**UQAR**

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

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Avertissement

*À mes parents, mes frères et soeurs, et ceux qui ont été patient.*

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Je tiens dans un premier temps à remercier mon directeur Dominique Gravel pour m'avoir donné l'opportunité de réaliser cette maîtrise. Dominique m'a redonné confiance et espoir dans toutes les étapes clés qui ont mené à la réalisation de ce mémoire. Il m'a impressionné par sa patience et ses nombreuses qualités humaines et m'a montré que la science est avant tout un travail d'équipe.

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*AVANT-PROPOS*

Je pourrais commencer cet avant-propos par, *"Depuis tout jeune, je souhaite comprendre comment la nature fonctionne..."*, mais je ne le ferais pas. Je n'ai pas atterri sur ce projet par simple mouvement brownien. Cette maîtrise est plutôt l'aboutissement d'un parcours scolaire ponctué par des rencontres et des discussions, animé par ma curiosité et ma passion pour les sciences environnementales. Après une technique en Bioécologie et un baccalauréat en Biologie, je me suis aperçu que mes centres d'intérêt ne portaient pas sur une espèce en particulier, mais plutôt sur la diversité des organismes et les rôles fonctionnels qu'ils remplissent au sein d'un écosystème. J'étais autant fasciné par les espèces du genre *Lombricus sp.* que par l'orignal. Ma curiosité me poussait donc vers la compréhension des mécanismes écologiques à une plus large échelle. Mon implication au sein du laboratoire de Dominique Gravel durant mon baccalauréat, m'a permise d'être initié à l'écologie théorique et la biogéographie ainsi qu'à l'approche scientifique par modélisation. Ce laboratoire m'offrait donc un cadre idéal pour réaliser ma maîtrise et satisfaire cette curiosité.

**Reproductibilité de mes travaux**

Le père du modèle hypothético-déductif, Karl Popper énonçait que l'un des critères fondamentaux dans la réalisation d'une bonne étude scientifique réside dans la reproductibilité de la méthode. Pour atteindre ce critère, des outils informatiques permettent aujourd'hui de dépasser la simple description méthodologique sur papier. Dans ce contexte, l'ensemble de mes scripts et programmes utilisé pour la réalisation de ce projet sont disponibles librement via une plateforme internet. Ainsi, le code nécessaire à la conceptualisation de la base de données QUICC-FOR est accessible à travers le dépôt : `https://github.com/QUICC-FOR/QUICCSQL`. Ce dépôt ne contient pas les données biologiques (celles-ci demeurant la propriété des Ministères ou entreprises privés partenaires du projet) mais seulement l'information permettant de reproduire l'architecture de la base de données SQL. Les scripts nécessaires à l'extraction des données pour la calibration et les projections du modèle sont ac-

cessibles à cette adresse `https://github.com/QUICC-FOR/STModel-Data`. Ils permettent de retracer l'ensemble des filtres, et des étapes de manipulation des données nécessaires à la réalisation des analyses. Le modèle d'automate cellulaire utilisé (States and Transitions model, STM) pour les simulations est également disponible (`https://github.com/QUICC-FOR/STModel-Simulation`), ainsi que les étapes de calibration (`https://github.com/QUICC-FOR/STModel-Calibration`) pour l'obtention des paramètres par la méthode de maximum de vraisemblance. Enfin, le post-traitement des simulations et les codes nécessaires à la production des figures est disponibles à cette adresse : `https://github.com/QUICC-FOR/STModel-CompAnalysis`. La mise à disposition de ces ressources constitue un gage de transparence auprès de mes pairs. Elle me permet également de valoriser mes compétences professionnelles en programmation scientifique. Enfin, elle garantit la possibilité de conduire les mêmes analyses dans les 20 ou 30 prochaines années lorsque de nouvelles observations/données seront accessibles ; un critère indéniable lorsque l'on connaît la lenteur dans la réponse d'un écosystème forestier à des changements environnementaux.

## *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, possèdent une forte longévité et disposent de faible capacité de dispersion. Les approches actuelles pour prédire l'aire de répartition future des espèces, telles que les modèles d'enveloppe climatique, ne peuvent pas tenir compte de ces particularités propres aux écosystèmes forestiers, car ils assument une dispersion infinie et une réponse instantanée aux changements climatiques. Nous proposons une nouvelle approche de modélisation basée sur la théorie des métapopulations pour tenir compte de cette capacité limitée de dispersion, des interactions biotiques et de la démographie propre à la forêt tempérée nordique du nord-est de l'Amérique du Nord. Notre objectif est d'évaluer si ce biome forestier sera en mesure de suivre sa niche climatique d'ici la fin de ce siècle. Nous avons effectué des simulations de l'écotone entre la forêt boréale et tempérée en utilisant un modèle d'états et de transitions (STM), dans lequel les communautés forestières sont classées dans 4 états : boréales, tempérées, mélangées et en régénération après une perturbation. Les transitions entre les états sont calibrées à partir des inventaires des parcelles permanentes présents aux États-Unis et au Canada. Les résultats des simulations du modèle indiquent que la forêt tempérée se déplacera seulement de 14 ± 2,0 km alors qu'un modèle de distribution d'espèces standard prédit un déplacement de 238,79 ± 34,24 km. Les simulations de l'écotone forestier mettent également en évidence que la majorité des transitions attendues seront une conversion des peuplements mixtes vers des peuplements purement décidus. L'utilisation du modèle avec un scénario de dispersion infinie révèle que les interactions biotiques et la démographie sont les facteurs les plus importants qui limitent la capacité d'expansion du biome de la forêt tempérée. En conclusion, la forêt tempérée possède une faible résilience au changement climatique en raison de sa lente démographie et des fortes interactions compétitives avec les espèces boréales.

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.

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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 XXI$^e$ 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**

Les forêts ont 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 est déjà observable sur la diversité végétale (G. Walther et al., 2002; Parmesan, 2006). Considérant l'augmentation de température de 4 à 7°C (Ouranos, 2015, Scénario RCP 8.5) attendu pour le Québec méridionale, plusieurs études prédisent que des espèces de la forêt tempérée (*Fagus grandifolia*, *Betula allegha-niensis*, *Acer saccharum*, *Quercus rubra*) vont étendre leur distribution vers le nord d'ici la fin du siècle (Iverson and Prasad, 2002; McKenney et al., 2007). Cependant, ce changement dans la composition végétale pourrait s'avérer difficile considérant que les conditions micro-climatiques que l'on retrouve sous les espèces boréales sont différentes de celles présentes en forêt tempérée. Au printemps, la température y est plus froide en raison de l'ombrage et par conséquent la neige y demeure plus longtemps, le sol y est plus humide et la litière est plus acide et plus fibreuse. Ainsi, même si les conditions climatiques à l'échelle de la région sont favorables à l'établissement des espèces tempérée, les microconditions particulières re-trouvées en forêt boréale pourraient nuire à sa régénération (De Frenne et al., 2013; Lafleur et al., 2010). Si c'est le cas, il est possible que la forêt tempérée nordique ne parvienne pas à s'installer en forêt boréale à la suite d'un réchauffement climatique et que cela contraigne l'expansion vers le nord de la distribution des espèces tempérées.

Pour étudier les changemens d'aire de répartition d'une espèce, les modèles com-

munément utilisé en biogéographie sont les mdèles d'enveloppes bioclimatiques. Ces derniers reposent sur des approches corrélatives mettant en relation la présence et l'abscence d'une espèce avec le climat. Ces outils présentent plusieurs limites puisqu'ils se basent sur la niche fondamentale et ne tiennent donc pas compte des facteurs biotiques (p. ex. capacité et taux de dispersion, compétition inter-spécifique) influençant l'aire de répartition des espèces [Guisan2005, Pearson2003]. Ces facteurs jouent pourtant un rôle prépondérant dans la dynamique d'un écosystème [Guisan2005, Araujo2007, Pearson2003]. Ces modèles assument également que la végétation ne présente pas de déséquilibre avec le climat et qu'elle répond de manière instantanée aux fluctuations climatiques [Austin2002]. Ils sont donc statiques et ne contiennent aucune composante dynamique (p. ex. les processus de dispersion, succession ou encore de perturbations tels que le feu ou le broutage) [Guisan2005, Austin2002].

# 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, possèdent une forte longévité et disposent de faible capacité de dispersion. Les approches actuelles pour prédire l'aire de répartition future des espèces, telles que les modèles d'enveloppe climatique, ne peuvent pas tenir compte de ces particularités propres aux écosystèmes forestiers, car ils assument une dispersion infinie et une réponse instantanée aux changements climatiques. Nous proposons une nouvelle approche de modélisation basée sur la théorie des métapopulations pour tenir compte de cette capacité limitée de dispersion, des interactions biotiques et de la démographie propre à la forêt tempérée nordique du nord-est de l'Amérique du Nord. Notre objectif est d'évaluer si ce biome forestier sera en mesure de suivre sa niche climatique d'ici la fin de ce siècle. Nous avons effectué des simulations de l'écotone entre la forêt boréale et tempérée en utilisant un modèle d'états et de transitions (STM), dans lequel les communautés forestières sont classées dans 4 états: boréales, tempérées, mélangées et en régénération après une perturbation. Les transitions entre les états sont calibrées à partir des inventaires des parcelles permanentes présents aux États-Unis et au Canada. Les résultats des simulations du modèle indiquent que la forêt tempérée se déplacera seulement de 14 ± 2,0 km alors qu'un modèle de distribution d'espèces standard prédit un déplacement de 238,79 ± 34,24 km. Les simulations de l'écotone forestier mettent également en évidence que la majorité des transitions attendues seront une conversion des peuplements mixtes vers des peuplements purement décidus. L'utilisation du modèle avec un scénario de dispersion infinie révèle que les interactions biotiques et la démographie sont les facteurs les plus importants qui limitent la capacité

d'expansion du biome de la forêt tempérée. En conclusion, la forêt tempérée possède une faible résilience au changement climatique en raison de sa lente démographie et des fortes interactions compétitives avec les espèces boréales.

Ce premier article, intitulé "*Slow demography constrains the North-Eastern Temperate Forest expansion under Climate Change*", fut corédigé par moi-même ainsi que mon Professeur Dominique Gravel et mes deux cosuperviseurs, Matthew Talutto (Ph.D) et Isabelle Boulangeat (Ph.D). L'article présenté sera soumis à "*Global Change Biologie*" pour évaluation par mes pairs à la fin de l'été 2016. Cet article constitue l'un des volets du projet stratégique QUICC-FOR, financé par le CRSNG, qui vise à cartographier et quantifier les conséquences des changements climatiques sur les forêts de l'Est de l'Amérique du Nord. Ma contribution en tant qu'auteur se résume en cinq points: (i) effectuer un état de la littérature; (ii) conceptualiser le modèle et l'implémenter grâce au langage de programmation C; (iii) créer une base de données nécessaire à la calibration et la validation du modèle; (iv) effectuer le post-traitement et l'analyse des simulations; (v) rédiger l'article. Dominique Gravel est à l'origine de l'idée du projet et a aidé à la conceptualisation, la validation du modèle et la révision du manuscrit. Matthew Talluto est responsable de la calibration bayésienne avec la méthode MCMC (*Monte Carlo Markov Chain*). Il a également contribué à l'implémentation du modèle en C ainsi qu'à la révision du manuscrit. Isabelle Boulangeat est responsable de l'estimation des paramètres par maximum de vraisemblance nécessaire à l'initialisation du MCMC. Elle a également contribué à la révision du manuscrit. L'ensemble de mon équipe d'encadrement a fourni une assistance technique inestimable dans la plupart des étapes scientifiques nécessaires à l'obtention de ces résultats.

Les résultats présentés ici reposent sur les paramètres issus la calibration par maximum de vraisemblance. De nouvelles simulations vont être amorcées en utilisant la distribution postérieure du MCMC afin d'obtenir une meilleure estimation de l'incertitude dans les projections. Les résultats de cet article ont été présentés à deux congrès internationaux et deux congrès provinciaux sous forme d'une affiche et d'une conférence. La conférence s'intitulait

"*Difficult migration of temperate tree species in boreal forest under climate change?*", présenté au 9$^e$ colloque du Centre d'étude de la Forêt (CEF) en avril 2015 et au 7$^e$ congrès eCANUSA sur les sciences forestières en octobre 2014. Enfin, l'affiche portait le titre "*A state transition model to investigate what constrains the northward migration of the temperate forest*" et a fait l'objet d'une présentation au colloque du Centre des sciences de la biodiversité du Québec (CSBQ) en octobre 2015 et au 9$^e$ congrès IALE en écologie du paysage en juillet 2015. L'ensemble de ces travaux peuvent être téléchargés à partir de mon site internet personnel (http://steveviss.github.io/paper/). En parallèle à cette maîtrise, je me suis impliqué à titre de coauteur dans l'un des chapitres de la thèse de Christian Marchese (UQAR) portant sur la phénologie du phytoplancton dans la région arctique de la mer de Baffin. Cette collaboration a aboutie à un article intitulé "*Changes in phytoplankton bloom phenology in the NOW polynya region: a response to changing environmental conditions*", soumis en mars 2016 dans la revue *Polar Biology*.

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

**ABSTRACT**

Many species are not migrating fast enough to keep pace with the rapidly changing climate. It is well known that trees experience long time lags in their migration responses because they are sessile, long-lived and have a relatively short dispersal ability. Current 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 an 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 northeastern American temperate forest will be able to track its climatic optimum by the end of this century. We performed simulations on the boreal-temperate ecotone using State and Transition Models (STMs), wherein forest communities are classified in 4 states: boreal, temperate, mixed and stands in regeneration. Transitions among states are calibrated from several long-term forest plot surveys from the United States and Canada. We find that the temperate forest will move only 14±2.0 km into the boreal forest by the end of this century, contrary to predictions from standard species distribution models that the temperate forest will shift northward by 238.79±34.24 km. We also find that 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.

**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 known for their shortcomings, in particular with respect to 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, SDM predictions of future distributions can be biased because of our inability to disentangle biotic from abiotic drivers of distribution (Kissling et al., 2012; Wisz et al., 2013). 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 (Boulangeat et al., 2012; Pulliam, 2000). Species might persist for a while at newly unsuitable locations because of the time-delayed extinction and source-sink 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 are particularly worth attention. Tree species may be 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 identi-

fied 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 the representation by these models, these two parameters point to fundamental quantities that are required 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, mycorrhizae and other types of biotic interactions also 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 is essential to improve our understanding of species migration (Normand et al., 2014).

Several North American temperate deciduous tree species (e.g. *Fagus grandifolia*, *Betula alleghaniensis*, *Acer saccharum*, *Quercus rubra*) are expected to expand their distributions northward (Iverson and Prasad, 2002; McKenney et al., 2007), where boreal forest is already established and dominated by conifers. 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 periods (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 stands, improving soil physical and chemical properties and facilitating temperate tree regeneration (Laganière et al., 2009). Thus, 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 favourable locations and pure

coniferous stands on less favourable 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 and 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 forest state (Stringham et al., 2003). For instance, several studies have 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 change (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 categorized 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 (Levins, 1969) could be viewed as a continuous time analogue 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, and has been applied empirically to study individual species' distributions in eastern North America (Talluto et al., 2016). 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 temperate deciduous 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 analytically and through simulations. Transitions 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.

## METHODS

We first describe the model representing the transitions among the four forest communities (i.e. boreal, temperate, mixed and regeneration communities). Then we explain the calibration using observations of transitions from permanent forest inventory plots in 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) identifying the relationship between climate and transition probabilities, (ii) characterizing the range shift dynamics under climate change over different scenarios, and (iii) disentangling via simulation scenarios the importance of demography, biotic interactions and dispersal limitations on migration rates.

### Modelling approaches

We consider a landscape made of a large number of patches that could be occupied by any of four vegetation types, defined by successional status and composition: Regeneration (R), Boreal (B), Temperate (T) and Mixed (M; Fig.1; see *Classification of states* below for a description). These four states summarize 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 are represented as a stochastic process influenced by climate, ecological interactions and dispersal. The state of focal plot $i$ at time step $t + 1$, given by $X_{t+1,i}$, is a random variable with a probability distribution conditional on the initial state $X_{t,i}$, climatic conditions a time $t$, and the prevalence of the four states in the neighbourhood of $i$ (Hereafter, we assume all equations are relative to a focal stand and omit the subscript $i$ for clarity of notation). The model dynamic is represented by the following ecological processes (Fig.1). A disturbance occurs with probability $\epsilon$ and converts T, B and M to Regeneration (R). 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 directly to state M, with probability $\alpha_T(T+M) \cdot \alpha_B(B+ M)$. Mixed stands can also arise via colonization of temperate stands by boreal trees, with probability $\beta_B(B + M)$, or conversely by the colonization of a boreal patch by temperate trees with probability $\beta_T(T + M)$. Competitive exclusion results in the transition from M patches to either B or T, respectively with probability $\theta_B$ and $\theta_T$. 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 $\alpha$, $\beta$, $\theta$, and $\epsilon$ were represented as a function of local climatic conditions.

To understand the long-term behaviour of the system, we first considered 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 the prevalence of states from the 8 immediately neighbouring cells. We then simulated the temperate-boreal forest ecotone, with each cell having 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 modelling scenarios in order to disentangle the mechanisms limiting the northward migration of the temperate forest.

The first modelling 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 neighbourhood 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 on the migration delay. All of these modelling approaches were run for the 23 Global Climate Models (GCMs, from the RCP 8.5 emission scenario) and repeated 120 times. GCMs used to project landscape dynamics 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).

**Calibration from forest inventory data**

**Classification of states**

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 the United States (O'Connell et al., 2007); Domtar a forest private company in Quebec; the Ministry of Forest, Wildlife and Parks in Quebec (MRN, 2013); the Ministry of Natural Resources and Forestry in Ontario (OMNR, 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 trees measurements and their location. For each database we extracted plot locations, plot surface, years of measurement, species names for every individual tree and diameter at breast height (DBH). We transformed the data for each individual tree into basal areas $m^2/ha$ 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 14 080 plots measured once, 16 626 plots measured twice, 14 837 plots measured up to twice. The time intervals between plot measurements are not constant among plot 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 intervals 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 $\phi_5$ 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.

To classify the plots into the (B)oreal, (T)emperate, (M)ixed, or (R)egeneration states, we examined the total biomass (as estimated by basal area) and species composition at each time step. Because the regeneration state represents post-disturbance stands, we used total basal area as the criterion for selection, where a plot was classified as R when basal area was less than $5m^2/ha$. The other states were determined by species composition. We classified temperate plots as those where at least one individual of the following species (*Prunus serotina*, *Acer rubrum*, *Acer saccharum*, *Fraxinus americana*, *Fraxinus nigra*, *Fagus grandifolia*, *Ostrya virginiana*, and *Tilia americana*) was present, and no boreal species (*Picea*

*mariana*, *Picea glauca*, *Picea rubens*, *Larix laricina*, *Pinus banksiana*, *Abies balsamea*, and *Thuja occidentalis*) were present. 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 were found in a stand. Based on this classification, we observed 3 910 transitions between different vegetation states and 45 133 non-transitions (Table SS1).

## Environmental data

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 modelling software (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 obtained from "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 random variable determined by a stochastic process conditional on the state at the 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 neighbourhood. We used simulated annealing (R package GenSA; Yang Xiang et al., 2013) to attain by maximum likelihood, the estimate of the parameters pertaining each transition probability illustrated at figure 1. Each of them is a function of mean annual temperature ($TP$, °C) and mean annual precipitation ($PP$, mm). Each of the per patch transition probabilities (i.e., $\alpha_T, \alpha_B, \beta_T, \beta_B, \theta_T, \theta_B$, and $epsilon$; Fig. **??**) was modelled as second order logistic function of climatic conditions. Thus, any parameter $\phi$ is modelled as:

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

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 are not available in the forest inventory databases and the incompatibility of stand classifications in the 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 (R package randomForest; 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, the mean diurnal range, slope aspect, soil pH and the $(X, Y)$ coordinates as explanatory variables. All of these variables were retained as the best descriptors of the state distributions. 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.

**Analysis**

Prior to analyzing the STM, we evaluated the strength of the relationship between transitions among states and climate conditions using a multinomial regression (R package nnet; Venables and Ripley, 2002). This model does not consider dispersal limitation (i.e., the prevalence terms in the full model) nor patch-scale ecological processes (i.e., the *alpha*, $\beta$, *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 average annual temperature and total precipitation, and then removed each of the terms one after the other to understand their contribution to the likelihood (using the $\delta AIC$). 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. This comparison was performed using 14 080 plots that were measured only once and therefore could not be used for calibration. For each of these plots, we computed the expected state by selecting the state with the highest occurrence probability from the STM. For the B, M, and T states, we then evaluated the classification skill of the model by computing correct (i.e., predicted and observed presence or absence or each state) and incorrect (i.e., prediction of presence or absence and observation of the opposite) classification and calculating the True Skill Statistic (TSS) (Allouche et al., 2006), which provides an estimate ranging from 0–1 where 0 indicates no classification skill and 1 indicates perfect classification. Because disturbances are largely driven by stochastic events and were relatively rare, we expected that the model would have high skill in predicting the absence of

disturbance (most plots are undisturbed), but little skill in predicting the precise spatial location of disturbances, rendering any TSS estimate uninterpretable. Thus, we did not compute TSS for the R state.

To understand transient states under climate change and analyze the migration rates, we ran 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 in equilibrium with initial climatic conditions. We used a five-year time step and ran the simulations from 2000 to 2095. At each time step, we recomputed the expected transition rates for each cell using the average climate of the preceding 15 years.

We subset from the grid into a band of 9.6km in longitude and 520 km in latitude in order to compute the migration rate of the temperate forest. The band started north of the city of Montreal in the maple bioclimatic domain and extended up to the spruce-moss domain, in the boreal forest near Chibougameau. The range limits 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. We then computed range expansion each time step and estimated the migration rate for any time interval as the annual movement northward (in km) along this south-north gradient.

**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 1). Mean average temperature had the strongest contribution to the likelihood of all transitions except for the transitions to M where the total annual precipitation was predominant ($\Delta AIC_{pp}$ = 28.60 ,Table 1). The transitions to T (competitive exclusion and colonization) and R (disturbance) were the most strongly correlated with climate ($R^2$ = 0.15 and $R^2$ = 0.22 respectively). The transitions from state R to M and T both increased with temperature (Figure 2). The disturbance probability remained low (¡0.005) through the entire climatic space (Fig. 2).

Similarly, we found strong relationships between the STM transition parameters and climate (Table 1). In particular, all transitions involving the invasion of temperate trees (i.e., R to M or T, B to M, and M to T) were all strongly positively related to temperature (Fig. 2). As expected, the competitive exclusion pathway for boreal trees (i.e., transitions from T to M and M to B) were strongly negatively related to temperature, however the successional pathway to boreal forest (R to B) showed little response to temperature (Fig. S3). The equilibrium solution of the dynamic model under the 2015 climatic conditions agreed well with the current distribution of temperate, mixed and boreal forest (Fig.S2), will relatively modest TSS values for the states B, T (0.46 and 0.43, respectively), and a lower value, 0.18, for M (Table 2). There was nonetheless a high correspondence between the match of presences and absences, with 0.70-0.98 of observations correctly predicted.

Our model predicts that temperate forests (i.e., pure stands of temperate species) cover an area of 339 359 km$^2$ in 2015. This is expected to expand by 37.8% 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 59% of their area (Fig.3). 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 (Fig.3). 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 ran four different modelling scenarios with climate change to investigate the main drivers of migration dynamics. We found for the full model a northward migration of 14±2.1km by 2095. By comparison, in the absence of dispersal limitation, demographic constraints, and biotic interactions, we found a migration of 238.79±34.24 km. In between, the simulation with infinite dispersal distance but with demographic constraints also has a very low north-ward migration at 14±2.0km, similar to the simulations with dispersal limitation. The main factor slowing down migration thus appears to be demography. This constraint is so se-vere that the vegetation does not even reach equilibrium after 10 000 years (Figure 4). The mismatch between the suitable climatic conditions for temperate species and their realized distribution consequently increases constantly through time.

## 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 (Renwick and Rocca, 2014; Vanderwel and Purves, 2014). We analyzed the northward shift in the distribution of temperate forests, a major biome covering the northeastern United States and Canada, into the domain presently dominated by boreal forests. The ecosystem properties of temperate forests contrast strikingly with those of boreal forests. Temperate forests are characterized by a disturbance regime generating small canopy gaps and with rapid processing of rich deciduous litter, compared to larger-scale dis-turbances (e.g. fire) and slow decomposition of an acidic and nutrient poor litter in boreal forests. We investigated the importance of key ecological processes—dispersal limitations,

biotic interactions and demography—for the migration dynamics of temperate forests. 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.

The transitions among forest community types represented in our model are driven by dynamic ecological processes such as disturbance, succession, competitive exclusion, and colonization. We expected that local climate is one factor driving the rate at which these transitions occur. Landhüsser et al. (2010) found that the rate of colonization by deciduous trees (in this case, *Populus tremuloides*) following disturbance is influenced by climate. Moreover, climate exerts a strong influence on the state of mature forests and their successional pathways (Anderson-Teixeira et al., 2013). Experiments at boreal and temperate latitudes show that rising temperatures affect all major chemical and biological processes and mediate forest successional dynamics (Saxe et al., 2002). 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 individual-scale processes. For example, Clark et al. (2011) found that some *Fagus* and *Pinus* are susceptible to moisture variation over the growing season, with lower moisture reducing germination success. Extreme drought can also increase mortality in several temperate deciduous tree species (Anderson-Teixeira et al., 2013). Spring and summer temperature has also been identified as

critical for fecundity rates (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 (Solarik et al., 2016). Sugar maple flower development is also affected by the timing of climatic events in the spring Chuine and Beaubien (2001) and as a consequence a mechanistic model of its distribution surprisingly fits well its distribution (Morin et al., 2008). 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 black spruce seeds which require a minimum number of degree-days to mature (Meunier et al., 2007). However, not all life stages are dependent on climatic conditions; some are more sensitive to competitive interactions than climate variation (Zhang et al., 2015). Future research will therefore be required to determine more precisely the processes underlying our observation that transitions among forest types are dependent on climate.

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 (Holt, 2009). It appears however that trees are not necessarily distributed where they grow best (McGill, 2012). Recenlty, Thuiller et al. (2014) 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 results 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 Holt et al. (2005), range limits could instead be driven by a balance between colonization and extinction processes. In this situation, in order for a species to persist it must

not only be able to establish a local population, as postulated by the traditional definition of the niche (Holt, 2009), but also maintain a colonization rate exceeding the local extinction rate. Our results demonstrate that such a regional approach to range limits of trees may be more relevant than an approach based on local dynamics. Incidentally, our analysis in this study is based on the same data as Thuiller et al. (2014), but we manage to better explain species distribution. Our results would explain the seemingly paradoxical observation that species such as sugar maple can establish and develop well outside of their current ranges (e.g., in the deep boreal forest; Kellman, 2004; Brown and Vellend, 2014). A regional approach to forest ecosystems also corresponds better to the long-held non-equilibrium view of forest ecosystems, where landscapes are composed of a mosaic of patches at different successional stages. Application of our approach broadly in other forested ecosystems may shed light on the generality of our results and contribute to the further development of theory for range limits.

We simulated the migration dynamics happening according to 23 climate change scenarios drawn from the most pessimistic scenario (RCP 8.5) from the CMIP5 project (Taylor et al., 2012). We found that despite an average annual temperate increase of 4 to 7°C at the ecotone (Ouranos, 2015), the temperate forest will barely move northward from its present distribution at the end of this century. Our model predicts rapid conversion of mixed forests to pure temperate stands, but the limit of the boreal-temperate transition zone (and thus the southern extent of boreal forests) ultimately constrains the expansion of the temperate forest. The inability of temperate species to migrate will thus 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 (Beckage et al., 2008; Talluto et al., 2016), in particular after these stands have been subject to forest management (Dupuis et al., 2011; Boucher et al., 2006). Fortunately, forest management could help reduce this increasing disquilibrium situation. If forest management simulates natural disturbances,

the analogous change under our model would be an increase in local extinction rate, which could speed one of the pathways from boreal to mixed to temperate forests. Further, because clearcutting and other methods of harvesting increase light availability, it tends to increase successionnal rate (Abrams and Scott, 1989). Diffusion theory also predicts that increasing the intrinsic population growth rate could speed up quite significantly the migration rate. Finally, assisted migration (Pedlar et al., 2012) as a part of forest management 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 is what will happen with maladapted boreal forests, that will stay in place for a certain time before temperate forest eventually migrate. There are currently no large and naturally occurring tracts of boreal forest stands found under temperate climatic conditions and on mesic soils. Boreal plantations (e.g., black spruce and jack pine) in warm climatic conditions indicate that the individual trees could stand warmer conditions and perform well. There is however considerable uncertainty as to whether such trees, in the absence of management, can successfully regenerate and tolerate natural disturbance. 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 temperate trees will not be able to migrate northward in response to climate change over short to medium time scales.

We found clear support for the hypothesis that climate drives transitions among forest types at the boreal-temperate ecotone (Figs. 2, S3). However, despite the strong link between temperature and colonization and succession, our model predicted very little replacement of boreal forest with mixed and temperate forest by 2095, along with very slow northward

migration of the temperate-boreal transition (14±2.0 km by 2095 with a rate of 740±0.11 m.yr$^{-1}$) (Fig. 3). This finding is consistent with Iverson et al. (2004) which predicted range shift of 10-20 km for several species confined to the eastern half of the United States at the end of this century. Additionally, analysis of fossil pollen records estimates migration rates of 100–1000 m/year during the quaternery period (Davis, 1981; MacDonald and Ritchie, 1986; McLachlan et al., 2005). The most probable reason for the discrepancy between climate-dependence of transition rates and the failure to migrate in response to climate change is demographic and dispersal lags. Despite the increasing tension between the optimal and realized climates over the 21st century, our simulations demonstrated that slow demographic and dispersal rates prevent any substantial movement in temperate forests, with much faster migration rates when these constraints were removed (Fig. 4). These limitations could be mitigated somewhat if local climatic conditions modify life history strategies (e.g., younger maturation age and higher fecundity) (Snell et al., 2014). However, over the relatively short time horizon encompassed by this study, such effects are unlikely to completely mitigate the effects of slow demographic rates. Thus, both temperate and boreal species within the transition zone are likely to experience increasing differences between optimal and realized climate in the coming century.

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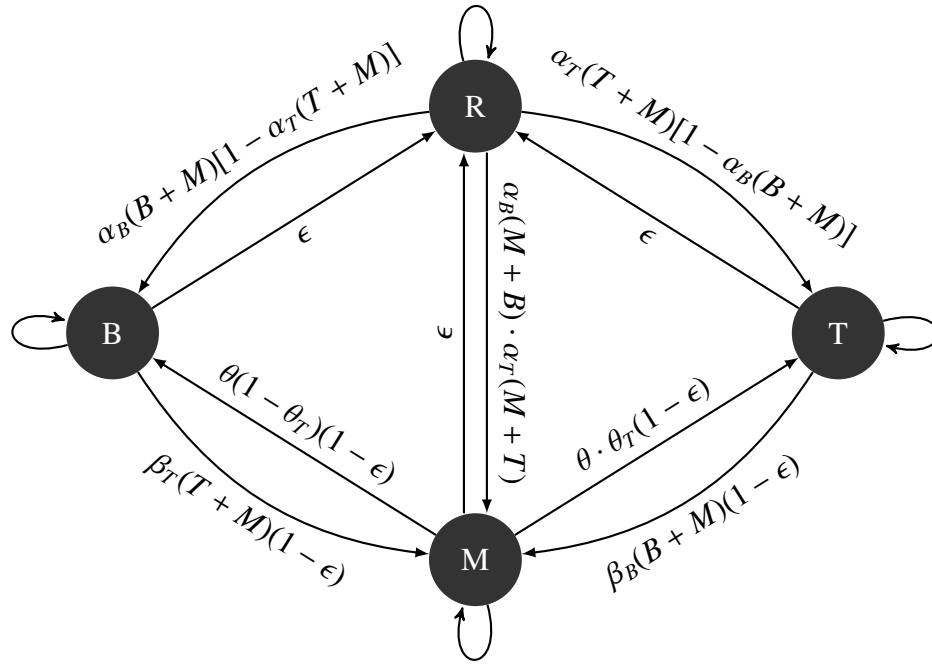
**FIGURES**

Figure 1: Schematic representation of the model with states (B)oreal, (M)ixed, (T)emperate and (R)egeneration. Transitions from B, M and T to R result from disturbances. Succession results in a transition from R to B, M or T, and colonization results in transitions from either B or T to M. Competitive exclusion causes with transitions from M to either B or T. All of the transitions involving the arrival of a new species are dependent on dispersal and thus on the occupancy in the neighbourhood ($T + M$ or $B + M$).
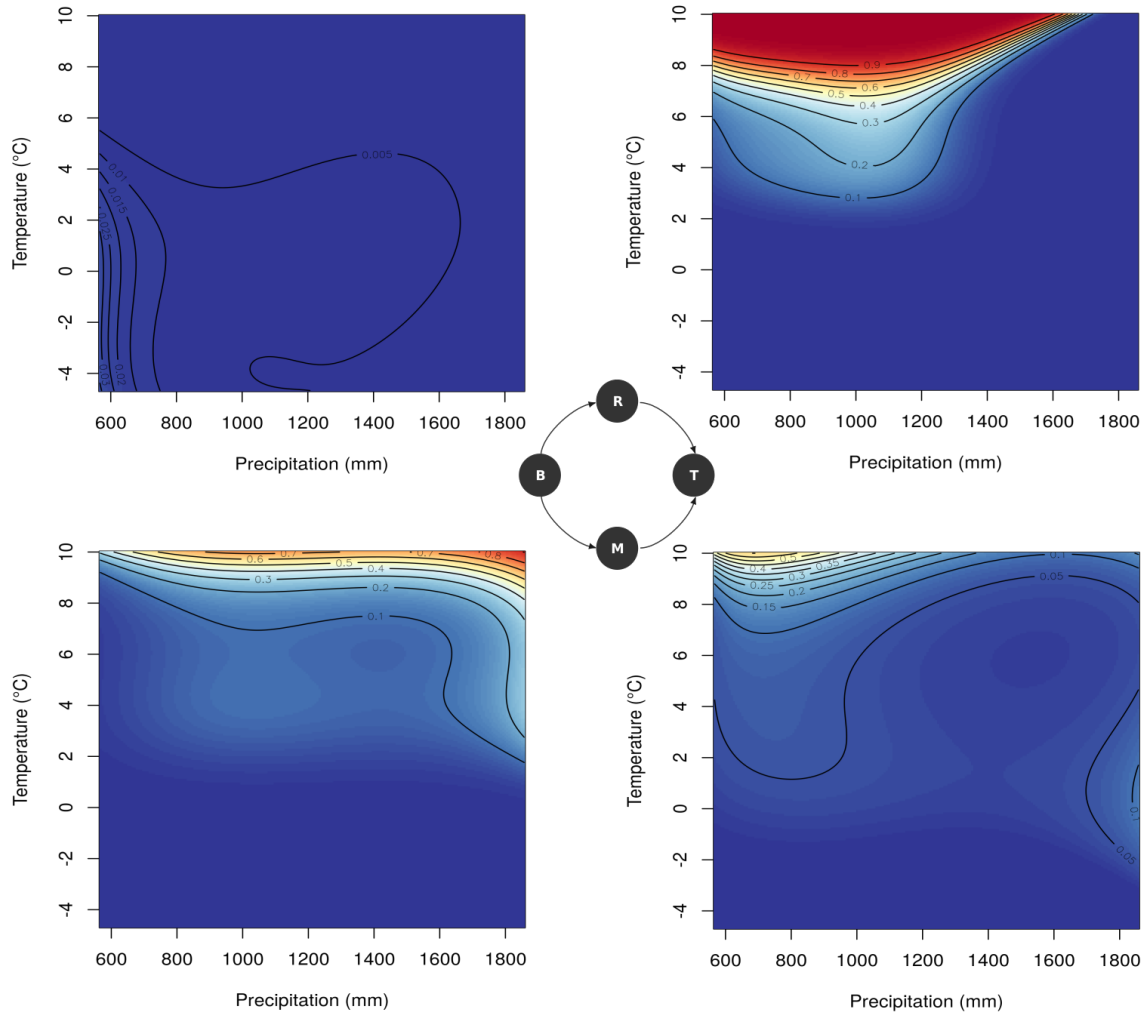
Figure 2: Transition probabilities of all pathways from (B)oreal to (T)emperate. Each panel corresponds to one pathway (also represented by arrows from Fig.1). Transition probabilities were estimated by multinomial regression accounting for the temperature (°C) on the y-axis and the precipitation (mm) on the x-axis.

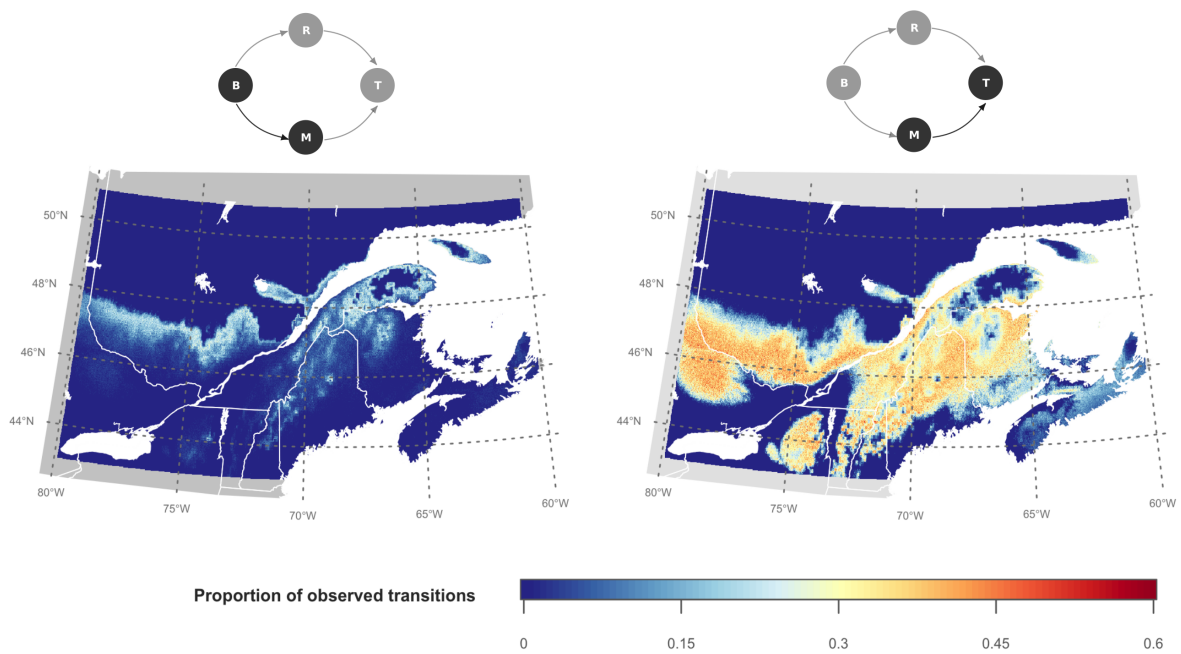Figure 3: Frequency of transitions from (B)oreal to (M)ixed (left panel) and (M)ixed to (T)emperate forest (right panel) between initial (2015) and final (2095) time steps. Transitions frequencies were obtained by dividing the number of transition observed by the number of simulations. Simulations used are only based on the first model scenario accounting for dispersal limitation, biotic and demographic constraints.
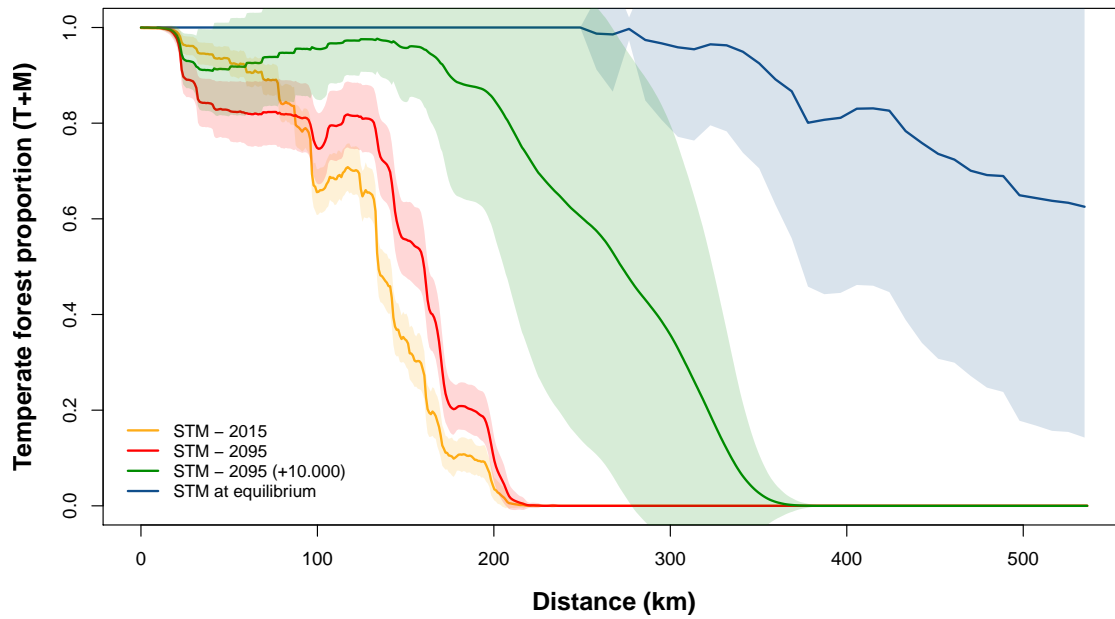
Figure 4: Mean proportion of temperate forests (with 95% quantiles) along a 520-km latitudinal band (in km, relative to the southernmost location of the band) showing the influence of dispersal and demographic constraints as well as long-term dynamics. We show the results of four modelling scenarios. The predictions of the STM for current climate (STM – 2015; yellow) is the best estimate of the current state of the system including dispersal and demographic constraints. When this constrained model is projected into the future with climate change (STM – 2095; red), we find very little increase in the proportion of temperate forest. When the constrained model is run for 10,000 years at 2095 climate (STM – 2095 + 10000; green), we see much greater movement, demonstrating that dispersal and demographic constraints introduce significant lags. Finally, the model solved at equilibrium (STM at equilibrium; blue) reveals that temperate forest will eventually expand to the entire gradient, but that this equilibrium is considerably farther than what was reached even with 10,000 years of equilibration.

**TABLES**

Table 1: Summary of the results of a multinomial regression estimating the relative contributions of mean annual temperature (tp) and total annual precipitation (pp) to transitions to each of the four states ($X_{t+1}$), with samples sizes $n$. We show the influence of each component of a third-order polynomial as the change in AIC ($\Delta$AIC) that results from removing the parameter from the model, where a larger value indicates a more important parameter and where $\Delta$AIC > 10 indicates strong support for a parameter (Burnham and Anderson, 2002). To account for uneven observation intervals, we also included the time interval as a parameter in the model (and show its contribution as $\Delta$AIC$_{time}$). We also show the to the Mc-Fadden pseudo-$R^2$ as an indication of the goodness-of-fit of the full model.

| $X_{t+1}$ | $n$ | $\Delta$AIC$_{tp}$ | $\Delta$AIC$_{tp^2}$ | $\Delta$AIC$_{tp^3}$ | $\Delta$AIC$_{pp}$ | $\Delta$AIC$_{pp^2}$ | $\Delta$AIC$_{pp^3}$ | $\Delta$AIC$_{tp:pp}$ | $\Delta$AIC$_{time}$ | $AIC_{tot}$ | $R^2$ |
|---|---|---|---|---|---|---|---|---|---|---|---|
| T | 16173 | 88.32 | 0.71 | 3.85 | -2.10 | 1.10 | -2.82 | 3.08 | 98.06 | 6757.46 | 0.15 |
| M | 16175 | 1.09 | 17.96 | 7.10 | 28.60 | -0.70 | 8.48 | 8.64 | 301.24 | 12034.80 | 0.04 |
| R | 503 | 15.43 | 48.21 | 12.69 | -5.91 | 7.54 | -0.74 | 0.06 | 18.34 | 1546.64 | 0.22 |
| B | 16144 | 26.89 | 159.57 | 42.68 | -2.94 | 17.69 | 1.31 | -3.47 | 305.03 | 9013.28 | 0.11 |

Table 2: Classification skill (TSS) for each state, where correct presences and absences indicate a predicted presence and absence and an observation that matched the predictions, and false presence/absence is the opposite.

|  | B | T | M | R | Total |
|---|---|---|---|---|---|
| a. Correct presences | 1380 | 6179 | 980 | 0 | 8539 |
| b. False presences | 1940 | 1141 | 2175 | 285 | 5541 |
| c. False absences | 830 | 3062 | 1648 | 0 | 5540 |
| d. Correct absences | 9930 | 3698 | 9277 | 13795 | 36700 |
| N | 3320 | 7320 | 3155 | 285 | 14080 |
| **TSS** | 0.46 | 0.43 | 0.18 |  | 0.48 |
| Proportion correct (a+d/N) | 0.80 | 0.70 | 0.73 | 0.98 | 0.80 |

**SUPPLEMENTARY MATERIALS**

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

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

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

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

Figure S1: Differential equations representing the boreal-temperate ecotone dynamic through the time. The rate of change in the proportion of patches occupied by each of the four forest states (T, B, R, and M for temperate, boreal, regenerating, and mixed forest, respectively) is a function of the local proportion of each of those states (again, T, B, R, and M) as well as the climate-specific transition parameters for each transition (Greek symbols; see main text and Fig. 1 for an explanation and diagrammatic representation).

Table S1: Number of transitions observed between all paired observations.

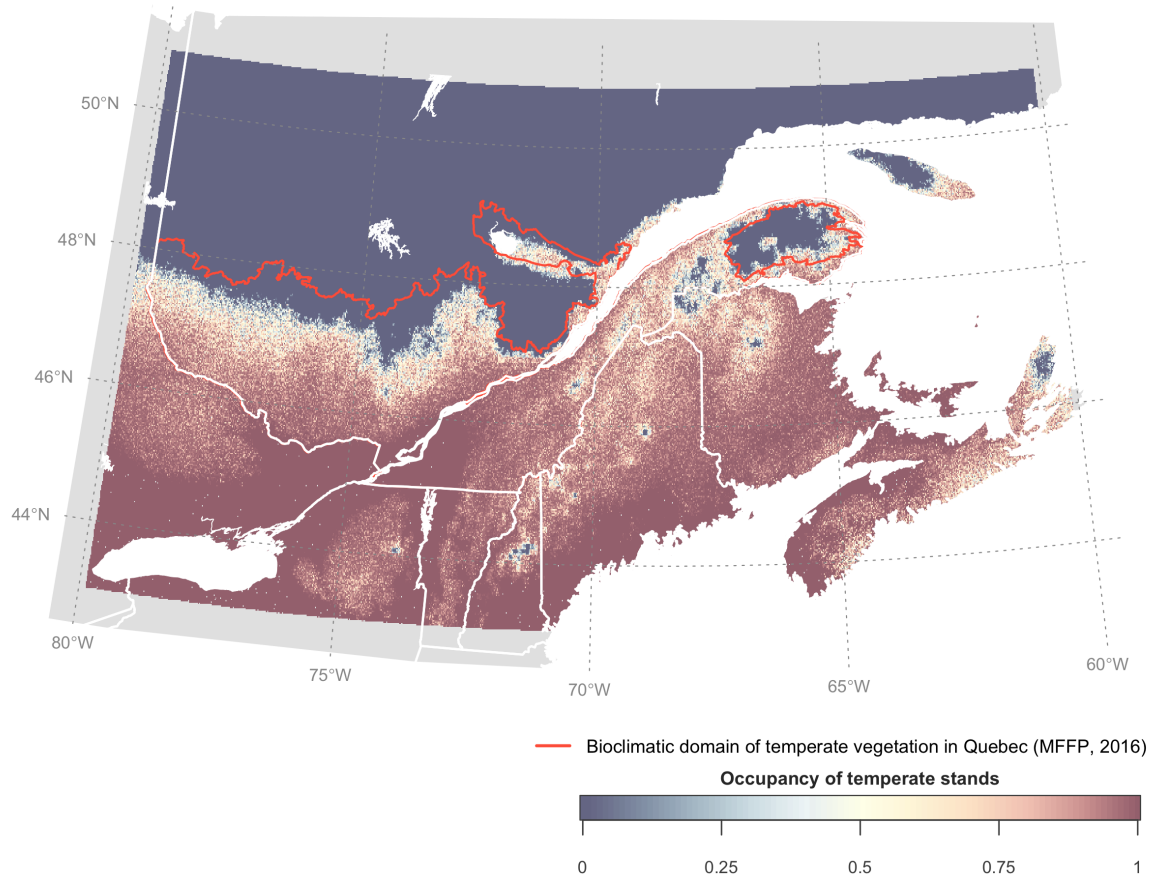| From \ To | B | M | R | T |
|---|---|---|---|---|
| **B** | 15357 | 794 | 203 | 0 |
| **M** | 302 | 14433 | 51 | 959 |
| **R** | 485 | 57 | 209 | 80 |
| **T** | 0 | 891 | 40 | 15134 |

Figure S2: The STM predictions of the present extent of temperate forest (colour scale) is largely concordant with expert-drawn maps (provided by the forest ministry of Quebec; MFFP 2016) delineating the extent of the temperate forest bioclimatic domain (red line), although there is some disagreement at the transition. Projections were made using the STM with demographic, biotic, and dispersal constraints and show the proportion of simulations where temperate or mixed forest was present.
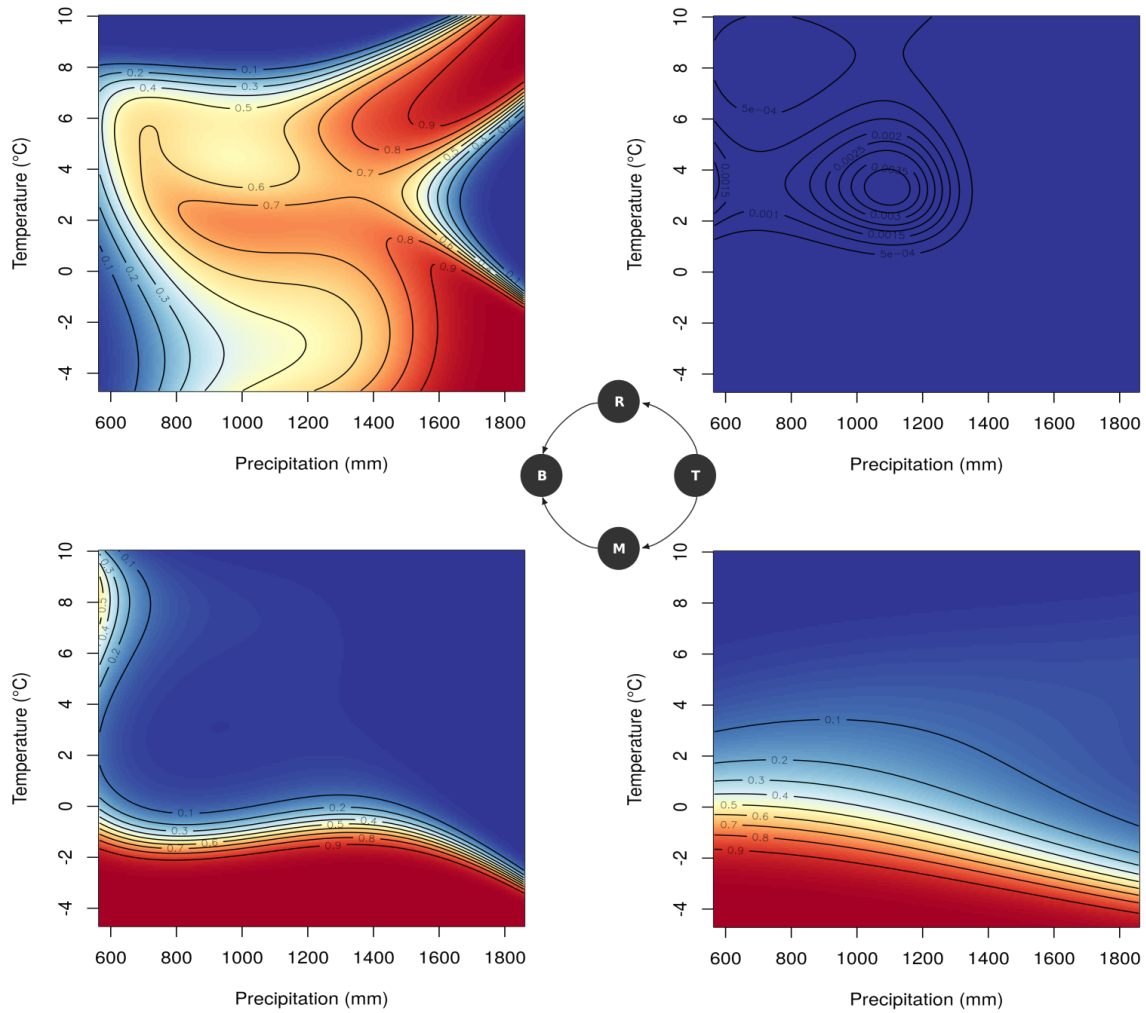
Figure S3: Transition probabilities of all pathways from (T)emperate to (B)oreal. Each panel corresponds to one pathway which can be attached to one arrows of the centered STM diagram (presented in Fig.1). Transition probabilities were estimated by multinomial regression accounting for the temperature (°C) on the y-axis and the precipitation (mm) on the x-axis.

# 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.]

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