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Article

Enemy release from beech bark disease coincides with upslope shift of American beech

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Abstract

Upslope shifts in plant distributions are often attributed to warming climate and lengthening of the growing season; however, biotic interactions may also contribute. The impacts of pests and pathogens are often sensitive to climate change and can vary along the climatic gradient associated with elevation. American beech (*Fagus grandifolia*) has moved upslope throughout the northeastern United States. Meanwhile, beech growth and longevity have decreased as a result of beech bark disease (BBD), a decline disease caused by the introduced European felted beech scale insect (*Cryptococcus fagisuga*) and native fungi from the genus *Neonectria*. Within a forested landscape spanning 250–1150 m elevation, we examined the relationships between elevation, beech demography and BBD to explore whether release from BBD at higher elevation may contribute to the upslope expansion of beech. Beech has shifted upslope at a rate of 1 m·year^{-1} coincident with lower mortality, higher recruitment, faster growth, lower BBD severity, and higher sapling densities at higher elevations. We suggest that climatic constraints on the beech scale insect at high elevations has led to a lower impact of BBD, which contributed to higher rates of beech growth, survival, and recruitment and in turn facilitated the regional upslope shift of beech.

Key words: range shift, enemy release, *Fagus grandifolia*, climate effects, Hubbard Brook Experimental Forest

Résumé

Les déplacements vers le haut de la distribution des plantes sont souvent attribués au réchauffement climatique et à l'allongement de la saison de croissance, mais les interactions biotiques peuvent également y contribuer. Les impacts des ravageurs et des pathogènes sont souvent sensibles au changement climatique et peuvent varier le long du gradient climatique associé à l'altitude. Le hêtre américain (*Fagus grandifolia*) s'est déplacé vers le haut de la pente dans tout le nord-est des États-Unis. Pendant ce temps, la croissance et la longévité du hêtre ont diminué en raison de la maladie corticale du hêtre, une maladie de dépérissement causée par la cochenille du hêtre feutré (*Cryptococcus fagisuga*) introduite en Europe et par des champignons indigènes du genre *Neonectria*. Au sein d'un paysage forestier s'étendant de 250 à 1150 m d'altitude, nous avons examiné les relations entre l'altitude, la démographie du hêtre et la maladie corticale du hêtre afin d'explorer si la libération de cette maladie à haute altitude peut contribuer à l'expansion du hêtre vers le haut de la pente. Le hêtre s'est déplacé vers le haut de la pente à un taux de 1m par an, coïncidant avec une mortalité plus faible, un recrutement plus élevé, une croissance plus rapide, une gravité moindre de la maladie et des densités plus élevées de gaules à des altitudes plus élevées. Nous suggérons que les contraintes climatiques sur la cochenille du hêtre à haute altitude ont conduit à un impact plus faible de la maladie corticale du hêtre, ce qui a contribué à des taux plus élevés de croissance, de survie et de recrutement du hêtre et a aussi facilité le déplacement régional du hêtre vers le haut de la pente. [Traduit par la Rédaction]

Mots-clés : déplacement de l'aire de répartition, libération d'ennemis, *Fagus grandifolia*, effets climatiques, forêt expérimentale de Hubbard Brook

Introduction

The mechanisms of population regulation and their role in species population shifts are shared at many scales including expansion of populations at their local edges, species introductions and invasions, and broader range expansions (Mlynarek et al. 2017). For a plant species to extend its range, even locally, there must be changes in the various biotic and abiotic factors that regulate the population. Changes in climate, avoidance of herbivores, shifts in the competitive hierarchy, and alterations of the disturbance regime can promote a plant species' range expansion (Engelkes et al. 2008; Peters et al. 2020; Nigro et al. 2022) while limitation by edaphic conditions and priority effects may impede expansion (Zhu et al. 2012; Solarik et al. 2018). Recent documentation of range expansion by American beech (*Fagus grandifolia* Ehrh.) in northeastern North America has been interpreted mainly as a response to climate change (Bose et al. 2017; Boisvert-Marsh et al. 2019) although land use legacies also have been suggested as a potential mechanism (Wason and Dovciak 2017). However, throughout northeastern North America beech has been infested with beech bark disease (BBD), a decline disease that causes increased morbidity and mortality particularly in large adult trees (Cale et al. 2017). Given the impact of the disease on survival, growth, and reproduction of beech (i.e., the vital rates), variation in the prevalence and (or) severity of BBD across beech's distribution may play a role in the recent range shifts of beech. In this study, we investigated whether a reduction in the exposure to BBD and its negative impacts contributed to the observed range expansion of beech through an enemy escape mechanism (Parker and Gilbert 2007).

BBD involves both an exotic insect, the introduced European felted beech scale (*Cryptococcus fagisuga* Lind.), and native pathogens, canker fungi of the genus *Neonectria*, as well as a native insect *Xylococcus betulae* (Cale et al. 2015). Typically, the invasion of the exotic beech scale insect precedes canker formation by the fungi by a decade such that limitations to insect dispersal, establishment or growth should stall disease progression (Dukes et al. 2009). At the landscape scale, a small fraction of beech (<2% of adult stems) appears resistant to BBD (Houston 1994) though there may be greater resistance with increasing latitude (Taylor et al. 2013; 2.2% resistance in south and 5.7% in the north). The beech scale insect is sensitive to cold winter temperatures (Houston and Valentine 1988), which also may explain increased resistance to BBD with increasing latitude.

To date, BBD has invaded about a third of the range of American beech and over half of the total beech stems (Garnas et al. 2011; Cale et al. 2017). Disease severity of BBD is influenced by a complex suite of factors operating at different temporal and spatial scales. Time since infection is the critical temporal factor (Garnas et al. 2011). At the scale of the individual, tree size, vigor, canopy position, and innate genetic resistance influence BBD severity (Evans et al. 2005; Cale et al. 2017). At the landscape-scale, BBD severity varies with slope, aspect, and elevation, but the impact of these landscape features on disease progression is inconsistent (Griffin et al. 2003; Evans et al. 2005; Mulder et al. 2020).

At the Hubbard Brook Experimental Forest (HBEF) in New Hampshire, BBD arrived around 1970 (Siccama et al. 2007) and its spread has been tracked since then (Cleavitt et al. 2021). Although research at a single site like the HBEF may limit broader generalization, it allows elucidation of processes that underlie broader patterns if the patterns also occur within the site (Fahey et al. 2015). We leveraged results from an intensive landscape-level plot network where tree population dynamics have been assessed for 20 years to address our overarching hypothesis that escape from BBD has contributed to range shift of beech. To evaluate this hypothesis, we answered the following questions: (*i*) Is the range of beech shifting upslope at the HBEF? (*ii*) What is the spatial pattern of BBD severity across the HBEF landscape? (*iii*) How does beech demography vary with elevation and BBD severity? (*iv*) How does the growth of individual beech trees vary with BBD severity? (*v*) Are there tree and plot-level factors associated with differences in BBD rating for individual beech trees?

Methods

Study area

The Hubbard Brook Experimental Forest (HBEF) is a 3160 ha long-term ecological research (LTER) site located in the White Mountains of central New Hampshire, USA (43°56′N, 71°45′W). The soils are primarily well-drained Spodosols (coarse, loamy, mixed, frigid, Typic Haplorthods) with sandy loam to loamy sand textures. The climate is continental, characterized by short, warm summers and long, cold winters. However, the climate has been getting both warmer and wetter over the measurement period (1969–present) particularly at low elevation south-facing stations (Supplementary Table S1). Warming has largely been in the winter with growing season length increasing at lower elevations but not at higher elevations (Supplementary Table S1). Increased precipitation has occurred in the growing season with a notable increase in high rainfall events (Supplementary Table S1).

The HBEF was selectively logged in the late 1800s and then again between 1906 and 1920. By 1920, 40% of the valley was "cutover" (C.V. Cogbill, 1989 unpublished manuscript). The 1938 hurricane created patches of blowdown; the most accessible patches were subsequently salvage logged. In 1998, an ice storm caused considerable structural damage to an elevation band between 600 and 800 m (Rhoads et al. 2002) on the south-facing slopes. The current age structure of the forest can be described as multiaged (mainly 60–120 years old), with most of the present-day trees established after the 1906 and 1920 harvests along with individual trees that predate these disturbances. The HBEF is dominated by the northern hardwood forest (71% by area) with the higher elevations supporting a subalpine conifer forest (20% by area). American beech, sugar maple (*Acer saccharum* Marsh.), and yellow birch (*Betula alleghaniensis* Britt.) are the most abundant species in the northern hardwood forest; red spruce (*Picea rubens* Sarg.) and balsam fir (*Abies balsamea* (L.) Mill.) are the two common species in the subalpine conifer stands found primarily on ridges and rocky areas (van Doorn et al. 2011). The lower reaches of the HBEF support mixed forest with eastern hemlock (*Tsuga canadensis* Ehrh.) abundant in the riparian areas and red maple (*Acer rubrum L.*) common in the uplands (9% by area).

Forest surveys

The footprint of the HBEF coincides with Hubbard Brook Valley defined by Mt. Cushman (northwestern flank) and Mt. Kineo (southwestern flank) at the head of the valley and Mir-

Table 1. Description of plot- and tree-level variables for plots containing American beech in the Hubbard Brook valley-wide plot network ($N = 286$ plots and 1263 trees included in this study).

Variable	Measurement	Measurement taken	Range in dataset	Mean in dataset
Plot level				
Elevation	Elevation above sea level of plot center in metres taken with a calibrated altimeter	Original survey	245–860 m	570 m
TASL	Slope corrected transformed aspect $(-1 \times \cos(a - 45) \times \sin(s))$	Original survey	−0.3684 (steep NE) to +0.3106 (steep SW)	0.0216
Plot BA	Total basal area of tagged trees (>10 cm) in 500 m^2 plot area	All surveys 1995	6.33–58.93 m^2·ha^{-1}	17.10 m^2·ha^{-1}
BBD gradient	Based on spatial analysis of BBD severity (% of trees with most severe (ratings 3 and 4) rating)	2015	High, neutral, low	NA
Sapling density	Species and size for all tree stems (2.0–9.9 cm DBH) in a 50 m^2 transect (2005 and 2015) and 24 m^2 transect (1995)	All surveys		
		1995	1–26 stems	6.2 stems
		2015	1–19	5.2
Tree recruitment	Per area rate of trees reaching the 10 cm DBH size class	1995–2015	0–180 trees·ha^{-1}·year^{-1}	5 trees·ha^{-1}·year^{-1} (median)
Tree mortality	Per area rate of trees that died	All resurveys	0–80 trees·ha^{-1}·year^{-1}	1 tree·ha^{-1}·year^{-1} (median)
Tree level				
Tree growth	Relative change in basal area increment (rBAI) between surveys for live trees >10 cm DBH	All resurveys	0%–1.77%·year^{-1}	0.32%·year^{-1}
BBD rating	Five-point scale used to rate extent of BBD on tree	Most recent survey	0, 1, 2, 3, 4	2 (median)
Crown position	Position of the tree canopy in relation to its neighbors, four classes	All surveys	Sup, Int, CoD, Dom	NA
DBH	Diameter of the tree at breast height (1.37 m from ground surface on the upslope side of the tree)	All surveys		
		1995	10–55.1 cm	18.5 cm
		2015	10–66.0 cm	21.1 cm

ror Lake at the mouth. A valley-wide network of permanent plots was installed over two field seasons (1995 and 1996) and consists of 371 circular plots 0.05 ha in area (Supplementary Fig. S1; Schwarz et al. 2003; van Doorn et al. 2011). The plots have been surveyed three times at 10-year intervals; for simplicity, we designate the year of each inventory by the first year of measurement (i.e., 1995, 2005, and 2015). Plot descriptions included elevation, aspect, and slope (Schwarz et al. 2003; Table 1). All live trees $\geq$10 cm diameter at breast height (1.37 m, DBH) were permanently tagged, measured to the nearest 0.1 cm DBH, and identified to species. For the 2005 and 2015 surveys, understory tree composition was measured in a 2 m wide transect that spanned the north–south diameter of each plot. In 1995, the sapling transect width was 1 m. Tree saplings ($\geq$2 cm DBH and <10 cm DBH) were measured to the nearest 0.1 cm DBH and identified to species. See Schwarz et al. (2003) and van Doorn et al. (2011) for details on survey protocols. For the two resurveys, live trees that had grown into the 10 cm DBH class were tagged and added to the database as recruits. For all tagged trees, we also assessed vigor and canopy position. Vigor is based on a visual evaluation of the canopy health and does not include wounds to the stem. Canopy position includes four categories: dominant, co-dominant, intermediate, and suppressed. These categories are judged visually relative to neighboring trees and reflect the amount of canopy exposure. Of the 371 plots, 294 total contained beech in at least one sample time as tagged beech trees (286 plots) or saplings (272 plots).

Tracking of BBD

The earliest observations of BBD at HBEF were from 1977 and only indicated the proportion of stems with the scale insect present or with canopy decline (Cleavitt et al. 2021). In 2012, a more detailed rating system for BBD presence and severity was added to our forest surveys. To better capture gradients in disease presence, we extended the rating system in the 2015 census to a five-point scale (similar to Rhoads et al. 2002): 0, tree clean of both scales and 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 cankering coalesced and the outline of the tree completely disfigured. We defined the ratings of 3 and 4 to represent “severe” BBD. There were few trees with a BBD rating of 0; therefore, for the growth analysis we combined these trees with category 1 trees.

We sampled *Neonectria* fungus on 15 of the valley-wide plots in late August of 2015 and 2016 using a chisel to remove a superficial layer of bark containing the fruiting bodies. *Neonectria* plots were selected to include beech-dominated plots across the full range of elevation and aspects (Supplementary Fig. S1). For each plot, we sampled the first five beech trees encountered with fruiting *Neonectria*; sometimes we had to sample trees adjacent to the plot. Samples were identified under the microscope using both macroscopic and microscopic features (after Kasson and Livingston 2009).

Analytical framework

We took a deliberatively conservative approach to detecting change in beech's distribution in the HBEF. Documenting range shifts in plant species is fraught with challenges particularly the potential to confound differences in space with differences in time (e.g., Crimmins et al. 2011). The valley-wide plot network is designed to quantify the landscape-level patterns and processes in community dynamics. We took advantage of this design and the repeated inventories. Thus, our analysis included an array of models that account for confounding spatial (e.g., spatial autocorrelation in BBD prevalence) and demographic processes (e.g., heterogeneity in subpopulations). To select among competing models, we employed an information theoretic approach but used caution in its application (Richards 2005). Analyses were limited to consideration of main effects given the ratio of potential variables (max = 7) to sample sizes (e.g., number of plots ≤286). Unless otherwise noted, statistical programming used R version 4.1.0 (R Core Team 2021).

Spatial analysis

To describe the extent of beech in the HBEF, plots were categorized by the status of beech in the plot through time. The categories were (*i*) plots where beech was present and tagged in 1995, (*ii*) plots where beech has recruited to tagged tree size since 1995, and (*iii*) plots where beech was absent in all surveys (Supplementary Fig. S2).

To quantify elevational range shifts of the major tree species, we first calculated the species mean elevation (SME) for each measurement interval (sensu Zhang et al. 2019). SME represents the center of each species' elevational distribution (Chen et al. 2009) and was estimated as the abundance-weighted mean for a given species across all plots. For trees, we used basal area as the measure of abundance; for saplings, we used density. Range shifts were evaluated as the change in SME, specifically,

$$\text{(1)}\qquad \mathrm{SES}_j = \frac{\sum_{i=1}^{N}\left(\mathrm{SME}_{i,j,t_2} - \mathrm{SME}_{i,j,t_1}\right)}{N}$$

where SES_j is the species elevation shift of species j, i is the plot, N is the total number of plots, t_2 represents the year of the remeasurement, and t_1 represents the year of the previous measurement. To evaluate the statistical significance of observed SES_j from 1995 to 2015, we generated null results by randomly shuffling assignments of plot elevation and calculating SES_j for 1000 iterations. Observed values that exceeded the 95% confidence interval of the null distribution were considered significant.

Spatial gradients in the prevalence of BBD (BBD gradient) were quantified using a hotspot analysis based on the severity of BBD in each plot. Severity was defined as the percent of trees in the plot with a severe (category 3 or 4) BBD rating. To account for spatial autocorrelation in the data (assessed with Moran's I), hotspot analysis was run using the Optimized Hotspot Analysis tool in ArcGIS Pro. We used the Getis-Ord Gi$*$ statistic (Getis and Ord 1992) to identify spatial clusters of features that deviated from values (z-scores) that would be expected to occur by random chance (ESRI 2013). The fixed distance band (817 m) was defined by the ArcGIS algorithm as the distance where z-scores peaked. This distance was used as a threshold for determining whether plots were considered as "neighbors" in the clustering analysis.

Demographic analysis

To describe the 20-year trends in beech population dynamics, we calculated annual, per capita (i.e., %·year^{-1}) rates of mortality (m) and recruitment (r) for beech and compared them to the collective rates for the nine most abundant tree species in the HBEF (defined as the tree community). The rate of change in species abundance, namely population growth (g), was calculated as the difference between mortality and recruitment rates. We applied a Bayesian analytical framework to account for the nonlinear functional forms of these vital rates and the heterogeneity among subpopulations (size for beech, size and species for the community analysis, Kohyama et al. 2018; Cleavitt et al. 2021). Statistical relevance was evaluated using 95% credibility intervals of the posterior distributions.

We calculated plot level, per area rates (i.e., trees·ha^{-1}·year^{-1}) of mortality (M_a) and recruitment (R_a) of beech trees (Kohyama et al. 2018) to understand how these vital rates varied with elevation and BBD gradient (as measured with hotspot analysis, above). This analysis was restricted to plots with at least one live beech tree present in the 1995 survey and 2015 surveys ($n = 249$ plots). Given that M_a and R_a represent count data and that our plot-level results had zero values, we applied negative binomial generalized linear regressions (Martin et al. 2005) with the dependent variable being the per-area vital rate. Differences in slope and aspect were accounted for with a single metric: the slope-corrected transformed aspect (TASL, Lookingbill and Urban 2004). Independent variables included TASL, plot elevation and BBD gradient (i.e., high, neutral, and low BBD) (Table 1). To account for differences in beech abundance among plots, we included additional fixed variables: beech basal area for M_a and beech sapling density for R_a. The best model among all additive combinations was determined using Akaike's information criterion (AIC) with the correction for small sample sizes (Burnham and Anderson 2002).

Tree-level analyses

Individual tree growth rate was calculated as the relative basal area increment (rBAI):

$$\text{(2)}\qquad \mathrm{rBAI} = \frac{\mathrm{BA}_{t1} - \mathrm{BA}_{t0}}{\mathrm{BA}_{t0}} / \triangle t \times 100$$

where rBAI is measured in $\%\cdot\text{year}^{-1}$; BA_{t0} is the basal area of tree at the initial measurement t_0 (time 0); BA_{t1} is the basal area of the tree at the next measurement, t_1 (time 1); and Δt is the time in years between the measurements ($t_1 - t_0$). We used a linear mixed model to estimate the relationships between growth rates for tagged beech trees that survived the most recent 10-year census period (2005–2015) and fixed terms for both plot level: plot basal area, elevation and TASL and tree level: tree diameter (DBH), crown position and BBD ratings (0–4) (Table 1). The influence of plot was included as random intercept term. The model with the lowest AIC value was selected.

We fit an ordinal regression model to investigate sources of variation in the 2015 BBD ratings (0–4) of individual trees. The regression model included a random effect of plot, with fixed terms that included DBH, crown position, plot elevation (rescaled to a mean of 0 and standard deviation of 1 due to large magnitude), plot basal area, and plot TASL (Table 1). We used the "ordinal" package within R to estimate the full additive model (Christensen 2019), and then the dredge function from the "MuMIn" package (Bartoń 2020) to estimate all possible model variable combinations from the full model. We selected the best-fit model based on AIC values.

Results

Plot-level demographic patterns and change

Total tree basal area (mean ± standard error) was remarkably stable over the 20 years (1995: $29.5 \pm 0.1\ \text{m}^2\cdot\text{ha}^{-1}$; 2005: $29.6 \pm 0.1\ \text{m}^2\cdot\text{ha}^{-1}$; 2015: $30.8 \pm 0.1\ \text{m}^2\cdot\text{ha}^{-1}$) while sapling density (mean ± standard error) decreased (1995: $1695 \pm 25\ \text{saplings}\cdot\text{ha}^{-1}$; 2005: $1413 \pm 24\ \text{saplings}\cdot\text{ha}^{-1}$; 2015: $1399 \pm 18\ \text{saplings}\cdot\text{ha}^{-1}$). Species composition was also stable through time. As measured by relative dominance, defined as relative basal area for trees and relative density for saplings, most species maintained their abundance in the community, although conifer species increased at the expense of birch species (Supplementary Table S2).

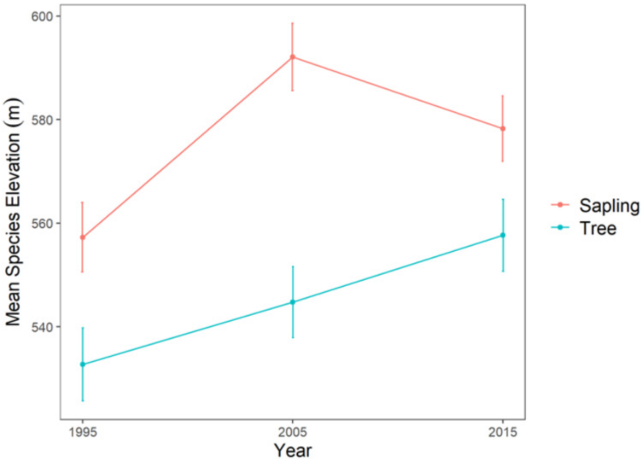
The extent of beech in the valley-wide plots has increased 5% (26 plots) for newly tagged trees (recruits) and 7.5% (28 plots) for saplings in 20 years (1995–2015) (Supplementary Fig. S2). Beech was present in the sapling layer in more than half of the valley-wide plots over the 20 years ($N = 272$ plots). Beech was the most demographically dynamic tree species with higher median recruitment, mortality, and population growth than the overall community (Supplementary Table S3).

Spatial patterns

Beech shifted upslope from 1995 to 2015 (Fig. 1). Mean elevation of saplings had a significant upslope shift (21.0 ± 9.8 m; Table 2; Supplementary Fig. S3), and beech trees exhibited the largest upslope shift of any species (24.9 ± 13.6 m; Table 2; Supplementary Fig. S4) although the shift was not significantly different from the null value.

Elevation and BBD gradient were highly correlated (Pearson's $r = 0.70$; $p < 0.0001$) (Table 3). For every 100 m increase in elevation, the BBD severity % (percentage of trees with BBD rating of 3 or 4) decreased overall by 7%. BBD was not significantly related to other plot variables but showed a pattern of greater severity at the eastern mouth of the valley where all the high BBD plots were located (Fig. 2). We found 32 BBD high spots and 27 BBD low spots (95% confidence) out of the 246 plots containing tagged and rated beech trees. All *Neonectria* collections regardless of elevation or aspect were identified morphologically from sporocarps as *N. faginata*.

Fig. 1. Change in mean species elevation for American beech saplings (2–9.9 cm diameter) and tagged trees (≥10 cm diameter) over 20 years at Hubbard Brook Experimental Forest, NH. Error bars represent the standard error of the mean. Statistical analysis for the data is given in Table 2. [Colour online]



Elevation or BBD gradient category was included in the best models ($\Delta\text{AIC}_c < 2$) for per-area vital rates (Supplementary Tables S4 and S5). Recruitment decreased in BBD high spots and increased at higher elevations (Fig. 3A). Mortality declined with increasing elevation (Fig. 3B) and increased with TASL (i.e., warmer, southwest facing slopes). For example, from 400 to 800 m in elevation, mortality decreased by half (4 to 2 $\text{trees}\cdot\text{ha}^{-1}\cdot\text{year}^{-1}$) and recruitment more than doubled (13 to 32 $\text{trees}\cdot\text{ha}^{-1}\cdot\text{year}^{-1}$; Fig. 3).

Tree-level patterns and change

Beech growth rate (relative basal area increment) was best predicted by tree DBH, plot elevation, tree crown position, plot basal area in 1995, and BBD rating (Fig. 4; Supplementary Table S6). Beech tree growth rate increased with elevation and decreased with increasing tree diameter, plot basal area, and higher BBD rating (Fig. 4; Supplementary Table S6). Surprisingly, trees with intermediate crown position were growing the fastest (Fig. 4).

The best-fit model (lowest AIC value) of all possible combinations of the full ordinal regression model for BBD rating included tree DBH, plot elevation and TASL (Supplementary Table S7). Elevation captured large effects on the BBD ratings, with lower BBD ratings at higher elevations. No "clean" beech (BBD rating = 0) and only a small percentage (11%) of lightly affected (BBD = 1) beech were found below 450 m. Tree DBH had a significant ($p < 0.05$), but small impact on BBD rating with bigger trees tending toward worse BBD ratings

Table 2. Species elevation shifts (SES in m) over 20 years (1995–2015) for the nine most common species (98% of the basal area) in 371 plots throughout the Hubbard Brook Experimental Forest, NH, USA.

Species	Mean elevation 1995 (m)	Mean elevation 2005 (m)	Mean elevation 2015 (m)	SES observed	SES$_{null}$ mean (95% CI)
Saplings (stems 2–9.9 cm in diameter)*					
American beech	557.3	592.1	578.2	21.0	– 0.1 (–19.9 – 18.6)
Balsam fir	788.8	781.0	776.0	– 12.9	0.6 (–37.7 – 40.4)
Eastern hemlock	331.1	362.7	393.5	62.4	– 1.4 (–118.7 – 119.5)
Paper birch	769.0	802.1	800.2	31.2	4.9 (–120 – 140.7)
Red maple	576.7	525.0	490.0	– 86.7	– 2.9 (–328.4 – 310.0)
Red spruce	678.4	695.1	684.0	5.6	0.5 (–30.6 – 33.6)
Sugar maple	565.9	575.3	571.2	5.3	0.7 (–60.7 – 58.6)
Yellow birch	618.4	651.6	669.2	50.8	– 0.2 (–65.5 – 64.9)
Trees (stems ≥10 cm in diameter)					
American beech	532.7	544.8	557.7	24.9	– 0.1 (–25.6 – 26.6)
Balsam fir	767.5	762.4	770.0	2.5	0.0 (–25.0 – 23.3)
Eastern hemlock	422.8	422.2	422.7	– 0.1	0.1 (–59.2 – 63.5)
Paper birch	763.7	768.3	784.5	20.8	0.0 (–31.7 – 32.7)
Red maple	507.2	506.5	507.8	0.5	– 0.4 (–39.3 – 43.9)
Red spruce	660.5	659.0	671.6	11.2	0.7 (–29.9 – 30.5)
Sugar maple	590.6	591.7	588.5	– 2.1	0.1 (–24.4 – 24.3)
White ash	459.1	460.3	459.6	0.5	– 0.9 (–66.7 – 63.3)
Yellow birch	596.3	593.7	594.0	– 2.3	0.3 (–19.2 – 20.3)

Note: The observed shifts are compared to null model from 1000 permutations.
*White ash had no saplings.

Table 3. Impact of beech bark disease (BBD) on beech demographic rates, recruitment and mortality, and correspondence with plot elevation for plots within the Hubbard Brook Experimental Forest, NH.

		Recruitment (trees·ha^{-1}·year^{-1})		Mortality (trees·ha^{-1}·year^{-1})		Elevation (m)	
BBD gradient	*n*	Mean	SE	Mean	SE	Mean	SE
Low BBD	27	4.0	6.1	1.0	0.5	602.7	10.4
Neutral	190	6.0	2.5	1.0	0.6	592.4	8.1
High BBD	32	2.5	3.8	4.5	0.7	361.4	10.0

Note: The BBD gradient is derived from hotspot analysis of spatial patterning of severity of BBD ratings across the valley (Fig. 2). Statistical results from negative binomial regression modeling (Supplementary Tables S4 and S5) include the sample size (*n*), the mean, and the standard error of the mean (SE).

(Supplementary Table S7b). While TASL improved model fit and decreased with BBD rating (lower ratings on cooler northeast facing slopes), it was not a significant parameter for BBD rating (Supplementary Table S7b).

Discussion

In the HBEF, both the extent of BBD and its impact on beech population dynamics were inversely correlated with elevation. The consistency of these patterns and processes suggests that the differential impact of BBD along the elevation gradients is important among the drivers of the documented upslope population shift of beech. Previous reports of beech advancing upslope in the region have posed climate change and land use history as explanations (Wason and Dovciak 2017; Bose et al. 2017). Escape from enemies has not been previously considered as an explanation for this range expansion. Although our observations are correlative, our results suggest that release from BBD plays a role in the regional pattern of beech expansion upslope.

Impact of a changing climate on beech elevation shift

In general, dominant tree species in montane forests are expected to shift their range uphill in response to warming (Frei et al. 2010). Warming trends at the HBEF during the last 20 years (1995–2015, Supplementary Table S1) follow the regional pattern, namely annual mean air temperature has increased with more warming in the winter than in the summer. However, we did not detect a consistent uphill shift of the other common tree species (Supplementary Figs. S3 and S4). Of the three northern hardwood species that share dominance at the HBEF (Supplementary Table S2), only beech moved uphill. Yet based on a regional analysis, the

Fig. 2. Valley-wide plot network in the Hubbard Brook Experimental Forest, NH showing the gradient in severe beech bark disease (BBD) with high BBD (red), low BBD (blue), and neutral (black) from the optimized hotspot analysis ($p < 0.05$). The gradient was based on the percentage of trees with severe (category 3 and 4) individual tree ratings in each plot. Open dots represent plots where beech is absent. [Colour online]

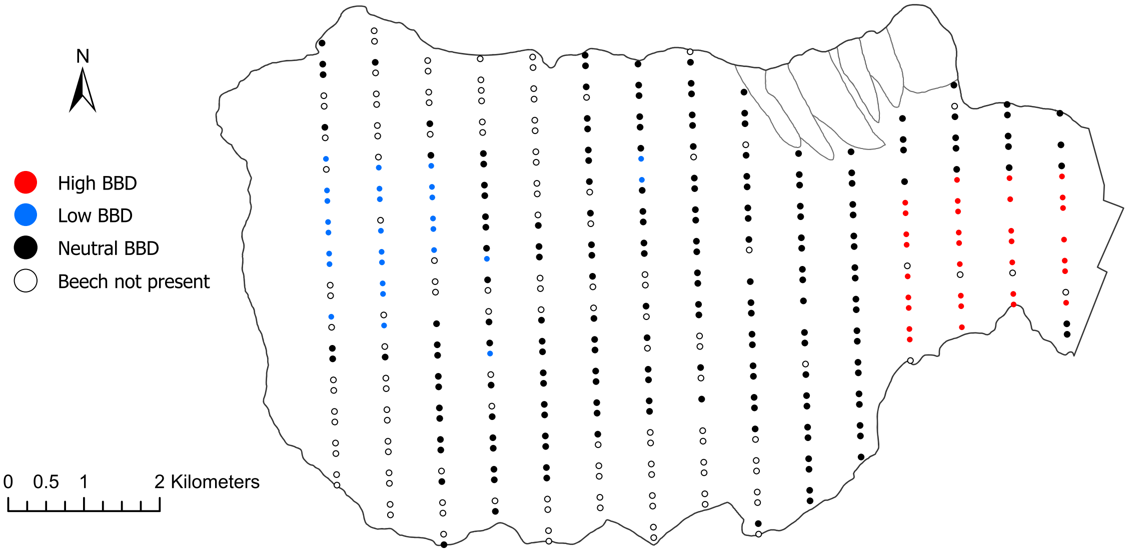
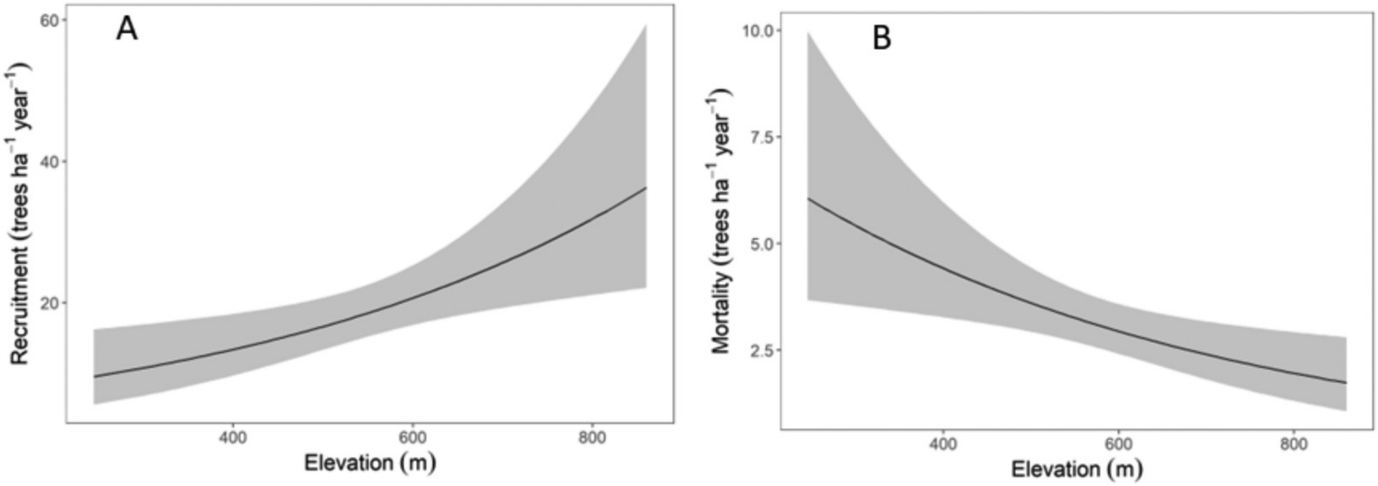


Fig. 3. Relationship of tree vital rates to elevation over 20 years at Hubbard Brook Experimental Forest, NH. Black lines represent the predicted value; gray shading denotes the 95% confidence interval of the predictions. (A) Predicted tree recruitment as a function of elevation (Model R ∼ Elevation; Supplementary Table S4). (B) Predicted tree mortality as a function of elevation (Model: M ∼ Elevation + TASL; Supplementary Table S5). TASL was assigned the mean value for these predictions.



distribution of beech is less sensitive to climate drivers in comparison to co-occurring species (Wason and Dovciak 2017). This regional result is consistent with species-wide traits: American beech is relatively insensitive to climate based on dendroclimatic analyses (Tardif et al. 2001; Nolet and Kneeshaw 2018) and its expected migration in response to climate change is modest compared to other tree species (Peters et al. 2020). American beech has the widest thermal range of any congeners globally (Fang and Lechowicz 2006), and although growing season warmth may be important to northward expansion most of the annual increase in temperature at the HBEF has been for the dormant season and not the growing season. Moreover, the growing season has only lengthened in the lowest elevations (Supplementary Table S1); a pattern also found on a broader elevational gradient in the White Mountains of NH (Seidel et al. 2009). Unless the warming results in increased growing season length it has very limited benefit to winter deciduous trees.

Climate change can differentially affect members of a pathosystem (Jactel et al. 2019; Dudney et al. 2021), and BBD is particularly complex because the impact on the host beech tree is the result of an interaction between an invasive insect and native fungi. However, both members of the BBD system appear to be sensitive to cold temperatures at higher elevations. In particular, beech scale insects are vulnerable to winterkill from low temperatures (−25 °C; Houston and Valen-

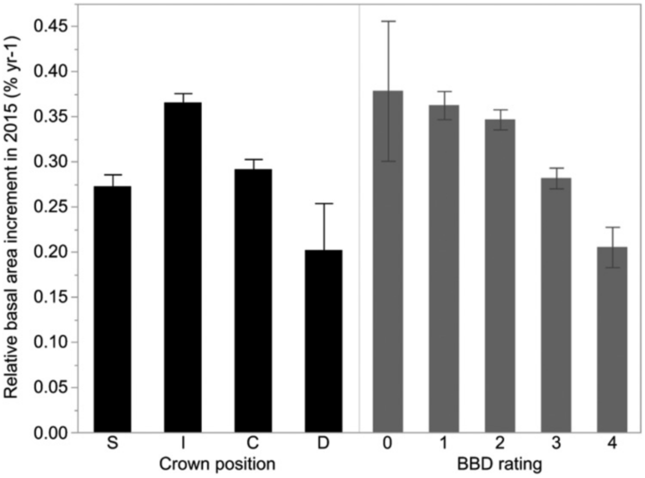


Fig. 4. Impact on beech tree growth rate as basal area increment (mean ± standard error) between 2005 and 2015 by canopy position: S, suppressed; I, intermediate; C, codominant; D, dominant and BBD rating: 0–4 from least to worst beech bark disease presence.

tine 1988; Kasson and Livingston 2011), and while warming winters could potentially allow the scale to extend its range upslope, the number of very cold (<−20 °C) days has remained relatively greater at higher than lower elevations (Supplementary Table S1). Similarly, the *Neonectria* fungus involved in BBD at the HBEF, *N. faginata*, is less cold tolerant than related species (Morrison et al. 2021). Thus, at the HBEF both the invasive scale insect and the dominant fungus are constrained from moving upslope into colder conditions.

Another aspect of the changing climate at the HBEF Hubbard Brook is the increase in annual precipitation and the frequency of heavy rainfall events (Supplementary Table S1). Although beech upslope expansion has been associated with increasing precipitation (Bose et al. 2017), this explanation seems unlikely for the HBEF. In temperate mountain climates, precipitation typically increases with elevation within the HBEF (Bailey et al. 2003); thus, because higher elevation sites already receive more precipitation than lower elevation sites, increasing precipitation would be unlikely to favor beech expansion upslope. However, heavy rain events in late summer and early autumn may wash beech scale insects from the tree stems in their exposed crawling stage (Kasson and Livingston 2011). At the HBEF, precipitation has increased most in summer with significantly more days with heavy rain events and a significant increase in maximal 24 h rainfall amounts during August–October window most relevant to decreasing scale populations (Supplementary Table S1). The increase in the intensity of summer and early autumn rain events may suppress the buildup of scale populations (Dukes et al. 2009; Kasson and Livingston 2011).

Other explanations for the beech elevation shift

As Wason and Dovciak (2017) note, disturbance legacies and edaphic factors can confound simple climate-envelope predictions of species range shifts. In their study, beech expansion was best explained by the extent of past logging. However, the most recent logging in HBEF was a limited salvage operation that followed the 1938 hurricane (Peart et al. 1992). The possible role of soil nutrient availability and soil acidification in the upslope expansion of beech is hard to evaluate, but beech is clearly less sensitive to base-poor soil than its associated species (Lee et al. 2005; Cleavitt et al. 2021).

The role of spatial constraints on spread of BBD in explaining the observed pattern within the HBEF deserves attention. The valley-wide plots were established in the mid-1990s, about 20 years into the local progression of BBD (Cleavitt et al. 2021). Thus, at the time of the 2015 inventory, BBD had been present throughout valley for about 40 years. Regional spread is predicted to be 14.7–16 km·year^{-1} (Cale et al. 2017), which is about twice the length of the Hubbard Brook Valley. Moreover, as noted earlier, there were very few beech trees in 2015 that were clean of the scale. Therefore, despite its ubiquity in the HBEF, severe BBD impacts remain concentrated in the lower elevation forests near the mouth of the valley (Cleavitt et al. 2021; Fig. 2).

Conclusion

Given the severe effects of BBD on growth and survival of beech (Gavin and Peart 1993; Gove and Houston 1996), advantages for beech in escaping these impacts would be exactly those we report here: improved growth, increased recruitment, and decreased mortality. The overall population shift reflects higher mortality in lower elevation plots, higher recruitment in higher elevation plots and some expansion of beech into plots where it was not previously present. We suggest that climatic constraints on the beech scale insect at high elevations has led to a lower impact of BBD, which contributed to higher rates of beech growth, survival and recruitment and facilitated the overall regional upslope shift of beech. The role of release from pests and pathogens in population shifts with climate has recently been highlighted (Urli et al. 2016) and our study adds to this emerging field of research that extends the enemy release hypothesis as a potential mechanism for local upslope expansions.

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Data availability

Data (Battles, Cleavitt, and Fahey 2022) are available through the Environmental Data Initiative at https://doi.org/10.6073/pasta/65b1f9e0111c189c68bc82083112fdeb. The following data were also used in this paper: USDA Forest Service, Northern Research Station. 2021*a*. Hubbard Brook Experimental Forest: Daily Temperature Record, 1955–present ver 10. Environmental Data Initiative. https://doi.org/10.6073/pasta/3afab60d54d5f2fcb1112e71f4be2106 USDA Forest Service, Northern Research Station. 2021*b*. Hubbard Brook Experimental Forest: Daily Precipitation Rain Gage Measurements, 1956–present ver 17. Environmental Data Initiative. https://doi.org/10.6073/pasta/453b49e8429a63b72419caf3b9ad6f98.

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Competing interests

The authors declare there are no competing interests.

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Supplementary material

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