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Moderate disturbances accelerate forest transition dynamics under climate change in the temperate–boreal ecotone of eastern North America

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Abstract

Several temperate tree species are expected to migrate northward and colonize boreal forests in response to climate change. Tree migrations could lead to transitions in forest types, but these could be influenced by several non-climatic factors, such as disturbances and soil conditions. We analysed over 10,000 forest inventory plots, sampled from 1970 to 2018 in meridional Québec, Canada, to identify what environmental conditions promote or prevent regional-scale forest transitions. We used a continuous-time multi-state Markov model to quantify the probabilities of transitions between forest states (temperate, boreal, mixed, pioneer) as a function of climate (mean temperature and climate moisture index during the growing season), soil conditions (pH and drainage) and disturbances (severity levels of natural disturbances and logging). We further investigate how different disturbance types and severities impact forests' short-term transient dynamics and long-term equilibrium using properties of Markov transition matrices. The most common transitions observed during the study period were from mixed to temperate states, as well as from pioneer to boreal forests. In our study, transitions were mainly driven by natural and anthropogenic disturbances and secondarily by climate, whereas soil characteristics exerted relatively minor constraints. While major disturbances only promoted transitions to the pioneer state, moderate disturbances increased the probability of transition from mixed to temperate states. Long-term projections of our model under the current environmental conditions indicate that moderate disturbances would promote a northward shift of the temperate forest. Moreover, disturbances reduced turnover and convergence time for all transitions, thereby accelerating forest dynamics. Contrary to our expectation, mixed to temperate transitions were not driven by temperate tree recruitment but by mortality and growth. Overall, our results suggest that moderate disturbances could catalyse rapid forest transitions and accelerate broad-scale biome shifts.

KEYWORDS
climate change, continuous-time multi-state Markov model, equilibrium, natural disturbances and logging, Québec, temperate–boreal ecotone, transient dynamics, transition probabilities

1 | INTRODUCTION

Global climate warming has led to altitudinal and latitudinal migration of species across the globe (Chen, Hill, Ohlemüller, Roy, & Thomas, 2011; Parmesan & Yohe, 2003). In ecotones, where transition between vegetation biomes occurs, these shifts in species distributions entail far reaching consequences for forest ecosystems (Evans & Brown, 2017). In some cases, climate-induced shifts in tree species distributions might trigger a 'regime shift' (Scheffer, Carpenter, Foley, Folke, & Walker, 2001) and transform treeless tundra into boreal forests (Harsch, Hulme, McGlone, & Duncan, 2009), tropical forests into savanna (Hirota, Holmgren, Van Nes, & Scheffer, 2011) or coniferous forests into deciduous forests (Boulanger et al., 2019). As ecological processes may strongly differ among these biomes, the reorganization of biodiversity not only impacts local species composition (Williams & Jackson, 2007) but also alters the functional and structural characteristics of communities (Esquivel-Muelbert et al., 2018; Scheffer, Hirota, Holmgren, Van Nes, & Chapin, 2012), hence feedbacks to microclimates, ecosystem functioning and biogeochemical cycles (Anderson et al., 2011). However, these large transitions in forest types are still poorly understood notably because ecotones are not solely controlled by regional climate but also by many other landscape- and local-scale factors that could accelerate or slow down these changes.

According to metapopulation theory, range dynamics ultimately arise from local demographic processes (e.g. recruitment, growth, mortality) that determine where a tree species can establish and persist (Godsoe, Jankowski, Holt, & Gravel, 2017; Levins, 1969). Whereas range expansion depends on dispersal and establishment of new individuals, range contraction is the result of declining vitality and mortality (Jump, Mátyás, & Peñuelas, 2009). In the temperate–boreal forest ecotone, recent climate warming has been shown to improve recruitment, survival and growth of some temperate tree species at their northern limits, whereas boreal species were competitively disadvantaged by slower growth and larger increase in mortality associated with heat and drought stress (Bolte, Hilbrig, Grundmann, & Roloff, 2014; Fisichelli, Frelich, & Reich, 2014; Goldblum & Rigg, 2005; Grundmann, Bolte, Bonn, & Roloff, 2011; Peng et al., 2011; Reich et al., 2015). Hence, as climate warms and tips the balance in favour of temperate over boreal species, forests at the ecotone are expected to transition from coniferous to mixedwood and from mixedwood to temperate deciduous (Boulanger et al., 2019; Chen, 2002; Lindner et al., 2010).

The reported shifts in species distributions are, however, much slower than the rate of climate change (Sittaro, Paquette, Messier, & Nock, 2017; Talluto, Boulangeat, Vissault, Thuiller, & Gravel, 2017). Such lags in species responses are hypothesized as primarily due to demographic constraints (Renwick & Rocca, 2015; Svenning & Sandel, 2013). Because trees are long-lived species that disperse over very short distances, colonization and extinction events in response to environmental changes are often delayed, such that forests are rarely in equilibrium with their environment (Talluto et al., 2017). Hence, if forests are undisturbed, transition rates between forest types following natural succession pathways will be mainly limited by the persistence and turnover of resident species (Bouchard, Aquilué, Périé, & Lambert, 2019; Loehle, 2000) as well as the dispersal and establishment rates of migrating species (Neilson, 1993), resulting in large disequilibrium and transient dynamics that may last a very long time (Hastings et al., 2018; Talluto et al., 2017).

Disturbance events, such as fire and harvesting, directly affect demographic processes and increase turnover, and are thus likely to influence forest responses to climate change (Bolte et al., 2014; Boulanger et al., 2019; Serra-Diaz, Scheller, Syphard, & Franklin, 2015). Indeed, as global climate warming slowly modifies the competitive balance among species, pulse disturbances remove the resident community in whole or in part, thus providing establishment opportunities for migrating species and making resources available for a fast growth. Consequently, following a disturbance, forest composition may shift to species that are better suited to current conditions and fail to return to its previous state (Johnstone et al., 2016; Renwick & Rocca, 2015; Turner, 2010). For example, canopy gaps have been shown to locally facilitate establishment of temperate species in mixed forests of Ontario (Leithead, Anand, & Silva, 2010). In a nature reserve of Scandinavia, Bolte et al. (2014) showed that Norway spruce (*Picea abies*) was particularly sensitive to the combination disturbances and warming which benefited the growth of European beech (*Fagus sylvatica*). In a previous study, we showed that moderate disturbances (i.e. disturbances that removed between 25% and 75% of the tree basal area) have favoured the increase of warm-adapted species and led to a broad-scale community thermophilization of forests at the temperate–boreal ecotone in Québec (Brice, Cazelles, Legendre, & Fortin, 2019).

Cross-scale interactions between landscape disturbances and global warming could drive abrupt transitions between forest types (Allen, 2007; Peters, Bestelmeyer, & Turner, 2007). Given that forests are increasingly subject to human disturbances, such nonlinear processes could play a key role in driving the climate shift in biomes. Some simulation studies have, however, concluded that disturbances are unlikely to promote extensive biome shifts in the coming decades because they would favour mainly the rapid recovery of resident species (Liang, Duveneck, Gustafson, Serra-Diaz, & Thompson, 2018) or the invasion by early-successional species (Vanderwel & Purves, 2014). It is possible that the effect of disturbances on forest dynamics depends on their intensity and type (natural or anthropogenic). Indeed, logging strongly differs from natural disturbances in severity, frequency, selectivity and spatial extent (McRae, Duchesne, Freedman, Lynham, & Woodley, 2001), which could alter successional pathways. For instance, in mixedwood forests of North America, natural canopy gaps and partial cutting can benefit shade-tolerant deciduous species (Danneyrolles, Arseneault, & Bergeron, 2016; Kneeshaw & Prévost, 2007), whereas clearcutting favours the expansion of pioneer species, such as the trembling aspen (*Populus tremuloides*; Grondin et al., 2018; Landhäusser, Deshaies, & Lieffers, 2010). Therefore, more empirical evidence is essential to evaluate how various intensities and types of disturbances may affect forest dynamics under recent climate change and whether their effects can scale-up to trigger punctuated and episodic shifts in forest types.

The northward migration of temperate species may nevertheless be contingent on their capacity to colonize different types of soil (Brown & Vellend, 2014; Carteron et al., 2020; Lafleur, Paré, Munson, & Bergeron, 2010). Soils of cold boreal forests generally have lower pH, lower microbial activity and slower decomposition rates of organic matter than warmer southern temperate forest soils (Goldblum & Rigg, 2010). These local and regional variations in soil properties are expected to slow down or inhibit the establishment of temperate trees into the boreal forest. For instance, transplant experimental studies have shown that seedlings of sugar maple (*Acer saccharum*) in boreal soils were negatively affected by soil biotic and abiotic conditions (Brown & Vellend, 2014; Carteron et al., 2020). In contrast, Kellman (2004) found a higher survival of *A. saccharum* seedlings in boreal stands than in hardwood stands, potentially because of better light availability. Hence, it has been suggested that soil properties in boreal forests may not be a major impediment to the migration of temperate species showing broad ecological tolerance (Barras & Kellman, 1998; Kellman, 2004; Lafleur et al., 2010). Nonetheless, suboptimal soil conditions under a boreal canopy could delay forest transitions under climate change (Solarik, Cazelles, Messier, Bergeron, & Gravel, 2019). While experimental studies provide valuable knowledge on the role of soils at local scales, the importance of such constraints on long-term forest dynamics should be evaluated at regional scale and across species to better anticipate future biome transitions.

One approach to investigating biome shifts in response to climate change is to model transition probabilities between forest states using a Markov chain approach. Given the unequivocal distinction between temperate and boreal forests, the dynamics of tree communities at the temperate–boreal ecotone of North America can be adequately characterized using discrete ecological and successional states, namely boreal (stands dominated by boreal coniferous species), mixed (mixed stands of coniferous and deciduous species), temperate (stands dominated by temperate deciduous species) and pioneer (stands dominated by early successional species, which can be found any disturbed habitats across the latitudinal gradient; Vissault, 2016). Using such classification, the forest dynamics thus can be formalized as a multi-state Markov model, where transitions among states are represented by a stochastic process influenced by their current state and environmental characteristics of interest (Jackson, 2011). The Markov framework has been previously used to study forest succession (Liénard & Strigul, 2016; Runkle, 1981; Waggoner & Stephens, 1970) notably because it is based on a straightforward definition of transitions between various forest states and provides a simple mechanistic interpretation of the estimated transition probabilities. This method thereby offers the possibility of exploiting the full complexity and temporal depth of forest inventory data, while buffering the idiosyncrasies of species responses (Strigul, Florescu, Welden, & Michalczewski, 2012).

Representation of forest dynamics with Markov chains allows us to link stand-scale ecological mechanisms (Wootton, 2001), which can be influenced by soils, disturbances and climate, to the emergent broad-scale biome shifts. For example, transitions to pioneer reflect disturbance, transitions from pioneer reflect colonization, dispersal and recruitment limitation and transitions between the other states reflect competitive exclusion. In addition, multi-state models can be used to investigate biome shifts from the perspective of both transient dynamics and long-term equilibrium. Markov transition matrices can be estimated from the model output and their well-established properties can then be compared under different scenarios (Boulangeat, Svenning, Daufresne, Leblond, & Gravel, 2018; Hill, Witman, & Caswell, 2004). For instance, the equilibrium or steady-state distribution can be derived from a transition matrix and used to infer the potential long-term forest composition under given environmental conditions (Scheffer et al., 2001), providing insights about the direction of current forest dynamics (Hill et al., 2004; Waggoner & Stephens, 1970). Moreover, transient periods can also be described: the time of convergence to equilibrium measures the length of the transient period; the turnover time indicates how fast the transitions occur and informs about the persistence of forest states; and the entropy reveals the uncertainty about the next transition. Contrasting empirically derived transition matrices and their properties among disturbance scenarios can shed new light on forest dynamics under climate change and may even provide hints about management measures.

Here, we investigate how regional-scale forest dynamics is influenced by disturbances and soil conditions under recent climate warming. In particular, we ask the following questions: (a) How recent forest transitions dynamics vary with climate, soil and disturbances? (b) Do different disturbance types and intensities impact the potential long-term equilibrium distribution of forest states? (c) How do different disturbance types and intensities influence the short-term transient dynamics under climate change? And (d) what is the relative importance of tree demographic processes underlying the transition dynamics? We answer those questions by estimating the influence of environmental covariates on transition probabilities among four forest states (boreal, mixed, temperate and pioneer) using a continuous-time Markov multi-state model. Using results from our model, we then examine the impact of disturbances on forest equilibrium and transient dynamics by comparing different complementary matrix properties.

We expect that climate warming should promote colonization by temperate species into mixed and boreal forests and competitive exclusion of boreal species, resulting in higher transition probabilities from boreal to mixed and from mixed to temperate, rather than the reverse. The most conspicuous effect of disturbances is expected to be the destruction of trees in place, which should provoke transitions from other states to pioneer. Nevertheless, we also anticipate that disturbances will favour climate-related transitions (boreal-mixed and mixed-temperate), whereas soil characteristics of coniferous forests (low pH and poor drainage) should slow down colonization by temperate trees. Disturbances should also accelerate the transient dynamics by shortening turnover and convergence times. Together, these effects on transitions should influence the steady-state distribution by promoting an increase in the proportion of temperate forests in the long run.

2 | METHODS

2.1 | Study area and forest inventory data

We used forest inventory plots in Québec, Canada, to investigate broad-scale transition dynamics in forest communities. Permanent plots have been sampled approximately every 10 years from 1970 to 2018 (and ongoing) by the *Ministère des forêts, de la Faune et des Parcs* (MFFP, 2016). The study area extends from approximately 45° to 52° North latitude (ca. 795,000 km^2). It covers six bioclimatic domains (Figure 1) and three different vegetation zones; the mixed forest, which corresponds to the balsam fir-yellow birch domain (from 47°N to 48°N; hereafter, the ecotone), marks the transition between the hardwood forest to the south, dominated by *A. saccharum*, and the boreal forest to the north, dominated by *Abies balsamea* and *Picea mariana*.

The natural disturbance regimes vary considerably along the latitudinal gradient of the study area, with fires in the northern boreal forests, spruce budworm outbreaks in the mixedwood forests and small windthrows and treefall gaps in the southernmost deciduous forests (Figure S1; Goldblum & Rigg, 2010). Anthropogenic disturbances are not homogeneously distributed either; clearcuts are more frequent in northern regions, while in southern regions, partial cuts are more common (Figure S1; Boucher, Arseneault, Sirois, & Blais, 2009).

We first selected all inventory plots that had been sampled at least twice. We then disregarded plots that were subjected to active reforestation (i.e. plantation) during the study period because we were interested in transition dynamics resulting from natural recolonization processes. Finally, we kept plots for which soil covariates were available. This yielded a total of 11,058 plots analysed (Figure 1). The time intervals between plot surveys varied from 3 to 39 years, with a mean interval of 11 years (*SD* = 3.45; Figure S2).

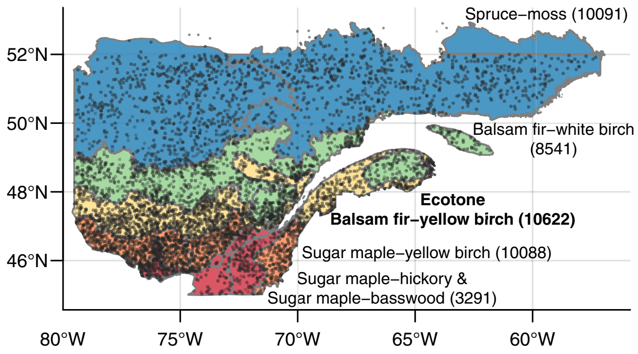


FIGURE 1 Locations of the 11,058 forest inventory plots in meridional Québec, Canada. Colours delimit the six bioclimatic domains. The two southernmost domains (red) are here combined. The number of plots in each domain is shown in parentheses. The balsam fir-yellow birch domain (in bold) is the ecotone between the hardwood and boreal forests [Colour figure can be viewed at wileyonlinelibrary.com]

2.2 | Forest states

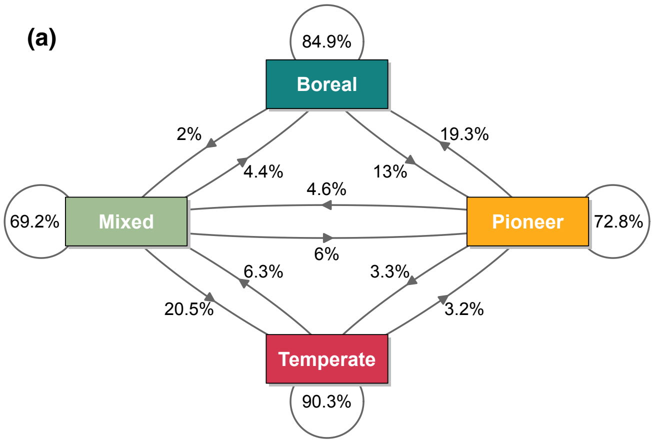
We classified the forest inventory plots into four forest states using species basal area and composition at each sampling date. We first assigned each studied species to a group based on their traits and their distribution (Table S1; see Brice et al., 2019 for details): boreal species are mostly coniferous trees with a northern distribution; temperate species are mostly deciduous trees with a southern distribution; and pioneer species have low shade tolerance and are generally found in any disturbed habitats. For each plot, we computed the total basal area of each species group and then classified the plot to one of the four states similar to the MFFP (2016) definitions; Boreal (boreal species representing >75% of the plot basal area), Temperate (temperate species representing >75% of the plot basal area), Mixed (when temperate and boreal species both occupy between >25% and <75% of the plot basal area) and Pioneer (when the basal area of pioneer species is superior to that of boreal and temperate species or when plot total basal area <5 m^2/ha). We analysed state transitions between consecutive plot surveys. Based on this classification, for the 42,633 observations (plots × number of years measured), we recorded 31,690 state transitions, including self-transitions (Figure 2; Table S2).

The definitions of forest states can affect the results to some extent. A higher threshold to define the boreal and temperate states (e.g. >85% instead of >75% of dominance of boreal and temperate, respectively) influences the transition probabilities, but the direction of the dynamics remains the same (see comparison between Tables S3 and S4).

2.3 | Environmental variables

Annual climatic conditions, covering a period from 1960 to 2018, were extracted from a 2 km^2 (60 arc sec) resolution grid for the entire study area using the ANUSPLIN climate modelling software (http://cfs.nrcan.gc.ca/projects/3/8; McKenney et al., 2011). Plot locations were intercepted with two bioclimatic variables hypothesized to influence tree establishment, survival and growth: the mean temperature during the growing season and the climate moisture index (CMI; difference between precipitation and potential evapotranspiration) from May to September (Table 1). To reduce the effect of inter-annual climate variability, each climate variable was averaged over a 10 year period prior to the plot measurement. From 1950 until the present day, growing season temperatures have increased by 0.17°C/decade in the plots, while CMI have shown no trends (Figure S3).

We also collected information pertaining to natural and anthropogenic disturbances that have affected the forest plots during the study period (Table 1; Figure S1). At each plot, the type of



(b)

$$Q=\begin{bmatrix} -\sum_{s\neq B} q_{Bs} & q_{BM} & q_{BP} & 0 \\ q_{MB} & -\sum_{s\neq M} q_{Ms} & q_{MP} & q_{MT} \\ q_{PB} & q_{PM} & -\sum_{s\neq P} q_{Ps} & q_{PT} \\ 0 & q_{TM} & q_{TP} & -\sum_{s\neq T} q_{Ts} \end{bmatrix}$$

(c)

$$q_{rs} = q_{rs.0} \times \exp(\beta_{rs.1} \times \text{climate} + \beta_{rs.2} \times \text{soil} + \beta_{rs.3} \times \text{disturbances})$$

for $r \neq s$ and $s \neq$ Pioneer

$$q_{rs} = q_{rs.0} \times \exp(\beta_{rs.3} \times \text{disturbances})$$

for $s =$ Pioneer

FIGURE 2 Multi-state transition diagram (a), intensity matrix *Q* (b) and equations of our full model (c). Directional arrows in the diagram (a) depict the allowed transitions between states. The numbers represent the percentage of observed transitions between states (nb_{rs}/nb_r × 100). Instantaneous transition from Boreal to Temperate and vice versa are considered impossible in the model (hence the absence of arrows in the diagram and the zeros in the *Q* matrix); however, rare transitions from Boreal to Temperate and from Temperate to Boreal were observed in the data (<0.2%). The *Q* matrix (b) contains the instantaneous risk to move from one state (row) to another (column), here: (B)oreal, (M)ixed, (P)ioneer and (T)emperate, in that order. Transitions from any other state to Pioneer were modelled as only dependent on disturbances (c) [Colour figure can be viewed at wileyonlinelibrary.com]

TABLE 1 Description of the explanatory variables used in the multi-state models

Variable name	Variable description
Climate	
Temperature	Mean temperature during growing season, 10 year average prior to plot measurement (°C)
CMI	Mean Climate Moisture Index from May to September, 10 year average prior to plot measurement (cm)
Soil	
pH	pH of the surface horizon
Drainage	Six classes of soil drainage, which range from excessive to very poor, that were treated as numeric
Disturbances	
Logging	Tree harvesting, including clearcutting, selection cutting, shelterwood cutting, seed-tree cutting etc. None or minor (0), moderate (1) or major (2)
Natural	Natural disturbances, including forest fires, insect outbreaks, windfall etc. No or minor (0), moderate (1) or major (2)

disturbances (21 types) and their level of severity were recorded during field surveys (see Figure S1 for details; MFFP, 2016). For our multi-state model, we differentiated two main types of disturbances: natural disturbances and logging, with three levels of severity each (0, no or minor; 1, moderate; 2, major). The MFFP defined major disturbances as events that have resulted in a loss of more than 75% of the total tree basal area, whereas moderate disturbances have caused between 25% and 75% of loss. When the loss in basal area is <25%, it is considered to be minor.

Finally, at each plot, several edaphic characteristics were recorded (MFFP, 2016). We selected drainage and pH because they largely affect nutrient availability, soil structural properties and vegetation development (Tan, 2009), and also because they captured most of the variance in soil characteristics in our plots.

Climate and disturbances were included as time-varying explanatory variables (often called covariates in survival models), while soil variables were considered as static. Climate variables at time t were used to model transitions during the interval t and $t+\Delta t$. Disturbances that occurred during the interval t and $t+\Delta t$ were used to model transitions during the same time period.

Note that we solely focused on a parsimonious set of variables that allowed us to determine how climate, disturbances and soils influence transition dynamics. We decided not to include an index of propagule availability, even though it is known to affect tree range shifts (Pearson, 2006), as forest composition is already very strongly correlated with our climate covariates (Figure S4; Goldblum & Rigg, 2010; Vissault, 2016). Our model is therefore well suited for our research goals; however, it is not designed to make future range shift projections.

2.4 | Analysis

2.4.1 | Continuous-time multi-state Markov model

We formalized forest dynamics with a continuous-time multi-state model (Jackson, 2011; Van Den Hout, 2016) in which transitions among states depend on the current state, time interval, climate, disturbances and soil characteristics (Figure 2). This type of model takes into account the fact that (a) time intervals between surveys were irregular, (b) multiple transitions were possible during an interval and (c) the exact moments of transitions were not observed (i.e. observations are interval censored; Logofet & Lesnaya, 2000; Van Den Hout, 2016).

In a four-state transition model in continuous time, the Markov process is governed by a 4 × 4 transition intensity matrix, Q, where rows are the current states and columns are the future states (Figure 2b). For each state r, $s \in B$, M, P, T, the transition intensity (q_{rs}) represents the instantaneous risk that a plot transitions from state r to state s. Because the states were defined based on stand basal area, instantaneous transitions from Boreal to Temperate (q_{BT}) or from Temperate to Boreal (q_{TB}) were impossible without disturbance; there is a necessary transition through Mixed or Pioneer. For this reason and the fact that these transitions were very rare in the data, we fixed q_{BT} and q_{TB} at 0 (Figure 2b). However, all states can transition directly to Pioneer when disturbed (Figure 2).

The intensities $q_{r,s}$ can be modelled as follows:

$$q_{rs}(t|x(t)) = q_{rs.0}(t)\exp(\beta'_{rs}x(t)),$$

where $x(t)$ is the matrix of explanatory variables (surveys as rows, covariates as columns), β_{rs} are coefficients to be estimated and $q_{rs.0}$ (t) is a baseline hazard that describes the risk when environment $x(t)$ = 0. Hence, $\exp(\beta'_{rs}x(t))$ is the relative increase or decrease in risk associated with a set of characteristics $x(t)$. In this model, time-dependent variables, such as climate and disturbances, are assumed to be piecewise constant, that is, the hazard is constant within a time interval $[t, t+\Delta t]$ and depends on the variable value at t, but can change between the intervals. The inclusion of time-dependent variables in the model allows one to fit a non-homogeneous Markov process. Estimation of model parameters was obtained by maximizing the log-likelihood (see Supplementary Methods for details).

We built five models: one baseline model that solely includes the $q_{rs.0}$, one model for each category of covariates independently (climate, soil and disturbances) and one full model, which combines all covariates (Table 1). Because multiple state transitions are estimated in a single model (all q_{rs} in Figure 2b), the number of parameters increases rapidly with the number of covariates (number of modelled transitions (here 10) × (number of covariates + 1)). Thus, to reduce the number of parameters, we assumed that transitions from any state to Pioneer were only determined by disturbances, while climate and soil variables should not directly influence these transitions. All quantitative variables were standardized ($\mu = 0$, $\sigma = 1$) prior to running the models.

2.4.2 | Model evaluation

We first evaluated the goodness of fit of each model containing covariates (climate, soil, disturbances and full) against the baseline model using likelihood ratio tests (Jackson, 2011), which evaluate if the addition of one or more new parameters significantly increases the likelihood of the model. We also compared and ranked the models using the Akaike information criterion (AIC; Burnham, Anderson, & Burnham, 2002). The model with the lowest AIC was considered to be the best model and thus used in further analyses.

2.4.3 | Model baseline and hazard ratios

We first evaluated the trends in recent forest transition dynamics. We used the baseline hazards ($q_{rs.0}$) estimated by our best model as indicators of the underlying forest response. For each pair of states, the baseline hazard describes the risk to make a transition for a mean forest plot (when all covariates are set to 0). We then investigated how environmental covariates influenced the transition dynamics (question 1) by comparing the estimated hazard ratios (HRs) derived from our best model ($\exp(\beta_{rs})$).

2.4.4 | Transient dynamics and equilibrium

We further investigated how disturbances modify the long-term equilibrium (question 2) and the forest transient dynamics (question 3). We computed different properties on the Markov transition matrix along the latitudinal temperature gradient and compared them among five disturbance scenarios defined by disturbance type and severity: (a) no or minor disturbances, when the covariates logging and natural were both fixed at 0; (b) moderate natural, with the covariate natural fixed at 1 and logging fixed at 0; and (c) vice versa for moderate logging; (d) major natural, with the covariate natural fixed at 2 and logging fixed at 0; and (e) vice versa for major logging. The temperature covariate was also allowed to vary from its lower 10th to its upper 90th percentile, whereas all other covariates were fixed at the average conditions found in the ecotone, the balsam fir-yellow birch domain (Figure 1), to focus solely on the effect of disturbances along the temperature gradient.

An extensive literature describes the multiple properties of discrete-time Markov transition matrices (Caswell, 2001; Hill et al., 2004) which can be adapted to continuous-time models. We chose four informative and complementary properties that fully characterize both the short- and long-time scale dynamics of our modelled system: (a) the steady-state distribution, which corresponds to the potential long-term proportion of forest states at equilibrium; (b) the half-life to equilibrium, which evaluates the time of convergence to the steady-state and the length of the transient period; (c) the turnover time, which measures the rate of transient successional changes; and (d) the entropy, which captures the uncertainty regarding the next transitions. While their absolute values should be interpreted with caution, their comparison under various disturbance scenarios can highlight essential features of the dynamics.

First, to measure the potential direction of forest dynamics under a given scenario, we estimated the steady-state distribution, π. For a regular Markov process, any initial state distribution converges to the same equilibrium as time approaches infinity. The vector of equilibrium π can be obtained by taking the left eigenvector of the intensity matrix Q, which has an eigenvalue of 0, normalized to sum to 1, or the left eigenvector of the transition probability matrix A, which has an eigenvalue of 1, normalized to sum to 1 (Norris, 1997).

Then, the convergence rate to the equilibrium distribution can be measured using the damping ratio (Hill et al., 2004):

$$\rho = \lambda_{A1} / \lambda_{A2} = \exp(\lambda_{Q1} - \lambda_{Q2}),$$

where λ_{A1} and λ_{A2} are the largest and second largest eigenvalues of A ($\lambda_{A1} = 1$ for stochastic A), whereas λ_{Q1} and λ_{Q2} are the largest and second largest eigenvalues of Q ($\lambda_{Q1} = 0$ for stochastic Q). The convergence time was approximated using the half-life to equilibrium:

$$t_{1/2} = \log(2) / \log(\rho).$$

We also measured the turnover time in each forest state, also called the sojourn time in multi-state models, which corresponds to the time spent in one state before transitioning to a different state. The turnover time can be estimated by $\text{Turnover}_r = -1/q_{rr}$, where q_{rr} is the rth entry on the diagonal of the estimated Q matrix. The turnover of the whole system is given by the average of each state turnover time over the steady-state distribution:

$$\text{Turnover} = -\sum_r \pi_r \times \text{Turnover}_r.$$

Finally, Hill et al. (2004) proposed to use the entropy of a discrete-time transition matrix as an index of the incertitude of successional changes. It measures how uncertain we are about the next new state of a site knowing its current state. For a continuous-time process, the entropy can be measured using the jump matrix (Spencer & Susko, 2005), which contains the probabilities that the next state after state r is state s:

$$j_{rs} = -q_{rs} / q_{rr}.$$

The entropy of state s is then:

$$H(j_{.s}) = -\sum_r j_{rs} \times \log(j_{rs}).$$

The normalized entropy of the whole system is the average of the entropies over the steady state, divided by $H_{\max} = \log(n_{\text{state}} = 4)$:

$$\text{Entropy} = \frac{-\sum_r \pi_r \times H(j_{.s})}{H_{\max}}.$$

Values of entropy closer to zero indicate more deterministic transition dynamics whereas values closer to one indicate more random dynamics.

2.4.5 | Demographic processes

We finally decomposed the transition dynamics into its underlying demographic components (question 4) for the most abundant species (i.e. three temperate, *Acer rubrum*, *A. saccharum* and *Betula alleghaniensis*; two boreal, *A. balsamea* and *P. mariana*; two pioneer, *Betula papyrifera* and *P. tremuloides*). The transitions between states can result from various combinations of increases in basal area through tree recruitment and growth and decreases in basal area through mortality and logging. We measured recruitment as the increase in basal area from new trees that had reached or exceeded the threshold diameter of 9.1 cm. Growth was measured as the increase in tree basal area between consecutive surveys. During the surveys, tree vitality was characterized. We used this information to separate mortality as either due to harvesting or to any other causes and measured the loss in basal area that resulted from each of these two mortality processes.

Next, we used an indicator value analysis to quantify the contribution of each demographic process and species to each of the 16 forest transitions (Dufrêne & Legendre, 1997). The indicator value (IV_{jk}), which measures the exclusiveness of a process j to a transition k, is given by the product of the relative abundance (specificity; RA_{jk}) and the relative frequency (fidelity; RF_{jk}):

$$\text{IV}_{jk} = 100 \times \text{RA}_{jk} \times \text{RF}_{jk}.$$

All analyses were performed using the R programming language version 3.6.1 (R Core Team, 2019). The list of R packages that were used to carry out the analyses is provided in the Supporting

Information (Table S5). All the data used in the study, in addition to R scripts to reproduce the analyses and the figures, can be found online at https://github.com/mhBrice/transition (https ://doi.org/10.5281/zenodo.3823355).

3 | RESULTS

During the study period, a large fraction of Mixed forests transitioned to Temperate forests (20.5%) but few did the opposite (6.3%). There were many transitions from Boreal to Pioneer (13.0%), and more from Pioneer to Boreal (19.3%). Temperate and Boreal forests were generally more persistent (90.3% and 84.9%, respectively, did not transition during the study period) than Mixed and Pioneer forests (69.2% and 72.8%, respectively; Figure 2a).

Overall, the full model, which includes climate, soil and disturbance variables, had the best fit and predictive performances for the observed data (Table 2; Figure S5). The second best model was the disturbance model, but it was far behind with a difference in AIC of almost 1,500 units from the full model (Table 2). All variable subsets improved significantly the likelihood of the model (all likelihood ratio tests were highly significant, $p \ll .001$; Table 2). Model performance was also evaluated using a 10-fold cross-validation (see Supplementary Methods); it revealed that including climate and disturbances improved overall model predictive performance, while soil variables had a negligible effect (Figure S5). Thereafter, all inferences about transition probabilities were derived from the full model.

3.1 | Baseline transition intensities

The baseline transition intensities of the full model provide insights about the background rate of forest changes (Figure 3). Forest dynamics over the whole study area was largely dominated by transitions from Pioneer to Boreal (q_{PB} = 0.0270) and from Mixed to Temperate (q_{MT} = 0.0229; Figure 3). Mixed forests were 1.6 times (q_{MT}/q_{TM}) more likely to transition to Temperate than the reverse, indicating an increase in proportion of temperate species relative to boreal species in mixedwoods during the study period. For Boreal forests, regeneration from Pioneer to Boreal was 3.9 times (q_{PB}/q_{BP}) more likely than transition from Boreal to Pioneer.

3.2 | Effect of covariates on transition probabilities

All transitions to Pioneer were highly influenced by disturbances (Figure 4; Table S3). As could be expected, major disturbances exert stronger effects than moderate disturbances (for both natural and logging), but, for each level of severity, logging had stronger effects than natural disturbances. For example, the risk of transition from Boreal to Pioneer has surged up to 213 times higher for plots that suffered major logging (logging 2) and 37 times higher for plots that suffered major natural disturbances (natural 2) compared to undisturbed plots (minor). Disturbances of all types and severities favoured transitions from Mixed to Temperate forests. Moderate disturbances (natural and logging) doubled the risk of this type of transition, whereas major disturbances increased it by ca. 5 times (HR = 5.76 and 5.32, for natural and logging, respectively). Although the effect of major disturbances on the instantaneous risk

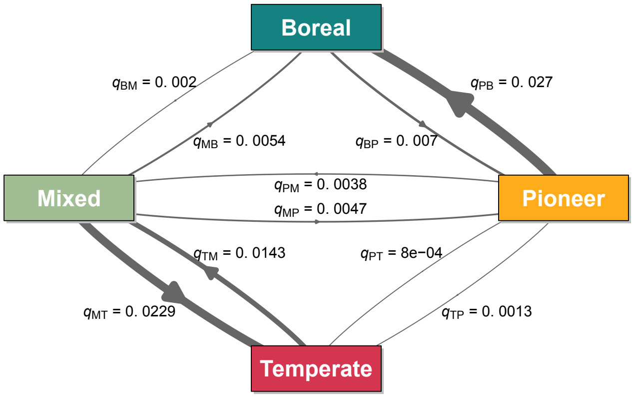


FIGURE 3 Baseline transition intensities as estimated from the best multi-state transition model. Arrows depict the direction of transitions between states. The numbers represent the estimated baseline hazards ($q_{rs.0}$), that is, the instantaneous risk of moving from one state to another when all covariates are set to 0 (i.e. the means of standardized covariates and disturbance level 0) [Colour figure can be viewed at wileyonlinelibrary.com]

TABLE 2 Comparisons of the five candidate multi-state models. The number of parameters used in each model corresponds to the number of modelled transitions (10) × the number of covariates − 1. The ΔAIC is the difference between the Akaike information criterion of each model (AIC_m) and the minimum of AIC among all models (AIC_{min}): $\Delta AIC = AIC_m - AIC_{min}$. Models are presented in decreasing order of their ΔAIC. Each model containing covariates was compared to the baseline model using a likelihood ratio (LR) test. The best model is the one in bold with ΔAIC = 0

	Covariates	Number of parameters	−2 Log-likelihood	Delta AIC	LR test
Baseline	Intercept	10	37,874.4	8,298.4	–
Soil	Drainage, pH	24	37,713.7	8,165.7	<0.001
Climate	Temperature, CMI	24	36,288.8	6,740.8	<0.001
Disturbances	Natural, logging	50	30,993.5	1,497.5	<0.001
Full	**All**	**78**	**29,440.0**	**0.0**	**<0.001**

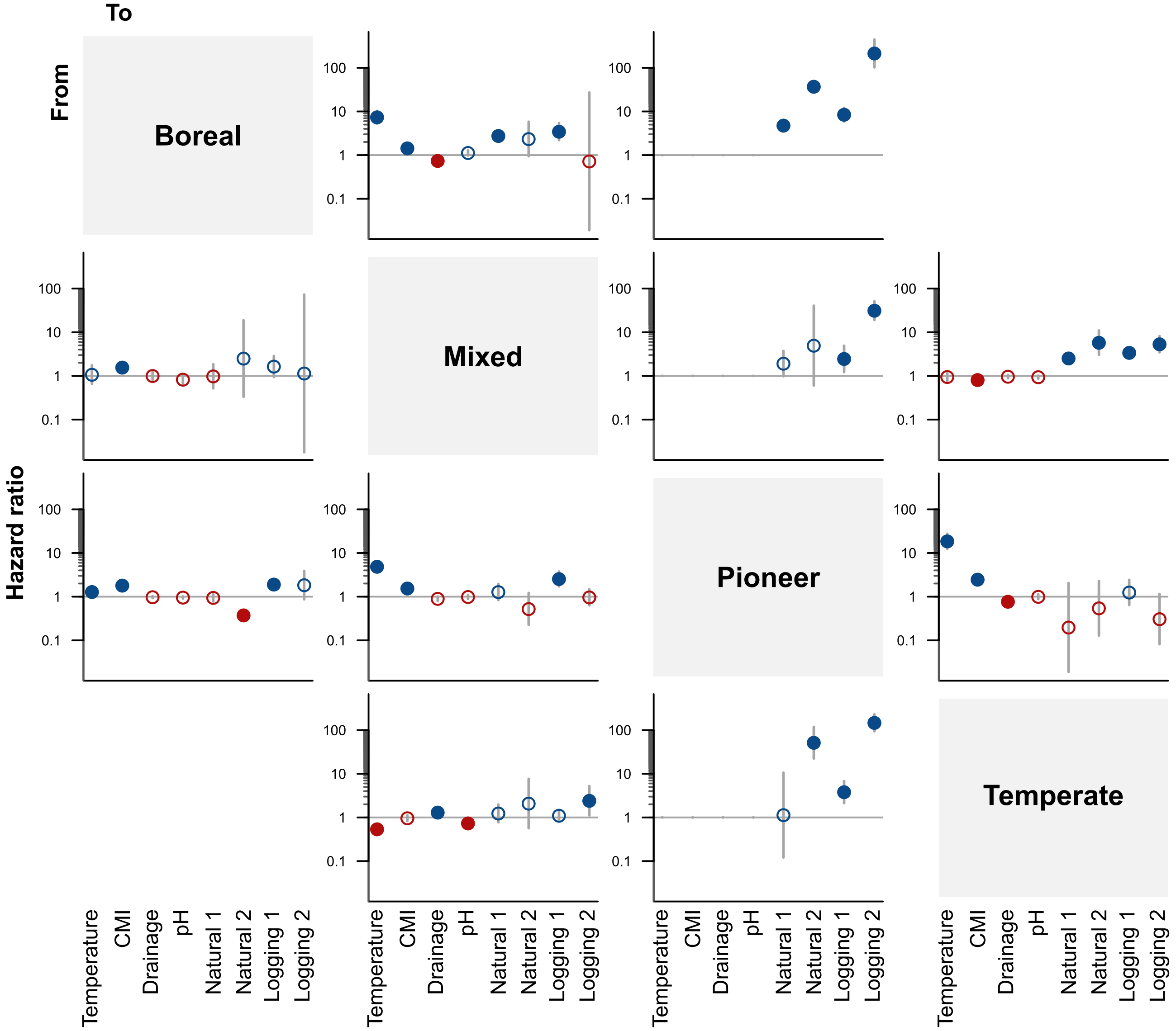


FIGURE 4 Hazard ratios (HR) and 95% confidence intervals as estimated from the best multi-state transition model. Each plot represents the estimated HR for transitions from row to column state, for example, the plot on the first row, second column shows the HR for the Boreal to Mixed transition. The ordinate is in log scale. The HR of predictors are interpretable as multiplicative effects on the hazard, where values above 1 (in blue) indicate that the predictor is associated with a greater risk of state transition, whereas values below 1 (in red) indicate a lower risk of transition. Predictors statistically different from 1 are represented by solid points. Numbers following disturbance predictors indicate their levels of intensity: 1 = moderate and 2 = major [Colour figure can be viewed at wileyonlinelibrary.com]

of transition from Mixed to Temperate was stronger than for moderate disturbances, the probability of this event decreased with time (Figure S6). Moderate disturbances also favoured transitions from Boreal to Mixed (HR = 2.76 and 3.45, respectively), while major disturbances had no significant effect on this type of transition. Overall, the effects of disturbances are well reflected by the radical change of structure of the 10-year transition probability matrix (Figure S7).

Climate variables also had a significant influence on most transitions (Figure 4). Warmer summer temperature (higher temperature) and higher humidity (higher CMI) favoured transitions from Boreal to Mixed as well as from Pioneer to Mixed and Pioneer to Temperate. Interestingly, warmer temperature did not significantly influence the risk of transition from Mixed to Temperate and higher CMI had a negative effect.

State transitions were also influenced by soil variables (Figure 4; Table S3). Holding the other covariates constant, the instantaneous risk of transition from Boreal to Mixed and from Pioneer to Temperate decreased by 27% and 23%, respectively, on poorer drainage (more humid), but the risk of transition from Temperate to Mixed increased by 30% (HR = 0.73, 0.77 and 1.30, respectively). Higher pH (acidic soil) had a negative effect on the transitions from Temperate to Mixed (HR = 0.73). These changes in risk ratios associated with soil variables appear almost irrelevant compared to the effect of disturbances, but a slight increase in drainage can dampen the positive effect of disturbances. For instance, under moderate natural disturbances, the instantaneous risk of transition from Boreal to Mixed is 0.007 at moderate drainage but decreases to 0.003 when increasing drainage by 1 point.

3.3 | Effect of disturbances on long-term equilibrium

The potential state proportion at equilibrium was strongly influenced by disturbances (Figure 5a). For the undisturbed scenario (minor), the predicted equilibrium at the ecotone was relatively close to the initial observed proportions, with signs of regeneration from Pioneer to Boreal states and slight increases in Mixed and Temperate states. The steady-state proportion of Temperate almost doubled with moderate disturbances (minor: 33%; moderate natural: 56%; moderate logging: 60%), while the boreal state was more than halved. At major disturbances, Pioneer forests dominated the equilibrium landscape, while the other states collapsed.

The steady-state proportion also changed as expected along the temperature gradient (Figure 5b,c). The Boreal state dominates at low temperature (high latitude) and the Temperate state dominates at high temperature (low latitude), highlighting the position of the boundary between these two biomes at a growing season temperature of about 12.9°C, which is found in the actual ecotone. Moderate disturbances (both natural and logging) displaced the temperate–boreal boundary at lower temperatures (ca. 12.2°C), hence further north of the current ecotone (Figure 5b,c). Because of the dominance of the Pioneer state, the boundary modestly moved north with major natural disturbances (12.7°C), while it retreated to the south with major logging (13.4°C).

3.4 | Effect of disturbances on transient dynamics

Disturbances affected forest transient dynamics with greater impact for higher disturbance severity (Figure 6). In the minor disturbance scenario, turnover time was generally longer at low temperature, indicating slower transition dynamics in northern forests (Figure 6a,b). The turnover time then rapidly declined to reach a minimum at ca. 13.25°C, at the southern limit of the ecotone, and went back up after this point. This trough, where transition dynamics is the fastest, is located just a little south of the boundary between Boreal and Temperate dominances found in Figure 5. Major disturbances accelerated transition dynamics all along the temperature gradient, while moderate disturbances also decreased turnover time but more strongly in the northern boreal region (Figure 6a,b). The effect on turnover time was similar for both disturbance types, except that the effect of major logging was much stronger in northern boreal forests than natural disturbances (Figure 6a,b). These spatial patterns reflect the turnover time of the dominant state at each point along the temperature gradient (Figure S8).

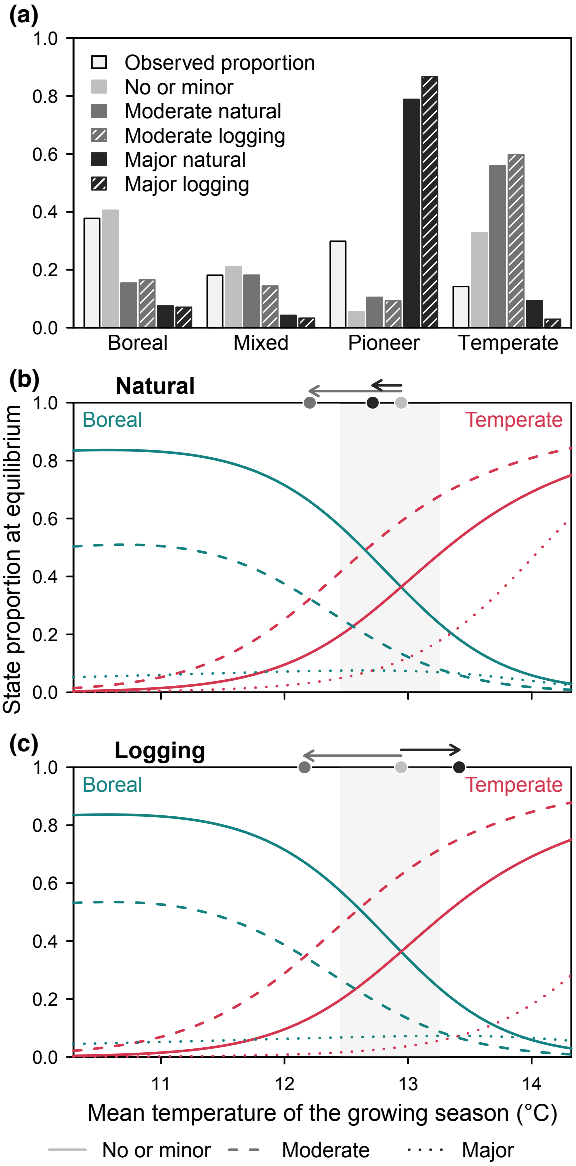


FIGURE 5 Changes in forest state proportions at equilibrium for different disturbance types (natural or logging) and intensity (no or minor, moderate, major). The barplot (a) compares the observed state proportion in the ecotone to the potential state proportion at equilibrium for different disturbance scenarios with all other covariates fixed at the average conditions found in the ecotone. The curved lines (b, c) show the proportions of Boreal (blue) and Temperate forests (red) at equilibrium along the temperature (latitudinal) gradient for no or minor (solid), moderate (dashed) and major (dotted) disturbances, with all other covariates fixed at the average conditions found in the ecotone. The light (no or minor), medium (moderate) and dark (major) grey circles indicate the positions of the boundary between dominance of Boreal and Temperate forests (i.e. the advancing front) while the corresponding arrows show how moderate and major disturbances move the boundary. The polygon approximates the position of the ecotone along the temperature gradient [Colour figure can be viewed at wileyonlinelibrary.com]

At minor disturbances, the entropy of the system generally increased from north to south and peaked at ca. 12.6°C, at the northern end of the ecotone (Figure 6c,d). This peak illustrates where the transition dynamics is most uncertain (transition to all states are possible at this point), while it is very predictable in northern boreal forests (Boreal stays Boreal until it transitions to Pioneer later on). The peak can be mainly attributed to the entropy

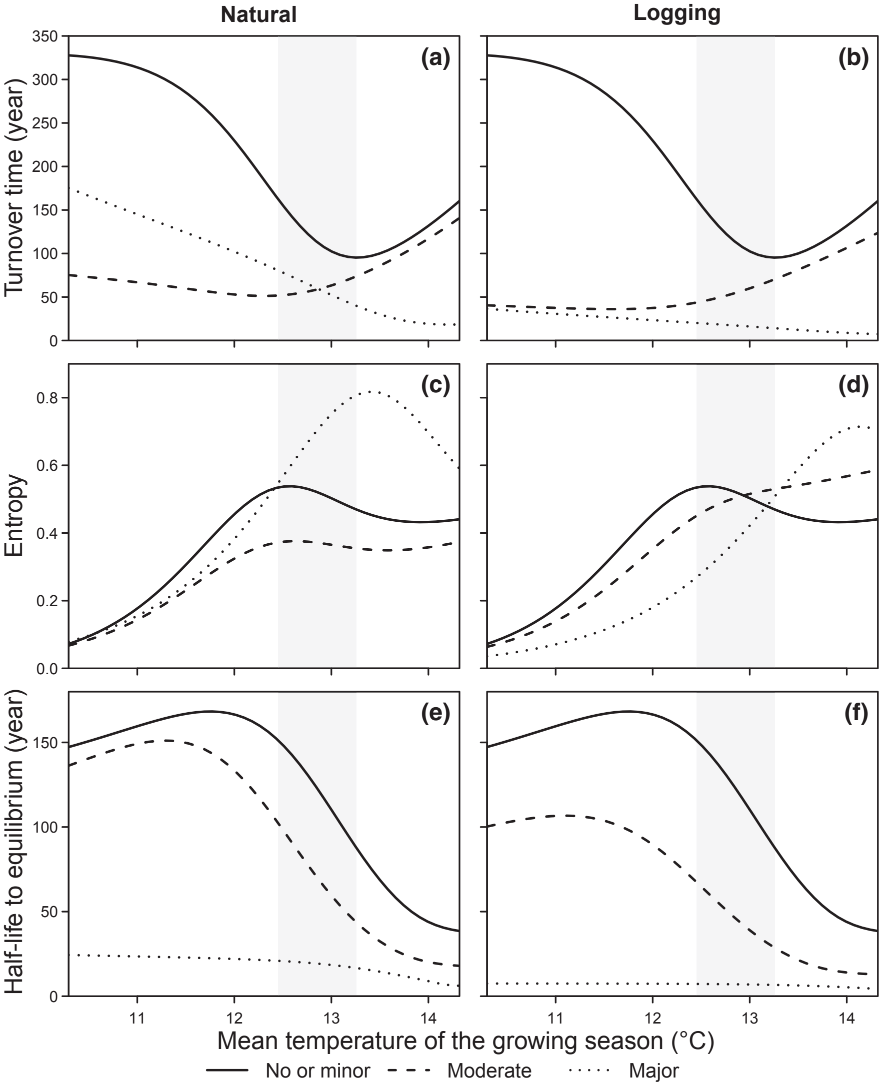


FIGURE 6 Changes in the characteristics of the forest transient dynamics along the temperature (latitudinal) gradient for different disturbance scenarios: no or minor (solid), moderate (dashed) and major (dotted) disturbances for both natural (a, c, e) and logging (b, d, f). All other covariates are fixed at the average conditions found in the ecotone to focus solely on the effect of disturbances along the temperature gradient. The turnover of the whole system (i.e. whole transition matrix; a, b) corresponds to the time spent in a state before transitioning to the next and is given by the average of each state turnover time over the steady-state distribution. The entropy of the whole system (c, d) corresponds to the uncertainty of the next transition and is given by the average of each state entropy over the steady-state distribution. The half-life to equilibrium (e, f) is the time taken to reach 50% of the steady-state distribution, that is, when the first eigenvalue becomes twice as large as the contribution of the second eigenvalue. The polygon approximates the positions of the ecotone along the temperature gradient

of the Boreal state at the ecotone, and the generally high values at low latitudes can be principally attributed to the Temperate state (Figure S9). This latitudinal pattern of entropy is modified by disturbances. Moderate natural disturbances decreased the entropy throughout the gradient, but especially where the peak is found (Figure 6c). With moderate logging, the peak disappeared, and entropy increased monotonically from north to south (Figure 6d). The peak of entropy was displaced to the south when major disturbances were included, whether natural or logging (Figure 6c,d), where it was dominated by the entropy of the Pioneer state (Figure S9).

Half-life to equilibrium was the longest at ca. 11.8°C, north of the ecotone, in the balsam fir-white birch domain, while it was the shortest in the southernmost latitudes (Figure 6e,f). Moderate disturbances flattened and shifted this peak to the north and the effect of moderate logging (Figure 6f) was stronger than natural disturbances (Figure 6e). In the balsam fir-white birch, the half-life to reach equilibrium distribution was reduced almost by half by moderate logging. With major disturbances, forests all along the temperature gradient can reach very quickly their steady-state distribution (maximum of about 8 years for major logging and 25 years for major natural disturbances).

3.5 | Contribution of demographic processes

Only the demographic processes of a few species contributed substantially to the observed transition dynamics (Figure 7). The importance of some processes was expected. For example, transitions from Boreal to Pioneer were dominated by mortality and logging of *P. mariana*, while the transitions from Pioneer to Boreal were characterized by recruitment and growth of *P. mariana* and *A. balsamea*. Most interestingly, the transitions from Mixed to Temperate were determined by the mortality of *A. balsamea* and the growth of temperate species, mainly *A. rubrum* and *B. alleghaniensis*, and to a lesser extent *A. saccharum*. The recruitment of temperate species was not indicator of the Mixed to Temperate transitions, but rather of the transitions from Pioneer to Temperate.

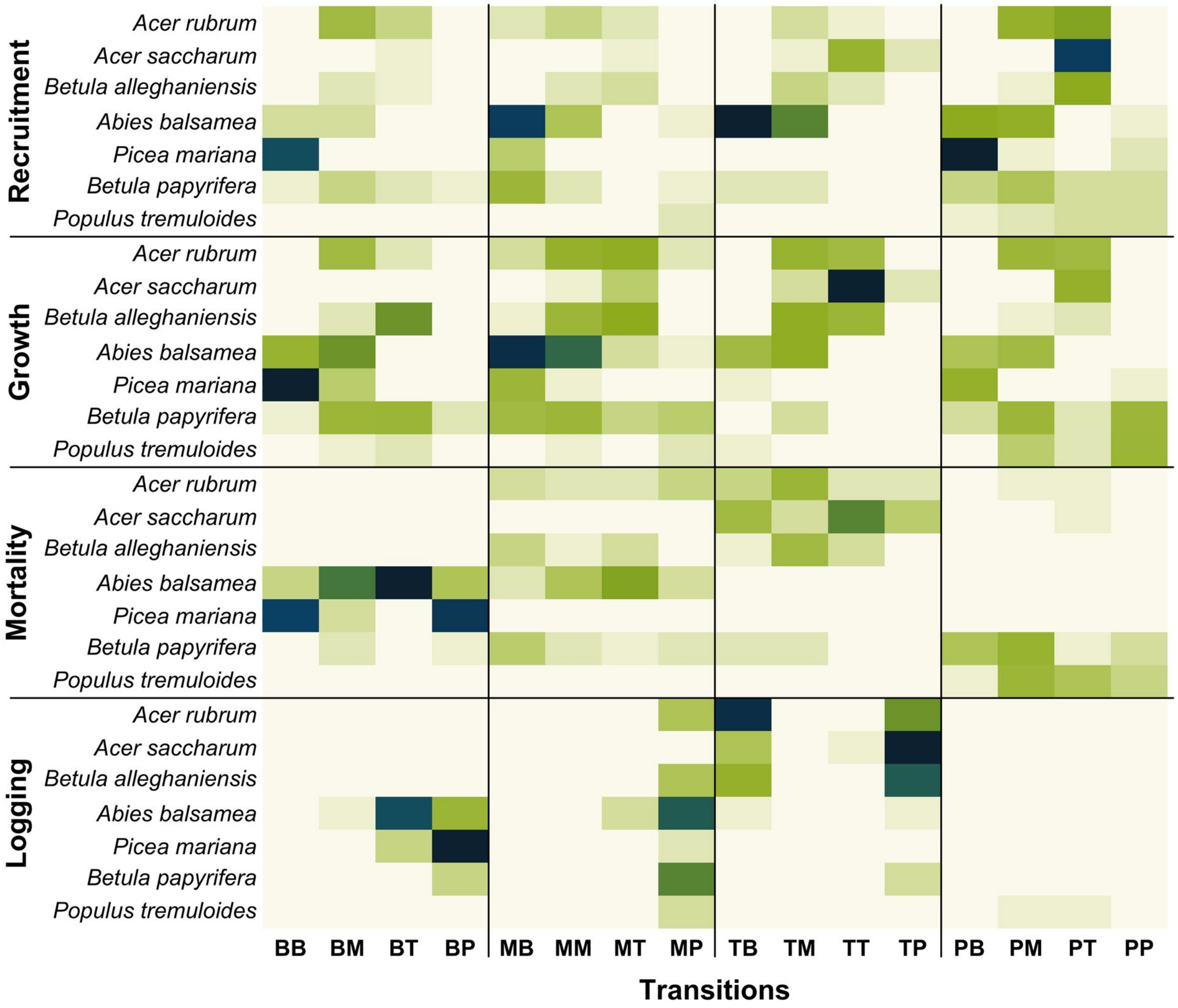


FIGURE 7 Species and demographic process contribution to all observed state transitions across the study area. Letters on the *x*-axis correspond to the four forest states: (B)oreal, (M)ixed, (P)ioneer and (T)emperate. Each pair of letters denotes a transition from one state (first letter) to the next (second letter), for example, BB is Boreal to Boreal. The darker colours indicate higher indicator value [Colour figure can be viewed at wileyonlinelibrary.com]

4 | DISCUSSION

Our study reveals that forest transition dynamics in the temperate–boreal ecotone was predominantly controlled by natural and anthropogenic disturbances and secondarily by climate, whereas local soil conditions exerted relatively minor constraints. While major disturbances only promoted transitions to the pioneer state, moderate disturbances increased the probability of transition from mixed to temperate states. Our analysis of the equilibrium further highlights that the long-term forest dynamics under moderate disturbances favours an increased proportion of temperate forests and thereby a northward shift of the temperate–boreal ecotone. Disturbances also modify the forest transient dynamics, accelerating both the turnover and convergence time and making the dynamics more predictable. Contrary to our expectation, transitions from mixed to temperate forests were not driven by recruitment but mostly by mortality and growth. In accordance with the hypothesis formulated in previous studies (Brice et al., 2019; Johnstone et al., 2016; Renwick & Rocca, 2015; Turner, 2010), our findings show that moderate disturbances catalyse transitions to the alternate, temperate-dominated forest state and could therefore promote regime shifts. Moreover, our results emphasize that forest dynamics are affected by multiple factors operating across different spatial and temporal scales. Predicting range shifts under climate change will thus require approaches that integrate multi-scale patterns and processes (Allen, 2007).

4.1 | Trends in recent forest transition dynamics in Québec

Forest dynamics in Québec during the last 48 years was dominated by transitions from pioneer to boreal and from mixed to temperate stands. The important regeneration of boreal forests could be attributed to past natural disturbances, notably the last spruce budworm outbreak. Indeed, the last outbreak, which occurred during the 1970s, has caused major mortality in coniferous species followed by important recruitment pulses and growth releases (Bouchard & Kneeshaw, 2006).

Although we did not directly evaluate the impact of climate change, our results suggest that recent climate warming may contribute to the forest transition dynamics. The high baseline transition rate from mixed to temperate is consistent with the expectation of a northward range shift of temperate trees into the mixed and boreal forests. In our study, these transitions were caused by the concomitant high mortality of an abundant boreal species, *A. balsamea*, and the increased growth of temperate species. Accordingly, the warming trend of the last decades (Figure S3) has been shown to increase growth and reproductive rates of temperate species at their northern limit (Boisvert-Marsh, Périé, & de Blois, 2019; Bolte et al., 2014; Fisichelli et al., 2014; Goldblum & Rigg, 2005; Reich et al., 2015), thus providing a competitive advantage to temperate over boreal species.

The increased transition rate to temperate forests is likely also a response to historical disturbances and climate change. Comparisons of pre-settlement and present-day forested landscapes of North America have highlighted an important deciduous encroachment in response to historical human activities (Boucher, Arseneault, & Sirois, 2006; Danneyrolles et al., 2019; Terrail et al., 2019). Historical legacies and recent climate change are presumably mutually non-exclusive explanations. Indeed, simulations by Boulanger et al. (2019) showed that the future climate-induced expansion in temperate species to the detriment of boreal species would amplify the already ongoing trend since preindustrial times.

4.2 | Disturbances catalyse forest state transition

Our study highlighted that moderate disturbances favour Mixed to Temperate transitions following climate warming, whereas major disturbances merely promote the Pioneer state. Disturbances directly remove trees, which lead to immediate and substantial changes in forest composition (Brice et al., 2019). Forests are expected to be resilient to normally experienced disturbances and should thus return to their preceding states (Gunderson, 2000). However, climate change alters the conditions that initially supported the persistence of a given state, making forests susceptible to transition to other states (Johnstone et al., 2016).

Following a disturbance, three mechanisms can contribute to the observed changes in tree cover: (a) the loss of a dominant species; (b) the growth release of advanced regeneration of co-occurring species; and (c) the pulse recruitment of new species. Our results show that the first two mechanisms may operate simultaneously, whereas the third had a limited influence.

In the study area, both natural and anthropogenic disturbances disproportionately affected *A. balsamea*, which has suffered significant mortality due to spruce budworm outbreaks and was also intensively harvested (Duchesne & Ouimet, 2008). The canopy gaps created by the loss of this ubiquitous and abundant boreal species probably allowed for the growth release of co-occurring temperate species. These findings are in line with a study in the temperate–boreal ecotone of Scandinavia where a boreal tree, *P. abies*, was particularly affected by a drought and an insect outbreak which then favour the growth of a temperate species, *F. sylvatica* (Bolte et al., 2014). Combined effects of selective disturbances and climate warming may thus initiate a shift in the competitive balance between boreal and temperate species (Bolte et al., 2014). We only found a weak contribution of temperate tree recruitment to the Mixed to Temperate transitions, likely because our analyses were based on tree basal area. However, other studies analysing abundance data suggest that moderate disturbances may also facilitate colonization and establishment by opportunistic temperate species under warmer conditions (Brice et al., 2019; Landhäusser et al., 2010; Leithead et al., 2010). Moreover, it is possible that, in the long run, the increased proportion of temperate species in forest communities could alter soil properties and ultimately facilitate the recruitment of even more temperate species.

In contrast to moderate disturbances, severe disturbances, primarily clearcutting but also large fires in the study area (Figure S1), may result in large forest dieback and create openings of very large extent. These newly opened landscapes can be colonized swiftly by early-successional species that benefit from a long-distance seed dispersal and a fast growth, such as *P. tremuloides* and *B. papyrifera* (Boucher, Auger, Noël, Grondin, & Arseneault, 2017; Grondin et al., 2018). In contrast, temperate species may be slower to come back following major disturbances because they dispersed over shorter distances (maximum of ca. 200 m for *Acer* compared to 5,000 m for *Populus*; Boulanger et al., 2017). Due to the increase in large-scale logging during the last century, the proportion of young recently disturbed forests have been found to have increased in North America (Boucher et al., 2006; Danneyrolles, Arseneault, & Bergeron, 2018; Thompson, Carpenter, Cogbill, & Foster, 2013). The expected increase in frequency and severity of climate-induced disturbances in combination with clearcuts may further promote the expansion of young pioneer forests in the future.

Compared to the catalysing effect of disturbances, local soil characteristics do not appear to represent a large impediment to state transitions, but transitions may be slower on some soil types. Poor drainage constrained climate-related transitions from Boreal to Mixed states, but not from Mixed to Temperate. This indicates that temperate species can readily colonize soils found in mixedwoods but may have more difficulty in colonizing hydric boreal soils. Thus, local soils may be important in explaining the low transition rate from Boreal to Mixed. Very poor drainage, often associated with peatland and thick organic layer, is usually thought to be improper for the regeneration of temperate species (Lafleur et al., 2010). Several studies found that *A. saccharum* regenerates well across the ecotone because of its large tolerance to various soil conditions (Barras & Kellman, 1998; Fisichelli et al., 2014; Goldblum & Rigg, 2002; Kellman, 2004). At their northern range limit, *A. saccharum* and *A. rubrum*, the species contributing most to compositional changes in Québec (Brice et al., 2019), are hypothesized to be mostly limited by cold soil temperature (Barras & Kellman, 1998; Goldblum & Rigg, 2002).

Moreover, disturbances may counteract any effect of soil properties. Indeed, disturbances, such as logging and fire, often remove the surface organic layers and expose mineral soil. They can, consequently, provide an appropriate seedbed for temperate species recruitment (Archambault, Delisle, Larocque, Sirois, & Belleau, 2006; Landhäusser et al., 2010). In combination with climate warming, disturbances may also facilitate temperate migration by increasing understorey air and soil temperatures (Stevens, Safford, Harrison, & Latimer, 2015).

4.3 | Changes in potential long-term equilibrium and biome boundary

Our model highlights the potential role of disturbances in influencing the position of the temperate–boreal boundary as well as the proportion of temperate and boreal biomes at equilibrium. As a result of the increased replacement of Mixed by Temperate states and a decline of Boreal to Pioneer states, the equilibrium temperate–boreal boundary shifts northward with moderate disturbances. While our results should not be interpreted as projections for the future, they are useful to highlight the direction of forest dynamics under different disturbance scenarios and underscore that short-term changes in the transition probabilities can impact long-term regional forest patterns. Our findings also support the simulations of Boulanger et al. (2019) where harvesting under future climate warming was projected to promote further invasions of pioneer species, such as *Populus*, and temperate species, such as *Acer* and *Fagus*, in mixedwoods of Québec.

Based on their simulations, Vanderwel and Purves (2014) concluded that logging would primarily accelerate the expansion of pioneer forests but would not promote extensive biome shifts over the next century in eastern United States. In contrast to their results, we found a clear range shift of the Temperate state under moderate disturbances, whereas the Pioneer state would have the advantage and become dominant at equilibrium only under major disturbances. We hypothesize that the northern shift of the Temperate state induced by moderate disturbances was mainly the result of the increased dominance of temperate species in areas where they are already present. Indeed, the current disturbance regime in our study area contributed to the decline of one boreal species in particular, *A. balsamea*, which in turn benefited the growth of co-occurring temperate species. Moreover, because of its positive response to past (Danneyrolles et al., 2019), recent (Brice et al., 2019) and future (Boulanger et al., 2019) disturbances in Québec, *A. rubrum* is likely to play a disproportionate role in the temperate biome shift. However, the low probability of transition from Boreal to Mixed suggests, like other studies, that migration of temperate trees into pure boreal forest will be a much slower process (Solarik et al., 2019; Vissault, 2016).

4.4 | Disturbances accelerate the transient dynamics

Beyond their impacts on the equilibrium, disturbances may substantially affect forest transient dynamics. We found that disturbances increased the rate of tree species replacement (reduced turnover time) and induced a convergence of the dynamics (reduced entropy), thereby accelerating transition dynamics towards a new equilibrium (reduced half-life). While disturbances are known to accelerate stand-scale forest succession (Abrams & Scott, 1989; Bolte et al., 2014), here we provided evidence that their effects could translate into an acceleration of regional-scale biome shifts.

In the continuous boreal zone (spruce–moss domain), forests dominated by *P. mariana* are usually characterized by dynamics of stand self-replacement with minimal compositional changes across disturbance cycles (Goldblum & Rigg, 2010). Consistent with this dynamics, the turnover time of undisturbed northern boreal forests was very long and the entropy very low in our results. The turnover was shortened by disturbances, but the entropy remained low, indicating that the dynamics was still very predictable (back and forth transitions between Boreal and Pioneer states) and that there was no directional shift associated with disturbances. Hence, boreal forests lose their persistence when moderately disturbed but remain resilient as they return to their previous boreal state. Under major disturbances, boreal forests collapsed to Pioneer state and reached this new equilibrium swiftly (short half-life). This observation is consistent with previous studies suggesting that boreal forests can easily shift into an alternative treeless state in response to severe or repeated disturbances (Payette & Delwaide, 2003).

In contrast, the ecotone is characterized by a rapid turnover and high entropy indicating abrupt compositional shift which can go in any direction. Compared to northern boreal forests, the short turnover time implies a low persistence of the forest states in this region even under minor disturbances. This result corroborates the predictions made by Vissault (2016), where mixed forests would undergo a swift conversion to temperate forests in the next decades, whereas boreal forests would present a large inertia presumably because of dispersal limitation. The dynamics of the ecotone appears unstable because it is caught between two stable states, that is, Boreal to the north and Temperate to the south. Under moderate disturbances, the probability of transitioning to Temperate increases to the detriment of the other possible states, hence the entropy is decreased, and the dynamics becomes more predictable. Such a clear directional shift strongly indicates non-equilibrium dynamics in this region. Although turnover is fast, half-life to equilibrium is long because a forest may not move towards equilibrium and may undergo multiple transitions.

4.5 | Ecological and management implications

A common assumption is that factors determining species distributions are hierarchical, such that climate would govern the distributions at regional scale while soil conditions would be more important at local scale (Pearson & Dawson, 2003). However, our study provides empirical evidence that, through their effect on demography, landscape disturbances and, to a lesser extent, local soil factors may interact with global warming to influence regional shifts in forest types. Specifically, natural and anthropogenic disturbances cause a widespread mortality of a dominant boreal species, while climate warming likely increases the growth of co-occurring temperate species in the newly formed canopy gaps, thus altering post-disturbance successional trajectories and catalysing regional forest transitions.

A shift in dominant forest cover from conifer to deciduous broadleaf species entails large changes in tree species diversity and composition (Berteaux et al., 2010) that can accumulate through time and space and induce a complete transformation of regional forest dynamics and functions (Peters et al., 2007). In the long term, this regime shift could increase carbon sequestration (Thurner et al., 2014), modify disturbance regimes (reduced flammability of broadleaf species Terrier, Girardin, Rie, Legendre, & Bergeron, 2013; and reduced sensitivity to current outbreak-prone pest MFFP, 2018), alter soil microbial activity (Laganière, Paré, & Bradley, 2010) and affect wildlife distribution (Mizel, Schmidt, Mcintyre, & Roland, 2016).

Such regime shifts will impact strongly on forest management strategies in area where silvicultural practices are tailored to the regional disturbance regimes and rely on natural regeneration. In Québec, ecosystem-based forest management seeks to maintain the composition and structure of a reference state, defined as the preindustrial forest conditions (Pinna, 2009). Yet, Boulanger et al. (2019) showed that such management would fail to restore historical forest conditions under future climate change, and that disturbances would only exacerbate the gap. While trying to maintain a historical state is likely impractical, our results emphasize that management should not only anticipate change, but should acknowledge that current forests have already undergone changes and are in the process of further transformation. Moreover, our study suggests that partial cutting could be used to increase temperate tree growth in mixedwoods. However, natural recruitment of temperate trees might not be sufficient. Thus, assisted migration could be necessary to facilitate range expansion, thereby increasing forest resilience to future climate warming (Duveneck & Scheller, 2016). The synergistic effects between climate change and disturbances are likely to further increase future uncertainty by fostering abrupt non-linear changes. In the face of this growing uncertainty, the role of forest management will be critical in building resilience and adaptative capacity of forest ecosystems (Messier, Puettmann, & Coates, 2013).

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The complete forest inventory data set used in this study is available online at https://www.donneesquebec.ca/recherche/fr/dataset/placettes-echantillons-permanentes-1970-a-aujourdhui. All the data used in the study, in addition to R scripts to reproduce the analyses and the figures, can be found online at https://github.com/mhBrice/transition (https://doi.org/10.5281/zenodo.3823355).

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SUPPORTING INFORMATION

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