

Role of alternative stable states on boreal-temperate forest ecotone (*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

Université du Québec à Rimouski
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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 [18, 8]. Sugar maple (*Acer saccharum*) is a widespread and abundant tree in north-eastern North America and is one of the most representative species of northern temperate forests [6, 13, 9, 1]. This species is one of the species expected to migrate northward towards the northern limit of the temperate forest [11, 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. 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 Québec (**Hypothesis ?**). Nevertheless, the expansion of species distribution occurring in Nordic temperate forest could be difficult to predict because microconditions can mitigate macroconditions as macroclimate warming on forest understories [2]. In boreal forest, colder temperatures from shading and excess soil moisture due to snow melt cause litter to be more acidic and fibrous during the spring. 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, 14, 2, 1]. In this case, the sugar maple could be unable to migrate in boreal forests as a result of negative local 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.

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 achieve 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) [18, 17, 7, 13] 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) [17, 16]. In this case, only one equilibrium can be observed given a specific environmental condition [17, 16, 15]. When the

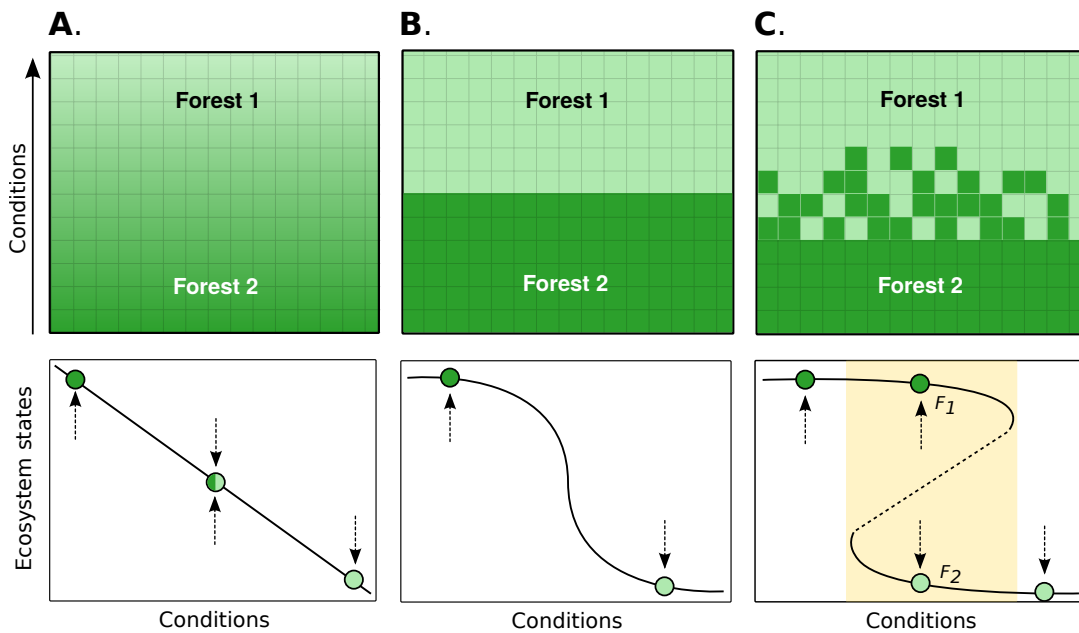


Figure 1: Schematic representation of different ways in which the equilibrium states from forest-forest system can vary with conditions such as temperature, precipitation or soil moisture. Three different kinds of response are presented, (A) gradual, (B) basic fold, (C) catastrophic fold. The first panels 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 environmental 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 environment 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 functioning. 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) [15]. Tree mortality can increase sharply when a toxin is added to the environment. [15]. In this case, the response curve of the natural system is not linear but lightly folded and a small change can drive the system to a threshold 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, response 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 smoothly to the lower branch. Small forcing on initial condition of the state F_1 transfer immediately 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 [15]. This range can be spatially structured as an intermixed of contrasted 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 establishment of those forests [2]. Distribution of deciduous and boreal forests within ecotone is not determined only along environmental gradients present on large scales but rather by local variation and conditions in substrate, drainage, physical soil properties, and nutrient availability [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 [13, 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 community's species as positive feedback 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, 14, 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 addressed on data used on the parametrization and calibration of this model. Whereas the transition between temperate and boreal forests is influenced by environmental conditions and proportion of coniferous 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 validation 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-successional 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. The model will be solved numerically and discretize (**Note:** Not sure to be enough comfortable to discuss about the last sentence).

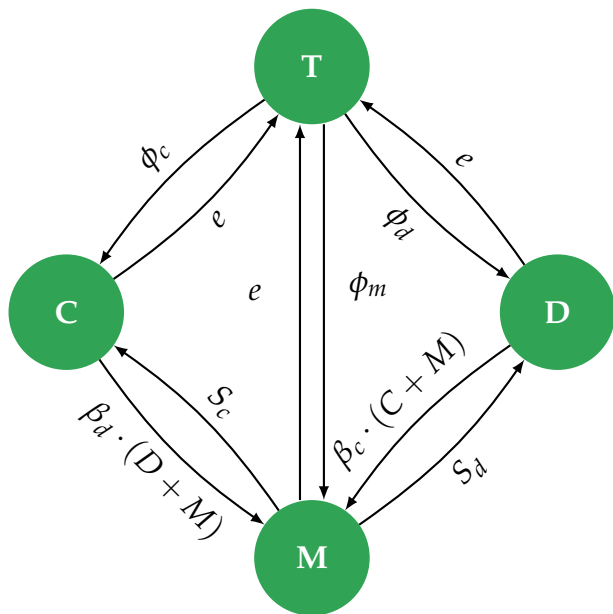


Figure 2: Conceptual transition model between forest stands deciduous (D), mixte (M) and coniferous (C). T corresponds to a transitionnal state where a perturbation are occurred with a frequency of e . Parameters β and S are referred as the colonisation and the succession rates respectively. We defined 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.

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). 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 [12]. The state and transitionnal model will take into consideration essentially rainfall (mm) and average temperatures ($^{\circ}\text{C}$) of the previous 30 years the year of the plot sampling. Those variables are used by many authors as external condition to detect alternative stable states and are often indicative of the distribution of biomes investigated in this present study [5, 7, 18]. (**More details on climatic**

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 28 species mostly representative of those communities will be take into account (more details in the parametrization section). Second filter is adressed to sugar maple who is central in this project and particularly well adapted to mesic soil, thus plots with only this drainage condition will be considered in this analysis. The last filter aims to remove all plots disturbed by human activities (mostly by forest harvesting) in order to focus on natural disturbances.

Paramerization. As previously announced, this model focuses mostly on representative species of the boreal and temperate forest. In this context and using the PESP network, the basal area (m^2/ha , BA) will be compute to provide a measure of relative growth by interests species (i) present in the plot (j) (BA_{ij}) at each time step (year of measurement). Each species is related to a patch C , D or T previously described in the model's section (Figure 2). Coniferious forest stand will be center on spruce, larch, grey pine, cedar, balsam fir and hemlock species. Deciduous stand will include ash, maples, iron wood, beech and lime. Finally, post- disturbance forest will be characterized by birch, red oak, aspen, white and red pine, balsam poplar and mountain ash (**Note:** Need to support classification of species in this section with MDS / PCA). 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 (**Note:** Do I add soil variables?), we will be able to use the Breiman and Cutler's classification method (randomForest R-package, [10]). This method allows 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).

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. 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).

Validation.

4 General timeline

Need to discuss with Matt and Dom

References

- [1] N. BARRAS AND M. KELLMAN, *The supply of regeneration microsites and segregation of tree species in a hardwood-boreal forest transition zone*, Journal of Biogeography, (1998), pp. 871–881.
- [2] P. DE FRENNE, F. RODRÍGUEZ-SÁNCHEZ, D. A. COOMES, L. BAETEN, G. VERSTRAETEN, M. VEL-LEND, M. BERNHARDT-RÖMERMAN, C. D. BROWN, J. BRUNET, J. CORNELIS, G. M. DECOCQ, H. DIERSCHKE, O. ERIKSSON, F. S. GILLIAM, R. HÉDL, T. HEINKEN, M. HERMY, P. HOMMEL, M. A. JENKINS, D. L. KELLY, K. J. KIRBY, F. J. G. MITCHELL, T. NAAF, M. NEWMAN, G. PETERKEN, P. PETRÍK, J. SCHULTZ, G. SONNIER, H. VAN CALSTER, D. M. WALLER, G.-R. WALTHER, P. S. WHITE, K. D. WOODS, M. WULF, B. J. GRAAE, AND K. VERHEYEN, *Microclimate moderates plant responses to macroclimate warming.*, Proceedings of the National Academy of Sciences of the United States of America, (2013), pp. 1–5.
- [3] L. FRELICH, R. CALCOTE, M. DAVIS, AND J. PASTOR, *Patch formation and maintenance in an old-growth hemlock-hardwood forest*, Ecology, 74 (1993), pp. 513–527.
- [4] D. GOLDBLUM AND L. RIGG, *Tree growth response to climate change at the deciduous boreal forest ecotone, Ontario, Canada*, Canadian Journal of Forest Research, 2718 (2005), pp. 2709–2718.
- [5] D. GOLDBLUM AND L. S. RIGG, *The Deciduous Forest - Boreal Forest Ecotone*, Geography Compass, 4 (2010), pp. 701–717.
- [6] N. GRAIGNIC, F. TREMBLAY, AND Y. BERGERON, *Geographical variation in reproductive capacity of sugar maple (Acer saccharum Marshall) northern peripheral populations*, Journal of Biogeography, (2013), pp. n/a–n/a.
- [7] M. HIROTA, M. HOLMGREN, E. V. NES, AND M. SCHEFFER, *Global Resilience of Tropical Forest and Savanna to Critical Transitions*, Science, (2011), pp. 232–235.
- [8] L. HUGHES, *Biological consequences of global warming: is the signal already apparent?*, Trends in Ecology & Evolution, 15 (2000), pp. 56–61.
- [9] M. KELLMAN, *Sugar maple (Acer saccharum Marsh.) establishment in boreal forest: results of a transplantation experiment*, Journal of Biogeography, 31 (2004), pp. 1515–1522.
- [10] A. LIAW AND M. WIENER, *Classification and Regression by randomForest*, R News, 2 (2002), pp. 18–22.
- [11] D. W. MC KENNEY, J. H. PEDLAR, K. LAWRENCE, K. CAMPBELL, AND M. F. HUTCHINSON, *Potential Impacts of Climate Change on the Distribution of North American Trees*, BioScience, 57 (2007), p. 939.
- [12] D. W. MCKENNEY, M. F. HUTCHINSON, P. PAPADOPOL, K. LAWRENCE, J. PEDLAR, K. CAMPBELL, E. MILEWSKA, R. F. HOPKINSON, D. PRICE, AND T. OWEN, *Customized Spatial Climate Models for North America*, Bulletin of the American Meteorological Society, 92 (2011), pp. 1611–1622.
- [13] Y. MESSAOUD, Y. BERGERON, AND A. LEDUC, *Ecological factors explaining the location of the boundary between the mixedwood and coniferous bioclimatic zones in the boreal biome of eastern North America*, Global Ecology and Biogeography, 16 (2007), pp. 90–102.

- [14] J.-D. MOORE, L. DUCHESNE, AND R. OUMET, *Soil properties and maple–beech regeneration a decade after liming in a northern hardwood stand*, *Forest Ecology and Management*, 255 (2008), pp. 3460–3468.
- [15] M. SCHEFFER, *Critical transitions in nature and society*, Princeton studies in complexity, Princeton University Press, Princeton, 2009.
- [16] M. SCHEFFER, J. BASCOMPTE, W. A. BROCK, V. BROVKIN, S. R. CARPENTER, V. DAKOS, H. HELD, E. H. VAN NES, M. RIETKERK, AND G. SUGIHARA, *Early-warning signals for critical transitions.*, *Nature*, 461 (2009), pp. 53–9.
- [17] M. SCHEFFER, S. CARPENTER, J. A. FOLEY, C. FOLKE, AND B. WALKER, *Catastrophic shifts in ecosystems.*, *Nature*, 413 (2001), pp. 591–6.
- [18] M. SCHEFFER, M. HIROTA, M. HOLMGREN, E. H. VAN NES, AND F. S. CHAPIN, *Thresholds for boreal biome transitions.*, *Proceedings of the National Academy of Sciences of the United States of America*, 109 (2012), pp. 21384–9.