



Soil abiotic and biotic properties constrain the establishment of a dominant temperate tree into boreal forests

Alexis Carteron¹ | Vlad Parasquive¹ | Florence Blanchard¹ | Xavier Guilbeault-Mayers¹ | Benjamin L. Turner² | Mark Vellend³ | Etienne Laliberté¹

¹Département de Sciences Biologiques,
Institut de Recherche en Biologie Végétale,
Centre sur la Biodiversité, Université de
Montréal, Montréal, QC, Canada

²Smithsonian Tropical Research Institute,
Balboa, Republic of Panama

³Département de Biologie, Université de
Sherbrooke, Sherbrooke, QC, Canada

Correspondence

Alexis Carteron
Email: alexis.carteron@umontreal.ca

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Abstract

1. Climate warming is expected to cause the poleward and upward elevational expansion of temperate plant species, but non-climatic factors such as soils could constrain this range expansion. However, the extent to which edaphic constraints on range expansion have an abiotic (e.g. soil chemistry) or biotic (e.g. micro-organisms) origin remains undetermined.
2. We conducted greenhouse experiments to test if the survival and growth of a major North American temperate tree species, *Acer saccharum* (sugar maple), is independently or jointly constrained by abiotic and biotic properties of field-collected soils from within and beyond the species' elevational range.
3. Abiotic factors, particularly low base cation concentrations, were major constraints to seedling establishment in boreal forest soils (beyond the range edge), but insufficient arbuscular mycorrhizal fungal inoculum (biotic factor) also strongly reduced seedling performance in these soils.
4. *Synthesis.* Our results suggest that forecasting future changes in forest composition under climate warming requires consideration of soil properties as well as the mycorrhizal status of tree species.

KEY WORDS

mycorrhizas, plant-soil interactions, range expansion, sugar maple, temperate–boreal ecotone

1 | INTRODUCTION

Climate warming has caused many terrestrial and aquatic organisms to expand their ranges poleward and upward in elevation (Parmesan, 2006; Pecl et al., 2017). If plant distributions were primarily determined by climatic conditions, plant distributions should shift geographically in concert with climate, but many studies show that suitable climatic conditions for a given species shift much faster than species range limits (Corlett & Westcott, 2013; Savage & Vellend, 2015; Zhu, Woodall, & Clark, 2012). Although such lags in species range expansion can be due to demographic factors such as propagule availability (Engler et al., 2009), they may also indicate negative impacts of non-climatic factors (Putnam & Reich, 2017; Van der Veken, der Rogister, Verheyen, Hermy, & Nathan, 2007). Reduction

in survival, growth and fecundity are often observed in plants that are transplanted beyond their range limits (Hargreaves, Samis, & Eckert, 2014; Stanton-Geddes & Anderson, 2011), but the underlying causes are rarely known. Further investigation—experimental studies in particular—are needed to understand the underlying processes and external drivers of species range limits and potential range shifts (Chen, Hill, Ohlemüller, Roy, & Thomas, 2011; Sexton, McIntyre, Angert, & Rice, 2009).

Plant establishment beyond current geographic range limits could be constrained due to biotic and/or abiotic factors, with many such factors involving below-ground soil characteristics (Chapin, Walker, Fastie, & Sharman, 1994; Lafleur, Paré, Munson, & Bergeron, 2010; Tomiolo & Ward, 2018). For example, beyond range edges, the positive effects of soil biota such as mutualists

can be reduced or absent and the negative effects of generalist soil-borne pathogens can be increased. Similarly, unfavourable soil chemical properties (e.g. low pH) or physical structure (e.g. thicker litter layer) beyond a species' range could impede plant establishment. By contrast, there are many reported cases of plant species that actually show higher establishment success outside their current range. For instance, species can escape their native soil-borne pathogens when establishing outside their range, as described for invasive plants under the 'enemy release hypothesis' (Keane & Crawley, 2002; Liu & Stiling, 2006). However, interactions among abiotic and biotic factors could lead to more complex outcomes such as the 'happy edge', where success is highest at the edge of a species' range (Urli, Brown, Perez, Chagnon, & Vellend, 2016). Abiotic and biotic factors have often been treated separately in studies of range limits, but they might interact in important ways—a topic largely unexplored to date (Gaston, 2009; Lau, McCall, Davies, McKay, & Wright, 2008; Sexton et al., 2009; but see Johnson, Miller, & Wilson, 2017).

Elevational gradients are valuable model systems to understand how abiotic and biotic factors independently or jointly influence range shifts in response to climate change (HilleRisLambers, Harsch, Ettinger, Ford, & Theobald, 2013), and they are comparable in many (but not all) respects to latitudinal gradients over longer distances (Diaz, Grosjean, & Graumlich, 2003; Sundqvist, Sanders, & Wardle, 2013). Strong gradients in vegetation composition can occur over short spatial scales at ecotones, with the temperate-boreal ecotone as a striking example (Evans & Brown, 2017). Temperate forests are usually dominated by broadleaf, deciduous trees. By contrast, boreal forests are dominated by coniferous trees on soils that tend to be more acidic and nutrient-poor than those of temperate forests, with important impacts on plant growth (Collin, Messier, & Bélanger, 2017; Evans & Brown, 2017). Soil microbial communities—also important for plant performance—can also be highly variable along elevational gradients and among forest types (Geml, 2017; Yang et al., 2014). For example, ectomycorrhizal associations are dominant in boreal forests, but coexist with arbuscular mycorrhizas in temperate forests (Phillips, Brzostek, & Midgley, 2013; Read & Perez-Moreno, 2003). Therefore, even if climatic conditions in the boreal forest become suitable for temperate plants, their establishment could nonetheless be strongly constrained not only by physical substrate conditions but also the absence of mutualistic organisms such as arbuscular mycorrhiza fungi (Evans & Brown, 2017). Therefore, understanding the abiotic and biotic below-ground processes constraining the establishment of temperate tree species into boreal forests is essential to predicting the future distribution of the temperate forest with increasing temperature.

Our study sought to determine the establishment success of a dominant temperate tree *Acer saccharum* (hereafter sugar maple) in soils sampled along an elevational gradient from the temperate (core range) to the boreal (beyond) forest, and to understand the relative importance of abiotic and biotic below-ground factors. To do so, we conducted two greenhouse experiments: one using unmanipulated

soil originating from the three forest types and a second involving manipulations of soil biota. Based on the hypothesis that abiotic and biotic soil properties constrain upward elevational range expansion, we predicted that: (a) sugar maple seedlings would show higher survival and performance in soils from within the species range, (b) these soil effects would be due both to abiotic conditions and also biotic factors, both of which should be more favourable within the species range. Alternatively, release from specialized soil pathogens could result in higher seedling performance at or beyond the species' range edge. If seedling survival or performance varies according to inoculum source on replicate samples of the same soil origin, we can infer an important role of biotic factors. Differences among sterilized samples of different soil origins would be indicative of effects of abiotic factors. Soil pH, carbon, nitrogen, phosphorus, cations, base saturation and root colonization by arbuscular mycorrhizal fungi (AMF) were measured as potential drivers of seedling survival and performance.

2 | MATERIALS AND METHODS

2.1 | Study system

The study system is located in Parc national du Mont-Mégantic, a protected area of 55 km² in south-eastern Québec, Canada. The study area has been described in detail elsewhere (Brown & Vellend, 2014; Savage & Vellend, 2015). Mont Mégantic is part of the Montréalian Hills, mainly composed of leucogranite and syenite at the surface (Feininger & Goodacre, 2003). Soils are ferro-humic and humo-ferric shallow podzols with a sandy loam texture derived from rocky glacial tills with talus slope at higher elevation (Marcotte & Grantner, 1974). The climate in this region is characterized by warm, wet summers and cold winters with abundant snowfall (Parc National du Mont-Mégantic, 2007). Elevation in the park ranges from 430 to 1,105 m above sea level (a.s.l.). Average temperatures range from -10.2°C in January to 17.3°C in July with possible daily maxima above 30°C and an annual mean of 3.9°C at low elevations (599 m a.s.l.). At high elevation (1,089 m a.s.l.), average temperatures range from -12.4°C in January to 14.9°C in July for an annual mean of 1.2°C (data available from 2013 to 2017 for weather stations IQUBECNO2 and IQUBECNO3 at www.wunderground.com/weatherstation/overview.asp). With decreasing temperature, the length of the growing season is reduced from c. 100 days at low elevations to c. 80 days at high elevations (Parc National du Mont-Mégantic, 2007).

Since 1950, the mean annual temperature in our study region of southern Québec has increased by up to 2°C, and by 2050, it is predicted to further increase between by 1.7–4.6°C (Ouranos, 2015). If temperature limits the distribution of sugar maple, the species is expected to migrate upward in elevation and northward in latitude (Frumhoff, McCarthy, Melillo, Moser, & Wuebbles, 2007). Studies have shown that sugar maple can successfully establish in boreal forests, probably favoured by the relatively broad

tolerance of seedlings and seed germination to variable soil conditions (Kellman, 2004; Solarik, Gravel, Ameztegui, Bergeron, & Messier, 2016), yet the species is known to be sensitive to acidic soils (St Clair, Sharpe, & Lynch, 2008). At least one study has reported upward elevational migration of sugar maple (Beckage et al., 2008). However, sugar maple establishment in boreal forests is known to be limited by both above-ground and below-ground factors, such as unsuitable soil and seed predation (Brown & Vellend, 2014; Collin et al., 2017). The studied gradient exhibits a striking elevational transition from a sugar maple dominated temperate forest at low elevation to the boreal forest at high elevation, where sugar maple is absent except near the ecotone. This elevational gradient constitutes an ideal study system for our research exploring the relative importance of abiotic and biotic factors on sugar maple establishment into boreal forests because it allows us to minimize variation in important factors such as parent material, aspect and regional climate (local temperature declines with increasing elevation—the gradient of primary interest).

2.2 | Study sites and soil sampling

Our soil sampling sites were on the eastern slope of Mont Saint-Joseph (45°27'N 71°06'W), which is underlain by uniform parent material (i.e. syenite), from 723 to 914 m a.s.l. Categorization of the plots was based on elevation as well as on the canopy dominance of sugar maple. Temperate forest plots were dominated by sugar maple, mixed plots had c. 50% canopy cover of sugar maple, whereas sugar maple was absent from boreal forest plots. To obtain 10 plots of 20 × 20 m distributed evenly within each forest type, sampling was performed along 10 elevational transects with one plot of each of the three forest types per transect (see Figure S1): temperate forest (723–821 m a.s.l.), mixed forest (748–882 m a.s.l.) and boreal forest (875–914 m a.s.l.), according to previous studies (Urli et al., 2016). The ecotone between these two forest types, the elevation of which fluctuates somewhat north to south, is a mixture of maple *Acer* spp., fir *Abies balsamea* and spruce *Picea* spp., with abundant yellow birch *Betula alleghaniensis*.

Soil samples were collected on the eastern slope of Mont Saint-Joseph in June 2016. In each plot, four soil pits were dug in order to obtain representative soil samples at the plot level. For each pit, soil from the top 20 cm was collected separately for different horizons. Organic horizons were separated as L (litter; original structures easily distinguishable), F (fragmented; partial decomposition, structures difficult to recognize) and H (humus; decomposed organic matter, original structures indistinguishable), while the mineral horizons were Ae (characterized by leaching/eluviation of clay, Fe, Al or organic matter) and B (characterized by illuviation/enrichment in organic matter and accumulation of Fe or Al oxides) (Soil Classification Working Group, 1998). Because soil profiles differed along the elevation gradient (Figure S2), the thickness of each horizon was recorded in each pit, so that it could be recreated in experimental pots. Samples were bulked for each horizon in each plot, and different horizons were kept separate.

2.3 | Experimental design

To test if boreal soils (biotic and abiotic properties combined) constrained sugar maple establishment, we used fresh untreated soil sampled from the three forests in a first experiment. Starting sample size was 10 for each forest type, so 30 pots in total. In the second (concurrent) experiment, to disentangle the effects of biotic (i.e. soil inoculum) and abiotic (i.e. soil origin) factors on tree establishment, we applied four soil treatments to the soil from each sampling site: (a) sterilization without inoculum (referred to as sterile soil), (b) sterilization followed by inoculation with boreal forest soil (boreal inoculum), (c) sterilization followed by inoculation with mixed forest soil (mixed inoculum), (d) sterilization followed by inoculation with temperate forest soil (temperate inoculum). Inoculation was done by adding 7% (mass basis) of fresh soil.

We used gamma ray irradiation to sterilize soils because it has fewer effects on soil chemistry compared to other soil sterilization methods (McNamara, Black, Beresford, & Parekh, 2003). The soils were irradiated to a minimum of 50 kGy (Nordion Inc.). An experimental unit consisted of a subsample of the soil from a given field plot, subjected to one of the four treatments. For the second experiment, starting sample size was 10 for each treatment combination, and so there were 120 pots: four treatments × three soil origins × 10 replicates (transects).

Prior to the experiment, sugar maple seeds were cold stratified to break dormancy. This was performed at the Berthier Seed Center (Sainte-Geneviève-de-Berthier). After emergence, seeds were planted in the experimental pots. Seedlings were grown for two growing seasons at c. 20–30°C (July 2016–June 2017) with a dormant winter pause of 3 months at c. 3–5°C (December 2016–February 2017). In all pots, horizons were kept separate (including inoculum) to maintain realistic podzolic soil profiles. The experiment was conducted under controlled conditions within research greenhouses of the Montréal Botanical Garden (Québec, Canada). Soil was placed into 1-L pots (20 cm high × 5 cm wide). The amount (i.e. thickness) of soil by horizon in the pots depended on actual site measurements (averaged by plot). One seedling was planted per pot after the radicle had emerged. During the first month after transplantation, dead seedlings were immediately replaced with live ones, but after 1 month, we considered mortality to be a treatment effect and not transplant shock. A shade cloth (allowing passage of 36% of natural light) was positioned over the pots to reduce light in the greenhouse and simulate a partially shaded environment during the first year of growth. Pots were arranged in 10 blocks, with all the samples from the three plots in a given transect (1–10 in Figure S1) in the same block. Soil inoculation after sterilization was done using inoculum from the same block (e.g. sterilized temperate soil inoculated with a boreal soil from the same transect).

2.4 | Soil chemical analyses

For each soil horizon in each field plot, we measured several chemical properties. Soil was first air-dried and sieved (2 mm

mesh size for organic horizons and 6 mm mesh size for mineral horizons) prior to analysis for organic carbon (C), total nitrogen (N), total phosphorus (P), labile inorganic P and pH. Total C and N contents were determined by automated combustion and gas chromatography with thermal conductivity detection using a Vario MICRO cube analyser (Elementar). Total P was determined by ignition at 550°C followed by extraction in 1 M sulphuric acid. Soil pH was determined in both deionized water and 10 mM CaCl₂ using a glass electrode, and a soil-to-solution ratio of 1:8 for L and F horizons, 1:4 for H horizon and 1:2 for A, B horizons. After Bray-1 extraction, Bray P (labile P) in the extraction material was determined using automated molybdate colorimetry on a Lachat Quikchem 8,500 (Hach Ltd). Exchangeable cations were determined for all H, Ae and B horizons by extraction in 0.1 M BaCl₂ (2 hr, 1:30 soil to solution ratio) and detection by inductively coupled plasma optical-emission spectrometry (ICP-OES) with an Optima 7,300 DV (Perkin-Elmer Ltd). Total exchangeable bases (TEB) were calculated as the sum of the charge equivalents of Ca, K, Mg and Na. Effective cation exchange capacity (ECEC) was calculated as the sum of the charge equivalents of Al, Ca, Fe, K, Mg, Mn and Na. Base saturation was calculated as (TEB/ECEC) × 100.

2.5 | Seedling measurements

Surviving seedlings from the two experiments were harvested in June 2017 and processed individually within 24 hr. For each seedling, leaves, petioles, stems and roots were separated, measured and weighed before and after oven-drying at 60°C for 72 hr. Total biomass was estimated as the dry weight of all structures combined. Other size traits were measured but not used in the analysis due to strong correlations and thus redundancy (Table S1). A representative sample of the roots of each seedling were cleared in 10% w/v KOH, then stained in an ink and vinegar solution at 90°C (Vierheilig, Coughlan, Wyss, & Piché, 1998). Colonization of the root system by fungal structures was determined using a semi-quantitative scale following a protocol (available at <https://doi.org/10.17504/protocols.io.36rgrd6>) modified from Zemunik, Lambers, Turner, Laliberté, and Oliveira (2018). Using standard light microscopy, we recorded structures of AMF such as hyphae, arbuscules, vesicles, coils as well as fungal endophytes (presence of chytrids, hyphae diameter <2 µm with the presence of microsclerotia).

2.6 | Statistical analysis

To quantify the effect of soil origin (forest type) on seedling survival and biomass (*Experiment 1*), we used a linear mixed-effect models to compare the impacts of the three types of forest soil (fixed factor) along 10 elevational transects (random factor). To test the relative importance of abiotic and biotic factors and their potential

interaction (*Experiment 2*) in a crossed experimental design, we used a hierarchical model; this model compared the impacts of the abiotic components of different soil origins (i.e. initially sterilized temperate, mixed or boreal soil) and the four biotic (inoculum source) treatments (i.e. sterile soil, inoculum of temperate, mixed or boreal soil) on seedling survival and biomass. Soil of Experiment 2 were sampled along the 10 elevational transects (random factor); therefore, soil origin and inoculum source (fixed factors) are nested within transects in the model. We calculated coefficients of variation among treatment means to compare the impact of biotic versus abiotic factors.

For both experiments, survival and final biomass were first modelled individually, and then jointly using a Hurdle analysis providing a measure of performance that integrates survival and biomass (hereafter, performance, which is survival multiplied by biomass). We used the Bernoulli distribution for survival, and the gamma distribution for biomass (see model specification in Supporting Information). For the biomass estimation, only surviving seedlings were used (see Tables S2 and S3 for corresponding sample sizes). We implemented a Bayesian approach using JAGS (Plummer, 2003), since initial data analyses with general linear mixed-effect models in R revealed significant issues regarding model convergence due to the large number of zeros in the data (>50%) and the hierarchical design. The model ran an update on three parallel chains of length 500,000 and a thinning rate of 10 following a run with three parallel chains of length 5,000 and a burn-in of 4,000 iterations with a thinning rate of 10, for a total of 150,000 iterations conserved. We used uninformative priors for the shape parameter and semi-informative priors for all betas (model coefficients) for both parts of the model (see model specification in Supporting Information for further details). Convergence was assessed for each parameter estimate by visually inspecting the three Markov chains and by examining the \hat{R} values which quantify consistency (Zuur & Ieno, 2016). Model validation was then assessed visually by plotting the residuals against the fitted values and with each covariate in the model. No significant heterogeneity issues, and no clear outliers in residual patterns, were found. Model fit was assessed using Pearson's residuals χ^2 by comparing the observed residuals over residuals from data simulated under the model. The lack-of-fit statistic $\chi_{\text{obs}}^2 / \chi_{\text{sim}}^2$, which is expected to be equal to 1 if the model fits the data perfectly (Kery & Schaub, 2011), was equal to 0.82, indicating a good model fit. Adjusted- R^2 values were used as approximate assessments of the percentage of variance that is explained by the models. This was done by linearly fitting observed values to their predicted values. Soil characteristics were modelled using linear mixed-effect models and root colonization by bootstrapping. Analyses with root hyphal colonization as an explanatory variable of dry mass, and with soil characteristics as explanatory variables of performance, were done using generalized linear mixed-effect models. For the statistical analysis, we used R (R Core Team, 2018) with the following packages: BRMS (Bürkner, 2017), DPLYR (Wickham, Francois, Henry, & Müller, 2017), EMMEANS (Lenth, 2019), GGPLOT2 (Wickham, 2016), GGPUBR (Kassambara, 2018), LATTICE (Sarkar, 2008),

NLME (Pinheiro, Bates, DebRoy, Sarkar, & Team, 2019), R2JAGS (Su & Yajima, 2015), RESHAPE2 (Wickham, 2007), RJAGS (Plummer, 2018).

3 | RESULTS

3.1 | Seedling survival, biomass and performance along the elevational gradient (Experiment 1)

Seedling survival and biomass of survivors were more than twice as high in untreated soils from temperate and mixed forests compared to soils from boreal forests (Figure 1a,b). However, we note that the 90% credible intervals for predicted seedling survival and biomass overlap among forest types. Overall seedling performance was much lower in boreal soils, and the most favourable soil tended to be from the mixed forest (Figure 1c); indeed, there was a 77% decrease in mean performance in boreal soils compared to mixed-forest soils, which differ from one another with >90% confidence (see Table S5 for a summary of the results).

3.2 | Overall performance impacted by abiotic and biotic factors (Experiment 2)

The integrated measure of performance (i.e. survival multiplied by biomass) showed differences of moderate magnitude among soil origins and inoculum sources (Figure 2; see also Table S6 for a summary of the results). Performance was lower in the treatments with boreal soil origin (on average 37% lower compared to temperate soil origin) and with boreal soil inoculum (44% lower). Performance was greatest in soils of temperate origin and with the temperate inoculum source. Considering soil origin and inoculum source simultaneously (Figure 2c), the performance of seedlings grown in temperate or mixed-forest soil was relatively low if the inoculum did not come from the temperate forest. For temperate and boreal inocula, the boreal soil origin had a detrimental effect on seedling performance. In the absence of inoculum (i.e. in sterile soils), seedling performance was always low.

The model that included the interaction term (soil origin \times inoculum source) fit the data better (higher adjusted- R^2), suggesting that the effects of inoculum source on overall performance depended on soil origin and vice versa (Figure 2c). For soils of temperate origin, mean values for each inoculum source (i.e. from temperate, mixed and boreal forests, not including sterile soils) had a coefficient of variation (CV) of 45%; the CV was 30% in the mixed-forest soil and 29% in the boreal

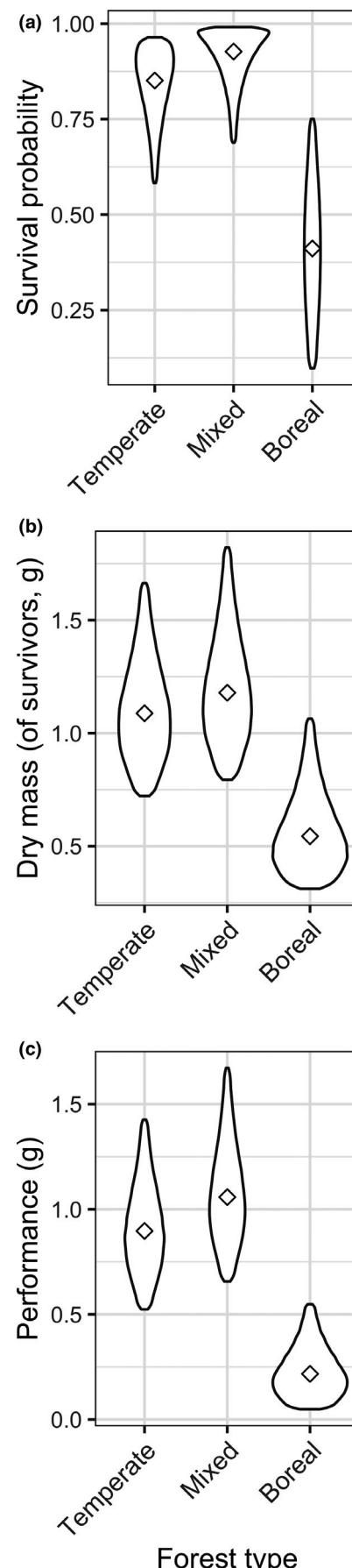


FIGURE 1 Effects of soils originating from the different forest types (along the elevational gradient) on the (a) survival probability, (b) dry mass and (c) performance (i.e. dry mass including survival probability) of sugar maple seedlings. In these violin plots, the width of the polygon represents the density of the expected values. Upper and lower limits of the violin plots represent 90% credible intervals (the vertical length of each polygon). Diamonds show medians

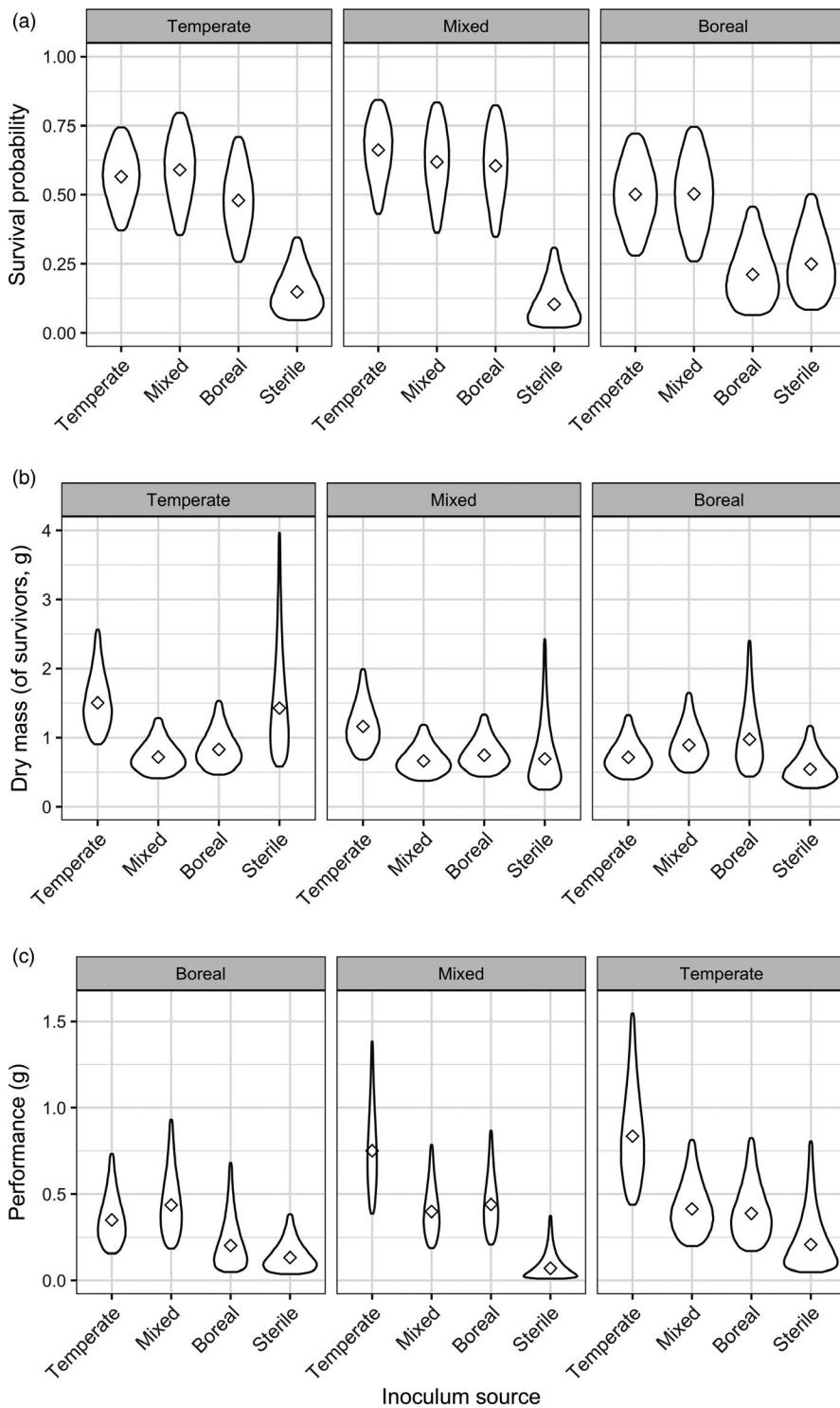


FIGURE 2 Effects of soil origin (abiotic and biotic factors) and inoculum source (only biotic factors) on sugar maple seedling (a) survival probability, (b) dry mass and (c) performance (i.e. dry mass including survival probability). Only one individual survived in sterilized temperate soil, so the expected dry mass showed large uncertainties which limit our predictions (i.e. the fit of the model). In these violin plots, the width of the polygon represents the density of the expected values. Upper and lower limits of the violin plots represent 90% credible interval. Diamonds show medians

soil. The magnitude of the soil origin effect on seedling performance (calculated as the CV among medians on sterilized soils) was 47%.

3.3 | Seedling survival and biomass impacted by abiotic and biotic factors (Experiment 2)

Survival was strongly impacted by the inoculum source (i.e. soil biota), but the magnitude of effect varied across soil origins. Survival was

especially low in sterile soil (Figure 2a). Overall, seedlings grown in sterile soil had, on average, 57% lower survival probability compared to the treatment with boreal inoculum and 89% lower compared to the treatment with temperate inoculum (see Supporting Information Table S6 for a summary of the results). Although the 90% credible intervals overlapped for survival among different inoculum sources, average survival was lower in boreal and sterile inoculum (Figure S3). When soil origin and inoculum source were considered simultaneously, the probability of survival was clearly lower within sterile soils regardless of soil origin.

The final biomass of surviving seedlings tended to be greater in soils originating in the temperate forest, being 36% and 44% greater than in mixed-forest and boreal soils respectively (Figure S3). When the impact of soil origin and inoculum source were considered simultaneously, biomass showed a large difference between the temperate inoculum and the other inocula if the

seedlings were grown in soils of temperate and mixed-forest origin (Figure 2b). The effect of the boreal soil origin on seedling biomass was negative regardless of the inoculum (mean biomass lower than 1 g). The effect of the temperate inoculum was approximately twice as high in temperate soil than in boreal soil.

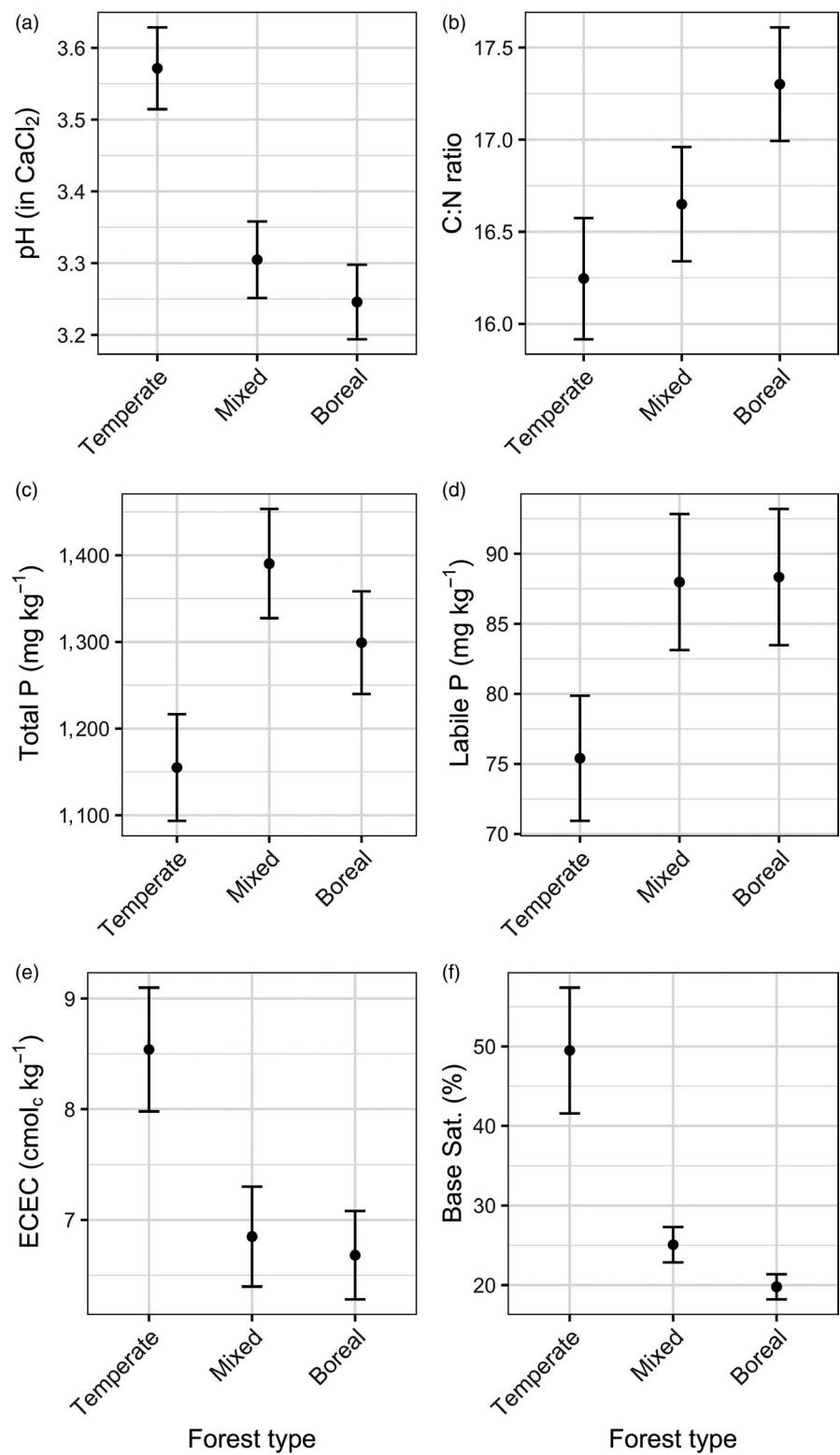


FIGURE 3 Soil characteristics for each forest type (temperate, mixed and boreal): (a) pH (in CaCl_2), (b) C:N ratio, (c) total P, (d) labile P, (e) effective cation exchange capacity (ECEC) and (f) base saturation. Values were averaged across horizons, and error bars represent the standard error of the mean of the estimated parameters

3.4 | Change in soil properties along the elevational gradient

Averaged across horizons, soil pH, ECEC and base saturation tended to decrease from temperate to boreal soils (Figure 3). In contrast, the soil C:N ratio and labile P tended to increase along the elevational gradient (Figure 3). As expected, soil in mixed forests tended to have intermediate values of soil characteristics except for total P, which was highest in mixed forests. All the soil physico-chemical parameters measured were strongly influenced by depth (see Supporting Information Figure S4). The first two organic horizons (L, F) had high pH, C:N ratio and labile P. The Ae horizons tended to have lowest values of pH, ECEC, C:N ratio and total P in all forest type. Soil properties in the Ae horizon in temperate forest were variable, but this horizon was encountered in only two plots. Seedling performance was positively correlated with ECEC (Figure S5), with an estimated effect size different from zero with 90% confidence.

3.5 | Abiotic and biotic factors impact root colonization by fungi

Seedlings grown in fresh (unsterilized) temperate soil tended to have higher colonization by hyphae, arbuscules and endophytes compared to seedlings grown in the mixed-forest and boreal soils (Experiment 1, Figure S6). Mycorrhizal root colonization in fresh soils was higher than in soils initially sterilized with or without subsequent inoculum (Experiment 2, Figure S7). Inoculum source and soil origin had important impacts on root colonization by fungi (Figure 4). Seedlings that were grown with the temperate inoculum had higher root colonization by arbuscular mycorrhizal fungal hyphae compared to seedlings with mixed-forest or boreal inoculum (Figure 4). Seedlings grown in soils of temperate origin were generally more strongly colonized (Figure 4). In sterile soil, hyphae were very rare and arbuscules never recorded (Figure 4 and Figure S8). Similar trends were observed for coils (Figure S8). As expected, colonization by endophytes was lower in sterilized soil and more evenly distributed among soil types and inoculum treatments (Figure S8). The presence of vesicles did not show a clear pattern. Seedling dry mass was positively correlated

with colonization by coils, arbuscules and hyphae, and negatively correlated with endophytes (Table S4). Furthermore, hyphal root colonization was positively correlated with higher biomass of seedlings that survived (Figure S9).

4 | DISCUSSION

Our study provides novel insights into the importance of non-climatic factors in constraining plant establishment and range expansion by disentangling the relative importance of soil abiotic factors (physico-chemical characteristics) and biotic properties (soil biota). The combined effects of abiotic and biotic soil factors greatly diminished the potential survival and growth of sugar maple seedlings in the boreal forest. In sterilized soils (i.e. with soil biota eliminated), seedling survival and growth were always very low, suggesting a crucial role of beneficial soil biota, most likely AMF. In addition, given strong differences in seedling performance among soils of different origin—even when sterilized—our study also points to an important role of soil abiotic properties, most likely base cations, in constraining the establishment of sugar maple in the boreal forest. Together, our results show how soil abiotic and biotic factors can jointly constrain the establishment of a dominant temperate tree species into boreal forests. Such below-ground factors should be considered when projecting future tree species distributions with climate change.

Under projected changes in climate, many temperate tree species have been predicted to expand their distributions beyond the current temperate–boreal ecotone (McKenney, Pedlar, Lawrence, Campbell, & Hutchinson, 2007). If not limited by dispersal and demographic factors, this shift is predicted to be of dozens of kilometres northward by the end of the current century. However, based on geographic distributions of seedlings versus adult trees, few North American tree species show signs of ongoing northward shifts (i.e. seedlings occurring further north than adult trees), despite recent increases in mean annual temperature (Zhu et al., 2012). Plant–soil interactions are known to influence plant performance and might be a major factor limiting temperate tree migration (Pither, Pickles, Simard, Ordonez, & Williams, 2018; Vissault, 2016). Sugar maple

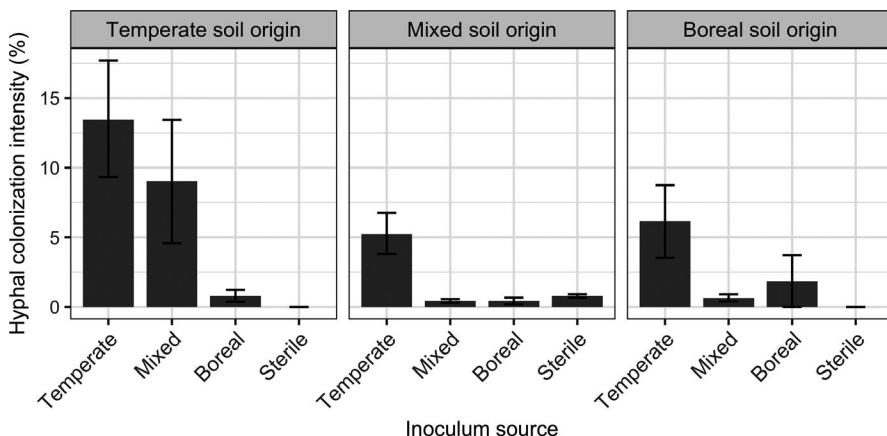


FIGURE 4 Effects of soil origin (abiotic and biotic factors) and inoculum source (only biotic factors) on observed root colonization intensity by hyphae in sugar maple seedlings. Error bars represent the standard error of the mean of the observed parameters

specifically is expected to migrate beyond its current range, towards the boreal forest (Frumhoff et al., 2007; Talluto, Boulangeat, Vissault, Thuiller, & Gravel, 2017), but edaphic conditions have been hypothesized to constrain such range expansion (Cleavitt, Battles, Fahey, & Blum, 2014). Our study shows that sugar maple expansion is likely to be constrained by lower seedling survival and growth on boreal soils (Figure 1) and, importantly, that such edaphic constraints have joint abiotic (e.g. low base cations) and a biotic (e.g. low arbuscular mycorrhizal fungal inoculum potential) causes. Declines in seedling performance are often observed in plants that are transplanted beyond their range limits, and our study contributes further evidence in the literature that non-climatic factors can play a central role (Tomiolio & Ward, 2018).

Mycorrhizal associations may be an important predictor of plant species distributions (Klironomos et al., 2011; Pringle et al., 2009). This symbiosis can even allow plants to expand their niche (Gerz, Bueno, Ozinga, Zobel, & Moora, 2018). The lack of mycorrhizal symbionts has been a major factor determining the spread of some introduced plants, as for ectomycorrhizal *Pinus* spp. (Dickie, Bolstridge, Cooper, & Peltzer, 2010; Nuñez, Horton, & Simberloff, 2009). However, AMF are very ancient plant symbionts (Field & Pressel, 2018) and many species have a cosmopolitan distribution (but see Bruns & Taylor, 2016; Davison et al., 2015; Morton & Bentivenga, 1994), dispersing over short and long distances (Correia, Heleno, da Silva, Costa, & Rodríguez-Echeverría, 2019; Egan, Li, & Klironomos, 2014), and showing low host specificity (van der Heijden, Martin, Selosse, & Sanders, 2015). Therefore, it has been suggested that the distributions of plants that form arbuscular mycorrhizal associations might not be constrained by the presence of the fungal symbionts (Richardson, Allsopp, D'Antonio, Milton, & Rejmánek, 2000). For example, an observational study that compared adult and seedling distributions suggested that differences in northward range expansion of North American temperate tree species are not predictable based on the type of mycorrhizal association (Lankau, Zhu, & Ordóñez, 2015). However, northward of temperate forests, there are boreal forests that are mainly dominated by trees that form ectomycorrhizal associations (e.g. *Picea* spp.) (Read & Perez-Moreno, 2003), which may act as a barrier for arbuscular mycorrhizal plant species since AMF are obligate symbionts. Our results suggest that boreal soils are not favourable to the symbiosis between AMF and the seedlings of sugar maple. As such, our study highlights the importance of considering the mycorrhizal status of plants in both 'donor' and 'recipient' communities when trying to forecast range expansions.

The poorer performance of seedlings under sterilized and boreal conditions further suggests that AMF are most likely to be the reason for the observed biotic effect. In fact, we found considerably lower root colonization intensity by AMF in seedlings inoculated with boreal forest soils (Figure 4), and a positive correlation between seedling biomass and the amount of mycorrhizal root colonization (Figure S9). The few AMF that might be present in boreal soils because of understorey plants or fungal spore dispersal (Öpik et al., 2008) appear to be insufficient for roots of sugar maple seedlings to be well colonized. This is supported by the fact that unsterilized

fresh soils (used in Experiment 1) tended to favour seedling performance and root colonization compared to the corresponding inoculum treatments on sterilized soil (see Figures S6 and S10). This is possibly due to the presence of a lower number of viable mycorrhizal propagules (e.g. fewer fragments of colonized roots) in the inoculated sterilized soil. Soil biotic factors strongly influenced the performance of sugar maple seedlings, and particularly their survival, as suggested by previous studies (Brown & Vellend, 2014; Cleavitt et al., 2014; Cleavitt, Fahey, & Battles, 2011; Putnam & Reich, 2017). It has also been shown that fungal and bacterial below-ground communities on sugar maple roots are different between areas of high abundance and the elevational range limit (Wallace, Laforest-Lapointe, & Kembel, 2018). In agreement with other studies, soil biota acted as important drivers of success of plant establishment (Ma et al., 2019; Pringle et al., 2009).

Performance of sugar maple seedlings was negatively impacted in terms of survival and subsequent growth by the abiotic component of boreal soil. Compared to soils from temperate forests, boreal soils tend to be more acidic and nutrient poor (e.g. lower availability of cations and nitrogen, Figure 3), characteristics that are known to affect the nutrition of sugar maple at early stages of development (Collin et al., 2017). This supports the hypothesis that upward and northward migration of sugar maple could be constrained by unsuitable soil physico-chemical properties. It is worth noting that soil chemistry was strongly influenced by depth. The Ae horizons characteristic of podzols tended to show the lowest concentrations of nutrients and pH, which could affect seedling growth, thus highlighting the importance of maintaining ecological realism by reconstructing soil profiles within the experimental units (Heinonsalo, Hurme, & Sen, 2004). Litter layer depth also can play an important role, acting as a barrier to seedling establishment (Cleavitt et al., 2011). Although sugar maple seedlings express broad tolerance for diverse abiotic soil factors (Arii & Lechowicz, 2002; Kellman, 2004), the presence of soil mutualists seems important as suggested by low performance in the sterile soil. AMF are also sensitive to abiotic factors, but their presence is crucial for the plant partner for nutrient acquisition, particularly phosphorus (Hodge & Storer, 2014; Smith & Smith, 2011), as well as for defence against pathogens (Jung, Martinez-Medina, Lopez-Raez, & Pozo, 2012; Smith & Read, 2010). Soil chemistry can influence seedlings both directly via nutrient availability and indirectly via effects on the soil biota. For example, sugar maple root colonization by AMF is known to diminish when soil pH is decreased (Coughlan, Dalpé, Lapointe, & Piché, 2000; Juice et al., 2006), which might explain the lower colonization and performance of seedlings grown in boreal soils (where pH was lower), thus negatively impacting their overall seedling performance, even when inoculated with temperate forest soil.

One must be cautious in using results from a greenhouse experiment to draw inferences about dynamics in the field, given additional, untested factors that can also influence plant performance. For example, intraspecific variation via local adaptation or maternal effects (e.g. on seed size)—not assessed in this study—may be important for sugar maple establishment (Solarik, Messier,

Ouimet, Bergeron, & Gravel, 2018; Walters & Reich, 2000). In addition, environmental parameters such as temperature can affect sugar maple germination, seedling survival and growth (Fisichelli, Stefanski, Frelich, & Reich, 2015; e.g. Solarik et al., 2016; Wright et al., 2018). Responses of soil micro-organisms to climate change are difficult to predict but will inevitably influence many abiotic and biotic factors (Jansson & Hofmockel, 2019), some of which that could feedback positively to plant performance, potentially facilitating range expansion. For example, it has been experimentally shown that higher soil temperature can stimulate microbial activity that increases mineralization of organically bound nutrients (Wan, Hui, Wallace, & Luo, 2005; Zak, Holmes, MacDonald, & Pregitzer, 1999), which can facilitate nutrient acquisition by sugar maple, although this also limits the benefits provided by AMF (St Clair et al., 2008). Availability of light and water can strongly influence sugar maple performance (discussed in detail by St Clair et al., 2008). These environmental features could interact in complex ways with mutualistic or harmful organisms (e.g. Hawkes, Hartley, Ineson, & Fitter, 2008; Sanders-DeMott, McNellis, Jabouri, & Templer, 2018). In our study, temperature, light and water availability were experimentally controlled to avoid any potential confounding effects with the factors of primary interest in this study—soil chemistry and microbiota. While it is possible that different levels of these environmental factors would have altered our experimental results, we have no *a priori* reason to suspect that the effects of soil factors specifically were qualitatively different than what one would expect in the field. Indeed, the relatively high temperatures experienced in the greenhouse might reflect expected future conditions with climate warming. A better understanding of the impacts of the interactions among temperature, light and water availability with biotic factors at the different stages of development of sugar maple would be needed to better forecast its future distribution.

Our study builds on several others at the same field site (Mont Mégantic) or in the same region (southern Québec) focused specifically on non-climatic below-ground factors that might limit or favour sugar maple's establishment into the boreal forest (Brown & Vellend, 2014; Collin, Messier, Kembel, & Bélanger, 2018; Urli et al., 2016). Our study highlights the importance of one group of beneficial soil biota, namely AMF. However, the possible effect of soil-borne pathogens merits further investigation. In previous studies, sugar maple showed negative conspecific density dependence (Johnson, Beaulieu, Bever, & Clay, 2012) and increased seedling survival in the boreal forest at Mont Mégantic (in a field experiment) with or without protection from insect herbivores, leading Urli et al. (2016) to hypothesize potential release from soil pathogens in the boreal forest. In contrast, our experiment points to an overall net positive effect of soil biota in this system, and other studies have not found strong negative plant-soil feedbacks for sugar maple (Bennett et al., 2017; McCarthy-Neumann & Ibáñez, 2012). The low performance of sugar maple seedlings on sterile soils from all sources suggests that the beneficial role of soil mutualists such as AMF outweighs potential negative impacts of soil-borne generalist pathogens, at least at our field site.

Furthermore, compared to sterile soils, seedlings showed marked positive responses to soil biota (inocula) when growing on soils from within their current range (temperate and mixed forests), and weaker responses when grown in boreal soil (Figure 2). That said, we must be cautious in extrapolating results from the greenhouse to the field. Our study focused mainly on soil micro-organisms as biotic factors, but sugar maple might also be susceptible to other enemies such as seed-consuming rodents for seed predation (Brown & Vellend, 2014) or insect herbivores (Urli et al., 2016). Beyond its elevational range, sugar maple seedlings appear to be favoured by release from insect herbivory (Urli et al., 2016); however, our results suggest that the presence of mutualist organisms might remain a key factor for its establishment, as other studies have suggested for annual plants and shrubs (Morriën & Putten, 2013; Sedlacek, Bossdorf, Cortés, Wheeler, & van Kleunen, 2014; Stanton-Geddes & Anderson, 2011).

Below-ground mutualists can be important determinants of plant distributions, especially in a context of range expansion and invasion (Richardson et al., 2000). Therefore, the incorporation of microbial ecology and especially mycorrhizal ecology into predictive ecosystem models might have great potential (Johnson et al., 2006; Treseder et al., 2012). Specifically, our results suggest that integrating below-ground traits such mycorrhizal status may improve modelling future changes in forest composition and functioning (Brzostek, Rebel, Smith, & Phillips, 2017). Some classic ideas in biogeography suggest that species distributions are limited by biotic factors (e.g. competition) at their warm edges (e.g. at low latitude or elevation) and by abiotic factors (e.g. harsh climate) at their cold edges (e.g. Dobzhansky, 1950; Pianka, 1966 and references therein). Evidence in support of this idea includes studies having shown that climatic and soil physico-chemical factors are important determinants of plant distributions (Beauregard & Blois, 2014; Bertrand, Perez, & Gégout, 2012; Coudun, Gégout, Piedallu, & Rameau, 2006). Our results indicate that even at cold range limits biotic factors such as soil microbial mutualists can be important determinants of potential range shifts, and thus need to be incorporated into forecasts of future changes in terrestrial ecosystems.

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AUTHORS' CONTRIBUTIONS

E.L., M.V. and A.C. conceived the ideas and designed methodology; A.C., V.P., F.B. and B.L.T. collected the data; X.G.-M. and A.C. analysed the data; A.C., E.L. and M.V. interpreted the results; A.C. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Data are available at: <https://doi.org/10.5281/zenodo.3524285> (Carteron, 2019a). Code for statistical analysis is available at <https://doi.org/10.5281/zenodo.3533170> (Carteron, 2019b).

ORCID

Alexis Carteron  <https://orcid.org/0000-0003-4162-9254>
 Xavier Guilbeault-Mayers  <https://orcid.org/0000-0002-4465-2153>
 Benjamin L. Turner  <https://orcid.org/0000-0002-6585-0722>
 Mark Vellend  <https://orcid.org/0000-0002-2491-956X>
 Etienne Laliberté  <https://orcid.org/0000-0002-3167-2622>

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SUPPORTING INFORMATION

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

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