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 northeastern North America. [12; 22; 15; 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 [21; 14]. According to McKenney (2007) [21], 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) [12; 16]. Thus, the expansion of Sugar maple and iis 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 [16; 1; 11; 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 composerd of a superficial leaf mat [1]. The temperature is colder, the snow melts later and the soil is wetter under coniforous trees [16; 11]. Soil acidification causes a reduction in the cation exchange capacity and subsequently decreases availability of some nutrients such as calcium [24]. Sugar maple seedlings have been recognized to be particularly sensitive to waterlogged conditions and soil nutrient content [24; 16; 5]. These properties of coniferous forest soils could hinder the local establishment of species associated with alkaline soils or unable to withstand waterlogged conditions [16]. Under these conditions, tree species migration is likely to be restricted or delayed [16]. 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 [15; 24; 1; 23].Sugar maple could thus be unable to colonize the boreal forests as a result of strong and localized plant-soil feedbacks [19].

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 [25]: 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 [11; 9]. 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 in areas where alternative stable states are susceptible to occur. In order to fulfill this objective and
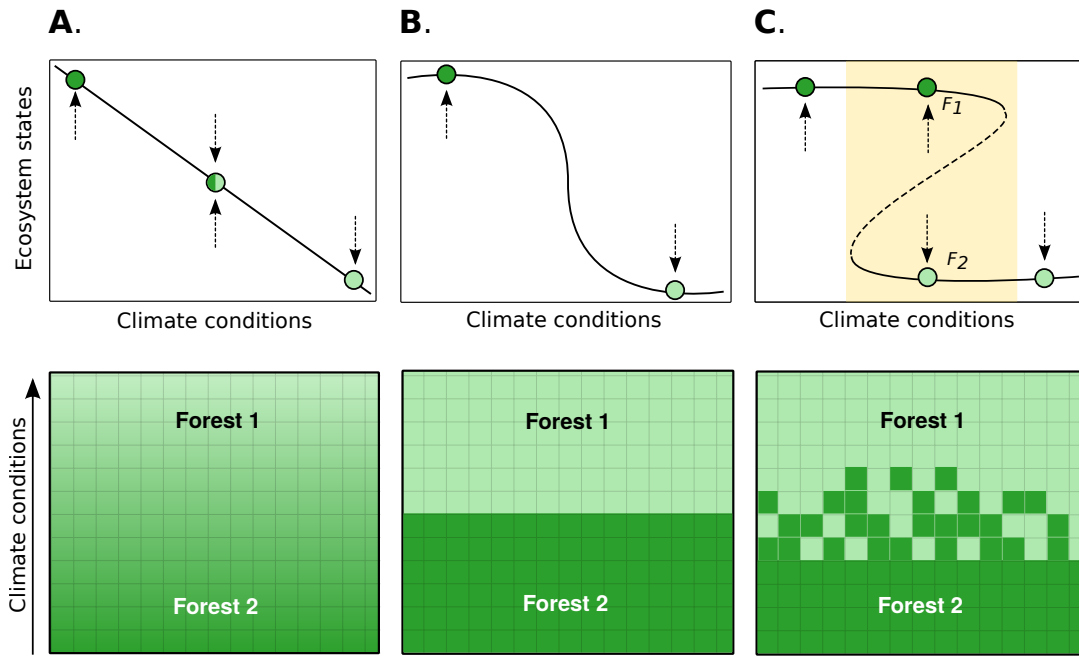
Figure 1: Schematic representation of different ways in which the equilibrium states from forest-forest system can vary over environmental gradients such as temperature, precipitation or soil moisture. Three different responses are presented, **(A)** gradual, **(B)** basic fold, **(C)** catastrophic fold. The first line presents the stable ecosystem states given a specific environmental condition. Arrows indicate the direction the system moves if not at the equilibrium. Solid lines represent stable states along the boreal-temperate transition, and the dashed line (in yellow highlight) unstable equilibrium. This zone, called hysteresis, is particularly unstable and small fluctuations in environment conditions give rise to a contrasted state representing an alternative stable states. (F_1 or F_2). The second line illustrates 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 emerged in the late 1960s [27; 2]. May (1977) highlights the fact than an ecosystem can be seen as a dynamic system where communities possess several different equilibrium points given a specific external conditions [18]. These equilibrium states are named alternative stable states. Suppose that a forest ecosystem can be usefully characterized by a set of dynamic state variables, with their relations to each other defined by a set of external conditions. In the present context, a state is defined as a forest species community given a time and a set of environmental conditions (e.g. annual precipitation and annual tempera-

ture). Changes on this set of environmental parameters can induce three different shapes of ecosystem response: **(A)** gradual, **(B)** basic fold, **(C)** catastrophic fold [27] (Figure 1, upper line). Firstly, when a small environmental change occurs, forest ecosystems can respond almost linearly, with no threshold leading to drastic changes in the species community (Figure 1.a, upper line) [27; 26]. In this case, forest ecosystems can be seen as a continuum of states along the climate gradient [27; 26; 25]. For instance, when the annual precipitation increases slightly in a deciduous stand, the new local condition gives rise to a new coniferous species establishment (e.g balsam fir). This forest stand reaches a new state wherein the species community has been smoothly changed. Secondly, such forest ecosystems are insensitive to small changes in environmental conditions over certain ranges but respond strongly when a threshold is reached [25]. For example, species mortality can increase sharply when the water level of a lake is rising permanently in response to changing hydrological conditions in the drainage basin. The new condition abruptly changes the entire species assemblage surrounding the lake. Hence, the response curve of the natural system is not linear but lightly folded and these changes can drive the forest ecosystem to a threshold and lead to major changes in the community (Figure 1 .b, upper line). Lastly, in some non-linear systems, the response curve can be folded backwards and alternative stable states could occur (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 [25]. The main ingredient to creating alternative stable states is positive feedbacks [25]. One well known is facilitation in ecological succession (i.e. the idea that pioneer species pave the way for later successional species) and this feedback seems to be present in the the boreal-temperate forests studied [1; 10].

Natural system studied. Many empirical and modelling studies have been conducted on the transition between forest to non-forests (e.g. Boreal-Tundra) [28; 27; 13; 22] but little attention has been given to evaluate the forest-forest ecotone [11; 12; 22]. At landscape scales, transitions between the temperate and boreal forests can be approached as a dynamical system where each forest biome community is a stable state (Figure 1, lower line). There is no distinct boundary at the boreal-temperate ecotone; instead a broad transition zone exists where stands of coniferous and deciduous species co-occur at the regional scale [11; 9]. A macromosaic landscape can be observed with either pure stands of northern temperate trees or boreal forest stands [11; 9]. In this study context, alternative stable state theory could applied to the hardwood-boreal forest patchiness structure often attributed to differences in soils, nutrient status and topographical factors [10]. This segregated patch distribution could be explained by the fact than microclimatic conditions can modulate establishment of those forests [6]. Distribution of deciduous and boreal forests within the ecotone is not determined by macroclimatic conditions, but rather by local variation of substrate, drainage, physical soil properties, and nutrient availability [11; 10]. Boreal and hardwood forests are dominated by trees with different physiognomy, which is expected to produce distinctive litter and light micro-environments [1]. 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) [10] hypothesized that Sugar maple is subject to such a feedback. 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 towards a better substrate to their own regeneration (positive feedback). In this context, we expect to find forest stands dominated by either boreal species or temperate species and with great sensitivity to initial conditions (i.e. soil conditions, abundance of deciduous or coniferous species in the forest stand). Thus, the soil condition and the role of dominant species in boreal and temperate forests need to be investigate as main drivers in shifts between alternative stable states [15; 24; 6; 1].

3. Methods
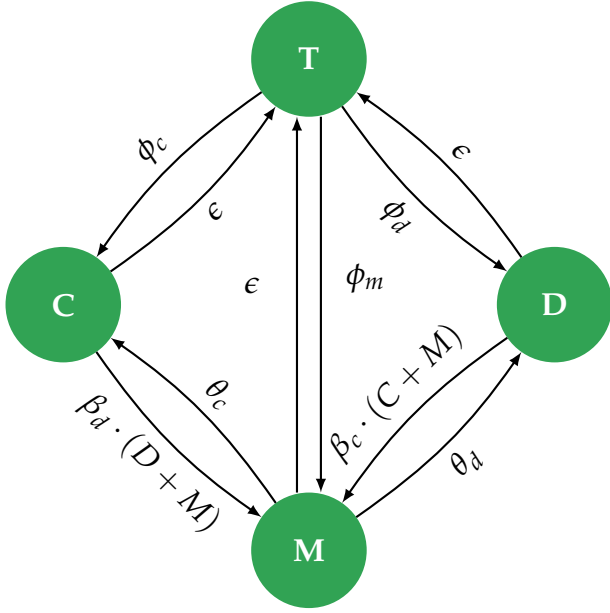
Figure 2: Conceptual representation of the transition model between deciduous (D), mixed (M) and coniferous (C) stands. T corresponds to a post-disturbance forest patch. Perturbations, natural and anthropogenic, occur with a frequence ϵ. Flows or transition rates between states are represented by arrows. 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.

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 [9]. 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 circle, 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 drivers leading the transition between two states. In fact, some disturbances might change state proportion in the landscape. 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 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 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- FOR[1] 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 [20] 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 [11; 13; 28]. 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-

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

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). This function will be calibrated using two statistical methods: (1) classification tree and (2) multinomial regression (eq. 1). Explanations on this calibration step will focus only on a specific transition, either $M \rightarrow T$ but the method used will be generalized on all transitions.

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

The Breiman and Cutler's classification method or classification tree (randomForest R-package, [17]) allows computation of $\hat{D}$ and $\hat{M}$ (eq. 1). They are the expected probability of observing state D or M in this area given climatic conditions. In this transition case (eq. 1), $\hat{D}$ and $\hat{M}$ is a proxy for the deciduous regeneration pressure surrounding the area. To compute the probability of state occurrence given the local climatic conditions encounter by a patch, we use a multinomial regression (nnet R-package, [29]). 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). The last part consists of implementing the model as a spatially explicit cellular automaton.

Validation and simulation. 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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