Role of alternative stable states on sugar maple (*Acer saccharum*) range shift in reaction to climate change.

Research proposal

Master in Wildlife management

By

Steve Vissault

For

Richard Cloutier, Pr. Director of the program committee

Dominique Arsenault, Pr. President of the jury

Matt Talluto, PhD Research Co-director

Dominique Gravel, Pr. Research Director

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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 [17, 8]. Sugar maple (Acer saccharum) is one of the species expected to migrate northward towards the northern limit of the temperate forest [10, 4]. Predicting shifts in the range of sugar maple under climate change is an important challenge because this species is highly desirable by hardwood and maple syrup producers, two large economic sectors in Quebec. Indeed, sugar maple is a widespread and abundant tree in north-eastern North America and is one of the most representative species of northern temperate forests [6, 12, 9, 1]. The expected northward migration of sugar maple and its vegetal community during climate change will increase the ecotone between the boreal and temperate forest of Quebec. Nevertheless, the expansion of species distribution occuring in Nordic temperate forest could be difficult to predict because microclimatic conditions found in boreal forests are different from those present in temperate forest. Colder temperatures from shading and excess soil moisture due to snow melt cause litter to be more acidic and fibrous during the spring in boreal forests . Therefore, even if the regional climate conditions are favorable [9], the microbiota and microclimatic conditions found in the boreal forest could affect the establishment of sugar maple [9, 13, 2, 1]. In this case, the sugar maple could be unable to migrate in boreal forests as a result of negative local conditions feedbacks. This phenomenon could increase the tension between the boreal and temperate forest and generate abrupt changes in the community composition and generating a patchy mosaic at landscape scale (H_0) .

Objectives. This project aims to develop a state and transition model (STM) of the boreal and temperate forests in order to investigate shifts in the distribution of sugar maple into the boreal-temperate forest dynamical system. To assess this main objective, I will (1) create a model of the transition between the temperate and the boreal forest; (2) investigate the spatial structure and presence of alternative stable states in the transitional zone; and finally (3) run simulations based on different climate change scenarios. In order to define the context of this study, the first section of this project proposal is a review subdivided into two parts. The first part presents the theoretical context on alternative stable states and abrupt changes in ecosystems functioning. The second part of this review focuses on the sugar maple, its community and co-existing species in the temperate forest and thus explain why alternative stable states is a relevant framework to study the dynamic of the boreal-temperate forests ecotone. The second section of this document describes the model and the methodology employed to assess the objectives. To conclude, the last part presents the general timeline associated with this project.

2 Review

Alternative stable state in forest ecosystems. Many ecotone studies and modeling efforts on transition between forest to non-forests (e. g. Boreal - Tundra) [17, 16, 7, 12] but little attention has been given to evaluate the transitional dynamics of forest- forest ecotones [5, 6]. At large scale, transition between the temperate and boreal forests can be approach as a dynamic system where each forest biomes is a stable state. The presence of different states at a location or a time depends on environmental conditions (e. g. soil, temperature) encountered by the system. When small environmental fluctuations occur, most dynamical system responds almost linearly with no threshold to drastic changes in the state of the ecosystem (Figure 1 .a) [16, 15]. In this case, only one equilibrium can be observed given a specific environmental condition [16, 15, 14]. When the

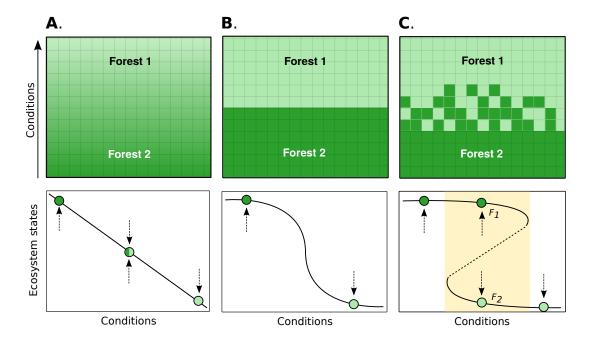


Figure 1: Schematic representation of different ways in which the equilibrium states from forest-forest system can vary with conditions such as temperature, precipitation or soil moisture. Three differents kinds of respond are presented, (A) gradual, (B) basic fold, (C) catastrophic fold. The first panels line is a conceptualization of a transitional landscape between the boreal (light green) and the nordic temperate forests (dark green). The second panels line presents the stable states rise by the forest given a specific environnemental condition. Each arrows in graphs indicate the point toward the system moves if it's not at the equilibrium. Every point on the plain line could be a stable state encounter by the boreal-temperate forests system, excepted for the dashed line (in yellow highlight). This zone, called hysteresis, are particularly unstable and little fluctuations in environnement conditions give rise to a contrasted state representing an alternative stable states. (F_1 or F_2).

soil moisture increase slowly, the new condition obtained might cause favorable conditions to a new species but this species establishment doesn't affect the community, thus the ecosystem functionning. Another kind of response occurs more frequently in nature. Natural systems are insensitive to environmental conditions over certain ranges but respond strongly when a threshold is reached (Figure 1 .b) [14]. Tree mortality can increase sharply when a toxin is added to the environment. [14]. 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. Small changes in the initial conditions can transform abruptly the species community composition and lead to a strong spatial division as representing in figure 1.c (Upper panel). In an other hand, respond curve can be folded backwards and the same threshold can conduct the system into catastrophic changes (Figure 1.c). When the system 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 *Bifurcation point* and small forcing on those critical states can drive the system into backward or forward shifts, increasing catastrophic events. In this situation, the system present alternative stable states who mean the presence of contrasted states over certain range of environmental conditions [14]. This range can be spatially structured as an intermixed of constrasted patches in a ecotone landscape like shown across the sub-figure 1.c (upper part). This layout could be easily rattached to the hardwood-boreal forest patchiness structure often attribute to differences in soils, nutrient status and topographical factors [3].

Natural system. In the boreal-temperate forest ecotone, there is no distinct boundary and a broad transition zone exists composed of mixed stands of coniferous-deciduous species [5]. Instead a macromosaic landscape can be observed with pure stands of deciduous trees on favorable sites and pure coniferous stands on less favorable sites [5]. This segregated patches distribution could be explain by the fact than microclimatic conditions can modulate at large scale, and on long term, establishement of those forest community's species [2]. Distribution of deciduous and boreal forests within ecotone is not determined only along environnemental gradients present on large scales but rather by local variation and conditions in substrate, drainage, physical soil properties, and nutrient avaiblity [5, 3]. By example, balsam fir (Abies balsamea) is often related to thick organic horizons and coarse xeric deposits while sugar maple is mostly present in opposite edaphic conditions [12, 9, 1]. Moreover, boreal and hardwood forests are dominated by trees of distinctive physiognomy which may be expected to produce distinctive litter and light micro-environments [1]. Those dominant species might induce conditions that differentially facilitate regeneration of the of the community's species as positive feeback which contribute to preserve the community type [1]. Frelich et al.(1993) [3] hypothesized sugar maple has one of those species. 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 [9, 13, 2, 1].

3 Methods

Following this review, the first methodology section will describe the general model reproducing the boreal-temperate ecotone dynamic. The second part will be adressed on data used on the parametrization and calibration of this 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. Two last sections will focus on simulation and validations techniques used in this project's context.

Models. This state and transition model will be based on three different forest states: **(D)** Deciduous and **(M)** Mixed patches characterizing temperate forests, then **(C)** Coniferous patch representing boreal forests (Figure 2). Disturbances regime is a main driver in those 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. Thus post-disturbance patches has been integrated within the model across the transitional patch **(T)** (Figure 2). On long term, late-succesional species from the understory will take up giving a new state (C, D or M). All states can change to another state except the direct transition between a deciduous and coniferous stands which doesn't occur in natural systems. Simulations of this model aims to assess the transition rate between each state in the overall landscape and identify if deciduous and coniferous patches are present as alternative stable states. When a coniferous patch *C* has been

disturbed with 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 paths unconverted into a deciduous state $(1-\alpha_d\cdot(D+M))$. In making the assumption that perturbation rate is similar between states, dynamic of a patch T can be formally describe by these differential equations: $\frac{\delta T}{\delta t} = e \cdot (C+M+D) - T \cdot (\phi_d + \phi_c + \phi_m)$. If a patch C is undisturbed, deciduous species (D+M) can spread over the patch with a colonisation rate β_d giving a new mixed patch. A mixed stand M might turn into a coniferous stand with a succession rate S_c . We can also summarize the coniferous dynamic by this differential equation: $\frac{\delta C}{\delta t} = \phi_C \cdot T + S_c \cdot M - \alpha_d \cdot (D+M) \cdot C - e \cdot C$. At this stage of this project, 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.

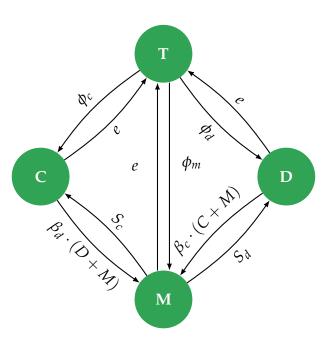


Figure 2: Conceptual transition model between forest stands deciduous (D), mixte (M) and coniferous (C). T corresponds to a transitionnal state where a perturbation are occurred with a frequence of e. Parameters β and S are referred as the colonisation and the succession rates respectively. We defined 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 finally get this equation $\phi_m = \phi_c \cdot \phi_d$. The parameter α mean the recovery rate after a patch has been disturbe.

sampling. (More details on climatic data?)

Data description. The parameterization and validation of this model will be conducted on the QUICC-FOR¹ database containing large permanent (PESP) and temporary (PEST) sample plots surveys from United- States and Canada. Those data are providing by several forest offices and covering 3 eastern canadian provinces (± 16.000 plots) and 31 states (± 50.000 plots). Data provides by the temporary sample plot (PEST) network will be use to validate the model while data from the permanent sample plot (PESP) network will addresses on the model calibration. Surveys started since 1970s including until 5 remeasurements varying between 5 and 10 years of time step and taken across many forest scales: seedling, tree, sapling and stand levels. Stem informations provide individual based measurements like diameter at breast height (DBH), species, state of the stem (e. g. alive or dead), height, age and canopy position. Seedling and sapling datas collected by subsample provide numbers of individuals by class of DBH and species. The stand forest datas include many relevant informations on soil, drainage, disturbances, cover type and, age and height of the stand. All plot inventories are geo-referenced in terms of latitude and longitude coordinates for a specific year. For each plot localisation, some climatic variables are include and extract by interpolation from the climatic model ANUSPLIN [11]. The state and transitionnal model will take into consideration essentially rainfall (mm) and average temperatures (degree celsius) of the previous 30 years the year of the plot

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

To focus on boreal and temperate forest dynamic, some filters will be apply on this database. In a first time, on 57 species contained in the current database, only species the most representative of those communities will be take into account in the model. Coniferious forest stand will be center on spruces, larch, grey pine, cedar, balsam fir and hemlock. Deciduous stand will include ash, maples, iron wood, beech and lime. Finally, post-disturbance forest stand

Second filter is addressed to sugar maple who is a central species in this project and particulary well adapted to mesic soil, thusplots with only this drainage condition will be considered in this analysis. I will also removed all plots disturbed by human activities (mostly forest harvesting) in order to focus on natural disturbances.

Paramerization.

As previously in the review, model focuses on most representative species of the boreal and temperate forest. Thus The basal area (m^2/ha , BA) will be compute to provide a measure of relative growth by species (i) present in the plot (j) (BA_{ij}).

Each plot will be classified into the four different states following their percent of deciduous and coniferious cover.

To include the climate, each model parameters will be calibrate as a function of probability based on climatic conditions.

Simulation. This model will be incorporated in a spatially explicit cellular automaton or lattice in order to evaluate the velocity of the transition into differents patches and differents climate change scenario.

Validation.

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