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Université du Québec
à Rimouski

**BIOGÉOGRAPHIE ET DYNAMIQUE DE LA FORÊT TEMPÉRÉE NORDIQUE
DANS UN CONTEXTE DE CHANGEMENTS CLIMATIQUES**

MÉMOIRE PRÉSENTÉ

dans le cadre du programme de maîtrise en gestion de la faune et de ses habitats

en vue de l'obtention du grade de maître ès sciences

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Avertissement

À mes parents et tous ceux qui

ont été patient...

REMERCIEMENTS

Je tiens dans un premier temps à remercier mon directeur Dominique Gravel pour m'avoir donné l'opportunité de réaliser cette maitrise. Je tiens également à remercier Isabelle Boulangeat et Matthew Talluto pour leurs implications et .

AVANT-PROPOS

[Cette page est facultative ; l'éliminer si elle n'est pas utilisée. L'avant-propos ne doit pas être confondu avec l'introduction. Il n'est pas d'ordre scientifique alors que l'introduction l'est. Il s'agit d'un discours préliminaire qui permet notamment à l'auteur d'exposer les raisons qui l'ont amené à étudier le sujet choisi, le but qu'il veut atteindre, ainsi que les possibilités et les limites de son travail. On peut inclure les remerciements à la fin de ce texte au lieu de les présenter sur une page distincte.]

RÉSUMÉ

De nombreuses espèces ne migrent pas assez vite pour suivre la rapidité des changements climatiques. Les arbres sont bien connus pour éprouver de longs délais dans leurs réponses au climat parce qu'ils sont sessiles, longévive et dispose de faible capacité de dispersion. Les approches actuelles pour prédire l'aire de répartition future des espèces ne peuvent pas tenir compte de ces particularités propre aux écosystèmes forestiers car ils assument une dispersion infinie et une réponse instantanée aux changements climatiques. À travers cette étude, nous proposons une nouvelle approche de modélisation basée sur la théorie des métapopulations pour tenir compte de la dispersion limitée, des interactions biotiques et de la démographie de la forêt tempérée. Notre objectif est d'évaluer si la forêt tempérée d'Amérique du Nord-Est sera en mesure de suivre son optimum climatique d'ici la fin du siècle. Les transitions entre les états sont calibrés à partir de plusieurs enquêtes sur les parcelles forestières à long terme des États United- et au Canada. Nous constatons que, même si les modèles de distribution des espèces classiques prédisaient un déplacement vers le nord de la distribution de la forêt tempérée de 328 ± 28,4 kms, la forêt tempérée sera à peine bouger 14 ± 2,0 km dans la forêt boréale à la fin de ce siècle. Nous constatons également que la plupart des transitions attendues sera la conversion du mélange à des peuplements purs tempérées. Une comparaison avec un scénario de dispersion infinie révèle que les interactions biotiques et la dynamique de remplacement des peuplements sont les facteurs les plus significatifs limitant le taux des arbres forestiers de migration. Nous concluons que la forêt tempérée a une faible résilience au changement climatique en raison de leur faible démographie et les interactions compétitives avec des arbres résidents.

Mots clés : [Inscrire ici 5 à 10 mots clés]

ABSTRACT

Many species are not migrating fast enough to keep pace with the rapidly changing climate. Trees are well known to experience long time lags in their migration responses because they are sessile, long-lived and have a relatively short dispersal ability. Actual approaches to forecast range shifts under climate change, such as Species Distribution Models, cannot account for the particularities of forest ecosystems because they assume infinite dispersal and instantaneous response to climate change. Here, we propose a new modelling approach based on metapopulation theory to account for dispersal limitations, biotic interactions and the demography of the temperate forest. Our objective is to assess if the North-Eastern American temperate forest will be able to track its climatic optimum by the end of this century. Transitions among states are calibrated from several long-term forest plots surveys from United States and Canada. We find that even if standard species distribution models would predict a northward shift of the temperate forest distribution of 328±28.4 km, the temperate forest will barely move 14±2.0 km into the boreal forest at the end of this century. We also find than most of the expected transitions will be the conversion from mixed to pure temperate stands. A comparison with an infinite dispersal scenario reveals that biotic interactions and stand replacement dynamics are the most significant factors limiting migration rate of forest trees. We conclude that the temperate forest has a low resilience to climate change because of their low demography and competitive interactions with resident trees.

Keywords : [Inscrire ici 5 à 10 mots clés]

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INTRODUCTION GÉNÉRALE

MISE EN CONTEXTE

Depuis l'ère industrielle, la forêt du Québec méridionale est en constante évolution (Arsenault) ; le paysage forestier tel que nous le connaissons aujourd'hui pourrait connaître de profondes modifications d'ici la fin du XXIe siècle. Ce paysage est occupé en grande majorité par la forêt tempérée qui couvre une superficie de 209 700 km^2 (MFFP, 2015). Cette forêt peut ainsi être désignée comme la forêt habitée du Québec considérant qu'elle se retrouve dans la zone la plus densément peuplée du Québec (Doyon). On y retrouve une multitude et une diversité d'activités socio-économiques tels que le tourisme, la chasse et l'acériculture et le prélèvement sylvicole. Au Québec, l'industrie forestière et l'acériculture génèrent XX et XX de dollars respectivement pour un total de XX millions d'emplois en 2015 (MFFP, Stats). La prospérité de ces activités repose sur l'intégrité écologique de ce biome forestier régionale. Sa gestion est donc primordiale, mais constitue un véritable défi de par la diversité des acteurs socio-économique, certains enjeux écologiques et les attentes de la société. Ce sont ces mêmes attentes qui ont contribué à l'adoption en XXXX d'un plan d'aménagement écosystémique visant à maintenir la diversité biologique et la viabilité de cet écosystème (MFFP,).

Depuis maintenant plusieurs années, la forêt tempérée est confrontée à de nombreux enjeux écologiques tels que les problématiques d'enfeuillement, la raréfaction de certaines essences ou envahissement par d'autres, la simplification des structures internes des peuplements (Varady-Szabo). Aujourd'hui, la forêt tempérée nordique doit faire face à une nouvelle problématique qui est celle des changements climatiques. Plusieurs enjeux écologiques majeurs découlent de cet problématique pour les aménagistes : (1) des modifications dans la composition de la régénération post-perturbation ; (2) une modulation de la productivité forestière chez certaines espèces ; (3) une modification du régime de perturbation (p.ex.

épidémies, verglas, chablis) ; puis enfin (4) des changements dans la répartition des espèces.
Ce mémoire porte sur ce quatrième volet en s'interressant à la biogéographie et la dynamique
de la communauté de la forêt tempérée nordique dans ce contexte de changements climatiques
(c.a.d. son écotone).

CADRE CONCEPTUEL

La biosphère a déjà connu plusieurs épisodes de changements climatiques. L'étude des
registres polliniques démontrent que ces fluctuations climatiques passées ont engendré des
contractions et expansions dans l'aire de distribution des espèces (e.g., Davis and Shaw 2001).
Aujourd'hui, l'effet des changements climatiques de ce siècle est déjà observable sur la diver-
sité végétale et animale (Parmesan and Yohe 2003 ; Walther et al. 2002). Considérant l'am-
pleur et la vélocité des changements climatiques prédis pour le XXIe siècle (IPCC, 2015),
la forêt tempérée nordique sera-t-elle en mesure de déplacer son aire de distribution assez
rapidement pour suivre son enveloppe climatique ?

ARTICLE 1

LA DÉMOGRAPHIE, UNE CONTRAINTE À L'EXPANSION DE LA FORÊT TEMPÉRÉE VERS LE NORD

1.1 Résumé en français du premier article

De nombreuses espèces ne migrent pas assez vite pour suivre la rapidité des changements climatiques. Les arbres sont bien connus pour éprouver de longs délais dans leurs réponses au climat parce qu'ils sont sessiles, longévive et dispose de faible capacité de dispersion. Les approches actuelles pour prédire l'aire de répartition future des espèces ne peuvent pas tenir compte de ces particularités propre aux écosystèmes forestiers car ils assument une dispersion infinie et une réponse instantanée aux changements climatiques. À travers cette étude, nous proposons une nouvelle approche de modélisation basée sur la théorie des métapopulations pour tenir compte de la dispersion limitée, des interactions biotiques et de la démographie de la forêt tempérée. Notre objectif est d'évaluer si la forêt tempérée d'Amérique du Nord-Est sera en mesure de suivre son optimum climatique d'ici la fin du siècle. Les transitions entre les états sont calibrés à partir de plusieurs enquêtes sur les parcelles forestières à long terme des États United- et au Canada. Nous constatons que, même si les modèles de distribution des espèces classiques prédisaient un déplacement vers le nord de la distribution de la forêt tempérée de 328 ± 28,4 kms, la forêt tempérée sera à peine bouger 14 ± 2,0 km dans la forêt boréale à la fin de ce siècle. Nous constatons également que la plupart des transitions attendues sera la conversion du mélange à des peuplements purs tempérées. Une comparaison avec un scénario de dispersion infinie révèle que les interactions biotiques et la dynamique de remplacement des peuplements sont les facteurs les plus significatifs limitant le taux des arbres forestiers de migration. Nous concluons que la forêt tempérée a une faible résilience au changement climatique en raison de leur faible démographie et les

interactions compétitives avec des arbres résidents.

En plus d'y consigner les grandes lignes de l'article, cette section sert de lieu pour préciser le contexte du projet. On y mentionne le nom de la revue où l'article a été soumis ainsi que le stade d'avancement de l'évaluation par les pairs. Un sommaire de la contribution de chacun des auteurs doit aussi être présenté. Voir l'exemple suivant :

Ce premier article, intitulé "*Combining Apparent Motion and Perspective as Visual Cues for Content-based Camera Motion Indexing*", fut corédigé par moi-même ainsi que par le professeur Frédéric Deschênes et ma collègue Joanie Pan. Il fut accepté pour publication dans sa version finale en 2009 par les éditeurs de la revue *Pattern Recognition*. En tant que premier auteur, ma contribution à ce travail fut l'essentiel de la recherche sur l'état de l'art, le développement de la méthode, l'exécution des tests de performance et la rédaction de l'article. Le professeur Frédéric Deschênes, second auteur, a fourni l'idée originale. Il a aidé à la recherche sur l'état de l'art, au développement de la méthode ainsi qu'à la révision de l'article. Joanie Pan, troisième auteure, a contribué à la recherche sur l'état de l'art ainsi qu'à l'exécution des tests de performance. Une version abrégée de cet article a été présentée à la conférence *Canadian Conférence on Computer and Robot Vision* à Washington D.C. (É.-U.) à l'automne 2008.]

1.2 Slow demography constrains the North-Eastern Temperate Forest expansion under Climate Change

AUTHORSHIP

1.3 Introduction

The current challenge biogeographers are facing today is not only to predict future species distribution, but also to assess if species will be able to follow their climatic optimum by migration (Lenoir and Svenning, 2014; Renwick and Rocca, 2014). Correlative Species Distribution Models (SDMs) are one of the most popular methods to evaluate the impact of climate change on biodiversity, but they are well know for their shortcomings, and in particular their ability to predict the rate of range shifts (Thuiller et al., 2008; Guisan and Thuiller, 2005). SDMs are based on the statistical relationship between distribution and the environment, and projections into the future often assume unlimited dispersal and instantaneous response to climate change (Thuiller et al., 2008). In some situations, SDMs can lead to biased estimation of the future distribution because of our inability to disentangle biotic from abiotic drivers of distribution (**??**). For instance, strong competitive interactions, slow demography and dispersal limitations can drive some species to local extinction, prevent colonization at the leading edge and create non- equilibrium situations in which species may be absent from suitable environments (**?**García-Valdés et al., 2013). Species might persist for a while at newly unsuitable locations because of the to time-delayed extinction and source-sinks dynamics (Schurr et al., 2012). These mechanisms could slow down spreading rates and explain why many species fail to migrate (Zhu et al., 2012) and keep pace with the rate of climate change (Renwick and Rocca, 2014; Svenning and Skov, 2004; Lenoir and Svenning, 2014).

Range dynamics of forest tree species particularly worth attention. Tree species may

be particularly vulnerable to migration lags because they are sessile, long-lived, have a small intrinsic growth rate, relatively short dispersal and often require long time to reach reproductive maturity (Renwick and Rocca, 2014; Vanderwel and Purves, 2014). Dispersal limitations and demographic rates (growth, mortality and reproduction) might modulate their response to climate change and further contribute to this lag (Svenning et al., 2014). Two parameters in particular, the intrinsic growth rate (*r*) and the average dispersal distance (*D*), are identified by classical diffusion models (e.g., Fisher-Skellam) as crucial drivers of migration rates (Skellam, 1951; Svenning et al., 2014). Even if forest range dynamics are more complex than supported by these models, these two parameters points to fundamental quantities required to evaluate in order to understand the transient phase between the initiation of climate change and a species reaching its new equilibrium distribution. For example, strong competition at distribution edges can reduce intrinsic growth rate, which coupled with dispersal limitations, might contribute to slow colonization (Moorcroft et al., 2006). Plant-soil feedbacks, seed dispersers, mycorhizae and other types of biotic interactions are contribute to local forest dynamics and consequently have potential implications on large-scale range dynamics (Afkhami et al., 2014; Ricklefs, 2004; Wootton, 2001). Integrating such demographic and spatial constraints on range shift projections are essential to improve our understanding of species migration (**?**).

Several north american temperate deciduous tree species (e.g. *Fagus grandifolia*, *Betula alleghaniensis*, *Acer saccharum*, *Quercus rubra*) are expected to expand their distribution through the north where boreal forest is already established and dominated by conifers (Iverson and Prasad, 2002; McKenney et al., 2007). The northward settlement of temperate species might be difficult as the success of their colonization is not only determined by climate, but also by subtle variation in substrate, drainage, physical soil properties and nutrient availability (Goldblum and Rigg, 2010; Lafleur et al., 2010; Brown and Vellend, 2014). Compared with soils in temperate forests, soil under coniferous trees tend to be poorly decomposed, colder, wetter and covered by snow for a longer period (Barras and Kellman, 1998; Lafleur et al., 2010; Goldblum and Rigg, 2010), potentially hindering the local establishment of temperate

species (Lafleur et al., 2010; Brown and Vellend, 2014). However, some boreal deciduous species such as *Populus tremuloides* can contribute to this transformation by colonizing pure coniferous stand, improving soil physical and chemical properties and facilitating temperate tree regeneration (Laganière et al., 2009). Plant-soil feedbacks may lead to patchy spatial structure in the boreal- temperate ecotone consisting of a mosaic of mixed stands of coniferous and deciduous species, pure stands of deciduous trees on favorable locations and pure coniferous stands on less favorable sites (Goldblum and Rigg, 2010; Fisichelli et al., 2013). Differences in soil properties and ecosystem functioning between deciduous and coniferous stands may impede stand conversions within the ecotone, consequently slowing down the migration process.

The persistence of a plant community at a single location depends on its ability to resist disturbances as well as invasion by other species. Environmental stressors, such as changes in climate conditions or biomass removal, can change forest successional trajectory and even make it jump to an alternative stable state (Stringham et al., 2003). For instance, several studies shown that the prevalence of deciduous (e.g., *A. saccarhum and rubrum*) and intermediate tree species (e.g., *P. tremuloide, Betula papyrifera*) have increased in the last decades along altitudinal and latitudinal gradients in response to management actions Dupuis et al. (2011); Boucher et al. (2006) and climate changes (Beckage et al., 2008). These findings suggest that the compositional changes at latitudinal and elevational ecotones are already observable and that forest stands are currently jumping from one attractor (i.e. dominance by coniferous trees) to another (i.e. deciduous trees).

The clear functional distinction between temperate deciduous and boreal coniferous stands facilitates the representation of the dynamics with a state and transition model (STM). STMs were introduced by Westoby et al. (1989) and have been commonly used to study vegetation dynamics(Briske et al., 2005; Bestelmeyer et al., 2011). They follow the long tradition of Markov Chain models used in forest ecology (Waggoner and Stephens, 1970; Horn, 1975; Binkley, 1980). An STM is based on the idea that plant communities can be cate-

gorized into discrete states (e.g., temperate, boreal, and mixed forest). A spatial unit (e.g., a grid cell in a lattice) can encompass scales from single individuals to entire communities (Briske et al., 2005). Vegetation dynamics are then driven by stochastic transitions between states. With typical datasets on forest communities, transitions can be evaluated from empirical observations, integrating demography, dispersal and species interactions effects and thus offering opportunities to disentangle which of these local mechanisms are limiting or increasing temperate species migration rates under climate change.

Stationary transition matrices are problematic to represent range expansion because they do not account for the build-up of the propagule pressure with the increase of a species abundance, nor do they account for climatic gradients in transition probabilities. Metapopulation theory fortunately provides an easy means to solve these issues. The standard metapopulation model (Levins, 1969) represents the stochastic transitions among two states (i.e., patches are either occupied or not) in a similar way to Markov Chain models of forest dynamics, with the addition of dispersal. The Levins model could viewed as a continuous time analog of such models with a non- stationary transition matrix that depends on the prevalence of the species. The model has already been extended to incorporate environmental gradients (Holt and Keitt, 2000; Holt et al., 2005), whereby a species can persist in a given landscape when the colonization rate of empty patches is higher than the extinction rate. Here, we explore a further extension of the Levins and Holt models to multi-species communities to better understand how climate change and regional-scale dynamic processes will influence the response of boreal and temperate forests to climate change.

Our first objective in this study is to assess if deciduous temperate tree species of eastern North America will be able to track their climate optimum over the next century. Secondly, we seek to investigate which ecological processes are delaying the migration response of temperate forest. We use an STM derived from metapopulation theory to represent the processes of colonization, competitive exclusion and disturbance dynamics at the temperate/boreal ecotone, and we analyze the model both analytically and via simulation. Tran-

sitions among states were calibrated using long-term forest plots surveys from the United States and Canada, where each possible transition was a function of the climatic conditions. We simulated the landscape dynamics over the most extreme climate change scenario (RCP 8.5, (Taylor et al., 2012)) in order to force range shifts. We further run four different versions of the model to investigate the importance of demography and dispersal limitations on range expansion rates. Our results reveal that the temperate forest has a low resilience to climate change because of a slow demography and significant dispersal limitations.

1.4 Methods

We first describe the model representing the transitions among four forest types and then its calibration with observations of transitions among them in permanent forest inventory plots of the United States and Canada. We consider plots from Southern Appalachians up to the boreal forest of Québec and Ontario. Then we describe the analysis performed in 3 steps: (i) identify the relationship the climate and transition probabilities, (ii) characterizing the range shift dynamics over different climate change scenarios , (iii) investigate with similation scenarios the relative importance of demography, biotic interactions and dispersal limitations on migration rates.

1.4.0.1 Modeling approaches

We consider a landscape made of an large number of patches that could be occupied by any of four vegetation types, defined from successionnal status and composition: Regeneration (R), Boreal (B), Temperate (T) and Mixed (M - Figure **??**). These four states summarizes the clustering of species found along the first two axes of a Principal Component Analysis of the relative abundance of dominant species across North-Eastern America (Supplementary Information Fig. S1).

Transitions among states is represented as a stochastic process influenced by climate, ecological interactions and dispersal. The state X_{t+1} at time step $t + 1$ is a probability conditional on the initial state X_t, climatic conditions a time t and the prevalence of the four states in the neighborhood of X. The model represents the following ecological processes. A disturance happens with probabiliy ϵ and converts T, B and M to Regeneration. Conversely, colonization of the R state by temperate trees happens with probability $\alpha_T(T + M)$, and similarly colonization by boreal trees happens with probability $\alpha_B(B + M)$. The colonization probability depends on the amount of propagules produced by neighbouring patches ($T + M$ or $B + M$), thus accounting for metapopulation dynamics. A joint colonization event is possible, leading to a transition to state M, with probability $\alpha_T(T + M) \cdot \alpha_B(B + M)$. Further colonization of a patch by boreal trees happens with probability $\beta_B(B + M)$, and conversely the colonization of a boreal patch by temperate trees happens with probability $\beta_T(T + M)$. Competitive exclusion happens with transition from M patches to either B or T, respectively with probability θ_B and θ_T. Direct transitions between T and B are not allowed, and must instead occur via disturbance and succession, with R as an intermediate state, or invasion and competitive exclusion, with M as an intermediate state. All parameters α, β, θ, and ϵ were modeled as a function of local climatic conditions.

To understand the long-term behavior of the system, we first consider a mean- field model, where the dynamics are represented by ordinary differential equations described in figure S1 and with the constraint that $B + T + M + R = 1$. The analytical solution of the mean-field model yields the expected occupancy of the four states for any given climatic condition. We then implemented the mean-field model into a stochastic cellular automaton to predict transient states and address the lag in migration following climate change. We represented the landscape as a regular grid of cells (600m in longitude and 900m in latitude) where each cell at each time step is occupied by one of the four forest states (R, B, T or M). Individual cells transition to a new state with a probability varying with the climate conditions as in the mean-field model. The model was made spatially explicit by computing neighborhood prevalence from each cell's 8 immediate neighbors. We then simulated the temperate-boreal

forest ecotone, with each cell having a climatic conditions obtained from the observed climate (to calibrate the model) or the projected climate from the RCP 8.5 emissions scenario (Taylor et al., 2012) (to project into the future). We selected this scenario because it predicts the largest temperature increase and we were interested in estimating the maximal migration rate possible. We then considered four modeling scenarios in order to disentangle the mechanisms limiting the northward migration of the temperate forest.

The first modeling scenario consists of simulations of the spatially explicit dispersal as described above. It is the most realistic scenario among the three cases we consider, including demographic and biotic constraints and dispersal limitations. Secondly, we solved the system of differential equations for the 2095 climatic conditions. This scenario is at the other extreme as it assumes, like standard species distribution model, that there are no dispersal limitations and no demographic and biotic interaction constraints. For the third scenario, instead of computing the occupancy of the four states in the immediate neighborhood of a focal cell as for the first scenario, we picked 8 cells at random in the entire grid. This third approach thus considers an infinite dispersal (a cell located at the northern edge of the distribution of boreal forest could be sown with propagules of temperate trees coming from the southern edge of the temperate forest). Demography is the only process limiting the migration in this situation. Finally, we also ran the spatially explicit dispersal model for 50 000 years in order to better understand the transient dynamics and the role of the demography in the migration delay. All of these modeling approaches were run for the 23 Global Climate Models (GCMs, from the RCP 8.5 emission scenario) and repeated 10 times. GCMs used to project landscape dynamic were downscaled at 10 km^2 by Ouranos, a Consortium on Regional Climatology and Adaptation to Climate Change, using the method of linear scaling of precipitation and temperature (Method description in Teutschbein and Seibert, 2012).

1.4.0.2 Calibration from forest inventory data

States classification and environmental data

We classified states using data from permanent sample plots in forest inventory databases from Eastern North America. This forest inventory network incorporated the Forest Inventory and Analysis National Program in United States (O'Connell et al., 2007); Domtar a forest private company in Quebec; the Ministry of Forest, Wildlife and Parks in Quebec (Ministère des Ressources naturelles, 2013); the Ministry of Natural Resources and Forestry in Ontario (Ontario Ministry of Natural Resources, 2014); the Ministry of Natural Resources in New-Brunswick (Porter et al., 2001). These databases differ in ontology but were integrated using their common information on tree measurements and their location. For each database we extracted plot locations, plot surface, year of measurement, species names for every individual tree and diameter at breast height (DBH). We transformed the data for each individual tree into basal area m^2/ha and summed it at the plot level. We considered living trees with a DBH $\geq$ 127 mm in order to standardize measurements across forest inventories. We extracted data for a total of 45 804 plots with a annual mean temperature lower than 10°C. Plot surveys started in 1960 and finished in 2012, with 14 341 plots measured once, 16 626 plots measured twice, 14 837 plots measured up to two times. The time intervals between plot measurements are not constant among plots databases with a median time of 5 years. We removed from the analysis plots with a time interval below than 5 years as no natural transitions are expected to be observed at this time scale. We also removed plots with time interval above 15 years to reduce the probability of "masked" transitions, where a single observation actually incorporates two transitions. For example, an observation of B $\rightarrow$ B could occur due to a lack of any transition, or due to a disturbance, causing B $\rightarrow$ R, followed by succession, resulting in R $\rightarrow$ B. Uneven transition probabilities were standardized to a 5-year interval via rescaling, where $\phi_5 = 1 - (1 - \phi_t)^{5/t}$, where ϕ_5 is any transition probability over a 5-year interval and t is the length of the observation interval. The analysis was thus made on 49 043 measurements located between 57°W to 96°W and 35°N to 52°N.

We classify forest stands in four different vegetation types: Boreal, Temperate, Mixed and Regeneration. The Regeneration state represents a post- disturbance stand, a critical aspect of forest dynamics at the boreal- temperate ecotone (Bergeron et al., 2004; Vanderwel

and Purves, 2014). A plot is classified as Regeneration if it has a basal area lower to $5m^2/ha$. The Temperate state is determined by the presence of at least one individual of the following species (*Prunus serotina*, *Acer rubrum*, *Acer saccharum*, *Fraxinus americana*, *Fraxinus nigra*, *Fagus grandifolia*, *Ostrya virginiana*, *Tilia americana*), and the absence of any boreal species (*Picea mariana*, *Picea glauca*, *Picea rubens*, *Larix laricina*, *Pinus banksiana*, *Abies balsamea*, *Thuja occidentalis*). Alternatively, the Boreal state was determined by the presence of boreal species and absence of temperate ones. The stand was classified as Mixed if both categories of species where found in a stand. Based on this classification, we observed 3 910 transitions between different vegetation states and 45 133 non- transitions (Table SS1).

Plot locations were intercepted with environmental data for 3 bioclimatic variables: the annual mean temperature (°C), the annual precipitation (mm) and the mean diurnal range (°C), as well as 2 soil descriptors: the slope (°) and soil ph. To reduce the effect of inter-annual climate variability, we computed each climate variable as the 15-year average prior to a plot measurement. The annual past climatic conditions were extracted from a $10km^2$ resolution grid using the ANUSPLIN climate modeling sofware (McKenney et al., 2011). ANUSPLIN is essentially a multidimensional "nonparametric" surface fitting method which is suited to interpolate various climate parameters from meteorological stations with historical records (Method description in McKenney et al., 2011). Soil pH was intercepted to "SoilGrids" — an automated system for global soil mapping provided by Global Soil Information Facilities (ISRIC, (Method description in Hengl et al., 2014) at a resolution grid of $1km^2$. Finally, we retrieved information on slope aspect using the Global 30 Arc-Second Elevation Data Set (GTOPO30) DEM courtesy of the U.S. Geological Survey Agency.

Calibration

We considered the state of a given sampling plot at time $t+1$, X_{t+1} as a stochastic process conditional on its state at time t, X_t, and climatic covariates E. It is a first-order markovian process since the transition is conditional only on the previous time step and independent of previous history. The probability function representing this process is $P(X_{t+1}|X_t, E, N)$, with

E being the set of climatic conditions and *N* the prevalence of the states in the neighborhood. We used simulated annealing (R package GenSA; Yang Xiang et al., 2013) to attain by maximum likelihood estimate of the parameters pertaining to each transition probability illustrated at figure **??**. Each of them is a function of mean annual temperature (TP, °C) and mean annual precipitation (PP, mm). Each of the per patch transition probability (i.e., α_T, α_B, β_T, β_B, θ_T, θ_B, and *epsilon*; Fig. **??**) was modeled as second order logistic function of climatic conditions. Thus, any parameter ϕ is modeled as:

$$logit(\phi) = a_0 + a_1 \cdot TP + a_2 \cdot PP + a_3 \cdot TP^2 + a_4 \cdot PP^2 \tag{1.1}$$

Transition probabilities involving the colonization by either temperate or boreal trees are dependent on the prevalence of B, M and T in the neighborhood of the plot. The evaluation of the model therefore requires data on the forest composition around the location of the plot. Such data is not available in the forest inventory databases and the incompatibilities of stand classifications in United States and Canada prevent the usage of stand maps. We therefore approximated the neighborhood composition by spatial interpolation of the forest composition using the multinomial Random Forest classification algorithm (Liaw and Wiener, 2002) to get the expected probability of finding the states B, M, T and R. The interpolation involved the annual mean temperature, the annual precipitation and the mean diurnal range, slope aspect, soil pH and the (X, Y) coordinates as explanatory variables. All of these environmental variables have been retained as the best descriptors of the states distribution. The classification algorithm was run on the entire dataset and the predicted occupancy of the different states were obtained for each plot based on its spatial coordinates and environmental conditions.

1.4.1 Analysis

Prior to analyzing the STM, we evaluated the strength of the relationship between transitions among states and climate conditions using a multinomial regression using the nnet

R package (Venables and Ripley, 2002). This model does not consider dispersal limitations (i.e., the prevalence terms in the full model) nor patch-scale ecological processes (i.e., the *alpha*, *β*, *theta*, and *epsilon* parameters), rather simply relates observed transitions to climate. This serves as a baseline for whether we could expect to observe climatic relationships within the more mechanistic STM. We considered a third order polynomial including both annual average temperature and total precipitations, and then removed each of the terms one after the other to understand their contribution to the likelihood (using the δAIC). The two climatic variables were standardized to mean 0 and unit standard deviation in order to compare regression coefficients. Other climatic variables were also considered but were found to be weaker predictors and are thus not considered.

We then solved the system of differential equations at equilibrium (i.e. mean field model) for each location of the climatic grid using the maximum likelihood estimates of the parameters. Analytical solutions were found using the deSolve R Package (Soetaert et al., 2010). We mapped the solution and compared it to the actual distribution in order to validate the predictions of the model. The validation was performed with the 14 080 plots that were measured only once and therefore not used for calibration. Each plot was classified according to the above criteria based on their composition. The expected state for each plot was attributed according to the state with the highest occurrence probability. We computed for each state the number of observed and expected presence (fraction "a"), observed presence and expected absence ("b"), observed absence and expected presence ("c") and finally the number of observed and expected absences ("d"). We calculated the True Skill Statistic for each of the four state s (REF).

We run the cellular automaton model on the spatially explicit climatic grid with climate change scenarios. The equilibrium solution obtained with the differential equations was used as the initial condition for conducting simulations to make sure than any observation of change in state distribution is caused by the changing climatic conditions and not by initial distributions that are not at equilibrium with initial climatic conditions. The time step was

five years and the simulations were run from 2000 to 2095. Expected transition rates for each cell on the landscape were recomputed at each time step according to the average climate of the preceeding 15 years.

We subset from the grid a band of 9.6km in longitude and 520km in latitude in order to compute the migration rate of the temperate forest. The band starts north of the city of Montreal in the maple bioclimatic domain and extends up to the spruce-moss domain, in the boreal forest nearby Chibougameau. The range limit of the temperate forest at any moment in time was recorded as the northernmost location (95th percentile) of a temperate or a mixed state along this band. The range expansion was computed between each time step and the migration rate for any time interval was estimated as the gain in km along this south-north gradient per year.

1.5   Results

We first investigated the relationship between transition probabilities and climatic variables using a multinomial regression and found that all transitions are significantly related to the annual mean temperature and the total annual precipitation (Table. **??**). Annual average temperature had the strongest contribution to the likelihood for all transitions except for the transition to M where the annual total precipitation is predominant (ΔAIC_{pp}= 28.60 ,Table. **??**). The transitions to T (competitive exclusion and colonization) and R (disturbance) were the most strongly related to climate (R^2 = 0.15 and R^2 = 0.22 respectively). The transitions from state R to M and T are both positively increasing with temperature (Figure **??**). The disturbance probability remained low (¡ 0.005) on the entire climatic space (Figure **??**).

Accordingly, we found that the State and Transition Model fitted well to the observed transitions. The model comparison reveals that all parameters are significantly related to climate (TABLE). The parameters most strongly related to climate were XX, while XX were more weakly related to climate. As a consequence, the equilibrium solution of the dynamic

model under the 2015 climatic conditions agreed with the current distribution of temperate, mixed and boreal forest (FIG). The validation reveals modest TSS values for the states B, T and R (TABLE), around 0.45, and a lower value for the state M at 0.18. There is nonetheless a high correspondance between the match of presences and absences, with 0.70 and 0.98 of observations correctly predicted.

B	T	M	R	TOTAL	
a	1380	6179	980	0	8539
b	1940	1141	2175	285	5541
c	830	3062	1648	0	5540
d	9930	3698	9277	13795	36700
NOBS	3320	7320	3155	285	14080
TSS	0.46	0.43	0.18	NA	0.48
(a+d)/N	0.80	0.70	0.73	0.98	0.80

The temperate forest (pure stand of temperate species) are predicted to cover a surface of XX km^2 in 2015. This surface is expected to expand to XX km^2 in 2095. The major change in forest composition is expected in the transition zone, where mixed forests will be rapidly converted to temperate forest, for a reduction of XX % of their surface (Figure **??**). As a consequence, the ecotone area found in 2015 (where temperate and mixed coexist at the landscape level) will almost disappear by the end of this century. The northern edge of the distribution does not change much however, with almost no movement toward the north for either temperate of mixed states.

We run four different modeling approaches with these climate change scenarios to investigate what are the main drivers of the migration dynamics. We found for the full model a northward migration of 14±0.2 kms by 2095. By comparison, we found that the migration would be 328±28.4 kms in absence of dispersal limitations, demographic constraints and biotic interactions. In between, the simulations with infinite dispersal distance but with demographic constraints also has a very low northward migration at XX±SD kms, comparable

to the simulations with dispersal limitations. The main factor slowing down migration thus appears to be demography. This constraint is so severe that the vegetation do not even reach equilibrium after 50 000 years (Figure **??**). The mismatch between the suitable climatic conditions for temperate species and their realized distribution consequently increases constantly through time.

1.6 Discussion

A clear understanding of the determinants of migration dynamics under climate change is essential to improve our ability to predict future biodiversity distribution (Svenning et al., 2014). Forest trees are expected to respond slowly to climate change because of their longevity, their low dispersal and slow demography. Here we analyzed the northward shift in distribution of temperate forest from North-Eastern America, a major biome covering North- Eastern United States and Canada. The dynamics and ecosystem properties of this ecosystem are strikingly contrasting with the ones of boreal forest, with on the one hand a small canopy gap disturbance regime with fast processing of a rich deciduous litter, and on the other hand a large scale disturbance regime with slow decomposition of an acidic and nutrient poor litter. We investigated the importance of key ecological processes - dispersal limitations, biotic interactions and demography - for the migration dynamics of this ecosystem. We found evidence for substantial lags in the response of these ecosystems to climate change; in particular the influx of temperate species into the boreal ecosystem was substantially slower than would be predicted based on climate envelopes alone. Moreover, these lags were principally due to the combination of slow demographic processes (i.e., the invasion of seedlings into uncolonised patches) and dispersal limitations. These results together demonstrate that, although temperate species can be expected to grow in dominance in areas where they are already present, the replacement of existing boreal ecosystems by temperate forest will be a much slower process.

Beyond rapid shift in forest structured induced by disturbances, the transitions we represented are driven by dynamical processes such as succession, competitive exclusion, and invasion. We expected that local climate is one factor driving the rate at which these transitions occur. For example, (REF) found that the rate of forest regrowth by colonization following disturbance is strongly influenced by climate. Moreover, there is clear evidence that climate exerts a strong influence on the state of mature forests and their succession pathways (Anderson-Teixeira et al., 2013). EXPLAIN MORE Our study shows that, at the stand scale, colonization and succession have strong relationships with climate, whereas competitive exclusion shows a weaker relationship. However, all of these larger-scale ecological processes are ultimately functions of individual- level demographic processes such as growth, mortality, seedling establishment and reproduction.

There is already substantial evidence that climate is influencing some of these processes. Some species such as *Fagus* or *Pinus* are already well known to be susceptible to moisture variation over the growing season, with lower moisture reducing germination success (CLARK et al., 2011). Extreme drought can also cause massing mortality of several temperate deciduous tree species (Palmer). Spring and summer temperature has also been identified as critical on the fecundity (CLARK et al., 2011; Graignic et al., 2014). The stratification of maple seeds for instance is strongly dependent on climate conditions prevailing in the spring, with strong evidence of local adaptation of Sugar maple seeds to cold temperatures at the northern edge of its distribution (Solarik2016). Sugar maple flower development is also affected by the timing of climatic events in the spring (Chuine2001) and as a consequence a mechanistic model of its distribution surprisingly fits well its distribution (Morin2008). Overall, these factors combine so that seedling density of Sugar maple is strongly related to the average temperature and precipitation in july (Graignic et al., 2014). Similarly, fecundity of boreal trees is also influenced by climate, such as the black spruce seeds requiring a certain amount of degree-days to mature (Sirois2006). Not all stages however are dependent on climatic conditions, some of them being more sensitive to competitive interactions than climate variation (He2015PNAS). Future research will therefore be required to determine more

precisely the processes underlying our observation of climate dependence of state transitions.

An important validation of our approach is that we successfully predicted the equilibrium distribution of these communities based on a dynamical model parameterized from observed transitions, rather than using static occurrence data such as is common in traditional species distribution models. The ecological niche is the conceptual backbone underlying most species distribution models. It posits that species distribution is constrained by local demography such that a species is found at locations where it has a positive intrinsic growth rate (Holt2009). It appears however that trees are not necessarily distributed where they grow best (McGill2012). Recenlty, Thuiller2014 found only weak and idiosynchratic relationship between the population growth rate, abundance, carrying capacity and the distribution of most temperate and boreal tree species of North America and Europe. These result suggest that tree range limits might be driven by processes happening at other spatial scales. Fortunately, metapopulation theory provides an alternative explantation to range limits. According to Holt2002, range limits could instead be driven by a balance between colonization and extinction processes. In such situation, not only a species must be able to establish a local population, as postulated by the traditional definition of the niche (Holt2009), but also that the colonization rate be larger than extinction. It appears from our results that a regional approach to range limits of trees would be more relevant to an approach based on local dynamics. Incidently, our analysis in this study is based on the same data as Thuiller2014, but we manage to better explain species distribution. Our results would explain the conflicting observation that species such as sugar maple could well establish and develop way outside of its current range, in the deep boreal forest (Kellman2004, Brown2014). A regional approach to forest ecosystems also correspond to the long-held non-equilibrium view of forest ecosystems, with landscapes being a mosaic of patches at different successional status. Our approach should be applied to other forest ecosystems in order to assist its generality and relevance for a more general theory of range limits of forest trees.

We simulated the migration dynamics happening according to 23 climate change sce-

narios drawn from the CMIP5 project, with the most pressimistic scenario (IPCC 2014, RCP 8.5). We found that despite an average increase of 4°C at the ecotone, the temperate forest will barely move northward from its present distribution at the end of this century. Mixed forests will be rapidly converted to temperate forests, but the transition zone will be squeezed at the southern limit of the boreal forest. The inability of temperate species to migrate will cause a spatial mismatch between the potential and realized species distributions, which could induce catastrophic shifts in forest ecosystems following anthropogenic and natural disturbances (G. Walther et al., 2002; Renwick and Rocca, 2014; Vanderwel and Purves, 2014). Such changes have been already observed at the boreal- temperate forest ecotone over the last decades (**?**), in particular after these stands have been subject to forest management (Dupuis et al., 2011; Boucher et al., 2006). Fortunately, forest management could help reducing this increasing disquilibrium situation. First, by increasing the transition to state R, forest management could speed up the transition from B to M. Further, because clearcutting and other methods of harvesting increase light availability, it tends to increase successionnal rate. Diffusion theory also predict that increasing the intrinsic population growth rate could speed up quite significantly the migration rate. Further, assisted migration (Aubin2012) can also increase the average dispersal distance by several orders, and thereby increase the resilience of forest ecosystems to climate change.

A critical question remaining however is what will happen with maladapted boreal forests, that will stay in place for a certain time before temperate forest eventually migrate. There is currently no spatial analog of large tracks of boreal stands, found under warm, temperate climatic conditions and on mesic soils. Planted boreal trees, such as black spruce and jack pine, in warm climatic conditions indicate that the individual trees could stand warmer conditions and well perform. There is however considerable uncertainty in the future regeneration capabilities of those trees, and their capacity to stand natural disturbances. Further, we have a limited understanding of the forest- climate interaction in the fire regime. According to our metapopulation approach, even though boreal trees could establish and grow under warmer conditions, they also need to have a sufficiently high colonization rate to balance

the extinction. If fires get more frequent with warmer temperatures, then we could face a no-analog situation where the boreal trees could suffer from climate change. This question remains open and will require substantial research given the evidence that temperature trees will not be able to response, at least over the mid-term, to the rapidly changing climate.

Despite the clear support for the hypothesis that climate drives transitions among forest types at the boreal-temperate ecotone, our model predicts that the temperate forest will barely move northward, with a mean change of 11 km by the year 20XX with a rate of XX km.yr^{-1}. This finding is consistent with Iverson et al. (2004) which predicted range shift of 10-20 kms for several species confined to the eastern half of the United States. In addition, analysis of fossil pollen distributions demonstrate that range shifted from 100 to 300 m/year during the quaternery period (**??**). However, our model includes several shortcomings which could lead to an over or underestimation of the migration predicted. If change in local climatic conditions modify life history strategies, we may expect to see faster migration rates (i.e. younger maturation age and higher fecundity) (Snell et al., 2014). Our model also assumes a constant dispersal ability (100m). But we found no evidence that the change on this grid resolution will impact migration rate until the end of this century. Consequently, STM is robust to predict the spread of the temperate forest on the short term horizon (2000-2095).

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CONCLUSION GÉNÉRALE

[C'est dans cette section qu'est mise en évidence la portée de l'étude ainsi que les liens entre les articles ou autres textes et une ouverture sur les perspectives de recherche dans le domaine concerné. On y fait état des limites de la recherche et on y propose, le cas échéant, des pistes nouvelles pour de futures recherches ou des façons de développer de nouvelles applications. La conclusion ne doit pas présenter de nouveaux résultats ni de nouvelles interprétations. Elle doit être rédigée de manière à faire ressortir la cohérence de la démarche.]

$$\frac{dT}{dt} = R \cdot \alpha_T(T + M)[1 - \alpha_B(B + M)] + M \cdot \theta \cdot \theta_T(1 - \epsilon) - T \cdot \beta_B(B + M)(1 - \epsilon) - T \cdot \epsilon$$

$$\frac{dB}{dt} = R \cdot \alpha_B(B + M)[1 - \alpha_T(T + M)] + M \cdot \theta(1 - \theta_T)(1 - \epsilon) - B \cdot \beta_T(T + M)(1 - \epsilon) - B \cdot \epsilon$$

$$\frac{dR}{dt} = \epsilon(M + B + T) - R \cdot \alpha_B(B + M)[1 - \alpha_T(T + M)] - R \cdot \alpha_T(T + M)[1 - \alpha_B(B + M)] - R \cdot \alpha_B(M + B)\alpha_T(M$$

$$\frac{dM}{dt} = B \cdot \beta_T(T + M)(1 - \epsilon) + T \cdot \beta_B(B + M)(1 - \epsilon) + R \cdot \alpha_B(B + M)[1 - \alpha_T(T + M)] - M \cdot \theta \cdot \theta_T(1 - \epsilon) - M \cdot$$

Figure S1: All differential equations representing the boreal-temperate ecotone through four different states. B, M, R and T mean Boreal, Mixed, Regeneration and Temperate respectively.

Tableau S1: Transition and none-transition observed between two measurements through all plots surveys without regard to the time interval. B, M, R and T mean Boreal, Mixed, Regeneration and Temperate.

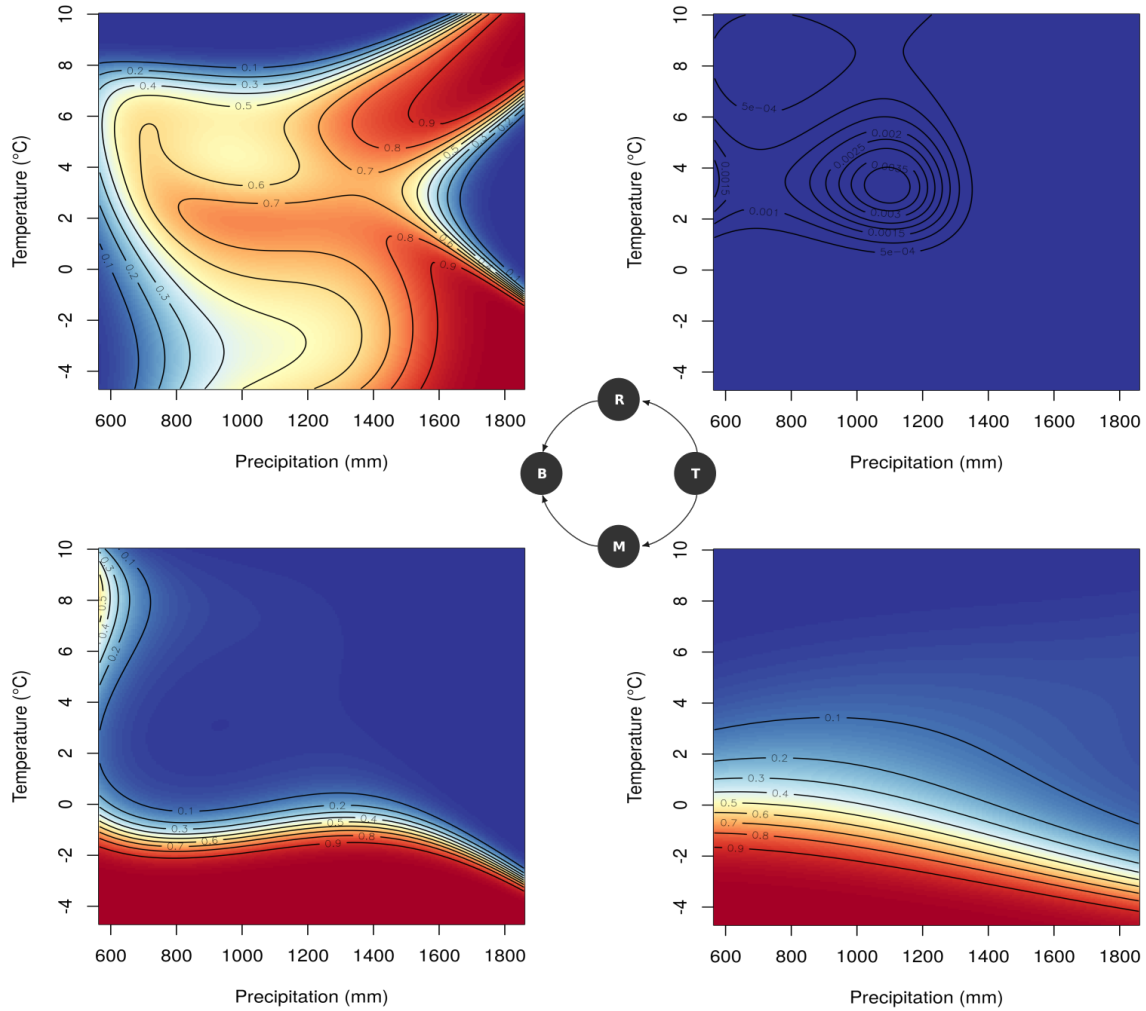| From \ To	B	M	R	T
B	**15 357**	794	203	-
M	302	**14 433**	51	959
R	485	57	**209**	80
T	-	891	40	**15 134**

Figure S2: Illustration of the transition probabilities of all pathway driving the conversion of a state Temperate (T) to Boreal (B). Probability functions are predicted by multinomial regression as a third degree polynomial which account for the temperature (°Cs) and the precipitation (mm). Transition pathways are described by the arrows of the centered diagram.

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