Moderate disturbances accelerate forest transition dynamics under climate change

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Running title

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Abstract [draft]

Several temperate tree species in North America are expected to expand their distribution northward, where the boreal forest is already established and dominated by conifers. However, these transitions from boreal to

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mixed and from mixed to temperate forests could be hampered by non-climatic factors, such as unsuitable soil conditions and competition by resident species.

In this paper, we describe the state transition dynamics of Quebec's forest communities in recent decades and identify the factors and processes that promote or prevent these state transitions. Specifically, we ask (1) Is forest transition dynamic affected by recent climate change? (2) How do disturbances and soil characteristics influence the transition probability among forest states under climate change? Can natural or anthropogenic disturbances accelerate climate related transitions? And, conversely, can soil characteristics constrain these transitions? (3) How do different disturbance type and intensity influence the transient dynamics and equilibrium distribution of forest states?

To answer these questions, we analyzed the transition dynamics in over 10,000 forest inventory plots of southern Quebec (1970-2016). Using a continuous time Markov multi-state model, we investigated the relationship between the transition probabilities between the different states of the forest community (temperate, boreal, mixed and pioneer) and variables related to climate, local soil conditions and disturbances. We also describe the long-term equilibrium state distribution under different disturbance scenarios, as well as the transient dynamics using complementary measures: the time to reach equilibrium, the turnover time and the entropy of the modeled system.

The transition probabilities are mainly related by natural and anthropogenic disturbances and secondarily to climatic variables, whereas soil characteristics (drainage and pH) were not a strong constraint. Moreover, moderate disturbances increased the probability of transition from Mixed to Temperate forests and thus accelerate long-term climate-induced transitions. [equilibrium... transient dynamic...]

Moderate disturbances were found to catalyze rapid transitions in forest communities and accelerate shift in response to recent climate change. In ecotones, areas of ecological tension, disturbances may provide opportunities for some migrating species to establish in otherwise competitive environments...

Keywords

Introduction

P1. Forest dynamics under CC

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

While tree climate niches are expected to shift northward by several hundred kilometers by the end of the century (McKenney, Pedlar, Lawrence, Campbell, & Hutchinson, 2007), multiple 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; Woodall et al., 2013). The slow response of forests to environmental changes is not surprising given that trees cannot walk, live for several decades to centuries and disperse over very short distance. Hence, if forests are undisturbed, the speed of transitions between forest biomes will be mainly limited by the natural turnover rate of the resident species as well as the dispersal and establishment rates of the migrating species (Neilson, 1993). However, as the disequilibrium between climate conditions and forest composition grows larger, alternative stable states become possible and forests may fail to return to their previous state following a disturbance (Johnstone et al., 2016).

P2. Disturbances

Both gradual and abrupt transitions from one biome to another will likely take place concurrently, but, as forests are increasingly subjected to both pervasive climatic stresses and direct human-related disturbances, catastrophic transitions are likely to play a dominant role in driving the climate shift in biomes. Established communities are generally though to be resistant to competitive displacement and resilient to commonly experienced disturbances (Grondin et al., 2018; Seidl, Rammer, & Spies, 2014). Resistance can be defined as the ability of an ecosystem to persist through time following a disturbance, whereas resilience is the capacity

to recover its pre-disturbance composition (Gunderson, 2000; Holling, 1973). Because the ability to persist and recover following a pulse disturbance (e.g., fire or logging) can be altered by a press disturbance (e.g., climate change), investigating resistance and resilience can provide precious insights into their interacting effects.

However, as climate change weaken forest resilience, disturbances can provide niche opportunities for migrating species and community composition can shift abruptly to species that are better suited to current conditions (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 favored the increase of warm-adapted species and led to a broad-scale community thermophilization of forests in Québec (Brice, Cazelles, Legendre, & Fortin, 2019). However, the coupling of warming and disturbances may depend on the intensity and type (natural or anthropogenic) of disturbances (Johnstone, Hollingsworth, Chapin, & Mack, 2010). Hence, in some cases, disturbances can promote invasions by early successional species which then displace long-lived shade-tolerant. For instance, clearcutting has been found to favor the expansion of 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). In contrast, other simulation studies have found that, although disturbances can influence some types of transitions, they are unlikely to drive extensive biome shifts in the coming decades (Liang, Duveneck, Gustafson, Serra-Diaz, & Thompson, 2018; Vanderwel & Purves, 2014). As a result, disturbances could accelerate shifts to an increasingly deciduous-dominated landscape, but empirical evidence of this process are necessary to understand how various intensities and types of disturbances may catalyze or hinder transitions between certain forest states.

other ref: Xu, Gertner, & Scheller (2012); Danneyrolles et al. (2019); Johnstone & Chapin (2003)

P3. Soil

The northward migration of temperate species might be further constrained by their capacity to colonize 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 rate of organic matter than warmer southern temperate forests (Goldblum & Rigg, 2010). These local and regional variations in soil properties (e.g., quality of drainage, availability of nutrients, pH, mycorrhizae) 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,

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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* seedling in boreal stands was high, even superior to that in the 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 could delay forest transition under climate change (Brown & Vellend, 2014) and, moreover, waterlogged conditions and deep organic matter accumulation may prevent the regeneration of several species (Lafleur et al., 2010). 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 dynamic, across species and across scales to better anticipate future biome transition.

P4. Markov multi-state models

One approach to investigating the process of biome shifts in response to climate change is to model transition probabilities of forest plots among states based upon the knowledge of their current state, as well as their current environmental characteristics. Given the unequivocal distinction between temperate and boreal forests, the dynamic of tree communities at ecotone can be adequately characterized using discrete functional and successional states, namely Boreal, Mixed, Temperate and Pioneer (Vissault, 2016) and thus can be formalized as a multi-state Markov model (Jackson, 2018). Markov models provide a useful framework for modeling changes of state over time using longitudinal data. In epidemiology, for example, the models are often used to describe the progression of diseases (Van Den Hout, 2016). In ecology, the models have been used to study processes such as ecological succession (Hill, Witman, & Caswell, 2004; Runkle, 1981), metapopulation dynamics (Hanski & Ovaskainen, 2003; Moilanen, 1999), landcover changes (Muller & Middleton, 1994; Yang, Zheng, & Chen, 2014), or stage class transitions (Caswell, 2008).

Despite the simplicity of a four-state transition model, this modeling framework allows to answer questions related to the coarse-scale dynamics of biome shift. Moreover, without explicitly modeling them, multi-state models represent mechanisms (Wootton, 2001). For example, transitions to pioneer reflect disturbance, transitions from pioneer reflect colonization, dispersal and recruitment limitation and transitions between the other states reflect competition. In addition to their simplicity, there exists numerous well-established properties of Markov transition matrices (Hill et al., 2004). Transition matrices can be estimated from the model output and their properties can then be compared under different scenarios to further explore the mechanisms of forest dynamics. For instance, the steady state distribution can be derived from a transition matrix and allow to infer the long-term forest composition [REF]. Multi-state models can not only be used to explicitly test hypotheses about equilibrium, but they can also be used to describe state changes during dynamic periods, i.e. transient dynamics (Boulangeat, Svenning, Daufresne, Leblond, & Gravel, 2018). As

most ecosystems never reach equilibrium (Holling, 1973), transient dynamics, especially in forests, may persist over very long time periods and are now thus recognized as crucial part of ecosystem dynamics [REF]. The time of convergence to reach the steady state distribution describes how fast the system converges; the turnover time indicates how fast the transitions occur and provides insights about the stability and the resistance of a forest state, while the entropy reveals the predictability of the transitions. 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 on management measures.

P5. Objectives

In this paper, we investigate the response of forests to recent climate warming by estimating the transition probability among four community states, boreal, mixed, temperate and pioneer. Specifically, we address these questions: 1. Is forest transition dynamic affected by recent climate change? 2. How do disturbances and soil characteristics influence the transition probability among forest states under climate change? Can natural or anthropogenic disturbances catalyze climate related transitions? And, conversely, can soil characteristics constrain these transitions? 3. How do different disturbance type and intensity influence the transient dynamics and equilibrium distribution of forest states?

We expect that the probability of self transitions will be the highest, i.e. most forests will not change states, because of tree slow demography. However, climate warming should promote more transitions from boreal to mixed forests and from mixed to temperate than the reverse. We also anticipate that natural and anthropogenic disturbances will further favor these climate-related transitions while soil characteristics will slow them down. We apply a time-continuous multi-state model to the dynamics of forest communities to estimate state transition probabilities and evaluate the influence of environmental covariates on these transitions. Using the result from our multi-state model, we investigate the impact of disturbances on forest equilibrium and transient dynamics under recent climate change using several measures: equilibrium state distribution, time to converge to equilibrium, turnover time and entropy.

Methods

Study area and forest inventory data

To investigate large-scale transition dynamics in forest communities, we used forest inventory plots in Quebec, Canada, which have been sampled approximately every ten years since 1970 and ongoing by the Ministère des forêts, de la Faune et des Parcs (MFFP, 2016). The study area extends from approximately 45° to 52°N of latitude (ca. 795 000 km^2) and covers six bioclimatic domains and three different forest subzones (Fig. 1).

The mixed forest (from 47°N to 48°N) marks the transition between the hardwood forest to the south, which is dominated by *Acer saccharum*, and the boreal forest to the north, which is dominated by *Abies balsamea* and *Picea mariana.*

We selected all inventory plots that were sampled at least twice as well as the ones where 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 recolonization. This yielded a total of 10,388 plots analyzed (Fig. 1). The time intervals between plot surveys varied from 4 to 43 years, with a mean time of 11 years ($\sigma = 3.85$).
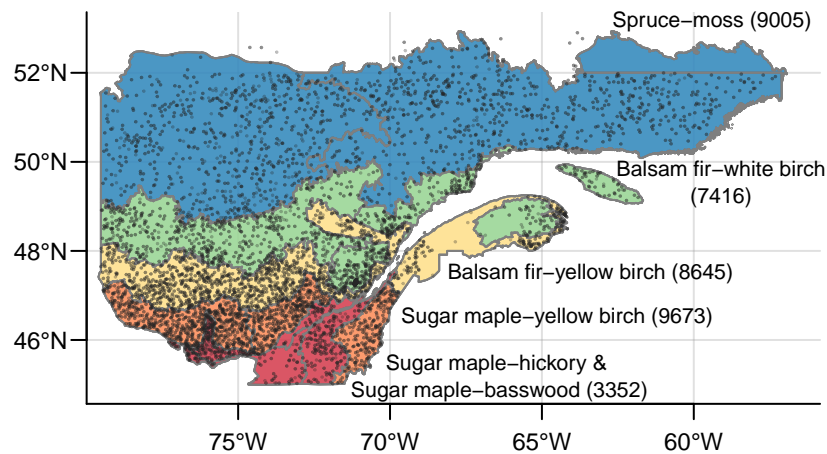

Figure 1: Locations of the 10,388 forest inventory plots in meridional Québec, Canada. Colors delimit the six bioclimatic domains. The two southernmost domains (red) are here combined. The number of forest plots in each domain is written in parentheses. The balsam fir-yellow birch domain is the ecotonal zone between hardwood and boreal forests.

Community states

We classified the forest inventory plots into four community states (Boreal, Mixed, Temperate and Pioneer) using species basal area and composition at each sampling date. We first assigned each studied species as boreal, temperate or pioneer according to their functional traits (see Table SX in Brice et al., 2019). For each plot, we computed the total basal area of each species group and then classified the plot following the MFFP (2016) definitions to one of the four states; Boreal (boreal species represent >75% of the plot basal area), Temperate (temperate species represent >75% of the plot basal area), Mixed (temperate and boreal species both occupy between >25% and <75% of the plot basal area) and Pioneer (pioneer species represent >75% of the plot basal area or plot total basal area <5m^2/ha). We analyzed state transitions between each consecutive plot survey. Based on this classification, from the 38,091 observations (plots x number of years measured), we observed 27,703 state transitions (Fig. 2).

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Environmental variables

The annual past climatic conditions, covering a period from 1960 to 2013, were extracted from a 2km^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 annual climate moisture index (CMI), which is the difference between annual precipitation and potential evapotranspiration (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. Over the past four decades, growing season temperature have increased by 0.14 °C/decade, while CMI has decreased by 1.2 cm/decade.

We also collected information pertaining to natural and anthropogenic disturbances that have affected the forest plots during the study period (Table 1). At each plot, the type of disturbances (21 types) and their level of intensity (moderate or major) were recorded (see Table S2 in Brice et al., 2019; MFFP, 2016). The MFFP defined major disturbances as events that have eliminated more than 75% of the 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 affects nutrient availability, soil structural properties and vegetation development [REF]. These two variables also capture most of the variance in soil characteristics in plots across Quebec and were orthogonal in a PCA (not shown).

Table 1. Description of the covariates used in the multi-state models.

Covariate name	Covariate description
Climate	
Temp	Mean temperature during growing season, 10-year average prior to first measurement (°C).
CMI	Mean annual Climate Moisture Index, 10-year average prior to first measurement (cm).
Soil	
pH	pH of of the surface horizon
Drainage	7 classes of soil drainage, which range from excessive to very poor, that were treated as numeric.
Disturbances	

Covariate name	Covariate description
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 (0), moderate (1) or major (2).

Analysis

NB: very detailed... where can we cut?

NB2: Lot of mathematical equations with different letters... verify if everything matches!

Continuous-time multi-state Markov model

We derived our modeling framework from methods widely used in survival analysis and disease progression model (Jackson, 2018; Van Den Hout, 2016). Similarly to Vissault (2016), we formalized forest dynamics as a four-state model, but here we used a continuous-time multi-state model (Jackson, 2018) in which transitions among states depend on the previous state, time interval, climate, disturbances and soil characteristics (Fig. 2).

In ecology, Markov models are often built using discrete time steps. However, because (1) time interval between surveys are irregular, (2) for each time interval, multiple transitions are possible and (3) the exact times of state changes are unobserved (i.e. observations are interval-censored), a continuous-time Markov model, in which time is treated as continuous, is preferable. Given observations at fixed time intervals, a homogeneous continuous-time Markov chain is a special case of a discrete-time Markov chain.

For states $r, s \in B, M, P, T$ and time $h, t \geq 0$, transition probabilities (p_{rs}) are defined as the probability that a plot in state r at time h is in state s at time $h + t$ and can be denoted by:

$$P_{r,s}(h,t) = P(S_{h+t} = s | S_h = r).$$

The Markov process is assumed to be time homogeneous, meaning that the transition probabilities are constant over time (i.e. independent of t, but dependent of the time interval), hence $P(S_{h+t} = s | S_h = r) = P(S_t = s | S_0 = r)$. However, this assumption can be relaxed (see below). In a four-state transition model, the transition probability matrix $P(t)$ is a 4×4 matrix, where the rows are the current state and the columns the future state, containing the transition probabilities $p_{rs}(t)$ for a specified time interval. For a time-homogeneous model, $P(t)$ can be solved by taking the matrix exponential of the intensity or generator matrix Q scaled by the time interval:

240 $P(t) = e^{tQ}$

241 The intensity matrix Q contains transition intensities $q_{r,s}$ which represent the instantaneous risk of moving

242 from state r to state s:

243 $q_{r,s} = \lim_{\Delta \to 0} \frac{P(Y_{t+\Delta}=s|Y_t=r)}{\Delta}$, on off-diagonal elements.

244 $q_{r,r} = -\sum_{s \neq r} q_{rs}$, on diagonal elements.

245 Transition-specific hazard regression models can be defined for those $r, s \in S$ between which a direct transi-

246 tion is possible according to the specified multi-state process (Fig. 2). The intensities $q_{r,s}$ can be modeled as

247 a combination of a baseline hazard $q_{rs.0}$ with a vector of explanatory variables $x(t)$ and a vector of coefficients

248 β_{rs} :

249 $q_{rs}(t) = q_{rs}(t|x(t)) = q_{rs.0}(t)exp(\beta'_{rs}x(t)),$

250 The definition of the log-linear regression hazard model allows to fit a site-specific and time-dependent

251 covariate vector $x(t)$ to transition intensities. Time-dependent covariates, such as climate and disturbances,

252 are assumed to be piecewise-constant, i.e. the hazard is constant within a specified time interval $[h, h+t]$ and

253 depends on the covariate value at h, but is allowed to change between the intervals. The time homogeneity

254 assumption is thus relaxed by the inclusion of time-dependent covariates in the model.

255 Estimation of model parameters can be obtained by maximizing the log-likelihood function using the tran-

256 sition probability matrix. The contribution of the plot i at time j to the likelihood is given by:

257 $LL_i(\theta|s, x) = \prod_{j=1}^{J} P(S_j = s_j | S_{j-1} = s_{j-1}, \theta, x),$

258 where θ is the vector with all the model parameters, x denotes the vector with the covariate values, and s

259 denotes the observed state trajectory $s_1, ..., s_J$ at times $t_1, ..., t_J$. The full likelihood function is the product

260 of contributions for all N plots:

261 $LL(\theta) = \prod_{i=1}^{N} LL_i(\theta|s, x),$

262 **Definition of candidate models**

263 It is important to consider which transitions can realistically occur in continuous time. Because the states

264 are defined based on the proportion of each species group, it is assumed that in order for a site to travel

265 from one state to a non-adjacent state, the plot also has to travel through the intermediate states. Thus,

266 in this model, we assumed that an instantaneous transition from Boreal to Temperate and from Temperate

267 to Boreal is impossible (necessary transition through Mixed), however all states can transition directly to

268 Pioneer when disturbed (Fig. 2).

269 We built five different models: one baseline model with intercept only, one for each subgroup of covariates

270 independently (climate, soil and disturbances) and one full model that is a combination of all the covariates

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(Table 1). Because we estimate multiple state transitions in a single model (all q_{rs} in Fig. 2), the number

272 of parameters increase rapidly with the number of covariates (number of modeled transitions (here 10) $\times$

273 number of covariates). Thus, to reduce the number of parameters, we hypothesized that transitions from any

274 state to Pioneer were only determined by disturbances while climate and soil variables should not directly

275 influence these transitions. All quantitative variables were standardized ($\mu = 0$, $\sigma = 1$) prior to running the
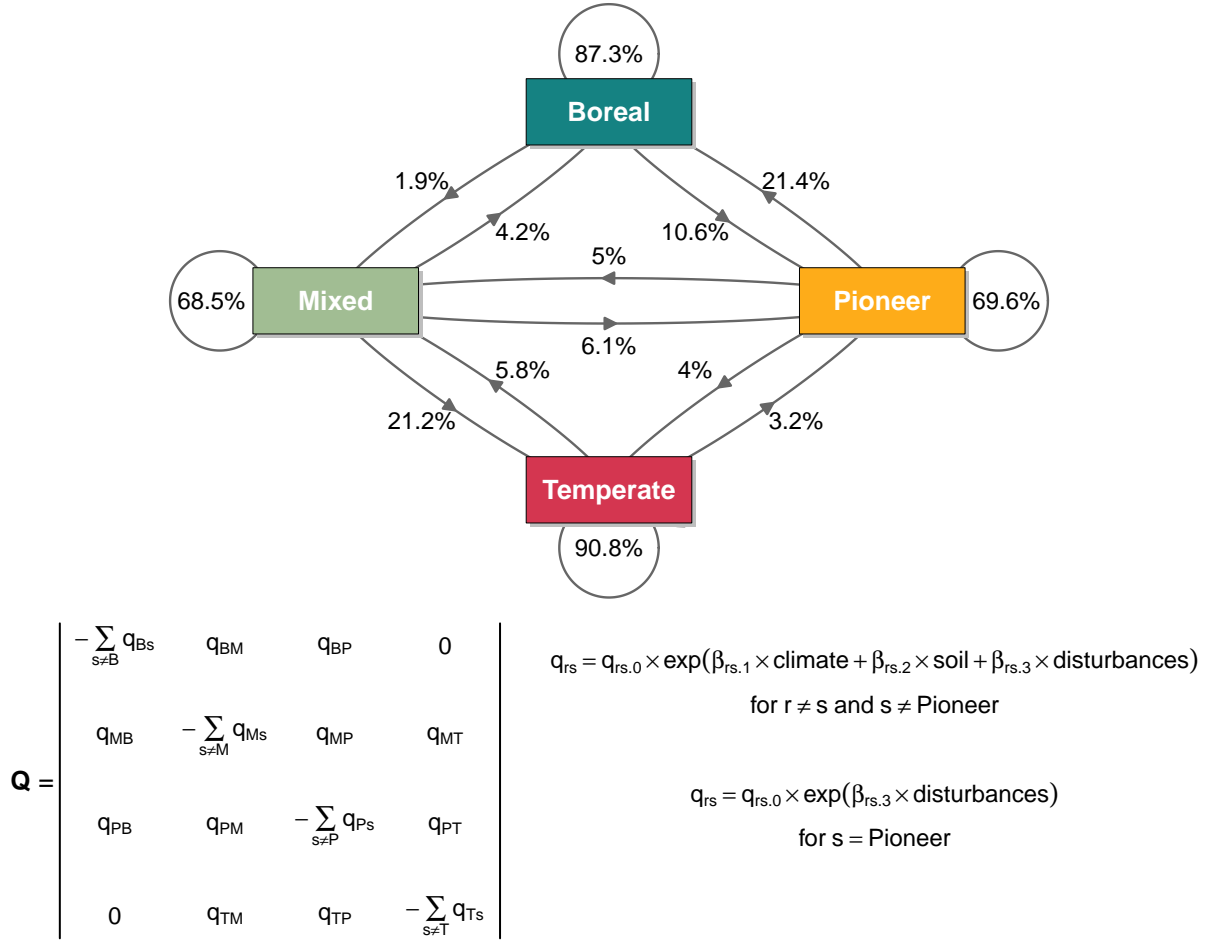
276 models.

Figure 2: Multi-state transition diagram (a), intensity matrix (b) and equations of our full model (c). Directional arrows in (a) depict the allowed transitions between states. The numbers represent the percentage of observed transitions between states ($nb_{rs}/nb_{r.}$ x 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%). All transitions from any states to Pioneer were modeled only as dependent of disturbances.

Evaluation of candidate models

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 test if the addition of one or more new parameters significantly increases the likelihood of the model. The statistical significance of individual covariates in the presence of the other was determined by comparing the full model with the correspondingly reduced model using likelihood ratio tests.

Prediction performance of candidate models

We fitted all models on the full data sets but also used cross-validation to estimate the predictive performance on held-out data. We used two statistics, the area under the receiver operating characteristic (ROC) curve (AUC) and the logarithmic scoring rule (LS), to assess the agreement between the observed state and the models' predictions. The AUC is a popular performance metric for binary classifiers that measures the probability of correct ranking of a random positive-negative pair. The AUC ranges from 0 to 1, where a score of 1 indicates perfect discrimination, while a score of 0.5 is as good as random. Hand & Hill (2001) has extended the AUC method to multi-class problems, here denoted mAUC. For any pair of states r and s, we can compute $\hat{A}(r|s)$, the probability that a randomly drawn member of state s has a lower estimated probability of belonging to state r than a randomly drawn member of state r. We can measure the discrimination rate between all pairs of states by computing the pairwise AUC:

$$\hat{A}(r,s) = [\hat{A}(r|s) + \hat{A}(s|r)]/2$$

The mAUC can be obtained by averaging the pairwise AUC:

$$mAUC = \frac{2}{c(c-1)} \sum_{r<s} \hat{A}(r,s)$$

The LS was proposed by Good (1952) and is often used in weather forecasts (Gneiting & Raftery, 2007). While AUC is a function of different classification thresholds, LS measures the degree to which predicted probabilities are close to the observed outcomes. We computed a global score for each model:

$$LS = \frac{1}{N} \sum_{i=1}^{N} -log(P(S_i = s_i))$$

where S_i is the random variable describing the state of the forest in the ith plot and s_i is the observed state. So, LS only depends upon the predicted probability of the realized state and not on the probabilities assigned to the other possible states. The score is very sensitive to incorrect predictions: if a model predicted the

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observed state with a probability of 100%, the score for that plot is 0, while if a probability of zero was assigned to the observed state, the score goes to infinity. Hence, this sensitivity allows to emphasize the differences between model predictions and strongly penalize a model that only gives high probabilities to self transitions.

To assess the quality of prediction for the four states individually, we also computed LS for each state r where we summed the predicted probability $P(S_i = r)$ if the observed state is indeed r and $1 - P(S_i = r)$ otherwise.

We evaluated and compared the predictive performance of our five models using the overall mAUC and the pairwise AUCs, as well as the overall LS and the state-specific LS. These metrics were estimated using stratified K-fold cross-validation [REF]. We first stratified the data set by bioclimatic domain to ensure that each fold was representative of the plot geographical distribution and randomly split the data set in k=10 folds. The cross-validation process was repeated k times, during which k − 1 folds were used to train the models and the remaining fold was used to validate the model predictions against the observed state transitions. The cross-validated performance metrics were then averaged for each model.

Effects of covariates on the transition dynamic

Using the result from the best model, we compared the estimated hazard ratios to investigate the influence of environmental covariates on transition dynamic. We also computed the predicted 10-year transition probabilities of forest plots under different disturbance scenarios, while keeping all other covariates at their average found in the ecotonal zone (i.e. the balsam fir-yellow birch domain), to facilitate visual interpretation of the impacts of disturbances on the matrix structure.

To further understand how disturbances can modify the forest dynamic under climate change, we characterized different properties of the transition dynamic 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, 2001; Hill et al., 2004) and these properties can also be measured for continuous time Markov models. We chose 4 informative and complementary properties that fully characterized the dynamic of our modeled system: (1) the steady state distribution, which corresponds to the long-term equilibrium state distribution of the system; (2) the time of convergence to the steady state; (3) the turnover time, which measures the speed of transient successional changes; and (4) the entropy, which captures the predictability of transitions.

First, we estimated the steady state distribution, π. For a regular Markov process, any initial state distribution $s(0)$ converges to the same equilibrium as t tends toward infinity:

$$\lim_{t \to \infty} s(0)P(t) = \pi$$

The vector of equilibrium π can be obtained by taking the left eigenvector of Q with eigenvalue 0, normalized to sum to 1 or by taking the dominant eigenvector of P with eigenvalue 1, normalized to sum to 1 [REF].

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

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

where λ_{P1} and λ_{P2} are the largest and second-largest eigenvalues of P ($\lambda_{P1} = 1$ for stochastic P) and λ_{Q1} and λ_{Q2} are the largest and second-largest eigenvalues of Q ($\lambda_{Q1} = 0$ for stochastic Q). The half-life to equilibrium is given by:

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

We also measured the turnover time in each forest state, also called the mean 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 generator 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 predictability 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). The jump matrix contains the probabilities that the next state after state r is state s:

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

where qrs is the transition intensity from r to s. 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 $H_{max} = log(n_{state} = 4)$:

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

Values of entropy closer to zero indicated a more deterministic transition dynamic and values closer to one indicated a more random dynamic.

All analyses were performed using the R programming language version 3.5.1 (R Core Team, 2018). The list of R packages that have been used throughout the analysis is provided in the Supporting Information (Table

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S1). All the data used in the study, in addition to R scripts to reproduce the analyses and the figures, will be made available online on Github unpon manuscript acceptance.

Results

Note: standardize verb tense + add letters to panel figures

Transition dynamics

In this study, there are a total of 38,091 surveys that were recorded for the 10,388 forest plots. At the beginning of the surveys, there were 4567 forest plots assigned as Boreal, 1143 as Mixed, 2712 as Pioneer, and 1966 as Temperate. At the end, there were 4795 Boreal plots, 1106 Mixed plots, 2176 Pioneer plots and 2311 Temperate plots (Fig. 2; Table S2). A large fraction of Mixed forests transitioned to Temperate forests (21.2%) but few did the opposite (5.8%). There were many transitions between Boreal and Pioneer, but more Pioneer recovered to Boreal than the reverse. Temperate and Boreal forests were generally more stable (large fraction of forests did not transition) than Mixed and Pioneer forests (Fig. 2).

Model evaluation

Overall, the full model including climate, soil and disturbance variables had the best fit and predictive performance (Fig. 3; 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 evaluation using 10-fold cross-validation revealed that including climate and disturbances improved overall model predictive performance (mAUC and LS), while soil variables had a negligible effect (Fig. 3). All models were good at distinguishing Boreal from Temperate (high pairwise AUC). Soil variables slightly help to predict Mixed and Temperate states. Including climate variables help to distinguish Mixed from the other states, while including disturbances help to distinguish Pioneer from the other states, especially Boreal. Hereafter, all inferences about transition probability parameters were derived from the full model.

AND/OR

OR

Table 2. Comparisons of the five candidate multi-state models. The number of parameters used in each model corresponds to the number of modeled transitions (10) $\times$ the number of covariates. The ΔAIC is the difference between the Akaike information criterion of each model (AIC_m) and the minimum of AIC among all the models (AIC_min): $\Delta\text{AIC} = \text{AIC}_\text{m} - \text{AIC}_\text{min}$. Multi-class area under the curve (mAUC) and
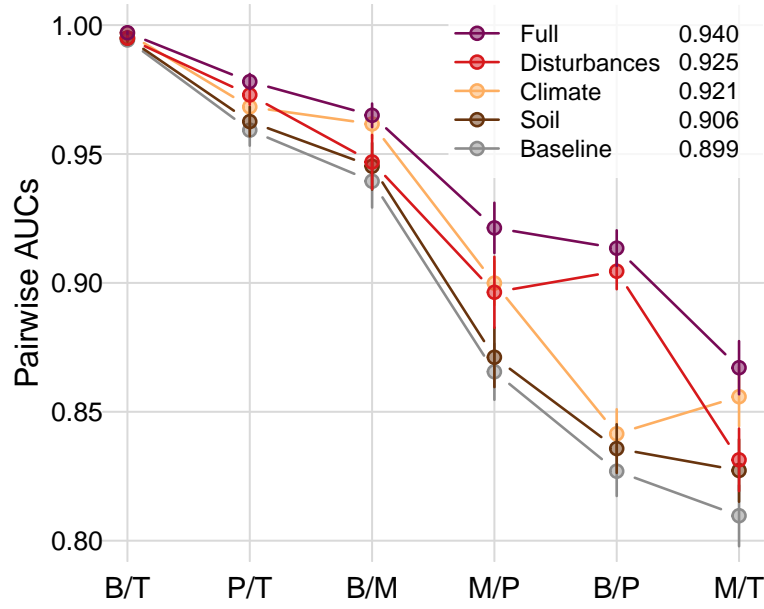
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Figure 3: Mean pairwise AUC (areas under the receiver operating characteristic curves) obtained through 10-fold cross-validation. Higher values indicate a better capacity to discriminate between the four forest states: (B)oreal, (M)ixed, (P)ioneer and (T)emperate. The overall mAUC of each model is given next to the legend.
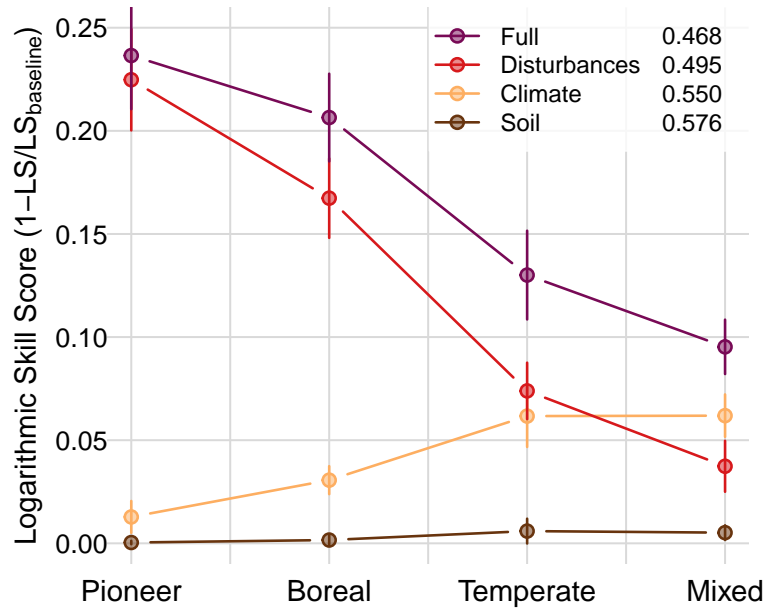

Figure 4: Mean state-specific logarithmic skill score where each model including covariates is compared to the baseline model. Values were obtained through 10-fold cross-validation. Higher values indicate a larger improvement (predicted probabilities are closer to the observed outcomes) compared to the baseline model. The overall logarithmic score of each model is given next to the legend.
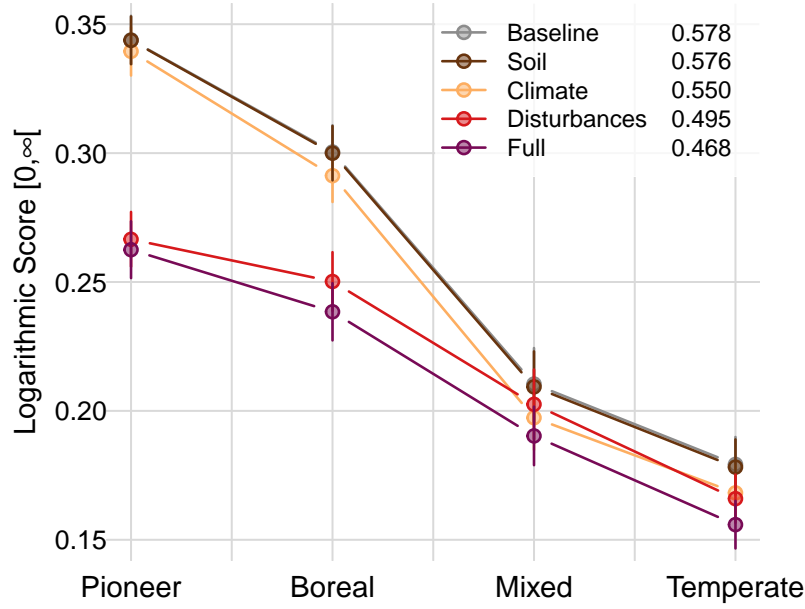
Figure 5: Mean state-specific logarithmic score obtained through 10-fold cross-validation. Lower values indicate that the predicted probabilities are closer to the observed outcomes. The overall logarithmic score of each model is given next to the legend.

logarithmic score were obtained through 10-fold cross-validation. Higher mAUC and lower LS indicate better model predictive performance. The best model is the one in bold with ΔAIC $= 0$.

	Covariates	Nb of parameters	-2 Log-likelihood	ΔAIC	LR test	mAUC	LS
Baseline	Intercept	10	32032.3	6132.6	< 0.001	0.899	0.578
Climate	Temperature, CMI	24	30438.7	4566.9	< 0.001	0.921	0.550
Soil	Drainage, pH	24	31886.9	6015.2	< 0.001	0.906	0.576
Disturbances	Natural, Logging	50	27341.3	1521.6	< 0.001	0.925	0.495
Full	**All**	**78**	**25763.7**	**0.0**	< 0.001	**0.940**	**0.468**

Effect of covariates on transition intensity

The full multi-state model allows to reveal interesting relationships between probabilities of forest state transition and environmental covariates. All transitions to Pioneer were highly influenced by disturbances (Fig. 4). As expected, major disturbances exert stronger effects than moderate disturbances (for both natural and logging), but logging had stronger effects for both levels of intensity. For example, the risk of transition from Boreal to Pioneer has surged up to 165 times higher for plots that suffered major logging (logging 2) compared to that which were not disturbed (minor). Disturbances of all types and intensities favored transitions from Mixed to Temperate forests. Major disturbances increase the risk of transition from Mixed to Temperate by ca. 5 times (Hazard Ratio (HR) = 4.51 and 5.32, for natural and logging, respectively). Moderate disturbances (natural and logging) also favored transitions from Boreal to Mixed (HR = 2.80 and 2.78, respectively), while major disturbances had no significant effect.

Climate variables also had a significant influence on most transitions (Fig. 4). Warmer summer temperature (higher sTP) and higher humidity (higher CMI) favored the 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.

Although less important (Fig. 3), soil variables also impacted state transitions (Fig. 4). Holding the other covariates constant, poorer drainage (more humid) decreased the instantaneous risk of transition from Boreal to Mixed by 29% and from Pioneer to Temperate by 17%, but increased the risk of transition from Temperate to Mixed by 32% (HR = 0.71, 0.83 and 1.32, respectively). Higher pH (acidic soil) had a considerable negative effect on the transitions from Temperate to Mixed and a smaller one on transitions from Pioneer to Boreal (HR = 0.80 and 0.93, respectively). These changes in risk ratio associated to soil variables appear almost irrelevant compare 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 estimated risk of transition from Boreal to Mixed is 2.12 (1.04-4.33) at moderate drainage but decreases to 1.50 (0.71-3.20) when increasing drainage by 1 point.
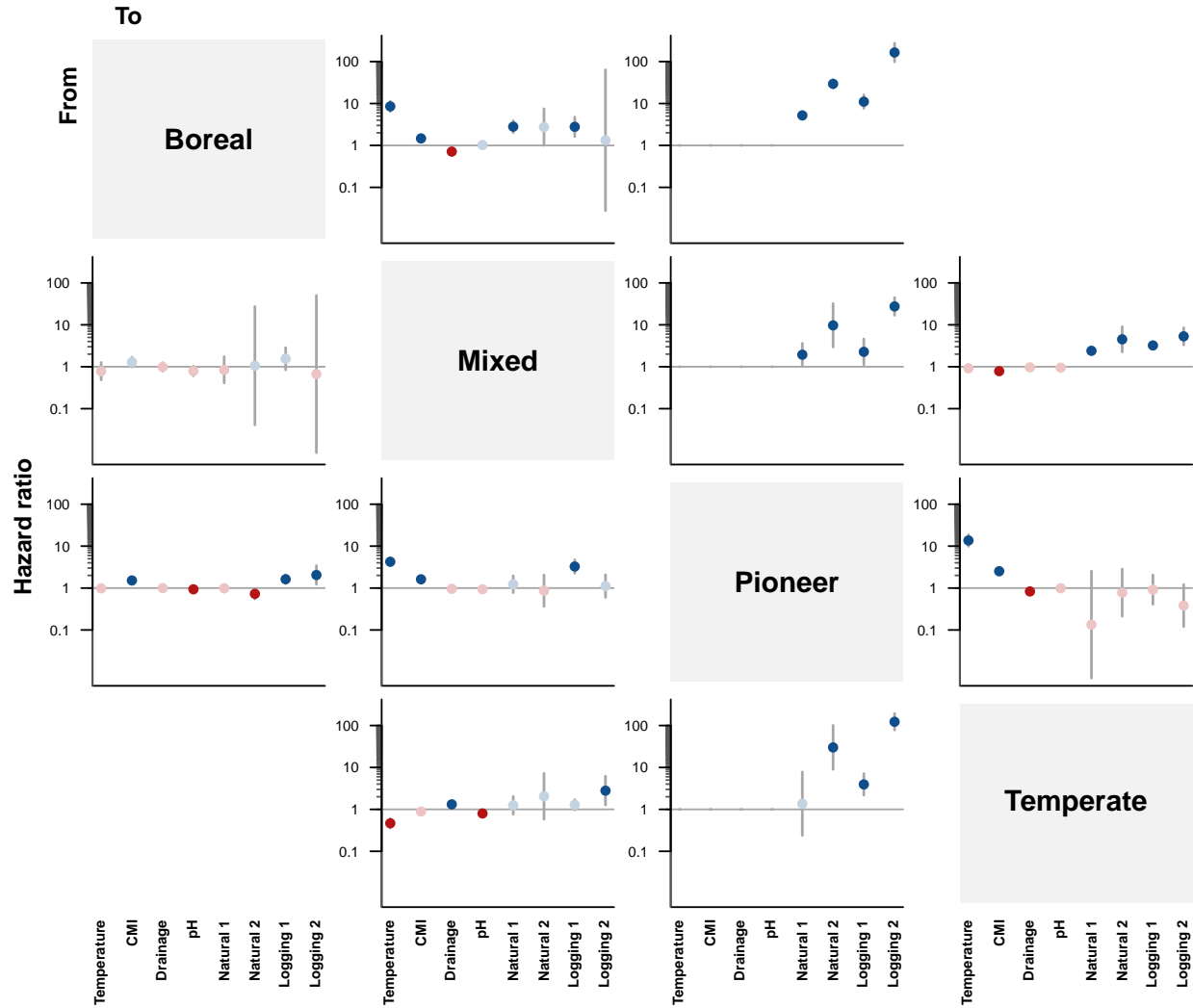
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Figure 6: Hazard ratios (HR) and 95% confidence intervals as estimated from the best multi-state transition model. The y-axis is in log scale. The HR of predictors are interpretable as multiplicative effects on the hazard, where values above 1 (in blue) indicate that the predictor is associated with a greater risk of state transition, while values below 1 (in red) indicate a lower risk of transition. Predictors different from 1 are colored 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 (characterized by the average environmental conditions of ecotone) remain in the same state after 10 years. For undisturbed forest plots (minor), the self transitions are very strong but transitions from Pioneer to Boreal, from Mixed to Temperate, and from Temperate to Mixed were not trivial. At moderate disturbances, probabilities of self transitions decrease, while transitions from Boreal to Pioneer, from Mixed to Temperate increase the most. Transitions from Mixed and Temperate to Pioneer do 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 emerges only at major disturbances. For both types of major disturbances, the probabilities in the third column, transitions to Pioneer, showed a great increase compare to moderate disturbances, but these values exploded in severely logged transition matrix, exceeding self transitions. Interestingly, the estimated probability of Mixed to Temperate remain quite high at major disturbances.
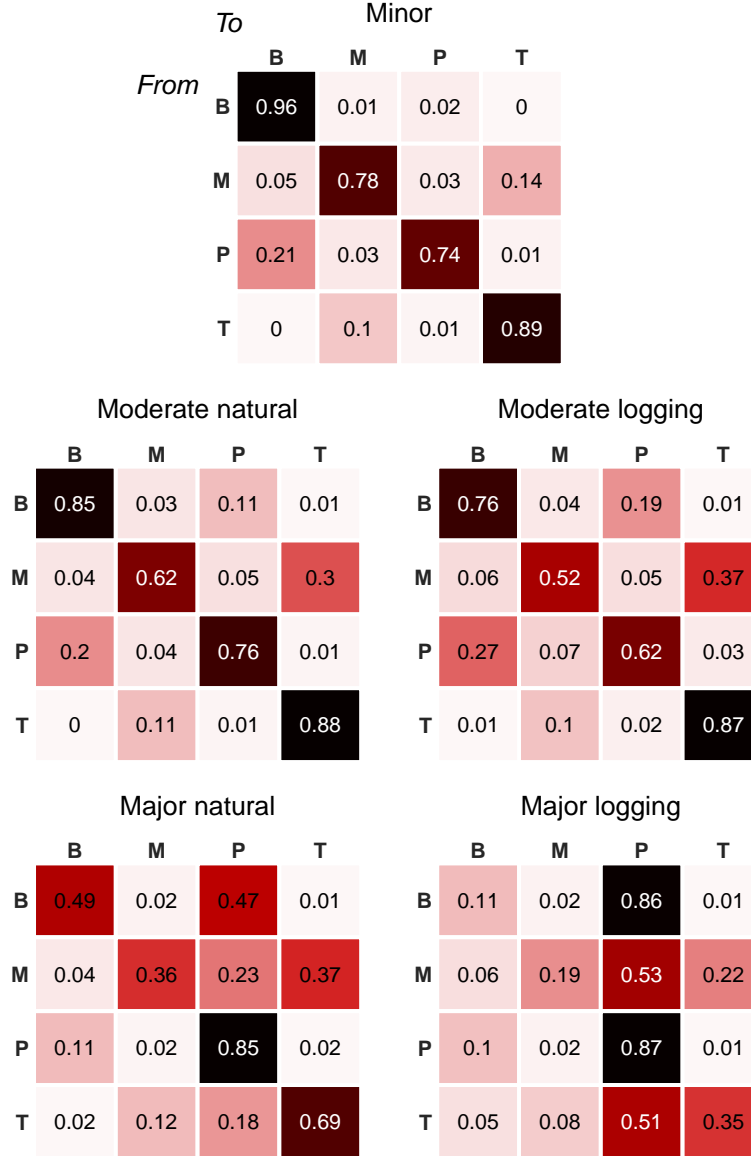
Figure 7: Predicted change in 10-year transition probabilities for different disturbance types and levels. All other covariates are fixed at the average conditions found in the ecotone, i.e. the balsam fir-yellow birch domain. Letters correspond to the four forest states: (B)oreal, (M)ixed, (P)ioneer and (T)emperate. Numbers are the modeled transition probabilities from rows to columns and darker color highlights stronger transitions.

Effect of disturbances on long term equilibrium

The steady state forest dominance changes as expected along the temperature gradient (Fig. 6); the Boreal state dominates at low temperature (high latitude) and Temperate and Mixed states dominate at high temperature (low latitude), with a transition boundary located at a growing season temperature of about 12.75°C, which falls in the ecotonal balsam fir-yellow birch domain. When moderate disturbances were included, the steady state proportion of Temperate and Mixed forests increases and the Boreal-Temperate boundary occurred at lower temperatures, hence further north in the balsam fir-white birch domain (Fig. 6). Moderate natural disturbances and logging had a similar positive effect on the proportion of Temperate and Mixed. For example, at 12.58°C, northern end of balsam fir-yellow birch domain, the steady state proportion of Temperate and Mixed almost doubles with moderate disturbances (minor: 36%; moderate natural: 58%; moderate logging: 60%). However, because there was a larger reduction in the proportion of Boreal to the benefit of Pioneer, the displacement of the boundary was slightly larger for logging than natural disturbances (displaced at 12.05°C for logging and at 12.18°C for natural disturbances; Fig. 6). Finally, for major disturbances, the proportion of Boreal forests at steady state collapsed while that of Temperate and Mixed forests also decreased to a lesser extent. The landscape is now dominated by Pioneer forests. The boundary modestly moved north with major natural disturbances (12.60°C), while it retreated to the south with major logging (13.05°C). Simulating change in frequency of disturbances (instead of all or nothing scenarios) shows that the Boreal-Temperate boundary slowly moved north with increasing moderate disturbance frequency (natural or logging), but it stagnates with increasing frequency of major natural disturbances and recedes south with increasing frequency of major logging (Fig. S3).

Effect of disturbances on transient dynamics

Natural disturbances and logging 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 a slow transition dynamic in forests of northern latitudes (Fig. 7a,b). The turnover time then rapidly declines to reach a minimum at 13.20°C, between the sugar maple-yellow birch and the balsam fir-yellow birch domains, and goes back up after this point. This trough, where transition dynamics are the fastest, is located just a little south of the point of transition between Boreal and Temperate dominance found in Figure 6. Major disturbances accelerate transition dynamics all along the temperature gradient, while moderate disturbances also decrease turnover time but more strongly in the boreal domains (balsam fir-white birch and spruce-moss domains; Fig. 7a,b). These spatial patterns reflect the turnover time of the dominant state at each point along the temperature gradient (Fig. S4).

At minor disturbances, the entropy of the system generally increases from north to south and peaked at 12.56°C, at the southern end of the balsam white-birch domain (Fig. 7c,d). This peak illustrates where
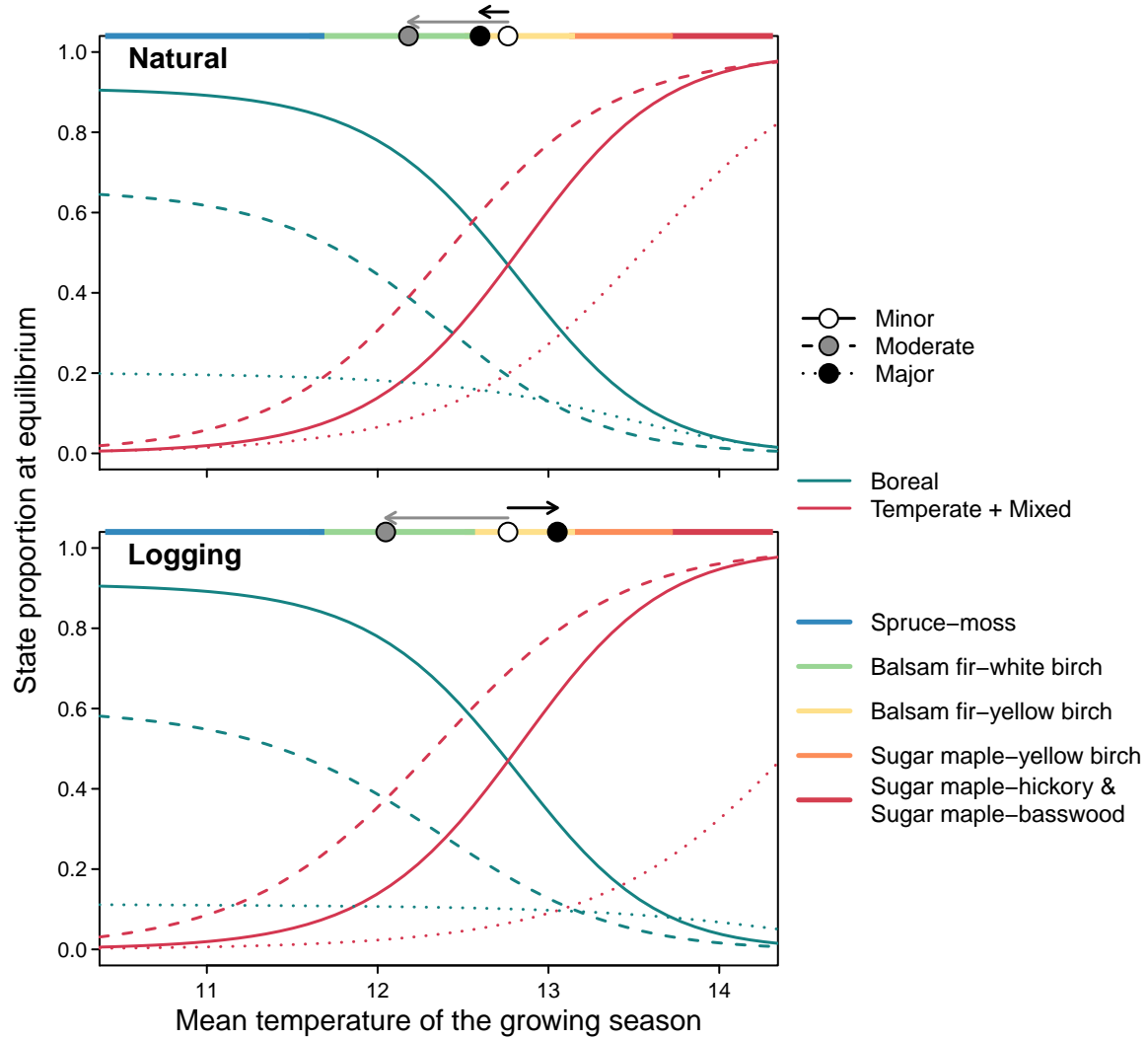
Figure 8: Changes in forest state proportion at equilibrium along the temperature (latitudinal) gradient for different disturbance scenarios. Proportion of Boreal (blue) and Temperate + Mixed forests (red) for minor (solid), moderate (dashed) and major (dotted) disturbances. All other covariates are fixed at the average conditions found in the ecotone, i.e. the balsam fir-yellow birch domain, to focus solely on the effect of disturbances along the temperature gradient. The white (minor), grey (moderate) and black (major) circles indicate the position of the boundary between dominance of Boreal forests and dominance of Temperate and Mixed forests (i.e. the advancing front). The colors at the top of the plots approximate the position of the bioclimatic domains along the temperature gradient.

the transition dynamic 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 and the generally high values at high temperature can be principally attributed to the Temperate state (Fig. S5). This latitudinal pattern of entropy is modified by disturbances. Moderate natural disturbances decrease the entropy throughout the gradient, but especially where was the peak (Fig. 7c). With moderate logging, the peak disappears and entropy increases monotonically from north to south (Fig. 7d). When major disturbances are included, wether natural or logging, the peak of entropy is displaced to the south (Fig. 7c,d) where it is dominated by the entropy of the Pioneer state (Fig. S5).

The half-life to equilibrium is the longest at 12.24°C, in the balsam fir-white birch domain, while it is the fastest in the southernmost latitudes (Fig. 7e,f). Interestingly, the peak for half-life closely matches the peak for entropy, but matches no feature of the turnover time curve. Moderate disturbances flatten and shift this peak to the north and the effect of moderate logging (Fig. 7f) is stronger than natural disturbances (Fig. 7e). Hence, in the balsam fir-white birch, the half-life to reach equilibrium distribution is 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

P1. Main results

Our study reveals that disturbances are likely to accelerate forest response to climate change by promoting transitions from boreal to mixed forests and, particularly, from mixed to temperate forests. Our analysis of the equilibrium further highlights that the long term forest dynamics under moderate disturbances favors 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, 2010; Vissault, 2016), our findings demonstrate that moderate disturbances catalyze transition to alternate, temperate-dominated forest state and, as a result, promote regime shifts.

P2. Is forest transition dynamic affected by recent climate change?

Our results seem to support the hypothesis that recent climate warming influences transition dynamics among forest states at the boreal-temperate ecotone. The higher number of transitions from mixed to temperate
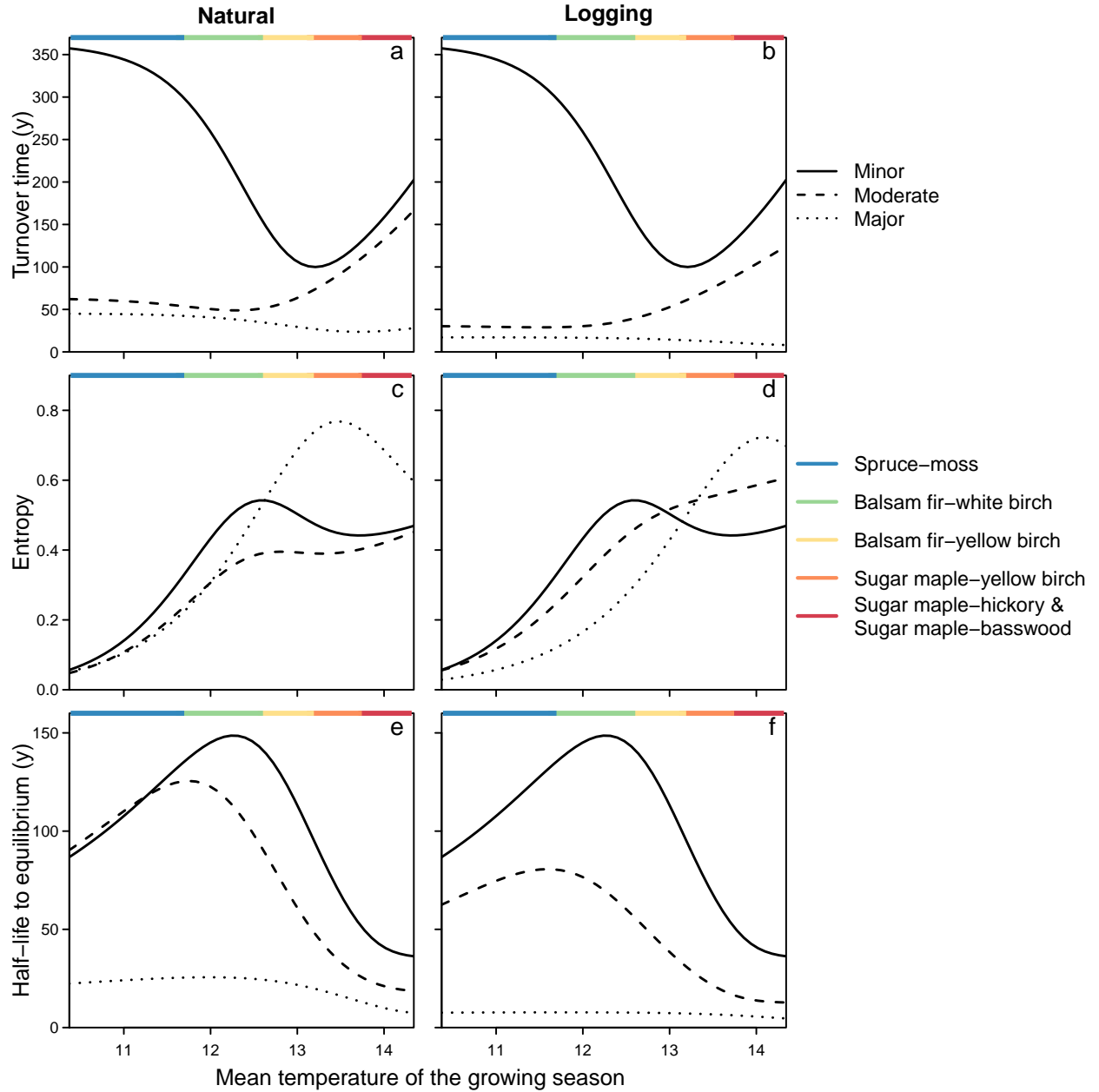
Figure 9: Changes in the characteristics of the forest transient dynamics along the temperature (latitudinal) gradient for different disturbance scenarios: minor (solid), moderate (dashed) and major (dotted) disturbances for both natural (a,c,e) and logging (b,d,f). All other covariates are fixed at the average conditions found in the ecotone, i.e. the balsam fir-yellow birch domain, 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 incertitude 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 to become twice as great as the contribution of the second eigenvalue. The colors at the top of the plots approximate the position of the bioclimatic domains.

is consistent with the expectation of a northward shift in range of temperate trees species into the mixed and boreal forests. Indeed, the warming trends of the last decades (fig supp?) have been shown to improve growth and reproductive rates of temperate species, but to reduce growth of boreal species (Boisvert-Marsh, Périé, & Blois, 2019; Fisichelli et al., 2014; Goldblum & Rigg, 2005; Reich et al., 2015), thus providing a competitive advantage of temperate over boreal species.

Alternatively, the increased transition to temperate species may be a response to other pressures. Comparisons of pre-settlement and present-day forested landscape of North America have demonstrated an important deciduous encroachment in response to historical human activities (Boucher, Arseneault, & Sirois, 2006; Danneyrolles et al., 2019; Terrail et al., 2019). Similarly, Johnstone & Chapin (2003) suggests that the northern range expansion of lodgepole pine following fire is not related to current climate change, but was rather a continued migration initiated in the early Holocene. However, historical legacies and climate change are likely mutually non-exclusive explanations. 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.

P3. Environmental catalysts and inhibitors of forest state transition

Our study demonstrated that moderate disturbances favor climate-related transitions, while major disturbances merely promote pioneer states. Disturbances directly remove trees which lead to immediate and substantial changes in forest composition and successional trajectories. Without climate change, forests are expected to be resilient to normally experienced disturbances and should thus return to their previous states. However, climate change alters the conditions that initially supported the persistence of a forest state, making them more vulnerable to disturbances (Johnstone et al., 2016). Hence, moderate disturbances remove resident species and reduce competition for light and nutrient, which likely facilitate colonization 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, create openings of very large extent which likely favor early-successional species that can disperse seed over long distances, such as *Populus sp* and *Betula sp* (Landhäusser et al., 2010).

Compared to the catalyzing effect of disturbances, soil characteristics do not appear as a large impediment to state transition but have the potential to slow down transitions. 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 to colonize hydric boreal soils. Very poor drainage, often associated with peatland and thick organic layer, is indeed considered as one of the only major edaphic limit for the regeneration of temperate species (Lafleur et al., 2010). Numerous studies found that *Acer saccharum* regenerate well across the ecotone because of its large tolerance to 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 hypothesized to be mostly limited by 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).

P4. Equilibrium and potential range limits

Our model highlights the potential role of disturbances in controlling 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 predictions of the future, they are useful to highlight the direction of the forest dynamic. Our results 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 accelerate the expansion of pioneer forests, but have little or no effect on extensive biome shifts over the next century in eastern United States. These apparently conflicting results could be due to the contrasting tree species responses to disturbance. 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.

- *Can we really compare?

- in all disturbance scenarios, boreal forests are losing ground primarily to pioneer forests

- Similar to Liang et al. (2018) and Vanderwel & Purves (2014) We also predict that major disturbances will only promote pioneer states to the detriment of boreal states…

Other results: Simulations by Vieira showed that plantation and enrichment planting shifted northward

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the boreal-temperate range limits, but not harvesting. Thinning increased the transition from mixed to temperate stands, but did not have any effect on range limits shift.

Boulangeat et al. (2018) even predicted a southern shift of the boreal-temperate boundary when including the effects of herbivores.*

P5. Transient dynamics

Help! Not sure how to interpret these results!

Beyond their impacts on steady state distribution, 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 characterized by a dynamic of stand self replacement with minimal compositional changes across disturbance cycles (Goldblum & Rigg, 2010). Consistent with this dynamic, the turnover time of undisturbed northern boreal forests is very long and the entropy very low. The turnover becomes very rapid with disturbances, but the entropy remains low indicating that the dynamic is still as predictable (back and forth transitions between boreal and pioneer states) and that there is no shift dynamic associated with disturbances. Hence, while resistant at low disturbances, boreal forests loose their resistance when moderately disturbed but remain resilient as they return to their previous boreal state. Under major disturbances, boreal forests collapse to pioneer state and reach this new equilibrium swiftly (short half-life). This interpretation 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 characterized by a rapid turnover and a high entropy indicating abrupt compositional shift which can go in all directions, hence this zone is neither resistant nor resilient. Compared to northern boreal forests, the short turnover time implies a low persistence, hence a low resistance, of the forest states in this region even under minor disturbances. This result corroborate the predictions made by Vissault (2016), where mixed forests undergo a swift conversion to temperate forests in the next decades whereas boreal forests present a large amount of inertia. The dynamic of the ecotone appear unstable because it is caught between the 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 (Fig. 6), hence the entropy is decreased and the dynamic becomes more predictable. Such a clear directional shift strongly indicates a non-equilibrium dynamic 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.

- *implication for resilience and resistance

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- long turnover = high persistence = high resistance?
- high entropy = low stability/resilience?

- Compare to Boulangeat et al. (2018) + Vieira -In contrast to our results, Boulangeat et al. (2018) showed that disturbances by browsers "reduced the asymptotic resilience of the system, decreasing the rate at which the new equilibrium was approached." Effect of browsers are likely less dramatic than tree logging (here moderate disturbances remove at least 25% of the basal area).

- active migration zone more sensitive

- at this scale there appear to be no difference between natural and anthropogenic disturbances.*

P6. Limitations of the study

Our goal was not to make predictions about the future state of Québec forests, but rather to explore how disturbances and soils may interact with recent climate change and modify transition dynamics. For this reason, it is inappropriate to regard the state distribution at equilibrium or the half-life to convergence as specific predictions about the extent and timing of biome shifts. Indeed, we did not simulate future climate change, we have only considered recent climate change that was observed during the surveyed period. Moreover, we did not include any dispersal limitations, although it is known to affect tree migration (Pearson, 2006). Because detailed temporal data on tree composition around each plot is not available, neighborhood composition should have been approximated using climate data, but we considered that it was redundant as they are already used in our multi-state model. Dispersal limitations could potentially reduce the effect of disturbances on long term forest distribution, but should not influence our empirically derived results.

Finally, the definition of states can affect to some extent the results. A higher threshold to define the boreal and temperate states (e.g., >90% instead of >75% of dominance of boreal and temperate, respectively) would change the transition probability but the direction of the dynamic would remain the same.

P7. Ecological and management implications

The relationships that we demonstrate between forest state transitions and disturbances provide a strong empirical basis for predicting the types of changes in forest dynamics that are likely to unfold in the coming century. A shift in dominant forest cover from conifer to deciduous broadleaf species not only entail 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 and productivity [REF], increase carbon sequestration (Thurner et al., 2014; as long as mortality is limited NRDC, 2018), modify disturbance regime (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 activities (e.g.

Laganière, Paré, & Bradley, 2010) and affect wildlife distribution (e.g. Mizel, Schmidt, Mcintyre, & Roland, 2016). However, such regime shift also have large repercussions on forest management strategies in area where silvicultural practices are tailored to regional disturbance regimes and rely on natural regeneration.

Our study reveals the potential of moderate disturbances to facilitate climate-related transitions and thus suggests that alternative silvicultural practices could be used to reduced tree migration lags. But even well planned logging may not benefit all species equally (Brice et al., 2019) and may interact will other natural disturbances to exacerbate tree mortality and compromise forest resilience in the long run (Buma & Wessman, 2011). In addition to alternative silvicultural strategies, some studies suggest that temperate species could be planted farther north to speed up succession [Iverson & McKenzie (2013); Duveneck & Scheller (2016); Vieira et al.]. However, whether promoting temperate tree migration is "desirable" or not depends on the decisions we make regarding forest management. Do we try to maintain historical conditions, let nature takes its course, or actively move species to climatically suitable locations outside their current ranges (Frelich & Reich, 2010)? In Québec, ecosystem-based forest management seek to maintain the composition and structure of a reference state, define by 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 or approach historical forest conditions under future climate change. In the context of ongoing climate change, our study reinforces that forest management have to consider the present system state in relationship to its transient dynamic as well as its likely trajectory. But even then, simulations by Duveneck & Scheller (2016) suggest that alternative management strategies, including modified silviculture and climate suitable planting, will have limited ability to increase resilience and resistance of forest under climate change. Therefore, in order to insure long term forest resilience at the boreal-temperate ecotone, adaptative management does not appear sufficient and drastic reduction of greenhouse gas emission is necessary to limit global warming (IPCC, 2014).

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