Role of alternative stable states on Sugar maple, *Acer saccharum*, 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 [25, 12, 15]. Sugar maple (*Acer saccharum*) is a widespread and abundant tree in north-eastern North America. [9, 20, 14, 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 [19, 13]. According to McKenney (20007), Sugar maple is one of those species expected to move closed to the Ungava bay [19]. 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) [9, 15]. 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 [4].

Species are responding differently to the soil conditions, and the soil properties found in boreal forests are different from those in temperate forest [15, 1, 8, 5]. 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 [15, 8]. Soil acidification is causing a reduction in the cation exchange capacity and subsequently decrease avaibility of some nutrients such as calcium [21]. Sugar maple regeneration has been recognized to be particulary sensitive to waterlogged condition and nutrients soil content [21, 15, 3]. This properties of coniferous forest soils could hinder the local establishment of species associated with base-rich soils or unable to withstand waterlogged conditions [15]. Under these latter conditions, tree species migration is likely to be restricted or delayed [15]. 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 [14, 21, 1]. Then the temperate forest including Sugar maple could then be unable to migrate in boreal forests as a result of local plant-soil feedbacks [17]. 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 [8, 6]. In this case, these forest communities are two alternative stable states, *i.e.* contrasted states occuring in the same climate conditions [22]. 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, I will (1) develop a climate-dependent model of state transition (STM) representing the dynamics of the boreal and temperate communities; (2) investigate the spatial structure of maple distribution and the occurrence of alternative stable states in the transitional zone; and finally (3) run simulations of maple migration 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

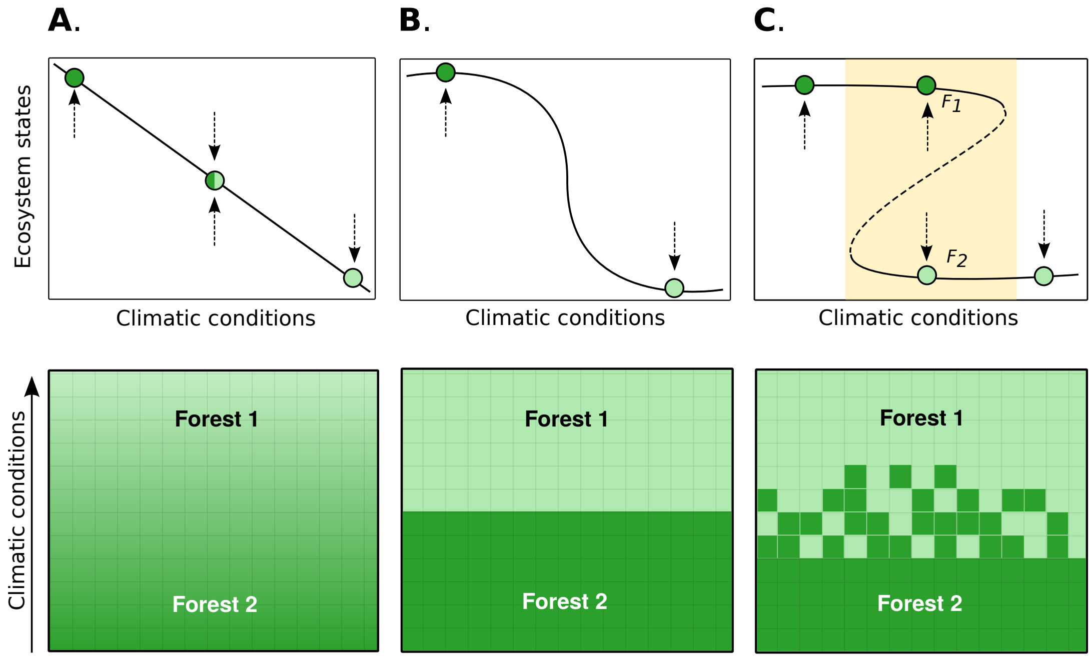

Figure 1: Schematic representation of different ways in which the equilibrium states from forest-forest system can vary over climatic gradients such as temperature, precipitation or soil moisture. Three differents responses are presented, **(A)** gradual, **(B)** basic fold, **(C)** catastrophic fold. 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).

part focuses on sugar maple, its 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 second section of this document describes the model and the methodology that I will employ to fill my specific objectives. To conclude, the last part presents the general timeline associated with this project.

2 Review

Alternative stable states in forest ecosystem. The idea that alternative stable states may exist in communities has been emerged in ecology since the late 1960s [24, 2, 11] (**Note:** alternative stable state has been quickly introduced and defined in the introduction).
Within the study context, a states is defined like a specific forest community given a time and a climatic conditions (e.g. annual precipitation or annual temperature). When a small environmental change occur, forest systems can respond almost linearly, with no threshold leading to drastic changes in the ecosystem functionning (Figure 1.a, upper line) [24, 23]. In this case, ecosystem can be seen further as a continuum of states along the environnemental gradient [24, 23, 22]. For instance, when the annual precipitation increase slightly in a forest deciduous stand, the new local condition gives rise to a new coniferious species establishment. This forest stand reaches a new state wherein the species community has been smoothly changed. Secondly, such systems are insensitive to small change in environmental conditions over certain ranges but respond strongly when a threshold is reached [22]. For exemple, species mortality can increase sharply when a toxin is added to the environment modifying the species assemblage. [22]. In this case, the response curve of the natural systeme is not linear but lightly folded and a small change can drive the sytem to a treshold and lead to major changes (Figure 1 .b, upper line). Small changes in the initial

conditions can transform abruptly the community composition. Lastly, the response curve can be folded backwards and alternative stable states could occur (Figure 1 .c). When the environmental conditions approach a tipping point on the folded upper branch, the system cannot pass smootly 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). This point is called a *Bifurcation point* and a small forcing on those critical states can drive the system into backward or forward shifts.
In this situation, the system present alternative stable states who mean the presence of contrasted states over certain range of environmental conditions [22]. An intermixed of constrasted patches in a ecotone landscape is expected in the area of bi-stability 1 .c (upper part).

Natural system studied. Many empirical and modeling studies have been conducted on the transition between forest to non- forests (e.g. Boreal- Tundra) [25, 24, 10, 20] but little attention has been given to evaluate the forest-forest ecotone [8, 9, 20]. 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. There is no distinct boundary at the boreal-temperate ecotone instead a broad transition zone exists where stands of coniferous deciduous species co-occur at the regional scale [8]. A macromosaic landscape can be observed with pure stands of northern temperate trees on favorable sites and boreal forest stands on less favorable sites [8, 6]. Thus, 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 [7].
This segregated patches distribution could be explain by the fact than microclimatic conditions can modulate establishement of those forests [4]. 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 [8, 7]. For instance, balsam fir (*Abies balsamea*) is often related to deep organic horizons and coarse xeric deposits, while Sugar maple is mostly present in opposite edaphic conditions [20, 14, 1].
Moreover, boreal and hardwood forests are dominated by trees of distinctive 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) [7] hypothesized that Sugar maple is subject to such a feedback. Knowing this, the alternative stable states is a relevant framework to study this ecotone dynamic because the soil conditions and role of dominant species in regeneration seems to act as main feedbacks on the temperate forest establishment generating a patchiness landscape (Figure 1.c, upper panel).
In this context, we expected to find patch dominated by boreal species and others dominated by temperate species under a certain range of climatic conditions. Thus, the soil condition and the role of dominant species in boreal and temperate forest need to be investigate as main drivers in alternative stable states [14, 21, 4, 1].

3 Methods

In this section I first describe the model representing dynamics at the boreal-temperate ecotone. Secondly, I present the data that will be used to parametrize the model.
Whereas the transition between temperate and boreal forests is influenced by environnemental conditions and proportion of coniferious and deciduous available in the neighbourhood, the third section section will dedicated on those factors and their parametrization. The last section describes the simulation and validation techniques.

Model description. The model represents the transition probability between four different forest states: **(D)** Deciduous, **(M)** Mixed and **(C)** Coniferous (Figure 2).

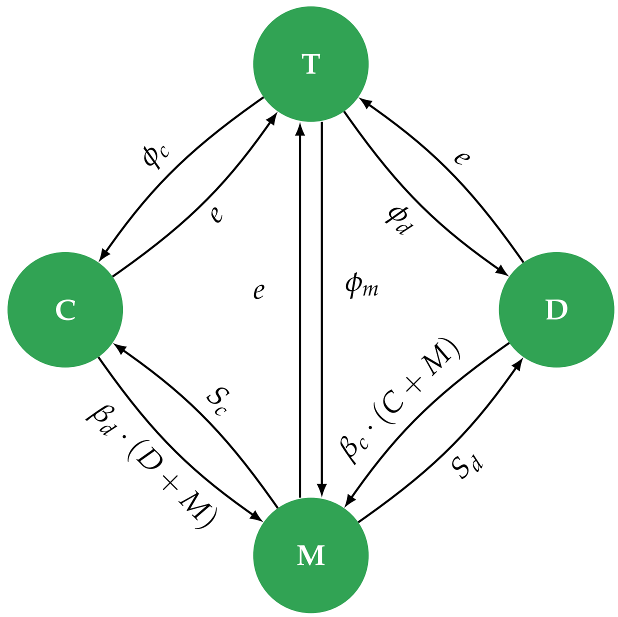

Figure 2: Conceptual representation of the transition model between deciduous (D), mixed (M) and coniferous (C) stands. T corresponds to a transitionnal state. Perturbations, natural and anthropogenic, occur with a frequence e. Parameters β and S are rates of colonisation and succession, respectively. We define the recovery rates (ϕ_c et ϕ_d) as $\phi_c = \alpha_c \cdot (M+C) \cdot [1 - \alpha_d \cdot (D+M)]$ and $\phi_D = \alpha_d \cdot (D+M) \cdot [1 - \alpha_c \cdot (C+M)]$, to finaly get this equation $\phi_m = \phi_c \cdot \phi_d$. The parameter α represents the recovery rate after a patch has been disturbed.

Disturbances is an important driver of forest dynamics (e .g. Fire in boreal forest or frost in temperate forest). When gap event occur in deciduous patch, species presents will be replaced by shade intolerant species as aspen and white birch, well adapted to the new shading condition.
Disturbances integrated within the model across the transitional patch **(T)** (Figure 2).
Dominance by late-succesional species are responsible for a transition from state T to other states (C, D or M). 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.
For exemple, when a coniferous patch C has been disturbed, a rate e, this can be recovered to another state following ϕ_c.
This term is taking in account a specific patch recovery rate (α_c), the availability of coniferous species ($M+C$) and the proportion of patches unconverted into a deciduous state ($1 - \alpha_d \cdot (D+M)$).
The dynamics of state T is described by the differential equation: $\frac{\delta T}{\delta t} = e \cdot (C+M+D) - T \cdot (\phi_d + \phi_c + \phi_m)$. If a patch C is undisturbed, deciduous species $(D+M)$ can spread over the patch at a rate β_d. Mixed stands M turn into coniferous stands at a rate S_c. The dynamic of coniferous states is described by the differential equation $\frac{\delta C}{\delta t} = \phi_C \cdot T + S_c \cdot M - \alpha_d \cdot (D+M) \cdot C - e \cdot C$.
The model is spatially implicit and assume that all space is occupied by one state, so that the proportions of land cover occupied by all types of patch sum to 1.
The model will be solved at equilibrium to understand if alternative stable states are possible and under which conditions.

Data description. The parameterization and validation of the model will be conducted using the QUICC-FOR[1] database containing large permanent (PP) and temporary (PT) sample plots from United States and Canada. Data are freely provided by partners. They and 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 includ 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 [18]. We will parameterize the model using annual rainfall (mm) and average temperatures (°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 distrbution of biomes investigated in this present study [8, 10, 25]. **(More details**

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

on climatic data?)

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 will be taken into account (more details in the parametrization section). Secondly, only plots with mesic soil conditions, ie thick deposite with fast to moderate drainage will be considered for the analysis. Lastly, plots disturbed by human activities (mostly by forest harvesting) will be removed in order to focus on natural disturbances.

Paramerization. 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 (C, D, M or T - Figure 2). Coniferious stands are dominated by either spruce, larch, grey pine, cedar, balsam fir and hemlock species. Deciduous stands are dominated by ash, maples, iron wood, beech and lime.
Finally, post- disturbance stands are dominated by birch, red oak, aspen, white and red pine, balsam poplar and mountain ash. Each plot will be classified into the four different states model following their percent of deciduous and coniferious or transitional species cover. In using the plots previously classified and their climatic variables associated, we will be able to use the Breiman and Cutler's classification method (randomForest R-package, [16]).
The model will be used to compute the probability of state occurency given the local climatic condition encounter by the patch (Or $P_s|X_1 + X_2 + X_i$... where s is a state's model and X_i, a climat variable). Probability P_s will be use as a proxy of the patch types (e.g. C or M) available in the neighborhood and present in the colonization's equation (e.g. $\beta_c \cdot (C + M)$). The final step is to conduct a multinomial regression (a generalized linear model) in order to get the transitional probability between each model's state. We can summarize this multinomial regression as follow: $P_d|P_m \sim (D + M) + X_1 + X_2 + X_i$... where $(D + M)$ correspond to the availability of patch types C and M in the neighborhood (previously presented).

Validation.
Simulation. This model will be implemented as a spatially explicit cellular automaton in order to evaluate the velocity of the migration of deciduous forest under differents climate change scenario. Simulation will be run in order to study states equilibrium of this model and allows to investigate some relevant points : (i) the sensitivity of the model on initials conditions (e.g state occurencies); (ii) evaluate if the landscape is spatially structured (e.g. mosaic structure) around alernatives stables states; (iii) impact of climatic conditions on transition rates between states (e.g. in increasing sharply temperature in the lattice).

4 General timeline

Need to discuss with Matt and Dom

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