

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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1. Introduction

Context. Sugar maple (*Acer saccharum*) is a widespread and abundant tree species in north-eastern North America. [12; 23; 15; 1]. Predicting shifts of the range of Sugar maple is of prime importance because this species is highly desirable for hardwood and maple syrup production, two large economic sectors in Quebec. This species is dominating the temperate forest up to the boreal-temperate ecotone at its northern range limit [1]. Some representative species of northern forest ecosystems are expected to expand their distribution towards the north following climate warming [22; 14]. According to McKenney (2007) [22], the climatic conditions favorable to Sugar maple will reach the Ungava bay within the next 100 years, which appears highly improbable because of dispersal limitations and slow population dynamics. This prediction relies on a species distribution model accounting only for climatic conditions; it is recognized that Sugar maple regeneration depends both on macro (*i.e.* regional climate) and micro environmental conditions (*i.e.* soil and microtopography) [12; 16]. De Frenne *et al.* (2013) revealed that shifts in species distribution in reaction to climate change can be mitigated by the microconditions (*i.e.* soil temperature within the forest understory) rather than the macroconditions (*i.e.* temperature rising at regional scale) [5]. Hence, we anticipate that the microconditions could also delay future sugar maple establishment into the boreal forest.

Soil-plant feedbacks are susceptible to impact sugar maple migration dynamics. Soil properties found in boreal forests differ from those in temperate forest [16; 1; 11; 6]. A deep and poorly-decomposed litter layer is usually found in boreal forests, while the litter of northern hardwood forests is thinner and mainly composed of a superficial leaf mat [1]. The temperature is colder, the snow melts later and the soil is wetter under coniferous trees [16; 11]. Acid soils in coniferous forests causes a reduction in the cation exchange capacity and subsequently decreases availability of some nutrients such as calcium [25]. Sugar maple seedlings have been recognized to be particularly sensitive to waterlogged conditions and soil nutrient content [25; 16; 4]. These properties of coniferous forest soils could hinder the local establishment of species associated with alkaline soils or unable to withstand waterlogged conditions [16]. Migration of temperate tree species therefore likely to be restricted or delayed by the dominance of coniferous trees [16]. Thus, even if the climatic conditions at the regional scale become favorable to Sugar maple after climate warming, the micro conditions found in the boreal forest could slow seedling establishment [15; 25; 1; 24]. Sugar maple could thus be unable to colonize the boreal forests as a result of strong and localized soil-plant feedbacks [20].

My general hypothesis that the temperate-boreal forest ecotone is as a system dominated by two alternative states, *i.e.* contrasted equilibrium states occurring under the same climate conditions [26]: the boreal community and the temperate community, including Sugar maple. Under this hypothesis, the landscape would be a patch mosaic where micro conditions and stand history are driving the spatial occurrence of boreal and temperate communities, despite a regional climate favourable to temperate species [11; 9]. I expect that a climate warming and the subsequent incapacity of Sugar maple to colonize boreal forest stands will create tension between the potential and realized forest composition and consequently that abrupt shifts in community composition are susceptible to occur at the boreal-temperate forest ecotone.

Objectives. The main objective of this project is to investigate the role of alternative stable states in the transition between the boreal and temperate forests under different climate change scenarios. We will test two specific hypotheses: (H_1) Alternative stable states do co-occur at the boreal-temperate forests ecotone, and (H_2) the response of Sugar maple to climate change will be delayed in areas where alternative stable states are susceptible to occur. In order to test these hypotheses, we will (1) develop a climate-dependent state-transition model (STM) representing the dynamics of the boreal and temperate communities at the landscape scale; (2) study the occurrence of alternative stable states at the temperate-boreal ecotone; and finally (3) 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. I present the concept of alternative stable states and critical transitions in forest ecosystem properties. Then after I focus on Sugar maple, its associated community in the temperate biome, and why alternative stable states are expected to occur at the boreal-temperate forests ecotone. The last

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

2. Review

Alternative stable states. A community is stable when it persists in a given state and is resilient to small perturbations [8]. Multiple stable states are however possible for a single system. The idea that alternative stable states may exist in community ecology was proposed in the late 1960s [28; 2]. May (1977) [19] shown that an ecosystem can be seen as a dynamic system where communities are not constant over time and can change following a modification of the environment. Ecological communities can reach several equilibrium points along an environmental gradient [19]. Stable states can persist according to various feedback mechanisms [8]. For instance, in the Sahel or some part of the Amazon area, vegetation may promote precipitation (i.e. positive feedback) and thus the persistence of large tracts of forests. However, loss of vegetation in this region following logging or natural fires can lead to a major change in climate, which becomes eventually too dry to support the vegetation needed to maintain precipitations [26]. Hence, larger perturbations encountered by the system can generate a change of the state of a community, i.e. the arrangement of species or populations and their interaction with the physical environment [8].

There are three possible responses of communities to a permanent change in the environment: **(A)** gradual, **(B)** basic fold, **(C)** catastrophic fold [28] (Figure 1, upper line). First, when a small modification on environmental condition occurs (e.g. temperature rises), the state of the community can change almost linearly (Figure 1.A) [28; 27]. In this case, the whole ecosystem can be seen as a continuum of communities along the environmental gradient [28; 27; 26]. Secondly, the entire community can be insensitive to changing environmental conditions over a certain range, but respond strongly when a threshold is reached [26]. For instance, some species mortality can increase sharply when a toxin is added to the environment and a lethal threshold is reached [26]. In this case, the response curve of this natural system is not linear but lightly folded. Hence, a small change of the environment such as adding a toxin, can lead to major changes in the community state. Lastly, in some strong non-linear systems, the response can be folded backwards and alternative stable states could occur (Figure 1 .C). This implies that, for a given environment, the ecosystem has two alternative stable states (F_1 and F_2) separated by an unstable equilibrium (yellow zone, 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 transfers the system immediately to a different state F_2 (Figure 1 .C). At this point, the system is particularly sensitive to the initial conditions. This point is called a bifurcation point and a small forcing can drive the system into backward or forward shifts towards either one of the alternative stable states F_1 or F_2 , also called "attractors" [26].

The main ingredient to create alternative stable states is the occurrence of positive feedbacks [26; 30]. One well known is the facilitation process in ecology and two kinds exist in nature. The first one is interspecific facilitation and can be observed across the ecological succession process. Pioneer species pave the way for later successional species, changing gradually the environment (e.g. shading, deeper litter) [26; 17]. In this case, the environmental modification by pioneer species can be seen as a positive feedback allowing the establishment of late successional ones. The second kind of facilitation is intraspecific, where a particular species can promote its own regeneration in the immediate environment. *Acer saccharum* and *Tsuga canadensis* seedling establishment for instance is impacted by the unique seedbed conditions created by each species, promoting self-replacement [10; 20]. By changing seedbed conditions, mature trees promote their own regeneration. When the intraspecific facilitation is higher than the interspecific competition, we can observe forest stands dominated by mature trees of *Acer saccharum* and else by *Tsuga canadensis*. Hence, either forest stand type can be considered as an alternative stable state. This kind of positive feedback is susceptible to occur at the boreal-temperate forest ecotone we will study [1; 10].

Natural system studied. Many empirical and modelling studies have been conducted on the transition between forest to non-forest communities (e.g. Boreal-Tundra) [29; 28; 13; 23]. However, little attention has been given to understand the forest-forest ecotone's dynamic [11; 12; 23]. The temperate-boreal transition could adopt

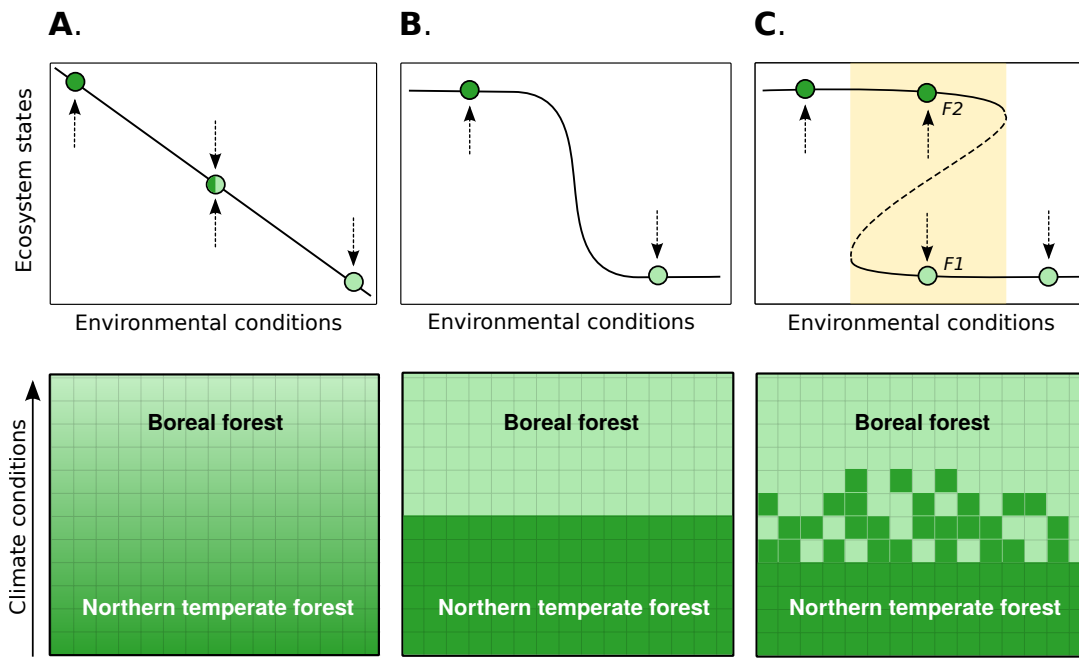


Figure 1: Change in communities composition over an environmental gradient (i.e. precipitation, temperature or soil moisture) can take three different shapes: **(A)** gradual, **(B)** basic fold, **(C)** catastrophic fold. Each of them are shown across the upper line. Solid lines represent all reachable stable states along the climate gradient. Arrows indicate where the system moves if not at the equilibrium (i.e outside of the solid lines). The yellow zone (in panel C), called hysteresis, is unstable and small fluctuations onto the environment conditions could give rise to abrupt changes into one of the alternative stable states (F_1 or F_2). In the temperate-boreal system and according to each response shape, the bottom line illustrate three different spatial repartitions of boreal and temperate communities over a climatic gradient.

three different structures along a climatic gradient (Figure 1, lower line). In the first case, the response of forest communities to climate is gradual and no distinct boundary is observed between the temperate and the boreal forests (Figure 1.A). Instead, a smooth transition occurs along a climatic gradient. On the other hand, distribution of temperate and boreal forest communities can be strongly linked to climate. Thus, climate highly segregate forest types and a net boundary appears between them (Figure1.B). Finally, a third response of the system is also possible. Previous studies highlighted that a broad zone in the boreal- temperate forests transition exists where stands dominated by either coniferous or deciduous species co-occur at the regional scale, but not within stands [11; 9]. Hence, this spatial configuration might correspond to the third case shown in figure 1.C. We hypothesize these communities to be alternative stable states. A strong positive plant-soil feedback might contribute to the maintenance of these communities: coniferous species generate acidic and wetter soils and deciduous species enrich the litter. Both types of forest stands are facilitating their own regeneration. These feedbacks help temperate species seedling establishment in favorable sites of an heterogeneous landscape.

Positive feedbacks should not increase the growth rate of temperate species within patches they already dominate, but they should increase local density and seed production [17]. A large disturbance could however contribute to modify the microconditions in a patch historically unfavorable to the other species. Following this event, this disturbed patch can switch abruptly into a temperate forest if a seed source is present in the neighborhood. These feedbacks might influence the spreading rate of temperate species into boreal forest [17]. In unfavorable patches, temperate species will have to cope with boreal soil properties that may hinder and delay their establishment. Climate change also has the potential to improve boreal soil conditions for temperate species establishment [16]. The outcome of these antagonistic forces could impact positively or negatively the migration of some temperate species in response to climate change.

3. Methods

State and Transitional Model. This study will be based on a STM representing landscape dynamics at the boreal-temperate transition. Three forest cover types are considered: (i) deciduous, (ii) mixed and (iii) coniferous [9]. Each of these stand types is represented as a state in the STM: **(D)** Deciduous, **(M)** Mixed, **(C)** Coniferous. We also consider the state **(T)** to represent transitional stands (green circles, figure 2). According to Briske *et al.* (2008), a state means a plant community phase occurring on similar soils that interact with the environment to produce persistent functional and structural attributes. Transition between states 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 probability (θ), transition probabilities vary with the proportion of coniferous or deciduous found in the neighbourhood to represent dispersal limitations. For instance, the succession rate of a coniferous patch (β_c) towards a mixed patch (M) depends also on the availability of D and M patches in the landscape (figure 2).

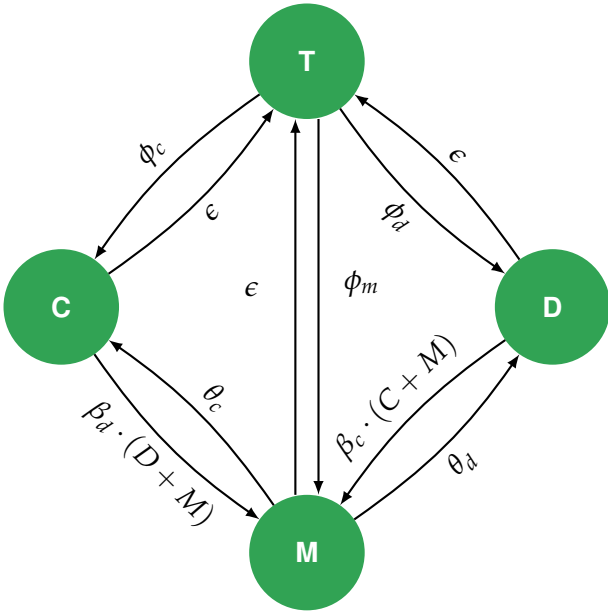


Figure 2: Conceptual representation of the transition model between deciduous (D), mixed (M) and coniferous (C) stands. T corresponds to a post-disturbance forest stand. Perturbations, natural and anthropogenic, occur with a probability ϵ . Flows or transition rates between states are represented by arrows. Parameters θ and β are colonization and succession probabilities, respectively. We define regeneration functions 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 regeneration rate after a patch has been disturbed.

Ecological processes such as succession and colonization are not the only mechanisms responsible for the transition between two states. Natural disturbances are important drivers of forest dynamics at the landscape scale (e.g. fire in boreal forest or large windthrow in temperate forest). Small fires promote dominance by deciduous species, while larger and intense fires favour 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 expansion (maples/aspen) or decline (cedar/spruce) of several species at the northern range limit of temperate trees in eastern Québec [7]. When a disturbance occurs in the actual model, the state affected is systematically converted into a transitional state (T). (Figure 2). Then after, any transitional patch (T) can switch into state C, M or D according to a probability ϕ . In the conversion case of state T towards C, this function of probability ϕ_c incorporates a specific patch regeneration rate (α_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 it could switch to a mixed stand after colonization by deciduous trees with a probability θ_c . The dynamics of a large number of patches following these rules can be described with a system of four differential equations. The dynamics of T over the time is described by the following differential equation:

$$\frac{\delta T}{\delta t} = \epsilon \cdot (C + M + D) - T \cdot (\phi_d + \phi_c + \phi_m) \quad (1)$$

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):

$$\frac{\delta C}{\delta t} = \phi_c \cdot T + \theta_c \cdot M - \alpha_d \cdot (D + M) \cdot C - \epsilon \cdot C \quad (2)$$

This model assumes that each patch is occupied by one state, thus the proportion of all states sum to 1.

Data description. The parameterization and validation of the model will be conducted using the QUICC- FOR¹ database of permanent (PP) and temporary (TP) sample plots from United States and Canada. The data has been freely provided by partners and covers 3 eastern Canadian provinces (ca. 16,000 plots) and 31 states of eastern USA (ca. 150,000 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 inventories are geo-referenced. Climatic variables are associated to each plot by interpolating the climatic model ANUSPLIN [21] . 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 good predictors of the distribution of the species investigated in this present study [11]. Filters will 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 dataset 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. The model focuses on representative species of the boreal and temperate forest. Relative abundance of each species will be computed from basal area 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 section (Figure 2). C, M, D and T states will be classified following their percentage of Ba in deciduous (Ba_d), coniferous (Ba_c) or transition species (Ba_t) in the plot (Table 1). The plots that do not satisfy any of the conditions shown in table 1 will be filtered out.

Table 1: Boundary of the coniferous (Ba_c), deciduous (Ba_d) and transition species (Ba_t) relative abundances to classify the four STM's states (D,C,M and T).

States	Boundaries
D	$Ba_d \geq 75\%$
C	$Ba_c \geq 75\%$
M	$Ba_c \geq 25\%$ and $Ba_d \geq 25\%$
T	$Ba_t \geq 75\%$

The second step of the parameterization consists of evaluating functions describing the probability of a transition between two states given specific climatic conditions (*Climate*, eq. 3) and the proportion of deciduous or coniferous in the neighborhood (\hat{D} and \hat{M} , eq. 3). Hereafter, will focus only on a specific transition $M \rightarrow T$ but the method is common to all transitions. In this example (eq. 3), \hat{D} and \hat{M} are the expected probabilities of observing state D or M in this area given climatic conditions. They are proxy for the deciduous propagule pressure coming from neighbors. They will be estimated using a standard species distribution model (Step 1, eq. 3) such as the random forest algorithm (R-package, [18]).

$$P(D_{t1}|M_{t0}, Climate) = f(\overbrace{Climate, \underbrace{\hat{D}, \hat{M}}_{\text{Step 1. RandomForest}}}^{\text{Step 2. Multinomial regression}}) \quad (3)$$

The probability of a transition between two states given the local climatic conditions encounter by a patch (Step 2, eq. 3) will be computed using a multinomial regression (nnet R-package, [31]). We can summarize this multinomial regression as $P(D_{t1}|M_{t0}, Climate) = \beta_0 + \beta_{\hat{D}} \cdot \hat{D} + \beta_{\hat{M}} \cdot \hat{M} + \beta_{X_i} \cdot X_i...$ where \hat{D} and \hat{M} correspond to the probability of observing any state in the immediate neighbourhood (previously presented) and

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

X_i a climate variable. Model selection will be performed using Akaike's information criterion (AIC). The selected model will be used to represent all transition probabilities between states.

Model validation and simulations. The model will be validated using the temporary sample plots (TP), an independent dataset for the Québec database. 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) and compare this distribution to the one predicted by the model. Highest R-square will be associated with the best predictive model. Bias (e.g. significant positive intercept, β_0 eq. 3) might indicate that the current forest composition is not at equilibrium and needs further investigations. After the validation, we will assess if alternative stable states are present in the boreal-temperate forests transitions (H_1). We will apply the model (eq 3.) in varying initial conditions i.e. states proportion and climate conditions. In studying the simulations, we expect to find abrupt changes in states proportion over the time. Also, we expect to observe bimodal distributions of states over a certain range of climate conditions (when the model is at the equilibrium). If these expectations are validated then alternative stable states are present in the boreal-temperate forests system. In the statistic model, rates of transition are related to the proportion of states available in the immediate neighborhood. To understand the spatial dynamic of the boreal-temperate forests ecotone, we need to simulate this model over a lattice (a cellular automaton), where each cell corresponds to a forest patch in the landscape (C,D,M or T). The succession (β) and regeneration (α) probabilities of transition will be positively affected by the composition of the eight neighboring cells. In making this model spatially explicit, we are able to assess the migration rate of sugar maple under climate change through his forest temperate patches. We will run simulations with a changing climate (e.g. increase the temperature) on an initial lattice where the upper zone consists of boreal-forest patches and the lower zone of temperate forests patches. In studying the front of the invasion of temperate species through boreal patches, we expect to observe a delayed rate of sugar maple migration where the alternative stable states appear.

4. General timeline

Session	General steps
Winter 2014	Exploring data and classifying forest states
Summer 2014	Processing on STM Model's parameterization and validation
Fall 2014	Coding cellular automaton and running simulations
Winter 2015	Analyzing model outputs and validating hypotheses
Summer 2015	Writing thesis

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. VELLEND, M. BERNHARDT-RÖRMERMANN, 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] K. FILBEE-DEXTER AND R. SCHEIBLING, *Sea urchin barrens as alternative stable states of collapsed kelp ecosystems*, Marine Ecology Progress Series, 495 (2013), pp. 1–25.
- [9] 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.
- [10] 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.
- [11] D. GOLDBLUM AND L. S. RIGG, *The Deciduous Forest - Boreal Forest Ecotone*, Geography Compass, 4 (2010), pp. 701–717.
- [12] N. GRAIGNIC, F. TREMBLAY, AND Y. BERGERON, *Geographical variation in reproductive capacity of sugar maple (Acer saccharum Marshall) northern peripheral populations*, Journal of Biogeography, (2014), pp. n/a–n/a.
- [13] 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.
- [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] J. M. LEVINE, E. PACHEPSKY, B. E. KENDALL, S. G. YELENIK, AND J. H. R. LAMBERS, *Plant-soil feedbacks and invasive spread.*, Ecology letters, 9 (2006), pp. 1005–14.
- [18] A. LIAW AND M. WIENER, *Classification and Regression by randomForest*, R News, 2 (2002), pp. 18–22.
- [19] R. MAY, *Thresholds and breakpoints in ecosystems with a multiplicity of stable states*, Nature, (1977).
- [20] 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.
- [21] D. W. MCKENNEY, M. F. HUTCHINSON, P. PAPADOPOULOS, 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.

- [22] 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.
- [23] 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.
- [24] 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.
- [25] 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.
- [26] M. SCHEFFER, *Critical transitions in nature and society*, Princeton studies in complexity, Princeton University Press, Princeton, 2009.
- [27] 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.
- [28] M. SCHEFFER, S. CARPENTER, J. A. FOLEY, C. FOLKE, AND B. WALKER, *Catastrophic shifts in ecosystems.*, Nature, 413 (2001), pp. 591–6.
- [29] 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.
- [30] A. SCHRÖDER, L. PERSSON, AND A. D. ROOS, *Direct experimental evidence for alternative stable states: a review*, Oikos, 110 (2005), pp. 3–19.
- [31] W. N. VENABLES AND B. D. RIPLEY, *Modern Applied Statistics with S*, Springer, New York, fourth ed., 2002.