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ECOSYSTEMS

Environmental Change Drivers Reduce Sapling Layer Diversity in Sugar Maple-Beech Forests of Eastern North America

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ABSTRACT

A century of beech bark disease (BBD) in North America has transformed hardwood forests by reducing the canopy biomass of American beech (*Fagus grandifolia*), even as beech has come to dominate the sapling layer of many forests. We do not understand the extent to which environmental change drivers such as climate, acidic atmospheric deposition (and its legacy of acidified soils), and invasive disease (BBD) may have contributed to this transformation. We investigated how BBD effects and tree community composition varied along a well-documented soil acidity gradient in the northeastern United States. We surveyed overstory and sapling layer tree species composition, BBD effects, and soil chemistry on 30 watersheds in forests co-dominated by beech and sugar maple (*Acer saccharum*). We analyzed potential drivers of community composition, BBD, and beech sapling density using linear models and non-metric multidimensional scaling. Predictors accounted for soil chemistry, climate, overstory beech (importance value, IV), mortality, and BBD defect. Overall overstory species composition varied most along the acidity gradient, while beech and BBD severity varied along their own distinct environmental gradient. Species composition of the overstory and sapling layers diverged significantly, with the latter dominated by beech. Beech sapling density was positively related to the proportion of standing dead overstory beech and soil exchangeable aluminum, but was unrelated to the overall proportion of overstory beech or their BBD severity. The dominance of sapling layers by beech may have resulted from a gradual accumulation of canopy-opening events precipitated by BBD and sugar maple decline, the latter driven by stressors such as acidification and climate change.

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INTRODUCTION

Worldwide, forests are under stress from introduced diseases, increasingly severe climatic disturbances, atmospheric sulfur (S) and nitrogen (N) deposition, and ongoing climate change (Bobbink and others 2010; McDowell and others 2020). These stresses are contributing to younger, shorter, and less diverse forests, altered ecosystem functions, and declining ecosystem services (Groffman and others 2012; Boyd and others 2013; Jones and others 2014; McDowell and others 2020). In the eastern United States and Canada, multiple studies have identified regeneration failures of forest tree populations, and compositional shifts in advance regeneration (seedlings and saplings) of forest tree communities, as threatening the maintenance of current overstory species composition into the future (Miller and McGill 2019; Vickers and others 2019). Forests with regeneration debts may be especially vulnerable to state shifts into non-forest communities following canopy-removing disturbances (Miller and McGill 2019). We need to understand the drivers of these demographic and structural shifts if we are to respond appropriately.

Together with sugar maple (*Acer saccharum*), American beech (*Fagus grandifolia*) is a foundational tree species of temperate deciduous (northern hardwood) forest ecosystems in the eastern United States and Canada, shaping biogeochemistry (Lovett and others 2010), provisioning food to wildlife (Rosemier and Storer 2010), and defining late succession (McNab and others 2007). Yet, beech bark disease (BBD), a complex of two scale insects (one non-native) and two necrotrophic fungi (Cale and others 2017), has transformed the functional niche of American beech by killing most large diameter stems and transitioning it to a smaller, denser component of the subcanopy (Giencke and others 2014; Lawrence and others 2018). In some cases, beech has been reported to establish thickets that undermine understory plant biodiversity (Cale and others 2013) and recruitment of co-dominants like sugar maple (Hane 2003), with negative effects on biodiversity similar to those of a dense shrub layer (compare Woodbridge and Dovciak 2022) or native-invasive species (Valéry and others 2009). While this "thicket formation" is often attributed to BBD (Cale and others 2017), high densities of beech have been reported prior to arrival of the BBD killing front (Duchesne and others 2005; Gravel and others 2011). The frequency of occurrence and density of these thickets is inconsistent relative to BBD (Cale and others 2017; Roy and Nolet 2018), with many other potential triggers, particularly land use history and climate (Nyland and others 2006). Given the potential ecological and economic implications of increasing beech densities (Cale and others 2013; Bose and others 2017), we need to develop a clearer understanding of the factors governing this change in biodiversity (Cale and others 2017).

Changing climate (for example, Huntington and others 2009; Wason and others 2017) and N and S deposition (Driscoll and others 2001; Shao and others 2020) are two well-studied aspects of global environmental change. Each is likely to interact with BBD, itself caused in part by a nonnative species of scale insect (Cale and others 2017). Such species introductions are another important component of anthropogenic global environmental change. Although research has considered interactions among BBD, climate, N and S deposition, and nutrient levels, the results are inconsistent (Cale and others 2017; Lawrence and others 2018). Recent evidence suggested that the observed increase in beech sapling density (as well as decreases in sugar maple) may be related to changing climate (Bose and others 2017). Others found contradictory associations between soil moisture, precipitation, or temperature and BBD infection frequency or severity (Cale and others 2017). While tree nutrition (bark N level) may predict disease severity (Latty and others 2003) there are few studies directly linking landscape-scale acidic deposition legacies (reduced soil pH and base cation nutrient levels) with BBD (Duchesne and Ouimet 2009; Lawrence and others 2018). Some observational studies found a negative relationship between small-diameter beech density and soil base cations (Duchesne and Ouimet 2009), while others detected a positive relationship between beech seedling density and soil pH (Roy and Nolet 2018). Given the uncertain future and uneven impacts of global environmental change, we need to know more about its potential interactions with this disease complex, the host's response, and the resultant impacts on forest structure (Cale and others 2017).

Our study investigates how biotic components of forest ecosystem health (disease, sapling density, and overstory species composition) vary with each other and with complex gradients of climate and soil chemistry (associated with historical acidic deposition). Our first objective was to determine if BBD severity and beech mortality varied with climate, soil chemistry, and the proportion of beech in the overstory. We expected that BBD would be more severe and the amount of standing dead beech greater where beech was (1) more common in the overstory and where (2) soils were more acidified. We reasoned that a greater abundance of overstory beech should lead to a greater probability of disease transmission (Giencke and others 2014), and more acidified soils with higher exchangeable aluminum (Al) content could increase physiological stress on beech (Kobe and others 2002), while past N enrichment of plant tissues might have exacerbated BBD (Latty and others 2003). Our second objective was to determine if beech sapling (thicket) density varied with measures of overstory BBD disease severity, forest structure (the proportion of beech overstory), climate, and soil chemistry. We anticipated that beech sapling density would be higher where beech was more common in the overstory, BBD symptoms were more severe, and beech mortality was higher (Giencke and others 2014). Our final, third objective was to determine how overstory and sapling species composition varied with BBD, climate, or soil chemistry. Given previous results from this soil-monitoring network (Beier and others 2012; Bishop and others 2015; Lawrence and others 2018; Page and Mitchell 2008; Sullivan and others 2013; Zarfos and others 2019), we expected that species composition in both the overstory and sapling layers would primarily be organized along the soil acidity gradient (beech and red maple more common, and sugar maple less common, in acidic soils) with additional sorting along gradients of disease severity and beech thicket density (Cale and others 2013).

METHODS

Study Area

This study was conducted in the 24,280 km^2 Adirondack Park of New York State, USA, part of a mountainous ecoregion dominated by hardwood and coniferous forests, with a mean annual growing season between 120 and 150 days (McNab and others 2007) (Figure 1). The average minimum and maximum daily temperature across the years analyzed in this study (2011 to 2015) was −1.35 and 11.05 °C respectively, while average annual precipitation was 1,384.22 mm (Thornton and others 2014). Our research was focused on the beech-maple-birch forest type (Bose and others 2017), co-dominated by sugar maple (*Acer saccharum*), American beech (*Fagus grandifolia*), yellow birch (*Betula alleghaniensis*), and red maple (*Acer rubrum*) (Refer to Table 1 for other species present) growing on coarse-textured, naturally acidic soils developed from granitic, and gneissic rock types (Baker and others 1990) that are interspersed with soils developed from a mix of rock types that provide higher acid-buffering (Darling and Peck 2016).

The Adirondacks is part of a broader ecoregion in the northeastern United States and southeastern Canada, where many forests are dominated by beech and sugar maple (McNab and others 2007; Duchesne and Ouimet 2009; Morin and Liebhold 2015; Périé and de Blois 2016; Bose and others 2017), precipitation and temperature are steadily increasing (Huntington and others 2009; Périé and de Blois 2016), and BBD is established or spreading (Cale and others 2017). Today Adirondack forests are in the "aftermath" phase of BBD (which arrived between 1960 and 1970), characterized by reinfection, mortality, high beech density, and a preponderance of small beech stems (Giencke and others 2014; Bose and others 2017; Cale and others 2017; Vickers and others 2019).

During the 1900's the Adirondacks experienced a southwest to northeast gradient of high to low acidic deposition that exacerbated a natural soil gradient that can be generally characterized by low pH, low base saturation and high exchangeable Al that gradually shifts to higher pH and base saturation and lower exchangeable Al, also in a southwest to northeast direction (Lawrence and others 2021; Sullivan and others 2013; Zarfos and others 2019). Repeated sampling of soils in the southwestern Adirondacks has shown some reversal of prior soil calcium (Ca) depletion by acidic deposition but increases in soil Ca availability were small. Within the forest floor—the primary rooting zone in the forests of this region—soil pH and exchangeable Ca have shown modest increases, while exchangeable Al has substantially decreased (Lawrence and others 2015; Lawrence and others 2021). The N deposition gradient in the Adirondacks has been linked to gradients of foliar N in overstory communities (McNeil and others 2012), regeneration, crown condition, and growth of sugar maple (Sullivan and others 2013), and plant species composition and richness in the understory (Zarfos and others 2019).

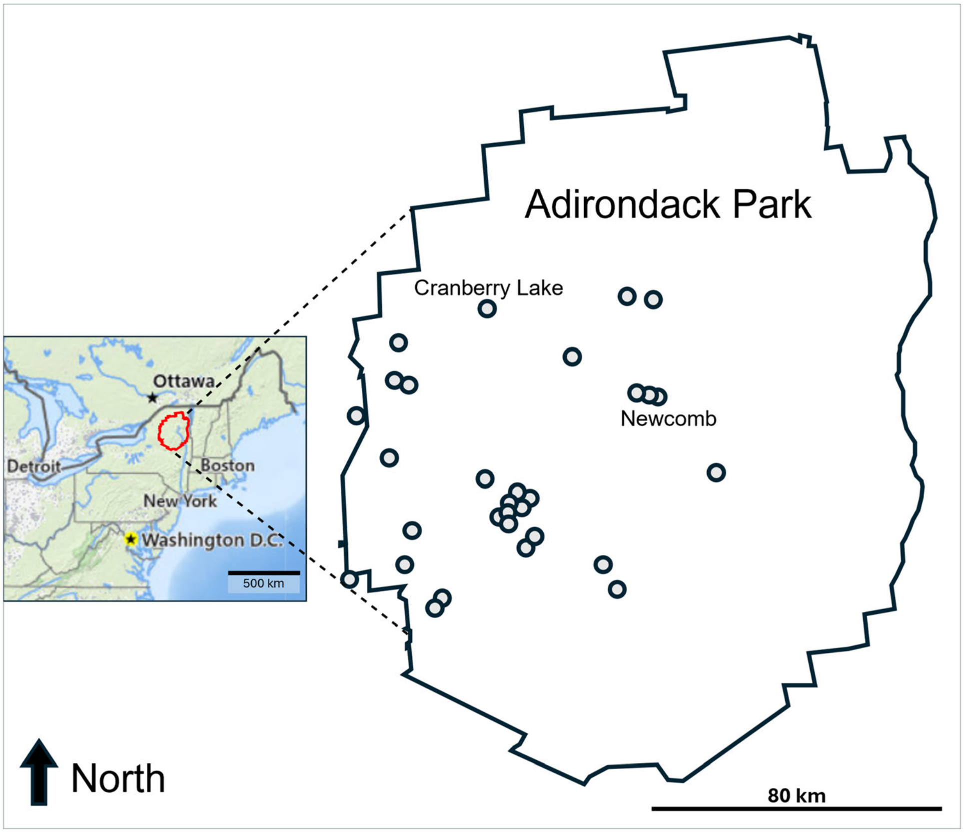

Figure 1. Locations of the 30 watersheds (points) surveyed in this study relative to the Adirondack Park Boundary and supporting research hubs of SUNY College of Environmental Science and Forestry (ESF) within the park: the Ranger School and Cranberry Lake Biological Station on Cranberry Lake, and the Adirondack Ecological Center at the Huntington Wildlife Forest in Newcomb. Inset on the left shows the location of the Adirondack Park in the context of the eastern United States (the base map is USGS National Map; https://apps.nationalmap.gov/viewer/; accessed on July 11, 2024).

Sampling Design

We conducted this study on 30 small watersheds (Figure 1) previously surveyed for soil chemistry in 2004 (n=7), 2009 (n=18), and between 2014 and 2018 (n=5) (Refer to Lawrence and others 2020, and Page and Mitchell 2008, for details on soil sampling and analysis). These watersheds have been the subject of research on relationships between acidic deposition and forest biodiversity and health (Beier and others 2012; Bishop and others 2015; Lawrence and others 2018; Sullivan and others 2013; Zarfos and others 2019). Watersheds capture a broad range of soil acidity, representative of soil conditions throughout the region (Zarfos and others 2019). For example, within our combined dataset of soils sampled between 2004 and 2018 (n=30), Ca in the O_a horizon ranged from 2.91 to 53.95 $cmol_c\ kg^{-1}$, Al in the upper B horizon ranged from 0.55 to 6.63 $cmol_c\ kg^{-1}$, and pH in the O_a and upper B ranged from 2.72 to 4.65 and 3.43 to 4.28 respectively. Importantly, all stands in our study were selected to be of comparable character (mature hardwood stands) to minimize any potential differences due to stand successional (developmental) stage (Lawrence and others 2020; Page and Mitchell 2008; Zarfos and others 2019).

The 30 sampled watersheds were selected from an initial population of 38 candidates. We evaluated potential plot (radius=80 m) locations within each watershed using a systematic process designed to reduce sampling bias. Representative soil sampling had been conducted across 33 of the 38 candidate watersheds (Lawrence and others 2020) while in five of the 38, soil samples were localized on a single historical plot (Page and Mitchell 2008). For the 33 candidate watersheds with representative soil sampling (25 of which were ultimately selected), we evaluated multiple candidate plots (radius=80 m) in each watershed (both randomly generated candidate plots and plots centered on historical soil samples). In the five watersheds that lacked representative soil sampling (all of which were included in the final selection), we only

Table 1. Glossary of Terms and Abbreviations for (a) Tree Size Classes, (b) Model Variables, and (c) Tree Species Used in the Analyses in This Study

(a) Tree size class	Description
Sapling	Stems 5 cm dbh (diameter at breast height): sampled at 16 subplots (2 m radius each) per plot
Overstory	Stems 10 cm dbh (diameter at breast height): sampled at 16 point-centered-quarter subplots per plot

(b) Model variable	Abbreviation	Units	Description
BBD defect score ^	BBD score		Index combining % cover estimates of defects on lower 2 m of overstory beech boles –refer to Table S1 for beech bark disease (BBD) defects
% Dead bole ^		%	Dead bark cover on lower 2 m overstory beech boles
Proportion dead ^			Fraction of standing dead overstory stems
Sapling count ^			Tally of beech saplings
Overstory beech IV ^	IV		Importance value of overstory beech: Sum of relative density, frequency, and basal area
Relative Density	RD		Proportion of stems of a species
Relative basal area	RBA		Proportion of total overstory basal area of a species
Total basal area ^	Total BA	cm^2	Sum of basal areas of all overstory stems
Total dead basal area ^		cm^2	Sum of basal areas for all dead overstory stems
Basal area		m^2/ha	Basal area per hectare of a species
Canopy openness ^		%	Mean canopy openness from densiometer
Temperature ^		°C	Mean annual air temperature (2011–2015; NASA Daymet)
Precipitation ^		mm	Mean total annual precipitation (2011–2015; NASA Daymet)
Snow		kg/m^2	Mean annual snow water equivalent (2011–2015; NASA Daymet)
Al ^		cmol$_c$ kg^{-1}	Exchangeable aluminum in O$_a$ or upper B horizon
Ca ^		cmol$_c$ kg^{-1}	Exchangeable calcium in O$_a$ or upper B horizon
pH ^		pH units	Acidity (pH) in calcium chloride in O$_a$ or upper B horizon

(c) Tree species	Abbreviation	Scientific Name
American beech ^+#	FAGGRA	*Fagus grandifolia*
sugar maple ^#	ACESAC	*Acer saccharum*
red maple ^#	ACERUB	*Acer rubrum*
yellow birch ^#	BETALL	*Betula alleghaniensis*
red spruce	PICRUB	*Picea rubens*
striped maple	ACEPEN	*Acer pensylvanicum*
white ash	FRAAME	*Fraxinus americana*
basswood	TILAME	*Tilia americana*
ironwood	OSTVIR	*Ostrya virginiana*
eastern hemlock	TSUCAN	*Tsuga canadensis*
black cherry	PRUSER	*Prunus serotina*

All variables averaged to the watershed level (one plot per watershed, 30 watersheds).

^ *Variable used in non-metric multidimensional scaling (NMS) secondary matrix: +indicates RD, #indicates RBA, soil variables included both horizons.*

evaluated a single candidate vegetation plot (radius =80 m), centered on the historical soil sample location in each watershed.

Candidate plots (radius=80 m) were chosen to capture a gradient of beech sapling densities including 15 thicket plots with at least 1 stem per m^2≤5 cm diameter at breast height (dbh) and≥ 1.4 m tall (satisfying the definition of a beech thicket; Cale and others 2013). However, none of the candidate plots reached this density while also satisfying our overstory criteria—a closed mature hardwood overstory presenting no evidence of management in the last 40 years and containing at least 30% beech (stems≥10 cm dbh). Ultimately, the selected plots (n=30—one 80 m radius plot per watershed) contained a range of beech basal area proportions (9–75%) and beech sapling densities (0.09–0.40 stems per m^2). Twenty-nine plots contained second growth, uneven aged, mature stands, while one plot was considered old growth. All but three of the plots were located on New York State lands excluded from management under the "forever wild" clause in Article XIV of the state constitution.

Vegetation Sampling

In 2016, we sampled the tree community in each of the 30 selected plots (radius=80 m, one plot per watershed). On each plot, we sampled a subplot located every 20 m along four transects emanating from the center in the four cardinal directions (4 subplots per each of 4 transects for the total of 16 subplots per plot). At each subplot (radius=2 m) we counted all saplings 5 cm dbh and 1.4 m tall. We then used the point-centered-quarter (PCQ) method to collect dbh, distance, and beech bark disease (BBD) data from 4 trees at each subplot (the closest tree in each quadrant of 10 cm dbh). We did not attempt to discriminate between stems originating from beech nuts or root suckers as that cannot be done in the field in a quick and reliable fashion. We calculated commonly used biotic variables (Refer to variable definitions in Table 1), averaging each to produce a single value per plot (and therefore watershed). We followed Mitchell (2010) in calculating variables from PCQ, including basal area per hectare and beech importance value (sum of relative density, relative frequency, and relative basal area). At each subplot we also took one estimate of canopy openness at 1 m height using a convex spherical densiometer (Lemmon 1956; Beeles and others 2022).

For each overstory beech that we sampled via PCQ (1,044 total), we estimated the percent coverage of defects, on the lower 2 m of bole that were likely to have resulted from the BBD complex (Table S1 shows proportions of each defect category), following Burns and Houston (1987), Giencke and others (2014), Houston and others (1979), Shigo (1962), Sinclair and others (1987), and Twery and Patterson III (1984). We combined these defects into a single index (BBD defect score), which summed to more than 100 due to overlap between categories. A tree that was covered in smooth, normal bark would have a score near or equal to zero, whereas a tree with heavily deformed bark would have a score near 100. We supplemented this estimate of BBD severity with a more conservative estimate of defect: the percent of the lower 2 m of bole covered in dead bark. This latter estimate also allowed us to tally "standing dead beech," including boles missing their crowns —a proxy for beech mortality in the preceding six or more years (Krasny and DiGregorio 2001). Standing dead trees in general can persist for many years, and tree boles, having lost their crown mass, might persist even longer (Krasny & DiGregorio, 2001), suggesting that this metric is useful in building landscape-scale models linking the distribution of standing dead beech to potential drivers of beech mortality.

Climate and Soil Data

We extracted surface climate data for each plot from the Daymet 1 km^2 raster of interpolated climate observations (Thornton and others 2014). For each plot we calculated the 2011 to 2015 average (compare Canham and Murphy 2016) of mean annual air temperature, mean total annual precipitation, and mean annual snow water equivalents (Refer to variable summaries, Table 1). These means capture climatic variation that may have impacted growth and survival of saplings, disease severity, and overstory mortality across the study watersheds at the time of field surveys. Both precipitation and temperature correlate with elevation in this region, while precipitation is also positively associated with the historical gradient of wet N deposition (Ito and others 2002; Ollinger and others 1993).

We retrieved soil data from records of previous sampling and analysis by Lawrence and others (2020) and Page and Mitchell (2008). For each watershed, we selected data from the most recent soil samples: 2004 (n=7), 2009 (n=18), and between 2014 and 2018 (n=5). While soils in this region are undergoing recovery from acidic deposition, the recovery is proceeding slowly (Lawrence and others 2015; Lawrence and others 2021). We did not detect systematic biases associated with differences in time elapsed since sampling during data exploration or model diagnostics. We had access to soil chemistry data from the uppermost 10 cm of the B horizon for all watersheds and the O_a horizon for 25 watersheds—both important rooting zones for trees across age classes (Sullivan and others 2013). For five watersheds (only sampled in 2004, Page and Mitchell 2008), the organic horizon data were predominantly from the O_a, but likely contained some O_e. As with dates, this sampling difference did not ultimately manifest as outlying or influential points in our analyses. For brevity, we will refer to all organic horizon data analyzed in this study as O_a data. For all soil variables analyzed (Table 1), a single mean value was calculated for the O_a and upper B horizon in each watershed, from all soil samples taken within the watershed, in the most recent year available. Lawrence and others (2020) and Page and Mitchell (2008) provide additional details of soil sampling and chemical analysis methods.

Modelling BBD Effects

We examined the potential drivers of BBD severity, beech mortality (standing dead beech), and beech sapling density (Objectives 1 and 2) using multiple ordinary least squares regression (OLS) and, where appropriate, generalized linear models (GLM) run in R (R Development Core Team 2020). All models were hypothesis-driven and pre-specified a priori based on peer-reviewed literature (Refer to model specifications below). We chose this approach rather than model selection, because our sample size was relatively small ($n=30$) (Heinze and others 2018). We considered these models as descriptive—valid for assessing the relationships between predictors and responses—and not meant for forecasting (Heinze and others 2018). Each of the 18 models evaluated was limited to a maximum of three predictor variables ($n/10$) (Harrell 2015) as follows:

Response = Biotic Predictor + Climate Predictor + Soil Predictor.

Before parameterizing models, we explored potential soil, climate, and biotic variables (Refer to Table 1 for definitions of each variable) following a standard protocol to identify potential outliers, collinearity among predictors, interactions, and nonindependence (Zuur and others 2010). This data exploration used functions in base R, and packages *car*, *ggplot2*, *PerformanceAnalytics*, *ape*, *sp*, and *gstat* (Pebesma and Bivand 2005; Gräler and others 2016; Wickham 2016; Fox and Weisberg 2019; Paradis and Schliep 2019; Peterson and Carl 2020; R Development Core Team 2020). Modelling assumptions were also assessed after each model run using residual diagnostic functions in base R, and packages *car*, *DHARMa*, *Performance*, and *effects* (Fox and Weisberg 2018, 2019; Hartig 2020; R Development Core Team 2020; Lüdecke 2021). Where necessary, models were advanced from the OLS to the GLM framework.

We selected Al in the upper B horizon and Ca in the O_a horizon as our two primary soil covariates of interest. Ca in the O_a is particularly relevant to tree seedlings and is generally collinear with the other base cations which are beneficial to plants (Lawrence and others 2018; Sullivan and others 2013; Zarfos and others 2019). When compared to Al and pH, Ca is generally more stable over time in northeastern forest soils undergoing recovery from acidic deposition (Lawrence and others 2015; Lawrence and others 2021). We selected Al because of its potential detrimental effects on beech seedlings (Kobe and others 2002) and the upper B horizon because this is generally the horizon where Al was mobilized by acidification (Lawrence and others 2015). Exchangeable Al in the upper B was our most normally distributed soil variable and was collinear with the largest number of alternative soil variables in patterns consistent with acidification effects from N and S deposition and natural precipitation. Since precipitation was highly collinear with our soil variables, we chose to use temperature as the predictor representing the effects of climate variation in our models.

For the first six models evaluated—our "BBD models"—we chose to model three different overstory response variables representing a range of BBD effects on beech at the landscape scale (Objective 1). BBD defect score was chosen to capture the cumulative effects of the disease complex's disparate components on individual beech trees. Percent dead bole was selected as the least ambiguous defect resulting from BBD, representing a failure to overcome localized infection or to recover from cambial necrosis. Proportion of dead beech in the overstory (standing dead) captured the terminal potential of the disease and represented a higher-level impact on the forest tree community. Each of these three responses was modeled twice (six total models), each model pair differing in the soil predictor included because of the high collinearity between Ca and Al. In addition to temperature, we included beech importance value as a third model predictor to account for any increased probability of BBD transmission where beech is a more frequent, larger, and denser component of the stand (Giencke and others 2014). Diagnostics generally suggested model compliance with OLS assumptions. Violations (slightly non-normal or patterned residuals) were always correctable by dropping one or two influential points. Because model results were unchanged by these manipulations, all data was ultimately retained. We also checked the validity of BBD defect score by running a simple OLS regression between it and the proportion of dead overstory beech.

For the final 12 models evaluated—our "thicket models" (Objective 2)—we chose to model the density rather than the relative density of beech in the sapling layer so that our results would be comparable to other work exploring the biodiversity and regeneration impacts of small-diameter beech (Hane 2003; Cale and others 2013). For ease of modelling, we used the total count of beech sapling stems per plot (summed across 16 subplots) as our response variable, rather than count per square meter. A Poisson family GLM is the standard approach to modelling a count (Bolker 2008). Ultimately, diagnostics indicated that we should progress to a negative binomial GLM (Allison 2012), which we ran in the *MASS* package (Venables and Ripley 2002). We evaluated four pairs of models for predicting beech sapling count; each included temperature as a predictor and alternated between soil variables (O_a Ca or upper B Al), while the biotic variable for each pair differed. As with the BBD models, we used beech importance value as a predictor in one model pair, but for the other pairs we used the three BBD model responses (BBD defect score, % dead bole, proportion dead overstory beech). Wherever a soil variable was found to be a significant predictor, we reran the model with soil pH from that horizon to confirm the result was not spurious and to broaden the applicability of the models.

Analysis of Community Composition

Differences in tree community composition along environmental gradients (Objective 3) were analyzed using non-metric multidimensional scaling (NMS) in R with package *vegan* (Oksanen and others 2020; R Development Core Team 2020). We characterized tree species composition on each plot using a primary matrix of individual species relative density (the count of individuals of a given species divided by the total count of all individuals of all species). In the case of overstory (PCQ) data, the denominator for this calculation was fixed at 64 (the total number of trees sampled per plot). Species that occurred in two or fewer plots within a given primary matrix were excluded to reduce the effects of rarity (Peck 2010).

We ran NMS ordinations on three different primary matrices, one with the sapling layer only, one with the overstory only, and one with the sapling and overstory layers combined in a single matrix. In this third ordination, we tested the compositional differences between the overstory tree and sapling communities using functions *ordiellipse* and *envfit* (Oksanen and others 2020). For all models, we used the latter function to calculate correlations between a secondary matrix of environmental variables listed in Table 1 and the ordination solution. Goodness of fit for correlations of continuous variables were given by the squared correlation coefficient (R^2) while R^2 for factors (saplings vs overstory) was calculated as 1 minus the within group sum of squares, divided by the total sum of squares. Significance was evaluated by comparing each fit with those of 999 random permutations (Oksanen and others 2020). We plotted the correlations of continuous variables (with $p < 0.05$) as vectors, with lengths scaled by $\sqrt{R^2}$, pointing in the direction of the variable's most rapid increase—the gradient. In this way, we explored the associations between environmental gradients and species composition. Ordinations were run three times for each primary and secondary matrix to confirm consistency in the distribution of watersheds, species centroids, and vectors in the ordination space for each solution. NMS function *metaMDS* (set to autotransform=TRUE, trymax=1000) settled consistently on 2-dimensional solutions using Bray distances, with stress between 0.10 and 0.09 (Oksanen and others 2020).

RESULTS

Overstory Disease and Mortality Unrelated to Soil and Climate (Objective 1)

Our index of BBD (BBD defect score) explained 54% of the variation in the proportion of standing dead beech in the overstory size class (10 cm dbh) (Figure 2). The six models parameterized to describe impacts of BBD ("BBD models") on overstory beech trees (responses of BBD defect score, % dead bole cover, or proportion of dead beech trees in the overstory), described between 40 and 46% of the variation in each response (R^{2a}, Table 2). Overstory beech importance value was a consistently significant positive predictor in each model, whereas temperature and soil variables (Al in the upper B

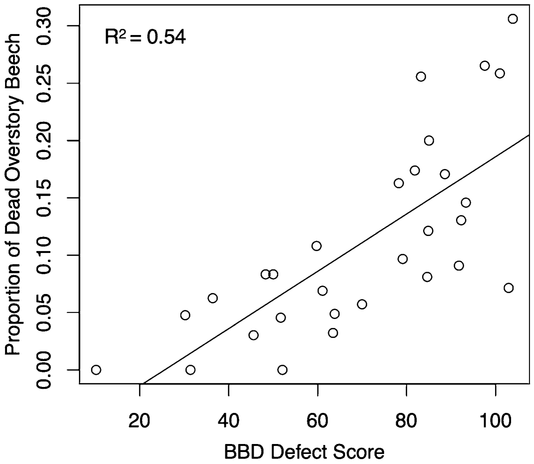

Figure 2. Beech bark disease (BBD) Defect Score significantly predicts the proportion of beech stems in the overstory that were dead (≥10 cm diameter at breast height (dbh)) in Adirondack Park, New York State, USA. Note: one outlier was removed due to heavy porcupine browse inflating the count of dead beech.

and Ca in the O_a horizons) were not significant predictors in any of the models (BBD models in Table 2; column A of Figure 3 provides visual examples for some of these relationships). Since none of these soil variables was significant, pH was not evaluated in alternative models.

Beech Sapling Densities Linked to Mortality and Acidification (Objective 2)

Conversely, of all the models explaining beech stem density in the sapling layer (5 cm dbh and 1.4 m tall) ("thicket models"), only three contained significant ($p < 0.05$) biotic predictors (Table 2). Percent dead bole (of overstory beech) and proportion of dead beech in the overstory were positive predictors of beech sapling density in three models, whereas beech importance value in the overstory and overstory BBD defect score were never significant predictors. Of the abiotic predictors in these models, Al in the upper B horizon was

Table 2. Results of 18 Hypothesis-driven Models Specified a priori to Describe the Variation in (a) Overstory Beech Bark Disease (BBD) and (b) Beech Sapling (Thicket) Density (Count) with Different Tripartite Combinations of Four Abiotic and Biotic Predictors, respectively, in Adirondack Park, New York State, USA

Response Variables	R^{2a}	R^{2b}	Biotic Predictors	Abiotic Predictors			
			Overstory Beech IV	T	Al	Ca	pH#
(a) BBD Models							
BBD defect score	0.46	0.40	13.90**	−5.28	−0.09		
	0.46	0.40	13.74**	−5.37		−0.54	
% Dead bole	0.42	0.35	6.41***	0.40	−1.28		
	0.41	0.35	6.34***	0.53		0.97	
Proportion of dead	0.41	0.34	0.063***	0.00	−0.02		
overstory beech trees	0.40	0.33	0.06***	0.00		0.01	
(b) Thicket Models							
Beech sapling count	0.34		0.08	0.03	0.15*		−0.16*
	0.19		0.09	0.02		−0.08	
			Overstory BBD Score				
Beech sapling count	0.39		0.12	0.05	0.15*		−0.16*
	0.23		0.13.	0.04		−0.09	
			Overstory % Dead Bole				
Beech sapling count	0.43		0.12.	0.04	0.16**		−0.15*
	0.29		0.14*	0.03		−0.10	
			Proportion Standing Dead				
Beech sapling count	0.44		0.13*^	0.05	0.16**		−0.16*
	0.31		0.15*	0.04		−0.11.	

For ordinary least squares regression (OLS) models (the first six), R^{2a} is the unadjusted and R^{2b} is adjusted-R-squared, whereas for negative binomial generalized linear models (GLMs) (sapling count models), R^{2a} is Nagelkerke's R^2. Significance: $P < 0.1$ '.', < 0.05 '', < 0.01 '**', and < 0.001 '***'. # pH in the upper B horizon was substituted for aluminum (Al) to confirm its significant coefficient estimate. ^ When pH is substituted for Al in this model, proportion dead loses significance. One outlier (9005) was removed from all models of sapling count due to heavy porcupinebrowse and human disturbance, the combination of which may explain atypically high beech sapling densities. T = temperature, Ca=calcium. Predictors were scaled and centered for comparison.*

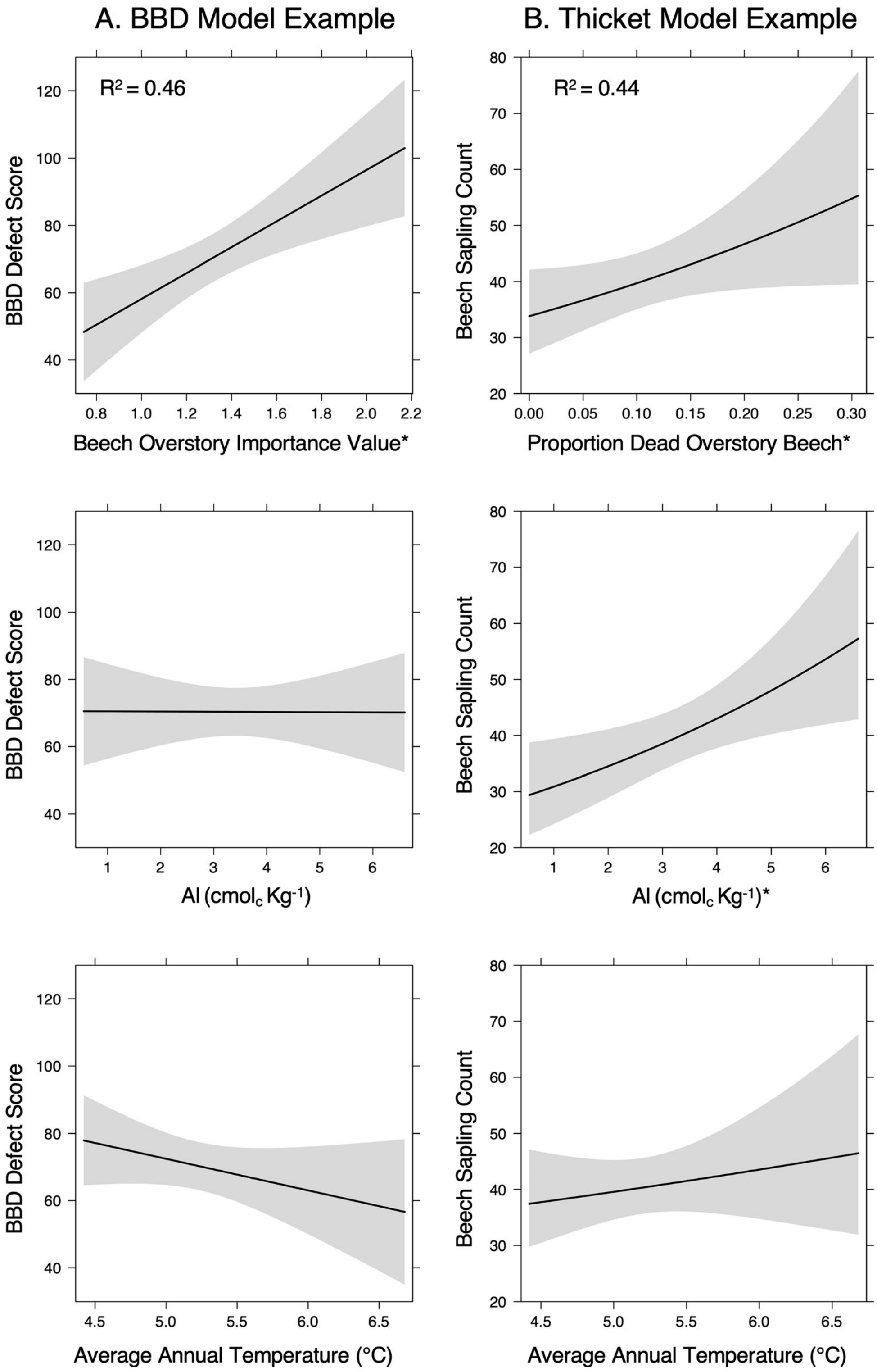

Figure 3. Examples of models predicting beech bark disease (BBD) (column A) and beech sapling count (column B) for Adirondack Park, New York State, USA. Lines represent the fitted values (with 95% pointwise confidence bands) for each predictor in the model (three total) when all other predictors are held at their mean. Sapling counts of 20 and 80 correspond to densities of 0.1 and 0.4 stems per m^2 respectively. Significant predictors are indicated by "*" on axis label. Refer to Table 2 for coefficient estimates and comparable models, figures for which are essentially identical to these. Al= aluminum.

a consistently significant positive predictor of beech sapling density (Figure 3, column B), while Ca and temperature were never significant. The significance of Al parameter estimates was generally greater than for the significant biotic predictors (Table 2). When models were rerun with pH in place of Al in the upper B horizon, pH was found to be a significant negative predictor of beech sapling density. Thicket models with significant coefficient estimates described between 29 and 44% of the variation in beech sapling densities (R^{2a}, Table 2). Note that one outlier (9005) was removed from all models of sapling count due to heavy porcupine browse and human disturbance, the combination of which may explain atypically high beech sapling densities.

Divergence of Tree Community Composition Between Overstory and Sapling Layers (Objective 3)

The combined sapling-overstory NMS analysis suggested a significant difference in the community composition of these two forest strata (Figure 4A), demonstrated by a distinct separation along ordination axis one (R^2=0.50, p=0.001) and a lack of overlap in the 95% confidence regions for each stratum. The sapling centroid was located on the positive end of axis one and two vectors were positively correlated (relatively weakly) with this axis: overstory beech importance value and overstory beech relative basal area (RBA). Three of the most shade tolerant species were positively correlated with axis one: beech (FAGGRA), red spruce (PICRUB), and striped maple (ACEPEN). These were the most common species in the sapling layer, respectively making up 84%, 7%, and 5% of stems on average. Of these three species, only beech was also a substantial component of the overstory (Figure S1).

Axis two of the combined sapling-overstory NMS was associated with a gradient of soil chemistry and precipitation (Figure 4B). Sugar maple (ACESAC), American basswood (TILAME), white ash (FRAAME), hophornbeam (OSTVIR), and eastern hemlock (TSUCAN) were positively correlated with axis two (Figure 4A), as were Ca and pH (Figure 4B). Red maple (ACERUB), yellow birch (BE-

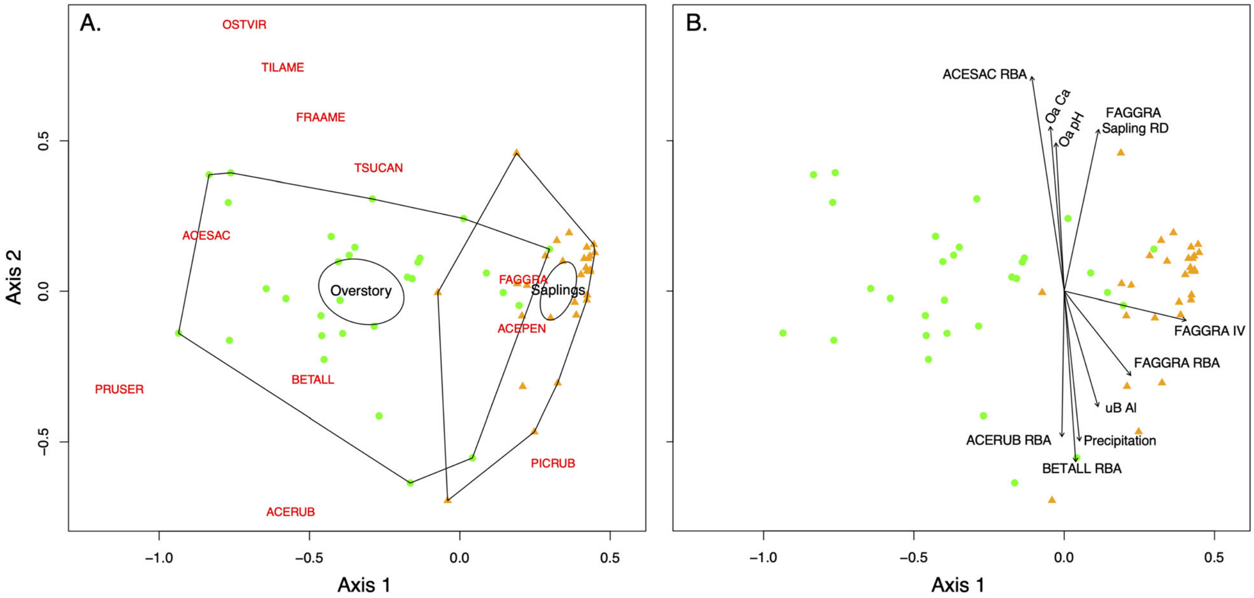

Figure 4. Trends in the species composition of the overstory (≥10 cm diameter at breast height (dbh), green circles) and sapling (≤5 cm dbh and ≥1.4 cm tall, orange triangles) layers across 30 watersheds in Adirondack Park, New York State, USA depicted using a non-metric multidimensional scaling (NMS) ordination (each panel depicts the same ordination). Points that are further apart are more dissimilar in species composition (relative density). Panel A: Species centroids (red acronyms) indicate the average species scores on the two axes relative to watershed scores (points near a species label contain a greater proportion of that species). Ellipses (black ovals) around "overstory" and "saplings" represent 95% confidence regions (standard errors) for the centroids of those strata. The spread of each layer is outlined by a descriptive polygon. Panel B: Vectors (arrows) show correlations between the NMS axes and key biotic and abiotic variables scaled by $\sqrt{R^2}$. Vectors plotted have a permutation-based p-value of ≤0.05. Refer to Table S2 for R^2 values and Table 1 for abbreviation definitions. Abbreviations: RBA=relative basal area, RD=relative density, IV=importance value, Oa=O_a horizon, uB=upper B horizon, Al=aluminum, Ca=calcium.

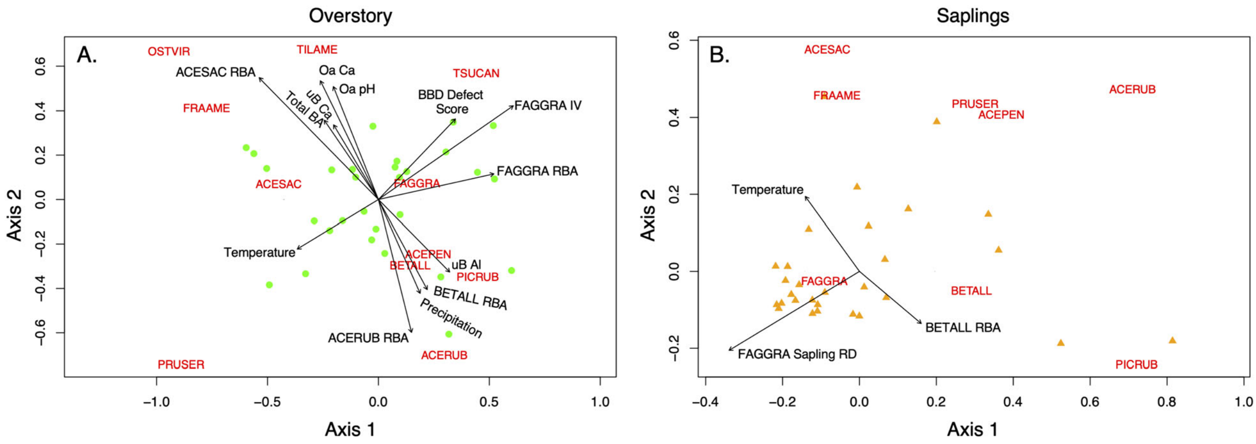

Figure 5. Trends in the species composition of the overstory (≥ 10 cm diameter at breast height (dbh), green circles in panel A) and sapling (≤ 5 cm dbh and ≥ 1.4 cm tall, orange triangles in panel B) layers across 30 watersheds in Adirondack Park, New York State, USA depicted using two separate non-metric multidimensional scaling (NMS) ordinations. Points that are closer together are more similar in their species composition (relative density). Species centroids are represented by red acronyms and indicate the average species scores on the two axes relative to watershed scores (points near a species label contain a greater proportion of that species). Vectors (arrows) show correlations between the NMS axes and key biotic and abiotic variables scaled by $\sqrt{R^2}$. Vectors plotted have a permutation-based p-value of ≤ 0.05. Refer to Table S2 for R^2 values and Table 1 for abbreviation definitions. Abbreviations: RBA=relative basal area, RD=relative density, IV=importance value, Oa=O_a horizon, uB=upper B horizon, Al=aluminum.

TALL), and black cherry (PRUSER) were negatively correlated with axis two, as were precipitation and Al. The locations of these species' centroids (based on relative density) generally corresponded with the directions of species-specific relative basal area (RBA) vectors (Figure 4).

While the relative positions of species centroids were conserved in the overstory-only ordination (Figure 5A), their change in the sapling-only ordination (Figure 5B) reflected beech (FAGGRA) dominance in this layer (Figure S1). The overstory-only ordination continued to exhibit an important soil-chemical gradient correlated with precipitation and sugar maple (ACESAC) overstory dominance and reflecting historical legacies of acidic deposition. However, this ordination also suggested a gradient of temperature, increasing as black cherry (PRUSER) became relatively more common and decreasing as beech overstory importance and BBD increased and eastern hemlock (TSUCAN) became relatively more common (Figure 5A, compare, Table S2).

The only abiotic gradient suggested by the sapling-only ordination was a weak temperature gradient negatively associated with birch (BETALL) and spruce (PICRUB), and positively associated with sugar maple, and ash (FRAAME). It was notable that no BBD-related variable was significantly correlated with the sapling-only ordination (Table S2), and beech sapling count was not correlated with any of the ordinations (compare, Table S2 and Figure S2).

DISCUSSION

We found no evidence to support the hypothesis that patterns of BBD-induced defect and mortality (standing dead beech) in aftermath forests (post-killing front) would vary with climate or soil conditions (Objective 1); instead, we found ample evidence that BBD impacts were more severe where beech was a more significant component of the overstory (compare, BBD Models, Table 2). This latter result agrees with others that found spatial patterning in the spread and impacts of BBD at fine scales (Giencke and others 2014), and positive relationships between relative beech basal area and disease severity at medium scales (Griffin and others 2003). Our results differed from others in finding a clear correlation between disease severity and beech mortality (Garnas and others 2013). Infected beech are likely sources of reinfection for resistant (Cleavitt and others 2021) and small-diameter beech (Giencke and others 2014). Thus, in locations where beech faces strong interspecific competition (for example, from sugar maple), or is at its bioclimatic limits (for example, elevation), its lower overall density and basal area may contribute to the less severe and frequent disease symptoms and mortality observed in other studies (Cleavitt and others 2021, 2022).

The lack of a significant relationship between BBD severity, beech mortality (standing dead), or beech sapling density and short-term (5 year) mean annual temperature (Objectives 1 and 2) was not surprising (Figure 3). This variable likely accounted for any spatial structure in our data (temperatures in the Adirondacks tend to be lower at higher elevations and further into the region's interior). Temperature failed as a proxy for the long-term accumulation of extreme outlying weather events, climatic variability, and gradual climate change, which if compared to the accumulation of BBD defects and mortality captured by a longitudinal study design, might prove to be significant. Others have found tentative links between climate change or conditions and BBD effects (Bose and others 2017; Cale and others 2017). Long term monitoring that tracks the accumulation of causal agents, defects, mortality, and small-diameter density, may elucidate climate influence on the disease complex and its ecosystem effects.

BBD Across the Soil-Acidity Gradient

While the literature suggests that beech is tolerant of acidic soils (Duchesne and others 2005; Nyland and others 2006; Nolet and others 2008; Tourville and others 2023), we were surprised to see no evidence that low pH and elevated Al could predict increased BBD defect or overstory beech mortality (Objective 1 and "BBD models," Table 2). There is substantial evidence that aluminum—which is more available in acidified soils—is toxic to plants, interfering with root development and function (Kinraide 2003). Yet, there are many genetically-linked mechanisms for aluminum tolerance (Kochian and others 2015). The study that inspired our hypothesis did not show significant detrimental effects of aluminum treatments on beech seedlings, but the results suggested reduced growth and survival (Kobe and others 2002). If aluminum were only marginally toxic to healthy beech, it followed that the additional stress of BBD on acidified soils might induce a significant effect. The soil-chemical boundaries of beech's niche space are not apparent in this system (Tourville and others 2023).

We found no relationship between the soil-acidity gradient captured in this study and either overstory beech importance value or relative basal area (Objective 3 and Figure 5A). This soil gradient was exacerbated by the historical gradient of N and S deposition (Bedison and Johnson 2010; Ito and others 2002; Johnson and others 2008; Shao and others 2021; Sullivan and others 2013). Previous work in the Adirondacks that found the nitrogen content of sugar maple foliage to be correlated with this N deposition gradient did not find the same for beech foliage (McNeil and others 2012). Although others found that bark nitrogen content in beech could be a predictor of BBD symptoms and infection, this signal was not evident in areas where the disease had been active longer and cumulative nitrogen additions had been greater (Latty and others 2003). More recent work in the Adirondacks suggests that complex interactions between bark nutrition, the BBD complex, and beech physiology govern disease progression at interannual scales (Cale and others 2015).

BBD, Light, and Beech Sapling Density

Our findings do not support the idea that BBD leads directly to the establishment of great densities of small diameter beech—often attributed to root sprouts (suckers) (Houston 1975; Hane 2003; Garnas and others 2011; Cale and others 2013; St-Jean and others 2021). That canopy beech importance value (and therefore presumably beechnut and surface root density) was not predictive of sapling density, but standing dead beech was (Objective 2 and "thicket models," Table 2), suggests that increased light associated with canopy gap formation due to past beech mortality is an important stimulus of beech sapling density in this system. It is not BBD's damage to the host that stimulates sprout formation (Jones and Raynal 1986), but rather crown decline and mortality that release beech seedlings and sprouts (Giencke and others 2014; Roy and Nolet 2018; Flinn and others 2022).

Legacies of Acidic Deposition

Canopy gaps formed by other agents of global environmental change may also disproportionately release beech into the sapling layer (Duchesne and Ouimet 2009; Giencke and others 2014; Morin and Liebhold 2015). We found that Al concentrations were the strongest positive, and pH the strongest negative, predictors of beech sapling density (Objective 2). Experimental additions of aluminum on plots experiencing significant canopy disturbance, benefited beech growth relative to sugar maple (without stimulating suckering) (Halman and others 2014). Sites acidified by N and S deposition have been associated with reduced sugar maple recruitment, crown condition, and growth (Sullivan and others 2013), experimental Ca additions have clearly benefited sugar maple (Cleavitt and others 2021). In the Northeast United States, elevational gradients of soil biotic and abiotic conditions—strongly correlated with acidity—appear to limit sugar maple seedling establishment relative to beech (Tourville and others

2023). Thus, anthropogenic soil acidification may also have favored recruitment of beech over sugar maple across the region.

Homogenization of the Sapling Layer by Global Environmental Change

We found little evidence that sapling layer species composition was related to any single environmental gradient (Objective 3, Figure 5B). The homogenization of the sapling layer by beech recruitment (Figure S1) is congruent with a broader trend over the past 50 years towards increasing dominance of subcanopy beech across the northeastern United States and southeastern Canada (Duchesne and others 2005; Nolet and others 2008; Gravel and others 2011; Cale and others 2013; Bose and others 2017). Where BBD was active, the tendency for increased density and mortality of ever smaller stems in the aftermath zone (Giencke and others 2014) would be gradually self-reinforcing, since beech was best adapted to exploit even small openings in forest canopy (Nyland and others 2006). Yet, beech bark disease could not have been the sole explanation for these trends because some increases in beech were observed before the killing front arrived (Twery and Patterson III 1984; Duchesne and others 2005; Gravel and others 2011). Acidic deposition, soil acidification, post-harvest establishment on acidic soils, and other sources of sugar maple decline such as defoliation events (Bal and others 2015) and climate change (Bose and others 2017; Oswald and others 2018), all likely contributed to varying degrees by undermining sugar maple's competitiveness and creating release opportunities for more shade-tolerant beech. In some regions, all of these perturbations were active simultaneously (Bal and others 2015; Cale and others 2017; Driscoll and others 2001; Lawrence and others 2015; Shao and others 2021). While preferential browse pressure could contribute to these shifts in species composition, white-tailed deer density in mature Adirondack forests is relatively low (Lesser and others 2019; Hinton and others 2022).

Beech Thickets

Although we succeeded in capturing a gradient of beech sapling densities, we did not encounter beech thickets (1 stem per m^2) as defined by important studies linking extremely high beech densities to reduced understory plant biodiversity (Cale and others 2013). Subcanopy beech dominance is often mentioned in the literature as suppressing economically important timber species (Hane 2003; Bose and others 2017; Elenitsky and others 2020). Logging (or other soil disturbance) is probably a major stimulant of beech root sprouting and release (Jones and Raynal 1986, 1988; Nyland and others 2006; Roy and Nolet 2018; Elenitsky and others 2020). Research that pools recently managed and unmanaged forests into a single analysis may be confounded by anthropogenically inflated beech sapling densities.

Spatial Versus Temporal Changes in Environmental Drivers of Forest Composition

To characterize the effects of broad regional gradients in soil acidity, climate and BBD on forest composition we integrated studies carried out across these gradients at different times. Consequently, soil chemistry, vegetation, BBD, and climate data in this study have been collected at different times and the dynamic nature of these variables makes it important to consider their changes over time relative to their changes across the studied spatial gradient.

Soil chemistry is of particular importance to consider since it played an important role in structuring forest composition. Soil chemistry on plots sampled in 2004 (n=7) and 2009 (n=18) may have changed to some degree by 2016 when vegetation and BBD data were collected. However, these changes were not likely to have been large relative to the regional soil chemistry gradient as rates of soil recovery are relatively slow and they differ between horizons and the cations being measured (Lawrence and others 2015; Lawrence and others 2021). To further reduce the influence of the potential changes in soil chemistry over time we considered two soil horizons and several chemical predictors. Importantly, we did not detect any systematic biases associated with the source of soil data or time since soil sampling. Unlike the soil data, climate data were available for our region continuously and we calculated 5-year means preceding 2016 vegetation and BBD surveys to characterize typical conditions experienced by trees at each plot. Our study specifically focused on the variation in BBD and forest structure along spatial gradients in climate and soil chemistry rather than disease temporal dynamics. BBD has been present in the study region since as early as 1960 and regional forests are now in the aftermath phase of the disease, although individual infections and disease progress tend to be asynchronous at the scale of individual stems (Giencke and others 2014; Cale and others 2017). While we cannot address temporal dynamics of BBD with the current data, our study provides the framework and the data for a future longitudinal study of BBD progression across extensive climatic and edaphic regional gradients.

CONCLUSION

Our study suggests that biotic and abiotic agents of global environmental change may combine to transform ecosystems. Our examples of these agents were N and S deposition (the measured soil acidity gradient) and an invasive species (the measured BBD gradient). We found that beech sapling densities were higher in locations with more standing dead overstory beech and more acidic soils. Yet, beech domination of the sapling layer (in terms of relative density) was unrelated to soil or BBD gradients. We connected these results with a rich literature on beech homogenization of sapling layers and sugar maple decline and mortality throughout northern hardwood forests in the United States and Canada. In this context, we suggest that BBD and acidic deposition may have combined to create many small canopy openings following decline and death of overstory beech and sugar maple. Though sugar maple would normally exploit the largest of these gaps (Nyland and others 2006; Nolet and others 2008), this species was suppressed on many sites in part by nutrient and/or acidity stress, often related to acidic deposition (Bal and others 2015). This process gradually released beech seedlings and sprouts, homogenizing the sapling layer over time. However subcanopy beech dominance may not continue in unmanaged forests, and beech may even decline over time, due to (i) BBD continuing to impact ever-smaller diameters of beech (Busby and Canham 2011; Giencke and others 2014), (ii) the novel beech leaf disease that appears to be fatal to small-diameter beech (Ewing and others 2019), and (iii) declining N and S deposition with associated recovery of acidified soils (Lawrence and others 2015). Future research focusing on differentiating the effects of climate change, acidic deposition, disease, and land use would further benefit our understanding of how these factors acting together shape species composition and structure in the sugar maple-beech forests of eastern North America.

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DATA AVAILABILITY

Data is available from the electronic supplemental information provided with this article.

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