

# **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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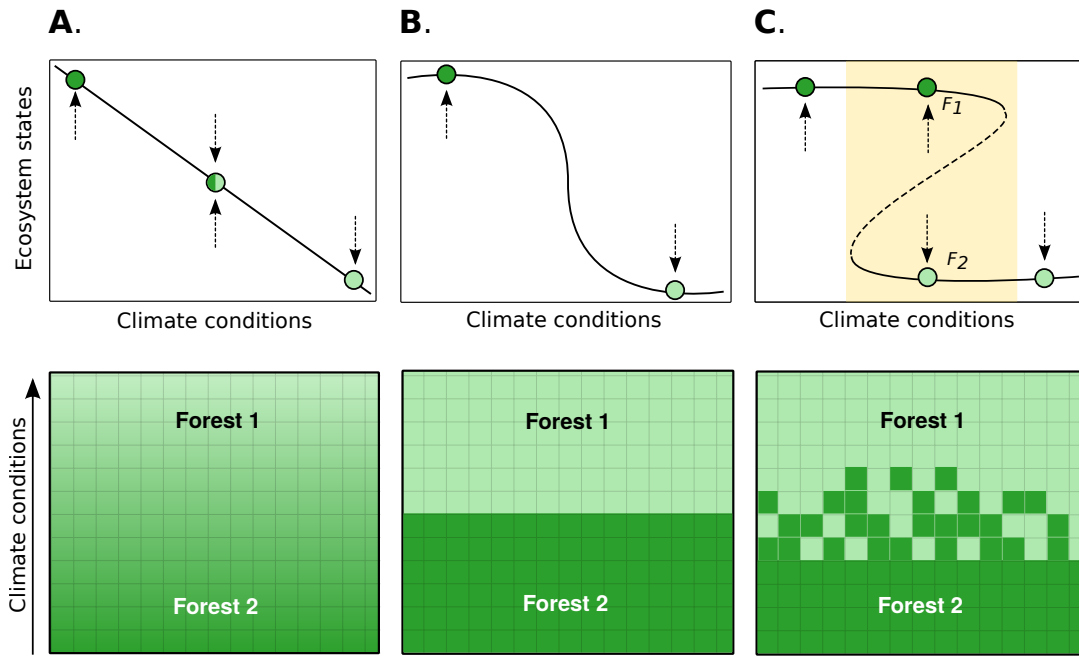
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# 1. Introduction

**Context.** Sugar maple (*Acer saccharum*) is a widespread and abundant tree in north-eastern North America. [12; 22; 15; 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. This species is dominating the northern temperate forest especially along the boreal-temperate forests ecotone at its northern range limit [1]. Some species mostly representative of northern forest ecosystems are forecast to expand their distribution broadly towards the north [21; 14]. According to McKenney (2007) [21], Sugar maple is one of those species expected to move closed to the Ungava bay which appear highly improbable. In fact, 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; 16]. Thus, the expansion of Sugar maple and its temperate species community is difficult to predict because micro conditions can mitigate macro conditions such as global warming [6].

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]. Conifer forests generally contain deep and poorly-decomposed litter 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 [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 latter conditions, tree species migration is likely to be restricted or delayed [16]. Thus even if the regional climate conditions are favorable, the micro conditions found in the boreal forest could slow the seedling establishment of these temperate species [15; 24; 1; 23]. Then the temperate forest including Sugar maple could be unable to migrate in boreal forests as a result of local plant-soil feedbacks [19]. To study the expansion of Sugar maple, the ecotone dynamic can be conceptualized as two dominant communities: the boreal community and the temperate community including Sugar maple. The landscape might be structured as a patchy mosaic where micro conditions are driving the spatial occurrences of boreal and temperate community species despite a regional climate favourable to temperate species [11; 9]. In this case, these forest communities are two alternative stable states, *i.e.* contrasted states occurring in the same climate conditions [25]. This situation generate a tension between the boreal and temperate forest meaning that modification of micro conditions (*i.e.* mainly soil conditions) can produce abrupt shifts 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 hypotheses: ( $H_1$ ) Alternative stable states are occurring in the boreal-temperate forests ecotone, and ( $H_2$ ) Time lags in the response to climate change will be larger in areas where alternative stable states are occurring. In order to achieve the general 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 landscape scale; (2) investigate the spatial structure of maple distribution through its temperate community; (3)



**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).

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, 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 document describes the model and the methodology that we will employ to achieve the specific objectives.

## 2. Review

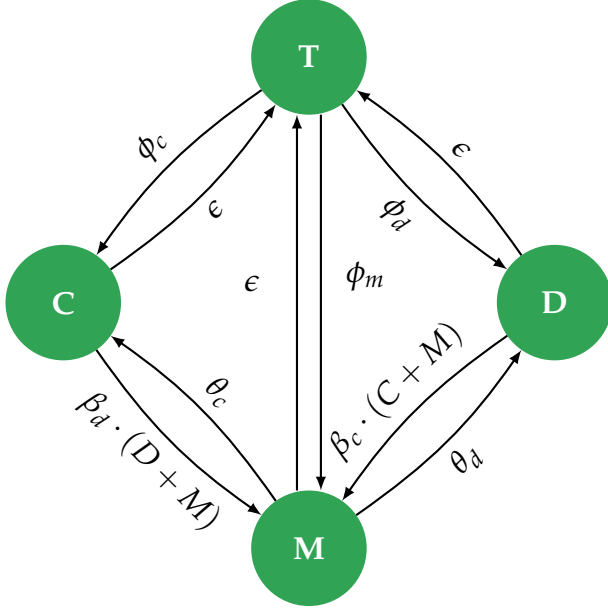
**Alternative stable states in forest ecosystems.** The idea that alternative stable states may exist in community ecology emerged in the late 1960s [27; 2]. May (1977) highlights the fact that an ecosystem can be seen as a dynamic system where communities possess several different equilibrium points 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 temperature). 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 frequency  $\epsilon$ . Flows or transition rates between states are represented by arrows. Parameters  $\theta$  and  $\beta$  are rates of colonization and succession, respectively. We define recovery functions  $\phi_c$ ,  $\phi_d$  as  $\phi_c = \alpha_c \cdot (M + C) \cdot [1 - \alpha_d \cdot (D + M)]$  and  $\phi_d = \alpha_d \cdot (D + M) \cdot [1 - \alpha_c \cdot (C + M)]$ .  $\phi_m$  include these both equations giving  $\phi_m = \phi_c \cdot \phi_d$ . Finally, parameter  $\alpha$  represents the climate-dependent recovery rate after a patch has been disturbed.

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  $\epsilon$  (Figure 2). After a perturbation, a patch **T** with can be recovered to state *C*, *M* or *D* following a function  $\phi$ . For instance when a patch **T** is recovered into a patch *C*, this flow described by the function  $\phi_c$  incorporates a specific patch

**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 ( $\theta$ ), transition rates vary with the proportion of coniferous or deciduous available in the closest neighbourhood. For instance, the succession rate of a coniferous patch ( $\beta_c$ ) 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 patches. Indeed, 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,

recovery rate ( $\alpha_c$ ), 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  $\theta_c$ .

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<sup>1</sup> 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. In this context, 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  $BA_D \geq 50\%$ ). 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 of computing a probability function of transition between

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

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.

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

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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