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. The boreal region is warming twice as fast as the global average and this will inevitably alter the species composition in boreal forests [29; 14; 17]. Sugar maple (*Acer saccharum*) is a widespread and abundant tree in north-eastern North America. [12; 23; 16; 1]. Predicting shifts in the range of Sugar maple is an important challenge because this species is highly desirable by hardwood and maple syrup producers, two large economic sectors in Quebec. Some species mostly representative of northern forest ecosystems are forecast to expand their distribution broadly towards the north [22; 15]. According to McKenney (20007), Sugar maple is one of those species expected to move closed to the Ungava bay [22]. This species is dominating the northern temperate forest especially along the boreal-temperate forests ecotone at its northern range limit [1]. Actually, Sugar maple predictions are built on species distribution models based only on climatic conditions, though Sugar maple regeneration depends both on macro conditions (*i.e.* regional climate) and micro conditions (*i.e.* soil and microtopography) [12; 17]. Thus, the expansion of Sugar maple and his temperate species community is difficult to predict because micro conditions can mitigate macro conditions such as global warming [6].

Species are responding differently to the soil conditions, and the soil properties found in boreal forests are different from those in temperate forest [17; 1; 11; 7]. Conifer forests generally contain deep and poorly-decomposed litter to layers, while those of northern hardwood forests are thinner but covered by a tough superficial leaf mat [1]. In boreal forest, the temperature is colder and the snow melts later, the soil is wetter and the litter is more acidic and fibrous [17; 11]. Soil acidification is causing a reduction in the cation exchange capacity and subsequently decrease avaibility of some nutrients such as calcium [25]. Sugar maple seedling has been recognized to be particulary sensitive to waterlogged condition and nutrients soil content [25; 17; 5]. This properties of coniferous forest soils could hinder the local establishment of species associated with base-rich soils or unable to withstand waterlogged conditions [17]. Under these latter conditions, tree species migration is likely to be restricted or delayed [17]. Thus even if the regional climate conditions are favorable, the micro conditions found in the boreal forest could slowing down the seedling establishment of these temperate species [16; 25; 1; 24]. Then the temperate forest including Sugar maple could then be unable to migrate in boreal forests as a result of local plant-soil feedbacks [20]. To study the expansion of Sugar maple, the ecotone dynamic can be conceptualized through two set of dominant species communities: the boreal community and the temperate community including Sugar maple. The landscape might be structured as a patchy mosaic structure where micro conditions are driving the spatial occurences of boreal and temperate community species despite a regional climate favorable to temperate species [11; 9]. In this case, these forest communities are two alternative stable states, *i.e.* contrasted states occuring in the same climate conditions [26]. This situation generate a tension between the boreal and temperate forest meaning that modification on micro conditions (i.e mainly soil conditions) can produce abrupt shift in community composition in 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 hypothesis: (H_1) Alternative stable states are occuring in the boreal-temperate forests ecotone; (H_2) Time lags in the response to climate change will be larger in areas where alternative stable states are occuring. In order to achieve my general objective and test these hypotheses, we will (1) develop a climate-dependent model of state transition (STM) representing
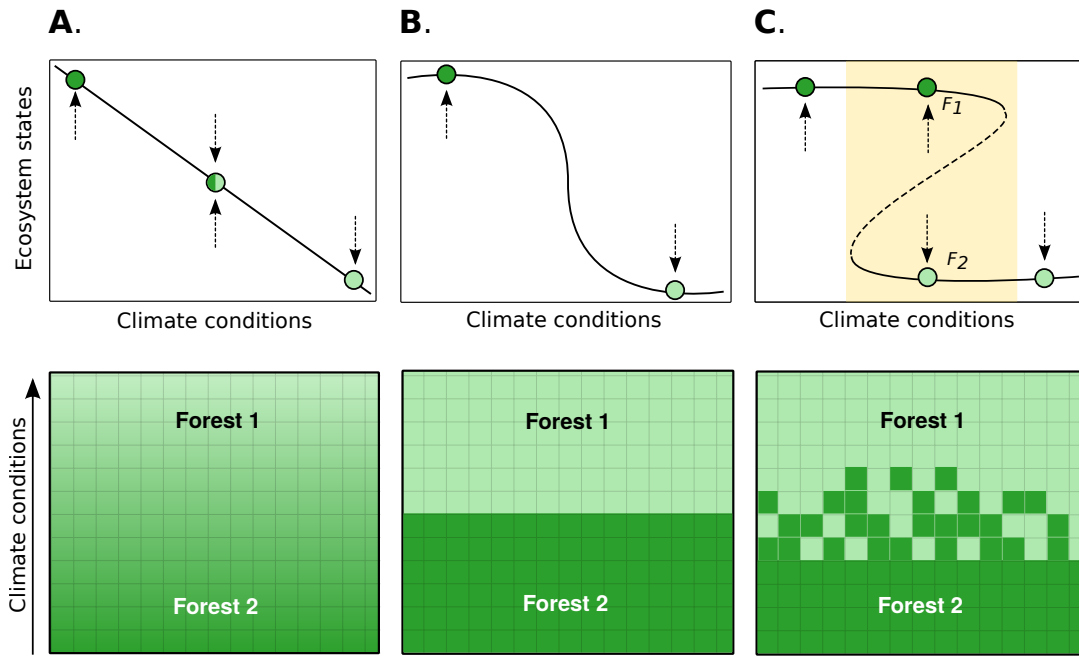
Figure 1: Schematic representation of different ways in which the equilibrium states from forest-forest system can vary over environnemental gradients such as temperature, precipitation or soil moisture. Three differents responses are presented, **(A)** gradual, **(B)** basic fold, **(C)** catastrophic fold. The first line presents the stable states rise by the forest given a specific environnemental 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 particulary unstable and small fluctuations in environnement 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).

the dynamics of the boreal and temperate communities at landscape scale; (2) investigate the spatial structure of maple distribution through his temperate community; (3) Study the occurrence of alternative stable states in the transitional zone; and finally (4) 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, it's associated community in the temperate biome and a justification about why alternative stable states are expected to occure at the boreal-temperate forests ecotone. The last section of this document describes the model and the methodology that we will employ to fill my specific objectives.

2. Review

Alternative stable states in forest ecosystems. The idea that alternative stable states may exist in community ecology has been emerged since the late 1960s [28; 2]. May (1977) highlights the fact than a ecosystem can be seen as a dynamic system where species communities possess several different equilibrium points given a specific external conditions [19]. 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 environnemental conditions (e.g. annual precipitation and annual

temperature). Changes on this set of environnemental parameters can induce three different shapes of ecosystem response **(A)** gradual, **(B)** basic fold, **(C)** catastrophic fold [28] (Figure 1, upper line). Firstly, when a small environmental change occur forest ecosystems can respond almost linearly, with no threshold leading to drastic changes in the species community (Figure 1.a, upper line) [28; 27]. In this case, forest ecosystems can be seen rather as a continuum of states along the climate gradient [28; 27; 26]. For instance, when the annual precipitation increase slightly in a forest 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 change in environmental conditions over certain ranges but respond strongly when a threshold is reached [26]. For example, species mortality can increase sharply when the water level of a lake is rising permanently in response to changing hydrologic conditions in the drainage basin. The new condition reached change abruptly the entire species assemblage surrounding the lake. Hence, the response curve of the natural systeme is not linear but lightly folded and these change can drive the forest ecosystem to a treshold 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 approach a tipping point on the folded upper branch, it cannot pass smoothly to the lower branch. Small forcing on initial condition of the state F_1 transfer immediatly the system into a contrasted state F_2 (Figure 1 .c). Hence, at this point, the system is particulary 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 [26]. The main ingredient to creating alternative stable states is positive feedbacks [26]. One well known is facilitation in ecological succession (i.e. the idea that pioneer species pave the way for later successionnal species) and this feedback seems to be present in the the boreal-temperate forests studied.

Natural system studied. Many empirical and modeling studies have been conducted on the transition between forest to non-forests (e.g. Boreal-Tundra) [29; 28; 13; 23] but little attention has been given to evaluate the forest-forest ecotone [11; 12; 23]. At landscape scale, transition 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 stabe state theory could applied to the hardwood-boreal forest patchiness structure often attribute to differences in soils, nutrient status and topographical factors [10]. This segregated patches distribution could be explain by the fact than microclimatic conditions can modulate establishement 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 avaiblity [11; 10]. Boreal and hardwoodl forests are dominated by trees with different physiognomy, which is expected to produce distinctive litter and light micro-environments [1]. A positive feedback contribute 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 delayed the temperate species regeneration (negative feedback) and in other hand, temperate species establishment can enriching the soil towards a better substrate to their own regeneration (positive feedback). In this context, we expected to find forest stand dominated by either boreal species or temperate species and particulary sensitive to initial conditions encountered (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 forest need to be investigate as main drivers in schifts between alternative stable states [16; 25; 6; 1].

3. Methods
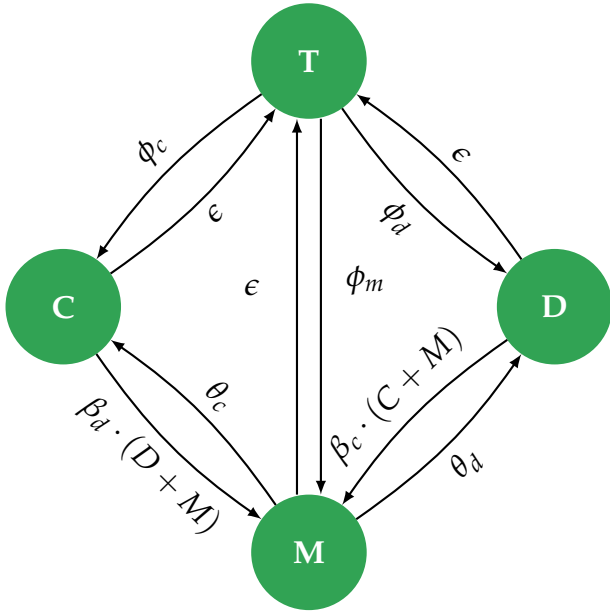
Figure 2: Conceptual representation of the transition model between deciduous (D), mixed (M) and coniferous (C) stands. T corresponds to a post-disturbance forest patch. Perturbations, natural and anthropogenic, occur with a frequence ϵ. Parameters θ and β are rates of colonization and succession, respectively. 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 on the STM representing dynamics in the boreal-temperate forests transition at landscape scale. In overall, the ecotone landscape includes three distinctive kind of forest canopies: (i) hardwood, (ii) mixedwood and finally (iii) softwood [9]. Each of these stands are represented as a state in the STM: **(D)** Deciduous, **(M)** Mixed and **(C)** Coniferous (see green circle, figure 2). According to Briske *et al.* (2008) and this STM context, state mean a plant community phases occurring on similar soils that interact with the environment to produce persistent functional and structural attributes [4]. Flows or transition rates between states are represented by arrows (figure 2). Theses rates are climate-depend. Transitions between all states are possible except the direct transition between a deciduous and coniferous stands, which does not occur because it systematically require an intermediate step in state M. Except for the colonisation rate (θ), transition rates are varying 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) depend also of the availability in C and M patches in the landscape (figure 2). Some disturbances might change state proportion in the landscape. Natural disturbances is 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 favoring 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 convert into a transitional patch **(T)** when one of those disturbances event occur at rate ϵ (Figure 2). Af-

ter 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 describe by the function ϕ_c incorporate a specific patch recovery rate (α_c), also the availability of coniferous ($C + M$) species and the proportion of patches unconverted into a deciduous state, either $1 - \alpha_d \cdot (D + M)$ (see caption, figure 2). If this patch C is undisturbed then the conferious stand turn into a mixed stands by deciduous colonization with a rate θ_c. 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 is 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 assume 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. Data are freely provided by partners. They are covering 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 including 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 include many relevant informations 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 are include and extract by interpolation from the climatic model ANUSPLIN [21]. We will parameterize the model using annual rainfall (mm) and monthly temperatures (minimum, maximum and average in °C) of the previous 30 years the year of the plot 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; 29]. Filters will be applied to the database prior to the model parameterization. In a first time, 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 deposite with fast to moderate drainage will be considered for the analysis. We will consider only the mature stands with dominant stratum within trees is superior to 50 years old. Lastly, plots disturbed by human activities (mostly by logging) will be removed in order to parametrize the model on natural disturbances.

Parametrization. As previously stated, the model focuses mostly on representative species of the boreal and temperate forest. In this context, the basal area (m^2/ha, BA) will be compute to provide a measure of relative species abundance in each of the plot 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 are classified following their percent 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 $BA_D \geq 50\%$). 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 second step consists to compute a probability function of transition between two states

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

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 calibrate in 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 $M \to T$ but the method used will be generalized on all transitions.

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

The Breiman and Cutler's classification method or classification tree (randomForest R-package, [18]) allows to compute $\hat{D}$ 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 of the deciduous regeneration pressure surrounding the area. To compute the probability of state occurency given the local climatic condition encounter by the patch, we use a multinomial regression (nnet R-package, [30]). 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 neighbourood (previously presented) and X_i a climate variable. Model selection will perform using Akaike information criterion (AIC). Model selected will serve to parameterize all flows between states in order to determine a transition matrix that will be funtion of the external conditions (i.e. neighbourood and climate). The last part consists to integrate the model in Julia programming language (parallelizable with CUDA) and implemented it in a spatially explicit cellular automaton.

Validation and simulation. Model validation will conduct on TP, an independent dataset present only in the Québec database. Temporary plots will be classified into the four different 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-squarred and lowest Akaike information criterion (AIC) will be associated with the best predictive model. Bias (i.e low R-squarred) might indicate that the current forest composition is not at equilibrium and needing further investigations. After the validation process, we will study states equilibrium of this model and investigate the first hypothesis by (i) evaluate the model sensitivity on initials conditions (e.g state occurencies), (ii) look up the spatial structure of the landscape (e.g. mosaic) and presence of alternatives stables states. Lastly, we will run simulations with increase or modification on the climatic gradient in the cellular automaton. This step relative to the second hypothesis, allows to assess Sugar maple migration (e.g velocity and time lag) through his temperate community under different climate change scenarios.

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