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Research article

Competitive interactions under current climate allow temperate tree species to grow and survive in boreal mixedwood forest

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With climate change, climatic optima are shifting poleward more rapidly than tree migration processes, resulting in a mismatch between species distributions and bioclimatic envelopes. Temperate hardwood tree species may take advantage of the release of climate constraints and forest management to migrate into the boreal forest. Here, we use the SORTIE-ND forest simulation model to determine the potential for the persistence of three temperate species (sugar maple, red maple and yellow birch) when introduced at seedling stage in typical balsam fir–paper birch (BF–PB) bioclimatic domain stands of eastern Canada, quantifying the consequences on the native species composition. SORTIE-ND is a spatially explicit, individual-based forest stand model that simulates tree growth, regeneration and mortality. We performed a novel parameterization of the SORTIE-ND tree growth equation allowing for the inclusion of climate modifiers on tree growth. After validating our model with data from permanent forest inventory plots, we modeled the dynamics of unharvested stands at different successional stages, as well as post-harvest stands, after the addition of sugar maple, red maple and yellow birch seedlings at different densities. Our results show that current BF–PB domain climate conditions do not limit growth and survival of temperate species in boreal stands. Of the temperate species introduced, sugar maple had the lowest ability to grow and survive by the end of the simulation. Species assemblages of host stands were impacted by the presence of temperate species when the addition of seedlings was above 5000 temperate seedlings per hectare at the beginning of the simulation. For stands that were recently clear cut, temperate seedlings were unable to grow due to intense competition from aspen regeneration. Our results suggest that both current climate and competitive interactions between temperate species and boreal species should not impede the ability of temperate species to grow and survive in the BF–PB domain.

Keywords: *Acer rubrum*, *Acer saccharum*, *Betula alleghaniensis*, competition effect, forest management, SORTIE-ND simulator

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Introduction

Global climate change is expected to produce complex impacts on forest ecosystems and tree species distributions (Boulanger et al. 2019, Brice et al. 2019, 2020). Under a warming climate, tree species are projected to migrate poleward, tracking their optimal climatic niche, as temperature and precipitation are known to shape the geographical range of tree species at the global scale (Morin et al. 2008, Lee-Yaw et al. 2016). At the local scale, other factors influence tree species distributions, including edaphic conditions, biotic mechanisms and dispersal abilities (Fisichelli et al. 2012, Solarik et al. 2018). Consequently, we observe a lag between shifts of bioclimatic envelopes and occupancy of these envelopes through migration. In particular, tree species with limited dispersal and late sexual maturity may be at greater risk of not keeping pace with high climate change velocity (Aitken et al. 2008, Boisvert-Marsh et al. 2014, Solarik et al. 2016).

The Canadian boreal mixedwood forest ecotone is composed of two distinct bioclimatic domains: the balsam fir–yellow birch (BF–YB) bioclimatic domain in the south and the balsam fir–paper birch (BF–PB) bioclimatic domain in the north (Saucier et al. 1998). The BF–PB domain corresponds with the northern limit of the temperate species sugar maple *Acer saccharum* and yellow birch *Betula alleghaniensis* (Saucier et al. 1998, 2003). The northern limit of red maple *Acer rubrum* is in the spruce–moss forest, further north (Tremblay et al. 2002). In the BF–PB domain, only marginal stands of these temperate species can be found on the top of hills where, due to frequent temperature inversions, climatic conditions are more favorable than in lower elevation plains and valleys (Jin et al. 2008). In addition, soil microsites on hilltops tend to be more favorable for the germination and growth of temperate tree species because of better drained soils (Goldblum and Rigg 2002). All three temperate species can maintain and reproduce in these marginal stands, but severe spring frost and low temperature during the growing season are known to affect their reproductive capacity (Tremblay et al. 2002, Drobyshev et al. 2014, Graignic et al. 2014). These marginal and isolated stands could act as seed sources, facilitating the colonization of temperate species from the BF–YB domain into the northern prevalent conifer matrix.

Even though the future climate may promote a northward expansion of temperate species into BF–PB domain (Fisichelli et al. 2014, Boulanger et al. 2017, Evans and Brown 2017, Taylor et al. 2017), other edaphic and biotic factors, natural disturbances and forest management activities could influence their migration success and rate (Lee-Yaw et al. 2016, Boulanger et al. 2018, Carteron et al. 2020, Solarik et al. 2020). For instance, competition of boreal species with temperate species may limit their northward expansion due to specific biotic mechanisms, such as the development of unfavorable acidic substrate with the decay of conifer needles and wood (Evans et al. 2020, Solarik et al. 2020, Cleavitt et al. 2021). Light competition could also be a limiting factor for temperate species expansion. Sugar maple is more shade tolerant than red maple and yellow birch, but its growth still increases with light availability (Beaudet and Messier 1998). Therefore, the ability of temperate species to grow and survive, especially red maple and yellow birch, may vary under different canopy compositions due to variability in canopy light interception (Messier et al. 1998). Temperate species could take advantage of gap dynamics created by natural disturbances or forest management in stands of the BF–PB domain due to the reductions in competitive pressure for light and space (Kellman 2004, Gasser et al. 2010, Bannon et al. 2015).

Modeling species distributions under climate change is an important and challenging task for understanding and predicting the fate of future ecosystems and natural resources. The most widely used tools to predict future species distribution are species distribution models (SDMs), largely based on bioclimatic envelope modeling (Guisan and Thuiller 2005). They are used to derive probabilities of occurrence in current and new geographical areas with climate change. Although SDMs can model species distributions at large scales, they are criticized because they generally only consider climatic variables and neglect biotic interactions, natural disturbances and other mechanisms of forest stand dynamics (Pellissier et al. 2012, Heads 2015). Some of these shortcomings can be mediated using process-based stand simulation models. Such models, which simulate the demographics of individual trees in a stand, are capable of simulating forest succession by considering competitive interactions for resources between trees (e.g. light and space) (DeAngelis and Grimm 2014, Maleki et al. 2019). Spatially explicit stand simulators model direct interactions between trees by considering their specific spatial positions, thus directly accounting for competition for light and space among trees. Further, these models simulate tree seed dispersal, recruitment and mortality using probabilistic approaches to evaluate changes in stand demography (Shugart and West 1977, Pacala et al. 1993, Shugart et al. 2018).

In this study, we used a forest stand simulation model to estimate the ability of temperate tree species to grow and survive under current climate conditions in western Quebec BF–PB domain stands where they are currently absent. We simulated stand dynamics of the BF–PB domain along a gradient of stands characterized by different ages and composition, from young pure aspen stands to older coniferous-dominated stands, representative of the regional landscape. Within each stand we 'added-in' different seedling densities of our target study species, i.e. sugar maple, red maple and yellow birch. We estimated the specific impact of initial seedling density on the resultant species assemblages (based on basal area) over 110 years duration simulations (1991–2100) keeping constant climate. The main objectives of this study were threefold: 1) to assess if current climatic conditions in the BF–PB domain may inhibit the growth and survival of temperate tree species; 2) to determine the role of intra- and inter-specific competition on the resultant basal area of temperate trees through time, considering 2a)

different successional stages and 2b) whether stands have been harvested or not; and 3) to determine the impact of the introduction of temperate tree species on native boreal tree communities.

Material and methods

Study area

The simulated study area was located in the Lake Duparquet Research and Teaching Forest (FERLD) in the Abitibi region of western Quebec, Canada. The growing season (May–September) is characterized by a mean temperature of 14°C and cumulative precipitation of 447 mm (mean from 1970 to 2019). The FERLD is located within the BF–PB domain (Fig. 1). The study landscape is fragmented by multiple past fire events staggered through time and space, resulting in a mosaic of different stand compositions from shade-intolerant species to late successional coniferous stands. Early succession stands are primarily composed of trembling aspen *Populus tremuloides*, paper birch *Betula papyrifera* and jack pine *Pinus banksiana*, and are replaced by balsam fir *Abies balsamea*, white spruce *Picea glauca* in mid-successional mixedwood stands and white cedar *Thuja occidentalis* in late successional stands (Bergeron 2000, Chen and Popadiouk 2002). Spruce budworm *Choristoneura fumiferana* outbreaks affect coniferous species, especially balsam fir, and create gaps that early succession species may colonize (Kneeshaw and Bergeron

1998, Bergeron et al. 2014). Concerning the three studied temperate species, red maple was scarcely present in the area and sugar maple and yellow birch were absent.

Model description and general application

The simulations were conducted with the SORTIE-ND model (hereafter SORTIE; ver. 7.05; Pacala et al. 1996, Murphy 2011). SORTIE is a spatially explicit, individual-based model that simulates stand dynamics by modeling the whole life cycle of trees within a stand (i.e. seedling, sapling, adult and snag). Each tree is modeled as a discrete object with different attributes such as diameter at breast height (DBH), height, crown dimension and age. Ecological processes, such as tree growth, mortality and recruitment, are simulated by specific modules within the main model. Modules, tree species lists, parameter values, tree initial conditions, local conditions (plot size, latitude, azimuth) and time step (minimal time units simulated) are specified in a parameter file. Time steps in SORTIE are generally one year, but can be longer. Within a timestep, SORTIE executes each biological–physical process considered in a predefined order: calculation of light received by each tree, diametrical tree growth, the number of seeds produced, their dispersal distance and mortality for both seedlings and trees. Initial conditions can be set in the SORTIE parameter file by indicating the number of trees per hectare for each 2 cm DBH class and species. SORTIE then randomizes tree positioning in the simulated plot. Alternatively, the position of each tree can be specified. We
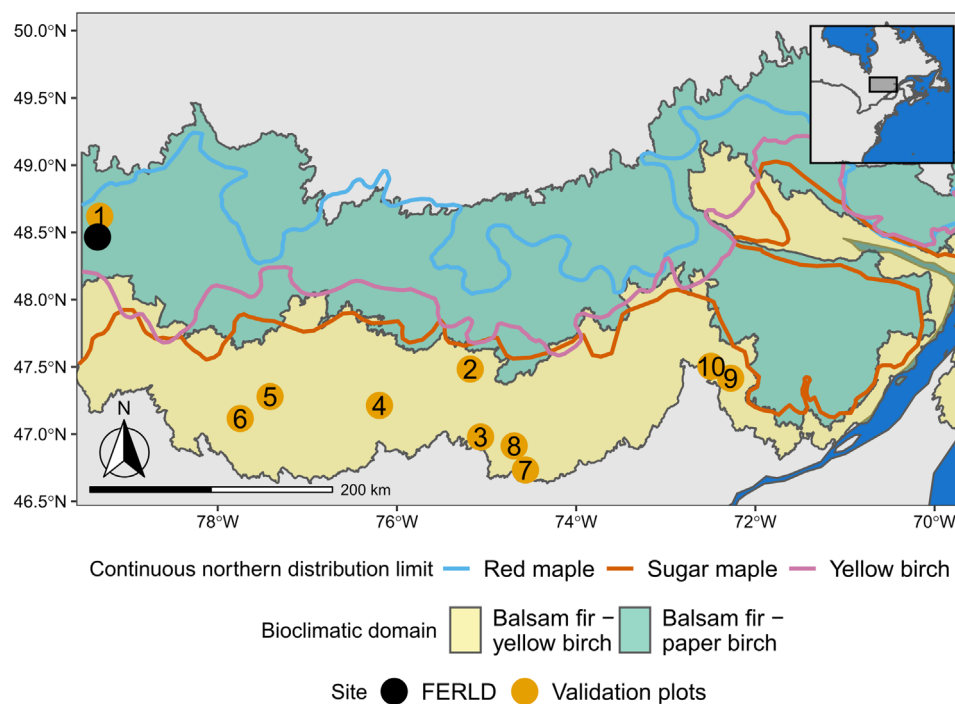

Figure 1. Map of the study area with points representing the location of the Lake Duparquet Teaching Research Forest (FERLD, in black) and the government permanent forest inventory plots used to validate the model (in orange). Numbers within dots correspond to the validation plots in Fig. 4. Bioclimatic domains and distribution limits of the temperate tree species are depicted as polygons and lines, respectively (C. Morneau, pers. comm., 2022).

consider SORTIE is a good candidate model to address our research objectives as it is flexible, permitting us to capture more realistically tree allometry, growth, dispersion and mortality using non-linear relationships and stochastic processes (Bose et al. 2015, Maleki et al. 2019, Benson et al. 2022).

The Supporting information describes the SORTIE submodels and our implementations. In the Supporting information, parameter values for yellow birch, red maple and sugar maple can be found along with six additional boreal tree species comprise into the BF–PB domain: trembling aspen, paper birch, balsam fir, white spruce, jack pine and white cedar. Tree allometry parameters, as well as those describing tree mortality and recruitment modules, were obtained from previous studies using SORTIE for those species (see references in Supporting information). To account for climatic effects on the tree growth of each species, as well as interspecific competition between temperate and boreal species, we produced a new parameterization of the adult growth modules of those species. We then validated our SORTIE parameterization by comparing simulations with independent data. Finally, we used the model to simulate the persistence of introduced temperate species seedlings in current climate conditions, with initial conditions based on a successional chronosequence of BF–PB domain stands at FERLD (Fig. 1). In each of the initial conditions we added different densities of temperate seedlings at the beginning of each simulation. Each of these steps is described in detail in the following sections (Fig. 2).

Parameterization of the SORTIE growth model

We used the growth module in SORTIE, based on a neighborhood competition index (NCI), to represent the growth of adult trees, i.e. trees ≥ 10 cm DBH. This module simulates tree growth through time (diameter at breast height increment in cm yr⁻¹, DBHI) as a proportion of maximum potential growth (*MaxPotGrowth*), which may be achieved under optimal growing conditions. In our study, the *MaxPotGrowth* parameter varies as a function of climate to account for differences in tree growth between plots and inventory years, and to simulate more accurately the tree growth across different forest domains. The realized growths were obtained by multiplying this potential growth by different limiting effects taking values between 0 and 1, representing the effects of tree size, shading from other trees and non-light-based competition or 'crowding' effects (Canham et al. 2004; Eq. 1).

$$\text{DBHI}\left(\text{cm yr}^{-1}\right) = MaxPotGrowth \times \text{size effect} \times \text{shading effect} \\ \times \text{crowding effect} \tag{1}$$

We parameterized Eq. 1 in two steps. First, we parameterized the effect of tree size, shading and crowding on tree growth with a hierarchical Bayesian model, using data from the Réseau d'Étude et de Surveillance des Écosystèmes Forestiers (RESEF) Quebec forest monitoring network, a network of 1-ha plots across Quebec where trees were inventoried every 5 years from 1986 to 2020, and where the position and DBH of all trees in the plot are known. In this study, we retained 37 RESEF plots where temperate tree species coexisted with boreal tree species. We also added to the RESEF data 6 additional mapped 1-ha plots located in the FERLD, which have been inventoried 5 times since 1991 (Maleki et al. 2021). The full parameterization dataset for our growth model thus included 43 plots, 19
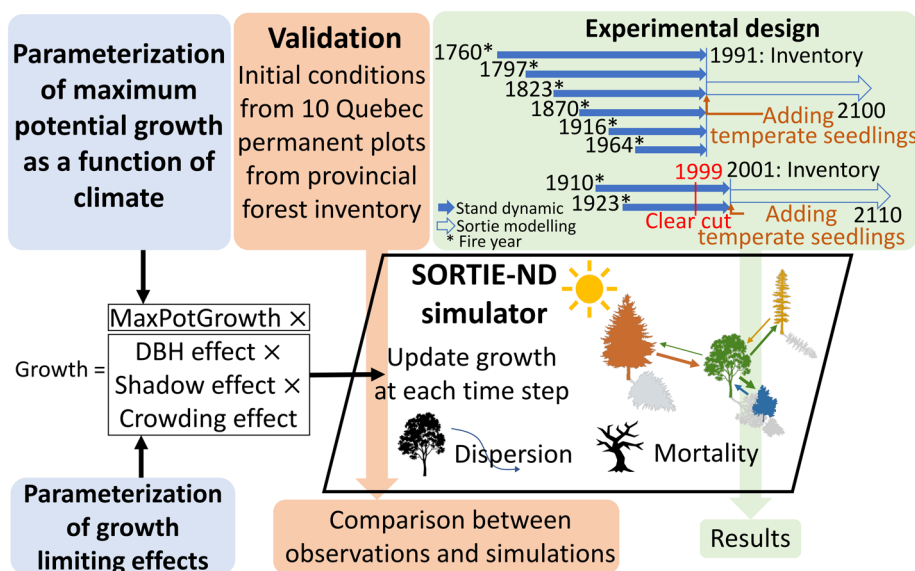

Figure 2. Conceptual framework of the model and the experimental design used in this study. The model has been parameterized in two steps represented by the two blue frames. Validation process is represented in orange frame; a map of the validation sites can be found in Fig. 1. The experimental design is represented in the green frame, where a timeline of the Lake Duparquet Teaching Research Forest (FERLD) forest stands used for initial modeling is represented. In each stand, different densities and combinations of temperate species have been added in the balsam fir–paper birch (BF–PB) domain stands.

184 different trees, for a total of 72 964 DBH observations. In this final dataset, all possible couples of species interactions were represented, so that SORTIE could adequately be parameterized.

Second, we estimated *MaxPotGrowth* as a function of four climate variables: mean annual temperature (MAT), growing degree days (DD5), mean summer precipitation (MSP) and summer climate moisture index (CMI). Because the RESEF plots are only located in Quebec and because the bioclimatic distributions of the considered species also lie outside of Quebec, we used an extensive network of inventory plots located across eastern North America to capture the whole species bioclimatic range. We used tree growth measurements from 4067 permanent forest inventory plots located across eastern North America, including 21 647 trees. We modeled tree growth as a function of climate using quantile Bayesian regression with the 95th percentile of observed growth as a substitute for the mean expected growth in the absence of competition. This second step also served to assess whether current climate conditions would be a limiting factor to tree growth affecting the performance of temperate species in the studied boreal stands (objective 1; see Supporting information for additional information).

In our parameterization of SORTIE, seedling and sapling growth only depended on the amount of received light, which was computed based on the crown space of neighboring trees. The species-specific sensitivity of seedling and sapling growth to light was parameterized previously (Pacala et al. 1994, Poulin et al. 2008). The resulting growth rate also determines their mortality probability.

Validation of the SORTIE model

Before executing our simulation experiments, we first verified if SORTIE, with the new tree growth parameterization, was able to reproduce observed stand dynamics. To do so, we used data from the permanent forest inventory network provided by the Quebec Ministry of Forests, Wildlife and Parks (MFFP; Fig. 1). These comprise 400-m² circular plots sampled on average every 10 years from the 1970s. At each inventory date, various data are collected on trees and saplings (e.g. composition, DBH) and of environmental attributes (e.g. soil conditions, topography, understory composition). We extracted the species and size distribution (trees ha⁻¹ for each species and size class) of trees and saplings of 10 permanent plots with repeated measurements for the validation process. The plots were selected according to the following criteria: they must be located within the boreal mixedwood forest in western Quebec (BF–PB and BF–YB domains); the studied species were present (i.e. sugar maple, red maple, yellow birch, paper birch, trembling aspen, jack pine, balsam fir, white spruce and white cedar); temperate tree species coexisted with boreal tree species; and the plots did not experience any major disturbances such as wildfires, logging or insect outbreak between the first and last inventory. The first inventory date in each plot was used as initial condition for the SORTIE simulations, with the position of each individual tree randomized respecting the DBH distribution of each species by SORTIE. This step was done automatically as an option in SORTIE if the x–y coordinates of each tree were not available. The length of the simulation was equal to the number of years between the first inventory and the last inventory, so that the simulation ended at the last inventory of the plot. We recorded tree DBH, growth and spatial coordinates over time in the simulations, and we extracted results only for the years when an inventory took place. For this validation exercise, the size of the simulated plots was 4 ha (200 × 200 m) and they were divided into 100 subplots of 400 m² to obtain 100 replicates at the same size of the observed plots. It was important to get replicates inside the simulation plots because SORTIE randomized the position of trees in the plot. Each replicate had different initial tree composition that may lead to different results at the end of the simulations. All these results were compared with the observation.

We evaluated SORTIE model performance by assessing the ability of the model to reproduce species assemblages observed in the validation plots using the following steps. We first performed a principal component analysis (PCA) of the adult basal area per hectare of each species (multivariate response) across all validation plots (observations and simulations). PCA was used to characterize stand species assemblages by deriving the position of each plot (observations and simulations) in multivariate space. For each simulation, we extracted the Euclidean distance between the observation position or the simulated subplots, and the centroid of the corresponding simulated subplots. We considered the simulations consistent with the observed data if the distance between the observation and the centroid was within the nearest 95% of the distances between simulated subplots and their centroid.

Simulation experiment design

For our simulation experiment, we obtained initial conditions for the SORTIE simulations from plots in the FERLD territory where tree DBH was sampled in a 400 m² area (Maleki et al. 2021). These plots were unharvested post-fire stands and harvested stands representing different successional forest stages and tree compositions (Maleki et al. 2021). Unharvested post-fire stands included plots with the following years of last fire: 1760, 1797, 1823, 1870, 1916 and 1964 (Fig. 2). Plots were inventoried in 1991 following a spruce budworm outbreak. We considered dead balsam fir, which is the primary host of the spruce budworm in that area, as alive in our initial conditions to remove the potential effect of spruce budworm outbreak (Bergeron et al. 1995). Two post-harvest stands that underwent clearcutting in 1999 were inventoried two years later, representing our initial conditions for harvested stands (Brais et al. 2013). These post-harvested stands originated by previous fires in 1910 and 1923. We extracted the mean density per species and DBH class of 153 available plots to initialize 8 stands for the SORTIE simulations (6 unharvested regenerated after specific fire years and 2 harvested in 1999; Supporting information).

At the beginning of each simulation for each initial stand, we added a variable number of temperate seedlings of sugar maple, red maple, yellow birch or all three species. Three seedling densities were considered: a low-density experiment (500 seedlings per hectare), a medium-density experiment (5000 seedlings per hectare) and a high-density experiment (10 000 seedlings per hectare). The number of seedlings for the high-density corresponded to one seedling per m²; we note that the density of temperate seedlings could be higher, i.e. more than 100 000 seedlings per hectare in particular conditions (Henry et al. 2021). However, such a high density leads to a very high seedling mortality and unnecessarily prolongs simulation times. For the medium- and low-density, we chose to have two times less the higher density and twenty times less, respectively. For the 'all species' scenario, the density levels above were applied to each temperate species, leading to an overall seedling density three times higher than the single species scenario. A simulation without introduced temperate seedlings was also executed as a control. For the simulation experiments, the size of the simulated plot was 1 hectare and we let the model randomize the position of trees at the beginning of the simulation. Because we used the option of SORTIE that randomized tree positions, we divided the simulated 1 ha plot into 25 subplots of 400 m² to have a range of plausible simulated results to analyze. We set the timestep as one year but recorded tree coordinates, DBH and growth every 5 years to reduce the memory requirement.

Basal areas at the last timestep (after 110 years of simulations, i.e. from 1991 to 2100 with constant climate) were extracted to assess the capacity of temperate trees to grow and survive in stands of the BF–PB domain. We compared these basal areas under the different conditions simulated, i.e. with different initial seedling densities (objective 2), at different stages of BF–PB stand dynamics (objective 2a) and in harvested and unharvested stands (objective 2b). To investigate the effect of temperate species establishment, growth and survival on native assemblages of the BF–PB domain (objective 3), we built a multivariate space using PCA analysis with the simulated basal area of all species in all simulations and time steps. For each simulation, we then extracted the position of each timestep in multivariate space and plotted the trajectory through time of the different simulations in the multivariate space, defined by the first two principal components. We compared the level of departures of these trajectories to that of the control group to assess the impact of the presence of temperate trees on the species assemblages in the stands.

Results

Climate effect on temperate species growth

MaxPotGrowth was equal to 0.66 cm yr^{-1} for sugar maple, 0.50 cm yr^{-1} for red maple and 0.85 cm yr^{-1} for yellow birch in the current FERLD climate, north of their continuous distribution range. Those parameter values were high enough to allow them to grow and survive in the BF–PB domain (Supporting information). Consequently, current climate conditions were not an important limiting factor. DD5 was the climate variable with the major influence on *MaxPotGrowth* for all species (Fig. 3).
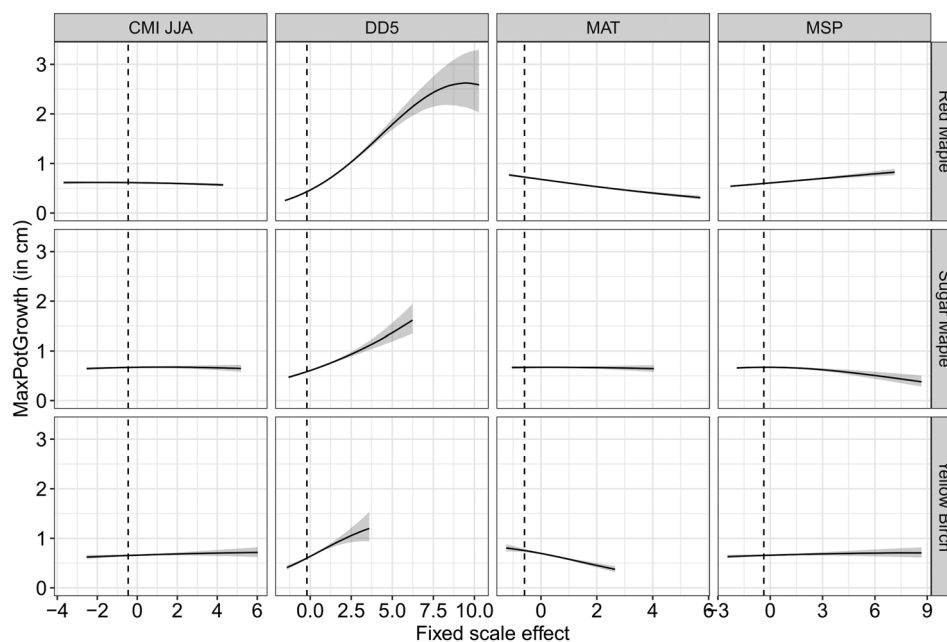

Figure 3. Climatic effects of the quantile Bayesian regression used to find maximum potential growth for temperate species. Values of the X axes correspond to the standardized climate variables (see panel column name). CMI JJA: climate moisture index for the months of June, July and August; DD5: annual growing degree days; MAT: mean annual temperature; and MSP: mean summer precipitation. The dashed vertical line represents present climate at the Lake Duparquet Teaching Research Forest (FERLD) study site.

Model validation

SORTIE simulations of species assemblages by basal area were consistent with observations, given that species assemblages were included in the 95% simulated interval for 9 out of 10 observed plots (Fig. 4). Plot 9 deviated from observations as the simulated basal area of balsam fir was slightly overestimated (Fig. 4a, Supporting information). The simulations did not reproduce the full range of variability in observed tree growth, which is to be expected since SORTIE does not include all sources of stochasticity on tree growth, but the comparison of simulated and observed growth of each species showed no systematic under- or overestimation of growth (Supporting information).

Growth and survival of temperate tree species in BF–PB stands

The simulated adult basal area of temperate tree species at the last time step (110 years) indicated that all temperate species

can grow and survive in the stands of the BF–PB domain under most simulated conditions (Fig. 5). Yellow birch displayed a higher basal area than sugar maple and red maple, indicating that yellow birch would be the most suitable species to grow and survive in the simulated stands. In harvested stands, yellow birch and sugar maple showed a lower basal area than in unharvested stands, while red maple did not survive in harvested stands after 110 years.

When temperate trees were simulated separately in unharvested stands, their basal area after 110 years increased according to their initial seedling from low- to medium-density. However, when going from a medium- to a high-density, only the basal area of red maple increased, whereas the two other species remained constant (Fig. 5 and 6). In harvested stands, the basal area of yellow birch and sugar maple increased between low- and medium-density, but not between medium- and high-seedling densities, whereas red maple basal area remained constant with increasing density.

The adult basal area of temperate species was lower when they were added altogether than when they were alone in
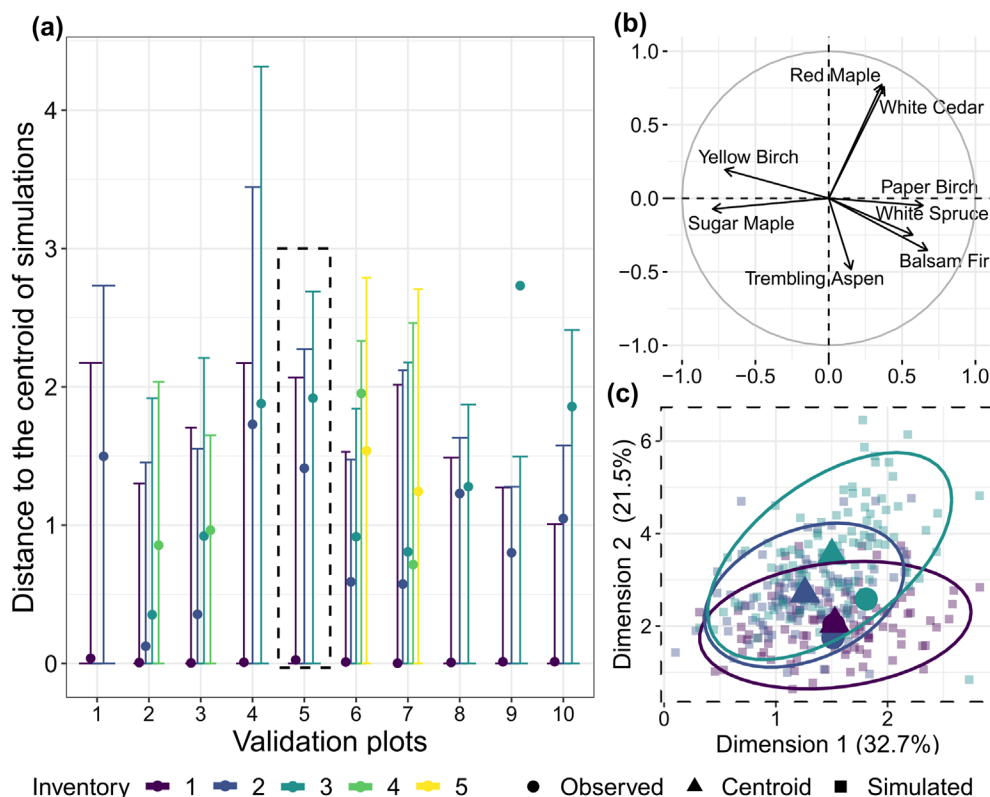

Figure 4. (a) Distance of the observed plot composition (point) and of the simulated subplot compositions (error bar, encompassing 95% of the simulations) to the centroid of simulated subplot compositions for the same plot and inventory date. The multivariate space was constructed by principal component analysis (PCA) with the simulated basal area (m² h⁻¹) of all species in the validation plots located in the balsam fir–yellow birch (BF–YB) stands. (b) Arrows showing the contribution of the basal area of each species on the main two axes of the PCA. (c) An example of the construction of the metrics presented in (a). First, the simulated basal area across replicated subplots is projected for each inventory (squared colored points). Second, the centroid of simulated points is computed by inventory (triangle points). Third, the observation points for each inventory are projected in the multivariate space (round points). Finally, the Euclidean distances between the centroid of the simulated subplots and the observation are calculated for each inventory. In (c), the orange triangle and the circle are superimposed since the centroid of the simulations corresponds to the observation at the beginning of the simulation, i.e. for the first inventory.

harvested and unharvested stands (Fig. 5b). In these conditions, yellow birch basal area increased with density; sugar maple basal area increased from low- to medium-density, but remained constant for higher density; and the basal area of red maple decreased with increasing seedling density up to extinction under high initial densities (Fig. 5b).

The basal area of temperate trees did not vary with the successional stage of the stand at the beginning of the simulation (time since last fire). However, for the younger stand (fire of 1964), basal area for red maple was higher than for the other stands (Fig. 5a).

Effect of temperate tree introduction on native BF–PB assemblages

The presence of temperate species had an impact on the native species composition of BF–PB domain stands, except under low temperate seedling densities (Fig. 6). Time trajectories of the control simulations moved in the multivariate space from stands with high presence of aspen towards stands with abundant white cedar and balsam fir typical of old forests in the study region. When adding a low-density of temperate seedlings in the unharvested stands, the trajectories shifted in the same direction as the control group, which means that the stand assemblages remained similar between

the control group and the low-density group. In contrast, we observed important differences between control stands and stands with medium to high seedling densities. The trajectories of stands with medium to high seedling densities shifted towards regions of the multivariate space that were correlated with high basal areas for the temperate species, indicating that temperate species have persisted in these stands. Furthermore, when adding red maple and yellow birch seedlings, the assemblages of stands at medium to high densities were similarly distributed in the multivariate space, indicating that an increase in density from medium to high did not further alter the species composition of the stands.

Discussion

In this study, we proposed a new parameterization of the SORTIE stand simulation model that allowed us to account for climate effects on growth as well as spatial interactions between trees in growth calculations. We aimed to assess whether sugar maple, red maple and yellow birch could grow and survive in stands of the BF–PB bioclimatic domain and what effect this would have on native species that currently dominate these stands. After parameterizing and validating the model, we showed that temperate tree species could grow
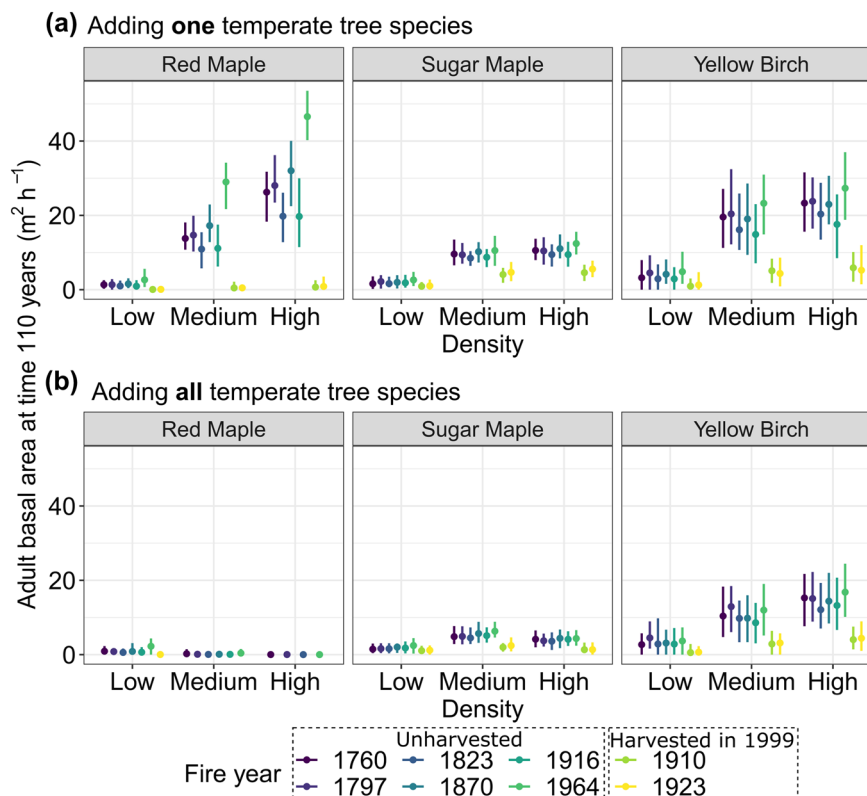

Figure 5. Simulated adult basal area at the last simulation timestep (110 years) for temperate tree species in stands of the balsam fir–paper birch (BF–PB) domain. Simulations consider different initial conditions relative to time since stand-replacing fire, harvesting and density of added temperate seedlings (one species at a time (a) or all species together (b)). Low, medium and high density seedlings correspond to 500, 5000 and 10 000 seedlings per hectare, respectively. Error bars are intervals containing 95% of the subplots in each simulation.
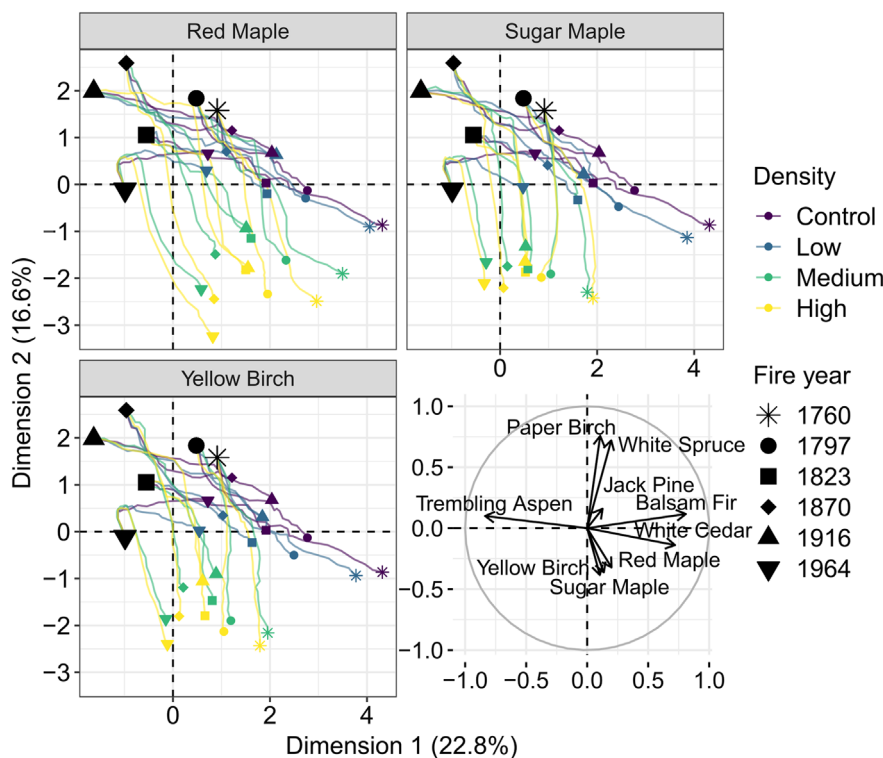
Figure 6. Simulated trajectories of stands assemblage in a multivariate space. The principal component analysis (PCA) is based on the basal area of adult trees across all simulation results. In each panel, various trajectories represent the chronology of the stands depending on the density of seedlings added in the balsam fir–paper birch (BF–PB) stands. The control group corresponds to simulations with no temperate tree species. Black dots correspond to the position of initial conditions in the multivariate space, and colored dots correspond to the results of the simulation at the last time step (110 years). This figure only displays unharvested stands, given the low ability of temperate tree species to grow and survive in recently harvested stands.

in current climate conditions of the BF–PB domain and persist in most stands we simulated after introduction.

Persistence of temperate species introduced in boreal mixedwood stands

The *MaxPotGrowth* parameter values of all temperate species were sufficiently high to allow them to grow in the current climate conditions of studied stands in the BF–PB domain (Supporting information; Leites et al. 2019, Brice et al. 2020). Maximum stand density is influenced in SORTIE by the impact of inter- and intra-specific competition on the mortality, i.e. the more the stand is crowded, the more intense is the competition for light and space with higher mortality rates for juveniles and adults (Bergeron et al. 2014). We showed that increasing temperate seedling density at the beginning of the simulation does not vary linearly with the basal area at the end of the simulation. When adding sugar maple and yellow birch in medium- and high-density situations, stands reached the maximum density for those species that can be supported. The addition of extra seedlings did not lead to higher final basal area.

Red maple had the lowest *MaxPotGrowth* parameter value but the highest capacity for growth and survival in stands with medium- and high-seedling density, indicating the importance of competitiveness, and its low mortality and high regeneration rates (Supporting information; Power et al. 2019). Yellow birch was the temperate species with the higher ability to persist when introduced in unharvested and low-density stands with its higher growth rate and thus higher basal area at the end of the simulation. In medium- and high-density stands, self-thinning of red maple was lower than that of sugar maple and yellow birch (Supporting information), resulting in a greater ability for red maple to persist when introduced in these stands, as reported by other studies (Andrews et al. 2018, Boulanger et al. 2019). Except for the younger stand, initial composition of stands seems to have little effect on the temperate tree species performance in unharvested stands, indicating that the establishment of seedlings on appropriate seedbeds is probably the most critical process in the mixedwood boreal forest (LePage et al. 2000, Charron and Greene 2002, Solarik et al. 2020).

Implications for forest management and native boreal species assemblages

Unexpectedly, temperate species had a lower performance in harvested stands, despite more favorable light conditions and the absence of adult trees (Boulanger et al. 2019). On clay soils like those at the FERLD site, trembling aspen

colonize harvested stands and any gaps rapidly after disturbances through root suckering (Landhäusser et al. 2010). The high density and growth of trembling aspen in harvested stands leads to a high level of seedling competition with neighboring trees (Bergeron et al. 2014). This high competition intensity from trembling aspen leads to high seedling mortality for the temperate trees, reducing their basal areas in harvested stands.

When temperate seedlings were added to the younger stand, i.e. the stand re-initiated in 1964, temperate species could persist better than in older stands, especially red maple. This stand had a lower initial total basal area (all species combined) since the stand was 27 years old when sampled. In this stand, temperate seedlings did not suffer from as much competition by trembling aspen seedlings and saplings, since the aspen cohort was already mature. The ability of temperate species to persist in stands may be higher in managed forests if temperate species colonize a sufficiently mature stand. Modeling studies at stand and landscape scales have shown that forest management coupled with climate change improved the ability of temperate species, particularly sugar maple and red maple, to persist when introduced in boreal mixedwood stands, especially in clearcuts (Steenberg et al. 2013, Fisichelli et al. 2014, Boulanger et al. 2019, Brice et al. 2020). These studies emphasized that, in stands regenerating from forest management, temperate species are more likely to persist in the boreal mixedwood forest with a climate favorable to their growth due to climate change. Boulanger et al. (2019), however, showed that even under Representative Concentration Pathway 8.5 (i.e. significant climate change), aspen abundance will remain very high in the boreal mixedwood forest after clearcutting, reducing the ability of temperate species to grow and survive.

According to our simulations, when medium and high seedling densities of a single temperate species are added to the stands, their survival has major consequences for the native species assemblage. Temperate species co-exist with the other species in the stands to the detriment of late-successional boreal species such as white cedar and balsam fir (Fisichelli et al. 2014, Frelich et al. 2021). In medium- and high-seedling density simulations, stands were at the maximum density they could attain, and a high mortality rate occurred for boreal tree species.

Other potential impediments to the northward expansion of temperate species

Our results show that current climatic conditions and interaction with boreal species may permit temperate species to grow and survive in the simulated BF–PB domain stands. However, these results do not indicate that all BF–PB domains will be dominated by temperate species by 2100, as our study was not designed to estimate future species distributions. Temperate species are currently present only as marginal stands. Additional constraints such as dispersal, edaphic conditions and disturbances may, therefore, limit their northward migration (Tremblay et al. 2002, Drobyshev et al. 2014,

Graignic et al. 2014). These constraints could be the subject of improvements to the simulations presented in this study.

In our study, temperate seedlings were only added at the initial step of our simulations, but if a seed source exists near a stand, a continuous flow of seeds should arrive in the stands. We did not model this potential constant seed flow, because we were interested in assessing the ability of temperate species to persist as a function of initial density of added temperate seedlings. Caspersen and Saprunoff (2005) demonstrated that inappropriate substrates, more than seed dispersal, limit the abundance of yellow birch and sugar maple at the northern limit of their distribution. In addition, at a broader spatial scale, the demographic characteristics of temperate species, such as late sexual maturity, reproductive strategies with cycles of 3–7 years and their seed dispersal, will constrain their poleward migration even with the projected shift of their potential bioclimatic range with the current rate of climate change (Aitken et al. 2008, Hossain et al. 2017, Boisvert-Marsh et al. 2022).

The substrate of coniferous stands is generally more acidic and drier than that of hardwood forests, limiting temperate species recruitment (Collin et al. 2018). Acidic and drier soil affects the uptake of nutrients by temperate species in coniferous stands and affects the probability of germination and growth of temperate juveniles (St.Clair et al. 2008, Caspersen et al. 2011, Solarik et al. 2018). However, the presence of temperate trees in stands was demonstrated to increase the recruitment of temperate species when the density of stands is not too high (Solarik et al. 2020). Thus, adding a substrate-modifying effect on recruitment in future model simulations could improve the plausibility of establishment rates in specific stands.

Although our results suggest that competition with boreal trees was not a critical determinant of the northern limit of temperate tree species, competition is not the only biotic factor that could influence their distribution (Evans and Brown 2017). Other biotic factors may also influence temperate species migration northwards. For instance, seed predation has been shown to reduce maple regeneration in northern Quebec (Brown and Vellend 2014). Presence or absence of pathogens, insect outbreak cycles and mycorrhizal facilitation might also be involved in supporting or limiting the northward migration of temperate species (Cleavitt et al. 2011, 2014, Frelich et al. 2012, Carteron et al. 2020, Evans et al. 2020).

In this study, we did not consider projected climate change and disturbances such as stochastic climate extreme events, or insect outbreaks. These may represent future improvements to this study. With projected climate change, the growing season will possibly be longer, consistent with the temperature increase, and increased growth of temperate species in the BF–PB domain may be observed (Taylor et al. 2017, Reich et al. 2022). With an increase in growth, temperate species have an even greater ability to persist when introduced into stands of the BF–PB domain (Boulanger et al. 2017, 2019). Meteorological events such as late frost, windthrow, flood or drought can directly affect the growth and mortality of the tree species we have considered, which could

facilitate or hinder the performance of temperate species in boreal mixedwood stands (Leithead et al. 2010, Moreau et al. 2020). The spruce budworm is the major defoliating insect in the study area (Bergeron et al. 2014). This insect causes mortality of balsam fir and spruce with a 30-year cycle during outbreaks, which are expected to be more intense with climate change (Pureswaran et al. 2019). The gaps created by the spruce budworm will lead to more light and space for the temperate tree species to grow and survive in stands (Kellman 2004, Gasser et al. 2010, Bannon et al. 2015). In the long term, the presence of temperate species may mitigate the intensity of the outbreaks, as spruce budworm host species will decrease in the stands (Cappuccino et al. 1998).

Conclusion

Our study shows that the seedlings of temperate tree species may grow and survive within mixedwood boreal tree species communities currently to the north of their geographic distribution under a range of native stand compositions, densities, loggings and under current climate conditions. More specifically, both current climate and competitive interactions between temperate and boreal species were not factors impeding temperate species persistence when introduced into stands of the BF–PB domain. Forest management had antagonistic effects on temperate tree species performance. Competition from trembling aspen seedlings limited the persistence of introduced temperate species in recently harvested stands, while temperate species had a higher ability to persist in later successional mature aspen stands. This study provides a new framework for investigating the abilities of temperate tree species to growth and survive in novel stands at the northernmost limit of their distributional range.

Author contributions

Maxence Soubeyrand: Conceptualization (lead); Data curation (lead); Formal analysis (equal); Investigation (equal); Methodology (equal); Software (lead); Visualization (lead); Writing – original draft (lead); Writing – review and editing (lead). **Fabio Gennaretti**: Conceptualization (supporting); Investigation (supporting); Methodology (supporting); Project administration (supporting); Resources (supporting); Supervision (equal); Validation (equal); Writing – review and editing (equal). **Olivier Blarquez**: Conceptualization (supporting); Funding acquisition (lead); Project administration (supporting); Supervision (supporting); Writing – review and editing (supporting). **Yves Bergeron**: Conceptualization (supporting); Writing – review and editing (supporting). **Anthony R. Taylor**: Data curation (equal); Investigation (supporting); Methodology (supporting); Resources (supporting); Writing – review and editing (equal). **Loïc D'Orangeville**: Methodology (supporting); Resources (supporting); Writing – review and editing (supporting). **Philippe Marchand**: Conceptualization (equal); Data curation (supporting); Formal analysis (equal); Investigation (equal); Methodology (equal); Project administration (equal); Resources (equal); Supervision (lead); Validation (lead); Visualization (supporting); Writing – review and editing (equal).

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Data availability statement

Data used in this study has been archived on GitHub and can be found at https://doi.org/10.5281/zenodo.6819495 (Soubeyrand et al. 2022); some data that was obtained under license from governmental organizations will be published with a one-year embargo.

Supporting information

The Supporting information associated with this article is available with the online version.

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