Impact of disturbances on forest transition dynamics under climate change

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Abstract

Keywords

Climate change, Disturbances, Forest, Continuous-time Markov model, Multi-state model, Québec, Temperate-boreal ecotone, Transition probabilities, Resilience

Introduction

P1. Forest dynamics under CC

P2. State transition / regime shift

P3. Disturbances

P3. Soil

P4. Multi state models

P5. Objectives

We investigate the response of forests to recent climate warming by studying the transition probability among four community states, boreal, mixed, temperate and pioneer: 1. Is forest transition dynamic affected by recent climate change? 2. How do disturbances and soil characteristics influence the transition probability among forest community 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?

We expect that most forests should not change states because tree response is slow. However, under climate warming, there should be more transitions from boreal to mixed forests and from mixed to temperate than the reverse. We also anticipate that natural and anthropogenic disturbances, combine with the underlying effect of climate change, will modify forest dynamics by providing establishment opportunities for some migrating species in otherwise competitive environments, thus triggering state changes in forest ecosystems. However, soil characteristics will likely impede some of these transitions. 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 explore the impact of disturbances on forest equilibrium and transient dynamics under climate change using several measures: equilibrium state distribution, time to converge to equilibrium, probability of persistence, recurrence time and entropy.

It is important to keep in mind that the goal here is not to make prediction about future ecosystem states and dynamics, but rather to explore how disturbances may interact with climate change and modify transition dynamics.

Methods

Study area and sites

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. XXX km^2) and covers three different forest subzones: the hardwood forest, the mixed forest, and the continuous boreal forest (Figure 1). The temperate mixed forest (from 47°N to 48°N) marks the transition between the hardwood forest to the south, which is dominated by *Acer saccharum* (sugar maple), and the boreal forest to the north, which is dominated by *Abies balsamea* (balsam fir) and *Picea mariana* (black spruce).

We selected all inventory plots that were sampled more than once as well as the ones where humus type was either mull, moder or mor... 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 9093 plots (Fig. 1) analyzed. The time intervals between plot surveys varied from 4 to 43 years, with a mean time of 11 years.

Community states

We classified the inventory plots into four community states (Boreal, Mixed, Temperate and Pioneer) using species basal area and composition at each time step. We first assigned each studied species as boreal, temperate or pioneer according to their functional traits (Brice et al.; see Table SX). 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 33557 observations (plots x number of years measured), we observed 24464 state transitions (Table Sx, Figure X).

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 several bioclimatic variables hypothesized to influence tree establishment, survival and growth: the annual mean temperature and total annual precipitation, the mean temperature and total precipitation during the growing season, the minimum temperature of the coldest period, the maximum temperature of the warmest period, and the annual climate moisture index (CMI), which is the difference between annual precipitation and potential evapotranspiration (see Table X). 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 (Fig. SX). *[not talk about other climate variables that were tested?]*

We also collected information pertaining to natural and anthropogenic disturbances that have affected the forest plots during the study period (Table 1, Fig. Sx). At each plot, 21 disturbance types and their level of intensity (moderate or major) were recorded (Table S2; 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 3 levels of intensity each (minor, moderate or major).

[What about old disturbances?]

Finally, at each plot, several edaphic characteristics were recorded (MFFP, 2016). Of the available variables, we selected (1) drainage class, (2) humus type, (3) humus depth, (4) texture, and (5) pH of the surface horizon.

Analysis

Continuous-time multi-state Markov model

(Ref: Jackson, 2011, @jackson_multi-state_2018, @spencer_continuous-time_2005, van den Hout 2017, @logofet_mathematics_2000)

We derived our modeling framework from methods widely used in survival analysis and disease progression model (REF). Similarly to Vissault et al., 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 (Figure X).

In ecology (vegetation succession, land use change), 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, 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. To our knowledge, this approach has been seldom used for ecological succession before.

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 site 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:

$P(t) = exp(tQ)$

The intensity matrix Q contains intensities $q_{r,s}$ which represent the instantaneous risk of moving from state r to state s:

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

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

Transition-specific hazard regression models can be defined for those $r, s \in S$ between which a direct transition is possible according to the specified multi-state process (Figure X). The intensities $q_{r,s}$ can be modeled as a combination of a baseline hazard $q_{rs.0}$ with a vector of explanatory variables $x(t) = (x_1(t), x_2(t), ..., x_p(t))$ and a vector of coefficients $\beta_{rs} = (\beta_{rs.1}, \beta_{rs.2}, ..., \beta_{rs.p})$:

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

The definition of the log-linear regression hazard model allows to fit a site-specific and time-dependent covariate vector $x(t)$ to transition intensities. Time-dependent covariates, such as climate and disturbances, are assumed to be piecewise-constant, i.e. the hazard is constant within a specified time interval $[h, h+t]$ and depends on the covariate value at h, but is allowed to change between the intervals. Including time-dependent covariates in the model is thus a simple workaround for the time homogeneity assumption.

Estimation of model parameters can be obtained by maximizing the log-likelihood function using the transition probability matrix. The contribution of the site i at time j to the likelihood is given by:

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

The full likelihood function is the product of contributions for all N sites:

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

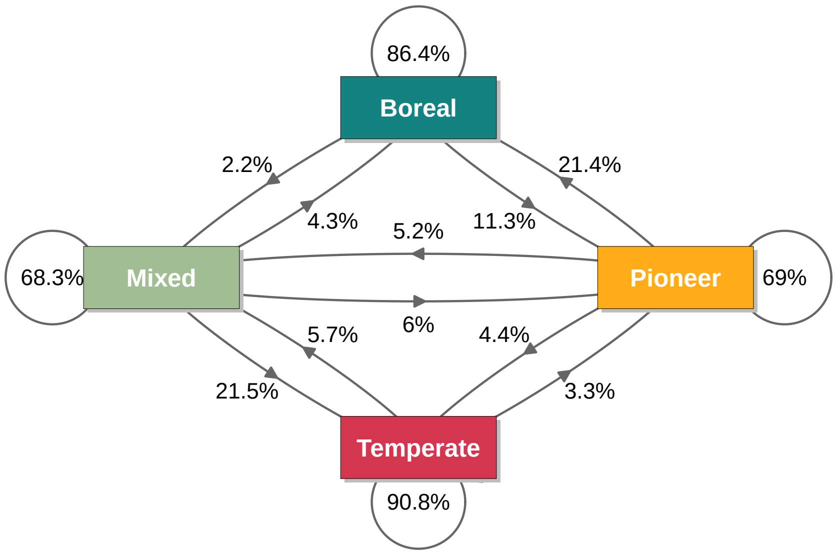
Definition and evaluation of candidate models

It is important to consider which transitions can realistically occur in continuous time. Because the states are defined based on percentage of the species groups, it is assumed that in order for a site to travel from one state to a non-adjacent state, the site also has to travel through the intermediate states. Thus, in this model, we assumed that a direct transition from Boreal to Temperate and from Temperate to Boreal is impossible, however all states can transition directly to Pioneer (Figure X).

Because we model multiple state transitions at once, the number parameters increase rapidly with the number of covariates (n(n-1)p). Hence, the full model was built in several steps to keep only the most relevant covariates. We first tested each subgroup of covariates independently (climate, disturbances and soil) and selected for the best sub-model using the lowest AIC in each subgroup. Moreover, a likelihood ratio test was used to compare each sub-model to the intercept only model. The best climate, disturbance and soil sub-models were then combined to construct the full model.

To determine the significance of a subset of covariates in the presence of the others, nested models were compared using likelihood ratio tests. The goodness-of-fit of the full model was evaluated using McFadden pseudo-R2 ($R_2 = 1 - (Deviance_{Full}/Deviance_{Null})$). The McFadden pseudo-R2 was also used to approximate the individual contribution of each subset to the full model.

We also computed predicted probabilities from the models to explore the relations between probability of transitions and environmental covariates of interest. All quantitative variables were standardized ($\mu = 0$, $\sigma = 1$) in order to compare their hazard ratios.



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

$$q_{rs} = q_{rs.0} \times \exp(\beta_{rs.1} \times \text{climate} + \beta_{rs.2} \times \text{disturbances} + \beta_{rs.3} \times \text{soil})$$
$$\text{for } r \neq s \text{ and } s \neq \text{Pioneer}$$

$$q_{rs} = q_{rs.0} \times \exp(\beta_{rs.2} \times \text{disturbances})$$
$$\text{for } s = \text{Pioneer}$$

Figure x. 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.

[Model fit: How to compare observed vs expected transition probabilities?]

Impact of disturbances on equilibrium and transient dynamics

Using the result from our full model, we characterized different properties of the forest transition dynamic. To further understand the impact of disturbances, we compared these properties between natural and anthropogenic disturbances and among levels. First, we estimated the forest equilibrium, or stationary distribution, which corresponds to the long-term state distribution of the system. For a regular Markov process, any initial state distribution $s(0)$ converges to the same equilibrium as t tends toward infinity:

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

The vector of equilibrium π can also be obtained by taking the left eigenvector of Q with eigenvalue 0, normalized to sum to 1 (REF) or by taking the dominant eigenvector of P with eigenvalue 1, normalized to sum to 1 (Hill *et al.*, 2004).

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

$$\rho = \lambda_1/\lambda_2$$

where λ_1 and λ_2 are the largest and second-largest eigenvalues of P ($\lambda_1 = 1$ for stochastic P). Community converges to the equilibrium, in the long run, at least as fast as $exp(\ -tlog(\rho))$ (Caswell 2001), so ρ provides a lower bound on the convergence rate. The half-life to equilibrium is given by:

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

We also explored how disturbances modify the resilience of the system's states by measuring the probability of persistence, the recurrence time as well as the entropy of each state (Hill *et al.*, 2004). Ecological resilience can be defined as the capacity of natural systems to absorb disturbances without undergoing change to a fundamentally different state and the time to recover after a disturbance (Gunderson, 2000, Holling 1996). The probability of persistence is directly given by the diagonal of the transition matrix (p_{rr}). The Smoluchowski recurrence time is the average time elapsing between a point leaving a given state and then returning to it again and is given by:

$$Recurrence = \frac{1-\pi}{\pi(1-p_{rr})}$$

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 on the jump matrix (Spencer & Susko, 2005). The jump matrix contains the probabilities $j_{rs} = -q_{rs}/q_{rr}$ that the next state after state r is state s, for each r and s. The entropy of state s is then:

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

The entropy of the community as a whole is:

$$H(S) = -\sum_s \pi_j \sum_r j_{rs} \times log(j_{rs})$$

The normalized entropy is: $H(S)/H(max)$ where $H(max) = log(4-1)$

[NB: these properties can also be computed on raw data]

All analyses were performed using the R programming language version 3.5.1 (R Core Team, 2018). Multi-state model was ran using the package 'msm' (Jackson, 2011).

Results

Table X. Multi-state model comparisons.

	Covariates	Nb of parameters	Delta AIC	-2 Log-likelihood	McFadden R2
Null	Intercept	10	0.00	29093.44	0.00
Climate	Temperature, CMI	30	-1721.41	27332.03	6.05
Disturbances	Natural, Harvesting	50	-3826.27	25187.17	13.43
Soil	Humus type	30	-982.90	28070.54	3.52
Full	All	90	-5758.33	23199.11	20.26

- Full model has a pseudo-R2 of 20%: not so bad but it indicates that there is still a lot of variation unaccounted for. Historical disturbances and prevalence of the state in the neighborhood could be considered, however it is difficult to add more covariates as the model does not converge…
- Transition dynamic is best explained by disturbance covariates (McFadden R2 is 13% for the disturbance model vs 6% and 3% for climate and soil, respectively)

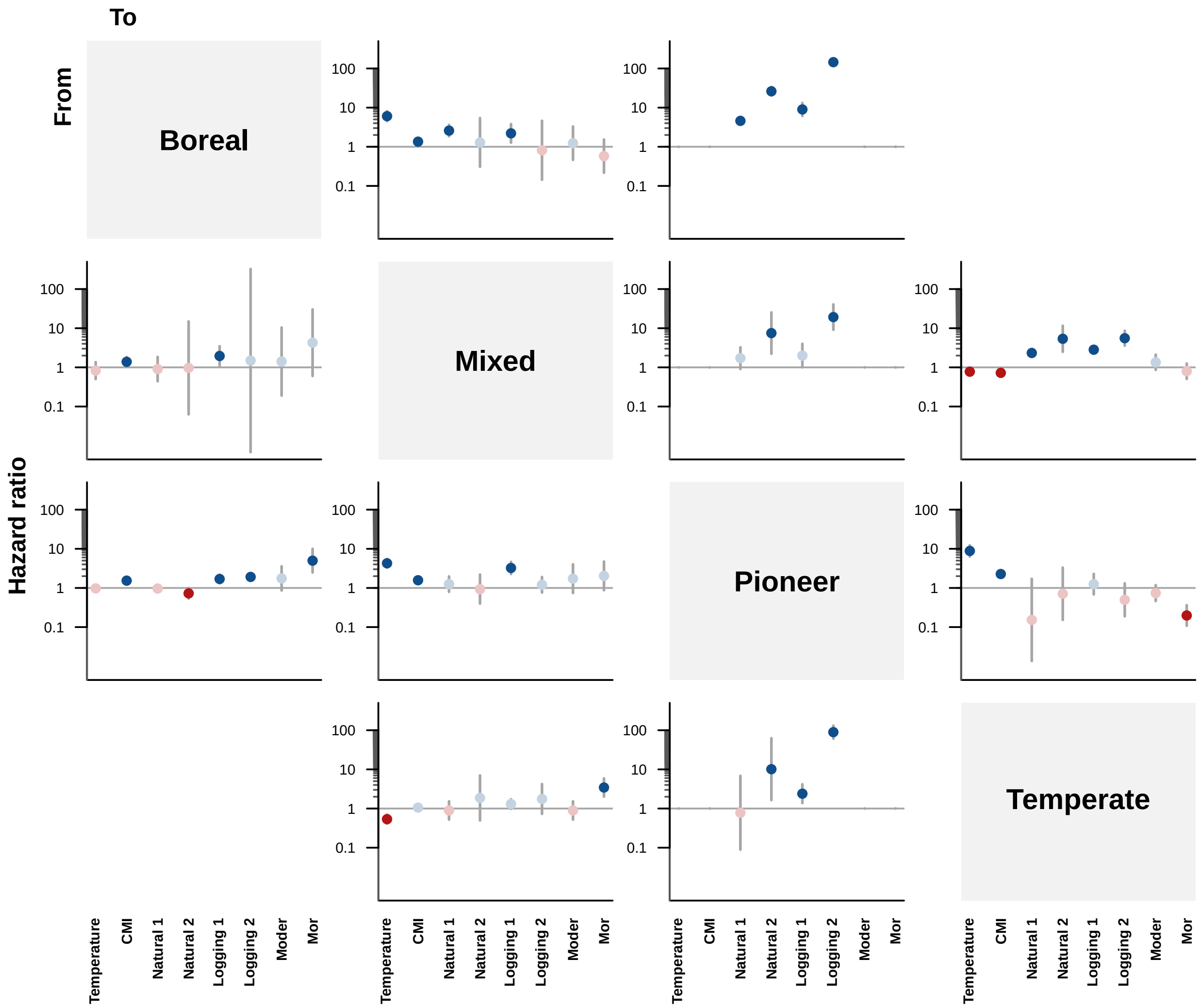


Figure x. Hazard ratios (HR) and 95% confidence intervals as estimated from the best multi-state transition model. The HR of predictors are interpretable as multiplicative effects on the hazard, where values above 1 (in blue) indicate that the predictor is associated with a greater risk of state transition, while values below 1 (in red) indicate a lower risk of transition. Predictors different from 1 are colored in dark blue or red.

Disturbances

- Natural disturbances and harvesting (both major and moderate) favor the transition from Mixed to Temperate forest. Major disturbances (natural and harvesting) increase the risk of transition from Mixed to Temperate by ca. 5 times.
- Moderate disturbances (natural and harvesting) increase the risk of transition from Boreal to Mixed by ca. 2 times, but not major ones.
- For all forest states, disturbances strongly favor the transition to Pioneer, particularly for Boreal forest.

Climate

- Warmer summer temperature favor the transition from Boreal to Mixed as well as from Pioneer to Mixed and Pioneer to Temperate.
- Interestingly, warmer temperature decrease the risk of transition from Mixed to Temperate.

Soil

- Baseline for comparison = Mull
- No effect of soil from Mixed to Temperate.
- The risk of transition from Pioneer to Temperate is decreased on Mor (compared to Mull) by 5 times (HR=0.19).
- In contrast, risk of transition from Pioneer to Boreal is increased on Mor (compared to Mull) by 5 times.

In the following figures, I explore the impact of different disturbance types and levels on the model predictions. The objective is to better understand how disturbances influence the transition dynamics, not to make predictions. Moreover, I modify the disturbance parameters while all other covariates remain fixed at their mean.

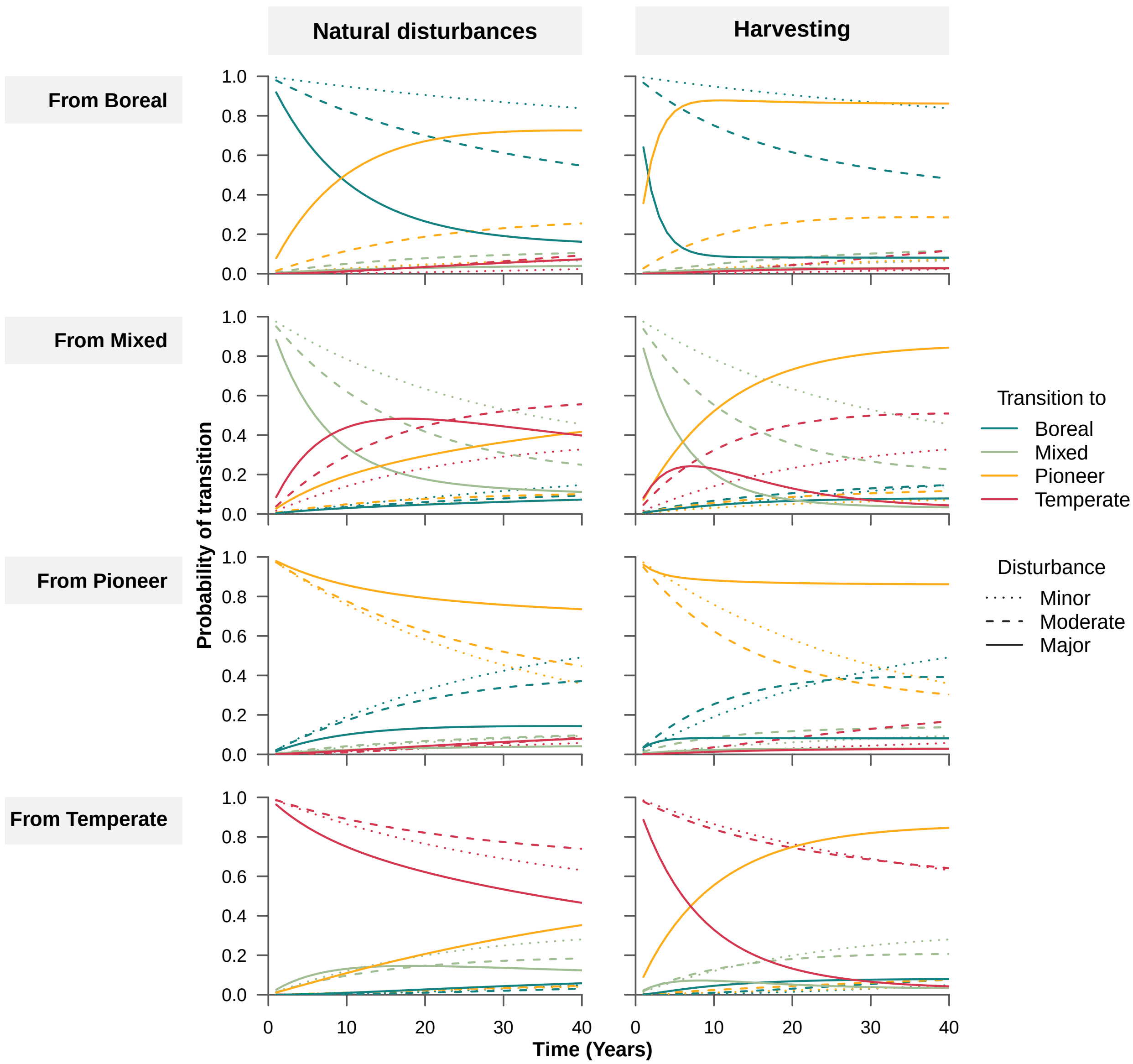


Figure x. Probability of transition between community states through time for natural and harvesting disturbances (columns) and for different levels (line type) as predicted by the best multi-state model. All other covariates are fixed at their mean.

- Moderate disturbances strongly increase the probability of transition from Boreal to Pioneer, and even more so with major disturbances. This effect seems long-lasting.
- Strong effect of major harvesting on the probability of transition from Temperate to Pioneer. Weaker

for major natural disturbances.

- Without disturbances (Minor), the transition probability from Mixed to Temperate increase constantly through time.
- Moderate disturbances further increase the transition probability from Mixed to Temperate through time.
- However, major disturbances increase the transition probability from Mixed to Temperate comparatively to moderate on the short term, but on the long term it decreases the transition probability. This effect is weak for major natural disturbances, but very pronounced for major harvesting.

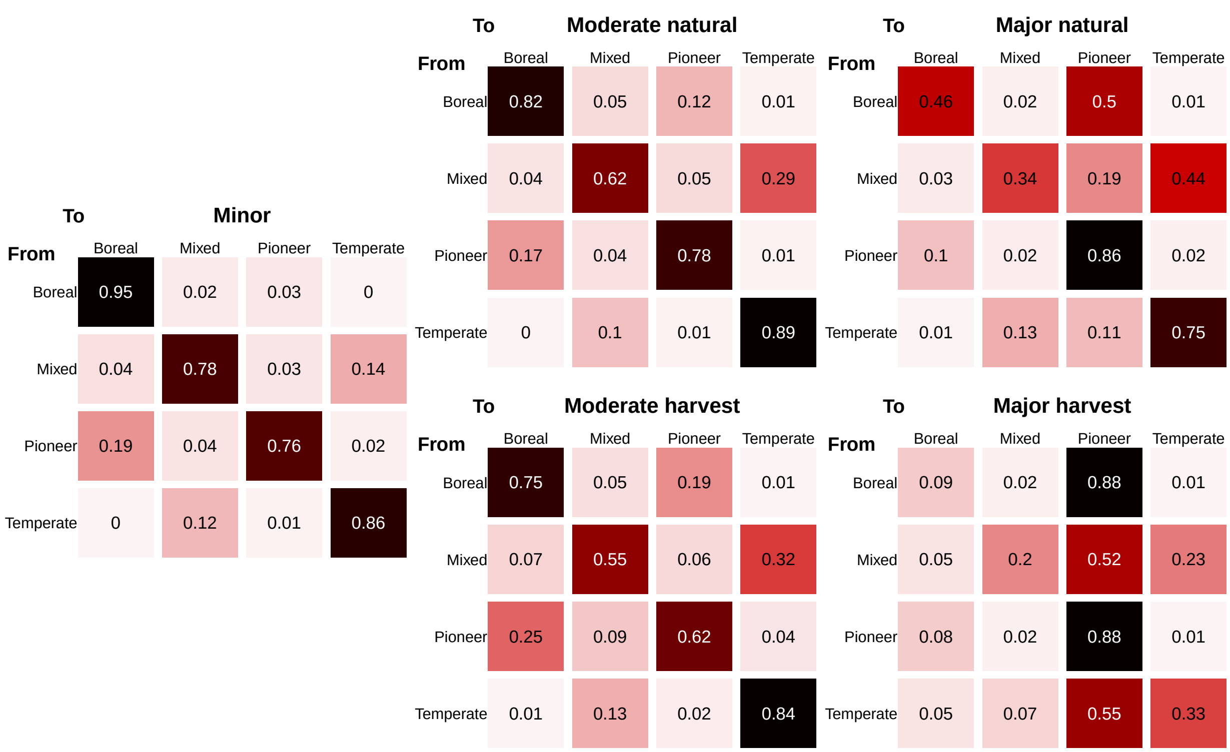


Figure x. Predicted change in transition probabilities for different disturbance levels for 10 years. All other covariates are fixed at their mean.

- Disturbances obviously modify forest transition dynamics…

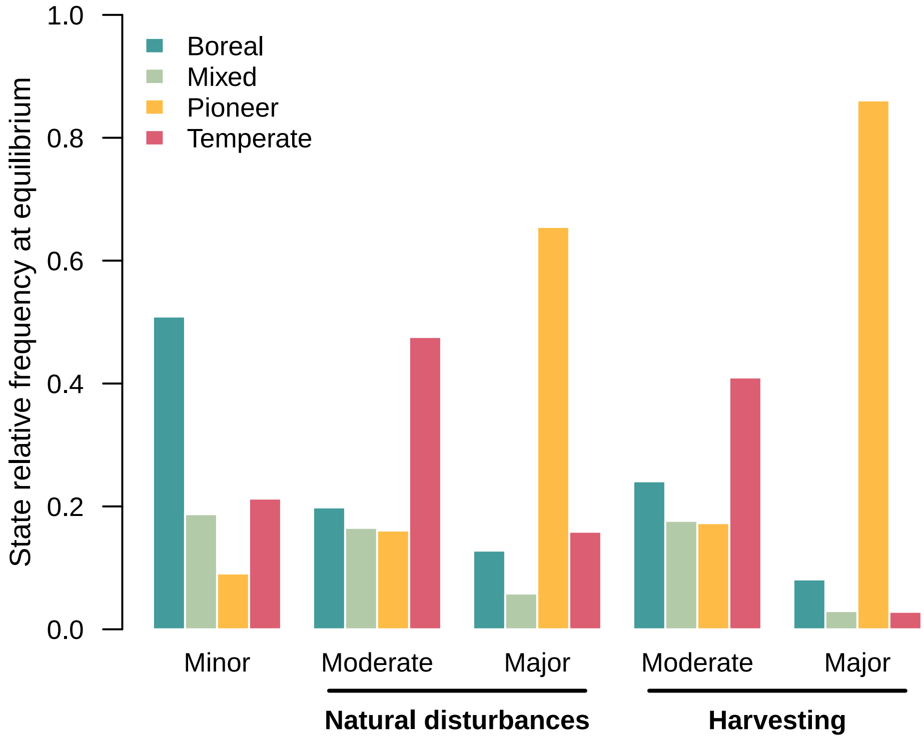


Figure x. Predicted equilibrium (stationary) distribution of states for different levels of disturbances. All other covariates are fixed at their mean.

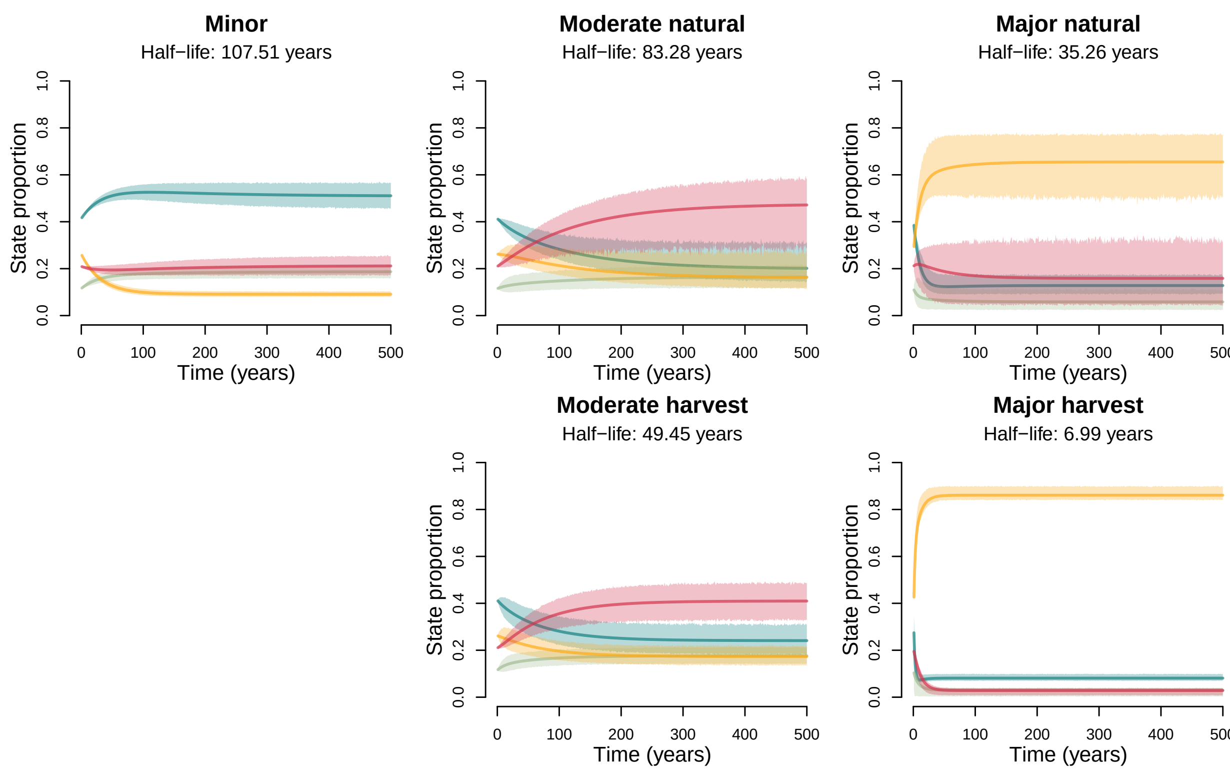


Figure x. Predicted time to reach equilibrium for different disturbance levels starting from observed initial state proportions. All other covariates are fixed at their mean.

- At minor disturbances, Boreal forests are dominant in the landscape. The steady state of minor disturbances is very similar to the initial state distribution.
- At moderate disturbances (both natural and harvesting), there is a large shift toward a dominance of temperate forests.
- At major disturbances (both natural and harvesting), there is a large dominance of Pioneer forests.
- Larger uncertainty at moderate disturbances

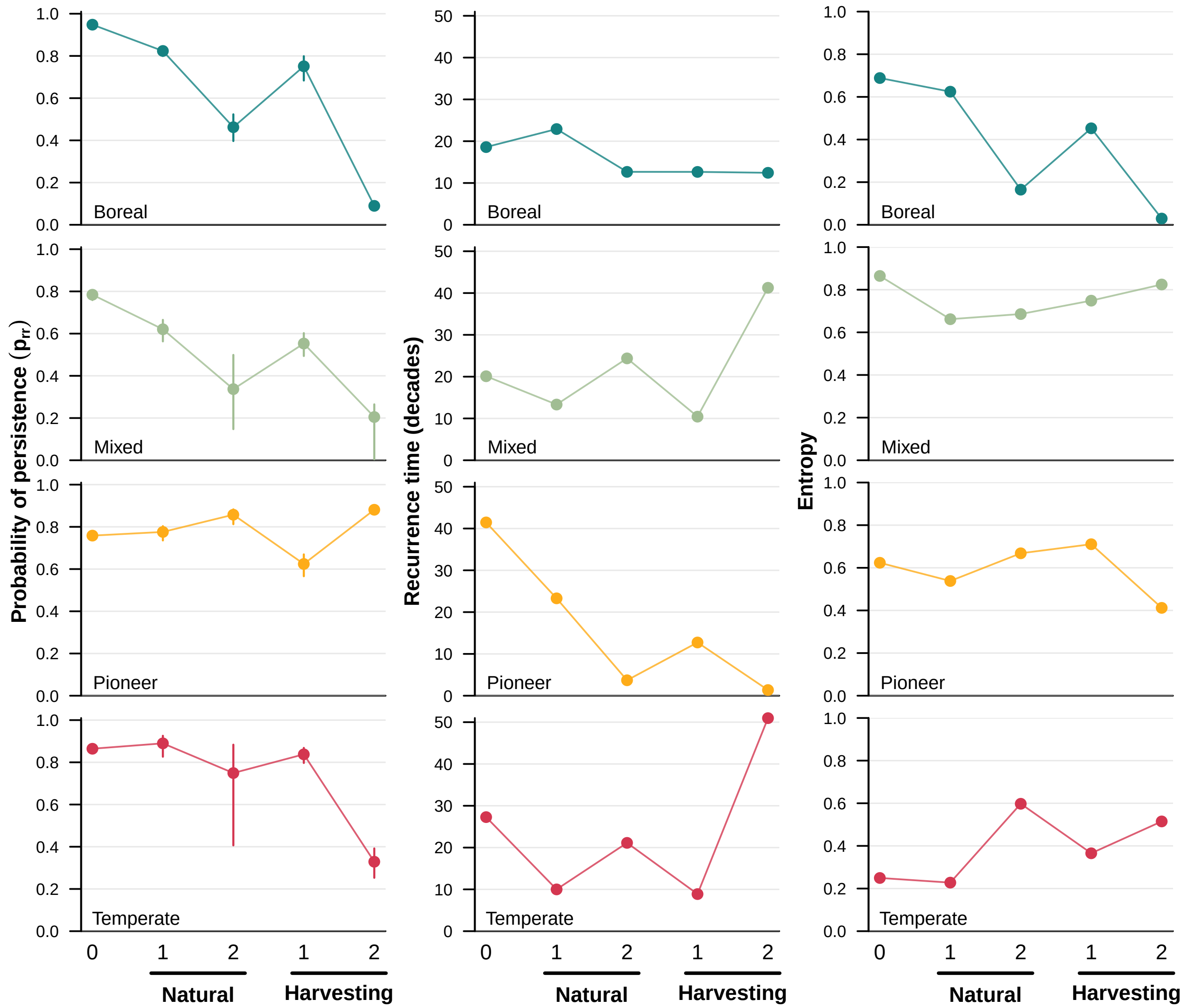


Figure x. Change in probability of persistence with 95% CI (left), recurrence time (middle) and entropy (right) for each community state (row) and for different levels disturbances (0 = minor, 1 = moderate, 2 = major). Probability of persistence is the diagonal of the transition matrix and corresponds to the probability that a point occupied by a state at time t is still occupied by that species at $t + \Delta t$ (here $\Delta t = 10$). Recurrence time measures the average time elapsing between a point leaving a state and then returning to it again. Entropy is the uncertainty of the next state knowing the current state; high values mean high uncertainty while low values mean high predictability. All other covariates are fixed at their mean.

Persistence

- Temperate and Boreal are more persistent when undisturbed than the other 2 states: high probability to stay.
- Relatively low resistance of Mixed forests.
- At moderately natural disturbances, there is a slight increase of Temperate persistence.

Recurrence

- Boreal forests are generally more resilient: less time to recover than other states
- Higher resilience at moderate disturbances for Temperate forests.

Entropy

- High entropy of Mixed forests for all disturbances types and levels: high uncertainty - can transition to all 3 states. But, uncertainty is slightly reduced at moderate natural disturbances (increased probability to transition to temperate relative to other states)
- Low entropy of Temperate forests at low disturbances and moderate natural disturbances: high predictability (very high probability that the next state will be Mixed forests).
- High entropy of Boreal forests at low disturbances and moderate natural disturbances: high uncertainty (50/50 that the next state will be Mixed or Pioneer). At major disturbances, high predictability of Boreal forests - they transition to Pioneer.

Overall, our results show that disturbances modify forest transition dynamics and accelerate transition from Mixed to Temperate.

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