

Increase in young forests, more than climate change may accelerate future colonization of temperate tree species in mixedwood boreal stands

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ABSTRACT

Temperate hardwood tree species may take advantage of climate change to migrate northward tracking their optimal growth and survival niches. Other factors than climate could constrain or facilitate their establishment north of their actual range, such as competitive interactions, their ability to disperse, and forest management. The objectives of this study were to model the ability of temperate tree species to colonize boreal mixedwood stands of Eastern Canada from a few temperate tree seeders, considering the effects of climate change, competitive interactions, and specific successional stages of the receiving stands. We used the individual based forest model SORTIE-ND with adult growth forced by four different projected climate change scenarios. To mimic the natural colonization of temperate trees from marginal populations eventually established by long-distance migration, we replaced a patch in the center of the simulated stands with temperate tree species, i.e., red maple, sugar maple or yellow birch. We then performed a sensitivity analysis on the parameters determining the growth, dispersal, and mortality of temperate tree species to determine which of these processes was critical to their expansion. All three temperate tree species were able to colonize the boreal stands with higher performance in younger stands, and greater colonization skills for yellow birch. At the 2100 horizon, the impact of the climate scenarios on the final basal area of temperate tree species was minor. Processes mostly driven by competition and species auto-ecology, including dispersion, mortality, and juvenile growth parameters, were the most important for the colonization capacity. Our results suggest that the expansion of temperate tree species from already established northern marginal populations would be minimally affected by climate change, and that forest management could have a more significant impact by rejuvenating boreal mixedwood landscapes.

FRENCH ABSTRACT

Les espèces d'arbres feuillus tempérés pourraient tirer parti du changement climatique pour migrer vers le nord, en suivant leurs niches optimales de croissance et de survie. D'autres facteurs que le climat pourraient contraindre ou faciliter leur établissement au nord de leur aire actuelle, tels que les interactions de compétition, leur capacité à se disperser et l'aménagement forestier. Les objectifs de cette étude étaient de modéliser la capacité des espèces d'arbres tempérés à coloniser les peuplements mixtes boréaux de l'est du Canada à partir de quelques espèces d'arbres tempérés, en tenant compte des effets du changement climatique, des interactions compétitives et des stades de succession des peuplements hôtes. Nous avons utilisé le modèle forestier basé sur les individus SORTIE-ND avec la croissance adulte forcée par quatre scénarios de changement climatique. Pour imiter la

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Open research statement: Data and code used in this study has been archived on GitHub and can be found at <https://rb.gy/tzt01y>.

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colonisation naturelle des espèces tempérées à partir de populations marginales établies éventuellement par migration longue distance, nous avons remplacé une placette au centre des peuplements simulés par des espèces d'arbres tempérés, c'est-à-dire l'érable rouge, l'érable à sucre ou le bouleau jaune. Nous avons ensuite effectué une analyse de sensibilité sur les paramètres déterminant la croissance, la dispersion et la mortalité des espèces tempérées pour déterminer quels processus étaient critiques pour leur expansion. Les trois espèces d'arbres tempérés ont pu coloniser les peuplements boréaux avec une meilleure performance dans les peuplements plus jeunes, et une meilleure capacité de colonisation pour le bouleau jaune. À l'horizon 2100, l'impact des scénarios climatiques sur la surface terrière finale des espèces d'arbres tempérés était mineur. Les processus principalement dirigés par la compétition et l'auto-écologie des espèces, y compris la dispersion, la mortalité et les paramètres de croissance juvénile, étaient les plus importants pour leur capacité de colonisation. Nos résultats suggèrent que l'expansion des espèces d'arbres tempérés à partir de populations marginales nordiques déjà établies serait peu affectée par le changement climatique, et que l'aménagement forestier pourrait avoir un impact plus significatif en rajeunissant les paysages mixtes boréaux.

1. Introduction

Temperature and precipitation have an important role on tree species distribution ranges at the continental scale (D'Orangeville et al., 2016). Consequently, tree species are projected to migrate poleward or at higher elevations under a warming climate, tracking their optimal climatic niche (Morin et al., 2008; Lee-Yaw et al., 2016). However, the speed of this process may vary according to many other factors operating at more regional and local scales, including species migration ability, climatic and edaphic conditions of microsites, biotic factors such as species competition, seed predation and disturbance factors such as fires, insect outbreaks and forest management (Fisichelli et al., 2012; Canham & Murphy, 2016a; Evans & Brown, 2017). The extent to which biotic factors interact with climate to shape tree species distributions remains an important unresolved issue (Oboite & Comeau, 2020; Soubeyrand et al., 2024).

The Quebec mixedwood ecotone is composed of two distinct forest: the southern temperate mixedwood forest and the northern boreal mixedwood forest (Saucier et al., 1998, 2003). The high abundance of temperate tree species such as sugar maple (*Acer saccharum* Marshall), red maple (*Acer rubrum* Linnaeus) and yellow birch (*Betula alleghaniensis* Britton) in the temperate mixedwood forest is the main difference between the two forests (Saucier et al., 2003). Red maple can also be found in hilltops of the boreal mixedwood forest where soil microsites and climatic conditions are more favourable than in the bottom of hills (Marquis et al., 2021). With climate change, the marginal populations of these three species are expected to expand northward, i.e. in the boreal mixedwood forest, and eventually colonize the bottom of hills due to the release of climate constraints (Boulanger et al., 2022; Paillard et al., 2023). However, site conditions of the boreal mixedwood forest may not be favourable for their establishment because of poor nutrient substrates, high tree density in the native stands or lack of facilitating soil microbiome (St.Clair et al., 2008; Collin et al., 2017, 2018; Carteron et al., 2020; Solarik et al., 2020).

Future migrations of temperate tree species may be studied through model simulations. Multiple models with a different degree of complexity and spatial and temporal resolutions may be used to simulate tree species expansion from current distribution ranges. Species distribution models (SDMs), based on the statistical relationship between current distribution and climate, were used to project the potential temperate tree species migration northward in the mixedwood boreal forest (McKenney et al., 2011). Although SDMs have been improved taking into account migration aspects, they do not consider some important local processes such as interspecific competition, stand dynamics or edaphic factors (Boisvert-Marsh et al., 2022). Alternatively, process-based landscape model were used to project future boreal and temperate tree species performance and biomass, but also this type of large-scale model does not include factors operating at the stand level, such as tree-specific competition for light and space (Boulanger et al., 2017, 2018). Conversely, spatially explicit stand models consider direct interactions between trees in a stand using their spatial positions to

compute competition for light and space among trees including potential inter-specific facilitation-exclusion (Pacala et al., 1993; Shugart & West, 1977; Shugart et al., 2018). These models can be used in a context of species migration to assess the short-distance ability of a species to colonize a neighbouring stand considering interaction with existing trees, recruitment and mortality processes. All this information may guide forest management by predicting the effects of climate change on compositional shifts of mixed boreal forests. These shifts will have profound implications for biodiversity and the timber industry (Gauthier et al., 2015; Noualhaguet et al., 2023).

The role of competition between temperate and boreal species in limiting the migration of temperate species northward remains unclear (Soubeyrand et al., 2023). Additionally, it is uncertain whether the projected increased growth of temperate broadleaf trees due to climate change will accelerate their colonization of stands north of their current distributional range (Zhu et al., 2012; Drobyshev et al., 2014; Zhang et al., 2015). To verify the relative importance of these mechanisms, we use a spatially explicit forest stand model to study compositional changes in stands of the boreal mixedwood forest after addition of a patch of temperate trees. This setup simulates the potential colonization capacity of temperate trees from northern marginal populations, eventually establishing through long-distance migration (Lazarus & McGill, 2014). Our initial hypotheses are that temperate tree species will demonstrate higher growth and colonization abilities as climate forcing increases, and that competition with conifers in mature boreal stands may slow down this northward expansion in the absence of recent external disturbances. Consequently, our simulations take into account tree-specific performance traits, inter-tree competitive interactions and different climate scenarios. Our objectives are threefold: (1) assess temperate tree growth in mixedwood boreal forests under different climate scenarios; (2a) determine the colonisation potential of temperate tree species from already established marginal population in boreal mixedwood stands, (2b) ranking the limiting impact of dispersal, mortality and growth processes; and (3) determine potential composition shifts in boreal mixedwood stands following the colonization of temperate tree species.

2. Methods

2.1. Study area

The study area is located at the Lake Duparquet Research and Teaching Forest (FERLD) in the Abitibi region of western Quebec, Canada. The growing season (May to September) is characterized by a mean temperature of 14°C and cumulative precipitation of 447 mm (mean from 1970 to 2019). The FERLD territory is within the boreal mixedwood forest western Quebec and is located in the clay belt characterized by glaciolacustrine clay deposits (Fig. 1, Saucier et al., 1998; Roy et al., 2015). The study landscape is fragmented by multiple past fire events and spruce budworm outbreak (*Choristoneura fumiferana* Clemens) staggered through time and space resulting in a mosaic of

different stand compositions (Bergeron et al., 2014). Early succession stands are composed of trembling aspen (*Populus tremuloides* Michaux), paper birch (*Betula papyrifera* Marshall) and jack pine (*Pinus banksiana* Lambert), and are replaced by balsam fir (*Abies balsamea* (Linnaeus) Miller), white and black spruce (*Picea glauca* (Moench) Voss and *Picea mariana* (Miller) Britton), white cedar (*Thuja occidentalis* Linnaeus) in mid and late successional stands (Bergeron, 2000; Chen & Popadiouk, 2002). Marginal red maple stands are scarcely present in the area mainly in the slope and top of the hills (Tremblay et al., 2002). Sugar maple and yellow birch are absent.

2.2. Overview of the model and of the simulation experiments

We performed the simulations using the spatially explicit and individual based SORTIE-ND model (hereafter SORTIE; version 7.05; Pacala et al., 1996; Murphy, 2011). SORTIE 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. At each timestep, usually one year, SORTIE simulates the interactions between trees, calculates their growth considering the impact of competition for light and space of neighboring trees, and updates tree attributes. Simultaneously, SORTIE computes the number of seeds produced and their dispersal distance and determines the mortality of both seedlings and trees. All significant equations for these processes are presented in the section Sensitivity analysis.

We modeled the increment of diameter at breast height of trees as a function of time (DBHI; in $\text{cm}\cdot\text{yr}^{-1}$) with the “Neighboring Competition Index (NCI) growth” module. This module calculates growth as a fraction of the maximum potential growth (*MaxPotGrowth*) that can be achieved under optimal growth conditions. We obtained the realized growth by multiplying *MaxPotGrowth* by various nonlinear limiting effects with values between 0 and 1, representing the effects of temperature, precipitation, tree size, shading from other trees, and non-light-based crowding effect including potential interspecific competition between trees, competition for space, nutrients and water accessibility (Canham et al., 2004; equation 1).

$$\begin{aligned} \text{DBHI}(\text{cm}\cdot\text{yr}^{-1}) = & \text{MaxPotGrowth} \times \text{temperature effect} \\ & \times \text{precipitation effect} \times \text{sizeeffect} \times \text{shadingeffect} \\ & \times \text{crowding effect} \end{aligned} \tag{1}$$

We used the parameter values from a new SORTIE parameterization procedure described in Soubeyrand et al. (2023) for the size effect, the shading effect and the crowding effect. Such parameterisation is available for yellow birch, red maple and sugar maple and for six additional boreal tree species composing the studied forest stands (trembling aspen, paper birch, balsam fir, white spruce, jack pine and white cedar). The *MaxPotGrowth* parameter, and the temperature and precipitation effects were parametrized for the 9 considered species using tree growth measurements on 21 647 trees from 4 067 permanent forest inventory plots located across eastern North America. Mean temperature during the growing season and mean summer precipitation were used for parameterizing the temperature and precipitation effects, respectively (parameterization method and parameter values are presented in Supporting Information). We modeled climate effect as:

$$\text{Climate effect} = \exp\left(-0.5 \times \left(\frac{\text{Climate}_i - C}{A}\right)^2\right) \tag{2}$$

where Climate_i is temperature or precipitation of the year i , A is the optimal temperature (C_t) or precipitation (C_p) value and A is the parameter that controls how quickly the growth decreases as the climate value deviates from optimal temperature (A_t) or precipitation (A_p).

In our simulations, tree allometry parameters, as well as parameters determining tree mortality and recruitment, were obtained from previous studies (Poulin et al., 2008; Maleki et al., 2019).

We used the model to simulate the colonisation of temperate tree species in 4 boreal mixedwood stands used as initial conditions. Such stands represent a successional chronosequence established after fire or harvesting (Fig. 1), determined using data from inventoried plots (Maleki et al., 2021; see section Stand initial conditions). In each of those stands (100 m x 100 m), we added various size of temperate tree subplots at their center at the beginning of the simulations. Each simulation was carried on with a specific climate scenario until 2100. We then performed a sensitivity analysis on important parameters to analyze the processes controlling the speed of the invasion of temperate trees in boreal mixedwood stands. The final simulations were compared in terms of growth and final basal area of temperate trees and of trajectories of composition changes. Each of these steps is described in detail in the following sections and is illustrated in Fig. 2.

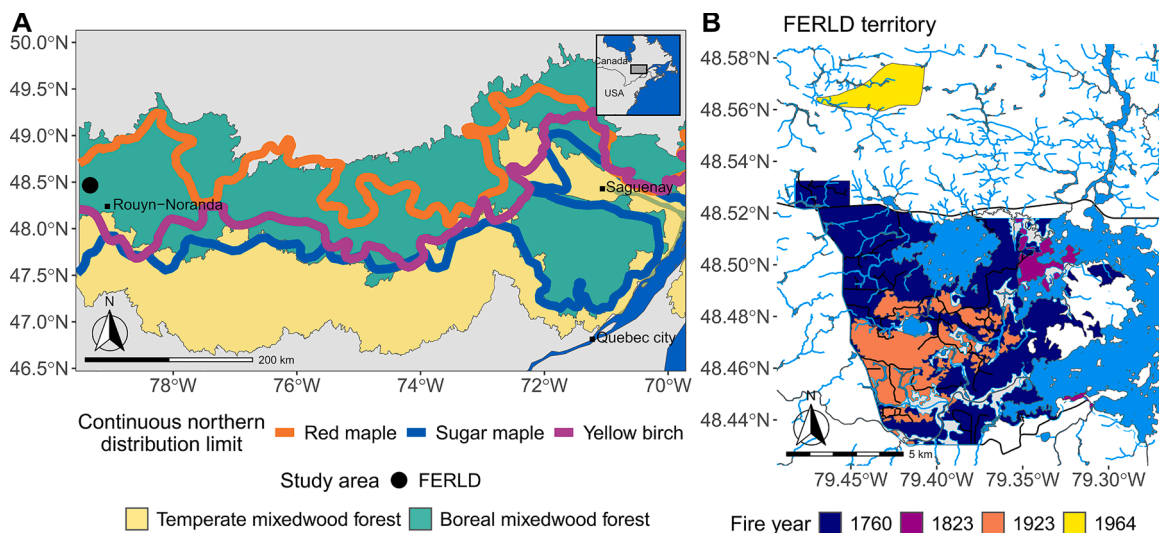


Fig. 1. Maps of the study area. (A) The two bioclimatic domains (polygons, Saucier et al., 2003) and the northward continuous distribution limits of the three studied temperate tree species (solid lines, respectively, Morneau, 2022). (B) Map of fires in the FERLD territory used as initial conditions for the simulations (Bergeron et al., 2004).

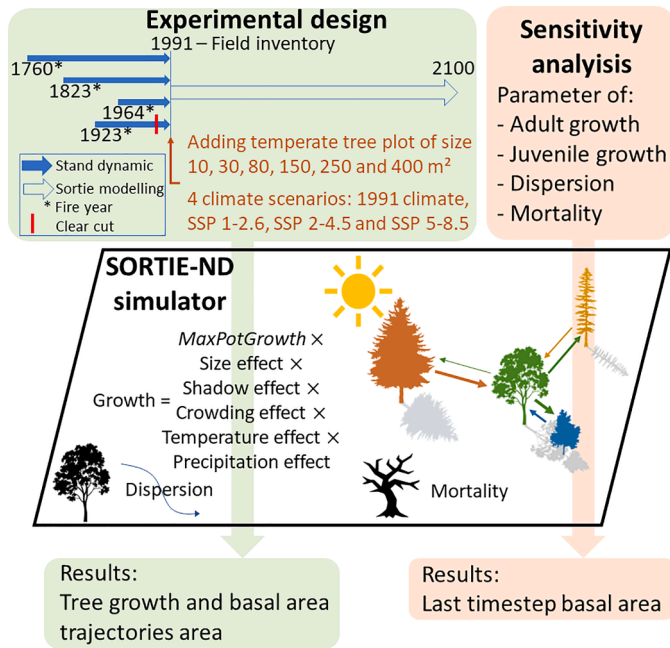


Fig. 2. Conceptual framework of the simulation experiments. We performed the sensitivity analysis only using the stand reinitiated in 1964 and the Shared Socioeconomic Pathways (SSP) 2-4.5 climate scenario.

2.3. Stand initial conditions

Boreal mixedwood tree DBH by species in 173 plots of 400 m² in stands previously burned during different fire years (Maleki et al., 2021). Such inventories provided 4 successional forest stages with different forest compositions to be used as stand initial conditions for our simulations (Fig. 3). The first stand is described by plots regenerated after a fire in 1760, the second after a fire in 1823 and the third after a fire in 1964. Plots were inventoried in 1991 following a spruce budworm

outbreak, which affected balsam fir trees. We considered dead balsam fir as alive to remove the potential effect of the spruce budworm outbreak in our simulation results. One fourth stand used plots originated by a fire in 1923 and was harvested in 1999 (Braiss et al., 2013). These plots were inventoried two years after the clearcut offering the possibility to consider recently harvested stands. We extracted the mean density per species and per DBH class of all available plots in each stand to initialize the SORTIE simulations by indicating the number of trees per hectare per each 2cm DBH class by species. SORTIE then randomized tree positioning in the simulated stand (100 m x 100 m).

At the beginning of each simulation, we replaced a round subplot at the center of the stands by a plot composed of temperate trees: sugar maple, red maple or yellow birch (Fig. 3). To produce the replacement plots, we extracted tree position and DBH from a pure mature sugar maple stand from the RESEF Quebec forest monitoring network (“Réseau d’Étude et de Surveillance des Écosystèmes Forestiers”). We considered the same tree position and DBH for the red maple and yellow birch experiments to allow the comparison of the results between the tree temperate tree species. Six plot size were considered: 10, 30, 80, 150, 250 and 400 m² to account for different sizes of the simulated marginal population. The 400 m² plot size encompassed the other plots. A simulation without introduction of a temperate plot was also executed as a control (Fig. 3).

These initial conditions allowed us for modelling the colonization of temperate tree species in the adjacent mixedwood boreal stands from the added patch of temperate trees. Such central patches are intended to emulate a long-distance migration event from which colonization of the boreal mixedwood forest could begin (Graignic et al., 2018).

2.4. Inclusion of climate scenarios

Daily downscaled future climate projections were extracted using the website <https://climatedata.ca>, generating a median ensemble from 25 general circulation models’ simulations with a resolution of 16 km². Daily values were aggregated to compute annual time series of mean temperature during the growing season (specify growing season) and mean summer precipitation (specify summer). We selected three Shared

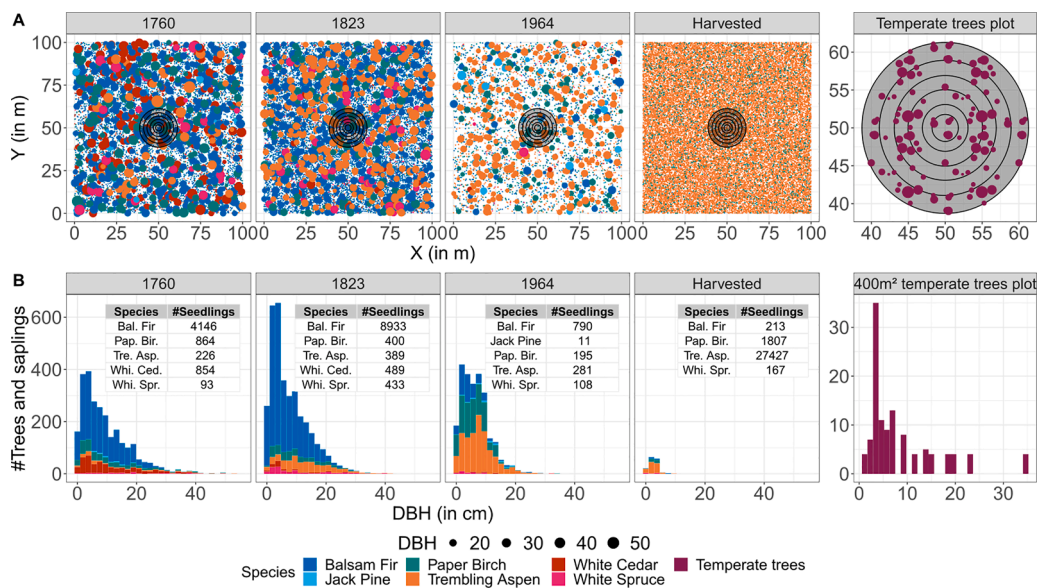


Fig. 3. Representation of the initial conditions used in the simulation. (A) Tree positioning in a one-hectare plot according to the year of the last fire. Initial conditions for the harvested plot correspond to two years following a clear-cut in a stand naturally regenerated after a 1923 fire event. Each species is represented by a color and the size of the circle indicates its diameter class. Circles in plots correspond to the sizes of temperate tree plots added in different simulations: 10, 30, 80, 150, 250, and 400 m² in area. The upper right panel (purple color) represents the position of temperate trees integrated in the central patch of each stand. (B) Number of seedling and histograms of adult and sapling trees according to their DBH in the stands. Right panel shows the 400m² temperate tree species plot added in the simulations.

Socioeconomic Pathways (SSPs) scenarios, (1) the optimistic SSP 1-2.6 (2) the plausible SSP 2-4.5 and (3) the pessimistic SSP 5-8.5. Historical climate data were extracted from 1991 to 2021 from the same website and median climate projection were extracted from 2022 and 2100. We also used a climate scenario with no climate change, i.e., the median climate from 1991 to 2022 unchanged.

In each of SORTIE simulations, we considered the time-dependent effect of climate warming on tree growth by using the temperature and the precipitation effect and updating at each 1-year timestep of the simulation the simulated climate (Eq. 2). Parameterization of temperature and precipitation effects along with size, shading and crowding effects is described in supplementary information 1.

2.5. Comparison and assessment of simulated results

To determine if temperate trees can grow in boreal mixedwood stands, we extracted the realized growth of each tree from the simulations with different climate scenarios and compared to the *MaxPot-Growth* of the species. We then evaluated the average impacts of each growth effect of equation 1 (objective 1).

We extracted the stand basal areas of temperate trees at last timestep (after 110 years of simulation, i.e., from 1991 to 2100) to assess the capacity of temperate trees to colonize boreal mixedwood stands. The central temperate tree plots were removed to consider only the basal area of temperate tree that invaded the adjacent stands. We compared these basal areas under the different conditions we simulated, i.e., with different initial central plot size of temperate trees, in different climate scenarios, at various initial stages of boreal mixedwood stands and in harvested and unharvested stands (objective 2a).

We performed Principal Component Analysis (PCA) to investigate the effect of the temperate tree species invasion on the assemblages of boreal mixedwood stands under different climate scenarios (objective 3). We used PCA for its ability to reduce the dimensionality of the simulation results highlighting the main variations in tree species composition across different tested scenarios. The PCA was computed on the data of species abundance including all stands and their temporal changes. We then displayed the trajectories of each simulated scenario along the first two principal components to visualize how species compositions evolved over time. The first two axes of the PCA explained the most variance in the simulation results, providing a clear view of the primary shifts in species composition when the trajectories were drawn. We finally compared these trajectories with the control trajectories (i.e., scenarios without inclusion of temperate trees) to assess the extent of compositional changes induced by the temperate tree colonisation.

2.6. Sensitivity analysis and main model equations

We performed a sensitivity analysis by varying parameters of four important modules of SORTIE to evaluate their influences on the invasion of temperate trees in boreal mixedwood stands: juvenile diametrical growth, adult diametrical growth, seed dispersal and mortality (objective 2b; Table 1). We choose these parameters because dispersion, mortality and growth process are directly implicated in the ability of temperate tree species to colonize mixedwood boreal forest (Urli et al., 2016; Solarik et al., 2016; Putnam & Reich, 2017).

In SORTIE, juvenile growth is simulated as:

$$Y = \log_{10}(\text{radial growth} + 1) = \frac{A \times GLI}{\frac{A}{S} + GLI} \quad (3)$$

where Y is the log 10 of the juvenile growth in $\text{cm} \cdot \text{year}^{-1}$, A is the maximum diameter growth on the log scale, S is the slope of the diameter growth response and GLI is the amount of light received by the tree which takes 1 when the tree received full light and 0 when the tree received no light.

The adult growth is defined by the Eq. (1) and depends on the

Table 1

List of the 20 parameters used in the sensitivity analysis with the associated optimal parameter values for sugar maple, red maple and yellow birch.

Module	Parameter	Sugar maple	Red maple	Yellow birch
Juvenile growth (eq. 3)	A	0.34	0.43	0.43
	S	0.68	0.11	0.58
Adult growth: maximum potential growth (eq. 1)	<i>MaxPotGrowth</i> ($\text{cm} \cdot \text{year}^{-1}$)	0.37	0.59	0.53
	A_t	6.27	5.18	1.82
Adult growth: temperature effect (eq. 2)	C_t	5.97	6.53	0.54
	A_p	6.32	5.95	5.99
Adult growth: precipitation effect (eq. 2)	C_p	1.51	3.09	3.99
	X_0 (cm)	21.65	20.19	16.18
Adult growth: size effect (eq. 4)	X_b	1.18	1.84	1.07
	m	1.16	0.56	0.8
Adult growth: shading effect (eq. 5)	c	$6.51 \cdot 10^{-4}$	0.044	0.018
	α	1.24	0.081	0.088
Adult growth: crowding Effect (eq. 6 and 7)	β	0.32	0.71	0.53
	STR	1.32	0.54	21
Dispersion (eq. 8)	d	$5.81 \cdot 10^{-4}$	$3.62 \cdot 10^{-5}$	$6.30 \cdot 10^{-5}$
	M_2	4.79	6.64	2.67
Juvenile mortality (eq. 9)	Random	0.01	0.01	0.01
	z	$3 \cdot 10^{-6}$	$3 \cdot 10^{-6}$	$4.33 \cdot 10^{-6}$
Adult mortality (eq. 10)	max	0.17	0.17	0.25
	Random	0.01	0.01	0.01

temperature and the precipitation effects as described in the Eq. (2), as well as on the other effects, including the size effect simulated as:

$$\text{size effect} = \exp \left(-0.5 \times \left(\frac{\ln \left(\frac{DBH}{X_0} \right)}{X_b} \right)^2 \right) \quad (4)$$

where DBH is the DBH of the tree in cm, X_0 is the DBH corresponding to maximum growth in cm and X_b determines the width of the Gaussian effect of $\ln DBH$ on growth.

The shading effect of the Eq. (1) is simulated as:

$$\text{Shading effect} = \exp(-m \times S) \quad (5)$$

here m is the shading effect parameter, S is the shading measurement, or the fraction of light intercepted by neighbors, as calculated by the ‘‘sail light’’ module in SORTIE.

The crowding effect of the Eq. (1) is simulated as:

$$\text{Crowding effect} = \exp(-C \times DBH \times NCI), \quad (6)$$

where C is the crowding effect parameter. The neighbor competition index (NCI) for each tree i is simulated by:

$$NCI_i = \sum_{j=1}^N \lambda_{ik} \left(\frac{DBH_j^\alpha}{dist_{ij}^\beta} \right) \quad (7)$$

where λ_{ik} strength of competition for different species pairs, k is the species of the neighbor j , α expresses the effect of the DBH of the neighbor tree, $dist_{ij}$ is the distance in meters of the neighbor j from the tree i and β is the exponent of the effect of distance on the NCI.

The density of dispersed seeds (R_i , in $\text{seeds} \cdot \text{m}^{-2}$) is calculated as

$$R_i = \frac{STR}{n} \times \sum_{j=1}^T \left(\frac{DBH_j}{30} \right) \times e^{-d \times m_j} \quad (8)$$

where R_i is the seed density produced per m^2 at a point i , STR is the

number of seeds produce by a tree of 30 cm DBH, $n = \int_0^\infty e^{-d \times m^q} , d$ is the Weibull canopy gap dispersal parameter that controls the probability of the presence of a seed at a distance m in meters of the seed maker.

Juvenile mortality occurs from two sources: a stochastic constant mortality rate specific to each species, and a mortality for seedlings and saplings based on their growth rate (depending on light availability, see Eq. 3):

$$P(\text{mortality}|\text{growth}) = 1 - e^{-e^{-M_2 \times G}} \tag{9}$$

where G is the growth of the tree (in $\text{cm} \cdot \text{year}^{-1}$) and M_2 is a parameter for the light dependent mortality.

Adults can die from three independent causes: a stochastic mortality rate specific to each species, a senescence-based mortality rate and a competition-based mortality rate. Senescence based mortality rate was not included in this sensitivity analysis because, temperate trees that colonize the stands didn't reach the senescence. Competition mortality depends on the ratio between the maximum growth the tree can attain relative to its DBH and the actual growth of the tree. The higher the shading effect and crowding effect, the higher the probability of mortality.

$$P(\text{mortality}|\text{competition}) = Z \frac{\frac{\text{growth}}{\text{MaxPotGrowth} \times \text{size effect}}}{\text{max}} \tag{10}$$

where Z is the competition mortality shape parameter, growth is the actual growth of the tree (in $\text{cm} \cdot \text{year}^{-1}$) and max is the competition mortality maximum parameter, which indicates the maximum relative increment ($\frac{\text{growth}}{\text{MaxPotGrowth} \times \text{size effect}}$) at which mortality may occur.

In the sensitivity analysis, we set the 20 selected parameters at 0.1, 0.2, 0.4, 0.6, 0.8, 1.2, 1.4, 1.6, 1.8 and 2 times the optimal parameter values obtained by parameterization (Table 1). In addition, for each species and each parameter, we assigned the parameter value of the other two species to know if specific parameter values allowed a species to better invade the stands. In the analysis, only one parameter varied iteratively while the others remain constant at their optimal value (480 simulations = 3 species x 16 parameters x 10 parameters values). The sensitivity analysis was done for the stand regenerated in 1964 with the SSP 2-4.5 climate change scenario and using the 150 m² central patch of

temperate trees.

3. Results

Climate at the FERLD should be warmer with more precipitations by the end of the century. More particularly, the mean temperature during growth season should increase of 2.95 to 7.16°C by 2100 according to the climate scenario (Fig. 4.A). On the other hand, the mean summer precipitation should increase of 1 to 5 mm.

The updated *MaxPotGrowth*, limited by the effects of temperature and precipitation according to the climate scenario, showed that red maple and sugar maple should benefit from climate change, increasing their potential growth in the FERLD territory (Fig. 4.B). For these two species, growth of adult trees should increase with the intensity of the climate scenario. For yellow birch, growth is expected to increase over time, reaching a plateau in 2030, and then decrease, with the decline being more abrupt with higher climate change intensity.

There was no variation in the precipitation effect due to the small changes in precipitation predicted in the climate scenarios (Fig. 4 and 5). We observed a reduced limiting temperature effect for sugar maple and red maple under the most pessimistic climate scenario (higher values of the effect, resulting in higher growth). Conversely, lower growth was observed for yellow birch with increasing temperature (lower values of the effect). The crowding effect was more limiting for red maple than for sugar maple and yellow birch, indicating that red maple poorly performs under intra- and interspecific competition. The shading effect decreased in younger stands where competition for light increases due to stand density.

Sugar maple and yellow birch could establish in all stand conditions whereas red maple could establish only in the harvested and 1964 stands (Fig 6. Supporting Information Video S1). Yellow birch displayed the highest basal areas at last timestep (e.g., mean basal area of 2.96 m²/h for yellow birch, 0.571 m²/h for sugar maple, and 0.914 m²/h for red maple for the largest patch size in the 1964 stand and for the SSP 2-4.5 climate scenario). Temperate tree species invasion increased with the size of the introduced central patch (Fig. 3 and 6). Younger and harvested stands were more easily invaded especially in the case of red maple. Climate scenarios did not appear to affect the invasiveness of temperate trees in boreal mixedwood stands.

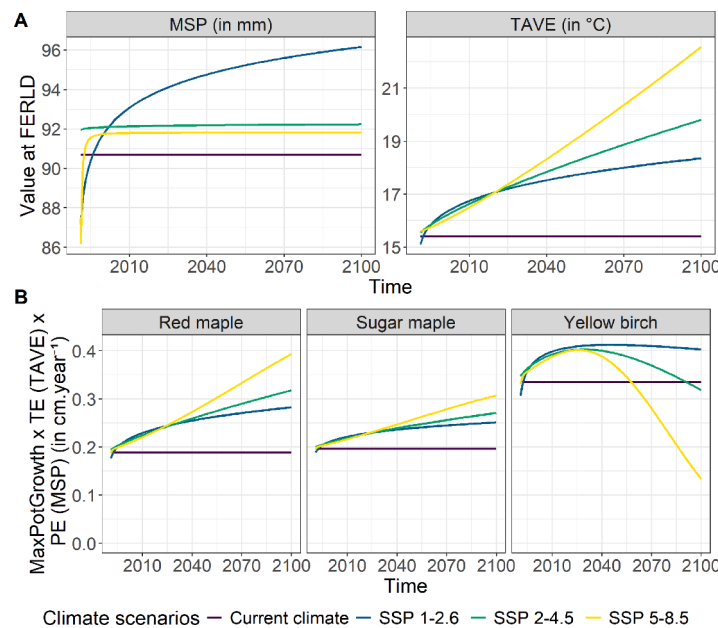


Fig. 4. (A) The future climate in the FERLD territory through the mean temperature during growing season (TAVE) and the mean summer precipitation (MSP) according to four climate scenarios. (B) *MaxPotGrowth* values estimations as a function of time and depending on the species and on the climate scenarios.

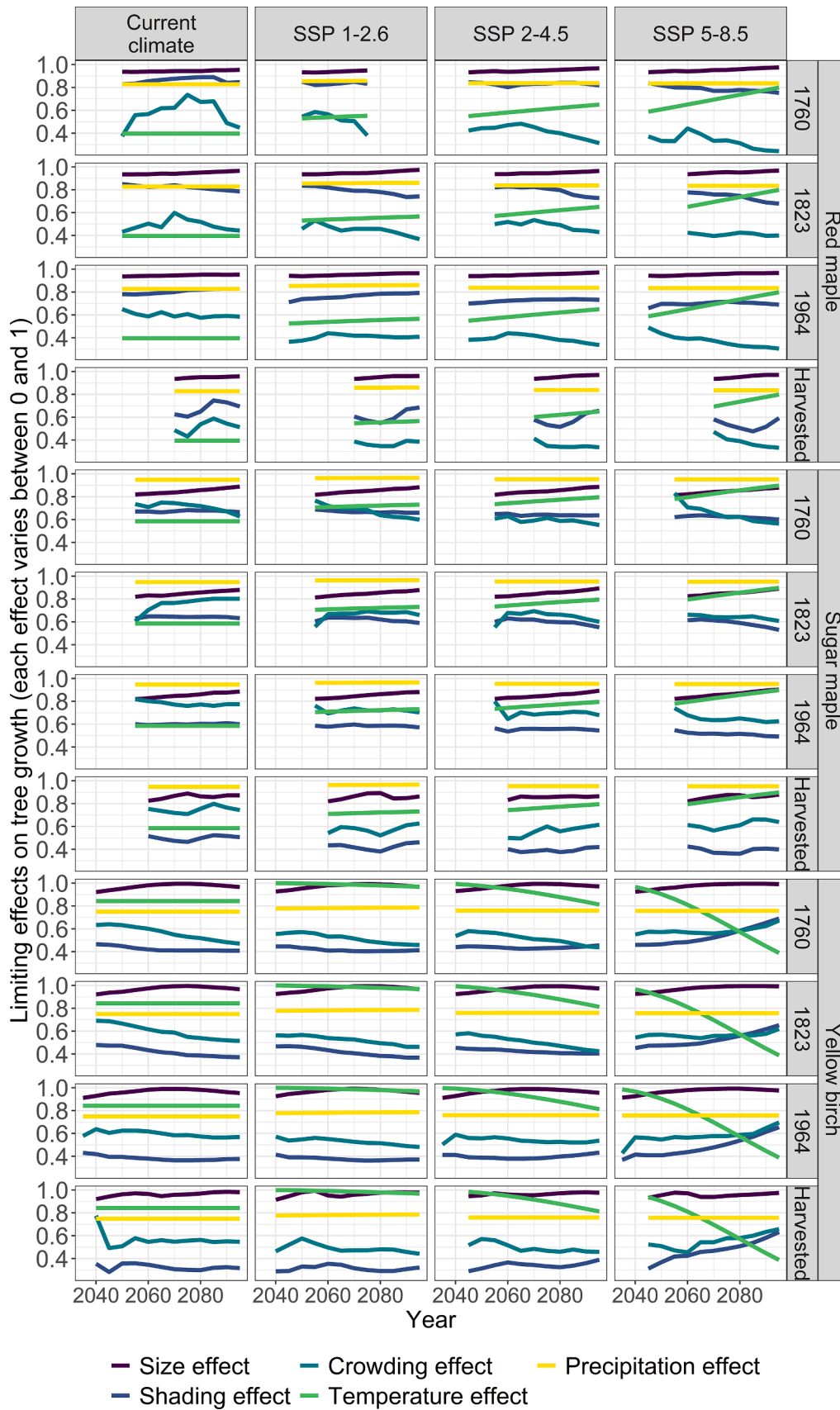


Fig. 5. Growth effect as a function of time depending on the temperate tree species, the considered stand, and the climate scenario. Simulations were performed with a 400m² central patch (Fig 3). Tree growth decomposition does not begin at the start of the simulation (1991) because trees are only juveniles at this time (DBH less than 10 cm). The closer the effect approaches zero, the greater its impact in reducing growth.

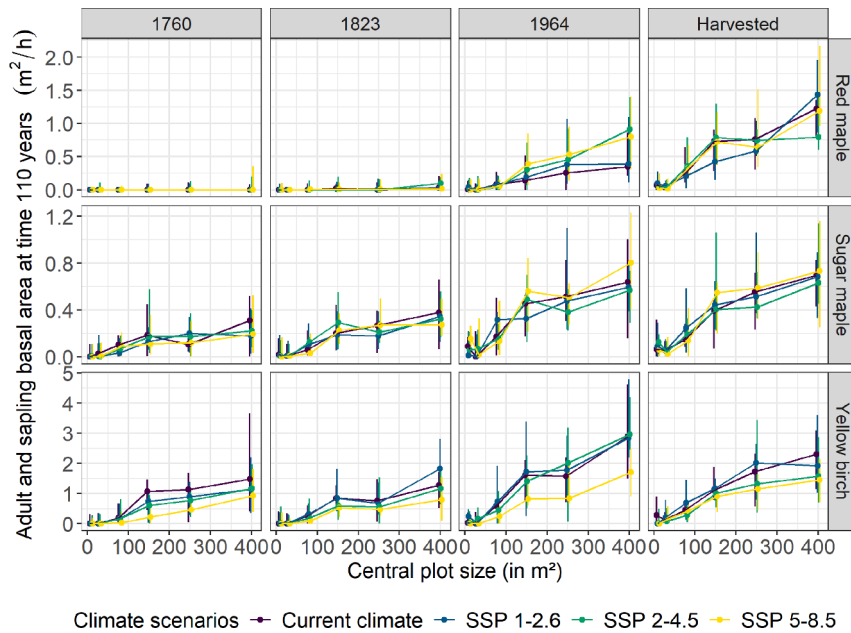


Fig. 6. Simulated adult basal area at the last simulation timestep (109 years corresponding to 2100) for temperate tree species in boreal mixedwood stands. Simulations consider different initial conditions relative to time since stand-replacing fire, harvesting, size of the central patch of temperate trees and climate scenarios. Central patches were removed when determining tree basal area to consider only those trees that have invaded the adjacent stand. Error bars correspond to the minimum and maximum of the replicates, i.e., the stand divided in eight equal plots then standardized to per hectare. Note different y-axis scales between rows.

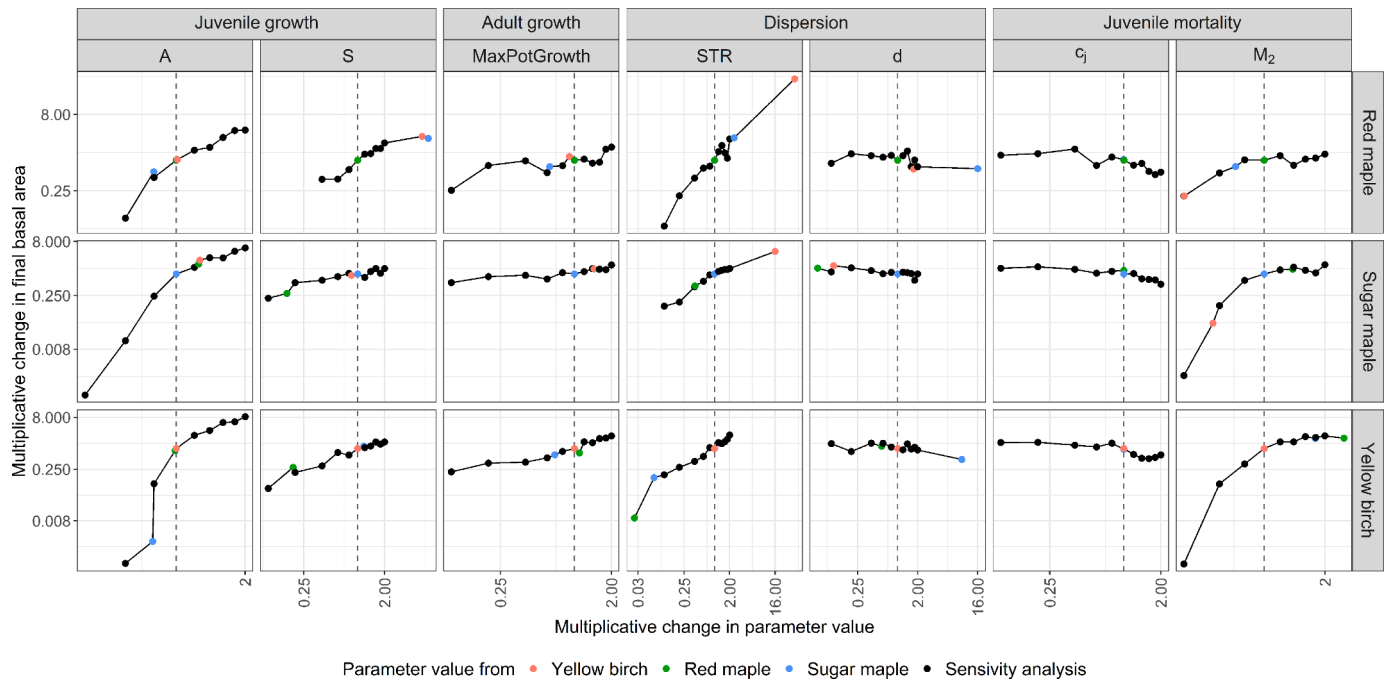


Fig. 7. Sensitivity analysis on 7 parameters influencing adult and sapling basal area at the last timestep. The sensitivity analysis has been performed on 13 other parameters of adult growth and adult mortality that can be found on the Supporting Information Fig. S1. These 13 additional parameters had a comparatively smaller effect on the final basal area of temperate species. Only the evaluated parameter varies while the others are fixed at their optimal value. Color points are the results of simulations with the parameter value of the species associated to that color. The vertical gray dashed lines correspond to the parameter value used for the experimental design. Here, we only used the SSP 2-4.5 climate scenario and a 150m² central patch of temperate trees in the stand reinitialized in 1964. The central plot has been removed to calculate the temperate tree basal areas.

The last timestep basal area of temperate trees was mostly responsive to variations of juvenile growth, juvenile mortality and dispersion parameters (Fig. 7, Supporting Information Fig. S1). We observed strong variations of last timestep basal area when modifying the *A* parameter of juvenile growth (maximum diameter growth, eq. 3); an increase of two time of the initial value of *A* caused an 8.3 times increase in last timestep

basal area of yellow birch, 5.4 for sugar maple and 3.9 for red maple. The *STR* dispersion parameter (the number of seeds produce by a tree of 30 cm DBH, eq. 8) was also an important parameter since this parameter set the number of seeds created by a tree of 30cm DBH. *STR* percentage increments produced similar percentage increments in the basal area at last timestep. *STR* for yellow birch were 15.9 times higher than sugar

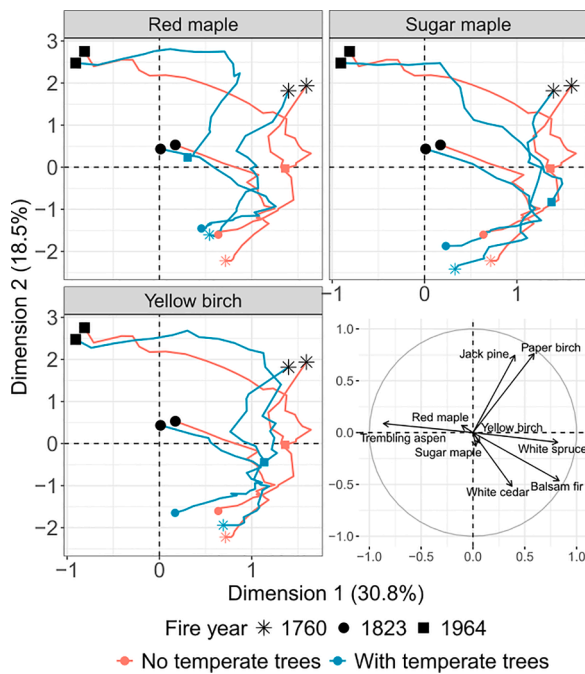


Fig. 8. Simulated trajectories of stand assemblages in a multivariate space built with a principal component analysis (PCA) based on the basal area ($\text{m}^2 \cdot \text{h}^{-1}$) of adults and saplings across all simulation results. Trajectories in each panel represent the chronology of the stand's composition depending on the absence (orange lines) or addition (blue lines) of the 400 m^2 patch of temperate tree species in the SSP 2.4-5 climate scenario. Black dots (square, circle, stars) correspond to the position at initial conditions of the vegetation in the multivariate space, and colored dots correspond to the results of the simulations at the last timestep (after 110 years). The PCA correlation circle used to generate the trajectories is shown in the lower right panel where the temperate tree species arrows are represented by short vectors located in the central part of the ordination.

maple and 38.9 times higher than red maple, explaining the better colonization performance of yellow birch. If the STR parameter value of yellow birch was attributed to the two other tree species, we observed an increase of basal area by a factor of 4.1 for sugar maple and of 41 for red maple. $MaxPotGrowth$ (maximum potential growth, eq. 1) had a little effect on basal area in the last timestep with a small increase of last timestep basal area with an increase of $MaxPotGrowth$. Last timestep basal area also responded to juvenile mortality and especially M_2 which is the parameter that related juvenile tree growth and mortality, with higher growth leading to lower mortality (light dependent mortality parameter, eq. 9). The parameterized value of M_2 for all temperate tree species was at about the threshold value where a decrease in M_2 would result in a major mortality and thus a drop in the species basal area per stand.

All temporal trajectories moved toward the space correlated with the basal area of white cedar and balsam fir consistent with the observed natural dynamics of stands in the boreal mixedwood forest (Fig. 8). Trajectories of the younger stand began in the space correlated with trembling aspen abundance and finished in the space correlated with coniferous species, the trajectories of the other two stands moved from mixed stands to coniferous dominated stands, particularly with high presence of white cedar. The most important deviations from the control trajectories (stands without temperate tree species) occurred in the youngest stand where the temperate tree species had the highest colonization ability. Trajectories were deviated because of the actual presence of temperate tree species, but also because of the consequences of the presence of temperate trees in stands which could affect regeneration, growth and survival of mixedwood boreal species.

4. Discussion

4.1. Temperate tree traits determining their colonization success in boreal stands

Our study considered three temperate tree species with contrasted auto-ecology and functional traits. Yellow birch and red maple are both moderately shade-tolerant species, but while red maple has a fast growth rate and is a typical pioneer species, yellow birch has a slower growth rate (Kobe et al., 1995). Sugar maple is shade-tolerant but slow growing, this species can colonize stands at all stages of the successional dynamic in their current distribution range (Beaudet & Messier, 1998). Sugar maple usually regenerates in gaps created by windthrow or insect outbreaks in mature stands and under the canopy, while yellow birch and red maple colonize stands in gaps and after major disturbances such as fire or harvesting (Fei & Steiner, 2009; Gasser et al., 2010; Duchesne & Prévost, 2013). Yellow birch has also higher ability to disperse far from the seed source because of the reduced mass of the seeds compared to maples (Ribbens et al., 1994; Caspersen & Sapruff, 2005; Hossain et al., 2017; Evans et al., 2020). In our simulations, these contrasted auto-ecology and functional traits resulted in different colonization performance of mixedwood boreal stands, in accordance with other studies (Boulanger et al., 2022). Yellow birch was the species with higher performance while sugar maple and red maple had similar and lower performance. All temperate tree species had similar realized growth per tree, slightly higher for red maple due to its pioneering behaviour. Yellow birch growth was significantly reduced by light availability in all conditions and by the high temperature of the more pessimistic climate scenario. Red maple growth was mostly reduced by highly competitive interactions with other trees in all mixed stands (Soubeyrand et al., 2024). Finally, as expected, sugar maple lacked sufficient light to grow in the denser and younger stands (Beaudet & Messier, 1998; Soubeyrand et al., 2024).

Our study showed that the number of seed produced per year and the seedling and sapling growth rate and mortality are the most important traits and processes determining the speed of the colonization of temperate trees in boreal stands (Aitken et al., 2008; Bouchard et al., 2019). Yellow birch took advantage of its high juvenile and adult growth, and its ability to disperse its abundant seeds more distant compared to red maple and sugar maple (Caspersen & Sapruff, 2005; Canham & Murphy, 2016b). Yellow birch was thus able to produce more stems developing faster than those of red maple and sugar maple, leading to higher birch basal area by 2100 (Supporting Information Fig. S2 and video S1). Soubeyrand et al. (2023) showed that all three studied temperate tree species may easily survive and grow in boreal mixedwood stands. The present study refines these results and shows that seed dispersal and seedling mortality are the prominent processes limiting the actual northward migration of temperate trees.

Marginal populations of temperate tree species located in the top and the slopes of the hills in the mixedwood boreal forest may act as pioneering outposts, facilitating the colonization and spread of temperate trees in the boreal forest in the context of climate change (Vogel et al., 2023; Vogel et al., 2024). Our study highlights that this colonization will be easier if the surrounding stands are young and recently disturbed. The greater seed dispersal capacity of yellow birch seems to be a key trait for a rapid migration and colonization of the mixedwood boreal forest. Yellow birch should colonize new stands from marginal populations and expand its distribution faster compared to the two other studied temperate tree species.

Our findings highlight the significance of juvenile growth in determining the basal area of temperate tree species several decades later. In our model, this growth stage is primarily influenced by the amount of light received by each seedling and sapling, in accordance with the literature (Godman & Krefting, 1960; Pacala et al., 1994; Collin et al., 2018). However, the establishment of temperate tree species in boreal mixedwood micro-sites may be limited by specific substrate and local

stand conditions (Collin et al., 2017, 2018; Carteron et al., 2020; Solarik et al., 2020). For instance, yellow birch seed germination is higher on dead wood, and seems to be even higher on coniferous dead wood, compared to dead deciduous trunks (Marx & Walters, 2008; Bolton & D'Amato, 2011; Lambert et al., 2016). Kellman et al. (2004) conducted in situ experiments to study sugar maple seed germination in various boreal stands (old conifers, young conifers, stands dominated by birch) and revealed that the probability of germination is more influenced by site-specific effects, such as seed predation, than by the species that dominates the stand. Conversely to seed germination, seedling mortality could depend on the tree species that dominates the stand, as for sugar maple seedlings that show high mortality in boreal stands, intermediate mortality in temperate stands, and minimal mortality in mixed stands (Kellman, 2004; Collin et al., 2018; Carteron et al., 2020). Although SORTIE-ND considers the abundance and suitability of different germination substrates, the performance of juvenile establishment and growth according to specific micro-site conditions merits further attention in future studies.

4.2. Effects of climate change

Our results are consistent with other studies showing that temperate tree species can grow north of their range under current climate, and that their growth should increase by 2100 due to the release of climatic constraints (Ashraf et al., 2015). However, temperate tree range expansion northward seems not currently limited by insufficient growth, but rather by stand-intrinsic factors, such as pre-existing species composition and disturbances (Zhu et al., 2012; Drobyshev et al., 2014; Y. Zhang et al., 2015). In line with the results of these studies, our simulations suggest that increased climate forcing would not enhance the northward colonization capacity of temperate broadleaf species, contrary to one of our initial hypotheses. Instead, increased temperatures and changes in water regimes would primarily have an indirect effect through alterations in disturbance regimes. Red maple and yellow birch should take advantage of stands disturbances increasing light availability such as budworm outbreaks, windthrows, or harvesting (Duchesne & Ouimet, 2008; Leithead et al., 2010; Hart et al., 2012; Duchesne & Prévost, 2013; Brice et al., 2019, 2020). When established, sugar maple should also be resilient to disturbed environments and increased fire activity, promoting the species expansion in the mixedwood boreal landscapes (Pilon & Payette, 2015; Payette et al., 2018). Temperate tree species may also take advantage of gaps created by natural tree mortality during stand succession (Gasser et al., 2010; Leithead et al., 2010; Hart et al., 2012; Després et al., 2014).

The species composition and density of the receiving stand had the greater effect on the realized growth of temperate tree species in accordance with previous studies (Zhu et al., 2012; Drobyshev et al., 2014; Y. Zhang et al., 2015; Power et al., 2019). The effects of projected climate on the colonization success were even negligible compared to those related to the receiving stand composition and density. However, we only consider the effects of climate on adult tree growth, while such effects may be important on the seed production and, at the seedling and sapling stage (Canham & Murphy, 2016a, 2017; Clark et al., 2021). Climate change could affect the regeneration of temperate species, for example, by reducing juvenile survival and seed production during droughts or disrupting phenology under high temperature regimes (Clark et al., 2021). Moreover, in our study, juveniles growth and mortality only depends on light availability without consideration of short-term meteorological events (Leithead et al., 2010; Moreau et al., 2020). For example, late-spring frost could highly affect seed production and juvenile growth and mortality of temperate trees, limiting their northward expansion (Godman & Krefting, 1960; Hufkens et al., 2012; Tao et al., 2021; Marquis et al., 2022). Future studies must focus on including climate and meteorological effects at all life stage of trees, including seed production and germination, seedling growth, and survival. However, at the moment, we lack quantitative field data to

properly include these effects in the simulations.

Climate-induced range shifts of tree species are not only influenced by average changes in temperature and precipitation, as modeled in our simulations. Other important bioclimatic variables and soil characteristics, such as those affecting soil water availability, may also play a critical role in shaping tree performance and potentially have a pronounced effect on the range of tree species (Puchałka et al., 2023). The northward expansion of temperate tree species may also be favored by the reduced fitness and local extinction of boreal tree species, which may struggle to cope with climate change (Zhang et al., 2017). The growth and survival of black spruce and balsam fir could be severely compromised in the future due to repeated drought episodes, particularly intense in the southern part of the boreal forest (Girardin et al., 2016; Sánchez-Pinillos et al., 2022). In contrast, species such as red maple, sugar maple, and yellow birch demonstrate better adaptation to warmer climates than boreal species. In our simulations, this possibility is considered by modeling the growth and performance of boreal tree species with a species-specific approach, accounting for their interactions and performance in a changing environment. However, we recognize that droughts and certain other processes, such as post-fire recolonization or increased pest outbreaks, cannot be fully accounted for (Maleki et al., 2019).

4.3. Implication for forest management

Colonization by temperate tree species was different in our simulations according to the age of the receiving mixedwood boreal stand. As suggested by one of our initial hypotheses, older stands had a higher proportion of coniferous species leading to high competitive interactions for light and space with high mortality of temperate tree species and reduced growth of juvenile and adult trees. This result is in accordance with the findings of other studies (St.Clair et al., 2008; Collin et al., 2017; Putnam & Reich, 2017). Conversely, the initial composition of the younger unharvested stand (reinitiated in 1964) was dominated by trembling aspen and had lower overall tree density compared to older stands. This led to lower level of competition for light and space and higher colonization success for temperate trees. This colonization modified the species assemblage at the expense of late-successional species, such as white cedar and balsam fir. Similar potential assemblage shifts are also described by other studies (Fisichelli et al., 2014; Frelich et al., 2021).

Forest fires can have a significant impact on the colonization of temperate tree species in mixedwood boreal stands by rejuvenating the host stands and providing appropriate substrates (Noualhuquet et al., 2023). As competition constraints for space are released, temperate tree species find favorable conditions to establish (Brice et al., 2020). The study area is also significantly impacted by the spruce budworm, which is a major defoliating insect (Bergeron et al., 2014). The outbreaks of this insect occur on average every 30 years, lead to the mortality of fir and spruce trees, and are expected to increase in severity due to climate change (Pureswaran et al., 2019). Such outbreaks create gaps within the stands, providing an opportunity for temperate tree species to thrive by accessing more light and space (Kellman, 2004; Gasser et al., 2010; Bannon et al., 2015). However, the increased presence of temperate species could potentially help mitigate the severity of future fires and spruce budworm outbreaks by decreasing the abundance of budworm's host species (Cappuccino et al., 1998).

Forest management, by rejuvenating the mixedwood boreal landscapes, could accelerate the migration of temperate tree species northward. Other landscape-scale modeling studies at the temperate-boreal ecotone showed that climate change coupled with forest management could modify the distribution of temperate tree species, which are facilitated especially after clearcuts (Steenberg et al., 2013; Fisichelli et al., 2014; Boulanger et al., 2019; Bouchard et al., 2019). The presence of young stands north of the distribution range of temperate tree species should accelerate the transition to forests dominated by hardwoods

(Brice et al., 2019, 2020; Molina et al., 2021). In accordance, our simulations showed that recently harvested and young post-fire stands are both suitable to temperate tree colonization. In recently harvested stands, our results show that seedlings and saplings of temperate tree species experience too high mortality rates due to competition for space with aspen, which produces abundant root suckers and grows rapidly during its juvenile stages. However, after the aspen self thinning (stands older than 20 years) and in stands where light availability is still high enough (stands younger than 140 years), the success of temperate tree colonization is maximized. Around the FERLD, 17% of the stands have an age between 20 and 140 due to forest management, and 24% due to fire events. This means that 41% of the forest landscape could eventually be favorable to colonization by temperate tree species if seed-bearing trees are near enough.

Other additional factors could limit the colonization of temperate trees into FERLD territory within the boreal forest such as edaphic factors (Drobyshev et al., 2014; Y. Zhang et al., 2015). The soil of boreal stands is generally more acidic than that of hardwood forest which could have an impact on temperate tree germination, growth and survival (Collin et al., 2017). In addition, the clay soils like in the clay belt and those around FERLD territory may be not favourable for the establishment of temperate tree species because of soil properties such as low drainage and lack of mycorrhizal symbionts (Carteron et al., 2020).

Our results suggest that fire- and logging-induced openings in the boreal forest cover will accelerate the northward expansion of temperate tree species by creating more easily colonizable forest assemblages and structures. The arrival of temperate tree species will further alter the soil environment, promoting the colonization of additional species (Paillard et al., 2023; Dumont et al., 2024).

While the conclusions of our simulations are informative from an ecological perspective and offer valuable insights for forest management, we want to emphasize that caution should be exercised when interpreting results from century-long simulations. For example, in a changing environment, entirely new biological interactions, such as those involving invasive species (Banasiak et al., 2019), may rapidly emerge and modify the outcomes.

5. Conclusion

Our study models potential colonization success of temperate trees into mixedwood boreal stands in the presence of available seeds sources. Our simulation set-up mimics the expansion from an already existing marginal population established, for example, by long distance migration. We demonstrate that, when a patch of temperate trees is introduced or already present in a mixedwood boreal stand, the trees can disperse, grow, and colonize the adjacent stand north of their current continuous distribution range. Current and projected climate scenarios excluding meteorological effect have low impact in the colonization success. Dispersal ability and juvenile growth and mortality are instead the most sensitive processes. The colonisation success depends on the successional stage of the adjacent mixedwood boreal stand, being maximum in younger stands and mixed stands with canopy openings. These results reinforce the conclusion that natural disturbances and forest management practices play a more critical role than the increase in temperature associated with climate change in facilitating the northward expansion of temperate tree species distributional ranges (Boucher et al., 2006; Danneyrolles et al., 2019).

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CRedit authorship contribution statement

Maxence Soubeyrand: Writing – review & editing, Writing – original draft, Visualization, Validation, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Fabio Gennaretti:** Writing – review & editing, Validation, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Conceptualization. **Marie-Hélène Brice:** Writing – review & editing, Validation, Supervision, Conceptualization. **Pierre Grondin:** Writing – review & editing, Validation, Investigation, Conceptualization. **Yves Bergeron:** Writing – review & editing, Supervision, Project administration, Funding acquisition, Conceptualization. **Philippe Marchand:** Writing – review & editing, Validation, Supervision, Resources, Methodology, Investigation, Conceptualization.

Declaration of competing interest

We have no conflict of interest to declare.

Data availability

Data and code used in this study has been archived on GitHub and can be found at <https://rb.gy/tzt01y>.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at [doi:10.1016/j.ecolmodel.2024.110892](https://doi.org/10.1016/j.ecolmodel.2024.110892).

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