Moderate disturbances accelerate forest transition dynamics under climate change

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Running title

Forest transition under climate change

Abstract

Several temperate tree species are expected to migrate northward and colonise boreal forests in response to climate change. Tree migrations could lead to transitions in forest types, and these could be facilitated by disturbances or hampered by unsuitable soil conditions.

Here, we model the state transition dynamics of Québec's forests in recent decades to identify the environmental conditions that promote or prevent these transitions. We also investigate how different disturbance types and intensities impact the potential long-term equilibrium as well as the short-term transient dynamics.

We analysed over 10,000 forest inventory plots, sampled from 1970 to 2018 in meridional Québec, Canada. We used a continuous-time multi-state Markov model to quantify the transition probabilities between forest states (temperate, boreal, mixed, pioneer) in relation to climate, soil conditions and disturbances. We described the equilibrium and transient dynamics under different disturbance scenarios, using properties of Markov transition matrices.

Although the majority of forests persist in the same state, most transitions were conversions from mixed to temperate stands, as well as regeneration from pioneer to boreal forests. Transition probabilities were mainly driven by natural and anthropogenic disturbances and secondarily by climate, whereas soils exerted only minor constraints. Moderate disturbances not only increased the probability of transition to pioneer, but also from mixed to temperate forests. At low disturbances, boreal forests were characterised by great inertia and predictable stand self-replacement dynamics, while mixed forests presented rapid and unpredictable transitions. Moderate disturbances reduced turnover and convergence times for all transitions and induced a clear directional shift toward temperate forests. In the long-term, these changes in the transition dynamics increase the equilibrium proportion of temperate forests, thus promoting a northward shift of the boreal-temperate boundary. Hence, moderate disturbances could catalyse rapid forest transitions and accelerate broad-scale biome shifts.

Keywords

Introduction

Global climate warming is forcing species to move their distribution (Parmesan & Yohe, 2003). Several temperate deciduous tree species at the temperate-boreal forest ecotone are slowly migrating northward, colonising conifer dominated forests (Boisvert-Marsh, Périé, & de Blois, 2014; Evans & Brown, 2017; Fisichelli, Frelich, & Reich, 2014; Sittaro, Paquette, Messier, & Nock, 2017). As climate warms up and tips the balance in favour of temperate over boreal species, forests are expected to transition from coniferous to mixedwood and from mixedwood to temperate deciduous (Boulanger et al., 2019; Price et al., 2013). While boreal forest dynamics is characterised by broad-scale disturbances (fires and insect outbreaks) and slow decomposition of an acidic and nutrient-poor litter, temperate forest dynamics is characterised by small-scale canopy gaps and rapid decomposition of a rich litter (Goldblum & Rigg, 2010). Hence, as ecological processes strongly differ among these biomes, climate-induced range shifts not only impact species distributions, but also alter the structure of communities, microclimates, biogeochemical cycles and ecosystem functioning and might trigger a "regime shift" (Scheffer, Carpenter, Foley, Folke, & Walker, 2001).

Climatic niches for tree species are expected to shift northward by several hundred kilometres by the end of the century (McKenney, Pedlar, Lawrence, Campbell, & Hutchinson, 2007), but many studies indicate that tree migration will not keep pace with global warming (e.g. Zhu, Woodall, & Clark, 2012; Renwick & Rocca, 2015; Sittaro et al., 2017; Talluto, Boulangeat, Vissault, Thuiller, & Gravel, 2017; Vissault, 2016). Indeed, warmer climate may improve recruitment, survival and growth of temperate species at their northern range limit (Boisvert-Marsh, Périé, & Blois, 2019; Goldblum & Rigg, 2005; Graignic, Tremblay, & Bergeron, 2014), while reducing growth and increasing mortality of boreal species at their southern range limit (Goldblum & Rigg, 2005; Peng et al., 2011). These demographic changes alter immigration and extinction rates which are driving recent species range shifts (Talluto et al., 2017), and should, in theory, continue until forests reach a new equilibrium with climate, i.e., the steady-state or long-term proportion of forest states. However, because trees are long-lived species that disperse over very short distances, immigration and extinction events in response to environmental changes are often delayed, and forests rarely reach their equilibrium (Talluto et al., 2017). If forests are undisturbed, transition rates between forest biomes will be mainly limited by the persistence and turnover of resident species as well as the dispersal and establishment rates of migrating species (Neilson, 1993), resulting in transient dynamics that may last a very long time (Hastings et al., 2018; Jackson & Sax, 2010; Talluto et al., 2017). While the study of equilibrium highlights the potential long-term attractor of forest dynamics, transient dynamics reveals the short-term response, which is more relevant to the changes likely to occur in the 21st century and within the time frame of management plans (Hastings et al., 2018). Knowledge of equilibrium and transient dynamics can thus expand our understanding of forest responses at different time scales.

Both gradual invasions and abrupt transitions from one biome to another will likely take place concurrently. However, given that forests are increasingly subjected to pervasive climatic stresses and direct human dis-

turbances, abrupt transitions are likely to play a key role in driving the climate shift in biomes. Indeed, as climate change slowly modifies the competitive balance among species, disturbances destroy the resident community in whole or in part, thus providing establishment opportunities for migrating species and making resources available for a fast growth. Consequently, forest composition may shift abruptly to species that are better suited to current conditions and fail to return to their previous state following a disturbance (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 Alaska, white spruce (*Picea glauca*) is invading black spruce (*Picea mariana*) stands following fire and permafrost degradation (Wirth, Lichstein, Dushoff, Chen, & Chapin, 2008). Similarly, moderate disturbances favoured the increase of warm-adapted species and led to a broad-scale community thermophilization of forests in Québec (Brice, Cazelles, Legendre, & Fortin, 2019).

While these examples suggest that disturbances have the potential to catalyse shifts to an increasingly deciduous-dominated landscape, other simulation studies have concluded that they are unlikely to drive extensive biome shifts in the coming decades (Liang, Duveneck, Gustafson, Serra-Diaz, & Thompson, 2018; Vanderwel & Purves, 2014). In some cases, disturbances have been shown to promote colonisation by early successional species which then displace long-lived shade-tolerant species. For instance, clearcutting has been found to favour the expansion of a pioneer species, the trembling aspen (*Populus tremuloides*), in mixed and boreal stands of Québec (Grondin et al., 2018; Laquerre, Leduc, & Harvey, 2009) and Alberta (Landhäusser, Deshaies, & Lieffers, 2010). These divergent results suggest that the effect of disturbances on forest dynamics may depend on their intensity and type (natural or anthropogenic). Therefore, more empirical evidence is essential to disentangle the role of various intensities and types of disturbances in broad-scale biome shifts.

The northward migration of temperate species may however be contingent on their capacity to colonise different types of soil (Bennett et al., 2017; Brown & Vellend, 2014; Lafleur, Paré, Munson, & Bergeron, 2010). Indeed, 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 conifer-dominated stands were negatively affected by seed predators and fungal pathogens (Brown & Vellend, 2014) as well as by soil acidity through reduced foliar nutrition (Collin, Messier, & Bélanger, 2017). However, Kellman (2004) found that, after initial high mortality due to seed predation, survival of *Acer saccharum* seedlings in boreal stands was high, even superior to temperate stands, potentially because of increased 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 transition under climate change (Solarik, Cazelles, Messier, Bergeron, &

Gravel, 2019). While experimental studies provide valuable insights on the potential role of soils at local scales, we need to test the generality of such constraints, or the lack thereof, on long-term forest dynamics 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 transitions of forest plots among states as a stochastic process influenced by their current state, as well as their current environmental characteristics. Given the unequivocal distinction between temperate and boreal forests, the dynamics of tree communities at the boreal-temperate ecotone can be adequately characterised using discrete functional and successional states, namely boreal, mixed, temperate and pioneer (Vissault, 2016) and thus can be formalised as a multi-state Markov model (Jackson, 2018). Markov models provide a useful framework for modelling changes of state over time using longitudinal data. In epidemiology, for example, these models are often used to describe the progression of diseases (Van Den Hout, 2016). In ecology, they have been used to study processes such as forest succession (Liénard, Gravel, & Strigul, 2015; Runkle, 1981; Waggoner & Stephens, 1970), metapopulation dynamics (Hanski & Ovaskainen, 2003; Moilanen, 1999), landcover changes (Muller & Middleton, 1994; Yang, Zheng, & Chen, 2014), or stage class transitions (Caswell, 2008).

Representation of forest dynamics with Markov chains allows to explore ecological mechanisms (Wootton, 2001) underlying biome shifts. For example, transitions to pioneer reflect disturbance, transitions from pioneer reflect colonisation, 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 matrix properties can then be compared under different scenarios (Boulangeat, Svenning, Daufresne, Leblond, & Gravel, 2018; Hill, Witman, & Caswell, 2004). For instance, the steady-state distribution can be derived from a transition matrix and used to infer the potential long-term forest composition under some environmental conditions (i.e., the attractor Scheffer et al., 2001), providing insights about the direction of the current forest dynamic (Hill et al., 2004; Waggoner & Stephens, 1970). Moreover, transient periods can be described using the time of convergence to reach the steady-state distribution, which 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 insights into management measures.

Here, we investigate the response of forests to recent climate warming by estimating the transition probabilities among four forest states: boreal, mixed, temperate and pioneer. We address the following questions: (1) What are the trends in recent forest transition dynamics? (2) How do disturbances and soil characteristics influence the transition probabilities among forest states? (3) Do different disturbance types and intensities impact the potential long-term equilibrium distribution of forest states? And (4) how do different

disturbance types and intensities influence the short-term transient dynamics following climate change?

We apply a continuous-time Markov multi-state model to the forest dynamics to estimate state transition probabilities and evaluate the influence of environmental covariates on these transitions. Using results from our multi-state model, we investigate the impact of disturbances on forest equilibrium and transient dynamics by comparing different complementary matrix properties.

We expect that most forests will not change states, i.e., high self-transition probabilities, because of the slow demography of trees. However, climate warming should promote colonisation 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 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), while soil characteristics of coniferous forests (low pH and poor drainage) should slow down the colonisation by temperate trees. Disturbances should also accelerate the transient dynamics by shortening turnover and convergence times. Together, these effects on transitions should result in an increased proportion of temperate forests at equilibrium relative to the current state distribution.

Methods

Study area and forest inventory data

We used forest inventory plots in Québec, Canada, to investigate large-scale transition dynamics in forest communities. Permanent plots have been sampled approximately every ten years from 1970 to 2018 (and ongoing) by the *Ministère des forêts, de la Faune et des Parcs* (MFFP, 2016) in order to monitor changes in forest productivity and growth. The study area extends from approximately 45° to 52°N of latitude (ca. 795 000 km^2). It covers six bioclimatic domains (Fig. 1) and three different forest subzones; 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 *Acer saccharum*, and the boreal forest to the north, dominated by *Abies balsamea* and *Picea mariana*. Plots were randomly positioned across these three subzones with a decreasing sampling intensity northward (MFFP, 2014).

We selected all inventory plots that had been sampled at least twice as well as those for which soil covariates were available. We disregarded plots that were subjected to active reforestation during the study period because we were interested in transition dynamics resulting from natural recolonisation processes. This yielded a total of 11,058 plots analysed (Fig. 1). The time intervals between plot surveys varied from 3 to 39 years, with a mean interval of 11 years (SD = 3.45).
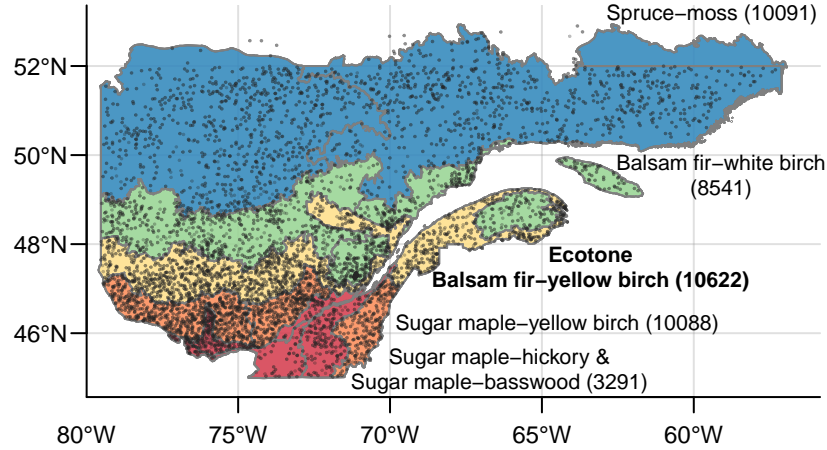
Figure 1: Locations of the 11,058 forest inventory plots in meridional Québec, Canada. Colours delimit the six bioclimatic domains. The two southernmost domains (red) are here combined. The number of forest plots in each domain is shown in parentheses. The balsam fir-yellow birch domain (in bold) is the ecotone between hardwood and boreal forests.

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 state: boreal, temperate or pioneer according to their functional traits (Table S1; see Brice et al., 2019 for details). 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 $<5\text{m}^2/\text{ha}$). 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 (Fig. 2, Table S3).

It should be noted that the definitions of forest states can affect the results to some extent. A higher threshold to define the boreal and temperate states (e.g., >90% instead of >75% of dominance of boreal and temperate, respectively) can influence the transition probabilities, but the direction of the dynamics would remain the same.

Environmental variables

The past 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 bio-

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climatic variables hypothesised 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. During the 1950 until the present day, growing season temperatures have increased by 0.17 °C/decade in the plots, while CMI have shown no trends (Fig. S1).

We also collected information pertaining to natural and anthropogenic disturbances that have affected the forest plots during the study period (Table 1; Figs. S2). At each plot, the type of disturbances (21 types) and their level of intensity (moderate or major) were recorded during field surveys (Fig. S2; MFFP, 2016). The MFFP defined major disturbances as events that have eliminated more than 75% of the total tree basal area, whereas moderate disturbances have eliminated between 25% and 75%. For our multi-state model, we differentiated two main types of disturbances: natural disturbances and harvest, with three levels of intensity each (minor, moderate or major).

Finally, at each plot, several edaphic characteristics were recorded (MFFP, 2016). Of the available variables, we selected drainage and pH because they largely affect nutrient availability, soil structural properties and vegetation development (Tan, 2009). These two variables also capture most of the variance in soil characteristics in plots across Québec and were orthogonal in a PCA (not shown).

Climate and disturbances were included as time-varying explanatory variables (often called covariates in survival models), while soil was 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.

Although we tested a well-founded set of variables, we did not attempt to include every ecological process affecting the forest dynamics. Our goal was not to make projections about the future state of Québec forests, but rather to explore how disturbances and soils influence transition dynamics under recent climate change. Therefore, we did not include propagule pressure as a covariate for transition intensities. Propagule availability is known to affect tree range shifts (Pearson, 2006), and would be important for making projections, i.e., when climate and distribution will be decoupled. Our model is therefore appropriate to study recent forest dynamics, as the neighbourhood composition is very strongly correlated with climate, which was included in our model.

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	6 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. None or minor (0), moderate (1) or major (2).

Analysis

Continuous-time multi-state Markov model

We formalised forest dynamics with a continuous-time multi-state model (Jackson, 2018; Van Den Hout, 2016) in which transitions among states depend upon the current state, time interval, climate, disturbances and soil characteristics (Fig. 2).

Markov models are often built using discrete time steps. However, a continuous-time Markov model was preferable because it takes into account the fact that (1) time intervals between surveys were irregular, (2) multiple transitions were possible during an interval, and (3) the exact times of transitions were unobserved (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 matrix transition intensity matrix, Q, where rows are the current states and columns the future states (Fig. 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, an instantaneous transition from Boreal to Temperate and from Temperate to Boreal was considered impossible (there is a necessary transition through the Mixed state). However, all states can transition directly to

₂₄₄ Pioneer when disturbed (Fig. 2).

₂₄₅ The intensities $q_{r,s}$ can be modelled as the product of a baseline hazard $q_{rs.0}$ and a log-linear effect of the
₂₄₆ explanatory variables $x(t)$ and their coefficients β_{rs}:

₂₄₇ $q_{rs}(t|x(t)) = q_{rs.0}(t)exp(\beta'_{rs}x(t))$.

₂₄₈ In this model, $q_{rs.0}(t)$ is a baseline hazard function that describes the risk for a reference plot i with
₂₄₉ environment $x_i(t) = 0$, and $exp(\beta'_{rs}x(t))$ is the relative increase or decrease in risk associated with the
₂₅₀ set of characteristics $x_i(t)$. In this model, time-dependent variables, such as climate and disturbances, are
₂₅₁ assumed to be piecewise-constant, i.e., the hazard is constant within a time interval $[t, t + \Delta t]$ and depends
₂₅₂ on the variable value at t, but can change between the intervals. Their inclusion in the model allows to
₂₅₃ fit a non-homogeneous Markov process. Estimation of model parameters were obtained by maximising the
₂₅₄ log-likelihood (see Supplementary Methods for details).

₂₅₅ We built five different models: one baseline model with intercept only, one for each subgroup of covariates
₂₅₆ independently (climate, soil and disturbances), and one full model, which combines all the covariates (Table
₂₅₇ 1). Because multiple state transitions are estimated in a single model (all q_{rs} in Fig. 2b), the number of
₂₅₈ parameters increases rapidly with the number of covariates (number of modelled transitions (here 10) ×
₂₅₉ number of covariates). Thus, to reduce the number of parameters, we hypothesised that transitions from any
₂₆₀ state to Pioneer were only determined by disturbances, while climate and soil variables should not directly
₂₆₁ influence these transitions. All quantitative variables were standardised ($\mu = 0$, $\sigma = 1$) prior to running the
₂₆₂ models.

₂₆₃ **Model evaluation**

₂₆₄ We first evaluated the goodness-of-fit of each model containing covariates (climate, soil, disturbances and
₂₆₅ full) against the baseline model using likelihood ratio tests (Jackson, 2011), which test if the addition of one
₂₆₆ or more new parameters significantly increases the likelihood of the model. We also compared and ranked
₂₆₇ the models using the Akaike's information criterion (AIC; Burnham, Anderson, & Burnham, 2002).

₂₆₈ **Baseline transition intensities**

₂₆₉ We first evaluated the trends in recent forest transition dynamics (objective 1). We used the baseline hazards
₂₇₀ ($q_{rs.0}$) estimated by our best model as indicators of the underlying forest response. For each pair of states,
₂₇₁ the baseline hazard describes the risk to make the transition for a mean forest plot (when all covariates are
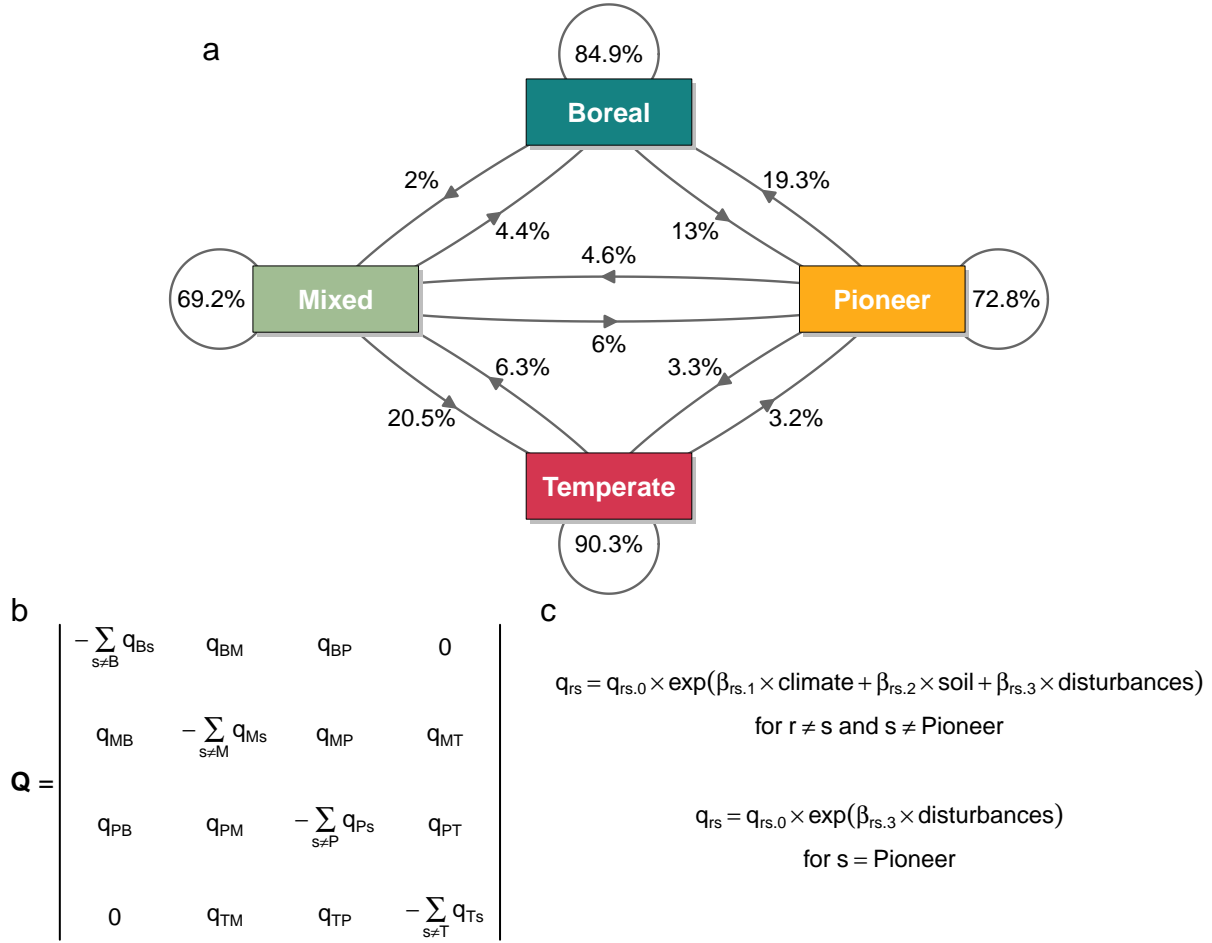₂₇₂ set to 0).

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a

84.9%

Boreal

2%   19.3%

4.4%   13%

4.6%

69.2%   **Mixed**   **Pioneer**   72.8%

6%

6.3%   3.3%

20.5%   3.2%

Temperate

90.3%

b

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

c

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

$$\text{for } r \neq s \text{ and } s \neq Pioneer$$

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

$$\text{for } s = Pioneer$$

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 ($nb_{rs}/nb_{r.} \times 100$). 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 (less than 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).

Effects of covariates on transition probabilities

We investigated the influence of environmental covariates on transition dynamics (objective 2). We compared the estimated hazard ratios derived from our best model ($exp(\beta_{rs})$). We also computed the predicted 10-year transition probabilities of forest plots under different disturbance scenarios, while keeping all other covariates at the average found in the ecotonal zone (i.e., the balsam fir-yellow birch domain, Fig. 1), to facilitate visual interpretation of the impacts of disturbances on the transition matrix structure.

Effects of disturbances on transient dynamics and equilibrium

We further investigated how disturbances modify the long-term equilibrium (objective 3) and the forest transient dynamics (objective 4). We computed different properties on the Markov transition matrix and compared them among levels and types of disturbances along the latitudinal temperature gradient. An extensive literature describes the multiple properties of discrete-time Markov transition matrix (Caswell, 2008; Hill et al., 2004) which can be adapted for continuous-time models. We chose four informative and complementary properties that fully characterise both the short and long-time scale dynamics of our modelled system: (1) the steady-state distribution, which corresponds to the potential long-term proportion of forest states at equilibrium; (2) the time of convergence towards the steady state, which measures the length of the transient period; (3) the turnover time, which measures the rate of transient successional changes; and (4) the entropy, which captures the incertitude of the next transitions. While their absolute values are likely inaccurate, 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 Q, which has an eigenvalue of 0, normalised to sum to 1, or the left eigenvector of P, which has an eigenvalue of 1, normalised 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):

$$\rho = \lambda_{P1}/\lambda_{P2} = exp(\lambda_{Q1} - \lambda_{Q2}),$$

where λ_{P1} and λ_{P2} are the largest and second-largest eigenvalues of P ($\lambda_{P1} = 1$ for stochastic P), 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 the next. The turnover time can be estimated by $Turnover_r = -1/q_{rr}$, 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:

$$Turnover = -\sum_r \pi_r \times Turnover_r.$$

Finally, Hill et al. (2004) suggested using 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 normalised entropy of the whole system is the average of the entropies over the steady state, divided by $H_{max} = log(n_{state} = 4)$:

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

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

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 throughout the analysis is provided in the Supporting Information (Table S1). All data used in the study, in addition to R scripts that reproduced the analyses and figures, will be made available online on Github upon manuscript acceptance.

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%), but even 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; Fig. 2a).

Model evaluation

Overall, the full model, which include climate, soil and disturbance variables, had the best fit and predictive performances for the observed data (Tables 2; Fig. S3). The second-best model was the disturbance model, but it was far behind with a difference in AIC of almost 1500 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 « 0.001; 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 (Fig. S3). Thereafter, all inferences about transition probability parameters were derived from the full model.

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. The ΔAIC is the difference between the Akaike's information criterion of each model (AIC_m) and the minimum of AIC among all the models (AIC_{min}): $\Delta AIC = AIC_m - AIC_{min}$. Models are ordered in terms of their ΔAIC. Each model containing covariates was compared to the baseline model using Likelihood Ratio (LR) test. The best model is the one in bold with $\Delta AIC = 0$.

	Covariates	Number of parameters	-2 Log-likelihood	Delta AIC	LR test
Baseline	Intercept	10	37874.4	8298.4	—
Soil	Drainage, pH	24	37713.7	8165.7	< 0.001
Climate	Temperature, CMI	24	36288.8	6740.8	< 0.001
Disturbances	Natural, Logging	50	30993.5	1497.5	< 0.001
Full	**All**	**78**	**29440.0**	**0.0**	**< 0.001**

Baseline transition intensities

The baseline transition intensities of the full model provide insight about the background rate of forest changes (Fig. 3). Forest dynamics over the whole study area was largely dominated by transitions from Pioneer to Boreal ($q_{PB} = 0.0270$) and from Mixed and Temperate ($q_{MT} = 0.0229$; Fig. 3). Mixed forests were 1.6 times (q_{MT} / q_{TM}) more likely to transition to Temperate than the reverse, indicating that temperate species had been successfully colonising mixedwoods, outcompeting boreal species, during the study period. For Boreal forests, regeneration from Pioneer to Boreal was 3.9 times (q_{PB} / q_{BP}) more likely than a succession resetting by disturbances.
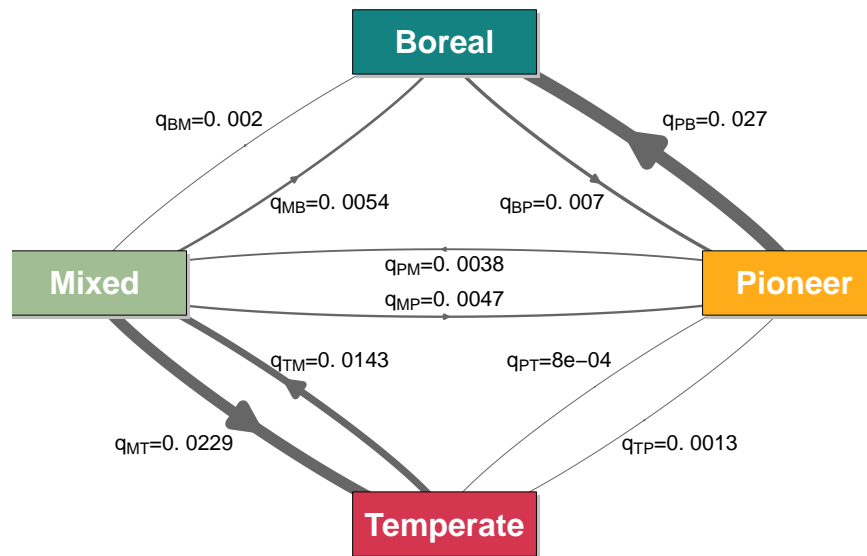
Figure 3: Baseline transition intensities as estimated from the best multi-state transition model. Arrows depict the direction of transitions between states. The numbers represent the estimated baseline hazard ($q_{rs.0}$), i.e., the instantaneous risk of moving from one state to another when all covariates are set to 0 (hence, the mean of standardised covariates and the no disturbance level).

Effect of covariates on transition probabilities

The full multi-state model indicates that forest state transitions are contingent upon environmental covariates. All transitions to Pioneer were highly influenced by disturbances (Fig. 4, Table S4). As could be expected, major disturbances exert stronger effects than moderate disturbances (for both natural and logging), but, for each level of intensity, logging had stronger effects than natural. 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) compared to undisturbed plots (minor). Disturbances of all types and intensities favoured transitions from Mixed to Temperate forests. Moderate disturbances (natural and logging) doubled the risk of this

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type of transition, whereas major disturbances increased it by ca. 5 times (Hazard Ratio (HR) = 5.76 and 5.32, for natural and logging, respectively). Although the effect of major disturbances on the instantaneous risk of transition from Mixed to Temperate was stronger than for moderate disturbances, the probability of this event decreases with time (Fig. S4). 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.

Climate variables also had a significant influence on most transitions (Fig. 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 (Fig. 4, Table S4). 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 ratio associated to 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.
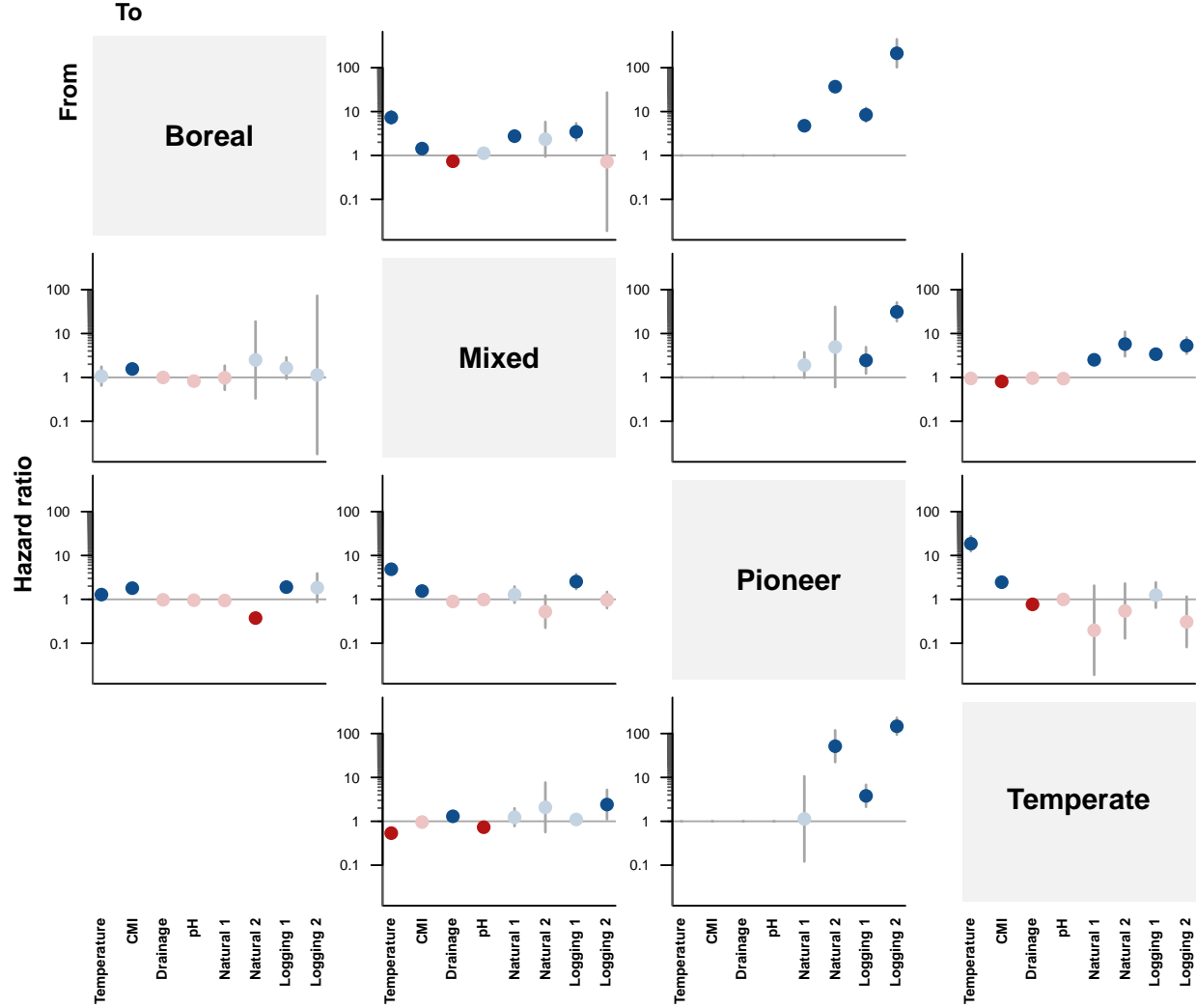
Figure 4: Hazard ratios (HR) and 95% confidence intervals as estimated from the best multi-state transition model. Each plot represents the estimated HR for transitions from row to column state, e.g., the plot on the first row, second column shows the HR for the Boreal to Mixed transition. The ordinate 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 coloured in dark blue or red. Numbers following disturbance predictors indicate their levels of intensity: 1 = moderate and 2 = major.

Disturbances completely altered the structure of the 10-year transition probability matrix (Fig. 5). The largest values across most matrices were generally associated with self-transitions (matrix diagonal), meaning that the vast majority of forest plots (characterised by the average environmental conditions found in the ecotone) remained in the same state after 10 years. For undisturbed forest plots (minor), the self-transitions were very strong but transitions from Pioneer to Boreal and from Mixed to Temperate were not trivial. At moderate disturbances, probabilities of self-transitions decreased, while transitions from Boreal to Pioneer, and from Mixed to Temperate increased the most. Transitions from Mixed and Temperate to Pioneer did not increase much at moderate disturbances, likely because such disturbances were less frequent and less severe than in Boreal forests. The difference between natural disturbances and logging was conspicuous only for major disturbances. For both types of major disturbances, the transition probabilities to Pioneer showed a great increase compared to moderate disturbances, but these values exploded in the severely logged transition matrix, exceeding self-transitions. Interestingly, the estimated probability of Mixed to Temperate transition remained quite high after major disturbances.

Figure 5: Predicted change in 10-year transition probabilities for different disturbance types and levels. All other covariates are fixed at the average conditions found in the ecotone. Letters correspond to the four forest states: (B)oreal, (M)ixed, (P)ioneer and (T)emperate. Numbers are the modelled transition probabilities from rows to columns and darker colour highlights stronger transition probability.

Effect of disturbances on long-term equilibrium

The potential state proportion at equilibrium was strongly influenced by disturbances (Fig. 6a). 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 (Fig. 6b,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 falls in the actual ecotone. Moderate disturbances (both natural and logging) displaced the Boreal-Temperate boundary at lower temperatures (ca. 12.2°C), hence further north of the current ecotone (Fig. 6b,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).

Effect of disturbances on transient dynamics

Disturbances also affected forest transient dynamics with greater impacts for higher disturbance intensity (Fig. 7). In the minor disturbance scenario, turnover time was generally longer at low temperature, indicating slower transition dynamics in northern forests (Fig. 7a,b). The turnover time then rapidly declined to reach a minimum at 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 the Boreal and Temperate dominances found in Figure 6. 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 (Fig. 7a,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 (Fig. 7a,b). These spatial patterns reflect the turnover time of the dominant state at each point along the temperature gradient (Fig. S5).

At minor disturbances, the entropy of the system generally increased from north to south and peaked at 12.59°C, at the northern end of the ecotone (Fig. 7c,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 of the Boreal state at the ecotone, and the generally high values at low latitudes can be principally attributed to the Temperate state (Fig. S6). This latitudinal pattern of entropy
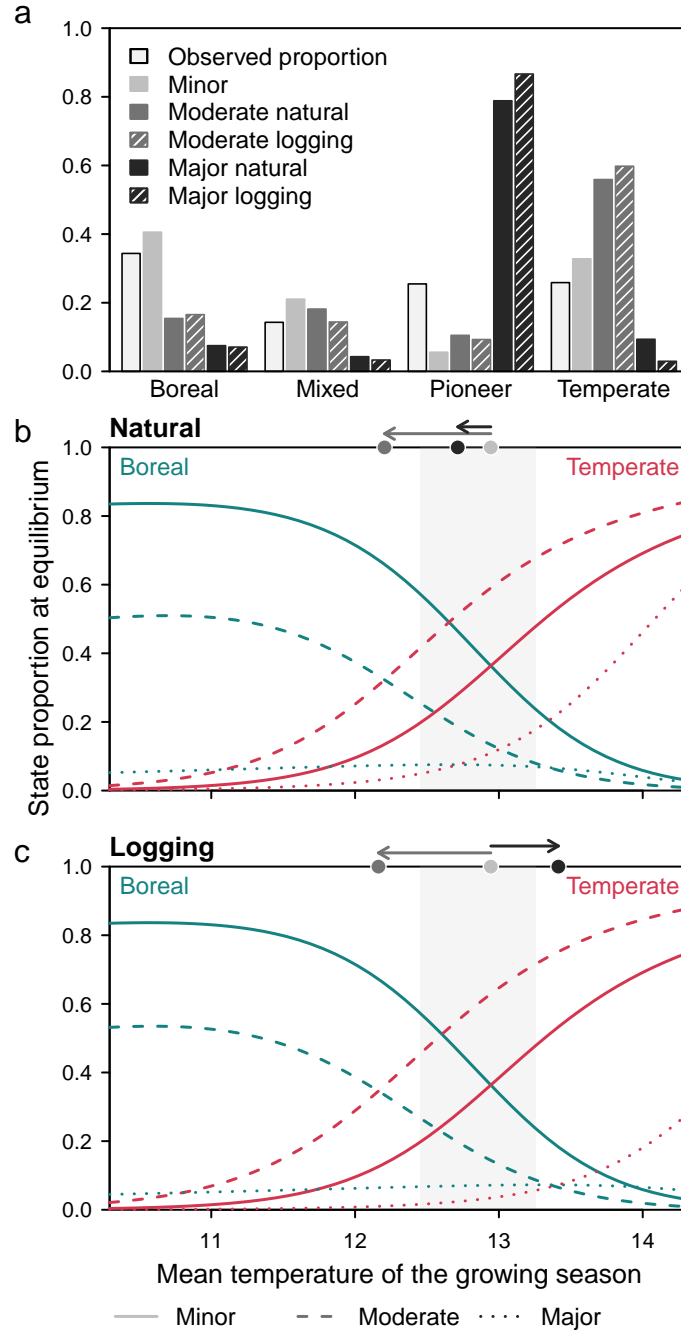
Figure 6: Changes in forest state proportions at equilibrium for different disturbance types (natural or logging) and intensity (minor, moderate, major). The barplot (a) compares the observed state proportion in the ecotone to the potential state proportion at equilibrium for different disturbance scenarios 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 minor (solid), moderate (dashed) and major (dotted) disturbances, with all other covariates are fixed at the average conditions found in the ecotone. The light (minor), medium (moderate) and dark (major) grey circles indicate the positions of the boundary between dominance of Boreal forests 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 positions of the ecotone along the temperature gradient.

is modified by disturbances. Moderate natural disturbances decreased the entropy throughout the gradient, but especially where was the peak (Fig. 7c). With moderate logging, the peak disappeared, and entropy increased monotonically from north to south (Fig. 7d). The peak of entropy was displaced to the south when major disturbances are included, whether natural or logging (Fig. 7c,d), where it is dominated by the entropy of the Pioneer state (Fig. S6).

The half-life to equilibrium was the longest at 11.77°C, north of the ecotone, in the balsam fir-white birch domain, while it was the shortest in the southernmost latitudes (Fig. 7e,f). Interestingly, none of the features in the three indices are aligned. Moderate disturbances flattened and shifted this peak to the north and the effect of moderate logging (Fig. 7f) was stronger than natural disturbances (Fig. 7e). 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).

Discussion

Our study reveals that disturbances are likely to accelerate forest response to climate change by promoting transitions from mixed to temperate forests. Our analysis of the equilibrium further highlights that the long-term forest dynamics under moderate disturbances favours an increase proportion of temperate forests and a northward shift of the boreal-temperate ecotone. Disturbances also modified the forest transient dynamics, accelerating both the turnover and convergence time and making the dynamics more predictable. In accordance with the hypothesis formulated by previous studies (Brice et al., 2019; Johnstone et al., 2016; Johnstone, Hollingsworth, Chapin, & Mack, 2010; Vissault, 2016), our findings show that moderate disturbances catalyse transitions to the alternate, temperate-dominated forest state and could therefore promote regime shifts.

Trends in recent forest transition dynamics

Forest dynamics in Québec during the last decades 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, that occurred during the 1970s, have 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 species into
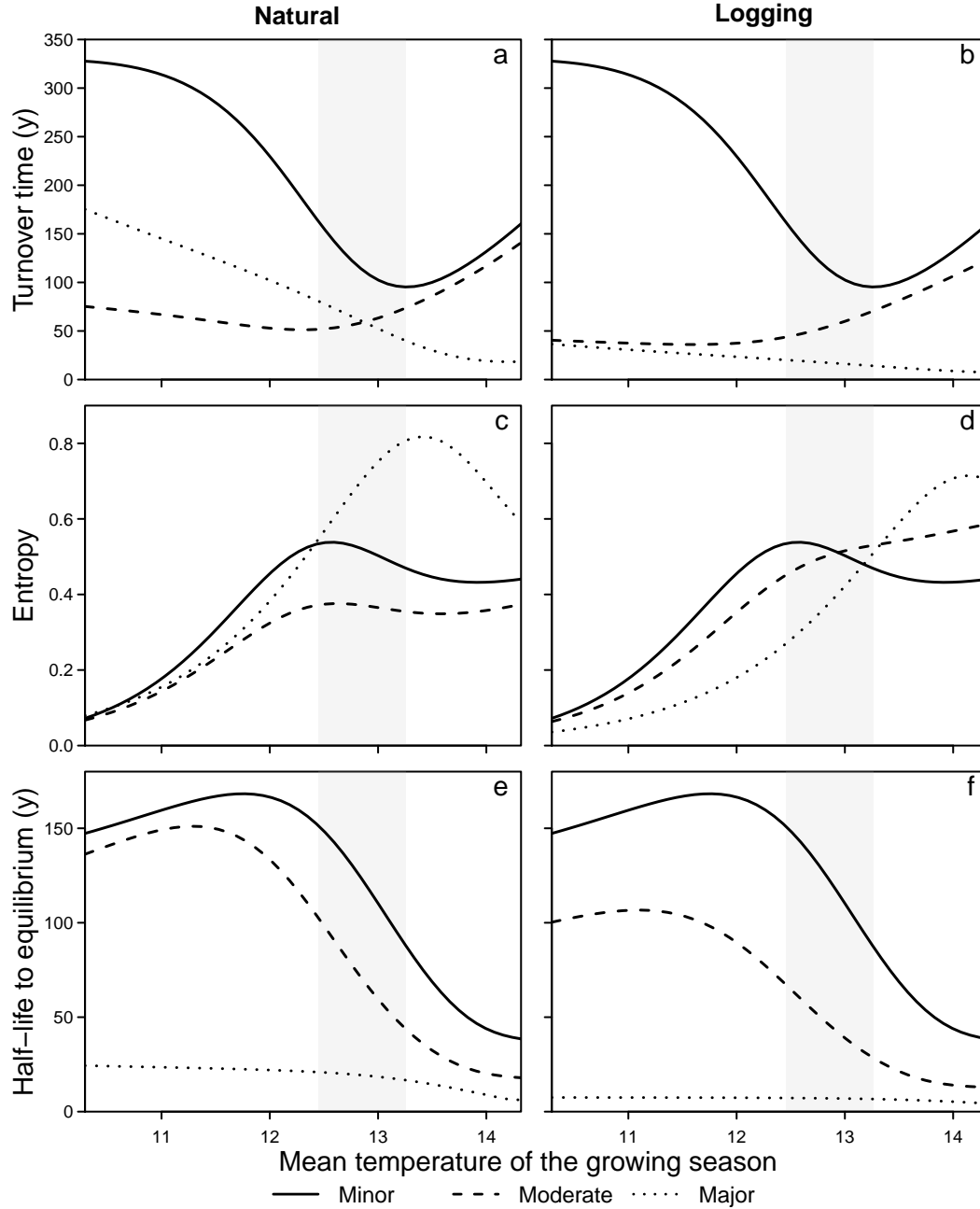
Figure 7: Changes in the characteristics of the forest transient dynamics along the temperature (latitudinal) gradient for different disturbance scenarios: minor (solid), moderate (dashed) and major (dotted) disturbances for both natural (a,c,e) and logging (b,d,f). All other covariates are fixed at 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 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, i.e. 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.

the mixed and boreal forests. These transitions were caused by a concomitant increase in temperate species and decrease in boreal species (Fig. S7). Accordingly, the warming trend of the last decades (Fig. S1) has been shown to increase growth and reproductive rates of temperate species and reduce growth of boreal species (Boisvert-Marsh et al., 2019; Fisichelli et al., 2014; Goldblum & Rigg, 2005; Reich et al., 2015), thus providing a competitive advantage of 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). Moreover, evidence suggest that the ongoing northern range expansion of some tree species is due to delayed postglacial migration (Svenning & Sandel, 2013). 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.

Disturbances catalyse forest state transition

Our study highlighted that moderate disturbances favour climate-related transitions, whereas major disturbances merely promote pioneer states. Disturbances directly remove trees, which leads to immediate and substantial changes in forest composition (Brice et al., 2019). Without climate change, forests are expected to be resilient to normally experienced disturbances and should thus return to their preceding states. 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). Hence, moderate disturbances likely facilitate colonisation and establishment by opportunistic temperate species under warmer conditions (Brice et al., 2019; Landhäusser et al., 2010; Leithead et al., 2010). In contrast, severe disturbances in the study area, primarily clearcutting but also large fires (Fig. S2), create openings of very large extent which are likely detrimental to temperate species and favour early-successional species that can disperse seed over long distances, such as *Populus sp* and *Betula sp* (Landhäusser et al., 2010).

Compared to the catalysing effect of disturbances, 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 colonise soils found in mixedwoods but may have more difficulty to colonise hydric boreal soils. 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 *Acer saccharum* regenerates well across the ecotone because of its large tolerance to

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various soil conditions (Barras & Kellman, 1998; Collin, Messier, Kembel, & Bélanger, 2018; 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 (Brice et al., 2019), are hypothesised 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 and 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 understory air and soil temperatures (De Frenne et al., 2013; Stevens, Safford, Harrison, & Latimer, 2015).

Changes in potential long-term equilibrium and biome boundary

Our model highlights the potential role of disturbances in influencing the position of the boreal-temperate 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 boreal-temperate 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. Our findings 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. In contrast, based on their simulations, Liang et al. (2018) and Vanderwel & Purves (2014) concluded that logging would primarily accelerate the expansion of pioneer forests, but would have little or no effect on extensive biome shifts over the next century in eastern United States. Divergence in tree species responses to disturbances could explain these apparently conflicting results. Disturbances may facilitate the range expansion of some species but hinder that of others depending on their functional traits (Aubin et al., 2016; Matthews, Marsh-Matthews, Cashner, & Gelwick, 2013). For instance, 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, *Acer rubrum* is likely to play a disproportional role in the temperate biome shift.

Disturbances accelerate the transient dynamics

Beyond their impacts on the equilibrium, our results suggest that disturbances may have a substantial influence on forest transient dynamics. In the continuous boreal zone (spruce-moss domain), forests dominated by *Picea mariana* are usually characterised 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. 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 agrees 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; Sánchez-Pinillos et al., 2019).

In contrast, the ecotone is characterised by a rapid turnover and a high entropy indicating abrupt compositional shift which can go in all directions. 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 limitations. The dynamics of the ecotone appears unstable because it is caught between two stable states, i.e. 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 in the right direction and may undergo multiple transitions.

Ecological and management implications

Our study provides a strong empirical basis for predicting the types of changes in forest dynamics that are likely to unfold in the 21st century. A shift in dominant forest cover from conifer to deciduous broadleaf species not only entails changes in tree species diversity and composition, but a complete transformation of forest dynamics and functions. In the long term, this regime shift could locally increase tree diversity (Berteaux et al., 2010) and 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_insectes_2018), alter soil microbial activity (Laganière, Paré, & Bradley, 2010) and affect wildlife distribution (Mizel, Schmidt, Mcintyre, & Roland, 2016).

Such regime shifts will impact strongly 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, Québec (Province), Ministère des ressources naturelles et de la faune, & Consortium en foresterie Gaspésie-Les-Îles, 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 emphasise that forest management should consider the present system state in relation to its transient dynamics as well as its most likely trajectory. Our study also reveals the potential of moderate disturbances to catalyse climate-related transitions. This suggests that thoughtful logging practices could be used to reduce extinction debt and colonisation credit, and thus tree migration lags. Other studies also recommend to plant temperate trees farther north outside their current range to facilitate their migration [Duveneck & Scheller (2016); Vieira et al. in prep]. However, before implementing such silvicultural strategies, key questions need to be answered. For instance, will multiple interacting disturbances exacerbate tree mortality? Which species will be able to benefit from the opportunities created by canopy openings? And how will these rapid transitions feedback to ecosystem processes and functions? The rate of recent climate change already outpaces tree migration capacity (Sittaro et al., 2017), and even more so the scientific capacity to understand and mitigate its consequences (Jackson & Sax, 2010). Therefore, in order to insure long-term forest health at the boreal-temperate ecotone, we need to simultaneously limit global warming through drastic reduction of greenhouse gas emission and intensify research effort to develop effective adaptation strategies.

Acknowledgements

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