

Role of alternative stable states on Sugar maple range shift in reaction to climate change.

Research proposal

Master in Wildlife management

By

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1. Introduction

Context. Sugar maple (*Acer saccharum*) is a widespread and abundant tree species in north-eastern North America. [13; 23; 16; 1]. Predicting shifts in the range of Sugar maple is of prime importance because this species is highly desirable for hardwood and maple syrup production, two large economic sectors in Quebec. This species is dominating the temperate forest up to the boreal- temperate ecotone at its northern range limit [1]. Some representative species of northern forest ecosystems are expected to expand their distribution towards the north following climate warming [22; 15]. According to McKenney (2007) [22], the climatic conditions favorable to Sugar maple will reach the Ungava bay within the next 100 years, which appears highly improbable because of dispersal limitations and slow population dynamics. Such predictions are built on species distribution models accounting only for climatic conditions; it is recognized that Sugar maple regeneration depends both on macro (*i.e.* regional climate) and micro environmental conditions (*i.e.* soil and microtopography) [13; 17]. Thus, the expansion of Sugar maple and is difficult to predict because micro conditions can mitigate macro conditions such as global warming [6].

Soil-plant feedbacks are susceptible to impact Sugar maple migration dynamics. Tree species respond differently to the soil conditions, and the soil properties found in boreal forests are different from those in temperate forest [17; 1; 12; 7]. A deep and poorly-decomposed litter layer is usually found in boreal forests, while the litter of northern hardwood forests is thinner and mainly composed of a superficial leaf mat [1]. The temperature is colder, the snow melts later and the soil is wetter under coniferous trees [17; 12]. Soil acidification causes a reduction in the cation exchange capacity and subsequently decreases availability of some nutrients such as calcium [25]. Sugar maple seedlings have been recognized to be particularly sensitive to waterlogged conditions and soil nutrient content [25; 17; 5]. These properties of coniferous forest soils could hinder the local establishment of species associated with alkaline soils or unable to withstand waterlogged conditions [17]. Under these conditions, tree species migration is likely to be restricted or delayed [17]. Thus, even if the climatic conditions at the regional scale become favorable to Sugar maple after climate warming, the micro conditions found in the boreal forest could slow seedling establishment [16; 25; 1; 24]. Sugar maple could thus be unable to colonize the boreal forests as a result of strong and localized plant-soil feedbacks [20].

I hypothesize that the temperate-boreal forest ecotone is as a system dominated by two alternative states, *i.e.* contrasted states occurring in the same climate conditions [26]: the boreal community and the temperate community, including Sugar maple. The landscape is made of a patch mosaic where micro conditions are driving the spatial occurrence of boreal and temperate communities, despite a regional climate favourable to temperate species [12; 10]. I expect that a climate warming and the subsequent incapacity of Sugar maple to colonize boreal forest stands will create tension between the potential and realized forest composition and consequently that abrupt shifts in community composition are susceptible to occur at the boreal-temperate forest ecotone.

Objectives. The main objective of this project is to investigate the transition between the boreal and temperate forests under different climate change scenarios. In this context, we will test two different hypotheses: (H_1) Alternative stable states do co-occur at the boreal-temperate forests ecotone, and (H_2) the response of Sugar maple to climate change will be delayed in areas where alternative stable states are susceptible to occur. In order to fulfill this objective and

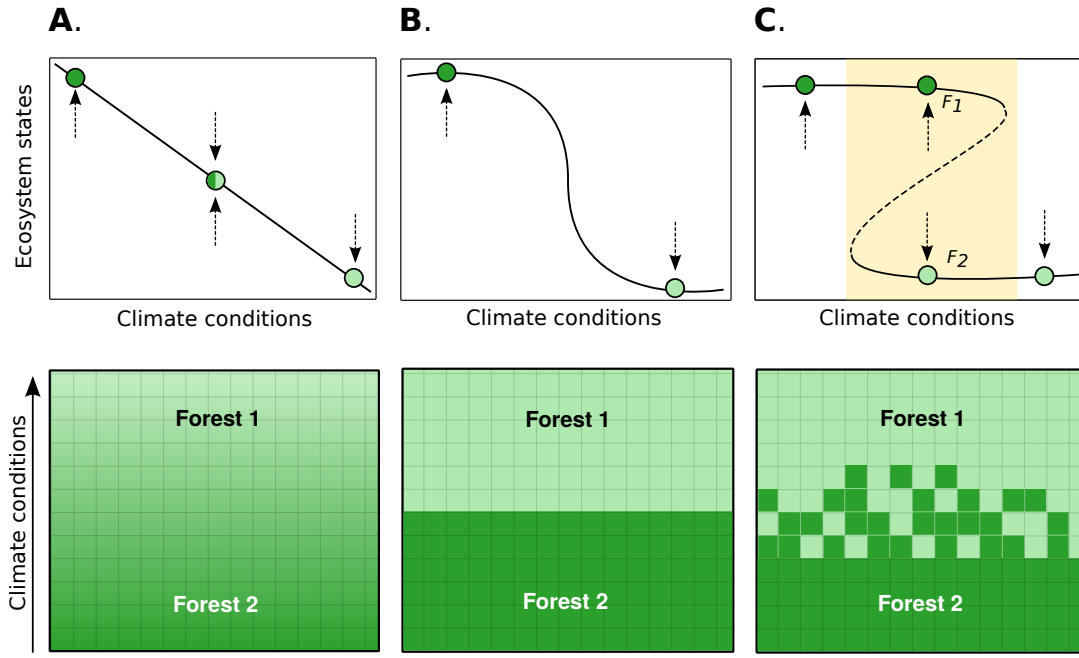


Figure 1: Schematic representation of different ways in which the forest-forest ecotone can vary over environmental gradients such as temperature, precipitation or soil moisture. Three different responses to an environmental gradient are presented, (A) gradual, (B) basic fold, (C) catastrophic fold. Upper panels represent the change in the ecosystem state over an environmental gradient. Solid lines represent stable states along the boreal-temperate transition, and the dashed line (in yellow highlight) unstable equilibrium. Arrows indicate the direction the system moves if not at the equilibrium. The zone with alternate stable states, called hysteresis, is unstable and small fluctuations in environment conditions give rise to abrupt changes in ecosystem state (F_1 or F_2). The bottom panels illustrate a conceptualization of a transitional landscape between the boreal (light green) and the nordic temperate forests (dark green).

test these hypotheses, we will (1) develop a climate-dependent state-transition model (STM) representing the dynamics of the boreal and temperate communities at landscape scale; (2) study the occurrence of alternative stable states at the temperate-boreal ecotone; and finally (3) run simulations of the temperate community species distribution under different climate change scenarios. The first section of this proposal reviews the context of the study. The first part of the review presents the concept of alternative stable states and critical transitions in forest ecosystem properties. The second part focuses on Sugar maple, its associated community in the temperate biome, and a justification about why alternative stable states are expected to occur at the boreal-temperate forests ecotone. The last section of this proposal describes the model and the methodology that we will employ to achieve the specific objectives.

2. Review

Alternative stable states in forest ecosystems. The idea that alternative stable states may exist in community ecology was proposed in the late 1960s [28; 2]. May (1977) [19] highlighted the fact that an ecosystem can be seen as a dynamic system where communities are not constant across the time and can change following environmental changes *i.e.* perturbation. These communities can reach several equilibrium points or stable states along an environmental gradient [19]. A community is stable when it persists in a given state, and resists or is resilient to small perturbations [9]. The community can persist according to various feedback mechanisms [9]. For instance, the growth of a population of deer is controlled by competition by

exploitation and predation, both can be viewed as feedbacks. Larger perturbations encountered by the system can generate changes on state of a community, i.e. the arrangement of species or populations and their interaction with the physical environment [9]. There are three possible community responses following these perturbations: **(A)** gradual, **(B)** basic fold, **(C)** catastrophic fold [28] (Figure 1, upper line). First, when a small modification environmental occurs, the state of the community can change almost linearly (Figure 1.a, upper line) [28; 27]. In this case, the whole ecosystem can be seen as a continuum of community along the climate gradient [28; 27; 26]. Secondly, the entire community can be insensitive to changing environmental conditions over a certain range, but respond strongly when a threshold is reached [26]. For instance, some species mortality can increased sharply when a toxin is added to the environment and a lethal threshold is reached [26]. In this case, the response curve of this natural system is not linear but lightly folded. Hence, small perturbations such as adding toxin can lead to major changes in the species communities. Lastly, in some strong non-linear systems, the response curve can be folded backwards and alternative stable states could occur (Figure 1.C). This implies that, for a certain environmental conditions, the ecosystem has two alternative stable states separated by an unstable equilibrium (yellow zone, figure 1.C). When the system approaches a tipping point on the folded upper branch, it cannot pass smoothly to the lower branch. Small forcing on initial conditions of the state F_1 transfer the system immediately into a different state F_2 (Figure 1.C). Hence, at this point, the system is particularly sensitive to the initial conditions. This point is called a bifurcation point and a small forcing on it can drive the system into backward or forward shifts towards either alternative stable states also called "attractors" [26]. The main ingredient to creating alternative stable states is the occurrence of positive feedbacks [26; 30]. One well known is facilitation in ecological succession (i.e. the idea that pioneer species pave the way for later successional species). this feedback seems to be present in the boreal-temperate forests studied [1; 11].

Natural system studied. Many empirical and modelling studies have been conducted on the transition between forest to non-forests communities (e.g. Boreal-Tundra) [29; 28; 14; 23]. Little attention has been given to understand forest-forest ecotones [12; 13; 23]. In the case of the boreal-temperate forests, there is no distinct boundary; instead a broad transition zone exists where stands of coniferous and deciduous species co-occur [12; 10]. At landscape scale and within the ecotone, the temperate and boreal forests biomes might be seen as alternative stable states (Figure 1, lower line). In fact, the temperate-boreal forest possess a patchiness structure often attributed to differences in soils, nutrient status and topographical factors [11].

A positive feedback contributes to the maintenance of the community type if the dominant tree species promotes conditions facilitating its own regeneration [1]. Frelich *et al.* (1993) [11] hypothesized such a soil-plant feedback impacts Sugar maple and hemlock spatial distribution. Hence, soil conditions and role of dominant species in regeneration seems to act as main feedbacks on the temperate forest establishment (Figure 1.c, upper panel). Boreal soil can delay temperate species regeneration (negative feedback) and, on other hand, temperate species establishment can enrich the soil so they promote their own regeneration (positive feedback).

In this context, we expect to find forest stands dominated by either boreal species or temperate species and sensitivity to initial conditions. Thus, the soil condition and the role of dominant species in boreal and temperate forests need to be investigated as main drivers in shifts between alternative stable states [16; 25; 6; 1].

3. Methods

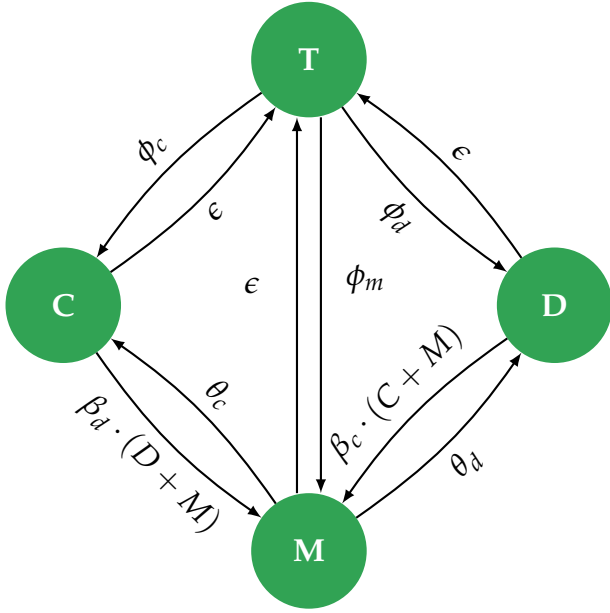


Figure 2: Conceptual representation of the transition model between deciduous (D), mixed (M) and coniferous (C) stands. T corresponds to a post-disturbance forest patch. Perturbations, natural and anthropogenic, occur with a frequency ϵ . Flows or transition rates between states are represented by arrows. Parameters θ and β are rates of colonization and succession, respectively. We define recovery functions ϕ_c , ϕ_d as $\phi_c = \alpha_c \cdot (M + C) \cdot [1 - \alpha_d \cdot (D + M)]$ and $\phi_d = \alpha_d \cdot (D + M) \cdot [1 - \alpha_c \cdot (C + M)]$. ϕ_m include these both equations giving $\phi_m = \phi_c \cdot \phi_d$. Finally, parameter α represents the climate-dependent recovery rate after a patch has been disturbed.

induce deciduous dominance and larger and intense fires favouring boreal communities [3]. Anthropogenic disturbances such as logging can also produce major change in the forest composition. Dupuis *et al.* (2011) revealed that historical disturbances affected the propensity of taxa to expand (maples/aspen) or decline (cedar/spruce) in the northern hardwood range limit in eastern Québec [8]. Thus, a state is systematically converted into a transitional patch (T) when one of those disturbances event occur at rate ϵ (Figure 2). After a perturbation, a patch T with can be recovered to state C , M or D following a function ϕ . For instance when a patch T is recovered into a patch C , this flow described by the function ϕ_c incorporates a specific patch recovery rate (α_c), as well as the availability of coniferous ($C + M$) species and the proportion of patches unconverted into a deciduous state, $1 - \alpha_d \cdot (D + M)$ (see caption, figure 2). If this patch C is undisturbed, then the coniferous stand turns into a mixed stand by deciduous colonization with a rate θ_c .

The dynamic of this model can be summarize through four differential equations. For instance, the dynamics of T over the time is described by this differential equation: $\frac{\delta T}{\delta t} = \epsilon \cdot (C + M + D) - T \cdot (\phi_d + \phi_c + \phi_m)$. The differential equations illustrating the dynamics of the other three

State and Transitional Model. The framework of this study lies is a STM representing dynamics in the boreal-temperate forest transition at the landscape scale. Overall, the ecotone landscape includes three distinctive kind of forest canopies: (i) deciduous, (ii) mixed and finally (iii) coniferous [10]. Each of these stand types is represented as a state in the STM: (**D**) Deciduous, (**M**) Mixed, (**C**) Coniferous and finally we added (**T**) a Transitional patch detailed later in the paragraph (green circles, figure 2). According to Briske *et al.* (2008) and this STM context, state means a plant community phase occurring on similar soils that interact with the environment to produce persistent functional and structural attributes [4]. Each transition rates between states are are climate-dependant. Transitions between all states are possible except the direct transition between a deciduous and coniferous stand, which requires an intermediate step through state M . Except for the colonization rate (θ), transition rates vary with the proportion of coniferous or deciduous available in the closest neighbourhood. For instance, the succession rate of a coniferous patch (β_c) towards a mixed patch (M) depends also on the availability of D and M patches in the landscape (figure 2). Natural processes such succession and colonization are not the only mecanisms leading the transition between two states. In fact, natural disturbances are an important driver of forest dynamics at landscape scale (e.g. fire in boreal forest or large windthrow in temperate forest). For instance, small fires in-

states (C,M and D) in the system are relatively similar and can be described (with coniferous state as example): $\frac{\delta C}{\delta t} = \phi_c \cdot T + \theta_c \cdot M - \alpha_d \cdot (D + M) \cdot C - \epsilon \cdot C$. The entire model is spatially implicit and assumes that each patch is occupied by one state, thus the proportion of all states sum to 1 in the entire matrix landscape.

Data description. The parameterization and validation of the model will be conducted using the QUICC- FOR¹ database containing large permanent (PP) and temporary (TP) sample plots from United States and Canada. The data have been freely provided by partners and covers 3 eastern Canadian provinces (*ca.* 16,000 plots) and 31 states of eastern USA (*ca.* 50,000 plots). Surveys started in the 1970s and include up to 5 remeasurements, with the interval between sampling ranging from 5 to 10 years. Data is recorded for seedlings, trees, saplings and stand level. Stem-level information includes diameter at breast height (DBH), species, state of the stem (e. g. alive or dead), height, age and canopy position. Seedling and sapling data provide numbers of individuals by class of DBH and species. The stand-level data includes relevant information about soil deposit, drainage, disturbances, cover type and age and height of the stand. All plot inventories are geo-referenced. For each plot location, some climatic variables extracted by interpolation from the climatic model ANUSPLIN [21] are included. We will parameterize the model using annual rainfall (mm) and monthly temperatures (minimum, maximum and average in °C) of the 30 years previous to the year of each plot’s sampling. Those variables are used by many authors as external conditions to detect alternative stable states and are often indicative of the distribution of biomes investigated in this present study [12; 14; 29]. Filters will also be applied to the database prior to the model parameterization. As a first step, out of the 57 species contained in the database, only 28 representative species of the whole sample plots network will be taken into account. Only plots with mesic soil conditions, *i.e.*, thick deposits with fast to moderate drainage, will be considered for the analysis. We will consider only mature stands with dominant strata containing trees greater than 50 years old. Lastly, plots disturbed by human activities (mostly by logging) will be removed in order to parametrize the model using only natural disturbances.

Parametrization. As previously stated, the model focuses mostly on representative species of the boreal and temperate forest. The basal area (m^2/ha , BA) will be computed to provide a measure of relative species abundance in each of the plots and at each time step (year of measurement). Stands will be considered in one of the four states previously described in the model’s section (Figure 2). C, M and D states will be classified following their percentage of BA in deciduous (BA_D) and coniferous (BA_C) species in the plot (*i.e.* D state if $BA_C < 25\%$ and $BA_D \geq 50\%$, C state if $BA_C \geq 50\%$ and $BA_D < 25\%$; and M state if $BA_C > 25\%$ and $BA_D > 25\%$). Lastly, each plot containing more than 75% of BA mostly representative of post-disturbance community species such as birch, aspen or pine is classified into transitional state (T). The rest of the plots are unclassified if they haven’t satisfied the previous statements. The second step consists of computing a probability function of transition between two states given a specific climate condition (*Climate*, eq. 1) and proportion of deciduous or coniferous available (\hat{D} and \hat{M} , eq. 1). Hereafter, will focus only on a specific transition $M \rightarrow T$ but the method used will be generalized on all transitions. In this example (eq. 1), \hat{D} and \hat{M} are the expected probability of observing state D or M in this area given climatic conditions. They are proxy for the deciduous regeneration pressure surrounding the area. They will be estimated using a classification method (Step 1, eq. 1) as for instance random forest (R-package, [18]).

¹Quantifying and mapping impact of climate change on the forest productivity in eastern Canada.

$$P(D_{t1}|M_{t0}, Climate) = f(\overbrace{Climate, \underbrace{\hat{D}, \hat{M}}_{\text{Step 1. RandomForest}}}^{\text{Step 2. Multinomial regression}}) \quad (1)$$

To compute the probability of state occurrence given the local climatic conditions encounter by a patch (Step 2, eq. 1), we use a multinomial regression (nnet R-package, [31]). We can summarize this multinomial regression as $P(D_{t1}|M_{t0}) \sim \hat{D} + \hat{M} + X_1 + X_2 + X_i...$ where \hat{D} and \hat{M} correspond to the probability of observing any state in the immediate neighbourhood (previously presented) and X_i a climate variable. Model selection will be performed using Akaike's information criterion (AIC). Model selected will serve to parameterize all flows between states in order to determine a transition matrix that will be a function of the external conditions (i.e. neighbourhood and climate).

Model simulations.

We will use the temporary plots (TP), an independent dataset present only in the Québec database, for model validation. Temporary plots will be classified into the same four states. We will compute the proportion of each state by ecoregion ("*Système de classification des types écologiques*", MRN). Secondly, we will run the model at equilibrium predicting the state proportions in same ecoregions and compare them with observed data from TP database. Highest R-squared and lowest Akaike information criterion (AIC) will be associated with the best predictive and parsimonious model. Bias (i.e low R-squared) might indicate that the current forest composition is not at equilibrium and needing further investigations.

After the validation process, we will study equilibrium states of the model and investigate the first hypothesis by (i) evaluate the model sensitivity on initials conditions (e.g state occurrences), (ii) analyze the spatial structure of the landscape (e.g. mosaic) for presence of alternatives stables states.

Lastly, we will run simulations with increases or modification of the climatic gradient in the cellular automaton. This step, in the context of the second hypothesis, allows us to assess Sugar maple migration (e.g velocity and time lag) through temperate communities under different climate change scenarios.

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