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# Slow demography and limited dispersal constrain the expansion of north-eastern temperate forests under climate change

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## Abstract

**Aim:** Tree species may be vulnerable to migration lags because they are sessile, long-lived, have a small intrinsic growth rate and relatively short dispersal. Our study assesses if those ecological mechanisms will mitigate the progression of the north-eastern American temperate forest leading edge into the boreal forest.

**Location:** The North-eastern boreal-temperate forest ecotone (from 43° to 51° North and 80° to 60° West).

**Taxon:** Our approach involved 15 forest species classified into four representative forest communities of the eastern boreal-temperate forest.

**Methods:** We performed simulations on the boreal-temperate ecotone using a state and transition model (STM), wherein forest communities are classified in four states: boreal, temperate, mixed and stands in regeneration. We propose a new modelling approach based on metapopulation theory to account for dispersal limitations and the demography of the temperate and boreal forests. We calibrated the STM model with an extensive dataset of 48,940 forest inventory plots. We projected the boreal-temperate forest landscape over 23 General Circulation models (GCMs) from the RCP 8.5 emission scenario to study the forest communities dynamics at the landscape scale under climate change.

**Results:** Simulations of climate changes predict a significant increase of temperate forest dominance within the ecotone, mainly due to the conversion of mixed stands into temperate stands. The leading edge of the temperate forest will however move only 304 m in latitude (95% CI: 0.18–0.56) into the boreal forest by the end of this century. In comparison, the average expansion rate was 2,555 m/year (95% CI: 1,969–2,932) when we released the dispersal constraint and even higher with an average rate of 7,197 m/year (95% CI: 5,722–9,776) when we released the dispersal and demography constraints.

**Main conclusions:** The northern edge of the temperate forest distribution does not change with almost no movement toward the north for either temperate or mixed communities by the end of this century. Slow demographic and dispersal rates

prevent any substantial movement in temperate forests, with much faster migration rates when these constraints are removed.

**KEYWORDS**

boreal forest, community range shift, ecotone, forest inventory databases, landscape dynamics, state and transition models

## 1 | INTRODUCTION

The current challenge biogeographers are facing today is not only to predict future species distributions, but also to assess if species will be able to follow their climatic optimum by migration (Lenoir & Svenning, 2015; Renwick & Rocca, 2015). Correlative species distribution models (SDMs) are one of the most popular methods to evaluate the impact of climate change on biodiversity, but they are well known for their shortcomings, in particular with respect to their ability to predict the extent of range shifts (Thuiller et al., 2008). In their basic form, SDMs are based on the statistical relationship between distribution and the environment, and projections into the future often assume unlimited dispersal and instantaneous response to climate change (Thuiller et al., 2008). In some situations, SDM predictions of future distributions can be biased because of our inability to disentangle biotic from abiotic drivers of distribution (Václavík & Meentemeyer, 2009; Wisz et al., 2013). This limitation inspired contemporary modellers to incorporate biotic components to SDMs, such as dispersal and population dynamics (Guisan & Thuiller, 2005). Incorporating these features is important as strong competitive interactions, slow demographic rates (growth, mortality and reproduction) and dispersal limitations can drive some species to local extinction, prevent colonization at the leading edge and create non-equilibrium situations in which species may be absent from suitable environments (Boulangeat et al., 2012; Solarik et al., 2018; Talluto et al., 2017). Species might persist for a while at newly unsuitable locations because of time-delayed extinction and source–sink dynamics (Schurr et al., 2012). These mechanisms could slow down spreading rates and explain why many species fail to migrate (Zhu et al., 2012) and keep pace with the rate of climate change (Lenoir & Svenning, 2015; Renwick & Rocca, 2015; Svenning & Skov, 2004).

Range dynamics of forest tree species are particularly worth attention. Tree species may be vulnerable to migration lags because they are sessile, long-lived, have a small intrinsic growth rate, relatively short dispersal and often require a long time to reach reproductive maturity (Renwick & Rocca, 2015; Vanderwel & Purves, 2014; although short-distance dispersal might modulate this when climatic gradients are steep, e.g. in mountains; Beckage et al., 2008; Dullinger et al., 2004; Engler et al., 2009). Dispersal limitation and slow demographic rates might modulate their response to climate change and further contribute to this lag (Svenning et al., 2014). Two parameters in particular, the intrinsic growth rate ($r$) and the average dispersal distance ($D$), are identified by classical diffusion models (e.g. Fisher-Skellam) as crucial drivers of migration rates (Skellam, 1951;

Svenning et al., 2014). Even if forest range dynamics are more complex than the representation by these models, these two parameters point to fundamental quantities that are required in order to understand the transient phase between the initiation of climate change and a species reaching its new equilibrium distribution. For example, strong competition at range margins can reduce the intrinsic growth rate, which, coupled with dispersal limitations, might contribute to slow colonization (Godsoe et al., 2017). Plant–soil feedbacks, seed dispersers, mycorrhizae and other types of biotic interactions also contribute to local forest dynamics and consequently have potential implications on large-scale range dynamics (Solarik et al., 2019). Integrating such demographic and spatial constraints on range shift projections is essential to improve our understanding of species migration (Normand et al., 2014).

In eastern North America, several temperate deciduous tree species (e.g. *Fagus grandifolia*, *Betula alleghaniensis*, *Acer saccharum*, *Quercus rubra*) are expected to expand their distributions northward (McKenney et al., 2007) into regions where boreal forest is already established and dominated by conifers. However, this migration might be inhibited because colonization success is not only determined by climate, but also by variation in soil properties and nutrient availability (Brown & Vellend, 2014; Lafleur et al., 2010; Solarik et al., 2018). Moreover, the persistence of a plant community at a single location depends on its ability to resist disturbances and invasion by other species. Local forest communities at the boreal-temperate ecotone are already experiencing species turnover in response to management actions (Danneyrolles et al., 2016; Dupuis et al., 2011) and climate change (Beckage et al., 2008). The prevalence of deciduous shade tolerant (e.g. *A. saccarhum* and *A. rubrum*) and intolerant tree species (e.g. *P. tremuloides*, *Betula papyrifera*) has increased in the previous decades along altitudinal and latitudinal gradients. These findings suggest that community shifts at latitudinal and elevational ecotones are already observable and that forest composition is currently changing from forest dominated by coniferous to deciduous species.

Temperate and boreal forests differ dramatically in terms of the functional traits of constituent species, and in terms of overall ecosystem functioning including carbon cycling and plant–soil interactions (Bonan, 2008; Magnani et al., 2007). This strong functional distinction marked by an abrupt change in ecosystem type facilitates the representation of the dynamics with a state and transition model (STM). STMs were introduced by Westoby et al. (1989) and have been commonly used to study vegetation dynamics (Briske et al., 2005). They follow the long tradition of Markov chain models

used in forest ecology (Binkley, 1980). An STM is based on the idea that plant communities can be categorized into discrete states (e.g. temperate, boreal and mixed forest). A spatial unit (e.g. a grid cell in a lattice) can encompass scales from single individuals to entire communities (Briske et al., 2005). Vegetation dynamics are then driven by stochastic transitions between states. With typical datasets on forest communities, transition probabilities among states can be estimated from empirical observations, integrating demography, dispersal and species interactions and thus offering opportunities to disentangle which of these processes are influencing most migration rates under climate change.

Stationary transition matrices are problematic to represent range expansion because they do not account for the build-up of the propagule pressure with the increase of a species abundance, nor do they account for climatic gradients in transition probabilities. Metapopulation theory fortunately provides an elegant solution to these issues. The standard metapopulation model (Levins, 1969) represents stochastic transitions among two states (i.e. patches are either occupied or not) in a similar way to Markov chain models of forest dynamics, with the addition of dispersal. The Levins model (Levins, 1969) could be viewed as a continuous time analogue of such models with a non-stationary transition matrix that depends on the prevalence of the species. The model has already been extended to incorporate environmental gradients (Holt & Keitt, 2000), whereby a species can persist in a given landscape when the colonization rate of empty patches is higher than the extinction rate. It has been applied to species distributions in eastern North America and shown to properly predict range margins (Talluto et al., 2017). Here, we explore a further extension of the Levins and Holt models by considering the state of entire communities, with the goal of better understanding how climate change and regional-scale dynamic processes will influence the response of boreal and temperate forests to climate change.

Our first objective in this study is to assess if temperate deciduous tree species of eastern North America will be able to track their climate optimum over the next century. Secondly, we seek to investigate which ecological processes are delaying the migration of temperate forest. We use an STM derived from metapopulation theory to represent demographic processes through colonization, competitive exclusion and disturbance dynamics at the temperate/boreal ecotone. Demographic processes are tracked inside the model as transitions among states. Those transitions were calibrated using long-term forest plots surveys from the United States and Canada, where each possible transition was modelled as a function of the climatic conditions and propagule pressure. We simulated the landscape dynamics over the most extreme climate change scenario (RCP 8.5, Taylor et al., 2012) in order to force range shifts. We further ran three different versions of the model to investigate the importance of demography and dispersal limitations on range expansion rates: the analytical model (no demograhic and dispersal constraints) and two STM variants (one including demographic constraint but no dispersal limitation, and a full model with demographic and dispersal limitations). Our results reveal that the temperate forest has a low
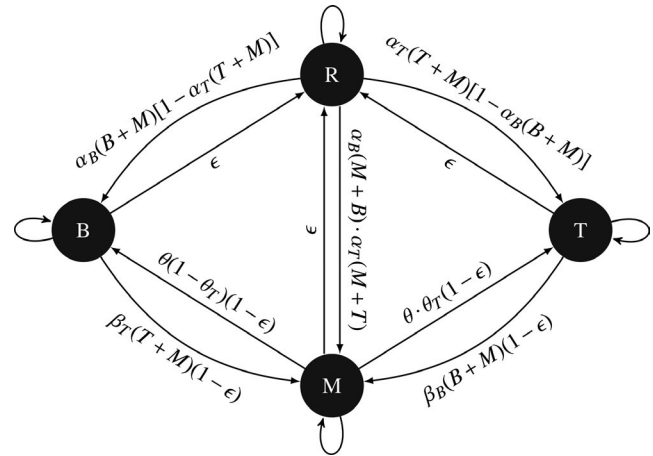


**FIGURE 1** Schematic representation of the model with states (B)oreal, (M)ixed, (T)emperate and (R)egeneration. Transitions from B, M and T to R result from disturbances. Succession results in a transition from R to B, M or T, and colonization results in transitions from either B or T to M. Competitive exclusion causes with transitions from M to either B or T. All of the transitions involving the arrival of a new species are dependent on dispersal and thus on the occupancy in the neighbourhood ($T + M$ or $B + M$)

adaptive capacity to climate change because of slow demography and significant dispersal limitations.

## 2 | MATERIALS AND METHODS

### 2.1 | Modelling approach

We consider a landscape made of a large number of patches that could be occupied by any of four vegetation types, defined by successional status and composition: Regeneration (R), Boreal (B), Temperate (T) and Mixed (M; Figure 1; see *States classifications* in Appendix S2 for a complete description). Temperate and Boreal states summarize the clustering of species found along the first axes of a principal components analysis of the relative abundance of dominant species across north-eastern America (see Appendix S2, Figure S5).

Transitions among states are represented as a stochastic process influenced by climate, ecological interactions and dispersal. The state of a focal plot $i$ at time step $t + 1$, given by $X_{t+1,i}$, is a random variable with a probability distribution conditional on the initial state $X_{t,i}$, climatic conditions at time $t$ and the prevalence of the four states in the neighbourhood of $i$ (hereafter, we assume all equations are relative to a focal stand and omit the subscript $i$ for clarity of notation). Ecological dynamics are represented by the following processes (Figure 1). A disturbance occurs with probability $\epsilon$ and converts T, B and M to Regeneration (R). Colonization of the R state happens with probabilities $\alpha_T (T + M)$ and $\alpha_B (B + M)$ for temperate and boreal trees respectively. The colonization probability depends on the amount of propagules produced by neighbouring patches ($T + M$ or $B + M$), thus accounting for metapopulation dynamics. A joint colonization event

is possible with probability $\alpha_T (T + M) \cdot \alpha_B (B + M)$, leading to a transition from R to state M. Mixed stands can also arise via colonization; boreal trees invade temperate stands with probability $\beta_B (B + M)$, and the converse occurs with probability $\beta_T (T + M)$. Finally, competitive exclusion results in the transition from M patches to either B or T, with probabilities $\theta$ and $\theta_T$. Direct transitions between T and B are not allowed, and must instead occur via the disturbance and succession (through R state) or invasion and competitive exclusion (through M state) pathways. We assume transitions will be gradual enough that either a mixed or a regeneration state must occur before a stand transitions from purely temperate to purely boreal; moreover, such transitions were almost absent from our calibration dataset (and thus it would be impossible to estimate it, see Appendix S1, Table S2). All parameters $\alpha$, $\beta$, $\theta$ and $\epsilon$ were represented as a function of local climatic conditions.

To understand the long-term behaviour of the system, we first considered a mean-field model, where the dynamics are represented by difference equations described in Figure S3 and with the constraint that $B + T + M + R = 1$. The analytical solution of the mean-field model yields the expected occupancy of the four states for any given climatic condition. We then implemented the model into a stochastic cellular automaton to predict transient states and compute migration rates. We represented the landscape as a regular grid of $100 \times 100$ m, where each cell at each time step is occupied by one of the four forest states (R, B, T or M). We made the model spatially explicit by computing the prevalence of states (i.e. the proportion of forest states in the eight immediately neighbouring cells of a focal cell) used in transition functions (T + M in the previous paragraph). Hence, each cell occupied by a specific state contributes to the expansion of his own state distribution within a radius of 100 m. Cell size is beyond the typical dispersal distance of most temperate tree species (Clark et al., 1998; Ribbens et al., 1994) and therefore we consider it to represent realistically the effect of rare long dispersal distance events. We also run extra simulations to assess if the migration rates were sensitive to this cell size by comparing two grid resolutions ($100 \times 100$ m, and $1,000 \times 1,000$ m, see Appendix S4). We then simulated the temperate-boreal forest ecotone, with each cell having climatic conditions obtained from the observed climate (McKenney et al., 2011; to calibrate the model) or the projected climate from the RCP 8.5 emissions scenario (Taylor et al., 2012; to project into the future). We selected this scenario because it predicts the largest temperature increase and thus provides the greatest potential mismatch between the present climatic equilibrium and future climate. We considered three modelling scenarios (below) in order to disentangle the mechanisms limiting the northward migration of the temperate forest. Finally, we used 600 m × 900 m cells to compute actual and expected distributions across entire Québec.

The first modelling scenario considered the spatially explicit model described above. It is the most realistic scenario we considered and includes demographic and dispersal limitations. Secondly, we solved the system of difference equations for every climatic condition of the landscape. This scenario is at the other extreme and similar to classic species distribution models as it assumes no

dispersal and demographic constraints. For the third scenario, we considered global dispersal by computing each cell's neighbours using cells randomly drawn from the entire grid, rather than the immediate neighbours. Demography is the only process limiting migration in this situation. All of these modelling approaches were run for the 23 General Circulation Models (GCMs, from the RCP 8.5 emission scenario), downscaled to 5 min by Ouranos, a Consortium on Regional Climatology and Adaptation to Climate Change. For analysis, we reprojected the grid to an Albers Equal Area Conic projection (to minimize the impacts of variable cell size, particularly in northern regions.)

## 2.2 | Data

We classified states using data from permanent sample plots in forest inventory databases from Eastern North America. This forest inventory network incorporated the Forest Inventory and Analysis National Program in the United States (O'Connell et al., 2007); Domtar, a private forest company in Québec; the Ministère Forêts, Faune et Parcs du Québec (Ministère des Ressources naturelles, 2013); the Ministry of Natural Resources in Ontario (Ontario Ministry of Natural Resources, 2014); the Ministry of Natural Resources in New Brunswick (Porter et al., 2001). These databases differ in ontology but were integrated using their common information on trees measurements and their location (all filters used are described in Appendix S2).

## 2.3 | Calibration

We described the state of a given sampling plot at time $t + 1$, $X_{t+1}$ with a random variable determined by a stochastic process conditional on the previous state $X_t$, prevalence $N$ (the methodology to estimate the initial prevalence with Random Forest algorithm is described in Appendix S2) and climatic covariates $E$. It is a non-stationary Markovian process since the transition is conditional only on the previous time step and independent of previous history. The probability function representing this process is $P(X_{t+1}|X_t, E, N)$. We used simulated annealing (R package *GenSA*; Gubian et al., 2002) to attain maximum likelihood estimates of the parameters pertaining to each transition probability (Figure 1). Each of them is a function of mean annual temperature (*TP*, °C) and mean annual precipitation (*PP*, mm). Each of the per patch transition probabilities (i.e. $\alpha_T$, $\alpha_B$, $\beta_T$, $\beta_B$, $\theta_T$, $\theta_B$, and $\epsilon$; Figure 1) was modelled as second order logistic function of climatic conditions. Thus, any parameter $\phi$ is modelled as:

$$\text{logit}(\phi) = a_0 + a_1 \cdot TP + a_2 \cdot PP + a_3 \cdot TP^2 + a_4 \cdot PP^2 \quad (1)$$

Prior to analysing the STM, we evaluated the strength of the relationship between transitions among states and climate conditions using a multinomial regression fit with an artificial neural network (ANN; R package *nnet*; Venables & Ripley, 2003). This model

**TABLE 1** Classification accuracy of the STM and the Random Forest classifier algorithm (RF) using the same climate predictors: annual mean temperature and total annual precipitation. The accuracy is presented for each state ($[a + d]/N_{total}$) and the overall model ($a/[b + d]$). Correct presences and absences indicate a predicted presence and absence and an observation that matched the predictions, and false presence/absence is the opposite

|  | B | T | M | R | Total |
|---|---|---|---|---|---|
| a. Correct presences | 1,380 | 6,179 | 980 | 0 | 8,539 |
| b. False presences | 1,940 | 1,141 | 2,175 | 285 | 5,541 |
| c. False absences | 830 | 3,062 | 1,648 | 0 | 5,540 |
| d. Correct absences | 9,930 | 3,698 | 9,277 | 13,795 | 36,700 |
| N | 3,320 | 7,320 | 3,155 | 285 | 14,080 |
| Classification accuracy (STM) | 0.80 | 0.70 | 0.73 | 0.98 | 0.57 |
| Classification accuracy (RF) | 0.95 | 0.95 | 0.95 | 0.99 | 0.91 |

does not consider dispersal limitation (i.e. the prevalence terms in the full model) nor patch-scale ecological processes (i.e. the $\alpha$, $\beta$, $\theta$ and $\epsilon$ parameters), rather it simply relates observed transitions to climate. This serves as a baseline for whether we could expect to observe climatic relationships within the more mechanistic STM. We used orthogonal third-order polynomials for mean annual temperature and total annual precipitation, with the variance of each term standardized to one (to allow comparison of regression coefficients). Other climatic variables were also considered but were found to be weaker predictors and are thus not considered. We also evaluated whether dropping the third polynomial terms was necessary by removing them from the model and computing the change in the Akaike's Information Criterion (ΔAIC); in most cases ΔAIC was less than 10, so we dropped the third-order terms for reporting the results (Burnham & Anderson, 1998). Because time intervals between observations were not uniform in our dataset, we limited this analysis to plots observed at a 5-year interval (consisting of 56% of observations).

We solved the system of difference equations at equilibrium (i.e. analytical model) for each location of the climatic grid using the maximum likelihood estimates of the parameters. Numerical solutions were found using the *deSolve* R Package (Soetaert et al., 2010). We mapped the solution and compared it to the actual distribution in order to validate the predictions of the model. This comparison was performed using 14,080 plots that were measured only once and therefore could not be used for calibration. For each of these plots, we computed the expected state by selecting the state with the highest occurrence probability from the STM. For the B, M and T states, we then evaluated the classification skill of the model by computing correct (i.e. predicted and observed presence or absence or each state) and incorrect (i.e. prediction of presence or absence and observation of the opposite) classification. Because disturbances are largely driven by stochastic events and were relatively rare, we expected that the model would have high skill in predicting the absence of disturbance (most plots are undisturbed), but little skill in predicting the precise spatial location of disturbances.

To understand transient states under climate change and analyse the migration rates, we ran the cellular automaton model on the spatially explicit climatic grid with climate change scenarios. The equilibrium solution obtained with the difference equations was used as the initial condition for conducting simulations to make sure that any observation of change in state distribution is caused by the changing climatic conditions and not by initial distributions that are not in equilibrium with initial climatic conditions. We used a 5-year time step and ran the simulations from 2000 to 2095. At each time step, we recomputed the expected transition rates for each cell using the average climate of the preceding 15 years.

We subset from the grid into a band of 46 km in longitude and 526 km in latitude in order to compute the migration rate of the temperate forest. The band started north of the city of Montreal in the sugar maple bioclimatic domain and extended up to the spruce-moss domain, in the boreal forest near Chibougameau. The range limit of the temperate forest at any moment in time was recorded as the northernmost location (95th percentile) of a temperate or a mixed state along this band. We computed range expansion each time step and estimated the migration rate for any time interval as the annual movement northward (in m/yr). The magnitude of the expansion was also reported as the proportion of the temperate forest along the north–south gradient.

## 3 | RESULTS

As a preliminary analysis, we first considered the relationship between transition probabilities and climate (mean annual temperature and total annual precipitation) using multinomial regression with an artificial neural network. In general, standardized parameter estimates for temperature were larger than those for precipitation, indicating a stronger effect of temperature in determining when and if transitions occurred (Table S1). The temperature terms were particularly largest for transitions from R to T (2.78 [1.06]), R to M (1.39 [0.75]), B to M (1.59 [0.45]) and M to B (–1.42 [0.97]; values are standardized effect sizes with standard errors in brackets). Response surfaces indicated that the disturbance probability (transitions to R) was low throughout the climatic space regardless of the initial states, whereas transitions to M and T increased as a function of temperature (Figure S1).

Similarly, we found a relationships between the STM transition parameters and climate (Table S1). In particular, all transitions involving the invasion by temperate trees (i.e. R to M or T, B to M and M to

T) were positively related to temperature (Figure S1). As expected, the competitive exclusion pathway for boreal trees (i.e., transitions from T to M and M to B) were negatively related to temperature, however the successional pathway to boreal forest (R to B) showed little response to temperature (Figure S2). The equilibrium solution of the dynamic model under the 2015 climatic conditions agreed well with the current distribution of temperate, mixed and boreal forests (Figure S4). There was a high correspondence between the match of presences and absences, with 0.70–0.98 of observations correctly predicted (Table 1).

Simulations from the full STM model (with demographic and dispersal constraints) predict that temperate forests (i.e. pure stands of temperate species) cover an area of 339,359 km$^2$ in 2015 and increase by 37.8% in 2095. The major change in forest composition occurs in the transition zone, where mixed forests will be rapidly converted to temperate forest, for an expected reduction of 59% of their area (Figure 2) at the end of the century. Our simulations suggest that competitive exclusion of boreal species by temperate species occurs at a higher rate than invasion of pure boreal forest stands by temperate species. As a consequence, the ecotone area found in 2015 (where temperate and mixed coexist at the landscape level) will almost disappear by the end of this century, while the northern edge of the temperate and mixed forest distribution will barely progress (Figure 2).

We ran the three different modelling scenarios with climate change to investigate the main drivers of migration dynamics. The full-STM simulations (accounting for demographic and dispersal constraints) predict that the leading edge of the temperate forest distribution (95th percentile) will progress by 304 m (95% CI: 0.18–0.56) at the end of this century. Simulations of this model show the slowest average rate of expansion into boreal forest (28.7 m/year with 95% CI: 20.0–59.7) among all RCP 8.5 models. In comparison, the average expansion rate was 2,555 m/year (95% CI: 1,969–2,932) when we released the dispersal constraint and even higher with an average rate of 7,197 m/year (95% CI: 5,722–9,776) when removing both constraints. Model simulations suggest that the temperate forest will reach 50.3°N in the absence of demographic and dispersal constraints in 2020–2030 and 2065–2095 with unlimited dispersal but demographic constraint. However, the leading edge of the temperate forest distribution will never reach this point at the end of the century according to the full STM (Figure 3). The main factors slowing down migration thus appear to be dispersal limitation followed by demography. The mismatch between the suitable climatic conditions for temperate species and their realized distribution consequently increases constantly through time (Figure 3).

## 4 | DISCUSSION

A clear understanding of the determinants of migration dynamics under climate change is essential to improve our ability to predict future biodiversity distribution (Svenning et al., 2014). Forest trees are expected to respond slowly to climate change because of their longevity, their low dispersal and slow demography (Renwick &
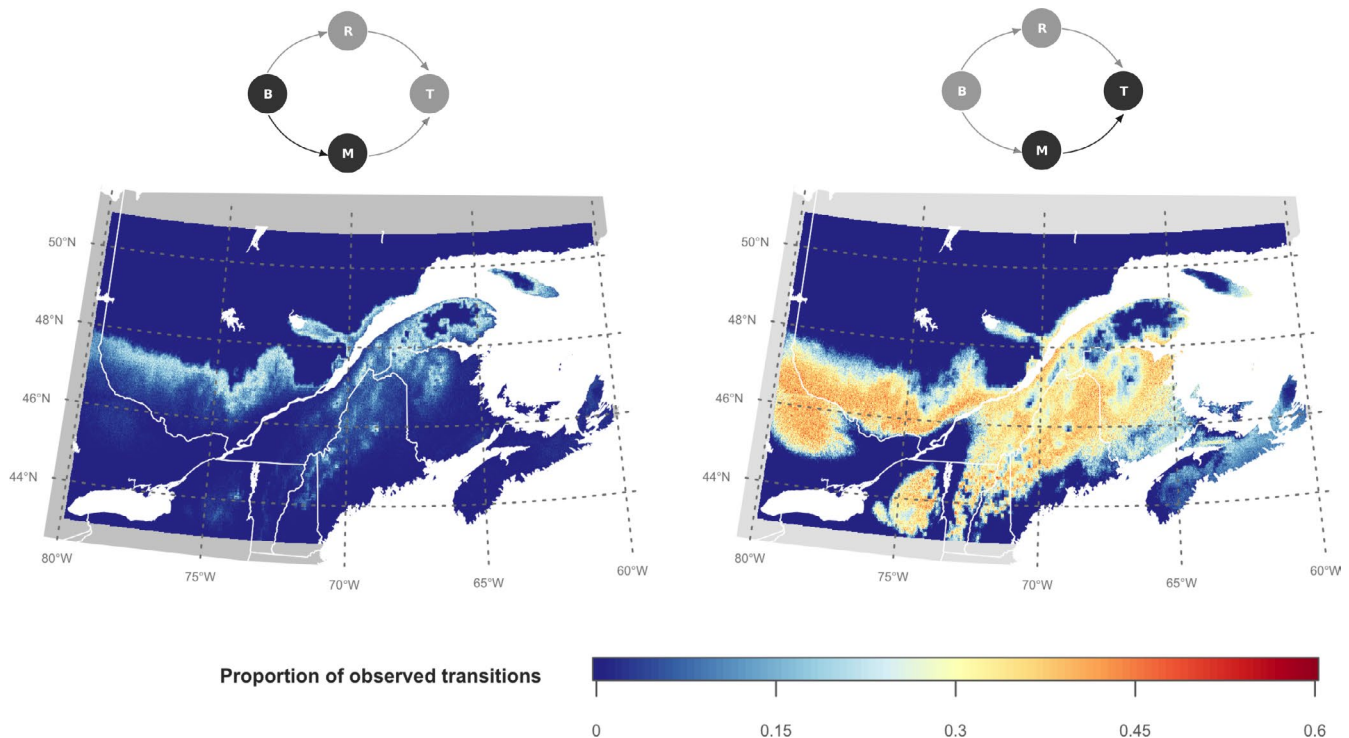


**FIGURE 2** Frequency of transitions from (B)oreal to (M)ixed (left panel) and (M)ixed to (T)emperate forest (right panel) between initial (2015) and final (2095) time steps. Transition frequencies were obtained by dividing the number of transitions observed by the number of simulations. Simulations used are only based on the first model scenario accounting for dispersal limitation, biotic and demographic constraints

**FIGURE 3** Mean proportion of temperate forests (with 95% quantiles) along a 520-km latitudinal band (in km, relative to the southernmost location of the band) showing the influence of dispersal and demographic constraints. We projected each STM variant over GCMs scenarios (RCP 8.5) and show the results in 2015 (left panel) and 2095 (right panel). The predictions of the full STM (blue line) for current climate (left panel) are the best estimates of the state of the system including dispersal and demographic constraints. When this constrained model is projected into the future with climate change (right panel), we find very little increase in the proportion of temperate forest. When the dispersal constraint (red line) is removed, we see much greater movement in 2095, demonstrating that dispersal introduces significant lags. Finally, when we released both constraints with the model solved at equilibrium (green line), simulations reveal that temperate forest will expand and occupy 100% of the band in 2095. This suggests that dispersal and demography are two ecological mechanisms delaying the expansion rate of the temperate forest
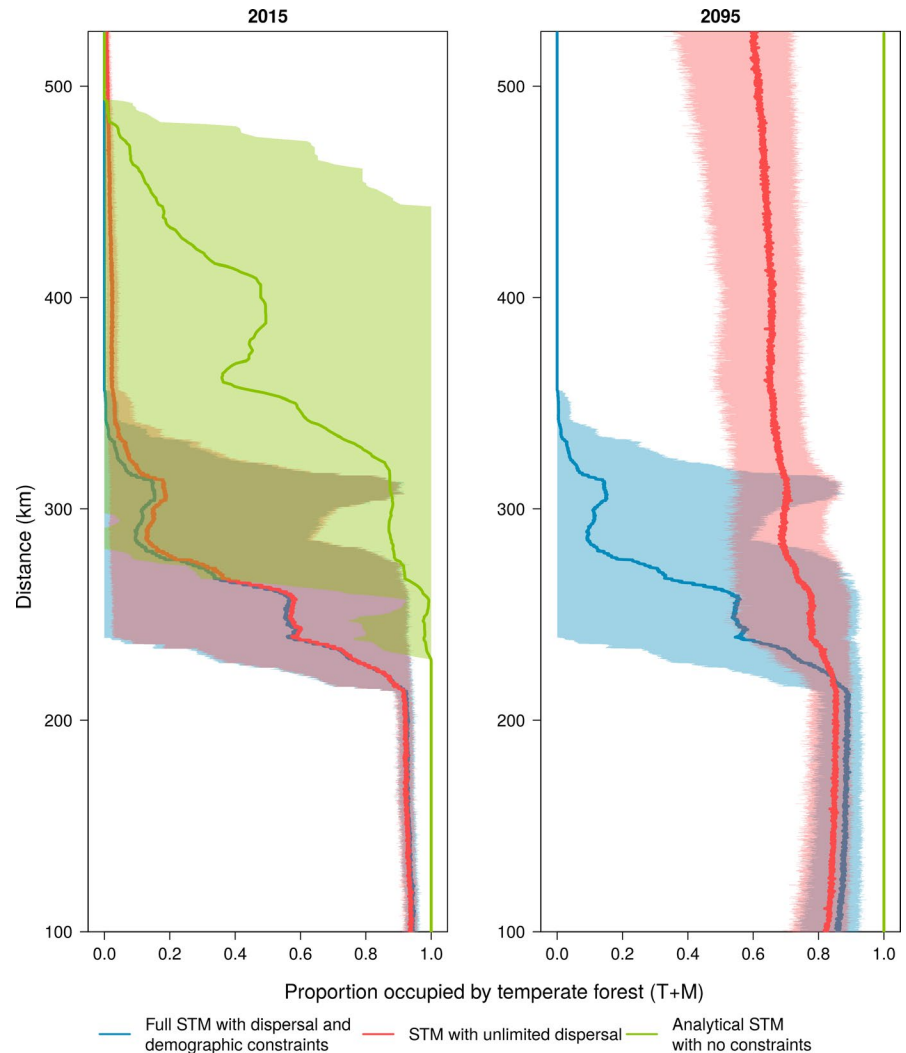


Rocca, 2015; Vanderwel & Purves, 2014). We analysed the northward shift in the distribution of temperate forests, a major biome covering the north-eastern United States and Canada, into the domain presently dominated by boreal forests. The ecosystem properties of temperate forests contrast strikingly with those of boreal forests. Temperate forests are characterized by a disturbance regime generating small canopy gaps and with rapid processing of rich deciduous litter, compared to larger-scale disturbances (e.g. fire) and slow decomposition of an acidic and nutrient poor litter in boreal forests. We investigated the importance of key ecological processes—dispersal limitations and demography—for the migration dynamics of temperate forests. We found evidence for substantial lags in the response of these ecosystems to climate change; in particular the influx of temperate species into the boreal ecosystem was slower than would be predicted at equilibrium with climate (analytical STM – Figure 3). Our results suggest that these lags were principally due to the combination of slow demographic processes (i.e. the invasion of seedlings into uncolonized patches) and dispersal limitations (Figure 3). Moreover, the equilibrium solution to our model under 2015 climate (Figure 3) suggests that the range of temperate forests may already be out of equilibrium with climate; temperate forests

under the equilibrium solution were shifted substantially further north than their present distribution. These results are consistent with previous research in this system showing disequilibrium in species ranges with respect to climate (Talluto et al., 2017). As the climate warms, the increasing tension between climatic equilibrium and distribution highlights that future changes in response to climate might be particularly sensitive to nonlinearities and stochastic dynamics (Jackson et al., 2009; Talluto et al., 2017). These results together show that, although temperate species can be expected to grow in dominance in areas where they are already present, the replacement of existing boreal ecosystems by temperate forest may be a much slower process.

The transitions among forest community types represented in our model are driven by dynamic ecological processes such as disturbance, succession, competitive exclusion and colonization. We expected that local climate is one factor driving the rate at which these transitions occur. Landhäusser et al. (2010) found that the rate of colonization by deciduous trees (in this case, *Populus tremuloides*) following disturbance is influenced by climate. Moreover, climate exerts a strong influence on the state of mature forests and their successional pathways (Anderson-Teixeira et al., 2013). Experiments

at boreal and temperate latitudes show that rising temperatures affect all major chemical and biological processes and mediate forest successional dynamics (Kreyling, 2010; Saxe et al., 2001). Our study shows that, at the stand scale, colonization and succession have strong relationships with climate, whereas competitive exclusion shows a weaker relationship. However, all of these larger-scale ecological processes are ultimately functions of individual-level demographic processes such as growth, mortality, seedling establishment and reproduction.

There is already substantial evidence that climate is influencing individual-scale processes. For example, Clark et al. (2011) found that some *Fagus* and *Pinus* are susceptible to moisture variation over the growing season, with lower moisture reducing germination success. Extreme drought can also increase mortality in several temperate deciduous tree species (Anderson-Teixeira et al., 2013). Spring and summer temperature has also been identified as critical for fecundity rates (Clark et al., 2011; Graignic et al., 2014). The stratification of maple seeds for instance is strongly dependent on climate conditions prevailing in the spring, with strong evidence of local adaptation of sugar maple seeds to cold temperatures at the northern edge of its distribution (Solarik et al., 2016). Sugar maple flower development is also affected by the timing of climatic events in the spring (Chuine & Beaubien, 2001). Overall, these factors combine so that seedling density of sugar maple is strongly related to the average temperature and precipitation in July (Graignic et al., 2014). Similarly, fecundity of boreal trees is also influenced by climate. In their study Meunier et al. (2007) show that black spruce seeds maturation is expected to increase under climate changes. However, not all life stages are dependent on climatic conditions; some are more sensitive to competitive interactions than climate variation (Zhang et al., 2015). Future research will therefore be required to determine more precisely the processes underlying our observation that transitions among forest types are dependent on climate.

An important validation of our approach is that we successfully predicted the equilibrium distribution of these communities based on a dynamical model parameterized from observed transitions, rather than using static occurrence data such as is common in traditional species distribution models. Recently, Thuiller et al. (2014) found only weak and idiosyncratic relationships between the population demographic rates and the probability of occurrence of most temperate and boreal tree species of North America and Europe. These results suggest that local-scale population dynamics may be insufficient to explain the presence or absence of species at larger spatial scales. A range dynamics model in a metapopulation framework provides an alternative to such population-based models to explain distributions, whereby range limits are driven by a balance between colonization and extinction (Holt et al., 2005) rather than being strictly linked to local demography. In this situation, in order for a species to persist it must not only be able to establish a local population, as postulated by the traditional definition of the niche (Holt, 2009), but also maintain a colonization rate exceeding the local extinction rate. Our results demonstrate that such a regional approach to range limits of trees may be more relevant and correspond

better to the long-held non-equilibrium view of forest ecosystems, where landscapes are composed of a mosaic of patches at different successional stages. Application of our approach broadly in other forested ecosystems may shed light on the generality of our results and contribute to the further development of theory for range limits.

One of the major findings from model projections was a conversion of mixed to pure temperate forest stands. Warmer climate tends to decrease the competitive ability of currently dominant boreal species in favour of temperate species as suggested by Reich et al. (2015). If such large landscape shifts happen, the decrease in mixedwood will reduce habitat availability for many species such as understorey plants, soil macrofauna, and birds, and impact the diversity of ectomycorrhizae (Cavard et al., 2011). Browsing pressure and seed predation could mitigate this trend by reducing temperate species' recruitement inside the patch and allow boreal species to persist longer (Brown & Vellend, 2014; Fisichelli et al., 2012; Kellman, 2004). Despite these changes within the ecotone, the leading edge of the temperate forest distribution will barely move northward from its present distribution at the end of this century under the most pessimistic scenario (RCP 8.5). The inability of temperate species to migrate will thus cause a spatial mismatch between the potential and realized species distributions, which could promote rapid episodic range shifts in forest ecosystems following anthropogenic and natural disturbances (Renwick & Rocca, 2015; Vanderwel & Purves, 2014). Increase in the dominance of northern hardwoods (e.g. Poplar, Maple) have been already observed in mixed forest over the previous decades in response to climate change (Beckage et al., 2008) or forest management (Boucher et al., 2006; Dupuis et al., 2011). Forest management could help reduce this increasing disequilibrium situation. If forest management simulates natural disturbances, the analogous change under our model would be an increase in local extinction rate, which could speed one of the pathways from boreal to mixed to temperate forests. Further, because clearcutting and other methods of harvesting increase light availability, it tends to increase successional rate (Abrams & Scott, 1989). Finally, a forest management plan including assisted migration (Pedlar et al., 2012) may increase the average dispersal distance by several orders, and thereby increase the rate of response of forest ecosystems to climate change.

In contrast to our results, historical migration studies based on palaeo records suggest that time-scales of centuries are necessary to observe changes between boreal and temperate forests (Davis & Botkin, 1985) and that migration rates for temperate trees can be orders of magnitude higher than those we report here (Feurdean et al., 2013). Changes in species composition within boreal forest may also be observable on similarly short time-scales (Lafontaine-Boyer & Gajewski, 2014). Thus, it is possible that we underestimate transition rates among ecosystems given that our model is parameterized from a half-century that includes a period of climate warming and because of the absence of long distance dispersal events. However, given that our model detects disequilibrium in the present distribution of temperate forest, it is clear that change in forest composition is already occurring in our data. Further, we still found

significant lags after extending the cell size way beyond the dispersal kernel of most temperate trees (Clark et al., 1998; Ribbens et al., 1994; Solarik et al., 2019). Thus, attaining similar rates of change to those observed in palaeoecological studies would require a rapid increase in transition from temperate to mixed and mixed to boreal forest, which would be possible if climatic tipping points result in little change in the early phases of warming followed by a period of rapid changes (Schaphoff et al., 2016). More rapid migration could also be attained if high-latitude refugia increase local prevalence of temperate trees (Clark et al., 1998; Feurdean et al., 2013). Although we attempt to address this issue with the unlimited dispersal scenario, ultimately our data sources do not have the spatial resolution to reliably detect both local high-latitude refugia and their influence on transitions in nearby locations. Our starting conditions for simulations were likely missing refugia at scales smaller than our climate grid. Thus, it is possible that our model underestimates the influence of small-scale refugia on the migration rate. It is also possible that changes from mixed to temperate forest, as predicted by our model, would result in pollen signatures similar to those observed since the last glacial maximum (Davis & Botkin, 1985), but that change from pure boreal stands to mixed stands would occur much more slowly. Our results are nonetheless consistent with more recent ecophysiological models (Duveneck et al., 2017) that suggest that changes to forest composition over a ca. 100-year time scale will be minimal. Thus, it is possible that forest dynamics under the combination of present human influence and current and predicted future climate differ from those that occurred in the past (where deglaciation dominated), and that forests will not migrate as they have in the past.

A critical question remaining is what will happen with maladapted boreal forests that will stay in place for a certain time before temperate forests eventually colonize. Several experimental studies found that boreal species are expected to exhibit decreasing growth rate under a warming climate (Fisichelli et al., 2012; Pedlar & McKenney, 2017; Reich et al., 2015). Jack pine (*Pinus banksiana*) and black spruce (*Picea mariana*) are not only unable to keep pace with the growth of temperate species (Fisichelli et al., 2012) but they are also less adapted as they approach their southern range limits (Pedlar & McKenney, 2017). Denser boreal canopy could compensate this disadvantage by reinforcing regeneration through thermophilization (De Frenne et al., 2013; Lenoir et al., 2013) or changes in soil condition (Lafleur et al., 2010) allowing boreal species to persist longer. If natural disturbances get more frequent (Flannigan et al., 1998; Girardin et al., 2016), then we could face a no-analog situation where the boreal trees can hardly recolonize sites after disturbances (Girardin et al., 2016). Our model prevented us to account for major shifts in disturbance regimes. Even if the model represents transition to the regeneration state as a function of climate, we have not found any type-specific climate dependence. The disturbance probability weakly responded to climate for all three states (see Appendix S0) and the modeling approach was also unable to create spatially structured disturbances (i.e fire, insect outbreaks). This question on what will happen with maladapted boreal forests therefore remains open and the first step will be to expand the disturbance model. Because

there is no-analog situation we could use to evaluate transitions in those maladapted forests, a more mechanistic approach may be required to extrapolate dynamics under warmer conditions. It will require substantial research given the evidence that boreal trees will be able to persist despite changes in disturbance regime and warmer conditions, and thus create a colonization credit of temperate species over short to medium time-scales.

We found clear support for the hypothesis that climate drives transitions among forest types at the boreal-temperate ecotone (Figures S1 and S2). However, despite the strong link between temperature and colonization and succession, our model predicted very little replacement of boreal forest with mixed and temperate forest by 2095 (Figure 2), along with very slow northward migration of the temperate- boreal transition (304 m – 95% CI: 180–560 by 2095 with a average rate of 28.7 m/year – 95% CI: 20.0–59.7). Despite the increasing tension between the optimal and realized climates over the 21st century, our simulations demonstrated that slow demographic and dispersal rates prevent any substantial movement in temperate forests, with much faster migration rates when these constraints were removed (Figure 3). These limitations could be mitigated somewhat if local climatic conditions modify life history strategies (e.g. younger maturation age and higher fecundity; Snell et al., 2014). However, over the relatively short time horizon encompassed by this study, such effects are unlikely to completely mitigate the effects of slow demographic and limited dispersal rates. Thus, both temperate and boreal species within the transition zone are likely to experience increasing differences between optimal and realized climate in the coming century.

## DATA AVAILABILITY STATEMENT

The Forest Inventory and Analysis National Program made their data publicly available at https://apps.fs.usda.gov/fia/datamart/datamart.html and the Ministère des Forêts, de la Faune et des Parcs at https://www.donneesquebec.ca/fr/. Domtar (Paper Products company) and two provincials forest inventories (Ontario and New Brunswick) data were provided under agreement. We released the classified states data with plot locations and environmental layers needed to perform the multinomial regression

and the model calibrations. These data and the original set of parameters can be downloaded at https://github.com/QUICC-FOR/STModel-Data (data: out_files/dataSTM.zip; estimated parameters: out_files/GenSaParams_STModel.txt). The States and Transitions model (C code) are accessible through a github repository under the https://doi.org/10.5281/zenodo.28215.

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**BIOSKETCH**

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**SUPPORTING INFORMATION**

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

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