

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

Université du Québec à Rimouski
March 15, 2014

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 [27, 13, 16]. Sugar maple (*Acer saccharum*) is a widespread and abundant tree in north-eastern North America. [11, 21, 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. Some species mostly representative of northern forest ecosystems are forecast to expand their distribution broadly towards the north [20, 14]. According to McKenney (20007), Sugar maple is one of those species expected to move closed to the Ungava bay [20]. 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) [11, 16]. 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 [5]. Species are responding differently to the soil conditions, and the soil properties found in boreal forests are different from those in temperate forest [16, 1, 10, 6]. 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 [16, 10]. Soil acidification is causing a reduction in the cation exchange capacity and subsequently decrease availability of some nutrients such as calcium [23]. Sugar maple regeneration has been recognized to be particularly sensitive to waterlogged condition and nutrients soil content [23, 16, 4]. This properties of coniferous forest soils could hinder the local establishment of species associated with base-rich 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 slowing down the seedling establishment of these temperate species [15, 23, 1, 22]. Then the temperate forest including Sugar maple could then be unable to migrate in boreal forests as a result of local plant-soil feedbacks [18]. 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 occurrences of boreal and temperate community species despite a regional climate favorable to temperate species [10, 8]. In this case, these forest communities are two alternative stable states, *i.e.* contrasted states occurring in the same climate conditions [24]. 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 occurring 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 occurring. 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 at landscape scale; (2) investigate the spatial structure of maple distribution through his temperate community; (3) Study the occurrence of alternative stable states in the transitional zone; and finally (4) run simulations of the

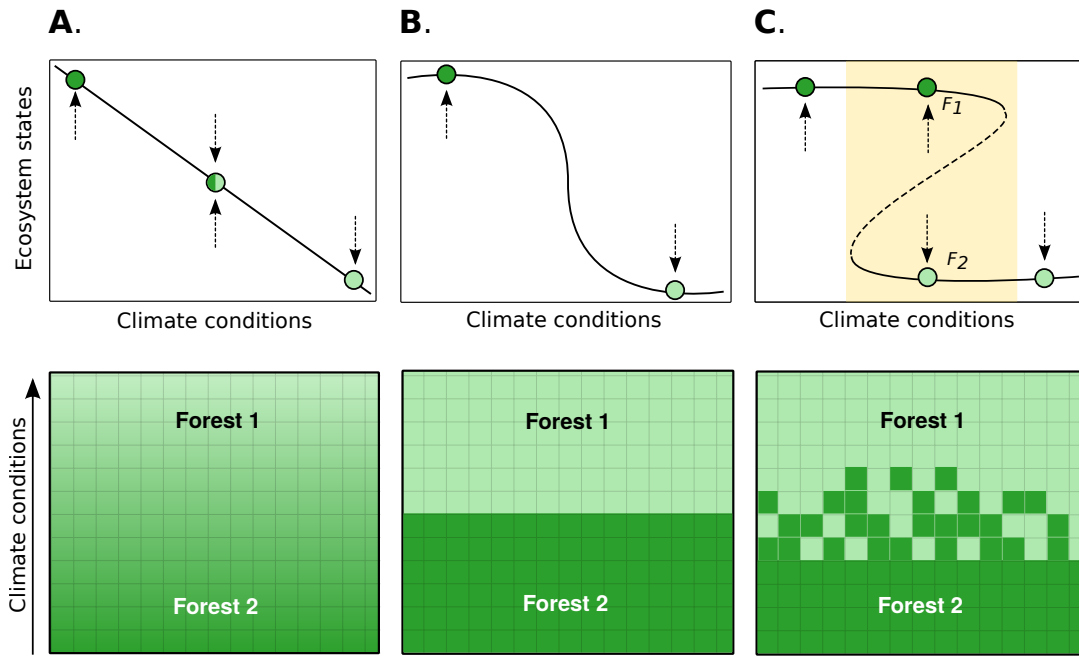


Figure 1: Schematic representation of different ways in which the equilibrium states from forest-forest system can vary over climatic gradients such as temperature, precipitation or soil moisture. Three different responses are presented, (A) gradual, (B) basic fold, (C) catastrophic fold. The first line presents the stable states rise by the forest given a specific 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 environmental 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).

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 I will employ to fill my specific objectives.

2. Review

Alternative stable states in forest ecosystems. The idea that alternative stable states may exist in communities has been emerged in ecology since the late 1960s [26, 2].

Within the theoretical context, a state is defined as a forest species 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 functioning (Figure 1.a, upper line) [26, 25]. In this case, ecosystem can be seen further as a continuum of states along the environmental gradient [26, 25, 24]. For instance, when the annual precipitation increase slightly in a forest deciduous stand, the new local condition gives rise to a new coniferous 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 [24]. For example, species mortality can increase sharply when a toxin is added to the environment modifying the species assemblage. [24]. 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 (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 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 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 presents alternative stable states which mean the presence of contrasted states over certain range of environmental conditions [24]. An intermixed of contrasted patches in an 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) [27, 26, 12, 21] but little attention has been given to evaluate the forest-forest ecotone [10, 11, 21]. 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 [10]. A macromosaic landscape can be observed with pure stands of northern temperate trees on favorable sites and boreal forest stands on less favorable sites [10, 8]. Thus, in this study context, alternative stable state theory could be applied to the hardwood-boreal forest patchiness structure often attributed to differences in soils, nutrient status and topographical factors [9].

This segregated patches distribution could be explained by the fact that microclimatic conditions can modulate establishment of those forests [5]. 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 [10, 9].

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 [21, 15, 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 contributes to the maintenance of the community type if the dominant tree species promotes conditions facilitating its own regeneration [1]. Frelich *et al.*(1993) [9] 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 investigated as main drivers in alternative stable states [15, 23, 5, 1].

3. Methods

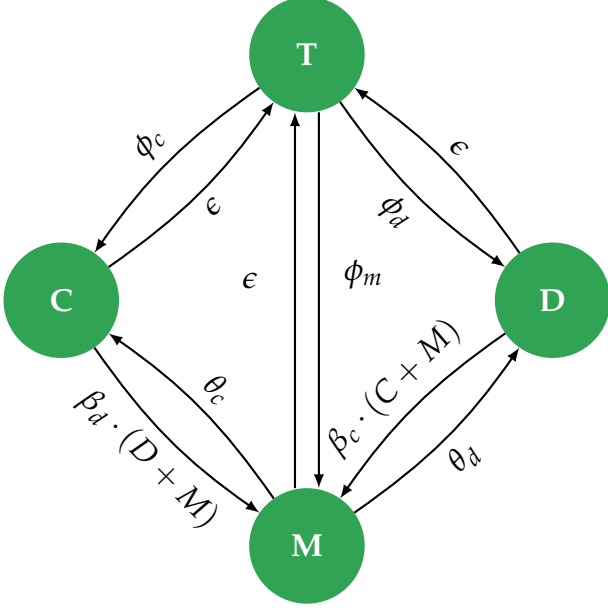


Figure 2: Conceptual representation of the transition model between deciduous (*D*), mixed (*M*) and coniferous (*C*) stands. *T* corresponds to a post-disturbance forest patch. Perturbations, natural and anthropogenic, occur with a frequency ϵ . Parameters θ and β are rates of colonization and succession,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

favoring 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 [7]. Thus, a state is systematically converted into a transitional patch (*T*) when one of those disturbances event occur at rate ϵ (Figure 2). After a perturbation, a patch *T* with can be recovered to state *C*, *M* or *D* following a rate ϕ . This term ϕ incorporate a specific patch recovery rate (α) and equally the availability of coniferous species ($M + C$) and the proportion of patches unconverted into a deciduous state ($1 - \alpha_d \cdot (D + M)$).

The model is spatially implicit and assume that all patch in the matrix landscape is occupied by one state, so we assume that the proportions of all patches sum to 1.

The dynamics of state *T* is described by the differential equation: $\frac{\delta T}{\delta t} = \epsilon \cdot (C + M + D) - T \cdot (\phi_d + \phi_c + \phi_m)$. 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 $\frac{\delta C}{\delta t} = \phi_c \cdot T + S_c \cdot M - \alpha_d \cdot (D + M) \cdot$

State and Transitional Model. The framework of this study lies on the STM representing dynamics in the boreal-temperate forests transition at landscape scale. In overall, the ecotone landscape includes three distinctive kind of forest canopies: (i) hardwood, (ii) mixedwood and finally (iii) softwood [8]. Each of these stands are represented as a state in the STM: (**D**) Deciduous, (**M**) Mixed and (**C**) Coniferous (see green circle, figure 2). According to Briske *et al.* (2008) and this STM context, state mean a plant community phases occurring on similar soils that interact with the environment to produce persistent functional and structural attributes. Flows or transition rates between states are represented by arrows (figure 2). Theses rates are climate-depend. 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*. Except for the colonisation rate (θ), transition rates are varying with the proportion of coniferous or deciduous available in the closest neighbourhood. For instance, the succession rate (β) of a coniferous patch (*C*) towards a mixed patch (*M*) depend also of the availability in *C* and *M* patches in the landscape (figure 2). Some disturbances might change state proportion in the landscape. Natural disturbances is an important driver of forest dynamics at landscape scale (e.g. fire in boreal forest or large windthrow in temperate forest). For instance, small fires induce deciduous dominance and larger and intense fires favoring boreal communities [3].

$$C - e \cdot C.$$

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-FOR¹ database containing large permanent (PP) and temporary (PT) sample plots from United States and Canada. Data are freely provided by partners. They are 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 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 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 included and extracted by interpolation from the climatic model ANUSPLIN [19]. 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 distribution of biomes investigated in this present study [10, 12, 27]. **(More details 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 deposit 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.

Parameterization. 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 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).

Coniferous 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 coniferous 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, [17]).

The model will be used to compute the probability of state occurrence given the local climatic condition encountered by the patch (Or $P_s | X_1 + X_2 + X_i \dots$ where s is a state's model and X_i , a climatic variable). Probability P_s will be used 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 tran-

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

sitional 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 different climate change scenarios. 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 initial conditions (e.g. state occurrences); (ii) evaluate if the landscape is spatially structured (e.g. mosaic structure) around alternative stable states; (iii) impact of climatic conditions on transition rates between states (e.g. in increasing sharply temperature in the lattice).

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] B. BEISNER, D. HAYDON, AND K. CUDDINGTON, *Alternative stable states in ecology*, Frontiers in Ecology and the Environment, 1 (2003), pp. 376–382.
- [3] Y. BERGERON, S. GAUTHIER, M. FLANNIGAN, AND V. KAFKA, *Fire regimes at the transition between mixedwood and coniferous boreal forest in northwestern Quebec*, Ecology, 85 (2004), pp. 1916–1932.
- [4] N. L. CLEAVITT, T. J. FAHEY, AND J. J. BATTLES, *Regeneration ecology of sugar maple (Acer saccharum): seedling survival in relation to nutrition, site factors, and damage by insects and pathogens*, Canadian Journal of Forest Research, 41 (2011), pp. 235–244.
- [5] P. DE FRENNE, F. RODRÍGUEZ-SÁNCHEZ, D. A. COOMES, L. BAETEN, G. VERSTRAETEN, M. VEL-LEND, M. BERNHARDT-RÖMMERMANN, 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.
- [6] J. DEMERS, T. LEE, AND J. BARRETT, *Substrate type and the distribution of sugar maple at its elevational limit in the White Mountains, New Hampshire*, Canadian Journal of Forest Research, 28 (1998), pp. 494–498.
- [7] S. DUPUIS, D. ARSENEAULT, AND L. SIROIS, *Change from pre-settlement to present-day forest composition reconstructed from early land survey records in eastern Québec, Canada*, Journal of Vegetation Science, 22 (2011), pp. 564–575.
- [8] N. A. FISICHELLI, L. E. FRELICH, AND P. B. REICH, *Temperate tree expansion into adjacent boreal forest patches facilitated by warmer temperatures*, Ecography, (2013), pp. no–no.
- [9] 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.
- [10] D. GOLDBLUM AND L. S. RIGG, *The Deciduous Forest - Boreal Forest Ecotone*, Geography Compass, 4 (2010), pp. 701–717.
- [11] 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.
- [12] 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.
- [13] L. HUGHES, *Biological consequences of global warming: is the signal already apparent?*, Trends in Ecology & Evolution, 15 (2000), pp. 56–61.

- [14] L. R. IVERSON AND A. M. PRASAD, *Potential redistribution of tree species habitat under five climate change scenarios in the eastern US*, *Forest Ecology and Management*, 155 (2002), pp. 205–222.
- [15] M. KELLMAN, *Sugar maple (*Acer saccharum* Marsh.) establishment in boreal forest: results of a transplantation experiment*, *Journal of Biogeography*, 31 (2004), pp. 1515–1522.
- [16] B. LAFLEUR, D. PARÉ, A. D. MUNSON, AND Y. BERGERON, *Response of northeastern North American forests to climate change: Will soil conditions constrain tree species migration?*, *Environmental Reviews*, 18 (2010), pp. 279–289.
- [17] A. LIAW AND M. WIENER, *Classification and Regression by randomForest*, *R News*, 2 (2002), pp. 18–22.
- [18] S. MCCARTHY-NEUMANN AND I. IBÁÑEZ, *Tree range expansion may be enhanced by escape from negative plant-soil feedbacks.*, *Ecology*, 93 (2012), pp. 2637–49.
- [19] 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.
- [20] D. W. MCKENNEY, J. H. PEDLAR, K. LAWRENCE, AND K. CAMPBELL, *Beyond traditional hardiness zones: using climate envelopes to map plant range limits*, *BioScience*, 57 (2007), pp. 929–937.
- [21] 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.
- [22] C. MESSIER, N. BÉLANGER, J. BRISSON, M. J. LECHOWICZ, AND D. GRAVEL, *Comment on “Present-day expansion of American beech in northeastern hardwood forests: Does soil base status matter?”* Appears in *Can. J. For. Res.* 39 : 2273–2282 (2009)., *Canadian Journal of Forest Research*, 41 (2011), pp. 649–653.
- [23] 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.
- [24] M. SCHEFFER, *Critical transitions in nature and society*, Princeton studies in complexity, Princeton University Press, Princeton, 2009.
- [25] 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.
- [26] M. SCHEFFER, S. CARPENTER, J. A. FOLEY, C. FOLKE, AND B. WALKER, *Catastrophic shifts in ecosystems.*, *Nature*, 413 (2001), pp. 591–6.
- [27] 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.