

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. [12; 23; 15; 1]. Predicting shifts of 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; 14]. 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. This prediction relies on a species distribution model 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]. De Frenne *et al.* (2013) revealed that shifts in species distribution in reaction to climate change can be mitigated by the microconditions (*i.e.* soil temperature within the forest understory) rather than the macroconditions (*i.e.* temperature rising at regional scale). Hence, the microconditions (e.g. soil, drainage) could delayed future sugar maple establishment towards the boreal forest.

Soil-plant feedbacks are susceptible to impact sugar maple migration dynamics. Soil properties found in boreal forests differ from those in temperate forest [16; 1; 11; 6]. 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 [16; 11]. Acid soils in coniferous forest 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; 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]. Migration of temperate tree species is likely to be restricted or delayed by the dominance of coniferous trees [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; 25; 1; 24]. Sugar maple could thus be unable to colonize the boreal forests as a result of strong and localized soil-plant feedbacks [20].

My general hypothesis that the temperate-boreal forest ecotone is as a system dominated by two alternative states, *i.e.* contrasted equilibrium states occurring in the same climate conditions [26]: the boreal community and the temperate community, including Sugar maple. Under this hypothesis, the landscape would be a patch mosaic where micro conditions and stand history 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 role of alternative stable states in the transition between the boreal and temperate forests under different climate change scenarios. In this context, we will test two specific 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 test these hypotheses, we will (1) develop a climate-dependent state-transition model (STM) representing the dynamics of the boreal and temperate communities at the 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. I present the concept of alternative stable states and critical transitions in forest ecosystem properties. Then after I focus 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. A community is stable when it persists in a given state, and resists or is resilient to small perturbations [8]. Multiple stable states are possible. The idea that alternative stable states may exist in community ecology was proposed in the late 1960s [28; 2]. May (1977) [19] shown that an ecosystem can be seen as a dynamic system where communities are not constant over time and can change following a modification of the environment. Ecological communities can reach several equilibrium points or stable states along an environmental gradient [19]. Stable states can persist according to various feedback mechanisms [8]. For instance, in the Sahel or some part of the Amazon area, vegetation may promote precipitation (i.e. positive feedback) and thus the persistence of large tracts of forests. However, loss of vegetation in this region following logging or natural fires can lead to a major change in climate, which because eventually too dry to support the vegetation needed to maintain precipitation [26]. Hence, larger perturbations encountered by the system can generate a change of the state of a community, i.e., the arrangement of species or populations and their interaction with the physical environment [8].

Ecologists recognize three possible responses of communities to a permanent change in the environment: **(A)** gradual, **(B)** basic fold, **(C)** catastrophic fold [28] (Figure 1, upper row). First, when a small modification to environmental conditions occurs (e.g. temperature rises), the state of the community can change almost linearly (Figure 1.A) [28; 27]. In this case, the whole ecosystem can be seen as a continuum of communities along the environmental 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 increase 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, a small change in the environment, such adding a toxin, can lead to major changes in the community state. Lastly, in some strong non-linear systems, the response can be folded backwards and alternative stable states could occur (Figure 1 .C). This implies that, for a given environment, the ecosystem has two alternative stable states (F_1 and F_2) 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 transfers the system immediately to a different state F_2 (Figure 1 .C). At this point, the system is particularly sensitive to the initial conditions. This point is called a bifurcation point and a small forcing can drive the system into backward or forward shifts towards either one of the alternative stable states F_1 or F_2 , also called "attractors" [26]. The main ingredient to create alternative stable states is the occurrence of positive feedbacks [26; 30]. One well known is the facilitation process in ecology and two kinds exist in nature. The first one is interspecific facilitation and can be observed across the ecological succession process. Pioneer species pave the way for later successional species, changing gradually the closest environment (e.g. shading, deeper litter) [26; 17]. In this case, the environmental modification by pioneer species can be seen as a positive feedback allowing the establishment of later successional species. The second kind of facilitation is intraspecific where a particular species can promote its own regeneration in the immediate environment. *Acer saccharum* and *Tsuga canadensis* regenerations are related to the unique seedbed conditions created by each species, to which conspecific seedlings are specialized [10; 20]. In changing seedbed condition, mature trees act as positive feedback to their own regeneration. When intraspecific facilitation is stronger than the interspecific competition, we can observe forest stands dominated either by mature trees of *Acer saccharum* or by *Tsuga canadensis*. Hence, either forest stand type can be considered as an alternative stable state. This kind of positive feedback could 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 and non-forest communities (e.g. Boreal-Tundra) [29; 28; 13; 23]. However, little attention has been given to the forest-forest ecotone's dynamic [11; 12; 23]. The temperate-boreal transition could adopt three different structures along a climatic gradient (Figure 1, lower row). In the first case, the response of forest communities to

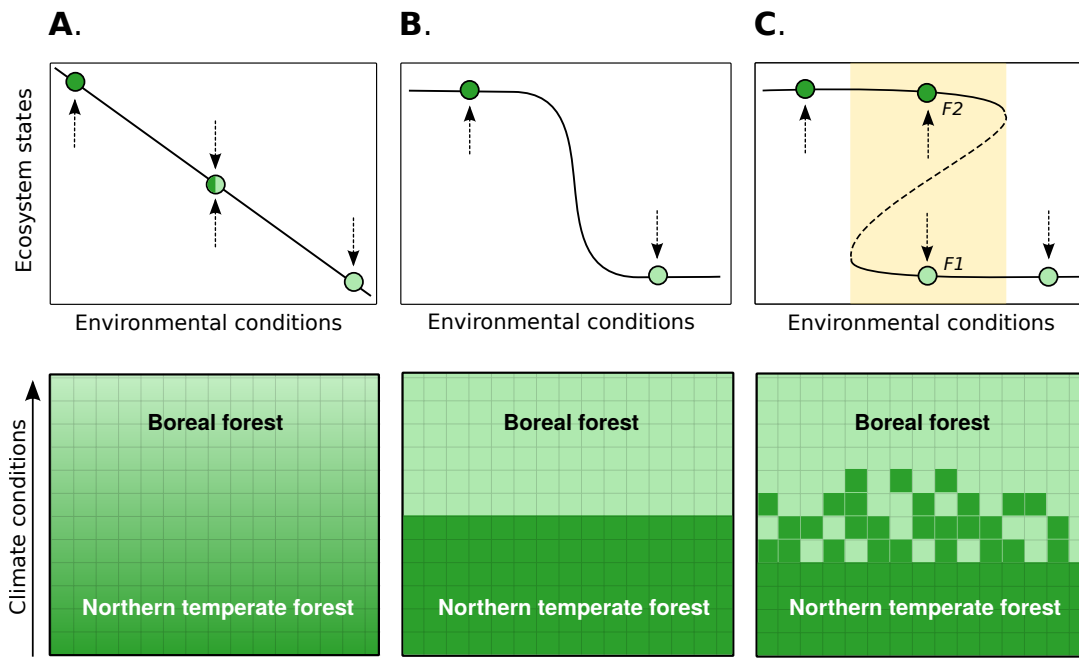


Figure 1: Change in communities composition over an environmental gradient (i.e. precipitation, temperature or soil moisture) can take three different shapes: **(A)** gradual, **(B)** basic fold, **(C)** catastrophic fold. Each of them are shown across the upper line. Solid lines represent all reachable stable states along the climate gradient. Arrows indicate where the system moves if not at the equilibrium (i.e outside of the solid lines). The yellow zone (in panel C), called hysteresis, is unstable and small fluctuations onto the environment conditions could give rise to abrupt changes into one of the alternative stable states (F_1 or F_2). In the temperate-boreal system and according to each response shape, the bottom line illustrate three different spatial repartitions of boreal and temperate communities over a climatic gradient.

climate is gradual and no distinct boundary is observed between the temperate and the boreal forests (Figure 1.A). Instead, a smooth transition where species assemblages are unique occurs for a given set of climatic conditions. On the other hand, distribution of temperate and boreal forest communities can be strongly linked to climate. Thus, climate highly segregates forest types and a net boundary appears between them (Figure 1.B). Moreover, a third response shape of the system is also possible. Previous studies highlighted that a broad zone in the boreal- temperate forests transition exists where stands dominated by either coniferous or deciduous species co-occur [11; 9]. Hence, this spatial configuration might correspond to the third case shown in figure 1.C. We hypothesize these communities to be alternative stable states. A strong positive plant-soil feedback contributes to the maintenance of these communities: coniferous species generate acidic and wetter soils and deciduous species enrich the litter. Both forest stands are using a facilitation process in order to promote their own regeneration. These feedbacks help temperate species seedling establishment in favorable sites of a heterogeneous landscape. These positive feedbacks do not increase the spread capacity of temperate species within their local favorable patches, they instead elevate local density and seed production [17]. A large disturbance could contribute to modifications of the microconditions in a patch historically unfavorable to the invader. Following this event, this post-disturbance patch can switch abruptly into a temperate forest state if favorable patches are available in the neighborhood. These feedbacks might influence the invasive spread of temperate species in boreal stand forest [17]. In unfavorable patches, temperate species will have to cope with boreal soil properties that may hinder and delay their establishment. Climate change also has the potential to improve boreal soil conditions for temperate species establishment [16]. The outcome of these antagonistic forces could impact positively or negatively the migration of some temperate species in response to climate change; we will investigate this deeply using an STM model.

3. Methods

State and Transitional Model. This study will be based on a STM representing landscape dynamics at the boreal-temperate transition. Three forest cover types are considered: (i) deciduous, (ii) mixed and (iii) coniferous [9]. Each of these stand types is represented as a state in the STM: **(D)** Deciduous, **(M)** Mixed, **(C)** Coniferous. We also consider the state **(T)** to represent transitional stands (green circles, figure 2). According to Briske *et al.* (2008) and this STM context, a state means a plant community phase occurring on similar soils that interact with the environment to produce persistent functional and structural attributes [4]. Transition between states 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 probability (θ), transition probabilities vary with the proportion of coniferous or deciduous found in the neighbourhood to represent dispersal limitations. 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).

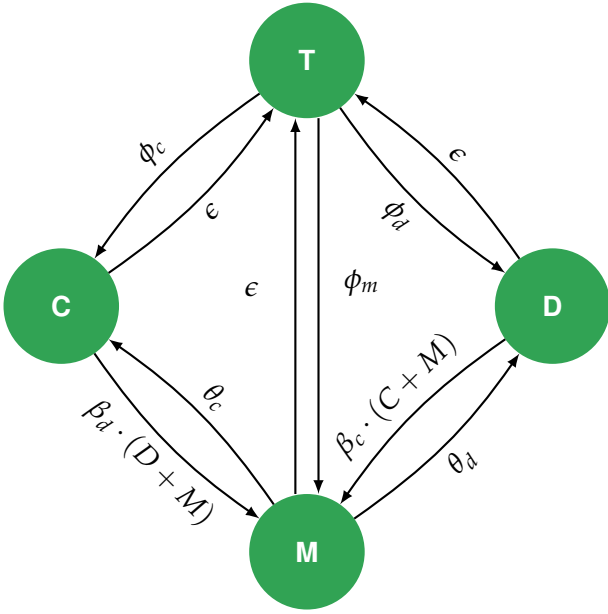


Figure 2: Conceptual representation of the transition model between deciduous (D), mixed (M) and coniferous (C) stands. *T* corresponds to a post-disturbance forest stand. Perturbations, natural and anthropogenic, occur with a probability ϵ . Flows or transition rates between states are represented by arrows. Parameters θ and β are colonization and succession probabilities, respectively. We define regeneration 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 regeneration rate after a patch has been disturbed.

Ecological processes such as succession and colonization are not the only mechanisms responsible for the transition between two states. Natural disturbances are an important drivers of forest dynamics at the landscape scale (e.g. fire in boreal forest or large windthrow in temperate forest). Small fires promote dominance by deciduous species, while larger and intense fires favour 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 expansion (maples/aspen) or decline (cedar/spruce) of several species at the northern range limit of temperate trees in eastern Québec [7]. When a disturbance occurs in the actual model, state affected is systematically converted into a transitional state (**T**). (Figure 2). Thereafter, any transitional patch (**T**) can be transferred into state C, M or D following a function of probability ϕ . In the conversion case of state T towards C, this flow ϕ_c incorporates a specific patch regeneration 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 it could switch to a mixed stand after colonization by deciduous trees with a probability θ_c . The dynamics of this model can be described with a system of four differential equations. The dynamics of *T* over the time is described by the following differential equation:

$$\frac{\delta T}{\delta t} = \epsilon \cdot (C + M + D) - T \cdot (\phi_d + \phi_c + \phi_m) \quad (1)$$

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):

$$\frac{\delta C}{\delta t} = \phi_c \cdot T + \theta_c \cdot M - \alpha_d \cdot (D + M) \cdot C - \epsilon \cdot C \quad (2)$$

This 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 has been freely provided by partners and covers 3 eastern Canadian provinces (ca. 16,000 plots) and 31 states of eastern USA (ca. 150,000 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 inventories are geo-referenced. Climatic variables are associated to each plot by interpolating 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 30 years previous to the year of each plot's sampling. Those variables are used by many authors as good predictors of the distribution of the species investigated in this present study [11]. Filters will 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. The model focuses on representative species of the boreal and temperate forest. Relative abundance of each species will be computed from basal area 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, D and T states will be classified following their percentage of *Ba* in deciduous (Ba_d), coniferous (Ba_c) or transition species (Ba_t) in the plot (Table 1). The plots that do not satisfy any of the conditions shown in table 1 are filtered out.

Table 1: Boundary of the coniferous (Ba_c), deciduous (Ba_d) and transition species (Ba_t) relative abundances to classify the four STM's states (D,C,M and T). The symbol (!) means that the forest plot hasn't been previously classified into one of the states C, D or M.

States	Boundaries
D	$Ba_c < 25\%$ and $Ba_d \geq 75\%$
C	$Ba_c \geq 75\%$ and $Ba_d < 25\%$
M	$Ba_c \geq 25\%$ and $Ba_d \geq 25\%$
T	$!D; !C; !M$ and $Ba_t \geq 75\%$

The second step of the parameterization consists of evaluating functions describing the probability of a transition between two states given specific climatic conditions (*Climate*, eq. 3) and the proportion of deciduous or coniferous in the neighborhood (\hat{D} and \hat{M} , eq. 3). Hereafter, will focus only on a specific transition $M \rightarrow T$ but the method is common to represent all transitions. In this example (eq. 3), \hat{D} and \hat{M} are the expected probabilities of observing state D or M in this area given climatic conditions. They are a proxy for the deciduous propagule pressure coming from neighbors. They will be estimated using a standard species distribution model (Step 1, eq. 3) such as the random forest algorithm (R-package, [18]).

$$P(D_{t1}|M_{t0}, Climate) = f(\overbrace{Climate, \underbrace{\hat{D}, \hat{M}}_{\text{Step 1. RandomForest}}}^{\text{Step 2. Multinomial regression}}) \quad (3)$$

The probability of a transition between two states given the local climatic conditions encountered by a patch (Step 2, eq. 3) will be computed using a multinomial regression (nnet R-package, [31]). We can summarize

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

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 be used to represent all flows between states.

Model validation and simulations. The model will be validated using the temporary sample plots (TP), an independent dataset present only in the Québec database. 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) and compare this distribution than predicted by the model. 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 investigation. After the validation, we will assess if alternative stable states are present in the boreal-temperate forests transitions (H_1). We will run multiple simulations of the spatially implicit model in varying initial conditions i.e. states proportion and climate conditions. In studying the simulations, we expect to find abrupt changes in the proportions of states over time. Also, we expect to observe a bimodal distributions of states over a certain range of climate conditions (when the model is at equilibrium). If these expectations are validated, then alternative stable states are present in the boreal- temperate forests system. In this implicit model, rates of transition depend to the proportion of states available in the general system, thus rates of transition are unconditional to the state of patches in the neighborhood. This property of the model makes it impossible to assess sugar maple range shift (i.e. dispersal and velocity rates of forest temperate patches) as proposed through hypothesis H_2 . To remedy it, we will embed this model into a cellular automaton where each cell corresponds to a forest patch in the landscape (C,D,M or T). The succession (β) and regeneration (α) probabilities of a patch will be affected by the presence of states in its eight neighboring cells. With this explicit model, we will run simulations and modulate climate in the lattice (e.g. increase the temperature). We expect to observe a delayed rate of sugar maple migration where the alternative stable states appear.

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