



Soil biotic and abiotic thresholds in sugar maple and American beech seedling establishment in forests of the northeastern United States

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Received: 5 April 2023 / Accepted: 11 June 2023

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Abstract

Aims Climate change is expected to shift climatic envelopes of temperate tree species into boreal forests where unsuitable soils may limit range expansion. We studied several edaphic thresholds (mycorrhizae, soil chemistry) that can limit seedling establishment of two major temperate tree species, sugar maple (arbuscular mycorrhizal, AM) and American beech (ectomycorrhizal, EM).

Methods We integrate two field surveys of tree seedling density, mycorrhizal colonization, and soil chemistry in montane forests of the Adirondack

and Green Mountains (Mtns) in the northeastern United States. We conducted correlation and linear breakpoint analyses to detect soil abiotic and biotic thresholds in seedling distributions across edaphic gradients.

Results In the Green Mtns, sugar maple seedling importance (an index of species relative density and frequency, IV) declined sharply with low pH (<3.74 in mineral soil) and low mycorrhizal colonization (<27.5% root length colonized). Sugar maple importance was highly correlated with multiple aspects of soil chemistry, while beech was somewhat sensitive to pH only; beech mycorrhizal colonization did not differ across elevation. Mycorrhizal colonization of sugar maple was positively correlated with soil pH and conspecific overstory basal area. In the Adirondacks, sugar maple importance, but not beech, plateaued above thresholds in soil calcium (~2 meq/100 g) and magnesium (~0.3 meq/100 g).

Conclusions The establishment of sugar maple, but not beech, was impeded by both biotic and abiotic soil components in montane conifer forests and by soil acidity in temperate deciduous forests. These differences in species sensitivity to edaphic thresholds will likely affect species success and future shifts in forest composition.

Responsible Editor: Michael Luke McCormack.

Supplementary information The online version contains supplementary material available at <https://doi.org/10.1007/s11104-023-06123-2>.

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Keywords Climate change · Northern hardwoods ·
Boreal forest · Seedling · Soil · Mycorrhizae

Introduction

Climate change is a foremost driver behind the documented shifts in species distributions on both regional and global scales (Pecl et al. 2017). Even more substantial changes in species distributions are expected to occur over the next century as climate change accelerates (e.g., Prasad et al. 2020). Tree species may be particularly susceptible to lags in migration given their slow growth, slow dispersal, and long lifespans; all of which can lead to slow population turnover and limited ability to adapt to a rapidly changing environment (Aitken et al. 2008). While prevailing theory and some empirical evidence indicates that tree species track changing climate by shifting range limits to higher elevations and latitudes (e.g., Beckage et al. 2008), some species have been observed to shift in unexpected directions; toward warmer climate (downslope or to lower latitudes) possibly due to past disturbance history and ongoing successional processes (Foster and D'Amato 2015; O'Sullivan et al. 2021; Tourville et al. 2022; Wason and Dovciak 2017). Other studies have revealed slow or delayed range shifts possibly due to other limiting factors, most notably soils and belowground biotic interactions (Alexander et al. 2018; Brown and Vellend 2014; Vellend et al. 2021). However, despite numerous attempts to model and predict future tree species distributions in the context of climate change, few studies have included these edaphic abiotic or biotic variables (de Bueno et al. 2016).

Montane slopes in northeastern North America are dominated by deciduous temperate (northern hardwood) tree species at low elevations and coniferous spruce-fir tree communities at high elevations (e.g., Wason and Dovciak 2017). In addition to a well-defined climatic gradient that covaries with elevation, soil texture and chemistry are also known to change across this gradient. Deeper, well-developed, relatively nutrient-rich soils in northern hardwood forests at low elevation generally give way to rocky, shallow, acidic, and nutrient poor soils at high elevations (Collin et al. 2017; Evans and Brown 2017). Sugar maple (*Acer saccharum*) and American beech (*Fagus grandifolia*), two ecologically important deciduous tree species that co-dominate low elevations, might migrate upslope as climate warming accelerates (Beckage et al. 2008; Urli et al. 2016). However, while sugar maple is generally more cold-tolerant

than American beech, sugar maple is also known to be sensitive to low base cation concentrations typical of acidic soils (Bal et al. 2015; Halman et al. 2015) which could prevent upslope migration. Further, American beech has been shown to be more tolerant of acidic, base-poor soils (Sullivan et al. 2013; Lawrence et al. 2018; Zarfós et al. 2019). Given this difference in acid-sensitivity, American beech could conceivably outcompete sugar maple at higher elevations. Further identification of soil chemistry thresholds that limit seedling establishment of these two species is helpful for understanding potential soil chemical controls across a broader region.

Soil acidity in northeastern North America is not predictable solely by variation across elevational gradients, but also by differences in parent material and anthropogenic acidification resulting from atmospheric nitrogen (N) and sulfur (S) deposition (Driscoll et al. 2001). N and S deposition, though much reduced following the 1990 amendments to the Clean Air Act (Lawrence et al. 2015), has acidified soils across the Northeast resulting in soil base cation depletion and mobilization of potentially toxic inorganic aluminum. As the industrial sources of much of this pollution were located in the Midwest, acidic deposition loads generally decreased from west to east and north, such that Adirondack soils were more exposed to acidifying deposition than soils in Vermont (Driscoll et al. 2001; Ollinger et al. 1993). Previous results in the Adirondacks have indicated that sugar maple recruitment is limited by soil acidification in a threshold response to base cation depletion (Sullivan et al. 2013).

Mycorrhizal associations and their influence on natural tree range expansions have received little attention in the ecological literature (Lankau et al. 2015). It is well documented that mycorrhizal symbioses are usually mutualistic and extremely widespread in nature (Van Der Heijden and Horton 2009); plants benefit from increased soil nutrient uptake via colonization by mycorrhizal fungi in exchange for plant-derived photosynthates. Given their known prevalence and positive influence on plant growth, mycorrhizal importance in aiding tree species establishment during climate change induced range expansions should be considered. Two dominant mycorrhizal types, arbuscular mycorrhizal fungi (AMF) and ectomycorrhizal fungi (EMF), are found in association with trees in northern hardwood forests

at low elevation, but EMF are the dominant colonizers of trees at high elevation spruce (*Picea sp.*) and fir (*Abies sp.*) (Evans and Brown 2017). Functionally, AMF and EMF also differ in resource acquisition strategies stemming from anatomical, physiological, and habitat idiosyncrasies (Tedersoo et al. 2020). EMF is generally more efficient than AMF at acquiring various forms of nitrogen (N), and can provide ample protection from plant-toxic heavy metals and pathogens in soils at high latitudes and elevations (Harley and Smith 1983; Van Der Heijden and Horton 2009; Tedersoo et al. 2020). Given these functional differences, and possible issues around local dispersal limitation, it is generally thought that the paucity of AMF propagules in soils at high elevations, assumed from a lack of AMF plant hosts, could impede the colonization of sugar maple, an AMF obligate species, but not American beech, a nominally EMF associated species (Carteron et al. 2020; Chaudhary et al. 2022; Tourville, *unpublished data*). However, to date, there has been no indication of the extent to which mycorrhizal root colonization is necessary to support seedling establishment beyond the existing ranges of these species.

The purpose of this analysis was to use plant and environmental survey data along elevation and putative soil acidity gradients in the northeastern United States to quantify soil biotic and abiotic thresholds beyond which the establishment of sugar maple and American beech seedlings is affected. We were particularly interested in (1) specific thresholds of mycorrhizal root length colonization and soil chemistry associated with seedling establishment (species importance values), and (2) comparison of threshold values between sugar maple and American beech which are colonized by different dominant mycorrhizal types (AMF versus EMF). We also sought to (3) evaluate general correlations between different soil chemical variables, mycorrhizal colonization, elevation, and overstory basal area to speculate on their individual influence on seedling establishment.

Methods

Study area

Field sampling was conducted along edaphic gradients related to elevation on four of the Green Mtns

in Vermont and at low elevations along a soil acidity gradient in the Adirondack Mtns of New York (Fig. 1). The Green Mtns are characterized by strong zonation in forest communities. Temperate deciduous northern hardwood forests dominated by sugar maple and American beech (and other AMF associated species, particularly other *Acer* species) occupy lower elevations, and spruce-fir forests dominated by balsam fir (*Abies balsamea*) and red spruce (*Picea rubens*) (both EMF associated species) occupy higher elevations. These forest communities are separated by a sharp ecotone around 800 m above sea level (asl) (Wason and Dovciak 2017). The Adirondack sites were established in temperate deciduous northern hardwood forests analogous to the low elevation forests sampled in the Green Mtns. Though glacial till accounts for much of the soil parent material in the Northeast, the geologic sources of that till differ between the Adirondack and Green Mtns, the former being generally more base-poor and acidic than the latter (Baker et al. 1990; Siccama 1974).

The northern region of New York and New England is comprised of diverse forests with the broad-leaf temperate forest biome to the south and the boreal conifer forest to the north and in the highest elevations (Janowiak et al. 2018). The region is officially situated in the Adirondack-New England highlands; and is characterized by highly variable terrain (generally ranging from 150 to 1,220 m asl, rocky Spodosol soils, a continental forest climate with warm summers and cold snowy winters (mean annual temperatures between 3 and 11°C; mean length of the frost-free period ~100 days; mean annual snowfall >2,550 mm), and evenly distributed precipitation across the year (annual mean precipitation of 890 mm, Albany, New York; Janowiak et al. 2018).

Soil and vegetation sampling – Green Mtns

Overstory and understory vegetation, soil chemistry, and seedling mycorrhizal status were assessed at 5–6 sites at intervals of 100 m elevation (from 500 to 1,000 m asl) on each of the four study mountains. Sites at each elevation were previously established and surveyed as described in Wason and Dovciak (2017) and Tourville et al. (2022). Briefly, we surveyed tree seedlings (juvenile woody tree species <0.5 m in height) on understory vegetation plots (1 × 1 m) placed systematically at each elevation

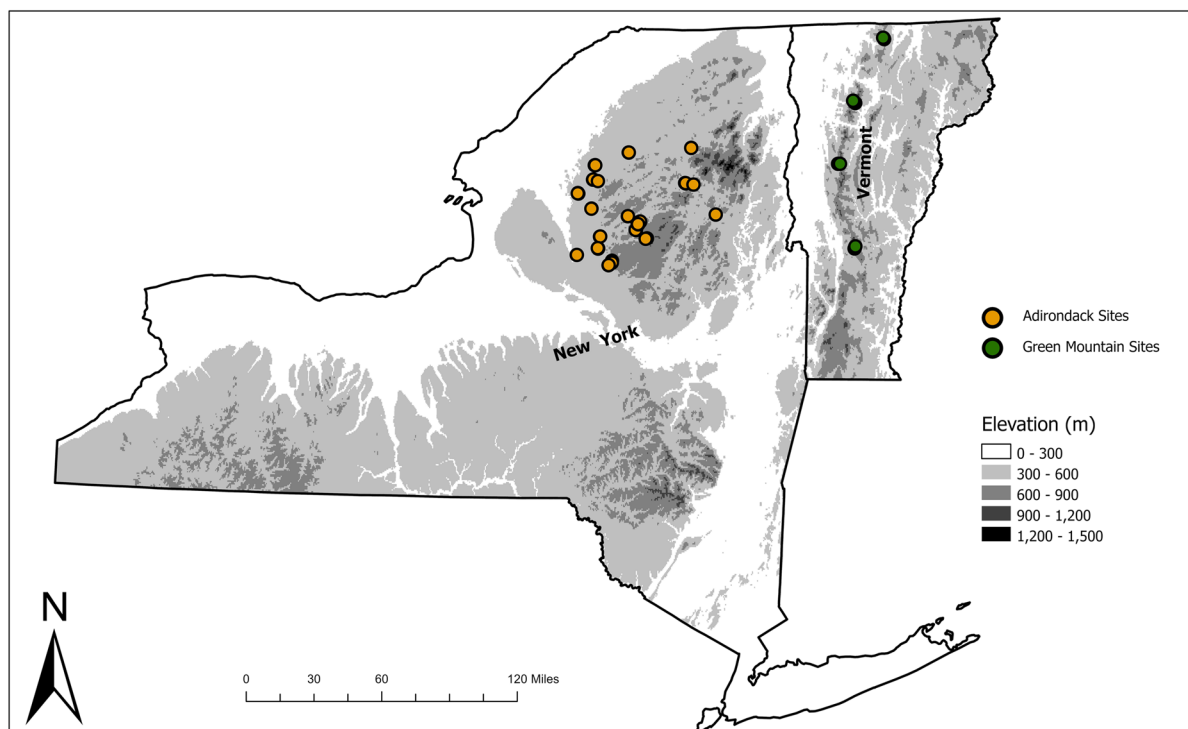


Fig. 1 Map indicating survey locations in the Adirondack Mtns (orange points; 20 watersheds with 2–3 plots each) of New York State ($n=50$), and Green Mtns (green points; 5–6 sites per each of the four study mountain) of Vermont ($n=22$).

Darker shading indicates higher elevations. Note that some points for both the Adirondacks and the Green Mtns are close together and overlap in this map

along 225 m transects along contour lines; 15 of these plots were established along each transect at 15 m intervals. We counted the number of seedlings per plot (by species). We subsampled up to 3 tree seedlings (<0.5 m in height) per elevation and mountain of both sugar maple and American beech for quantifying mycorrhizal colonization (see below). Overstory trees were surveyed using the point-center-quarter method at each elevation using transect vegetation plots as sampling points (Wason and Dovciak 2017), which allowed for the quantification of basal area partitioned between AMF and EMF associated trees (see Brundrett and Tedersoo 2020). Adult trees were defined as individuals > 10 cm diameter at breast height (DBH).

To assess soil chemistry across gradients of elevation, a total of 30 soil cores (5 cm diameter $\times$ 15 cm depth) were extracted from each mountain in the fall of 2019 (see Tourville et al. 2022 for site and sampling details). Five cores per elevation were mixed to form a composite sample ultimately yielding 6

soil samples per elevation (5–6 elevations $\times$ 4 mountains = 130 samples total). All soil cores were processed to separate the mineral upper B horizon from other soil horizons and any organic (leaf litter) material, and sieved using a 2 mm sieve to remove the coarse soil fraction. Sieved upper B horizon soils were processed to quantify soil pH via electrometric methods, and soil organic matter (SOM) was determined via the loss on ignition procedure in the Soil Analysis Laboratory at SUNY-ESF following Carter and Gregorich (2007). Additionally, soil subsamples from each elevation were sent to the University of Vermont Agricultural and Environmental Testing Lab to analyze for effective cation exchange capacity (ECEC, sum of exchangeable base cations plus exchangeable acidity), base cation concentrations (Ca, Mg, K, Na), and metal concentrations (Al) using a modified Morgan procedure (McIntosh 1969).

Mycorrhizal colonization was estimated from stored seedling roots (preserved in 70% ethanol) collected during the field surveys (see above) using

staining and light microscopy methods. Specifically, root samples were cleared using a 10% KOH solution via a 30-min autoclave liquid cycle, stained with Chlorazol Black E in another 30-min liquid autoclave cycle, and stored in a 50% glycerin solution. The grid-line intercept method was used to estimate AMF colonization, defined as the percent total examined root length with mycorrhizal structures present; structures that include arbuscules, vesicles, coils, and hyphae, as described in McGonigle et al. (1990) and Brundrett et al. (1996). We also noted any dark-septate endophytes (DSE), and other unknown endophytes present in seedling roots (see Supplemental Table S1). A simplified gridline intercept procedure was used to estimate EMF colonization (defined as % of examined root tips with a fungal sheath present) for unstained fungi (Brundrett et al. 1996).

Soil and vegetation sampling – Adirondack Mtns

Overstory and understory vegetation and soil chemistry were assessed at two to three plots (50 total) in 20 watersheds selected to capture a gradient of soil acidity across the western Adirondacks. Sites were previously established and surveyed as described in Sullivan et al. (2013) and Zarfos et al. (2019). Briefly, during the summers of 2009 and 2015 we counted each species of seedling encountered within five subplots (1×1 m), spaced 10 m apart along the midline of each 20×50 m plot. We defined seedlings as any species of tree > 5 cm tall and < 1 cm DBH. In 2009, we recorded the DBH of all trees in each plot with a DBH > 10 cm.

Soil sampling was carried out in 2009 by the U.S. Geological Survey (USGS), USDA Forest Service, and E&S Environmental Chemistry. We used soil data gathered from the upper 10 cm of the B horizon at each plot to enable comparison with results derived from this horizon in Sullivan et al. (2013). All chemical analyses were done in the U.S. Geological Survey (USGS) New York Water Science Center Soil and Low-Ionic Strength Water Quality Laboratory (see Lawrence et al. 2020 for soil data and also Sullivan et al. 2013 for the details of soil-chemical analysis methods). Full documentation of analysis methods and all data are available in Lawrence et al. (2020). ECEC was calculated as the sum of exchangeable base cations (K, Na, Ca, and Mg) plus exchangeable acidity.

Statistical analysis

Seedling relative frequency and relative density were averaged across plots to calculate a species importance value (IV) (index ranging from zero to one) for each elevation (site) on each mountain in the Green Mtns ($n=22$) and for each plot in the Adirondack Mtns ($n=50$). Raw soil chemical and mycorrhizal colonization data were also averaged for each elevation and mountain (Green Mtns) or for each plot and watershed (Adirondack Mtns). A Spearman rank correlation analysis was conducted first to assess correlation estimates and significance ($\alpha=0.05$) between species importance and soil abiotic and biotic variables, elevation, and conspecific overstory basal area. In addition, generalized linear (GLM) breakpoint analyses were conducted using the “segmented” package in R (Muggeo 2008) to identify variable values beyond which species importance rapidly declined to zero or reached a plateau (using a binomial distribution). Only variables with significant correlations with species importance for either species were included in the breakpoint analyses. To assess the validity of estimated breakpoints, model Akaike Information Criterion (AIC) values were calculated for both segmented models and generalized linear models (the latter served as a null model) for each bivariate comparison (using the R package “lme4”). Breakpoints were considered meaningful if the segmented models performed better than their corresponding generalized linear models ($> 2 \Delta AIC$). GLM diagnostic plots (plots of jackknife deviance residuals against linear predictor, qq-plots, plots of approximate Cook statistics against leverage, and case plots of Cook statistics) were examined using the “boot” package in R. Lastly, both mean AMF and EMF root length colonization for each elevation, combined across all study mountains (Green Mtns), were plotted with mean basal area of total AMF or EMF associated trees. All analyses were conducted using the R statistical programming language (R Development Core Team 2022).

Results

The root length colonized by AMF of naturally occurring sugar maple seedlings decreased below 20% above 800 m asl, just above the temperate-boreal

ecotone in the Green Mtns (Fig. 2, panel A). AMF colonization declined with the basal area of AMF associated tree species as elevation increased (Fig. 2, panel A; also see Supplemental Table S1). EMF root length colonization of American beech seedlings remained between 40 and 50% along the elevation gradient, even as EMF associated basal area increased with elevation (Fig. 2, panel B).

In the Green Mtns, sugar maple species importance was significantly positively correlated with AMF colonization, soil pH, sugar maple overstory basal area, and base cation concentrations including

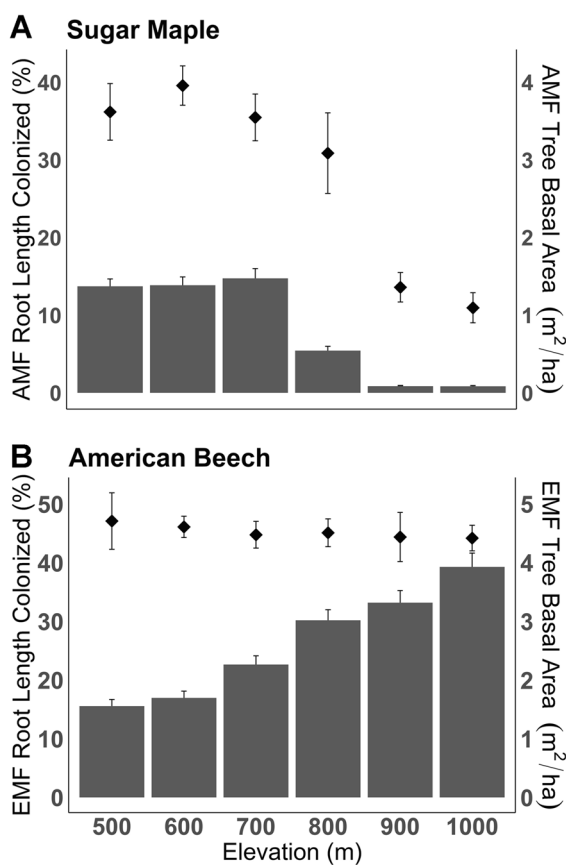


Fig. 2 Mycorrhizal (arbuscular mycorrhizal fungi, AMF or ectomycorrhizal fungi, EMF) root length colonized (%) of sugar maple (**A**) and American beech (**B**) seedlings for each elevation surveyed averaged across the study mountains in the Green Mtns (filled points; ± 1 SE indicated by the whiskers) on the left axis compared with averaged plot overstory basal area (m²/ha, partitioned between AMF and EMF associated trees) on right axis (with ± 1 SE whiskers). AMF colonization for sugar maple is displayed in the top plot while EMF colonization of American beech is displayed in the bottom plot

Ca and Mg (Table 1, Supplemental Fig. S1). Sugar maple importance value was significantly negatively correlated with elevation and SOM. Similarly, American beech importance value was significantly negatively correlated with elevation and SOM while positively correlated with soil pH and overstory basal area of both sugar maple and beech, although these relationships were weaker than for sugar maple (see Fig. 3 for relationships with pH). As expected, there was a negative relationship between elevation and most soil biotic and abiotic variables. EMF colonization was not correlated with any soil chemical variable with the exception of a positive relationship with Mg. Elevation was negatively correlated with soil pH, ECEC, base cation concentrations, and AMF colonization while positively correlated with SOM (Table 1).

In the Adirondacks, sugar maple importance was significantly positively correlated with pH (as with the Green Mtns), sugar maple overstory basal area, and base cation concentrations including Ca and Mg (Table 2, Supplemental Fig. S2) and was significantly negatively correlated with Al concentrations. American beech importance was only significantly positively correlated with its overstory basal area and had a weak negative correlation with soil Ca (Table 2).

Bivariate breakpoint analyses revealed that sugar maple seedling importance in the Green Mtns declined to zero around a root length colonization <27.5%, a pH <3.74, a SOM >21.2%, and plateaued around 0.7 at Ca concentrations of <26.1 meq/100 g, although sugar maple importance also declined to 0 below ~5.0 meq/100 g (Table 3; Fig. 4). Breakpoints could not be resolved for elevation (linear relationship). American beech importance was insensitive to biotic and abiotic soil variables and only declined to zero as a linear function of elevation (>700 m asl) and hardwood overstory basal area. For the Adirondacks, sugar maple seedling importance plateaued around 0.8 for values of Ca above 2.09 meq/100 g and values of Mg >0.35 meq/100 g (from 2015 data, Table 3; Fig. 4). Species importance declined to 0 at higher concentrations of Al >3.51 meq/100 g although the segmented regression did not perform better than a generalized linear model (see Supplemental Table S2). While sugar maple was negatively correlated with SOM up to the 21.2% breakpoint in the Green Mtns (where SOM exceeded 50%),

Table 1 Spearman rank correlation matrix of all soil chemical variables, mycorrhizal root length colonization (arbuscular mycorrhizal fungi, AMF and ectomycorrhizal fungi, EMF, %), overstory basal area of sugar maple (SM BA) and American beech (AB BA, m²/ha), and species importance value (IV, %) of sugar maple (SM IV) and American beech (AB IV) from the Green Mtns

Elevation	pH	SOM	ECEC	Mg	Ca	Al	AMF Colo- nization	EMF Colo- nization	SM BA	AB BA
pH	-0.74									
SOM	0.80									
ECEC	-0.18	-0.18								
Mg	-0.45	-0.51	0.80							
Ca	-0.42	-0.52	0.80	0.79						
Al	-0.03	-0.20	-0.43	-0.49	-0.20					
AMF Colonization	-0.92	-0.82	0.12	0.43	0.41	0.02				
EMF Colonization	0.19	0.37	0.32	0.46	0.37	-0.28	0.15			
SM BA	-0.75	-0.79	0.15	0.42	0.46	0.23	0.77	0.06		
AB BA	-0.60	-0.49	-0.17	0.15	0.07	-0.03	0.66	-0.20	0.74	
SM IV	-0.85	-0.86	0.31	0.58	0.60	0.19	0.79	NA	0.84	0.48
AB IV	-0.72	-0.65	0.12	0.19	0.21	0.17	NA	-0.10	0.84	0.91

Soil chemical variables include pH, SOM (soil organic matter, %), ECEC (effective cation exchange capacity, meq/100 g), Mg (soil magnesium concentration, meq/100 g), Ca (soil calcium concentration, meq/100 g), and Al (soil aluminum concentration, meq/100 g). Statistically significant correlations (alpha=0.05) are in bold font

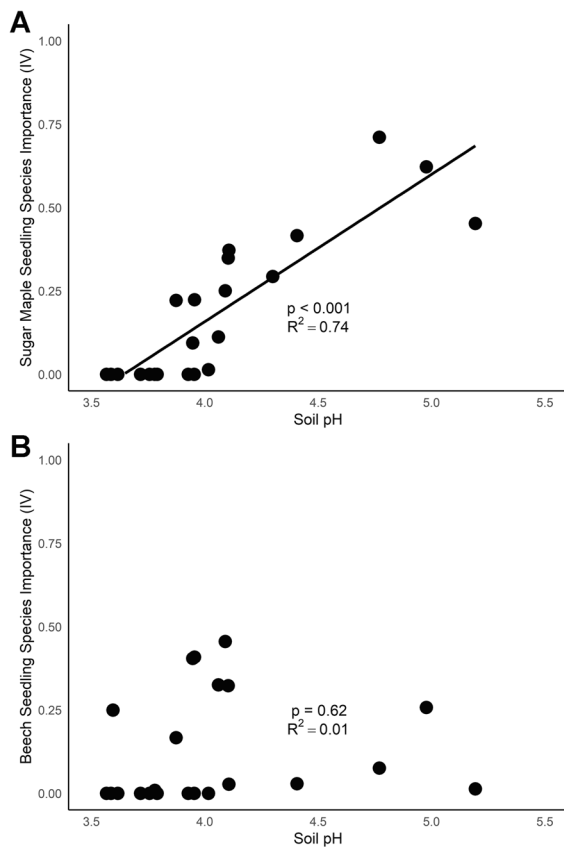


Fig. 3 Bivariate relationships between sugar maple (**a**) species importance value (IV) and American beech (**b**) species importance value (IV) and pH in the Green Mtns. Relationships are fitted with a linear model (p -values and R^2 reported in figure)

this relationship was flat in the Adirondacks, where SOM did not exceed 26%.

Discussion

Patterns and role of soil abiotic environment

Our results indicate that sugar maple seedlings are much more sensitive to acidic soils than American beech, which may lead to beech becoming more dominant in hardwood forests expanding to higher elevations on montane slopes, where soils tend to be more acidic than lower elevations. We find that sugar maple importance value is particularly sensitive to low soil pH and low base cation concentrations, corroborating previous work and theory focused around this species (Bal et al. 2015; Lawrence et al. 2015;

Sullivan et al. 2013, see Fig. 3). This apparent difference in soil-chemical niche space is also supported by more recent work in the region and may have significant consequences for future forest composition both within the northern hardwood forest biome and at higher elevations where range expansions of these species may occur (Carteron et al. 2020; Cleavitt et al. 2011). Recent work investigating factors that control seedling distributions indicates that both climate and soils are significant drivers (Tourville et al. 2022). Assuming climate becomes favorable for both sugar maple and American beech within the boreal forest at high elevations, acidic soils with low base cation saturation may impede sugar maple seedlings but allow for the establishment of acid-tolerant beech seedlings and possibly other less abundant species such as red maple (*Acer rubrum*), striped maple (*Acer pensylvanicum*), mountain maple (*Acer spicatum*), and birch species (*Betula sp.*) (Tourville et al. 2022). While not addressed through this study, given previous research that has indicated that beech saplings are generally absent in drier sites, the high soil moisture content of mesic and high elevation forests (which will remain so with greater future precipitation) will not likely give sugar maple or beech an advantage over one another (Arii and Lechowicz 2002).

Given the observed ability of American beech (via advanced seedling recruitment and vegetative sprouting) to compete with and suppress sugar maple seedlings (Hane 2003; Nyland et al. 2006), especially given the increase of sapling basal area and stem density largely as a result of beech bark disease (Giencke et al. 2014), the establishment of beech at higher elevations may further hinder upslope sugar maple migration (cf. Cleavitt et al. 2018, 2022). While somewhat speculative, it is possible that the observed increase of American beech basal area and upslope establishment throughout the Northeast relative to sugar maple (Bose et al. 2017; Wason and Dovciak 2017; but see Tourville et al. 2022) may be in part due to historical soil acidification across the region due to acidifying deposition; however, this anthropogenic influence was not evenly distributed across the region (cf. Ollinger et al. 1993). However, we should add that while we were largely able to distinguish between beech vegetative sprouts and independent seedlings in our study, it is possible that the perceived tolerance of beech to acidity is partly a result of access to parental resources by beech sprouts.

Table 2 Spearman rank correlation matrix of all soil chemical variables, overstory basal area (BA) of sugar maple (SM BA) and American beech (AB BA, m²/ha), and species importance

value (IV, %) of sugar maple (SM IV) and American beech (AB IV) from the Adirondack Mtns for both 2009 and 2015

	Elevation	pH	SOM	ECEC	Mg	Ca	Al	SM BA	AB BA
pH	−0.07								
SOM	0.08	−0.25							
ECEC	0.16	−0.31	0.64						
Mg	0.40	0.01	0.20	0.42					
Ca	0.40	0.31	0.10	0.29	0.8				
Al	0.02	−0.61	0.72	0.53	−0.10	−0.22			
SM BA	0.05	0.52	−0.55	−0.38	0.20	0.42	−0.61		
AB BA	0.28	−0.41	0.33	0.36	0.14	0.01	0.37	−0.36	
2009 SM IV	0.37	0.43	−0.15	−0.02	0.58	0.73	−0.41	0.73	−0.09
2015 SM IV	0.35	0.34	0.05	0.10	0.48	0.65	−0.15	0.50	0
2009 AB IV	0.05	−0.02	0.06	0.01	−0.10	−0.11	0.16	−0.14	0.59
2015 AB IV	0.10	−0.11	0.15	−0.01	−0.26	−0.35	0.23	−0.27	0.39

Soil chemical variables include pH, SOM (soil organic matter, %), ECEC (effective cation exchange capacity, meq/100 g), Mg (soil magnesium concentration, meq/100 g), Ca (soil calcium concentration, meq/100 g), and Al (soil aluminum concentration, meq/100 g). Statistically significant correlations ($\alpha=0.05$) are in bold font

Table 3 Threshold values beyond which species importance value (IV) rapidly declines to zero, or reaches a plateau as revealed via linear breakpoint analysis ($\pm$ SE)

Breakpoint variable	Study area	Year data collected	Species	IV to 0 or Plateau	Value ($\pm$ SE)	Δ AIC
Root Length Colonized (%)	Green Mtns	2019	Sugar maple	0	$< 27.5 \pm 4.62$	2.42
pH	Green Mtns	2019	Sugar maple	0	$< 3.74 \pm 0.19$	4.30
SOM (%)	Green Mtns	2019	Sugar maple	0	$> 21.2 \pm 4.42$	4.16
[Ca] (meq/100 g)	Green Mtns	2019	Sugar maple	Plateau	$> 26.1 \pm 1.87$	2.65
[Ca] (meq/100 g)	Adirondacks	2009	Sugar maple	Plateau	$> 1.44 \pm 0.26$	13.26
[Ca] (meq/100 g)	Adirondacks	2015	Sugar maple	Plateau	$> 2.09 \pm 0.69$	8.12
[Mg] (meq/100 g)	Adirondacks	2009	Sugar maple	Plateau	$> 0.24 \pm 0.09$	5.28
[Mg] (meq/100 g)	Adirondacks	2015	Sugar maple	Plateau	$> 0.35 \pm 0.12$	4.57

Only significant correlations between IV for either tree species and elevation, mycorrhizal colonization, or soil chemical variables were included in breakpoint analyses. Variables for which no breakpoints were resolved or where linear breakpoint models did not improve model fit over generalized linear models as determined by Δ AIC (< 2) are also not shown. AIC = Akaike Information Criterion; SOM = soil organic matter

Seedling threshold responses to soil abiotic environment

Our breakpoint analysis highlighted three categories of species response to abiotic gradients: linear, thresholds beyond which a species was absent, and thresholds beyond which the species response plateaued at a non-zero value. Plateaus indicate that the predictor (or its close correlates) reaches a level at which additions no longer produce a benefit to the

species, perhaps loosely reflecting Liebig's Law of the Minimum (cf., Rubio et al. 2003). For example, this was the case for sugar maple's relationship with Mg and Ca in the Adirondacks, but not with pH – a close chemical correlate. Sugar maple had a strong, positive, linear association with pH in another study within the region, reflecting a potential for nutrient colimitation (Mg and Ca; cf., Vadeboncoeur 2010). The Green Mtns provided the only examples of thresholds beyond which a species was always absent.

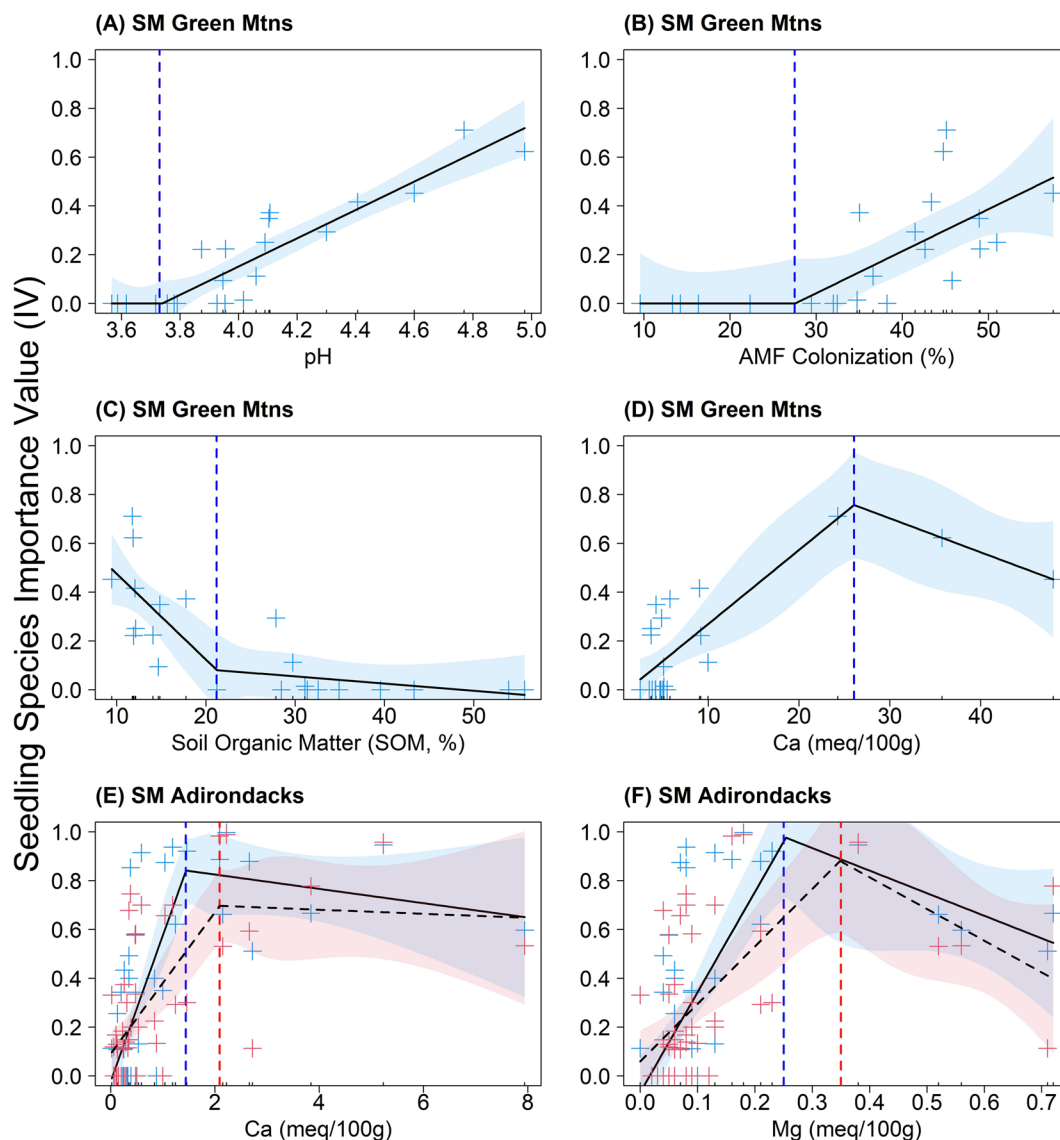


Fig. 4 Results of generalized linear breakpoint analyses of sugar maple (SM) seedling species importance value, in the Green Mtns and Adirondack Mtns relative to soil chemical and environmental variables (only significant relationships shown, panels A–F). Points (+) indicate raw data; shading represents 95% confidence intervals. The solid lines in A–D display data derived from 2019. The vertical dotted line represents the esti-

mation of the breakpoint (change between slopes of the two linear segments – see Supplemental Table S2 for diagnostics of segmented fits). For Adirondack Ca and Mg comparisons, the solid lines display data derived from 2009 (with blue vertical dashed line) and the dashed lines show 2015 data (with red vertical dashed line)

This reflects the study design, wherein samples captured the full transition in community composition from northern hardwood to spruce-fir.

Another notable difference between results from the Adirondacks and those from the Green Mtns were the relationships observed among elevation, SOM,

ECEC, and pH. In the Green Mtns, SOM increased with elevation, where colder conditions slow decomposition, similar to findings in the unglaciated Great Smoky Mountains (Garten et al. 1999; Tewksbury and Van Miegroet 2007), and in New York’s Catskills (Lawrence et al. 2000). In the Adirondacks, SOM

was weakly related to overstory species composition, possibly reflecting differences in decomposition rate between beech and sugar maple litter (Melillo et al. 1982). As with surveys in the Catskill Mountains to the south (Johnson et al. 2000), SOM in the Adirondacks appeared to be an important component of ECEC (SOM was ECEC's strongest potentially explanatory predictor). In the Green Mtns, where SOM was unrelated to ECEC, but was negatively correlated with pH, it is possible that organic matter accumulation at high elevations has contributed to soil acidification.

Patterns and role of mycorrhizal associations

Mycorrhizal colonization of tree seedling roots also seems to play an important role in seedling establishment across our elevation gradients. It has previously been indicated that AMF propagules are not present in sufficient abundance within the boreal forest to support beneficial colonization of expanding sugar maple (Carteron et al. 2020). Indeed, AMF associated tree basal area (represented solely by *Sorbus sp.* at high elevations) is extremely low at high elevations generally dominated by EMF associated trees like red spruce, balsam fir, and cordate birch (*Betula cordifolia*). Although this indicates low diversity of tree AMF hosts at high elevation, AMF colonization of understory herbaceous plants does occur. Our analysis revealed a steep decline in AMF root length colonization beyond the temperate-boreal ecotone, coincident with a sharp decline in sugar maple importance value. While we cannot fully decouple the decline in sugar maple importance at high elevations from the effects of climate and soil chemistry (but see Tourville et al. 2022), recent manipulative seedling growth experiments along regional elevation gradients done both in a greenhouse and in a field setting indicates a central role of mycorrhizal colonization in potentially controlling sugar maple establishment in the boreal forests considered in our study (Carteron et al. 2020; Tourville, unpublished data).

While mycorrhizal colonization of sugar maple roots was much reduced in boreal forests relative to northern hardwoods, it remained non-zero. Our study identified a threshold value of colonization (~30%) below which sugar maple importance value rapidly declined to zero. Importantly, colonization is not only a function of inoculum availability, but a

response to resource availability modulated by functional differences between AMF and EMF species (Tedersoo et al. 2020). However, we posit that availability of inoculum was more relevant for colonization rates in this study. For AMF which specializes in phosphorus (P) acquisition, concentrations of P were not low (compared to lower elevations) at high elevations sites in the Green Mtns (see Supplemental Fig. S3). For EMF which efficiently harvest nitrogen (N), high N deposition at high elevations, known to occur in the northeastern United States, did not significantly reduce EMF colonization of beech (Miller et al. 1993). While the lack of colonization intensity itself likely impedes successful establishment of sugar maple in boreal forests, it is also possible that a less beneficial AMF community (i.e., fungal species that exchange a relatively smaller amount of critical nutrients than other species) is dominant in higher elevation spruce-fir forests compared to lower elevation hardwoods forests. Species turnover and declining fungal richness at higher elevations and latitudes has been noted across other such gradients across the globe and this could be at play in our system (Kivlin et al. 2017; Urcelay et al. 2019; De Bellis et al. 2022). It is also possible that environmental changes spurred in part by climate change could also shift fungal community composition to favor fungal species better suited to function under an altered climate, which in turn could have unpredicted effects on plant host performance (Kivlin 2020). In contrast, EMF colonization of beech remained consistent across the elevation gradient in our study, even though EMF species turnover may also have occurred (Kivlin et al. 2017), which would indicate that beech can partner with a variety of generalist fungal species. Given the lack of consistent strong correlations between American beech species importance and soil abiotic or biotic variables, limitation of American beech seedling establishment at high elevation may be more controlled by climate or other biotic interactions.

Conclusions

Despite numerous efforts to forecast changes in future tree species distributions under climate change, models often lack crucial information on the edaphic factors or biotic interactions that can dramatically alter the realized niche of a species.

Based on data collected along well-defined elevation and soil acidity gradients, we have quantified specific soil abiotic and biotic thresholds that can limit the establishment of sugar maple that do not appear to be relevant for American beech. The threshold values reported here could be used to continue and expand studies of the fundamental limitations of sugar maple seedling establishment beyond its current realized niche. Furthermore, our work highlights the importance of considering information related to plant associations with mycorrhizal fungi when forecasting distributional shifts of tree species. Ultimately, we hope that our results can contribute to the development of more sophisticated species distribution models that can be used to evaluate tree community shifts and inform the conservation and management of forest ecosystems in a changing world.

Acknowledgements Green Mountain research was supported partly by the US National Science Foundation award to Martin Dovciak (NSF award # 1759724) and partly by a Botanical Society of America Graduate Student Research Award, a New York Flora Association Research Award, and the Lowe-Wilcox Award from SUNY-ESF to Jordon Tourville. We thank Hailey Lynch, Heather Zimba, Ben VanderStouw, and Adam Busman for their help with data collection; local, state, and federal organizations located in Vermont for providing research permits, access to sites, and logistic support; and the Forest Ecology Monitoring Cooperative and the Green Mountain Club for providing site access and logistic support. We thank the Adair lab, Marie English, and the Aiken Forestry Sciences Laboratory at the University of Vermont for support and facilities for all mycorrhizal lab work. Adirondack research was funded by grants from the New York State Energy Research and Development Authority (NYSERDA), under the direction of Greg Lampman, to E&S Environmental Chemistry, Inc. (with a subaward to SUNY-ESF). We acknowledge the New York State Department of Environmental Conservation for permits for fieldwork in the Adirondack Park. The Adirondack Ecological Center in Newcomb and Ranger School in Wanakena (both SUNY-ESF) provided field housing and logistical support. Jay Wason, Tim Callahan, Charlotte Ruth Levy, M. Brand and M. Leopold helped with field work, and Mariano Arias helped with data entry. We thank the Dovciak plant ecology lab members for useful and critical feedback. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

Author contributions All authors contributed to the initial study conception and design. Material preparation, data collection and analysis were performed by Jordon Tourville and Michael Zarfós. The first draft of the manuscript was written by Jordon Tourville and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

Funding Green Mountain research was supported partly by the U.S. National Science Foundation award to Martin Dovciak (NSF award # 1759724) and partly by a Botanical Society of America Graduate Student Research Award, a New York Flora Association Research Award, and the Lowe-Wilcox Award from SUNY-ESF to Jordon Tourville. Adirondack research was funded by grants from the New York State Energy Research and Development Authority (NYSERDA), under the direction of Greg Lampman, to E&S Environmental Chemistry, Inc. (with a subaward to SUNY-ESF).

Data availability The datasets generated during and/or analyzed during the current study are available for download in Springer Nature figshare repository.

Declarations

Competing interests The authors have no relevant financial or non-financial interests to disclose.

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