increased in the most recent census (Table 2). In the most recent census, sugar maple mortality was much lower on CAL, 1.3% versus 1.8%/year, with no overlap of the credibility intervals (Table 2). There was no treatment effect on beech mortality (Table 2).

3.7 | Tree growth rates

Although beech trees grew relatively faster than sugar maple in both watersheds, the treatment had opposite effects on the two

FIGURE 4 Sapling abundance over 20 years on treated (CAL: calcium addition) and reference (REF) watersheds at Hubbard Brook Experimental Forest, NH, USA for sugar maple, American beech and all tree species. Saplings defined as stems between 2 and 9.9 cm in diameter at breast height (breast height = 1.37 m). Abundance reported as mean stem density $\pm$ SE. The gray vertical line indicates the calcium addition in October 1999

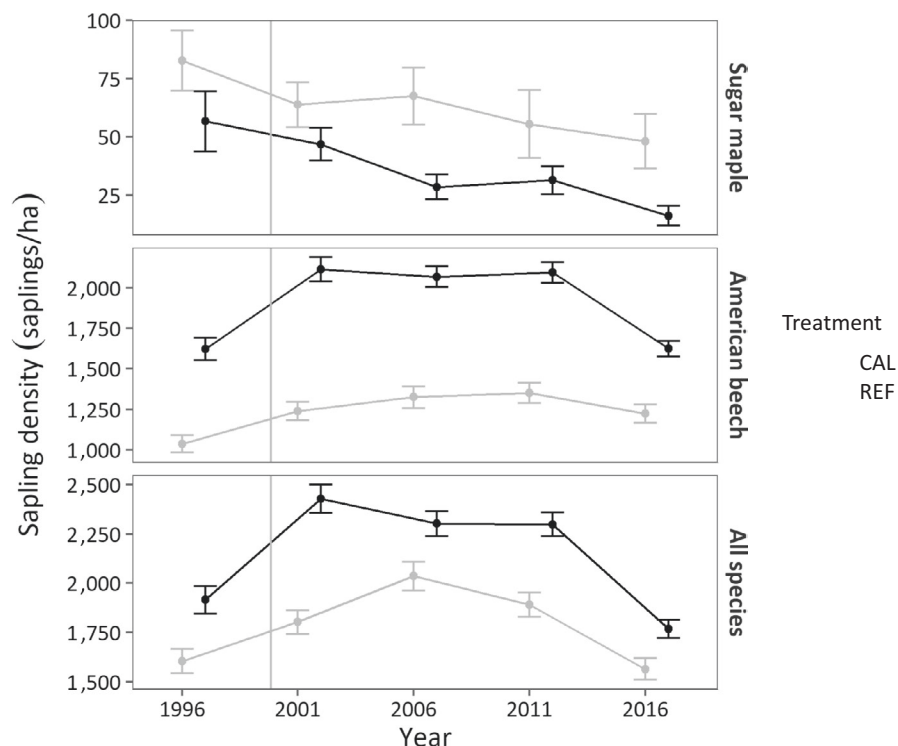
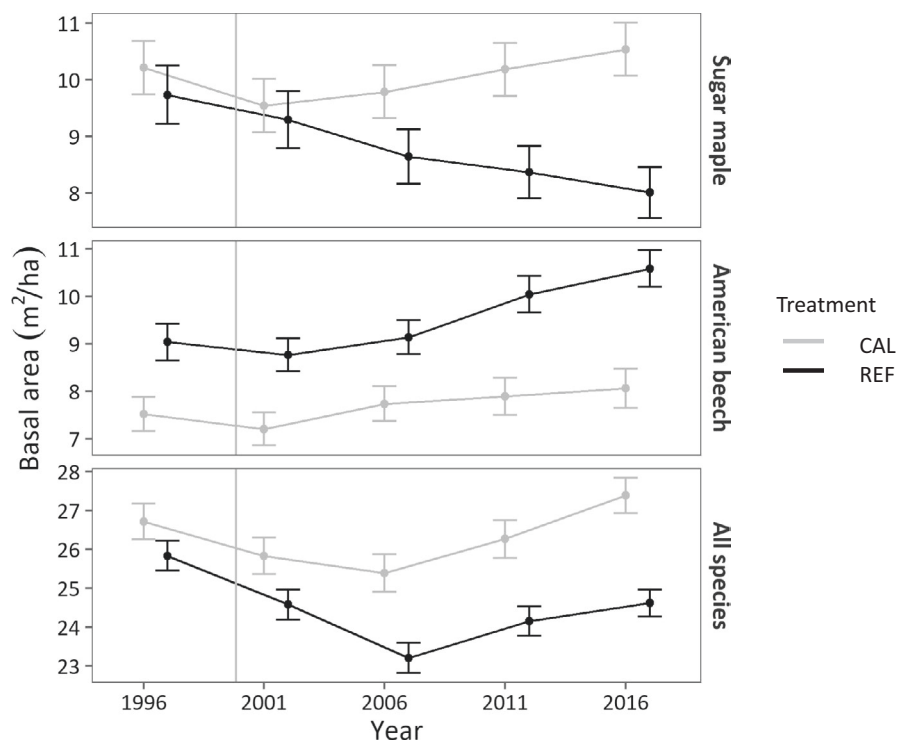


FIGURE 5 Tree abundance over 20 years on treated (CAL: calcium addition) and reference (REF) watersheds at Hubbard Brook Experimental Forest, NH, USA for sugar maple, American beech and all tree species. Trees defined as stems ≥ 10 cm diameter at breast height (breast height = 1.37 m). Abundance reported as the mean basal area $\pm$ SE. The gray vertical line indicates the calcium addition in October 1999



species (Table 3). Sugar maple grew almost twice as fast on CAL than REF, and beech trees grew significantly faster on REF than CAL (Table S9). Total basal area and basal area of non-target species (mostly yellow birch) were significant predictors of growth only for American beech. Relative growth was lower in plots with greater basal area (Table S9). No such effects were observed for maple.

3.8 | Beech bark disease progression

Overall, the progression of BBD was greater on REF than CAL. In the 2016/2017 census, the most severe BBD ratings of 3 and 4 represented 47% of the population on REF and only 18% on CAL. A striking result was that relative growth rate of beech trees decreased

TABLE 1 Final density-based annual recruitment (%/year) of trees for two recent measurement periods on a calcium treated (CAL) and reference (REF) watershed at Hubbard Brook Experimental Forest, NH, USA. Values are the medians with the 95% credibility intervals in parentheses. Values with non-overlapping credibility intervals are considered significantly different. Estimates for all trees in a watershed include heterogeneity due to species differences and the elevation gradient. Estimates for species include heterogeneity across the elevation gradient

Census interval	Sugar maple		American beech		All trees	
	CAL	REF	CAL	REF	CAL	REF
2006/7–2011/2	0.68 (0.51–0.88)	0.41 (0.28–0.58)	2.38 (2.09–2.68)	4.38 (4.09–4.71)	2.20 (2.03–2.38)	3.31 (3.11–3.51)
2011/2–2016/7	0.48 (0.35–0.63)	0.39 (0.27–0.55)	3.25 (2.95–3.61)	4.80 (4.51–5.11)	2.61 (2.43–2.81)	3.64 (3.44–3.85)

TABLE 2 Annual mortality (%/year) of trees for two recent measurement periods on a calcium treated (CAL) and reference (REF) watershed at Hubbard Brook Experimental Forest, NH, USA. Values are the medians with the 95% credibility intervals in parentheses. Values with non-overlapping credibility intervals are considered significantly different. Estimates for all trees in a watershed include heterogeneity due to species differences and the elevation gradient. Estimates for species include heterogeneity across the elevation gradient

Census interval	Sugar maple		American beech		All trees	
	CAL	REF	CAL	REF	CAL	REF
2006/7–2011/2	1.40 (1.19–1.65)	1.72 (1.44–2.01)	1.33 (1.12–1.56)	1.25 (1.09–1.42)	1.59 (1.44–1.75)	1.56 (1.42–1.71)
	N = 1,880	N = 1,611	N = 2,265	N = 3,305	N = 5,483	N = 5,841
2011/2–2016/7	1.31 (1.09–1.42)	1.81 (1.53–2.12)	2.18 (1.94–2.46)	2.15 (1.96–2.37)	1.80 (1.65–1.97)	2.01 (1.86–2.17)
	N = 1,808	N = 1,510	N = 2,389	N = 3,907	N = 5,651	N = 6,422

TABLE 3 Tree growth (relative basal area increment) of tagged trees on calcium treated (CAL) and reference (REF) watersheds for two main species (sugar maple and American beech) in Hubbard Brook Experimental Forest, NH, USA. rBAI is the mean relative basal area increment (%/year) with standard error in parentheses. N refers to the number of trees in each category

Species	2006/7–2011/12				2011/12–2016/17			
	CAL		REF		CAL		REF	
	N	rBAI (%/year)	N	rBAI (%/year)	N	rBAI (%/year)	N	rBAI (%/year)
Sugar maple	1,732	2.42 (0.06)	1,473	1.34 (0.04)	1,798	1.81 (0.07)	1,509	0.91 (0.07)
American beech	1,970	3.25 (0.06)	2,955	4.15 (0.06)	2,219	2.82 (0.08)	3,679	3.58 (0.07)
All species	4,719	3.12 (0.05)	5,157	3.40 (0.05)	5,248	2.51 (0.06)	6,052	2.90 (0.05)

significantly with increasing severity of BBD on CAL, but not on REF (Figure 6; Table S10).

Repeat observations of tagged trees across three censuses provided the basis for tracking the fate of these individual beech trees. The most prominent treatment effect was that many more unhealthy trees (>50% canopy dieback) recovered on CAL than REF, whereas many more trees became unhealthy on REF during the census intervals (Figure S3). Thus, over the last decade, the number of unhealthy beech trees on REF increased markedly (from 131 to 230 trees) whereas they decreased on CAL (from 160 to 49 trees), with the largest change in the most recent census (Figure S3).

The percentage of trees in all three size classes (saplings, recruits and original tagged trees) with more severe BBD was greater in REF than CAL (Table S11). In addition, the progression of BBD appeared to be slower on CAL. That is, the proportion of stems in the lowest severity BBD class (category 1) declined with increasing size class

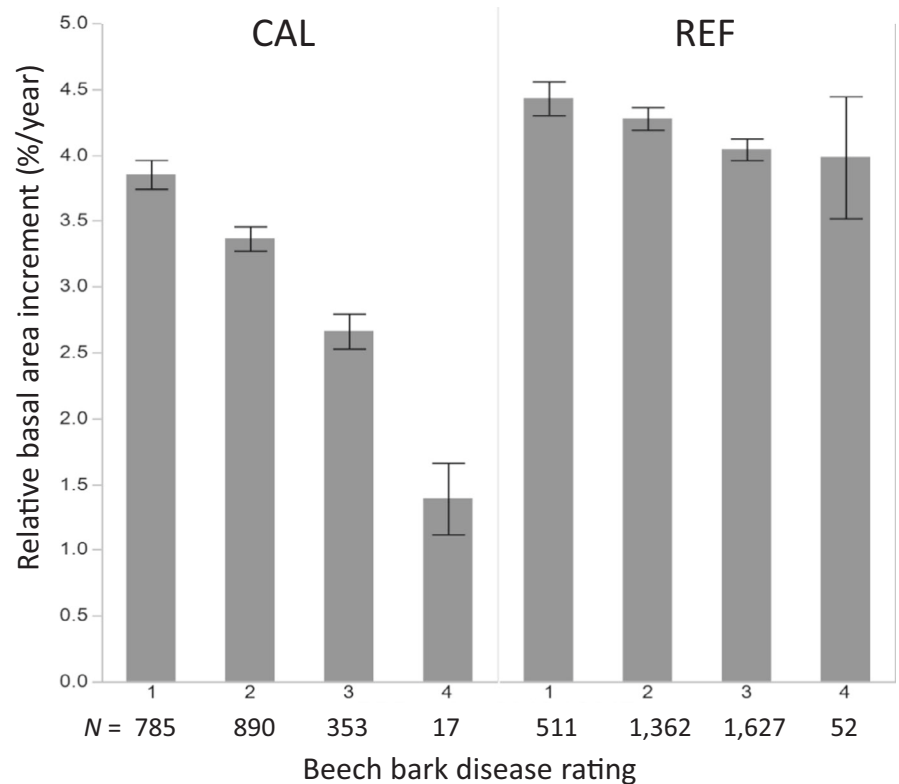
(saplings, recruits and canopy trees) in both watersheds, but it declined much more steeply in REF than CAL.

4 | DISCUSSION

4.1 | Hypotheses

Our overarching hypothesis was that relaxation of stresses associated with soil acidification (Cronan & Grigal, 1995) would strongly favour sugar maple in competition with beech which is suffering from the stresses of an introduced disease complex (BBD; Cale et al., 2017). This hypothesis was supported based on differential mid-term (20 year) changes in abundance of the two species on a reference watershed compared with a watershed where Ca was added to replace losses due to acid deposition in the 20th century

FIGURE 6 Impact of beech bark disease (BBD) severity on growth of American beech trees on treated (CAL: calcium addition) and reference (REF) watersheds at Hubbard Brook Experimental Forest, NH, USA. Disease severity defined as categorical classes between 1 and 4 with 1 being least BBD and 4 being most severe BBD. Growth was calculated as the relative basal area increment from the two most recent census years for each watershed and reported as the mean increment $\pm$ SE



(Figure 5; Battles et al., 2014). Over longer time-scales the outcome of competition between sugar maple and beech depends upon species-specific responses at various stages in the complex life history of forest trees. The aggregate effect of these responses will be expressed in the vital rates of the two species. Based on our ecosystem level understanding, we advanced the simplistic hypothesis that the effects of the watershed Ca treatment would be concordant across all life-history stages of the two species; that is, sugar maple fecundity, recruitment, survivorship, growth and stem abundance in all life-history stages would increase in the treated watershed whereas those of beech would decrease. Not surprisingly, support for this hypothesis was mixed, as some responses of beech to the treatment were positive (seed production, Figure 1; and BBD severity and progression, Figure S3; Table S11), and some responses of sugar maple were delayed (seed production; Figure 1) or non-significant (sapling abundance; Figure 4).

We hypothesized that the principal interaction between the two stresses would be associated with improved competitive performance of sugar maple. As expected, growth rates of diseased beech on the treated watershed were much lower than on the reference watershed, indicating the competitive influence of more healthy sugar maple (Table 3; Figure 6). However, beech mortality was not higher on CAL (Table 2) and several indicators of BBD effects on the beech populations actually indicated healthier beech trees there, namely overall lower rates of severe cankering, slower progression across size classes (Table S11), and better recovery of beech trees with canopy damage (Figure S3).

We note that given the expense and logistical constraints on the landscape of replicating catchment-scale treatments,

watershed experiments rely on pairing a treated watershed with a reference watershed as an alternative to randomized controlled trials to mitigate the confounding effects of any differences between the watersheds (Brown et al., 2005). Prior to the Ca addition, the two watersheds were similar but not identical in terms of forest composition and structure (Table S1). For some of our key response variables (Table S3), we were able to control for differences in starting conditions using a before-after-control-impact design (Christie et al., 2019). For other variables, we could not rule out the potentially confounding effects of initial differences. However, the length and very large samples sizes (tree and plot level) lend a strength to our findings that other designs would lack.

Overall, our study provided insights into the key contextual features operating on interspecific competition in forest trees. First, both of the stresses we studied result in canopy dieback (Cale et al., 2017; Juice et al., 2006). Thus, the competition for crown space is the first-order response to the change in the stressors. One possible outcome of Ca addition is the improved competitive performance of sugar maple. Enhanced competitive abilities could interact with BBD if increased competition interacts with disease severity or tree decline and eventual mortality. Second, because of the unusual ability of American beech to produce vegetative root sprouts (Held, 1983) that remain connected to the mother trees and receive a carbon subsidy (Farahat & Lechowicz, 2013), the sensitivity of the beech seedling bank and sapling layer to competition with sugar maple may be reduced, thereby contributing to smaller differences between watersheds (Figures 3 and 4). This understorey layer may play an inordinate role in regulating interspecific interactions

because sugar maple regeneration is strongly suppressed in beech sapling thickets (Hane, 2003).

4.2 | Regeneration impacts

The increase in sugar maple seed production on CAL required 20 years of observation to detect and was not significant prior to the 2017 mast event (Cleavitt & Fahey, 2017; Cleavitt et al., 2011), even though it has been reported for other Ca addition studies (Halman et al., 2013; Long et al., 2011). Both sugar maple and American beech seed production increased in response to Ca addition (Figure 1). The response of beech seed production to Ca addition appears to represent an exception to the acid soil tolerance of this species (Ouimet et al., 2017). However, this result matches observations for European beech (*Fagus sylvatica*; Övergaard et al., 2007) in Sweden where seed production increased in response to soil liming. The explanation of this response could be complex and involve other nutrient requirements of fruit and seed production in *Fagus* spp. such as high nutrient requirements for flower, cupule and fruit production (Jonczak, 2013). This complexity is further implied by the correlation of masting with shifts in foliar chemistry, including nitrogen (Han et al., 2017; Muller-Haubold et al., 2015), and the rarity occurrence of consecutive mast years (Cleavitt & Fahey, 2017; Övergaard et al., 2007). These observations highlight the need for further study of the interaction of soil base status with other nutrients in regulating seed production of beech.

Both sugar maple (Marks & Gardescu, 1998) and American beech (Cleavitt et al., 2008) rely on the accumulation of a seedling bank to increase the likelihood of recruitment into the sapling layer in response to canopy gaps. The increased seedling bank density for sugar maple in the treated watershed confirms previous observations at the HBEF (Juice et al., 2006) and elsewhere (Sullivan et al., 2013) and emphasizes the likely long-term effects of soil Ca depletion in contributing to declining sugar maple populations on acidified soils. The situation for beech is more complex because reproduction includes both seedlings and root sprouts. Beech produced more seeds on CAL than REF, and the impact of this investment was apparent in the seedling bank as the seedling-to-sprout ratio was two times higher on CAL. While current evidence for greater beech seedling survival on Ca sufficient soils is weak, there is evidence for the effects of changing soil fertility on root growth and morphology of European beech seedlings (Leuschner et al., 2004). Over time, higher beech seed production on CAL should also lead to higher seedling density even with similar seedling survival rates of beech between watersheds.

Twenty years after Ca treatment, beech continues to dominate the sapling layer in both watersheds. A large cohort of understorey beech existed in the watersheds from an establishment period noted in the late 1960s (T. G. Siccama, unpubl. data). Although the origins of this cohort remain obscure, its presence restricts the possibilities for recruitment of other species. Perhaps most importantly, this dense sapling layer has been shown to strongly suppress sugar

maple reproduction (Hane, 2003), thereby limiting its response to the more favourable soil conditions on CAL. Tree recruitment into the 10 cm diameter class was over 50% higher for beech on REF than CAL (Table 2), and overall beech recruitment has been three to seven times greater than sugar maple even on the treated site. Presumably, increased competition from overstorey sugar maples in response to Ca addition has reduced the recruitment of beech on the treated watershed to some extent, but this mechanism requires further study and is likely mediated through an effect of lower light levels under healthier sugar maple canopies.

4.3 | Canopy tree responses

Juice et al., (2006) reported a striking improvement of crown condition of sugar maple on CAL within 3 years of Ca addition in this experiment. This initial response has been sustained. Canopy sugar maples in CAL have maintained significantly increased growth (Table 3) and decreased mortality (Table 2) 20 years after treatment. Lawrence et al., (2018) suggested that on soils with base saturation above the threshold where Al mobility is reduced (about 17%, Sullivan et al., 2013), sugar maple may outcompete beech for crown space. Our observations of significantly slower growth of beech on CAL support this conjecture as does the significance of plot basal area in predicting individual tree growth for beech, but not maple (Table S9). Plot basal area can be considered a proxy for the amount of crowding and competitive pressure. In addition, a study of neighbourhood effects at the HBEF, conducted in a low elevation area with similar forest composition to these south-facing watersheds, revealed that sugar maple is a stronger competitor than beech, causing greater growth suppression of neighbouring trees (van Doorn, 2014). Measurements of the canopy interactions of sugar maple and beech on REF and CAL could help to clarify this competitive interaction.

The depletion of soil base cations by acid deposition on a site that was naturally close to the threshold values of base saturation for healthy sugar maple has resulted in maple decline, including regeneration failure and increased overstorey mortality (Battles et al., 2014; Juice et al., 2006). The reduced competitive ability of sugar maple on acidified soils has favoured persistence of diseased beech and greater survival of beech sprouts; together these responses have facilitated the recruitment of more BBD susceptible beech trees and promoted the chronic sublethal persistence of BBD in the population (Table S11). Thus, the typical observation of a 'killing front' of this invasive disease (Houston, 1975), where all the larger beech trees have been lost, apparently can be absent in some BBD aftermath forests where mortality is not greatly elevated.

Release of beech from competition with sugar maple, owing to acid rain-induced maple decline, results in less severe growth impacts of BBD (Figure 6; Table S10) and consequently, large diseased trees can survive for decades after infection (see also, Cale & McNulty, 2018). Conversely, we would anticipate that eventual

recovery of soil base status as a result of stringent pollution controls should result in healthier sugar maple populations and may select out the most diseased beech in the populations through enhanced impact of the disease on growth (Figure 6). The increased cost of having BBD in a competitive environment may be the mortality of the most diseased individuals. This idea is also supported by the lower severity of cankering and slowed progression of BBD on CAL (Table S11). Susceptibility to BBD has a distinct genetic component (Calić et al., 2017), so that beech trees left on CAL are probably more resistant to BBD and their progeny of sprouts and seedlings in the understorey should also have higher resistance. Hence, while overall beech mortality did not differ between the watersheds, the pattern of death in relation to BBD may differ, with profound potential effects on the composition of the population. The extent to which the genetics of beech resistance to BBD may have shifted in CAL is an intriguing avenue for future research.

4.4 | Episodic disturbance events

For longitudinal studies, the paired watershed approach provides the means to account for the influence of natural disturbances events. In a long-term, large-scale experiment, natural disturbance events inevitably influence treatment responses, and understanding the implications of interacting disturbances for forest health has been cited as a key knowledge gap (Pautasso et al., 2015). Such episodic stressors may increase with climate change (Rockel & Woth, 2007; Seidl et al., 2017) and could play a key role in shaping competitive interactions.

During the present study two intermediate disturbance events (*sensu* Woods, 2004) occurred, a severe ice (glaze) storm in winter 1998 (Rhoads et al., 2002) and a microburst windstorm in 2013 (Battles et al., 2017). The principal effect of both of these events was on beech. First, overstorey beech is particularly susceptible to mortality caused by wind and ice loading in part because of wood rot associated with BBD (Calić et al., 2017). Second, canopy damage favoured the persistence and growth of beech in the understorey. Canopy damage from the 1998 ice storm spurred an increase in the density of the sapling layer, particularly for American beech, through opening the canopy (Rhoads et al., 2002), which 20 years later has returned to very near pre-ice storm densities (Figure 4).

These two disturbances influenced not only the treatment response but also the progression of BBD. The prevalence of *Neovectria*-caused cankers increased following both the ice storm (Rhoads et al., 2002) and the windstorm (Figure S2a). The increase in BBD severity following episodic disturbances may represent a previously underappreciated aspect of local variation in the disease progression. Episodic disturbances appear to both increase the number of trees infected and the severity of the infection (Figure S2; Rhoads et al., 2002). American beech was the most impacted species in both disturbance events at the HBEF (Battles et al., 2017; Rhoads et al., 2002; elevated mortality in most recent census post-windstorm, see Table 2). Interestingly, following the

2013 windstorm, BBD progression and canopy health diverged between the two watersheds with greater impact on REF; that is, with more severe BBD, worsened canopy health and damaged these trees were more likely to die than to recover (Figures S2 and S3). This difference may be explained partly by a greater impact of the microburst on REF (Battles et al., 2017; Cleavitt, unpubl. data); however, the pattern suggests local variation in BBD may be related to the extent and severity of past disturbance events. Further work in this area would be required to substantiate a cause and effect relationship.

4.5 | Future implications

A key question that remains from the present study is whether the restoration of soil base status will ultimately translate into a return to shared dominance between sugar maple and beech trees in northern hardwood forests subject to BBD and to a history of acid rain depletion of soil base cations. Our results indicate that the beech dominated sapling layer has created inertia in the re-balancing of sugar maple and American beech abundance on the landscape. Moreover, large-scale surveys indicate that sugar maple abundance has not increased significantly in northeastern North America even though BBD is present throughout the region (Garnas et al., 2011). Despite the improvements in sugar maple health on the treated watershed, tree mortality (Table 2) still exceeded recruitment (Table 1) in both watersheds. Likewise, growth of sugar maple remains below that of beech (Table 3) even though in the 1950s and 1960s, before the recent decline, this was not the case at the HBEF (see fig. 5 in Siccama et al., 2007). In contrast, the number of beech trees continued to increase even in CAL (Table S1). Others have posited to a link between climate change, specifically increased precipitation in the northeastern USA, and the recent increase in American beech prevalence (Bose et al., 2017). The shifting conditions created by global change effectively alters the 'playing field' not only along the edges where contractions and expansions are predicted, but even near the current centre of species' ranges, such as those studied here.

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AUTHORS' CONTRIBUTIONS

N.L.C. wrote the first draft of the paper and led revisions; T.J.F. and J.J.B. added substantial contributions to paper writing and revisions; N.L.C., N.S.v.D. and J.J.B. took part in data collection and curating; J.J.B. and N.L.C. analysed the data; T.J.F. was central to CAL treatment design. All authors have read and commented on the current paper.

PEER REVIEW

The peer review history for this article is available at <https://publons.com/publon/10.1111/1365-2745.13687>.

DATA AVAILABILITY STATEMENT

Hubbard Brook data are archived in the Environmental Data Initiative Repository (<https://portal.edirepository.org>). Watershed 1 inventory: <https://doi.org/10.6073/pasta/cab9ced139ba8e5ee1aa-be4c86e7d0bb>. Watershed 6 inventory: <https://doi.org/10.6073/pasta/0593ba15fb76a4f085797126a1bea3a7>.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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