

Université de Montréal

**Dynamique spatio-temporelle des forêts dans l'écotone
boréal-tempéré en réponse aux changements globaux**

par

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Résumé

Le principal objectif de ma thèse était de comprendre et de quantifier l'effet combiné du changement climatique récent et des perturbations sur la dynamique des communautés forestières de l'écotone boréal-tempéré au cours des dernières décennies. Pour ce faire, j'ai analysé les changements au niveau de la composition en espèces, de la dynamique de transition et du recrutement dans les forêts du Québec de 1970 à 2018.

Dans le premier chapitre, j'ai montré que les perturbations naturelles et anthropiques étaient les principaux moteurs des changements de composition, i.e. la diversité β temporelle. Malgré la prévalence des perturbations, l'analyse des traits écologiques de la communauté a révélé une thermophilisation des forêts à travers le Québec, i.e. une augmentation des espèces de climat chaud au détriment des espèces de climat froid. Ce phénomène de thermophilisation a même été amplifié par les perturbations modérées, soulevant une nouvelle question : si les perturbations peuvent favoriser une telle réorganisation des communautés, pourraient-elles catalyser un basculement des forêts vers des états alternatifs ?

Le second chapitre a apporté des réponses à cette question en analysant la dynamique de transition des forêts du Québec avec un modèle à quatre états, soit boréal, mixte, tempéré et pionnier. La dynamique de transition était principalement influencée par les perturbations et secondairement par le climat et les conditions édaphiques. Les perturbations majeures ont entraîné surtout des transitions vers l'état pionnier, tandis que les perturbations modérées ont favorisé les transitions de mixte à tempéré. À long terme, les perturbations modérées pourraient catalyser un déplacement plus rapide de l'écotone boréal-tempéré vers le nord sous l'effet du changement climatique. Toutefois, le recrutement des espèces tempérées a joué un rôle négligeable dans cette dynamique comparativement aux processus de mortalité et de croissance.

Les deux premiers chapitres s'appuient sur des analyses de l'évolution des communautés d'arbres matures. Cependant, pour comprendre la dynamique forestière, une analyse de la dynamique de régénération est nécessaire, étude que j'ai menée au troisième chapitre. J'ai d'abord mis en lumière des déplacements de plusieurs kilomètres vers le nord pour les gaulis de *Acer rubrum*, *Acer saccharum* et *Betula alleghaniensis* dans les forêts non perturbées. Toutefois, sous l'influence des perturbations modérées, seuls les *Acer spp.* ont migré ; aucune

espèce ne s'est déplacée sous l'influence des perturbations majeures. En revanche, les gaulis de *Fagus grandifolia* n'ont pas du tout migré. Bien que les coupes partielles aient favorisé une augmentation du recrutement des quatre espèces, elles n'ont pas entraîné de migration plus au nord, possiblement parce que le recrutement était freiné par une faible capacité de dispersion, une forte compétition par les espèces boréales et des conditions édaphiques défavorables.

Dans l'ensemble, mes résultats ont souligné que les communautés forestières de l'écotone boréal-tempéré répondent déjà au changement climatique récent et que les perturbations accélèrent cette réponse. En effet, le réchauffement érode la résilience des forêts mixtes tandis que les perturbations éliminent les espèces boréales en place, ce qui accélère le processus de succession et facilite l'établissement des espèces tempérées.

Mots-clés

Changement climatique, Diversité beta, Dynamique de transition, Écologie des communautés, Écotone boréal-tempéré, Équilibre et dynamique transitoire, Forêts, Inventaire forestier du Québec, Migration des arbres, Perturbations naturelles et coupes forestières, Recrutement des gaulis, Thermophilisation.

Abstract

The main objective of my thesis was to understand and quantify the combined effect of recent climate change and disturbances on forest community dynamics in the boreal-temperate ecotone over the past decades. To do so, I analysed the evolution of forest composition, transition dynamics and recruitment dynamics in Quebec from 1970 to 2018.

In the first chapter, I showed that natural and anthropogenic disturbances were the main drivers of forest compositional change, i.e. temporal β diversity. Despite the prevalence of disturbances, analysis of community ecological traits revealed a thermophilization of forests across Québec, i.e. an increase of warm-adapted species at the expense of cold-adapted species. This thermophilization was further amplified by moderate disturbances, leading to a new question: if disturbances can favour such a community reorganization, could they catalyse a permanent shift to alternative states?

The second chapter provided answers to this question with an analysis of forest transition dynamics in Québec based on a four-state model, i.e. boreal, mixed, temperate and pioneer. Transition dynamics was primarily influenced by disturbances and secondarily by climate and edaphic conditions. Major disturbances mainly triggered transitions to the pioneer state, while moderate disturbances promoted transitions from mixed to temperate states. In the long run, moderate disturbances may catalyse a faster northward shift of the temperate-boreal ecotone under climate change. However, contrary to my expectations, temperate species recruitment played a negligible role in this dynamic compared to mortality and growth processes.

The first two chapters were focussing on the evolution of mature tree communities. However, to understand forest dynamics, a detailed analysis of regeneration dynamics is necessary. Such a study was conducted in the third chapter where I highlighted northward shifts of several kilometres for the saplings of *Acer rubrum*, *Acer saccharum* and *Betula alleghaniensis* in undisturbed forests. However, under the influence of moderate disturbances, only *Acer spp.* had migrated and there were no shifts under the influence of major disturbances. In contrast, I found no evidence of migration for the saplings of *Fagus grandifolia*. Although partial cutting increased recruitment success of all four species, it did not result in larger

northward range shifts, presumably because recruitment was constrained by short-distance dispersal, strong competition by boreal species, and unfavourable edaphic conditions.

Overall, my results highlighted that forest communities in the temperate-boreal ecotone are already changing in response to recent climate warming and that disturbances are accelerating this response. While climate warming erodes the resilience of mixed forests, disturbances remove resident boreal species, thereby accelerating the successional process and facilitating the establishment of temperate species.

Keywords

Beta diversity, Boreal-temperate ecotone, Climate change, Community ecology, Equilibrium and transient dynamics, Forests, Natural disturbances and logging, Québec Forest Inventory, Thermophilization, Transition dynamics, Tree migration, Tree sapling recruitment.

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Liste des sigles et des abréviations

AIC	Critère d'information d'Akaike, de l'anglais <i>Akaikes Information Criteria</i>
DBH	Diamètre hauteur poitrine (1.3m), de l'anglais <i>Diameter at breast height</i>
CTI	Indice de température de la communauté, de l'anglais <i>Community Temperature Index</i>
GES	Gaz à effet de serre
GIEC	Groupe d'experts intergouvernemental sur l'évolution du climat
PCA	Analyse en composantes principales, de l'anglais <i>Principal component Analysis</i>
sd	Écart standard, de l'anglais <i>standard deviation</i>
SDM	Modèle de distribution des espèces, de l'anglais <i>Species Distribution Model</i>

STI	Indice de température des espèces, de l'anglais <i>Species Temperature Index</i>
TBI	Indice de diversité beta temporelle, de l'anglais <i>Temporal Beta diversity Index</i>

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Avant-propos

Cette thèse est rédigée sous forme d'articles scientifiques, qui forment le cœur du document, tandis que l'introduction et la conclusion générales viennent compléter l'histoire. Deux des articles sont déjà publiés ou acceptés à des revues avec comité de lecture, et un article reste en préparation pour soumission.

1. Brice, M.H., Cazelles, K., Legendre, P., & Fortin, M. (2019). Disturbances amplify tree community responses to climate change in the temperate–boreal ecotone. *Global Ecology and Biogeography*, 28(11), 1668–1681. <https://doi.org/10.1111/geb.12971>
2. Brice, M.H., Vissault, S., Vieira, W., Gravel, D., Legendre, P., & Fortin, M. Moderate disturbances accelerate forest transition dynamics under climate change in the temperate-boreal ecotone of eastern North America. *Global Change Biology*. <https://doi.org/10.1111/gcb.15143>
3. Brice, M.H., Chalumeau, A., Grondin, P., Fortin, M.J & Legendre, P. Northern range shifts of temperate tree saplings in Québec : the role of climate, stand composition, soils and disturbances on recruitment dynamics. (En préparation)

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Accessibilité et reproductibilité de mes travaux

L'ensemble des données et des scripts utilisés dans le cadre de ma thèse sont disponibles librement. Ainsi, les codes nécessaires à la mise en forme des bases de données climatiques et des données d'inventaires forestiers sont accessibles à travers le dépôt : https://github.com/mhBrice/Quebec_data. Ce dépôt permet de nettoyer et mettre en forme les données utilisées dans mes trois chapitres de thèse. Ensuite, chaque chapitre a un dépôt indépendant qui contient toutes les données nettoyées ainsi que les scripts R pour reproduire les analyses et les figures. Les scripts pour reproduire les analyses du chapitre 1 sont disponibles en ligne à l'adresse : <https://github.com/mhBrice/thermophilization>. Les scripts du chapitre 2 peuvent être consultées en ligne à l'adresse : <https://github.com/mhBrice/transition>. Enfin, le dépôt du chapitre 3 se trouve à l'adresse : <https://github.com/mhBrice/recrutement>.

Introduction

0.1. L'écologie à l'ère de l'Anthropocène

L'espèce humaine est aujourd'hui une force prédominante gouvernant les processus biogéochimiques et la distribution de biodiversité mondiale, marquant, selon plusieurs chercheurs, le début d'une nouvelle ère géologique, l'Anthropocène (Crutzen, 2002). Depuis plus d'un siècle, les activités humaines ont largement perturbé l'équilibre dynamique des cycles naturels. Les humains ont modifié plus de 50% des surfaces terrestres, consomment chaque année environ 40% de la productivité primaire de la planète et émettent tellement de gaz à effet de serre qu'ils ont changé le climat mondial (McGill *et al.*, 2015). Les changements d'utilisation du territoire et la surexploitation des ressources causent la dégradation et la perte des habitats et comptent ainsi parmi les plus grandes menaces actuelles pour la biodiversité (IPBES, 2019). Au cours du siècle dernier, les températures ont augmenté d'environ 1°C et, selon les projections, le 21^e siècle assistera à des bouleversements climatiques sans précédent (IPCC, 2014). Alors que la destruction d'habitats peut avoir des conséquences rapides et directes sur la biodiversité, le réchauffement climatique est un processus persistant et comparativement plus graduel dont les effets continueront à s'intensifier au cours des prochaines décennies (IPBES, 2019). Les effets synergiques entre les nombreuses perturbations anthropiques risquent d'aggraver leurs effets individuels sur la biodiversité et mettent en péril la persistance à long terme des espèces. Dans l'ouest de l'Amérique du Nord, par exemple, le changement climatique a favorisé l'expansion des populations d'insectes ravageurs et a affaibli les arbres, tandis que l'exploitation forestière a homogénéisé le paysage forestier. Ces deux phénomènes ont ainsi engendré des épidémies d'insectes sans précédent tuant des arbres par millions (Raffa *et al.*, 2008). Un nombre croissant de preuves révèle une perte de biodiversité et un déclin des populations exceptionnellement rapide au cours des derniers siècles, dont les conséquences se répercuteront sur les fonctions et les services des écosystèmes (Ceballos *et al.*, 2015; IPBES, 2019). Par exemple, le déclin rapide des pollinisateurs menacent nos systèmes alimentaires puisque plus de 75% des cultures, notamment les fruits, les légumes et le café, en dépendent directement (IPBES, 2019). L'ampleur, la vitesse et l'intensité de ces menaces mondiales soulignent la nécessité de développer de nouveaux outils d'analyse

pour comprendre, détecter et quantifier les changements de la biodiversité en cours et évaluer les causes de ces changements de façon à adapter les méthodes de gestions et atténuer les conséquences préjudiciables à venir.

0.2. Changement climatique

Déjà en 1979, un rapport scientifique produit aux États-Unis informe d'une menace climatique grandissante causée par l'émission massive de dioxyde de carbone (CO_2) par l'activité humaine (National Research Council, 1979) :

« We now have incontrovertible evidence that the atmosphere is indeed changing and that we ourselves contribute to that change. Atmospheric concentrations of carbon dioxide are steadily increasing, and these changes are linked with man's use of fossil fuels and exploitation of the land. [The consensus of number of investigations] has been that increasing carbon dioxide will lead to a warmer earth with different distribution of climatic regimes. »

Ainsi, près d'une décennie avant la création du groupe d'experts intergouvernemental sur l'évolution du climat (GIEC), les scientifiques nous avertissaient très clairement du danger potentiel vers lequel nous nous dirigions. La crise climatique aurait-elle pu être évitée ou du moins atténuée ? En réalité, la vitesse, l'ampleur et les conséquences du réchauffement climatique étaient encore peu connues en 1979. À cette époque, et pendant plusieurs années, même les scientifiques considéraient le changement climatique comme une perspective lointaine. Nous savons maintenant que cette vision était erronée. Depuis, le GIEC a produit cinq rapports d'évaluation sur l'état des connaissances relatives au changement climatique, ainsi qu'une dizaine de rapports spéciaux sur des thèmes précis (entre 1990 et 2019). Au fil de ces rapports, à mesure que les connaissances s'accumulent et que les modèles climatiques deviennent plus robustes, on prend conscience de la gravité de la crise climatique et le ton devient de plus en plus alarmant.

Selon le 5e rapport du GIEC, le réchauffement climatique mesuré sur l'ensemble de la planète durant les dernières décennies est maintenant sans équivoque, et la responsabilité de l'humain par l'émission de gaz à effet de serre (GES) est clairement établie (IPCC, 2014). Les activités humaines ont déjà contribué à une hausse entre 0.8 et 1.2 °C au-dessus des températures préindustrielles (IPCC, 2018). Des projections récentes des changements climatiques indiquent que les températures moyennes mondiales pourraient augmenter de 2.6 à 4.8°C d'ici la fin du XXI^e siècle dans le nord-est de l'Amérique du Nord, s'il n'y a pas de progrès sur le contrôle des émissions de GES anthropiques (IPCC, 2014). Le climat étant un déterminant central de la distribution des espèces (Pearson et Dawson, 2003), de telles augmentations de température auront un impact majeur sur la biodiversité et le fonctionnement de tous les écosystèmes (Bellard *et al.*, 2012; Gauthier *et al.*, 2015a).

Dans les écosystèmes forestiers, les variations de température et de régimes de précipitation influencent de nombreux processus biologiques, autant des processus saisonniers, comme la floraison, le débourrement et la fructification, que des processus à long terme comme la croissance, la survie et la régénération des espèces (Saxe *et al.*, 2001). Pour survivre, les espèces devront soit s'adapter localement aux nouvelles conditions environnementales (par exemple, en modifiant leur phénologie), soit se déplacer vers de nouveaux habitats (Aitken *et al.*, 2008). Certaines projections suggèrent que de nombreuses espèces d'arbres se déplaceront vers le nord sur des centaines de kilomètres (McKenney *et al.*, 2007) ou plus haut en altitude d'une centaine de mètres (Jump *et al.*, 2009) au cours des prochaines décennies, modifiant la composition, la structure et la diversité des forêts (Price *et al.*, 2013; Reich *et al.*, 2015). Or, de tels changements peuvent avoir des répercussions environnementales considérables sur les fonctions et les services rendus par les écosystèmes forestiers, tels que le stockage du carbone, le cycle des nutriments, la purification de l'air et de l'eau et le maintien d'habitats pour la faune et la flore (Mitchell *et al.*, 2013; Mori *et al.*, 2017). Ces changements soulèvent aussi des enjeux socio-économiques majeurs. Par exemple, comment adapter les stratégies de gestion forestière pour assurer un approvisionnement durable en bois ? Ou encore, quel est l'avenir de certaines espèces économiquement et culturellement importantes, comme l'érable à sucre au Québec ? Comprendre et quantifier les conséquences du changement climatique sur les écosystèmes forestiers représente donc l'un des grands défis actuels pour la communauté scientifique (Garcia *et al.*, 2014; Pereira *et al.*, 2010).

0.3. Distributions géographiques des espèces et niche écologique

La biogéographie, l'étude des facteurs qui influencent la distribution des espèces, a une longue histoire en écologie (von Humboldt, 1805; MacArthur, 1972; Wallace, 1881). Étant donné la vitesse et l'ampleur des changements globaux et de leurs impacts sur la biodiversité, cette question fondamentale suscite aujourd'hui un intérêt renouvelé. Ainsi, notre cadre contemporain d'analyse et d'interprétation de la diversité trouve ses sources dans les théories fondatrices de l'écologie des communautés (Ricklefs, 2004; Vellend, 2010). Notamment, de nombreux modèles de prédictions de la distribution des espèces (SDM, *Species Distribution Model*) reposent sur le concept de la niche écologique (Guisan et Thuiller, 2005). Parmi les nombreuses définitions de la niche qui existent dans la littérature écologique (Godsoe, 2010; Soberón, 2007), la plus influente est sans doute celle de G. Evelyn Hutchinson (Hutchinson, 1957). En l'absence de dispersion et d'interaction, la niche fondamentale d'Hutchinson est définie comme l'ensemble de toutes les conditions environnementales dans lesquelles une espèce peut persister. Alors que la niche fondamentale est un espace théorique déterminé par les limites physiologiques abiotiques d'une espèce et dépend uniquement des conditions

environnementales (e.g., le climat, la topographie, le sol, et la disponibilité des ressources), la niche réalisée est la fraction de la niche fondamentale qui est effectivement occupée lorsque sont considérées les interactions avec les autres espèces, particulièrement la compétition pour les ressources. Exprimée en termes démographiques, la niche est constituée de tous les environnements dans lesquels le taux de croissance intrinsèque de la population est positif ($r > 0$), i.e. quand le recrutement surpassé la mortalité en l'absence de dispersion (Chase et Leibold, 2003; Maguire, 1973). La variation spatiale de r peut donc déterminer la répartition géographique d'une espèce (Fig. 0.1 ; Holt *et al.*, 2005) et, par conséquent, l'assemblage des communautés d'espèces (Chase et Leibold, 2003).

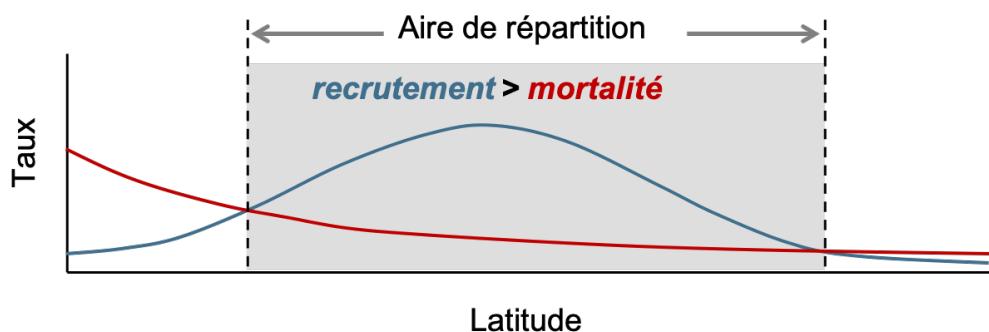


Figure 0.1. Représentation schématique de la niche écologique défini en termes démographiques. La niche d'une espèce, ou sa répartition géographique, représente la région où le taux de croissance intrinsèque de la population est positif ($r > 0$), i.e. quand le recrutement surpassé la mortalité. Les limites de l'aire de répartition correspondent au moment où il y a autant de recrutement que de mortalité. Schéma inspiré de Talluto *et al.* (2017).

Cependant caractériser la niche par r seulement est inadéquat dans un contexte de populations ouvertes à la colonisation (Holt et Keitt, 2000). En effet, la composition des communautés dépend non seulement ces processus locaux d'interaction entre les espèces et de tolérance aux conditions environnementales, mais également de processus à l'échelle régionale tels que la dispersion entre les différentes communautés d'un paysage (Leibold *et al.*, 2004). Le concept de métacommunauté permet de réconcilier les processus locaux et régionaux qui déterminent la répartition des espèces dans une théorie plus inclusive de l'assemblage des communautés (Leibold *et al.*, 2004).

La métacommunauté est définie comme un ensemble de communautés locales liées par la dispersion de plusieurs espèces potentiellement en interaction (Leibold *et al.*, 2004; Leibold et Chase, 2017). Plusieurs mécanismes d'assemblage de la communauté contribuent conjointement à la coexistence locale des espèces au sein d'une métacommunauté. Ces différents mécanismes se distinguent le long de trois grands axes : la dispersion des espèces ; l'hétérogénéité des habitats (i.e. leurs caractéristiques biotiques et abiotiques) ; et l'équivalence entre

les espèces selon leur niche écologique (Logue *et al.*, 2011). L'importance relative de ces différents axes influencera la dissimilarité entre les communautés (diversité β). Par exemple, alors qu'une grande hétérogénéité environnementale augmente la diversité β , un haut taux de dispersion homogénéise les communautés.

Les perturbations peuvent exercer une influence majeure sur les mécanismes d'assemblage des communautés (Chase, 2005) et sont ainsi un élément clé permettant la coexistence des espèces au sein des communautés (Hastings, 1980). Les perturbations peuvent agir autant à l'échelle locale (par exemple, un chablis dans une forêt) que régionale (par exemple, un grand feu de forêt). Selon les cas, les perturbations peuvent libérer des sites les rendant disponibles pour la colonisation ou encore fragmenter le paysage diminuant ainsi la connectivité entre les sites et donnant un avantage aux espèces qui ont une grande capacité de dispersion. Les perturbations peuvent aussi modifier les conditions environnementales et changer le rapport de force de compétition entre les espèces. D'ailleurs, il a souvent été observé que la diversité locale est maximisée à des niveaux intermédiaires de perturbation (Connell, 1978; Hastings, 1980; Wilkinson, 1999) ; quand il n'y a pas assez de perturbations, les espèces compétitives excluent toutes les autres espèces, tandis que quand il y en a trop, seules les espèces pionnières et tolérantes aux stress peuvent survivre. Ce n'est qu'à des taux de perturbation intermédiaires que la coexistence entre les différents types d'espèces est la plus probable.

L'ensemble de ces facteurs abiotiques et biotiques n'agissent pas tous à la même échelle spatiale et temporelle. L'hypothèse traditionnelle était que leur influence sur la distribution des espèces est spatialement hiérarchisée (Diez et Pulliam, 2007; Pearson et Dawson, 2003). À une échelle continentale, la distribution des espèces est principalement contrôlée par le climat. Par exemple, la limite nord des forêts tempérées feuillues en Amérique du Nord correspond approximativement à l'isotherme de température minimale annuelle moyenne de -40°C (Arris et Eagleson, 1989). À l'échelle d'un paysage, la topographie et l'utilisation du sol deviennent plus déterminantes. Enfin, à l'échelle locale, si les conditions aux niveaux supérieurs sont satisfaites, la présence des espèces dépendra des caractéristiques du sol, des interactions biotiques et du microclimat (Pearson et Dawson, 2003). Cependant, cette représentation hiérarchique, du haut vers le bas (*top-down*), des processus est de plus en plus remise en cause par les données empiriques qui montrent que des processus locaux peuvent influencer les distributions régionales des espèces (Gotelli *et al.*, 2010; McGill, 2010) et que les processus à une échelle spatiale ou temporelle peuvent interagir avec des processus à une autre échelle (Peters *et al.*, 2007; Soranno *et al.*, 2014). Par exemple, le climat contraindrait la distribution des espèces à leur limite nord, tandis que le rôle des interactions serait plus important à la limite sud et à l'intérieur de l'aire de répartition, là où les conditions environnementales sont plus favorables (Louthan *et al.*, 2015). Un bon exemple de ce phénomène est la distribution de l'épinette noire (*Picea mariana*), une espèce ayant une niche écologique très large, mais

dont la distribution au sud est limitée aux sites où la compétition est faible, comme des sites où le drainage très mauvais ou excessif (Burns et Honkala, 1990).

Ma thèse vise à comprendre l'effet combiné du changement climatique et des perturbations sur les communautés d'arbres dans l'écotone boréal-tempéré. Mes questions de recherches sont donc ancrées principalement dans une approche communauté-centrée avec un intérêt particulier pour les processus d'assemblage liés à l'environnement, la niche des espèces et les interactions de compétition, ainsi que l'effet des perturbations sur ces processus. Une des prédictions importantes qui découlent de cette approche théorique est une adéquation entre les conditions environnementales et les tolérances physiologiques des espèces d'une communauté. Cette perspective implique qu'une modification du climat entraînera un changement de distribution des espèces. Les écotones séparant les grandes zones de végétation sont donc présumés être très sensibles aux changements dans les conditions climatiques (Evans et Brown, 2017; Loehle, 2000). Par contre, d'autres processus agissant à différentes échelles spatiales pourraient également influencer la dynamique des arbres et interagir avec les effets du changement climatique, complexifiant ainsi les signaux de réponse. Comme mes recherches portent sur les forêts de l'écotone boréal-tempéré, les exemples seront orientés principalement sur celles-ci.

0.4. Les perturbations et la dynamique forestière

Les perturbations font partie intégrante de la dynamique des forêts. Feux, épidémies d'insectes, chablis, inondations sont des événements de mortalités aiguës et à court terme (*pulse disturbance*; Bender *et al.*, 1984) qui s'inscrivent dans la dynamique naturelle des forêts et permettent leur renouvellement (Attieill, 1994; Johnstone *et al.*, 2016). Les perturbations éliminent partiellement ou totalement la végétation en place, rendent disponibles les ressources (e.g., nutriments, lumière), créent des espaces vacants pour la colonisation et peuvent mélan-géer les différentes couches de sol et même exposer le sol minéral. Suite à une perturbation, la succession est réinitialisée et on observe généralement une invasion d'espèces intolérantes à l'ombre, tels que le bouleau blanc (*Betula papyrifera*) et le peuplier faux-tremble (*Populus tremuloides*), qui seront progressivement remplacés par des espèces compétitives tolérantes à l'ombre. La grande variabilité spatio-temporelle des perturbations (fréquence, intensité, durée et étendue spatiale) permet de créer une mosaïque d'habitats hétérogènes, complexes et dynamiques favorisant la coexistence de nombreuses espèces à travers le paysage forestier (Bouchard et Kneeshaw, 2006).

Les régimes de perturbations naturelles varient considérablement entre les différents biomes forestiers (Chen et Popadiouk, 2002; Goldblum et Rigg, 2010; Pastor et Mladenoff, 1992). Dans les forêts boréales de l'Amérique du Nord, les feux sont la principale perturbation et entraînent une dynamique de remplacement entre les peuplements matures d'épinette

noire (*Picea mariana*) et les peuplements de régénération (Chen et Popadiouk, 2002). Dans les forêts mixtes dominées par le sapin baumier (*Abies balsamea*), les forêts sont surtout affectées par les épidémies de tordeuse des bourgeons de l'épinette dans les forêts mixtes (Holling, 1992). Plus au sud, les forêts tempérées feuillues se régénèrent principalement par une dynamique de trouée, suivant la chute de vieux arbres ou un chablis (Pastor et Mladenoff, 1992; Runkle, 1981). Ainsi, les espèces forestières d'un région sont généralement bien adaptés à un régime de perturbation naturelle, défini par la superficie, la sévérité et la fréquence (Turner, 2010). Par exemple, dans la forêt boréale, les cônes sérotineux du pin gris (*Pinus banksiana*) nécessitent des températures élevées pour s'ouvrir et lui permettent de coloniser rapidement un site après un feu (Burns et Honkala, 1990). Dans la forêt tempérée, les semis et les gaulis de l'érable à sucre (*Acer saccharum*) peuvent persister longtemps dans un sous-bois ombragé jusqu'à ce qu'une trouée créée par la chute des vieux arbres lui permette de rejoindre la canopée rapidement (Burns et Honkala, 1990). Les communautés forestières ont donc généralement une bonne capacité à se rétablir et à revenir à leur état initial suite à une perturbation naturelles, i.e. elles sont résilientes (Gunderson, 2000).

Les perturbations anthropiques viennent s'ajouter ou se substituer aux perturbations naturelles pour créer un tout nouveau régime de perturbations (Boucher *et al.*, 2014). L'exploitation forestière diffère grandement des perturbations naturelles en termes de sévérité, de fréquence, de sélectivité et d'étendue spatiale (Boucher *et al.*, 2006; Kuuluvainen, 2009; Schulte *et al.*, 2007), ce qui peut modifier les trajectoires de succession. En général, les coupes forestières ont des temps de retour plus court que les perturbations naturelles et des patrons spatio-temporels beaucoup plus uniformes (Bergeron *et al.*, 2002; McRae *et al.*, 2001). Plusieurs études ont montré que les coupes tendent à rajeunir et homogénéiser les paysages forestiers, à simplifier la structure des peuplements et à modifier leur composition (Boucher *et al.*, 2006; Boucher et Grondin, 2012; Cyr *et al.*, 2009; McRae *et al.*, 2001; Schulte *et al.*, 2007). Les forêts présentent une certaine résilience face aux coupes forestières ; tant que le régime de coupes forestières restent dans la plage de variabilité naturelle des forêts (Grondin *et al.*, 2018), la plupart des espèces peuvent se régénérer après coupe. Toutefois, à long terme, des coupes répétées peuvent entraîner d'importants changements de composition. Par exemple, entre 1930 et 2002, la coupe forestière dans une région à la limite nord des espèces tempérées au Québec a engendré un changement majeur de composition et de structure d'âge ; en 1930, le paysage était largement dominé par des vieilles forêts (>100 ans) de conifères, tandis qu'en 2002, les jeunes forêts (<70 ans) dominant et près de 40 % du paysage est passé d'un couvert coniférien à un couvert mixte et près de 20 % est devenu feuillu (Boucher *et al.*, 2006).

0.5. Réponses des communautés forestières au changement climatique

Sous l'influence du réchauffement climatique, les espèces doivent s'adapter, migrer ou disparaître (Aitken *et al.*, 2008). Contrairement aux espèces mobiles, comme les oiseaux qui peuvent se déplacer et suivre rapidement leur niche climatique (Gaüzère *et al.*, 2015), la réponse des arbres n'est pas immédiate et se fait sur plusieurs générations. Un arbre mature peut persister pendant de nombreuses années après que les conditions locales soient devenues défavorables, simplement parce qu'il est là, bien enraciné. Par contre, cet arbre finira par mourir, ne laissant derrière lui aucune régénération. Le trou dans la canopée laissé par sa chute sera colonisé par de nouvelles espèces mieux adaptées aux nouvelles conditions et, à terme, toute la composition de la forêt pourrait être modifiée.

0.5.1. Réponses démographiques

Les changements de température et de précipitations ont des effets directs sur la croissance, la mortalité et le recrutement des arbres (Vanderwel *et al.*, 2013b; Zhang *et al.*, 2015a). Par exemple, les augmentations récentes des taux de mortalité des arbres dans l'ouest de l'Amérique du Nord ont été attribuées à des températures élevées et à des sécheresses (Peng *et al.*, 2011; van Mantgem *et al.*, 2009). Or, c'est l'équilibre entre les gains par la croissance et le recrutement et les pertes par la mortalité qui détermine, localement, la niche climatique où une espèce d'arbre peut s'établir et persister (Godsoe *et al.*, 2017; Schurr *et al.*, 2012) et, régionalement, les limites d'aires de répartition (Holt *et al.*, 2005). Des changements même très faibles dans les taux démographiques peuvent modifier le rapport de force de la compétition interspécifique (Luo et Chen, 2013; Reich *et al.*, 2015), de même que la dynamique et la trajectoire de succession des forêts (Prach et Walker, 2011), modifiant par conséquent leur structure et leur composition (Stephenson *et al.*, 2011; van Mantgem *et al.*, 2009).

À long terme, ces changements démographiques agissent donc pour contrôler les limites géographiques des différents types de forêts (Holt *et al.*, 2005). Alors que l'expansion de l'aire de répartition dépend de la dispersion et de l'établissement de nouveaux individus, la contraction de l'aire de répartition est le résultat de la perte de vitalité et de la mortalité (Jump *et al.*, 2009). Le processus de recrutement est d'ailleurs reconnu comme une étape cruciale pour les déplacements d'aires de répartition et peut fournir un signal précoce de la migration des espèces d'arbres (Woodall *et al.*, 2009; Zhu *et al.*, 2012). Certaines études ont en effet montré une augmentation du recrutement d'espèces d'arbres à la limite de leur aire de répartition plus haut en altitude (Lenoir *et al.*, 2008) et plus au nord en latitude (Boisvert-Marsh *et al.*, 2014; Fisichelli *et al.*, 2014; Sittaro *et al.*, 2017). Plus généralement, dans l'écotone de la forêt boréale-tempérée, le récent réchauffement climatique a amélioré le recrutement, la survie et la croissance de certaines espèces d'arbres tempérés à la limite nord

de leur aire de répartition (Boisvert-Marsh *et al.*, 2019; Bolte *et al.*, 2010; Fisichelli *et al.*, 2014; Grundmann *et al.*, 2011). Dans le même temps, les espèces boréales ont été désavantagées par une croissance plus lente et une augmentation plus importante des mortalités associées au stress de la chaleur et de la sécheresse (Bolte *et al.*, 2010; Goldblum et Rigg, 2005; Grundmann *et al.*, 2011; Peng *et al.*, 2011). Ainsi, à mesure que le climat se réchauffe et fait pencher la balance en faveur des espèces tempérées plutôt que boréales, les forêts de l'écotone pourraient passer d'une dominance coniférienne à mixte, puis de mixte à feuillue (Fig. 0.2 ; Boulanger *et al.*, 2019; Chen, 2002; Lindner *et al.*, 2010; Price *et al.*, 2013).

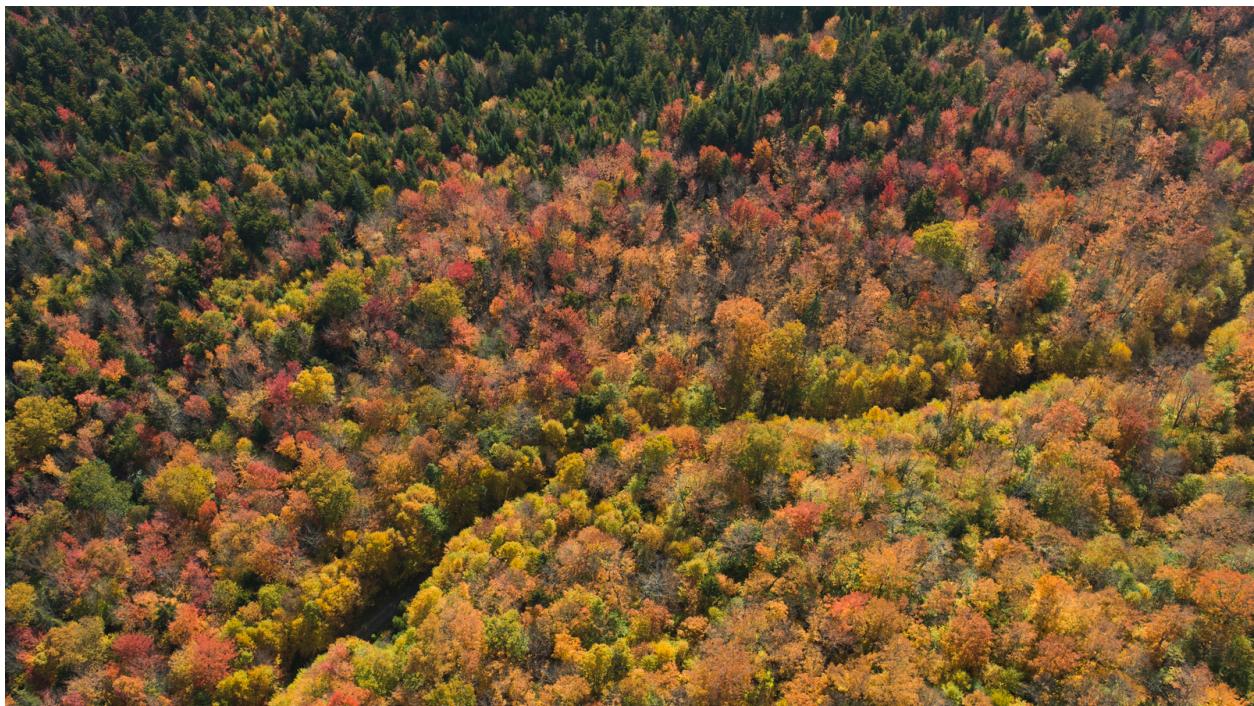


Figure 0.2. Cette photo illustre une zone de transition le long d'un gradient altitudinal entre la forêt feuillue, qui arbore son feuillage d'automne coloré, en bas de la pente et la forêt résineuse, toujours verte, en haut de la pente où la température est généralement plus froide. Avec le réchauffement climatique, les espèces feuillues peuvent migrer vers le haut de la pente et se mélanger avec les conifères et éventuellement les remplacer. Ce même phénomène commence à apparaître le long du gradient latitudinal, mais sur des distances beaucoup plus grandes. Photo de Blake Gordon pour The Nature Conservancy.

0.5.2. La course vers le nord

Des changements de distribution liés au climat ont déjà été observés pour de nombreuses espèces d'arbres à travers le monde (Chen *et al.*, 2011; Parmesan et Yohe, 2003; Walther *et al.*, 2002), particulièrement dans les zones de transition où les changements sont plus facilement détectables (Boulanger *et al.*, 2017; Jump *et al.*, 2009). Ainsi, il existe un nombre croissant de preuves de changements contemporains dans la distribution des espèces d'arbres

le long des gradients d’altitude en montagne (Beckage *et al.*, 2008; Gottfried *et al.*, 2012; Kapralov *et al.*, 2006; Lenoir *et al.*, 2008; Savage et Vellend, 2015), où les écotones sont étroits et bien définis (Jump *et al.*, 2009). Par exemple, dans les Montagnes Vertes du Vermont, les arbres tempérés ont monté en altitude, conduisant à un déplacement des limites de l’écotone boréal-tempéré d’environ 100 m (Beckage *et al.*, 2008), tandis que sur le mont Mégantic au sud du Québec, les arbres se sont déplacés en élévation de près de 30 m en moyenne (Savage et Vellend, 2015).

Des tendances similaires commencent également à apparaître pour les changements de latitude (Boisvert-Marsh *et al.*, 2019; Chen *et al.*, 2011; Fisichelli *et al.*, 2014; Lindner *et al.*, 2010; Sittaro *et al.*, 2017). Par exemple, à l’échelle locale, Fisichelli *et al.* (2014) ont observé une avancée de la régénération d’espèces d’arbres tempérées dans la forêt boréale de la région à l’ouest des Grands Lacs et ce processus semblait être facilité par des températures plus chaudes. Leithead *et al.* (2010) ont observé que les trouées causées par la mort des arbres boréaux dans une forêt du nord de l’Ontario facilitent l’établissement d’espèces tempérées du sud. À l’échelle régionale, Boisvert-Marsh *et al.* (2014) et Sittaro *et al.* (2017) ont montré une migration à prédominance vers le nord des essences d’arbres à travers le Québec, avec les gaulis (jeunes arbres de diamètre entre 1 et 9 cm) présentant une réponse plus rapide que les arbres adultes.

0.5.3. Réorganisation des communautés

Malgré la tendance générale des déplacements vers les pôles et en altitude, le moment, l’ampleur et même la direction des déplacements des espèces varient considérablement d’un taxon et d’une région à l’autre (Fei *et al.*, 2017; VanDerWal *et al.*, 2013). Selon leur capacité à migrer vers de nouveaux habitats ou à s’adapter aux conditions locales plus chaudes, certaines espèces “gagnantes” peuvent augmenter en abondance et étendre leur aire de répartition, tandis que les “perdantes” peuvent diminuer en abondance et s’éteindre localement (McGill *et al.*, 2015). Alors que les gains et les pertes d’espèces peuvent avoir lieu simultanément au sein des communautés, la diversité locale (diversité α) peut montrer des tendances variées (Vellend *et al.*, 2013; Dornelas *et al.*, 2014), déconnectées du déclin de la biodiversité observé à l’échelle globale (Ceballos *et al.*, 2015; IPBES, 2019). Toutefois, cette apparente stabilité peut cacher un remaniement majeur des espèces présentes dans la communauté (diversité β ; Dornelas *et al.*, 2014; McGill *et al.*, 2015). Ces grands remaniements d’espèces pourraient même donner lieu à de nouvelles associations d’espèces (*no-analog communities*; Williams et Jackson, 2007) et par conséquent de nouvelles interactions entre espèces (Van der Putten, 2012). Ainsi, en mettant l’accent sur les limites d’aires de répartition, il est possible que l’empreinte du changement climatique ait été sous-estimée et que d’importantes réorganisations de la biodiversité soient en cours à l’intérieur des limites d’aires de répartition.

À long terme, la dynamique non aléatoire des pertes et des gains en espèces peut amener des changements au niveau des caractéristiques fonctionnelles de la communauté. En effet, le réchauffement climatique devrait favoriser les espèces adaptées au chaud au détriment des espèces adaptées au froid, entraînant une “thermophilisation” des communautés (De Frenne *et al.*, 2013; Gottfried *et al.*, 2012). De plus, l’effet de ces pertes et ces gains sur la dynamique et le fonctionnement des communautés sera d’autant plus important si les nouvelles espèces ont des caractéristiques très différentes par rapport à celles des espèces résidentes (Wardle *et al.*, 2011).

Dans les écotones, ces changements de composition induits par le climat pourraient même déclencher un changement de régime (*regime shift*; Scheffer *et al.*, 2001). Par exemple, le changement climatique pourrait transformer la toundra sans arbres en forêt boréale (Danby et Hik, 2007; Kapralov *et al.*, 2006), les forêts tropicales en savane (Boulanger *et al.*, 2019; Hirota *et al.*, 2011) ou les forêts de conifères en forêts de feuillus (Fig. 0.2 ; Price *et al.*, 2013). Étant donné que les caractéristiques des espèces et la dynamique des écosystèmes diffèrent fortement entre ces biomes, cette réorganisation de la biodiversité n’a pas seulement un impact sur la composition et la biodiversité locale (Williams et Jackson, 2007), mais modifie également les caractéristiques fonctionnelles des communautés (Danneyrolles *et al.*, 2019; Esquivel-Muelbert *et al.*, 2018; Scheffer *et al.*, 2012) et, par conséquent, le microclimat, les cycles biogéochimiques et le régime de perturbations (Anderson *et al.*, 2011). De tels changements de régimes auront donc un impact majeur sur la dynamique forestière, mais sont encore mal compris et difficiles à prédire, notamment parce que les écotones ne sont pas uniquement contrôlés par le climat mais par de nombreux autres facteurs non climatiques qui pourraient accélérer ou ralentir ces changements.

0.6. Délais de réponse et déséquilibre

Bien qu’on prévoie un déplacement des niches climatiques des arbres de plusieurs centaines de kilomètres vers le nord d’ici la fin du siècle (McKenney *et al.*, 2007), un nombre croissant d’études suggèrent que le déplacement des arbres en Amérique du Nord ne réussira probablement pas à suivre le rythme du réchauffement climatique (Fig. 0.3 ; Bertrand *et al.*, 2011; Sittaro *et al.*, 2017; Vissault, 2016; Woodall *et al.*, 2013; Zhu *et al.*, 2012). Par exemple, alors qu’on observe un déplacement des aires de répartition vers le nord, les vitesses de migration des espèces d’arbres au Québec étaient en moyenne inférieures à 50% de la vitesse de l’avancée géographique du changement climatique récent (Sittaro *et al.*, 2017). De plus, alors que les projections estiment que les taux de migrations des arbres au cours du prochain siècle devront atteindre plus de 1000 mètres par an (Iverson *et al.*, 2008; Malcolm *et al.*, 2002), les taux postglaciaires estimés sont beaucoup plus lents (<100 m/an) que ceux requis (McLachlan *et al.*, 2005).

Les arbres sont particulièrement susceptibles de montrer de longs délais de réponse aux changements parce que ces espèces sont sessiles, ont une faible capacité de dispersion, une longue durée de vie, une croissance lente et une maturité sexuelle tardive (Iverson et McKenzie, 2013; Lenoir et Svenning, 2015). Ces caractéristiques démographiques pourraient expliquer le haut niveau d'inertie des forêts malgré les changements de climat, de sorte que l'équilibre entre l'environnement et les forêts est rarement atteint (Talluto *et al.*, 2017). En d'autres termes, il y a un décalage entre la niche hutchinsonienne d'une espèce et la répartition géographique observée (Fig. 0.3 ; Holt, 2009). Les délais de réponse peuvent entraîner l'accumulation de crédits de colonisation et de dettes d'extinction par rapport à la situation d'équilibre (Jackson et Sax, 2010; Tilman *et al.*, 1994). Certaines espèces sont vouées à disparaître d'un habitat parce que les conditions environnementales ne sont plus adéquates, mais des populations relictuelles peuvent persister pendant un certain temps, en raison, par exemple, de la longévité des individus ou de la reproduction végétative ; ces espèces représentent une dette d'extinction. Inversement, malgré que les conditions d'une région soient devenues favorables, de nouvelles espèces adaptées ne sont pas encore parvenues à la coloniser, du fait d'une faible capacité de dispersion, de barrières à la dispersion ou encore d'un effet prioritaire des espèces résidentes ; ces espèces constituent un crédit de colonisation (Jackson et Sax, 2010; Tilman *et al.*, 1994). Ainsi, étant donné que l'environnement est dynamique et que les arbres sont caractérisés par d'importants délais de réponse, l'atteinte de l'état d'équilibre pourrait prendre plusieurs décennies ou siècles, laissant les écosystèmes forestiers dans une longue dynamique transitoire (*transient dynamics* ; Hastings *et al.*, 2018; Jackson et Sax, 2010; Talluto *et al.*, 2017). En corollaire, il est probable que les réponses des forêts au changement climatique dépendent des dynamiques transitoires déjà amorcées par d'autres perturbations récentes ou historiques. Pourtant, la majorité des modèles de distribution d'espèces supposent que les espèces sont en équilibre avec leur environnement, ignorant la dynamique transitoire.

D'importants délais de réponse des forêts au changement climatique sont déjà observables puisque la distribution de plusieurs espèces d'arbres de l'est de l'Amérique du Nord n'est pas à l'équilibre avec le climat aux marges de leur aire de répartition, avec davantage de dettes d'extinction au sud et de crédits de colonisation au nord (Talluto *et al.*, 2017). Leurs résultats montrent aussi que la vitesse de la contraction d'aire de répartition dans le sud est plus rapide que l'expansion dans le nord (Talluto *et al.*, 2017). Des simulations ont aussi montré que le décalage entre la niche climatique optimale des espèces tempérées et leur distribution réalisée ne fera que s'accroître avec le temps (Vissault, 2016). Cette tension grandissante entre la distribution réalisée et potentielle des espèces risque d'autant plus de causer des changements brusques (*regime shift*) dans les écosystèmes forestiers suite à une perturbation anthropique ou naturelle (Renwick et Rocca, 2015; Vanderwel et Purves, 2014).

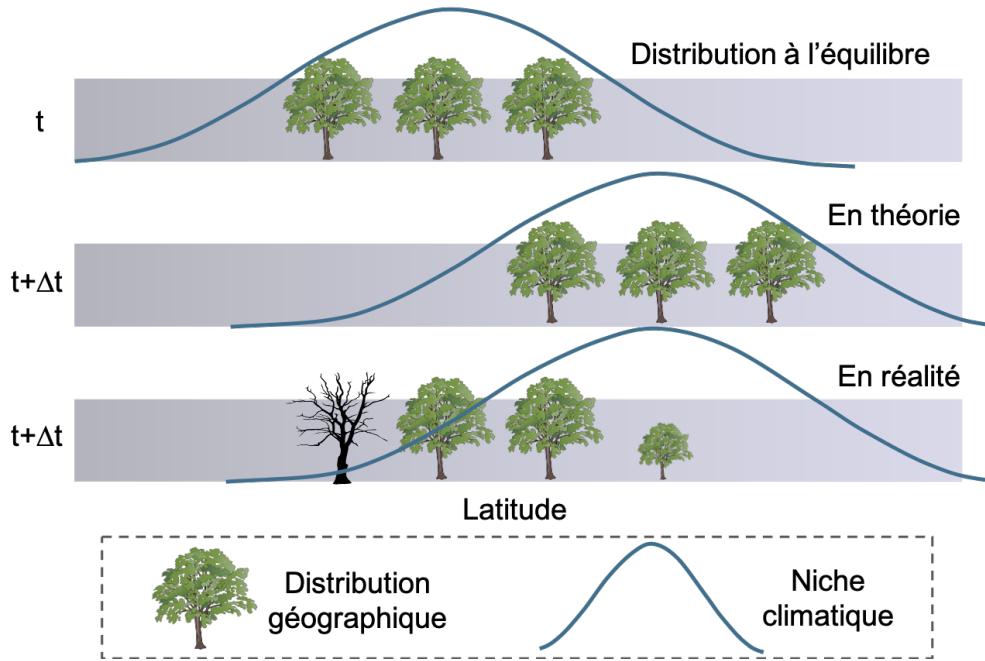


Figure 0.3. Selon la théorie des niches, la distribution géographique d'une espèce devrait correspondre à ses tolérances environnementales ; on dit alors que la distribution est à l'équilibre avec les conditions environnementales (schéma du haut). Ainsi, en théorie, lorsque le climat se réchauffe, la niche climatique d'une espèce se déplace également et on s'attend à un déplacement de la distribution équivalent (schéma du centre). Toutefois, en réalité, le changement du climat est beaucoup plus rapide que la capacité de migration des espèces (schéma du bas). Il y a donc un décalage grandissant entre la niche climatique et la distribution observée des espèces. À une extrémité de la niche, on observe une dette d'extinction causée par la persistance d'individus voués à l'extinction. À l'autre extrémité, on observe un crédit de colonisation causé par le retard de recrutement.

0.7. Interaction entre le changement climatique et les perturbations

Tandis que les forêts répondent lentement aux changements environnementaux, les perturbations peuvent causer des épisodes de mortalité accrue et déclencher des altérations rapides et profondes de la composition, de la structure et des trajectoires de succession (Bergeron *et al.*, 2017; Boulanger *et al.*, 2017; Gauthier *et al.*, 2015a; Keane *et al.*, 2013; Serra-Diaz *et al.*, 2015). De plus, la fréquence, l'intensité et la durée des perturbations naturelles ont déjà augmenté au cours des dernières décennies avec le changement climatique (Seidl *et al.*, 2017). Depuis plus d'un siècle, les forêts sont également soumises à d'importantes pressions anthropiques, tout particulièrement les activités d'exploitation forestière.

Les perturbations, autant naturelles qu'anthropiques, pourraient moduler la vitesse de réponse des forêts au changement climatique. Alors que le climat global change graduellement (*press disturbance*; Bender *et al.*, 1984) et modifie lentement l'équilibre compétitif entre les

espèces, les perturbations de type *pulse* diminuent ou éliminent la compétition par les espèces résidentes et créent ainsi des opportunités de colonisation pour les espèces migratrices (Serra-Diaz *et al.*, 2015; Vanderwel et Purves, 2014; Xu *et al.*, 2012). Par conséquent, suite à une perturbation, la forêt pourrait être rapidement colonisée par des espèces mieux adaptées aux nouvelles conditions climatiques et même basculer vers un autre nouvel état alternatif persistant (Fig. 0.4; Johnstone *et al.*, 2016; Renwick et Rocca, 2015; Turner, 2010). Dans l'écotone boréal-tempéré, par exemple, il a été montré que les trouées de la canopée facilitent localement l'établissement d'espèces tempérées dans les forêts mixtes de l'Ontario (Leithead *et al.*, 2010). En Scandinavie, Bolte *et al.* (2010) a montré que l'épinette de Norvège (*Picea abies*) était particulièrement sensible à la combinaison des perturbations et du réchauffement qui ont favorisé la croissance du hêtre européen (*Fagus sylvatica*). Certaines études de simulation ont toutefois conclu qu'il est peu probable que les perturbations entraînent des grands changements d'aires de répartition dans les décennies à venir parce qu'elles favoriseraient principalement le rétablissement rapide des espèces résidentes (Liang *et al.*, 2018) ou l'invasion par des espèces en début de succession (Vanderwel et Purves, 2014).

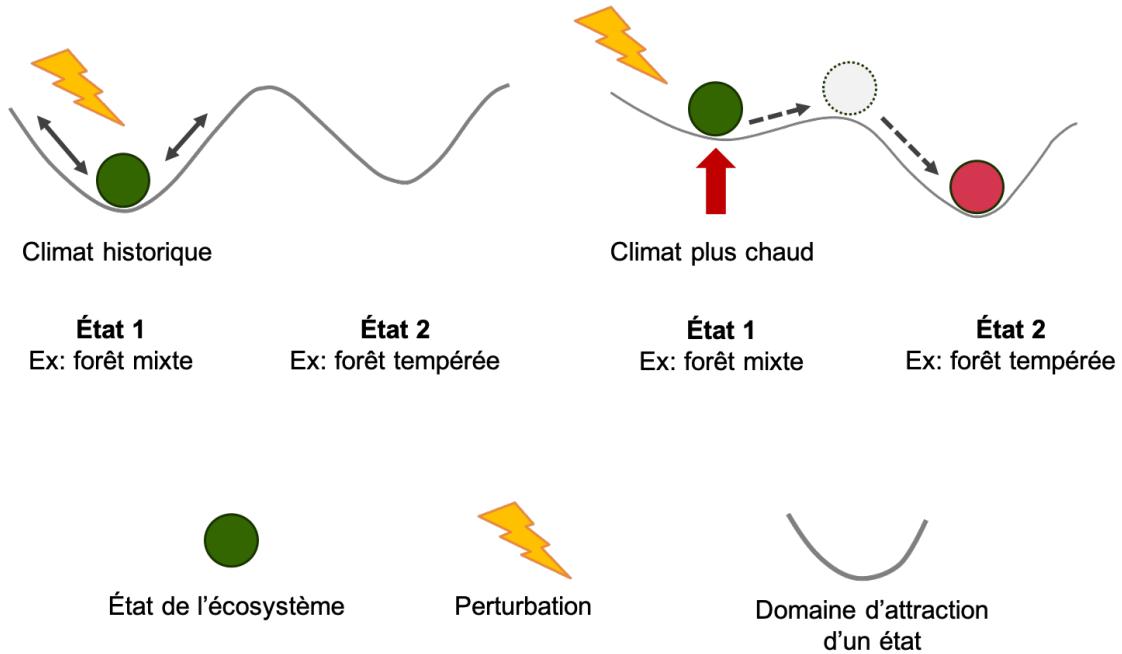


Figure 0.4. Représentation du concept d'états alternatifs stables. Les états stables d'un écosystème correspondent à des bassins d'attractions (vallées) vers lesquels le système (boule) tend à se stabiliser. À gauche, la forêt (boule) est résiliente, c'est-à-dire qu'une perturbation peut entraîner des changements de composition dans la forêt (faire bouger la boule dans le bassin d'attraction), mais la forêt tendra à revenir à sa composition initiale (la boule retourne au creux de son bassin d'attraction). À droite, le réchauffement climatique diminue la résilience de la forêt (le bassin est déformé et moins stable) et une perturbation peut alors facilement la faire basculer vers un nouvel état forestier alternatif. Cette hypothèse est au coeur de ma thèse de doctorat. Figure inspirée de Johnstone *et al.* (2016).

Face aux nombreuses perturbations que subissent les forêts, il est certain que la réponse des arbres au futur changement climatique dépendra et interagira avec des dynamiques de transition déjà en cours. Les forêts risquent de perdre leur résilience et, par conséquent, devenir plus vulnérables et plus lentes à se rétablir. Discerner les effets du changement climatique et ceux des perturbations naturelles et anthropiques et leurs rétroactions potentielles est nécessaire à la fois pour informer les modèles prédictifs de distribution de la biodiversité sous le changement climatique et pour élaborer des stratégies de gestion forestière permettant un aménagement durable des forêts.

0.8. Contraintes à la migration

Malgré l'empreinte indéniable du changement climatique, la réponse récente des communautés forestières n'est pas aussi unidirectionnelle et linéaire que prévu, vraisemblablement parce que d'autres facteurs non climatiques, tels que les interactions biotiques et les propriétés du sol, imposent des contraintes supplémentaires à la migration des espèces. Selon l'importance relative de ces contraintes par rapport au climat à la limite nord des aires de répartition des espèces, les projections de migration sous le changement climatique qui ignorent ces facteurs pourraient surestimer l'effet des températures sur l'expansion des aires (Beauregard et de Blois, 2016; Ettinger et HilleRisLambers, 2017).

Bien qu'elles répondent de manière indépendante, les espèces ne sont pas isolées, mais interagissent avec les autres membres de leur écosystème. Avec le changement climatique, les conditions favorables se déplacent et forcent de nouvelles interactions à la marge des aires de distributions (Kissling et Schleuning, 2015). Par exemple, à moins qu'un dépérissement massif de la forêt ne se produise, les espèces migratrices devront s'établir sur des sites qui sont déjà colonisés par d'autres espèces et devront donc vraisemblablement compétitionner pour les ressources lors de leur établissement (phénomène appelé l'effet prioritaire ; Gilman *et al.*, 2010). Une étude de simulation a d'ailleurs révélé que les taux de migration sont plus faibles dans les forêts établies et diversifiées que dans les forêts de début de succession (Meier *et al.*, 2012). Tel que discuté précédemment, les perturbations pourraient diminuer la compétition par les espèces résidentes.

En plus de la compétition entre les espèces d'arbres, les espèces migratrices coloniseront des sols qui sont déjà développés et qui présentent des propriétés (e.g. qualité du drainage, disponibilité en nutriments, pH, mycorhizes) qui varient localement ou régionalement, lesquelles pourraient retarder ou contraindre leur établissement (Brown et Vellend, 2014; Carteron *et al.*, 2020; Collin *et al.*, 2017; Lafleur *et al.*, 2010; Solarik *et al.*, 2019). Dans l'écotone boréal-tempéré, les forêts dominées par les conifères au nord où la température moyenne est froide présentent généralement des sols acides, une activité microbienne faible et une décomposition lente de la matière organique comparativement aux forêts tempérées décidues

plus chaudes du sud (Goldblum et Rigg, 2010). Les populations résidentes pourraient ainsi inhiber indirectement l'établissement de nouvelles espèces par leur effet sur les propriétés du sol (Solarik *et al.*, 2019). Par exemple, Collin *et al.* (2017) ont montré que l'acidité du sol forestier sous une canopée dominée par les conifères affecte négativement les semis de l'érable à sucre (*Acer saccharum*) via un débalancement nutritif foliaire. De plus, l'absence d'espèces mycorhiziennes arbusculaires dans les sols de la forêt boréale pourraient également réduire la survie des semis d'érable à sucre (Carteron *et al.*, 2020). En revanche, d'autres études ont montré une bonne régénération de cette espèce emblématique dans la forêt boréale, suggérant que les propriétés du sol ne constituent peut-être pas un obstacle majeur à la migration des espèces tempérées présentant une large tolérance écologique (Barras et Kellman, 1998; Fisichelli *et al.*, 2014; Kellman, 2004). D'ailleurs, il est possible que les espèces migratrices puissent influencer leur propre taux d'invasion, par leur effet sur la qualité chimique de la litière et sur la composition des micro-organismes du sol (Laganière *et al.*, 2010; Légaré *et al.*, 2005). Néanmoins, des conditions édaphiques sous-optimales pourraient tout de même retarder la migration des arbres vers le nord. Bien que les études expérimentales sur l'érable à sucre fournissent des connaissances précieuses sur l'influence des sols à l'échelle locale, l'effet de ces contraintes sur la dynamique forestière à long terme devrait aussi être quantifié à l'échelle régionale et pour différentes espèces.

0.9. Problématique et enjeux

La question des effets du changement climatique sur la dynamique forestière soulève de nombreux enjeux, notamment au niveau de la gestion des forêts. La gestion actuelle repose grandement sur une conception statique de la dynamique forestière sous l'influence d'un climat stable. Par exemple, l'aménagement écosystémique des forêts se base sur des états de références historiques, comme les forêts préindustrielles, i.e. avant l'exploitation industrielle (Pinna, 2009; Vaillancourt *et al.*, 2009). Dans le contexte du changement climatique, maintenir la composition et la structure des forêts historiques de références pourrait devenir de plus en plus difficile à atteindre et mener à des écosystèmes forestiers non résilients (Boulanger *et al.*, 2019; Duveneck et Scheller, 2016).

De plus, l'aménagement forestier repose actuellement sur des modèles de possibilités forestières, “lesquelles correspondent au volume maximum des récoltes annuelles que l'on peut prélever à perpétuité, sans diminuer la capacité productive du milieu forestier” (Bureau du forestier en chef, 2016). Le calcul de possibilité forestière tient compte de plusieurs critères tels que la dynamique naturelle des forêts, leur composition, leur structure d'âge et la probabilité de perturbation par les feux, les insectes et les maladies. Cependant, il ne tient toujours pas compte du changement climatique. Or, ce calcul fait des prédictions à long

terme et la coupe forestière dépend de ces prédictions. On devine que le changement rapide du climat risque de bousculer ces prédictions. Par exemple, une espèce d'importance commerciale pourrait ne pas se régénérer après coupe et être remplacée par des espèces de moins grande valeur économique. L'amplification des perturbations naturelles combinée à l'homogénéisation du paysage par les coupes forestières et aux stress climatiques pourrait avoir des effets synergiques menant à un dépérissement des forêts.

Les modèles de distribution d'espèces permettent de dresser un portrait des répartitions potentielles des arbres sous un climat futur et d'estimer leur vulnérabilité (Berteaux, 2014; Périé et de Blois, 2016). Toutefois, les projections issues de des modèles reposent bien souvent sur la relation statistique entre les occurrences d'espèces et l'environnement. Et, tel que discuté tout au long de cette introduction, la relation climat-présence n'est qu'une facette du lien qui unit les espèces à leur aire de répartition. À l'heure actuelle, il manque de nombreuses informations quantitatives sur les contraintes et les moteurs aux changements de distribution des espèces. Notre capacité à prédire les effets futurs du changement climatique sur la dynamique forestière dépend de la quantification et de la compréhension de ses effets passés et de son interaction avec les perturbations naturelles et anthropiques.

0.10. Objectifs et structure de la thèse

La question au cœur de la présente thèse est : quel est l'effet combiné du changement climatique récent et des perturbations sur la dynamique forestière ? Pour y répondre, j'ai quantifié les changements dans les communautés forestières du Québec méridional au cours des dernières décennies (1970 à 2018) et évalué les causes de ces changements selon trois différents points de vue :

- (1) *la diversité et la composition des communautés ;*
- (2) *le dynamique de transition entre les types forestiers ;*
- (3) *la dynamique de régénération des espèces tempérées à leur limite nord.*

Cette thèse s'articule autour de ces trois points de vue, qui correspondent aux chapitres qui structurent la thèse. Pour l'ensemble de ces projets, j'ai utilisé le vaste réseau de placettes forestières permanentes échantillonnées de 1970 à 2018 au Québec, Canada (jeu de données présenté dans la section *Les forêts du Québec*, plus bas).

0.10.1. Chapitre 1 — Diversité β et composition des communautés

L'objectif du chapitre 1 (Brice *et al.*, 2019) est de quantifier les changements de composition des communautés d'arbres entre une période historique (1970-1980) et une période contemporaine (2000-2016) et d'évaluer les contributions relatives du changement climatique et des perturbations sur ces changements.

La réorganisation des communautés forestières a été quantifiée en examinant la diversité β temporelle (TBI, en référence à *Temporal Beta Diversity Index*), ainsi que ses composantes sous-jacentes, les pertes et les gains en espèces (Legendre, 2014, 2019). Cette méthode permet de faire le lien entre les changements de diversité et les changements démographiques dans les communautés, puisque les pertes et les gains sont en fait des mortalités et des recrutements lorsque calculés sur des données d'abondance, et des extinctions et colonisations lorsque calculés sur des données de présence-absence. Les effets du climat et des perturbations sur la diversité β temporelle ont été évalués à l'aide de régressions multiples et de partitionnement des variations.

Afin de discerner les effets du changement climatique de ceux des perturbations, des indices de traits de la communauté en lien avec la niche thermique (CTI, en référence à *Community Temperature Index*) et la tolérance à l'ombre (CSI, en référence à *Community Shade Index*) des espèces ont été utilisés. Cette approche, ancrée dans l'écologie fonctionnelle, permet de décrire la composition d'une communauté au regard d'un trait spécifique et d'estimer la dynamique des assemblages des espèces en réponse à un changement environnemental donné (Violle *et al.*, 2007). Étant donné que le CTI reflète l'abondance relative des espèces adaptées aux conditions chaudes par rapport aux espèces adaptées au froid, on s'attend à ce que l'indice augmente avec le réchauffement climatique (Fig. 0.5). Les changements dans les valeurs de ces indices de communauté ont été comparés entre différents niveaux de perturbation. Ainsi, le réchauffement climatique devrait favoriser les espèces adaptées aux conditions chaudes, résultant en une augmentation du CTI, tandis que les perturbations devraient favoriser les espèces intolérantes à l'ombre au détriment des espèces tolérantes à l'ombre, résultant en une diminution du CSI. Enfin, une méthode d'analyse a été développée pour quantifier la contribution des gains et des pertes d'espèces à la variation des indices.

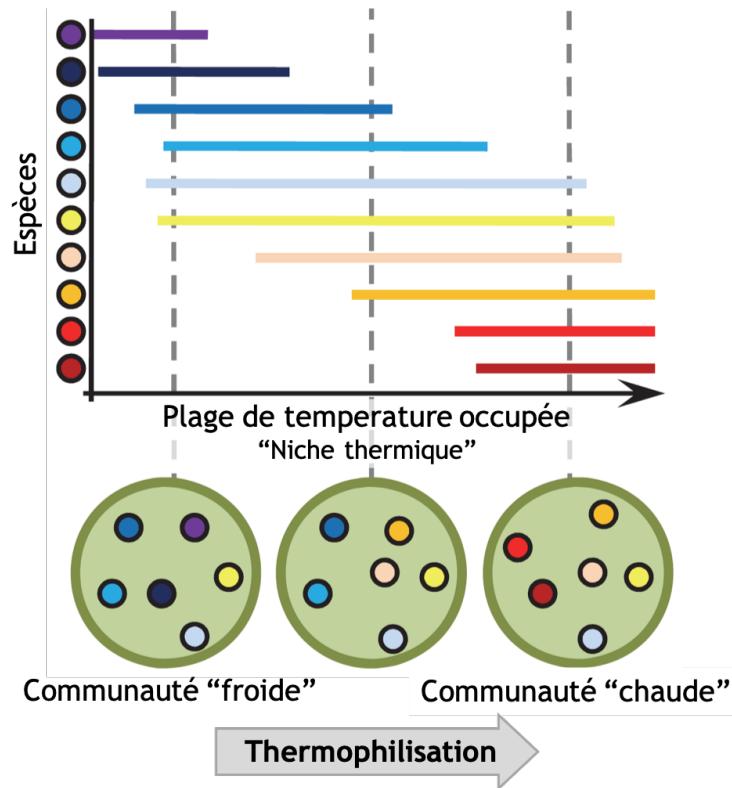


Figure 0.5. Représentation schématique du processus de thermophilisation des communautés. Les espèces (cercles de couleur) du pool régional se distribuent le long d'un gradient de température (les bars représentent leur distribution dans l'espace ou leur niche thermique). Les espèces adaptées au chaud (tons de rouge) se trouvent dans les habitats plus chauds, tandis que les espèces adaptées au froid (tons de bleu) se trouvent dans les habitats froids. Ainsi, la composition moyenne des communautés variera le long de ce gradient et un réchauffement des températures devrait mener à une thermophilisation, i.e. une augmentation de la proportion d'espèces chaudes par rapport aux espèces froides. Schéma inspiré de Bertrand *et al.* (2011).

0.10.2. Chapitre 2 — Dynamique de transition des forêts

Dans le chapitre 2 (Brice *et al.*, 2020), l'objectif est de caractériser la dynamique de transition des forêts au Québec et d'identifier les conditions environnementales qui favorisent ou empêchent les transitions forestières. Les effets des perturbations ont également été analysés plus précisément en étudiant la dynamique transitoire et l'équilibre à long terme. Ce chapitre vise tout particulièrement à vérifier si les perturbations peuvent catalyser des transitions rapides entre différents types de forêts (e.g., mixte à tempérée) et ainsi accélérer les changements de biome à grande échelle.

Pour répondre à cet objectif, la dynamique forestière a été simplifiée à une dynamique de transition entre quatre états forestiers distincts déterminés en fonction de la composition des communautés : boréal, mixte, tempéré et pionnier (Fig. 0.6). La dynamique a ainsi été

formalisée sous la forme d'un modèle de Markov multi-états. La représentation de la dynamique forestière par des chaînes de Markov offre une interprétation mécanistique simple des probabilités de transition estimées (Vissault, 2016; Wootton, 2001) en lien avec les changements d'aire de répartition. Par exemple, les transitions vers l'état pionnier reflètent les perturbations, les transitions à partir de pionnier reflètent les processus de colonisation et de dispersion, alors que les transitions entre les autres états reflètent l'exclusion compétitive. Les propriétés de ce type de modèle permettent aussi d'étudier la dynamique transitoire ainsi que l'équilibre à long terme. L'analyse d'espèces indicatrices (Dufrêne et Legendre, 1997) a été adaptée afin de faire le lien entre les changements démographiques et les transitions forestières.

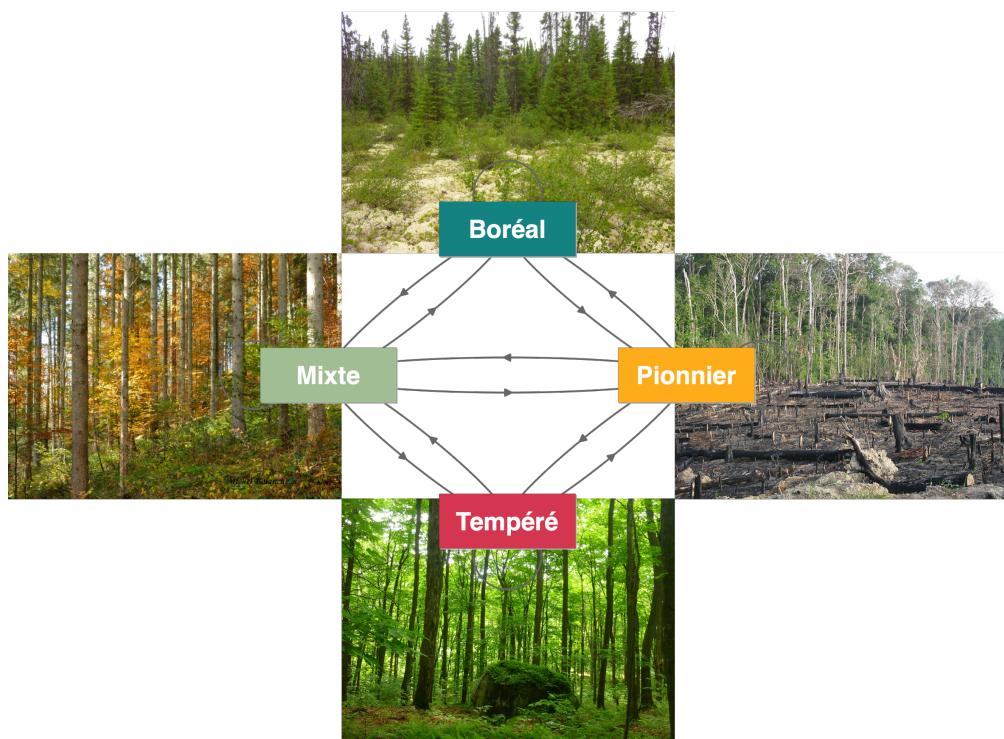


Figure 0.6. Représentation schématique de la dynamique de transitions entre les quatre états forestiers. Cette simplification de la dynamique forestière permet d'étudier les processus d'intérêt. Par exemple, les transitions vers l'état pionnier sont causées par des perturbations, tandis que la transition de l'état mixte vers l'état tempéré peut être causée par la perte des espèces boréales ou le gain en espèces tempérées.

0.10.3. Chapitre 3 — Dynamique de recrutement des gaulis des espèces tempérées

Enfin, le chapitre 3 s'intéresse plus en détails au processus de recrutement des espèces tempérées à leur limite nord. L'objectif est de quantifier les changements d'aires de répartition des gaulis, avec un intérêt particulier pour quatre espèces tempérées (*Acer rubrum*, *Acer saccharum*, *Betula alleghaniensis* et *Fagus grandifolia*) et d'identifier les facteurs environnementaux sous-jacents des processus de recrutement.

Des études récentes ont montré qu'un changement temporel dans la limite latitudinale ou altitudinale de la répartition des jeunes arbres peut agir comme un signal de changement d'aire de répartition (Boisvert-Marsh *et al.*, 2014; Sittaro *et al.*, 2017), puisque la régénération devrait réagir plus rapidement aux changements environnementaux. Cependant, en ignorant les effets des perturbations sur la dynamique de régénération, des différences importantes pourraient être masquées. La comparaison des changements de distribution latitudinale des gaulis dans le temps (de 1970-1981 à 2005-2018) entre les niveaux de perturbations me permet de déterminer si les perturbations promeuvent ou freinent de nouveaux recrutements au-delà des limites de l'aire de répartition.

Enfin, pour identifier les facteurs environnementaux qui contrôlent le recrutement des espèces tempérées à leur limite nord, j'ai utilisé des modèles en deux parties (aussi connu sous le nom de *hurdle model*) pour chaque espèce en fonction du climat, des conditions topographiques et édaphiques, de l'abondance d'arbres parents dans le peuplement et aux alentours, du couvert en résineux et des perturbations. Ce type de modèle permet de modéliser d'abord la probabilité de présence d'une recrue et ensuite le nombre de recrues conditionnel à l'occurrence du recrutement. Ainsi, d'une certaine façon, cette approche permet de considérer les rétroactions réciproques entre les filtres régionaux sur le recrutement (e.g., climat, dispersion) et les filtres locaux (e.g., compétition avec les espèces boréales et réponse aux conditions du sol).

0.10.4. Chapitre 4 — Conclusion

Dans ce dernier chapitre, je résume mes conclusions et intègre mes résultats dans un cadre conceptuel plus large. Je tente également de faire le pont entre mes recherches et l'aménagement forestier. Pris ensemble, les trois chapitres principaux de la thèse fournissent un éventail complémentaire de méthodes et d'approches récentes et nouvelles pour mieux comprendre l'effet combiné du changement climatique et des perturbations sur la dynamique forestière. En accordant une attention particulière aux différents aspects des variations de la diversité et de la composition des communautés forestières, cette thèse apporte des perspectives originales et révèle des changements précédemment imperceptibles sous l'angle de l'analyse des limites des aires de répartition des espèces. Les résultats présentés ici aideront à améliorer

notre compréhension des réponses de la biodiversité forestière aux multiples facteurs de stress anthropiques qui se sont accélérés au cours des dernières décennies.

0.10.5. Les forêts du Québec

Afin de détecter les changements à long terme dans les communautés forestières, j'ai analysé les données du réseau d'inventaires forestiers du Québec méridional. Depuis les années 1970, plus de 12 000 parcelles d'échantillonnage permanentes ont été établies et mesurées périodiquement par le ministère des Forêts, de la Faune et des Parcs du Québec dans le but d'améliorer la base de connaissance sur les ressources forestières provinciales (MFFP, 2016). La profondeur temporelle et l'étendue spatiale de ce réseau de placettes d'inventaire permanentes en font un outil indispensable pour étudier les différents aspects de la dynamique spatio-temporelle des communautés forestières en réponse aux changements globaux.

Au Québec, la composition et la distribution des forêts sont fortement structurées par le gradient latitudinal de la température. Ainsi on aura un gradient de biodiversité décroissant, allant des forêts feuillues au sud jusqu'au forêts de conifères au nord, qui reflète étroitement celui de la température moyenne. Le territoire forestier du Québec peut donc être classifié en différents groupes de végétation (sous-zones) : la forêt mélangée ($98\ 600\ km^2$), écotone où se côtoient les espèces feuillues et résineuses, marque la transition entre la forêt décidue ($111\ 100\ km^2$) au sud dominée par l'érable à sucre et le bouleau jaune ; et la forêt boréale continue ($551\ 400\ km^2$) au nord composée majoritairement d'épinette noire et de sapin baumier (Fig. 0.7; Saucier *et al.*, 2009). Au cours des dernières décennies, une forte augmentation des températures a été observée à travers le Québec. Alors que les écotones sont particulièrement vulnérables au changement climatique, la distinction marquée entre les différents types de forêts de la région d'étude facilite la détection rapide des changements de composition récents.

Zones de végétation et domaines bioclimatiques du Québec

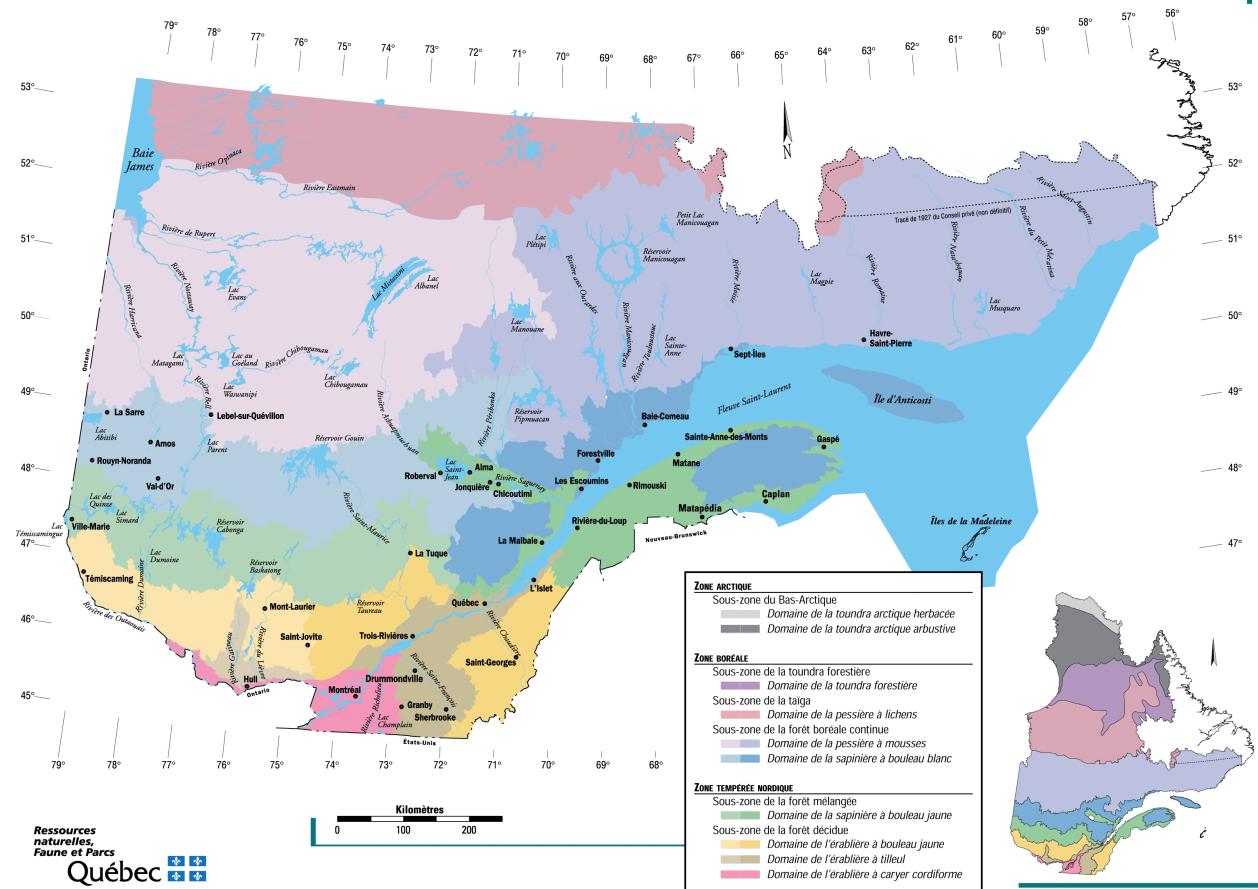


Figure 0.7. Carte des domaines et sous-domaines bioclimatiques du Québec méridional. La zone d'étude de cette thèse couvre 761 100 km² et s'étend du domaine de l'érablière à caryer cordiforme, à l'extrême sud de la forêt décidue, jusqu'au domaine de la pessière à mousse, à la limite nord de la forêt boréale continue. La structure latitudinale est principalement déterminée par le gradient de température, tandis que les divisions est-ouest correspondent à des variations de précipitation.

First Article.

Disturbances amplify tree community responses to climate change in the temperate-boreal ecotone

by

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ABSTRACT.

Aim Climate change causes major shifts in species distributions, reshuffling community composition and favouring warm-adapted species ("thermophilization"). Tree community response is likely to be affected by major disturbances such as fire and harvest. Here, we quantify the relative contributions of climate change and disturbances to temporal shifts in tree composition over the last decades and evaluate whether disturbances accelerate community thermophilization.

Location Québec, Canada

Time period 1970–2016

Taxa studied Trees

Methods Using 6281 forest inventory plots, we quantified temporal changes in species composition between a historical (1970–1980) and a contemporary period (2000–2016) by measuring temporal β diversity, gains and losses. The effects of climate and disturbances on temporal β diversity were quantified using multiple regressions and variation partitioning. We compared how community indices of species temperature preference (CTI) and shade tolerance (CSI) changed for forests that experienced different levels of disturbance. We quantified the contribution of species gains and losses to change in CTI.

Results Temporal β diversity was mainly driven by disturbances, with historical harvesting as the most important predictor. Despite the prevailing influence of disturbances, we revealed a significant thermophilization ($\Delta\text{CTI} = +0.03^\circ\text{C}/\text{decade}$) throughout forests in Québec. However, this shift in community composition was weakly explained by climate change and considerably slower than the rate of warming ($+0.14^\circ\text{C}/\text{decade}$). Importantly, thermophilization was amplified by moderate disturbances ($+0.044^\circ\text{C}/\text{decade}$), almost a three-fold increase compared to minor disturbances ($+0.015^\circ\text{C}/\text{decade}$). The gains and losses of a few tree species contributed to this community-level shift.

Conclusions Our study provides evidence that disturbances can strongly modify tree community responses to climate change. Moderate disturbances, such as harvesting, may reduce competition and facilitate gains of warm-adapted species, which then accelerate thermophilization of tree communities under climate change. Although accelerated by disturbances, community thermophilization was driven by the gains and losses of a small number of species, notably gains of maples.

Keywords: Beta diversity, Climate change, Community temperature index, Community temporal change, Disturbances, Forest, Québec, Temperate-boreal ecotone, Thermophilization.

1. Introduction

Climate warming over the past century has led to distribution shifts in many species (Parmesan et Yohe, 2003). Despite the general trend of poleward and upward (in altitude) range shifts, the timing, magnitude and even direction of species shifts vary considerably among taxa and regions (VanDerWal *et al.*, 2013). Major reshuffling of community composition is therefore expected. Yet, we lack an understanding of the community-level consequences of climate-driven shifts. This knowledge gap is even greater in forests where tree response is slow (Sittaro *et al.*, 2017) relative to the short duration of typical ecological studies. So far, much of the emphasis has been placed on detecting species shifts at their range edge, where early signs of changes are expected to be readily detectable (Jump *et al.*, 2009). As such, there is a growing body of evidence for contemporary shifts in tree species distributions along altitudinal gradients in mountains (Beckage *et al.*, 2008; Lenoir *et al.*, 2008; Savage et Vellend, 2015), where ecotones are narrow and well-defined (Jump *et al.*, 2009). Similar evidence is also beginning to emerge for latitudinal shifts (Boisvert-Marsh *et al.*, 2019; Fisichelli *et al.*, 2014; Sittaro *et al.*, 2017). Though, because of the focus on shifts at range limits (e.g., leading and rearing edges of species ranges), there has been little empirical work on the effect of climate change on tree community composition and abundance distributions within the core of species range itself (e.g. Esquivel-Muelbert *et al.*, 2018; Searle et Chen, 2017).

Worldwide increases in tree mortality rates triggered by drought and heat stresses have been documented recently (Allen *et al.*, 2010). In the long term, even minor changes in demographic rates can modify the balance between local species gains and losses, leading to temporal change in community composition. Yet, as trees are long-lived species, mortality and recruitment rates are low (Iverson et McKenzie, 2013). Thus, tree community responses to contemporary climate warming are likely to be lagged, resulting in extinction debts (Svenning et Sandel, 2013; Talluto *et al.*, 2017). Consequently, tree community-level response to climate change remains difficult to quantify and is probably underestimated.

Furthermore, in northern temperate and boreal regions, natural disturbances (fires and insect outbreaks) and anthropogenic disturbances (timber harvesting) are major drivers of tree community dynamics (Goldblum et Rigg, 2010). These pulse disturbances are likely to dominate local, short-term biotic changes, resulting in increased prevalence of young forests dominated by early successional species. These short-term effects could easily mask climate-induced changes that are expected to occur on much longer time scales and broader spatial scales. For this reason, disturbances are often considered to be inconvenient confounding factors instead of an inherent part of contemporary ecosystems. Thus, numerous studies have searched for trends in relatively undisturbed systems (Parmesan et Yohe, 2003) rather than accounting for their effects. Yet, disturbances and climate change have a high potential

for interactions, which can lead to synergistic or antagonistic ecological effects that are difficult to predict (Brook *et al.*, 2008). Indeed, disturbances create canopy openings that could facilitate the northward migration of temperate species (Boisvert-Marsh *et al.*, 2019; Leithead *et al.*, 2010; Vanderwel et Purves, 2014; Xu *et al.*, 2012). In addition, the frequency and intensity of natural disturbances can increase as an indirect effect of climate change (Seidl *et al.*, 2017).

Although it is widely assumed that positive synergy between disturbances and climate warming should play a key role in contemporary tree community changes, empirical studies have reached conflicting conclusions. For example, comparison of early industrial (early 1900) to contemporary forests in the Bas-Saint-Laurent region of Québec showed that logging practices turned old-aged conifer forests into young mixed and deciduous forests (Boucher *et al.*, 2006, 2009). Leithead *et al.* (2010) also observed that the establishment of southern temperate species in the temperate-boreal ecotone of northern Ontario increased with the size and age of canopy gaps. While Boisvert-Marsh *et al.* (2019) found that climate change outweighs disturbances in explaining latitudinal shifts of tree saplings in Québec in the last decades, Danneyrolles *et al.* (2019) found larger impacts of anthropogenic disturbances than climate warming on forest compositional changes in southern Québec over the last centuries. Hence, to anticipate and adapt to future forest changes, large-scale empirical studies are required in order to unravel individual and aggregated impacts of multiple stressors on forest composition.

Even though disturbances may mask slow community responses to climate change, these two drivers leave distinguishable signatures on communities. Climate warming should favour warm-adapted species at the expense of cold-adapted species, leading to a “thermophilization” of communities (De Frenne *et al.*, 2013; Savage et Vellend, 2015). Conversely, disturbances should increase the prevalence of young forests dominated by shade-intolerant species (Boucher et Grondin, 2012; Savage et Vellend, 2015). Hence, analysing shifts of relevant functional traits and ecological affinities in communities using large-scale monitoring data should disentangle the role of different environmental drivers in shaping communities (Viole *et al.*, 2007). For instance, the Community Temperature Index (CTI) has been used to measure thermophilization in various communities, such as plants, trees, birds and fishes (Becker-Scarpitta *et al.*, 2019; Cheung *et al.*, 2013; Danneyrolles *et al.*, 2019; De Frenne *et al.*, 2013; Devictor *et al.*, 2008; Feeley *et al.*, 2013; Gaüzère *et al.*, 2015). The CTI is a community abundance-weighted average of the Species Temperature Indices (STI; proxy for species thermal preference computed as the mean temperature of a given species distribution). Because CTI reflects the relative abundance of warm-adapted (high STI) vs cold-adapted species (low STI), it is expected to increase following climate warming if species are moving according to their temperature requirements.

Here, we quantify the temporal shifts in tree community composition in the temperate-boreal ecotone, and test whether recent climate change is impacting forest composition. We analysed data from a long-term forest inventory program across meridional Québec, where vegetation ranges from northern hardwood forests dominated by *Acer saccharum* at low latitudes (up to 47°N) to mixed forests dominated by *Abies balsamea* (from 47°N to 48°N), to boreal forests dominated by *Picea mariana* at high latitudes (from 49°N to 52°N). This dataset allowed us to compare community responses to recent climate change in plots that experienced different levels of disturbances along a broad latitudinal gradient. We address four questions: (1) how has the composition of forest communities changed during the last decades across different bioclimatic domains? (2) What is the relative contribution of climate change and disturbances to these temporal community changes? (3) Have forest communities experienced a thermophilization during the last decades? And can disturbances accelerate community thermophilization? (4) How do gains and losses of specific tree species contribute to thermophilization?

Specifically, we measured temporal β diversity (Legendre, 2019) over 6000 resurveyed communities between a historical (1970–1980) and a contemporary (2000–2016) period. Temporal β diversity, which describes the temporal dissimilarity in community composition between survey times, was decomposed into gains and losses to investigate the underlying mechanisms of change. Then, we quantified the effects of climate change and disturbances on temporal β diversity using multiple regressions and variation partitioning. Using community indices for temperature (CTI) and shade tolerance (CSI), we quantified community-level changes associated with thermophilization and succession and compared these changes among levels of disturbances. We finally quantified the species-specific contributions to thermophilization.

2. Methods

2.1. Study area

To analyse large-scale temporal changes in forest community composition, we used the Québec forest inventory plots that have been sampled in six bioclimatic domains, south of the 52nd parallel, since 1970 by the Ministère des forêts, de la Faune et des Parcs (Fig. 1.1; MFFP, 2016). For each plot, we compared the tree composition between the first and last surveys. To maximise the time interval between surveys, only plots that were inventoried in two distinct time periods (historical period: 1970–1980; contemporary period: 2000–2016) were retained for analysis. We disregarded plots that were subjected to active reforestation during the study period as we were interested in compositional changes resulting from natural post-disturbance recolonisation. We also eliminated plots without trees (due to a disturbance)

either at their first or last year of sampling. This yielded a subset of 6281 plots analysed (Fig. 1.1), with a median of 35 years between surveys (1st quartile: 33 and 3rd quartile: 41 years).

Within each circular plot (400 m^2), trees larger than 9 cm in diameter at breast height (DBH) were identified to species, measured and their vitality noted (MFFP, 2016). The selected plots included a total of 51 tree species, from which we eliminated introduced and planted species as well as species with a single occurrence, yielding 45 analysed species (Table A.1). Rare species were included in the analyses because even the rarest can contribute to temporal changes; their identity does not bias our analyses and, contrary to mobile species, there is little detection bias in tree surveys. Each species was assigned according to their functional traits to one of three species groups of interest: boreal (6 species), pioneer (9 species) and temperate (30 species; see Table A.1 for details).

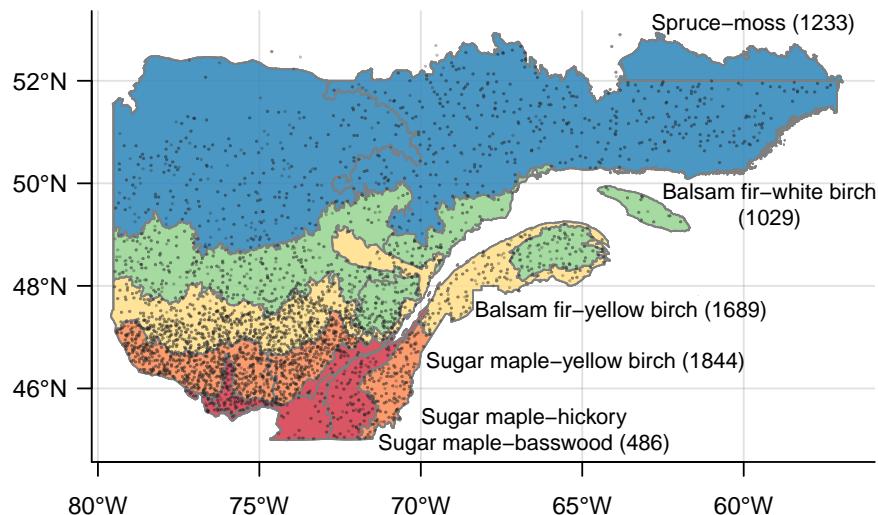


Figure 1.1. Locations of the 6281 forest inventory plots in meridional Québec, Canada. Colours delimit the six bioclimatic domains. The two southernmost domains (orange) were combined in our analyses. The number of forest plots in each domain is written in parentheses.

2.2. Environmental variables

The annual past climatic conditions, covering a period from 1960 to 2013, were extracted using a 2 km^2 (60 arc sec) resolution grid for the entire study area using the ANUSPLIN climate modelling software (<http://cfs.nrcan.gc.ca/projects/3/8>; McKenney *et al.*, 2011). Bioclimatic variables hypothesised to influence tree survival were intercepted at plot locations: the mean temperature and total precipitation during the growing season, minimum temperature of the coldest period, maximum temperature of the warmest period and the annual climate moisture index (CMI; difference between annual precipitation and potential

evapotranspiration). From these bioclimatic variables, we derived different predictors (see Table 1.1 for details). Over the past four decades, growing season temperature and precipitation have increased by 0.14 °C/decade and 9.5 mm/decade, respectively, while CMI has decreased by 1.2 cm/decade (Fig. A.1).

Table 1.1. Description of the predictors used in the multiple linear regression models. See Table A.2 for details about disturbance types.

Variable name	Variable description
Baseline conditions	
Temp, Temp ²	Mean temperature during growing season and its second order polynomial. 10-year average prior to first survey of each plot (°C).
Precip, Precip ²	Total precipitation during growing season and its second order polynomial. 10-year average prior to first survey of each plot (mm).
ΔTime	Time interval between first and last measurements (years).
Climate change	
ΔTemp	Slope between Temp and time (°C/y).
ΔPrecip	Slope between Precip and time (mm/y).
ΔCMI	Slope between Climate Moisture Index and time (cm/y).
Temp min	Extreme minimum temperature. Difference between minimum and mean temperature of the coldest period (°C).
Temp max	Extreme maximum temperature. Difference between maximum and mean temperature of the warmest period (°C).
CMI min	Extreme minimum Climate Moisture Index (CMI). Difference between minimum CMI and mean CMI (cm), as a proxy of drought.
Disturbances	
Age	Stand age (years).
Old harvest	Tree harvesting (clearcutting, partial cutting, selection cutting, etc.) that occurred before the study period. Minor (0), moderate (1) or major (2).
Recent harvest	Tree harvesting (clearcutting, partial cutting, selection cutting, etc.) that occurred during the study period. Minor (0), moderate (1) or major (2).
Old natural	Natural disturbances (fire, insect outbreak, windfall, etc.) that occurred before the study period. Minor (0), moderate (1) or major (2).
Recent natural	Natural disturbances (fire, insect outbreak, windfall, etc.) that occurred before the study period. Minor (0), moderate (1) or major (2).

We also collected information pertaining to natural and anthropogenic disturbances that have affected the forest plots both before and during the study period (Table 1.1, Fig. A.2). At each plot, 21 disturbance types and their level of intensity (moderate or major) were recorded (Table A.2; MFFP, 2016). The MFFP defined major disturbances as events that resulted in a loss of at least 75% of the tree basal area, whereas moderate disturbances have caused between 25% and 75% of loss. For our regression models, we differentiated two main types of disturbances: natural disturbances and harvest, with 3 levels of intensity each (minor, moderate or major) and 2 periods (old: occurred before the first inventory, and recent: occurred during the study period). To compare diversity measures among disturbance levels, we also assigned each forest to the level of intensity of the worst disturbance it experienced (regardless of the type or timing).

Core samples were also collected on selected trees during surveys to measure their age. Stand age was estimated as the mean of these measures to account for forest succession processes after disturbances. Finally, because the time interval between the first and last measurements varies among the forest plots, it was included as a predictor.

2.3. Analysis

2.3.1. β diversity

For each plot, we computed temporal β diversity (Legendre, 2019), which is the dissimilarity in species composition between two surveys of a given plot, by comparing local tree abundance (i.e. number of individuals) in forest plots between the historical (1970-1980, t_1) and contemporary (2000-2016, t_2) periods. The dissimilarity (β) was computed using the Ružička coefficient (Fig. A.3):

$$\beta = (B + C)/(A + B + C) \text{ where, for } n \text{ species:}$$

$A = \sum_{j=1}^n a_j$: unscaled similarity. a_j represents the abundance of species j that is common between t_1 and t_2 ;

$B = \sum_{j=1}^n b_j$: unscaled species abundance losses. b_j represents the abundance of species j present at t_1 but not at t_2 ; when species j increases in abundance, $b_j = 0$;

$C = \sum_{j=1}^n c_j$: unscaled species abundance gains. c_j represents the abundance of species j present at t_2 but not at t_1 ; when species j decreases in abundance, $c_j = 0$;

This temporal β diversity varies from 0 (community compositions at t_1 and t_2 are exactly the same) to 1 (communities have no shared species). The use of this dissimilarity index enabled us to decompose the compositional change into relative gains ($C/(A + B + C)$) and losses ($B/(A + B + C)$) in tree abundances (Fig. A.3). Throughout this paper, gains and losses refer to these relative metrics.

This additive framework allowed us to partition further the different components contributing to β diversity. Temporal dissimilarity in tree community can be decomposed into

the dissimilarity (gains and losses) of different species groups of interest, here boreal, pioneer and temperate species (Table A.1). The temporal dissimilarity of a given group, for instance boreal, relative to all species is simply: $\beta_{boreal} = (B_{boreal} + C_{boreal})/(A + B + C)$, with $(A + B + C)$ the denominator computed over all tree species. As a consequence, β can be decomposed as follows:

$$\beta = \beta_{boreal} + \beta_{pioneer} + \beta_{temperate}$$

2.3.2. Assessing the relative importance of drivers of community changes

We evaluated the effects of multiple drivers on temporal β , gains and losses using multiple regressions, in combination with variation partitioning analyses (Borcard *et al.*, 1992; Peres-Neto *et al.*, 2006). For these analyses, we used a logit transformation $y' = \log(y/(1 - y))$ of the response variables (β , gains, losses) as they were all in the standard unit range [0, 1].

In order to quantify the variation explained by climate change and disturbances, while controlling for the baseline climate gradient and different time intervals, we classified our predictor variables into three subsets: baseline conditions, climate change and disturbances (see Table 1.1). We then generated regression models predicting β , gains and losses, for each of the three subsets. We also tested relevant interactions between disturbance and climate predictors: Natural (old and recent) \times Δ CMI and Natural (old and recent) \times Δ Temp, because drought and heat stress can increase natural disturbance frequency; Harvest (old and recent) \times Δ Temp, because the effect of harvest was hypothesised to be influenced by warmer temperatures. A forward selection of explanatory variables based on two stopping criteria (significance level α and global R^2_{adj} ; Blanchet *et al.*, 2008) was performed to obtain parsimonious regression models for each of the three subsets. The predictors had been previously standardised to z -scores to allow comparison of their slope coefficients. We also ensured that residuals met the assumptions of normality and homoscedasticity.

We assessed the unique contributions of each predictor subset (baseline conditions, climate change and disturbances) as well as their shared effect on forest community changes using variation partitioning analysis on the parsimonious regression models.

2.3.3. Functional index of community change

To test whether or not climate warming contributed to community changes, we examined the temporal changes in the distribution of species temperature values within every plot. We quantified such changes by the shift in the mean (Community Temperature Index or CTI; Devictor *et al.*, 2008), as well as the lower 10th percentile and the upper 90th percentile of this plot-level distribution (De Frenne *et al.*, 2013).

To compute these metrics, we first combined climate and tree occurrence data to obtain species temperature distributions. Specifically, we overlaid interpolated climate data (mean annual temperature averages for 1970–2000 at a spatial resolution of 1 km², available online

<http://worldclim.org/version2>; Fick et Hijnmans, 2017) and occurrence data from multiple forest inventory databases of eastern North America (collected in the QUICC-FOR project; <https://github.com/QUICC-FOR>) for the focal species. The mean annual temperature for each occurrence was extracted to infer species temperature distributions. Following Devictor *et al.* (2008), we used the mean of these temperature values as a proxy for species thermal preference (Species Temperature Index, STI, in Celsius; Table A.1). For each plot in each time period, the CTI was then calculated as the mean of the STI values weighted by the abundances of the species present in that plot.

Following De Frenne *et al.* (2013), we computed the 10th and 90th percentiles of the plot-level temperature distributions, which correspond to the cold and warm tails of the distribution. To do so, for every plot and every species, we sampled 1000 temperature values per individual from the species' temperature distribution. The plot-level temperature distributions corresponds to the combination of the temperature values for all individuals in a given plot. From these distributions, which accounted for species composition and their relative abundances, we computed the 10th and 90th percentiles. Note that contrary to De Frenne *et al.* (2013), we used the entire distribution for each species instead of modelling species thermal response curves because numerous species distributions were not Gaussian.

To evaluate the directionality of the changes in communities between the historical (t_1) and contemporary (t_2) periods, we computed the temporal shift in the mean CTI, the cold tail and the warm tail (in °C per decade) as follows:

$$\Delta CTI = \frac{CTI_{t2} - CTI_{t1}}{t_2 - t_1} \times 10$$

The shifts in the cold and warm tails were computed in the same way as for the shifts in mean CTI. A positive value of ΔCTI indicates an overall thermophilization of the tree community in degrees per decade. A positive shift of the cold tail indicates a decrease of cold-adapted species, while a positive shift of the warm tail indicates an increase of warm-adapted species; both result in thermophilization.

We also quantified how each species contributed to ΔCTI through gain or loss in abundances. Species contributions were assessed following these steps: for each species, (1) we replaced its abundance at t_2 by its abundance at t_1 , as if this species abundance had not changed over time; (2) we computed a new CTI_{t2}' ; (3) then we calculated $\Delta CTI'$ using CTI_{t2}' and CTI_{t1} as above; and (4) we measured the difference between $\Delta CTI'$ and ΔCTI in each plot. A positive value indicates that the change (gain or loss) of a given species abundance increases thermophilization in a plot. Then, we determined the role of species gains and losses in ΔCTI by averaging their contributions for plots where they increased and where they decreased.

To test the hypothesis that community changes are resulting from post-disturbance succession, we collected traits about species shade tolerance (Species Shade Index, SSI; Niinemets et Valladares, 2006), which represents a species ability to grow in shade conditions. Shade tolerance indices ranged from 1 (very intolerant to shade) to 5 (very tolerant) on a continuous scale. As for CTI, a Community Shade Index (CSI) was computed for each plot as the mean of the SSI values weighted by the abundances of the species present in that plot. Temporal shift in CSI between the historical and contemporary time periods, Δ CSI, was computed in the same way as for Δ CTI, where a positive value indicates a progress in stand succession toward climax, in units per decade.

All analyses were performed using the R programming language version 3.5.1 (R Core Team, 2018). The list of R packages that have been used throughout the analysis is provided in Table A.3. All the data used in the study as well as R scripts to reproduce the analyses and the figures can be found online at <https://github.com/mhBrice/thermophilization> (<https://doi.org/10.5281/zenodo.3242773>).

3. Results

3.1. Temporal β diversity

The mean temporal β diversity was 0.56 over all sites in the study area ($n = 6281$), and these temporal changes in composition were attributable to slightly more gains in abundances (52.5%) than losses (47.5%; Fig. 1.2a). Temporal β diversity varied along a latitudinal gradient; it tended to decrease northward, reaching its maximum at 48°N of latitude, which corresponds to the northern limit of the balsam fir-yellow birch domain, the ecotone between boreal and deciduous forests. North of the 49°N of latitude, in the spruce-moss domain, temporal β changes were dominated by losses whereas, south of this limit, gains prevailed. Latitudinal patterns were also visible in the contributions of the three species groups to temporal β (Fig. 1.2b). At minor disturbance level, community changes were mainly determined by gains in temperate species south of 47°N and by gains in boreal species north of 47°N (where boreal species are the most abundant species group).

The magnitude of compositional changes in forests was highly influenced by disturbances (Figs 1.2b-d, 1.3, A.4). In each domain, the β diversity values of highly disturbed forests are strongly skewed (Fig. 1.3). The mean temporal β was 0.43 at minor disturbance level, whereas it was 0.53 at moderate disturbance level and reached 0.74 at major disturbance level (all domains combined). Moreover, the fraction of changes attributed to losses was generally lower at minor, than at moderate and major disturbance levels (minor: 41%; moderate: 48%; major: 50%, all domains combined), especially for the spruce-moss domain (minor: 40%; moderate: 73%; major: 64%; Fig. 1.3). At minor disturbance level, both

boreal and temperate species groups experienced more gains than losses (Fig. 1.2b), while at major disturbance level, we observed a strong surge in losses of boreal tree species along with larger gains of pioneer species (Fig. 1.2d). In contrast, gains in temperate species were higher at moderate disturbance level (Fig. 1.2c). Some species have experienced great changes in abundance and occurrence throughout these domains, namely *Picea mariana*, *Acer rubrum*, *Betula alleghaniensis*, *Fagus grandifolia* and *Populus tremuloides*, and likely contributed largely to the pattern of temporal β diversity (Fig. A.5).

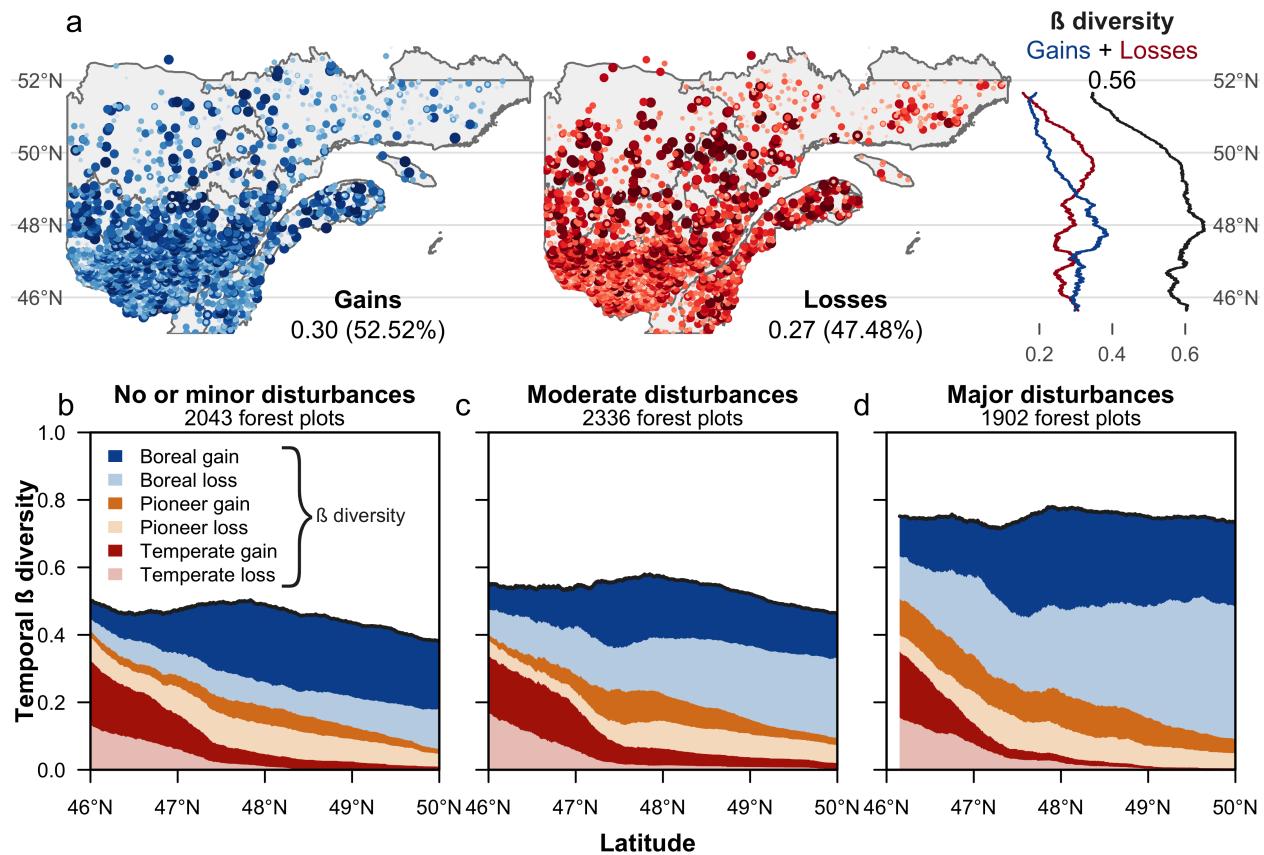


Figure 1.2. Maps of gains and losses in tree abundances (a) and latitudinal trends in temporal β diversity, decomposed into gains (blue) and losses (red) of boreal, pioneer and temperate trees, for different levels of disturbance (b-d). The sizes and colours of the points on the maps are proportional to the values of interest. The latitudinal trends in temporal β in a-d are based on moving averages computed on each index against latitude (window size of 500 plots in panel a and 400 plots in panels b-d), to smooth out local-scale fluctuations and highlight broad-scale trends.

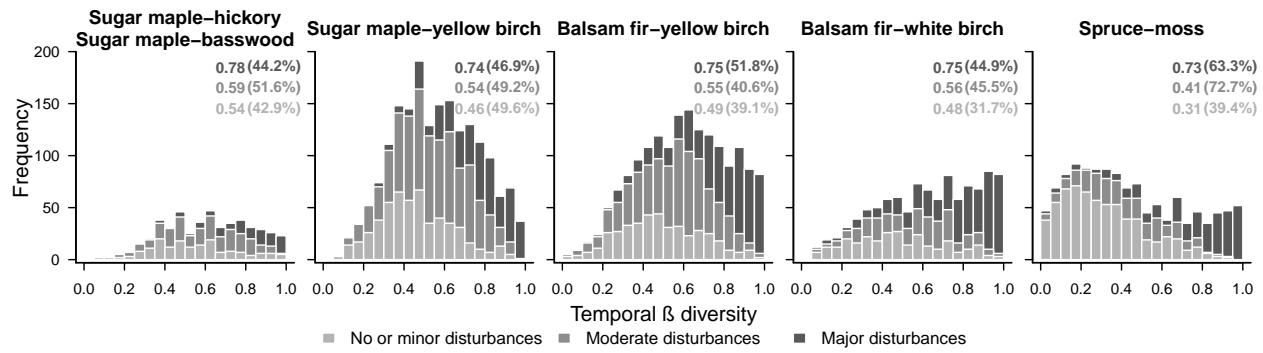


Figure 1.3. Frequency distributions of temporal β diversity in forest plots by bioclimatic domains. Forests of different disturbance levels are stacked on top of each other. The values written in the panels are the mean temporal β diversity values followed by the percentage of losses in parentheses. The distribution of β diversity values is skewed to the right for higher disturbance levels.

3.2. Drivers of temporal changes

Once combined, predictors from the three subsets (baseline, climate change and disturbances; Table 1.1) explained together 40% of the variation of temporal β diversity, and 30% for both gains and losses (Fig. 1.4). As revealed by the variation partitioning analyses, community temporal changes were mainly driven by disturbances (R^2_{adj} for β : 31%; gains: 25%; losses: 26%), whereas the unique influence of climate change as well as that of baseline conditions were significant but comparatively modest ($R^2_{adj} < 1\%$; Fig. 1.4d-f).

Overall, disturbances enhanced temporal β diversity, with old major harvest (Old harvest₂) being the most important driver, followed by old major natural disturbances (Old natural₂; Fig. 1.4a-c). Interestingly, while recent disturbances (natural and harvest) promoted losses and reduced gains, old disturbances had the opposite effect (Fig. 1.4b-c). As time-since-disturbance increased and the forests grew old (Age), forest composition changed less and colonisation by new individuals became less frequent (Fig. 1.4a-b).

Regression models provided only weak evidence of climate change effect on forest community changes. Mainly, extreme minimum climate moisture index (CMI min) and extreme cold (Temp min) contributed to community changes through losses in tree abundances (Fig. 1.4a,c). Increase in precipitation (Δ Precip) favoured tree gains. Only one interaction was retained, which indicated that stronger warming (Δ Temp) mitigated the effect of recent moderate harvest (Recent harvest₁) on losses. Variables related to baseline conditions were more important than climate change variables; the effects of mean temperature (Temp) and total precipitation (Precip) likely reflect the latitudinal gradient in community change, while the effect of time interval between surveys (Δ Time) reflects the fact that community change takes time.

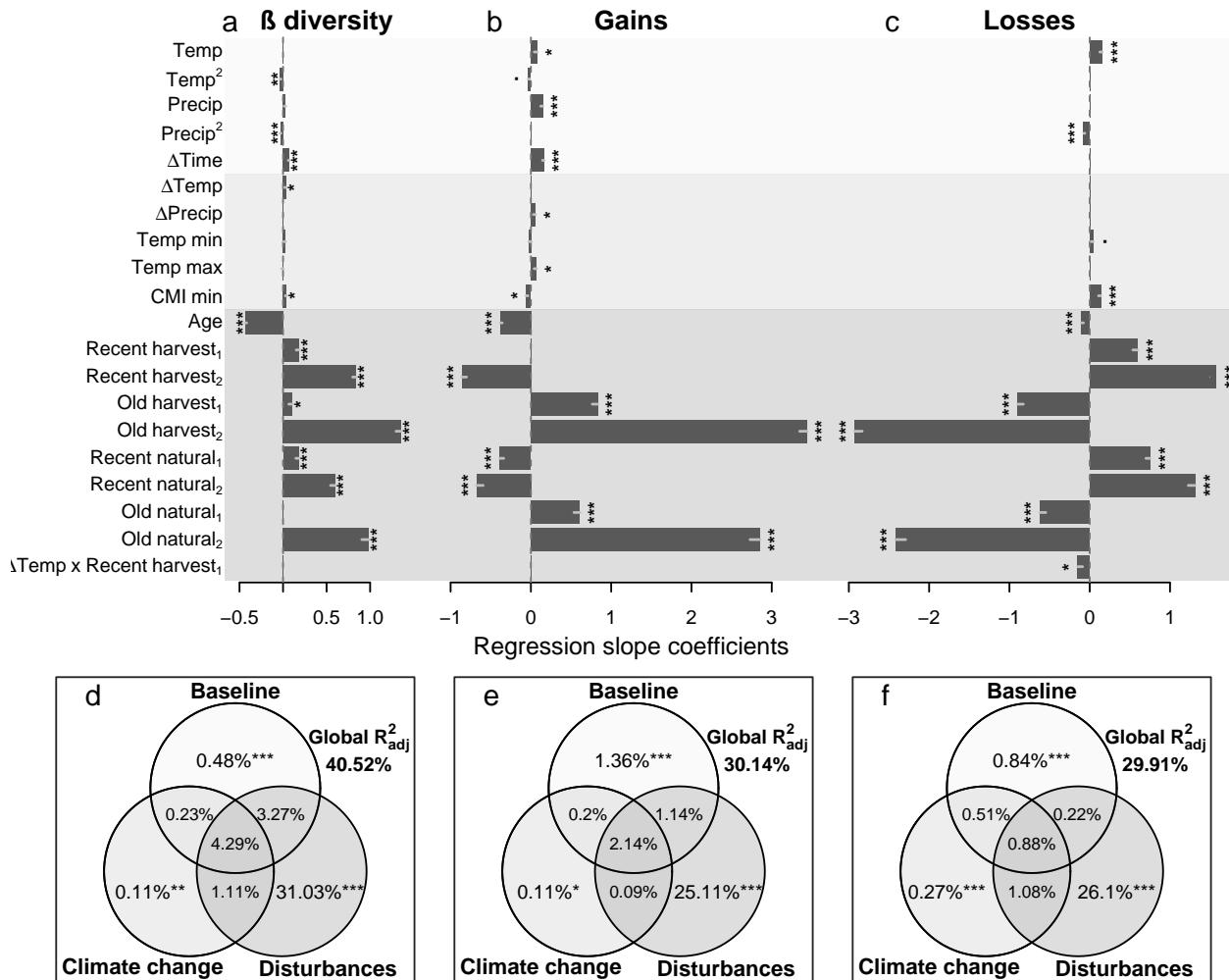


Figure 1.4. Slope coefficients from multiple regression models for (a) temporal β diversity, (b) species gains and (c) species losses and the corresponding variation partitioning diagrams (d, e, f). Error bars represent one standard error of the slope coefficient. For the regression models, only the selected predictors are shown. Subscripts following disturbance predictors indicate their levels of intensity: 1 Moderate and 2 Major. In each variation partitioning, significance of each unique fraction was tested using 9999 permutations, while shared fractions cannot be tested. Stars indicate the level of significance of the p -values (* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$). See Table 1.1 for description of the predictor variables.

3.3. Changes in community temperature and shade indices

The community temperature index (CTI) increased significantly between the historical and contemporary periods (paired t -test p -value < 0.001 ; mean of $+0.03$ °C/decade for all plots combined, ranging from -0.02 to $+0.05$ across domains), which indicates a generalised community thermophilization throughout the study area. During the same time period, the community shade index (CSI) also increased ($+0.01$ unit/decade), suggesting a transition towards late successional forests (Fig. 1.5).

Thermophilization was significantly larger in moderately disturbed forests ($\Delta\text{CTI} = +0.044 \text{ }^{\circ}\text{C}/\text{decade}$) than in undisturbed ($+0.015 \text{ }^{\circ}\text{C}/\text{decade}$) or highly disturbed forests ($+0.018 \text{ }^{\circ}\text{C}/\text{decade}$; ANOVA $F_{2,6278} = 14.59$, $p\text{-value} < 0.001$; a post-hoc Tukey test showed significantly higher ΔCTI at moderate disturbance than at the other levels). Moreover, the latitudinal pattern of ΔCTI varied with the disturbance level: the thermophilization in moderately disturbed forests extended further north than in undisturbed forests, exceeding 48°N , up in the balsam fir-yellow birch domain (Fig. 1.5b,e), while at major disturbances, thermophilization was more or less constant across the latitudinal gradient (Fig. 1.5c,f). Despite the influence of disturbances on thermophilization, change in CTI was weakly explained by our complete set of environmental predictors (R^2_{adj} ca. 3%). Moreover, the relationship between thermophilization and climate change predictors was surprisingly weak ($R^2_{adj} < 1\%$), with no correlation at all with temperature change.

The analysis of ΔCSI revealed that major disturbances resulted in a large decrease in CSI (Fig. 1.5c; mean $\Delta\text{CSI} = -0.037$), consistent with higher gains in pioneer species (Fig. 1.2), while minor disturbances led to an increase in CSI (Fig. 1.5a; mean $\Delta\text{CSI} = +0.060$). Both influenced by disturbances, ΔCTI and ΔCSI were negatively correlated (Pearson $r = -0.2$, $p\text{-value} < 0.001$) indicating that the two ecological processes are intertwined. However, ΔCTI was more strongly correlated to gains in temperate species and losses of boreal species than to gains in pioneer species (Fig. A.6), which suggests that thermophilization was not trivially driven by successional processes.

Community thermophilization was asymmetrical and mainly driven by larger gains in warm-adapted species, as indicated by the larger increases in the warm-tail of the temperature distributions than in the cold-tail (Fig. 1.5d-f). Moderate disturbances exacerbated this effect from the sugar maple-yellow birch up to the balsam fir-white birch domain (larger increase in the warm tail; Fig. 1.5e). The positive correlation between ΔCTI and gains in temperate species in all domains, except in the spruce-moss, also corroborates the role of warm-adapted species (Fig. A.6).

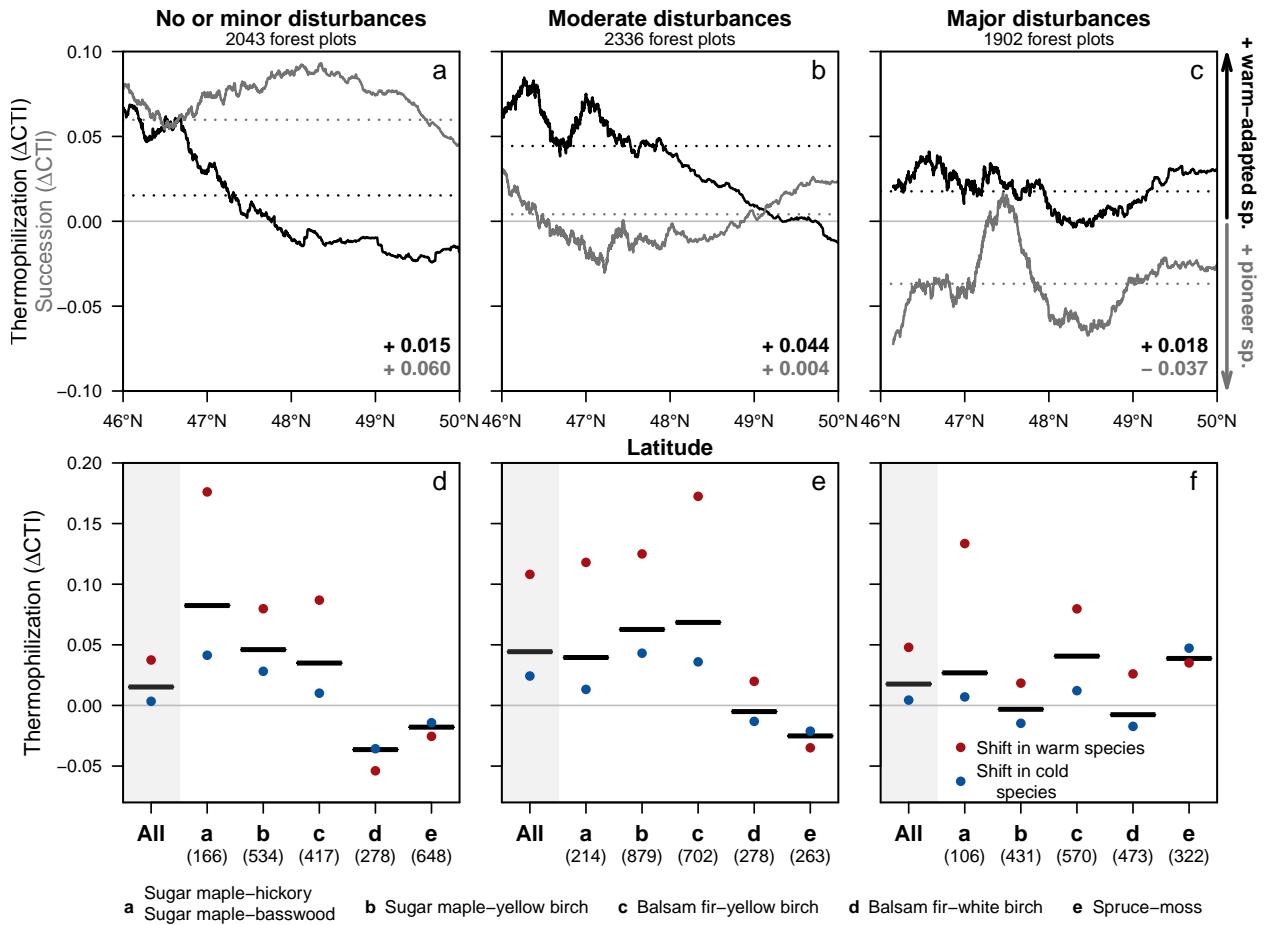


Figure 1.5. Thermophilization (i.e., change in community temperature index, ΔCTI) and successional process (i.e., change in community shade index, ΔCSI) of forests for different levels of disturbance. In the upper panels (a-c), the latitudinal trends in ΔCTI (black curve) and ΔCSI (grey curve) are based on moving averages computed on the indices against latitude (window size of 400 plots). Positive values indicate an increase in warm-adapted species (black) or in late-successional species (grey) over time. The dotted lines in panels a-c represent the mean ΔCTI (black) and ΔCSI (grey) values for different levels of disturbance. The lower panels (d-f) show thermophilization of the forest plots across the study area (All) and by bioclimatic domain. Positive values for the temporal shift of the mean (black line), left tail (red) and right tail (blue) of the distribution of CTI indicate overall thermophilization, increases of warm-adapted and decreases of cold-adapted species, respectively.

Only a few species contributed substantially to community thermophilization (Fig. 1.6). Gains of *Acer rubrum* and *Acer saccharum*, as well as losses of *Abies balsamea* and *Picea mariana*, contributed strongly to the thermophilization of all bioclimatic domains. In addition to the change of these four species, the losses of *Betula papyrifera* and *Picea glauca* also played a key role in the thermophilization of ecotonal forests in the balsam fir-yellow birch domain. Moreover, temperate species such as *Fagus grandifolia*, *Quercus rubra* and *Fraxinus americana* contributed mostly to the thermophilization of southern domains (Fig. 1.6) where

their abundance has increased (Fig. A.5). In contrast, the surge in CTI north of the 49°N (spruce-moss) in highly disturbed forests (Fig. 1.5) was likely due to the replacement of boreal species by pioneer species (Fig. A.6), such as *Betula papyrifera* and *Salix spp.* (Fig. 1.6).

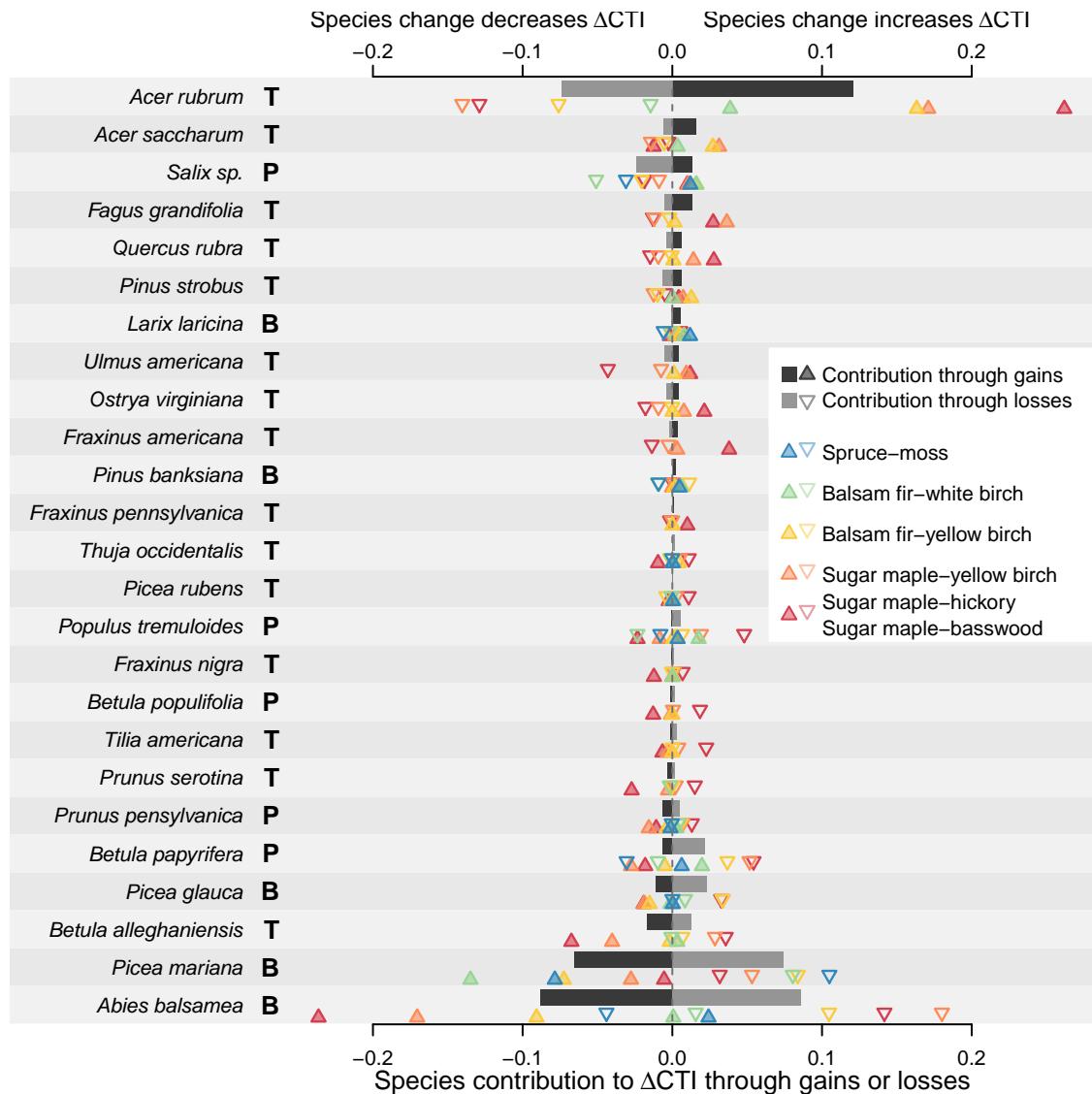


Figure 1.6. Individual species contributions, through gains and losses, to thermophilization of forest communities across the study area and for each bioclimatic domain. The bars represent the mean contributions of given species through gains (dark grey) or losses (light grey) across the study area, while the coloured triangles represent the mean contributions of given species through gains (filled) or losses (open) by domain. For example, the Δ CTI increased by an average of 0.12 for all plots where *Acer rubrum* has increased in abundance (dark grey bar), whereas the Δ CTI also increased by an average of 0.09 for all plots where *Abies balsamea* has decreased in abundance (light grey bar). Letters next to species names correspond to (T)emperate, (P)ioneer and (B)oreal species. Only species that contributed more than 0.01 in at least one domain are shown.

4. Discussion

Taken together, our results suggest that disturbances accelerate tree community responses to climate change, revealing potential synergies that are yet to be investigated. Local and short-term influences of disturbances mask long-term and lagging climate-induced changes in communities. Yet, we revealed a generalised thermophilization of forests throughout the temperate-boreal ecotone of Québec, driven by a concurrent gain of temperate species and loss of boreal species. Moreover, we found that moderate disturbances likely accelerated thermophilization. Hence, moderate disturbances, but not major ones, could facilitate gains in warm-adapted species under climate change.

4.1. Impact of disturbances on tree community changes

Our results suggest that disturbances (e.g., clear-cutting, insect outbreaks, fires) are the primary drivers of forest community changes in the temperate-boreal ecotone. Such findings are in agreement with previous work showing that disturbances alter rapidly and profoundly tree communities that otherwise respond slowly to environmental changes (Vanderwel *et al.*, 2013a).

Furthermore, our study underscores the importance of historical disturbances, particularly harvesting activities, on the forest dynamics of the temperate-boreal ecotone. Disturbance effects on communities may persist from decades to centuries (Johnstone *et al.*, 2016) and, here, the effects of historical disturbances even superseded that of recent disturbances. Such findings stress that disturbances cannot be ignored when modelling the future of forests with climate change, as they not only drive community changes, but also have long-lasting impacts. Tree harvesting was the most frequent type of disturbance (Fig. A.2) and alone accounted for 24.7% of all tree mortality during the study period, thus impacting severely all components of temporal community changes. However, in contrast to natural disturbances, tree harvesting has been shown to disrupt the relationship between vegetation and local environmental conditions and, because of its short return interval, to favour young even-aged stands to the detriment of old-growth forests (Boucher *et al.*, 2009; Boucher et Grondin, 2012).

4.2. Climate-induced change in tree community

Our findings highlight an ongoing shift toward more warm-adapted tree species in forests across the temperate-boreal ecotone. This overall thermophilization trend of tree communities is consistent with the hypothesis of climate-induced range shift, expanding on earlier findings that forests are responding to climate warming (e.g. Fisichelli *et al.*, 2014; Leithead *et al.*, 2010; Sittaro *et al.*, 2017). However, the observed increase of tree community temperature of +0.03 °C/decade is considerably smaller than the rising trend in growing season

temperature of 0.14 °C/decade (Fig. A.1). Although these measures have different origins and should thus be compared cautiously, our findings support the conclusion of numerous studies that tree responses often lag behind environmental changes (Renwick et Rocca, 2015; Sittaro *et al.*, 2017; Svenning et Sandel, 2013; Talluto *et al.*, 2017). Considering the velocity of the predicted future climate change, the gap between species distributions and their optimal climate niches will likely widen and lead to greater reshuffling of biodiversity.

4.3. Feedback between climate change and disturbances

Our most striking finding is that community thermophilization was amplified by moderate disturbances. Our combined analysis of change in CTI and CSI also allowed us to disentangle climate change effects from successional processes, highlighting that the observed thermophilization was not simply correlated with the replacement of boreal by pioneer species. Our work provides a broad-scale community perspective on the role played by disturbances in promoting northward migration of tree species, which is in agreement with the conclusions of recent empirical (Boucher *et al.*, 2006; Leithead *et al.*, 2010) and simulation (Vanderwel et Purves, 2014; Wang *et al.*, 2015) studies.

Disturbances likely accelerate forest changes by reducing competition and providing establishment opportunities to warm-adapted temperate tree species (Leithead *et al.*, 2010; Svenning et Sandel, 2013). Indeed, in the absence of disturbances, trees grow slowly, their mortality rates are low and competition for space and light is strong, thus preventing warm-adapted species from colonizing new areas, despite the suitability of climatic conditions; community thermophilization is consequently very slow. Moderate disturbances, however, remove individuals of resident species and reduce competition, which enhances the replacement of boreal by temperate trees, thereby increasing the thermophilization rate. Furthermore, moderate disturbances can also modify local microclimates (De Frenne *et al.*, 2013; Stevens *et al.*, 2015) which may alter the survival rates of tree saplings. In contrast, major disturbances only favour early successional species. Such findings echo the well-known intermediate disturbance hypothesis (Connell, 1978); as in the classical hypothesis, intermediate disturbances lower interspecific competition but here, not only do they increase local species richness (not shown), but they also accelerate ecological transitions.

Our complete set of predictors poorly explained the observed forest thermophilization, likely because this process was highly variable among localities. Forest composition is thus changing as expected under climate warming, but thermophilization does not appear to be directly driven by rising temperatures. As suggested by Renwick et Rocca (2015), we surmise that, as climate warms up, moderate disturbances could foster punctuated and episodic migration of warm-adapted species in localities where conditions are otherwise favourable.

However, it raises questions about the specific conditions in which the thermophilization process can effectively take place. Further analyses are required to determine which factors can trigger (e.g. type, size, frequency of disturbances) or constrain (e.g. soil type, competition, precipitation) the invasion by warm-adapted species.

Our results contrast with those of Boisvert-Marsh *et al.* (2019) who found that climate was more important than disturbances in explaining tree sapling recruitment at their northern limit in Québec. This suggests that the pattern we uncovered might be primarily caused by an increase in abundance of species already present rather than by new colonization. Danneyrolles *et al.* (2019) also found that forest compositional changes over the last centuries (between 1790–1900 and 1980–2010) in deciduous forests of southern Québec were largely driven by land-use changes, favouring more disturbance-adapted tree species, but did not find any signs of thermophilization. In contrast to our study that covers a period of pronounced climate warming, Danneyrolles *et al.* (2019) investigated a period dominated by land-use and population changes which may explain the absence of thermophilization signal in their results. In light of their results, we hypothesize that some of the thermophilization we reported here in the sugar maple domains is in fact the result of secondary succession after historical disturbances.

4.4. Species contributions to community thermophilization

We found that the observed community thermophilization was caused by gains and losses in abundance of a restricted group of species. This differential rate of species response entails that other species lag even more behind climate change and that larger reshuffling of communities is still ahead of us. The interaction between climate and disturbances likely promotes generalist tree species adapted to disturbances with high dispersal abilities (Aubin *et al.*, 2016). For instance, generalist species like *Acer sp.*, especially *Acer rubrum*, have been expanding in eastern North America since the pre-industrial period (Boucher *et al.*, 2006; Danneyrolles *et al.*, 2019; Thompson *et al.*, 2013) and recently established themselves in boreal forests (Leithead *et al.*, 2010; Sittaro *et al.*, 2017) because they quickly take advantage from disturbances and thrive in a wide variety of ecological conditions. In contrast, some species limited by dispersal, such as *Carya sp.* and *Tilia americana*, or constrained to specific habitat, such as *Acer saccharinum*, might not benefit from these opportunities.

The magnitude of change in CTI varied by bioclimatic domains reflecting the spatial patterns of species changes in response to climate warming and disturbances. The thermophilization of the sugar maple domains was facilitated by the presence of a large pool of warm-adapted species. When disturbed, these southernmost domains had lower thermophilization because they gained pioneer species. We showed that the balsam fir-yellow birch domain was particularly sensitive to moderate disturbances. The thermophilization

of this ecotonal zone was primarily due to increase in *Acer rubrum* and, to a lesser extent, increase in *A. saccharum* and decrease in *Abies balsamea* and *Betula papyrifera*. Although *A. rubrum* is already well established in this domain, our results suggest that it will continue to thrive and spread, likely in response to a combination of climate warming, historical and recent disturbances as well as natural forest dynamics. *A. saccharum* is presently constrained on hilltops in the southern part of this domain (Gosselin, 2002), but our results suggest that it could expand in nearby habitats. In contrast, the decrease in CTI in the balsam fir-white birch and spruce moss domains could be explained by the fact that temperate species are rare in these two northernmost domains, hence changes in CTI resulted mostly from a dynamic of replacement between pioneer and boreal species in response to disturbances. *A. rubrum* was the only temperate species to increase in the balsam fir-white birch domain (Fig. A.5) and, when it did, it contributed to increase its CTI (Fig. 1.6). Similarly to *A. saccharum*, *A. rubrum* distribution is spatially constrained within the balsam fir-white birch domain (Blouin et Berger, 2008) and will likely expand from existing existing patchy populations in the future.

4.5. Long-term perspectives for the temperate-boreal ecotone

Although the time period covered by our study (46 years) is sufficient to observe significant trends in forest compositional changes, it is not long enough to test whether warm-adapted temperate species will persist and thrive in these novel assemblages or if boreal species will out-compete them in the long run. Therefore, an important question remains: does the current forest thermophilization indicates an ongoing ecosystem shift or only a transient dynamic? Multiple studies suggest a persistence of these novel assemblages. For instance, after a century of logging disturbances, temperate species were found to have increased and persisted in forests formerly dominated by conifers (Boucher *et al.*, 2006). Furthermore, Fréchette et de Vernal (2013) provided evidence that, during the last interglacial period (6-7°C warmer), the northern limit of the temperate biome was located about 500 km north of its actual limit, suggesting that a northward shift of the ecotone is possible. Hence, while climate warming erodes forest resilience by affecting competitive advantages and generating colonization debt, our findings suggest that moderate disturbances play a major role in promoting regime shift by speeding up the transition from one ecosystem state to another. Such a conclusion stresses the importance of accounting for the synergistic effect of disturbances and climate change in forest management strategies as well as in models of forest responses to climate change.

5. Acknowledgements

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6. Data Accessibility Statement

The complete forest inventory dataset used in this study is available online at <https://www.donneesquebec.ca/recherche/fr/dataset/placettes-echantillons-permanentes-1970-a-aujourd-hui>. All the data used in the study, in addition to R scripts to reproduce the analyses and the figures, can be found online at <https://github.com/mhBrice/thermophilization> (<https://doi.org/10.5281/zenodo.3242773>).

Second Article.

Moderate disturbances accelerate forest transition dynamics under climate change in the temperate-boreal ecotone of eastern North America

by

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ABSTRACT.

Several temperate tree species are expected to migrate northward and colonise boreal forests in response to climate change. Tree migrations could lead to transitions in forest types, but these could be influenced by several non-climatic factors, such as disturbances and soil conditions.

We analysed over 10,000 forest inventory plots, sampled from 1970 to 2018 in meridional Québec, Canada to identify what environmental conditions promote or prevent regional-scale forest transitions. We used a continuous-time multi-state Markov model to quantify the probabilities of transitions between forest states (temperate, boreal, mixed, pioneer) as a function of climate (mean temperature and climate moisture index during the growing season), soil conditions (pH and drainage) and disturbances (severity levels of natural disturbances and logging). We further investigate how different disturbance types and severities impact forests' short-term transient dynamics and long-term equilibrium using properties of Markov transition matrices.

The most common transitions observed during the study period were from mixed to temperate states, as well as from pioneer to boreal forests. In our study, transitions were mainly driven by natural and anthropogenic disturbances and secondarily by climate, whereas soil characteristics exerted relatively minor constraints. While major disturbances only promoted transitions to the pioneer state, moderate disturbances increased the probability of transition from mixed to temperate states. Long-term projections of our model under the current environmental conditions indicate that moderate disturbances would promote a northward shift of the temperate forest. Moreover, disturbances reduced turnover and convergence time for all transitions, thereby accelerating forest dynamics. Contrary to our expectation, mixed to temperate transitions were not driven by temperate tree recruitment but by mortality and growth. Overall, our results suggest that moderate disturbances could catalyse rapid forest transitions and accelerate broad-scale biome shifts.

Keywords: Climate change, Natural disturbances and logging, Continuous-time multi-state Markov model, Québec, Temperate-boreal ecotone, Transition probabilities, Equilibrium, Transient dynamics.

1. Introduction

Global climate warming has led to altitudinal and latitudinal migration of species across the globe (Chen *et al.*, 2011; Parmesan et Yohe, 2003). In ecotones, where transition between vegetation biomes occurs, these shifts in species distributions entail far reaching consequences for forest ecosystems (Evans et Brown, 2017). In some cases, climate-induced shifts in tree species distributions might trigger a “regime shift” (Scheffer *et al.*, 2001) and transform treeless tundra into boreal forests (Harsch *et al.*, 2009), tropical forests into savanna (Hirota *et al.*, 2011) or coniferous forests into deciduous forests (Boulanger *et al.*, 2019). As ecological processes may strongly differ among these biomes, the reorganisation of biodiversity not only impacts local species composition (Williams et Jackson, 2007), but also alters the functional and structural characteristics of communities (Esquivel-Muelbert *et al.*, 2018; Scheffer *et al.*, 2012), hence feedbacks to microclimates, ecosystem functioning and biogeochemical cycles (Anderson *et al.*, 2011). However, these large transitions in forest types are still poorly understood notably because ecotones are not solely controlled by regional climate but also by many other landscape- and local-scale factors that could accelerate or slow-down these changes.

According to metapopulation theory, range dynamics ultimately arise from local demographic processes (e.g., recruitment, growth, mortality) that determine where a tree species can establish and persist (Godsoe *et al.*, 2017; Levins, 1969). Whereas range expansion depends upon dispersal and establishment of new individuals, range contraction is the result of declining vitality and mortality (Jump *et al.*, 2009). In the temperate-boreal forest ecotone, recent climate warming has been shown to improve recruitment, survival and growth of some temperate tree species at their northern limits, whereas boreal species were competitively disadvantaged by slower growth and larger increase in mortality associated to heat and drought stress (Bolte *et al.*, 2014; Fisichelli *et al.*, 2014; Goldblum et Rigg, 2005; Grundmann *et al.*, 2011; Peng *et al.*, 2011; Reich *et al.*, 2015). Hence, as climate warms and tips the balance in favour of temperate over boreal species, forests at the ecotone are expected to transition from coniferous to mixedwood and from mixedwood to temperate deciduous (Boulanger *et al.*, 2019; Chen, 2002; Lindner *et al.*, 2010).

The reported shifts in species distributions are, however, much slower than the rate of climate change (Sittaro *et al.*, 2017; Talluto *et al.*, 2017). Such lags in species responses are hypothesised as primarily due to demographic constraints (Renwick et Rocca, 2015; Svenning et Sandel, 2013). Because trees are long-lived species that disperse over very short distances, colonisation and extinction events in response to environmental changes are often delayed, such that forests are rarely in equilibrium with their environment (Talluto *et al.*, 2017). Hence, if forests are undisturbed, transition rates between forest types following natural succession pathways will be mainly limited by the persistence and turnover of resident species

(Bouchard, 2019; Loehle, 2000) as well as the dispersal and establishment rates of migrating species (Neilson, 1993), resulting in large disequilibrium and transient dynamics that may last a very long time (Hastings *et al.*, 2018; Talluto *et al.*, 2017).

Disturbance events, such as fire and harvesting, directly affect demographic processes and increase turnover, and are thus likely to influence forest responses to climate change (Bolte *et al.*, 2014; Boulanger *et al.*, 2019; Serra-Diaz *et al.*, 2015). Indeed, as global climate warming slowly modifies the competitive balance among species, pulse disturbances remove the resident community in whole or in part, thus providing establishment opportunities for migrating species and making resources available for a fast growth. Consequently, following a disturbance, forest composition may shift to species that are better suited to current conditions and fail to return to its previous state (Johnstone *et al.*, 2016; Renwick et Rocca, 2015; Turner, 2010). For example, canopy gaps have been shown to locally facilitate establishment of temperate species in mixed forests of Ontario (Leithead *et al.*, 2010). In a nature reserve of Scandinavia, Bolte *et al.* (2014) showed that Norway spruce (*Picea abies*) was particularly sensitive to the combination disturbances and warming which benefited the growth of European beech (*Fagus sylvatica*). In a previous study, we showed that moderate disturbances (i.e., disturbances that removed between 25–75% of the tree basal area) have favoured the increase of warm-adapted species and led to a broad-scale community thermophilization of forests at the temperate-boreal ecotone in Québec (Brice *et al.*, 2019).

Cross-scale interactions between landscape disturbances and global warming could drive abrupt transitions between forest types (Allen, 2007; Peters *et al.*, 2007). Given that forests are increasingly subject to human disturbances, such non-linear processes could play a key role in driving the climate shift in biomes. Some simulation studies have however concluded that disturbances are unlikely to promote extensive biome shifts in the coming decades because they would favour mainly the rapid recovery of resident species (Liang *et al.*, 2018) or the invasion by early-successional species (Vanderwel et Purves, 2014). It is possible that the effect of disturbances on forest dynamics depend on their intensity and type (natural or anthropogenic). Indeed, logging strongly differs from natural disturbances in severity, frequency, selectivity and spatial extent (McRae *et al.*, 2001), which could alter successional pathways. For instance, in mixedwood forests of North America, natural canopy gaps and partial cutting can benefit shade-tolerant deciduous species (Danneyrolles *et al.*, 2016; Kneeshaw et Prévost, 2007), whereas clearcutting favours the expansion of pioneer species, such as the trembling aspen (*Populus tremuloides*) (Grondin *et al.*, 2018; Landhäusser *et al.*, 2010). Therefore, more empirical evidence is essential to evaluate how various intensities and types of disturbances may affect forest dynamics under recent climate change and whether their effects can scale-up to trigger punctuated and episodic shifts in forest types.

The northward migration of temperate species may nevertheless be contingent on their capacity to colonise different types of soil (Brown et Vellend, 2014; Carteron *et al.*, 2020;

Lafleur *et al.*, 2010). Soils of cold boreal forests generally have lower pH, lower microbial activity and slower decomposition rates of organic matter than warmer southern temperate forest soils (Goldblum et Rigg, 2010). These local and regional variations in soil properties are expected to slow down or inhibit the establishment of temperate trees into the boreal forest. For instance, transplant experimental studies have shown that seedlings of sugar maple (*Acer saccharum*) in boreal soils were negatively affected by soil biotic and abiotic conditions (Brown et Vellend, 2014; Carteron *et al.*, 2020). In contrast, Kellman (2004) found a higher survival of *Acer saccharum* seedlings in boreal stands than in hardwood stands, potentially because of better light availability. Hence, it has been suggested that soil properties in boreal forests may not be a major impediment to the migration of temperate species showing broad ecological tolerance (Barras et Kellman, 1998; Kellman, 2004; Lafleur *et al.*, 2010). Nonetheless, suboptimal soil conditions under a boreal canopy could delay forest transitions under climate change (Solarik *et al.*, 2019). While experimental studies provide valuable knowledge on the role of soils at local scales, the importance of such constraints on long-term forest dynamics should be evaluated at regional scale and across species to better anticipate future biome transitions.

One approach to investigating biome shifts in response to climate change is to model transition probabilities between forest states using a Markov chain approach. Given the unequivocal distinction between temperate and boreal forests, the dynamics of tree communities at the temperate-boreal ecotone of North America can be adequately characterised using discrete ecological and successional states, namely boreal (stands dominated by boreal coniferous species), mixed (mixed stands of coniferous and deciduous species), temperate (stands dominated by temperate deciduous species) and pioneer (stands dominated by early successional species, which can be found in any disturbed habitats across the latitudinal gradient) (Vissault, 2016). Using such classification, the forest dynamics thus can be formalised as a multi-state Markov model, where transitions among states are represented by a stochastic process influenced by their current state and environmental characteristics of interest (Jackson, 2018). The Markov framework has been previously used to study forest succession (Liénard et Strigul, 2016; Runkle, 1981; Waggoner et Stephens, 1970) notably because it is based on a straightforward definition of transitions between various forest states and provides a simple mechanistic interpretation of the estimated transition probabilities. This method thereby offers the possibility of exploiting the full complexity and temporal depth of forest inventory data, while buffering the idiosyncrasies of species responses (Strigul *et al.*, 2012).

Representation of forest dynamics with Markov chains allows us to link stand-scale ecological mechanisms (Wootton, 2001), which can be influenced by soils, disturbances and climate, to the emergent broad-scale biome shifts. For example, transitions to pioneer reflect disturbance, transitions from pioneer reflect colonisation, dispersal and recruitment limitation, and transitions between the other states reflect competitive exclusion. In addition,

multi-state models can be used to investigate biome shifts from the perspective of both transient dynamics and long-term equilibrium. Markov transition matrices can be estimated from the model output and their well-established properties can then be compared under different scenarios (Boulangeat *et al.*, 2018; Hill *et al.*, 2004). For instance, the equilibrium or steady-state distribution can be derived from a transition matrix and used to infer the potential long-term forest composition under given environmental conditions (Scheffer *et al.*, 2001), providing insights about the direction of current forest dynamics (Hill *et al.*, 2004; Waggoner et Stephens, 1970). Moreover, transient periods can also be described: the time of convergence to equilibrium measures the length of the transient period; the turnover time indicates how fast the transitions occur and informs about the persistence of forest states; and the entropy reveals the uncertainty about the next transition. Contrasting empirically derived transition matrices and their properties among disturbance scenarios can shed new light on forest dynamics under climate change and may even provide hints about management measures.

Here, we investigate how regional-scale forest dynamics is influenced by disturbances and soil conditions under recent climate warming. In particular, we ask the following questions: (1) How recent forest transitions dynamics vary with climate, soil and disturbances? (2) Do different disturbance types and intensities impact the potential long-term equilibrium distribution of forest states? (3) How do different disturbance types and intensities influence the short-term transient dynamics under climate change? And (4) what is the relative importance of tree demographic processes underlying the transition dynamics? We answer those question by estimating the influence of environmental covariates on transition probabilities among four forest states (boreal, mixed, temperate and pioneer) using a continuous-time Markov multi-state model. Using results from our model, we then examine the impact of disturbances on forest equilibrium and transient dynamics by comparing different complementary matrix properties.

We expect that climate warming should promote colonisation by temperate species into mixed and boreal forests and competitive exclusion of boreal species, resulting in higher transition probabilities from boreal to mixed and from mixed to temperate, rather than the reverse. The most conspicuous effect of disturbances is expected to be the destruction of trees in place, which should provoke transitions from other states to pioneer. Nevertheless, we also anticipate that disturbances will favour climate-related transitions (boreal-mixed and mixed-temperate), whereas soil characteristics of coniferous forests (low pH and poor drainage) should slow down colonisation by temperate trees. Disturbances should also accelerate the transient dynamics by shortening turnover and convergence times. Together, these effects on transitions should influence the steady-state distribution by promoting an increase in the proportion of temperate forests in the long run.

2. Methods

2.1. Study area and forest inventory data

We used forest inventory plots in Québec, Canada, to investigate broad-scale transition dynamics in forest communities. Permanent plots have been sampled approximately every ten years from 1970 to 2018 (and ongoing) by the *Ministère des forêts, de la Faune et des Parcs* (MFFP, 2016). The study area extends from approximately 45° to 52° North latitude (ca. 795 000 km²). It covers six bioclimatic domains (Fig. 2.1) and three different vegetation zones; the mixed forest, which corresponds to the balsam fir-yellow birch domain (from 47°N to 48°N; hereafter, the ecotone), marks the transition between the hardwood forest to the south, dominated by *Acer saccharum*, and the boreal forest to the north, dominated by *Abies balsamea* and *Picea mariana*.

The natural disturbance regimes vary considerably along the latitudinal gradient of the study area, with fires in the northern boreal forests, spruce budworm outbreaks in the mixed-wood forests, and small windthrows and treefall gaps in the southernmost deciduous forests (Fig. B.1; Goldblum et Rigg, 2010). Anthropogenic disturbances are not homogeneously distributed either; clearcuts are more frequent in northern regions, while in southern regions partial cuts are more common (Fig. B.1; Boucher *et al.*, 2009).

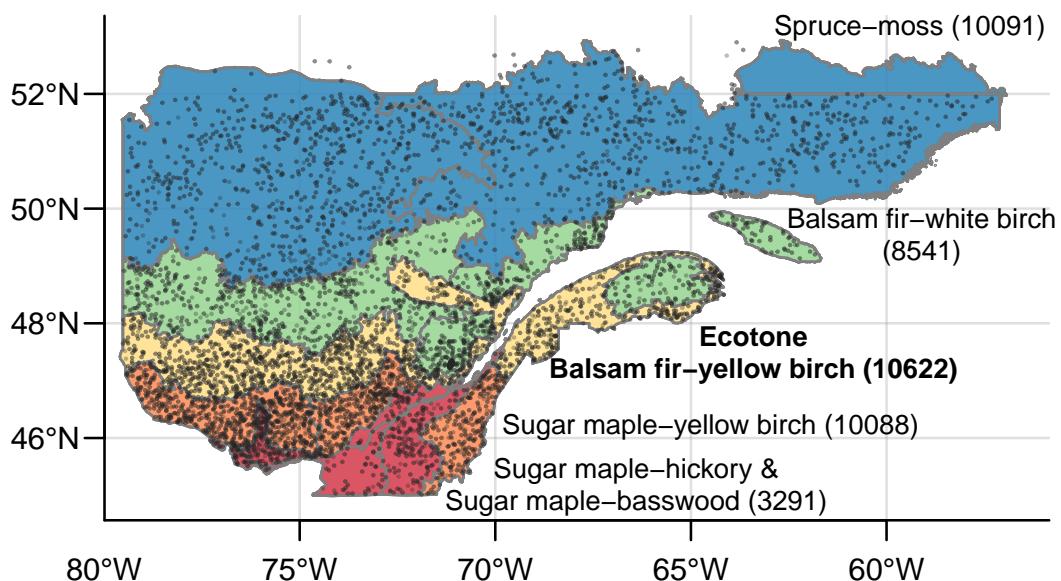


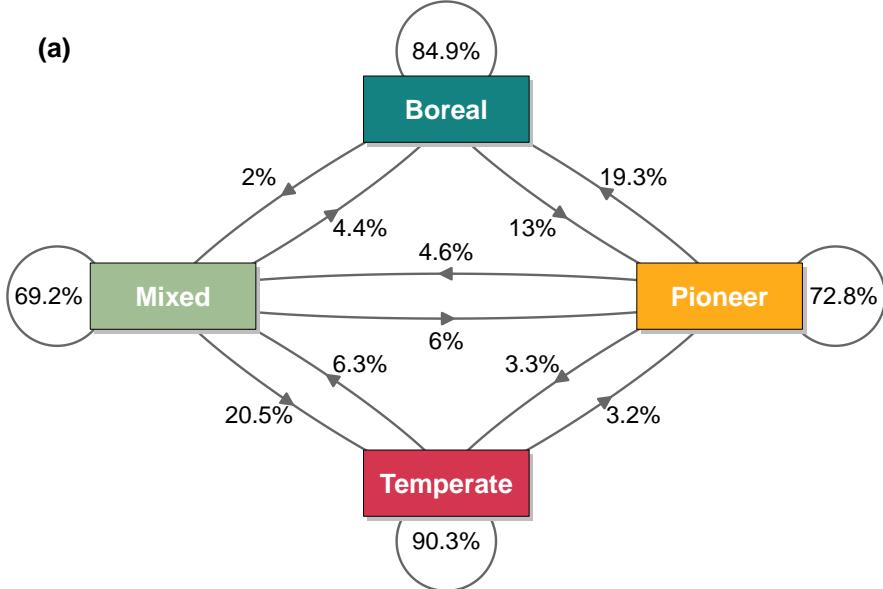
Figure 2.1. Locations of the 11,058 forest inventory plots in meridional Québec, Canada. Colours delimit the six bioclimatic domains. The two southernmost domains (red) are here combined. The number of plots in each domain is shown in parentheses. The balsam fir-yellow birch domain (in bold) is the ecotone between the hardwood and boreal forests.

We first selected all inventory plots that had been sampled at least twice. We then disregarded plots that were subjected to active reforestation (i.e., plantation) during the study period because we were interested in transition dynamics resulting from natural recolonisation processes. Finally, we kept plots for which soil covariates were available. This yielded a total of 11,058 plots analysed (Fig. 2.1). The time intervals between plot surveys varied from 3 to 39 years, with a mean interval of 11 years ($sd = 3.45$; Fig. B.2).

2.2. Forest states

We classified the forest inventory plots into four forest states using species basal area and composition at each sampling date. We first assigned each studied species to a group based on their traits and their distribution (Table B.1; see Brice *et al.*, 2019, for details): boreal species are mostly coniferous trees with a northern distribution; temperate species are mostly deciduous trees with a southern distribution; and pioneer species have low shade tolerance and are generally found in any disturbed habitats. For each plot, we computed the total basal area of each species group and then classified the plot to one of the four states similar to the MFFP (2016) definitions; Boreal (boreal species representing $>75\%$ of the plot basal area), Temperate (temperate species representing $>75\%$ of the plot basal area), Mixed (when temperate and boreal species both occupy between $>25\%$ and $<75\%$ of the plot basal area), and Pioneer (when the basal area of pioneer species is superior to that of boreal and temperate species or when plot total basal area $<5m^2/ha$). We analysed state transitions between consecutive plot surveys. Based on this classification, for the 42,633 observations (plots \times number of years measured), we recorded 31,690 state transitions, including self-transitions (Fig. 2.2, Table B.2).

The definitions of forest states can affect the results to some extent. A higher threshold to define the boreal and temperate states (e.g., $>85\%$ instead of $>75\%$ of dominance of boreal and temperate, respectively) influences the transition probabilities, but the direction of the dynamics remains the same (see comparison between Tables B.3 and B.4).



(b)

$$Q = \begin{vmatrix} -\sum_{s \neq B} q_{Bs} & q_{BM} & q_{BP} & 0 \\ q_{MB} & -\sum_{s \neq M} q_{Ms} & q_{MP} & q_{MT} \\ q_{PB} & q_{PM} & -\sum_{s \neq P} q_{Ps} & q_{PT} \\ 0 & q_{TM} & q_{TP} & -\sum_{s \neq T} q_{Ts} \end{vmatrix}$$

(c)

$$q_{rs} = q_{rs,0} \times \exp(\beta_{rs,1} \times \text{climate} + \beta_{rs,2} \times \text{soil} + \beta_{rs,3} \times \text{disturbances})$$

for $r \neq s$ and $s \neq \text{Pioneer}$

$$q_{rs} = q_{rs,0} \times \exp(\beta_{rs,3} \times \text{disturbances})$$

for $s = \text{Pioneer}$

Figure 2.2. Multi-state transition diagram (a), intensity matrix Q (b) and equations of our full model (c). Directional arrows in the diagram (a) depict the allowed transitions between states. The numbers represent the percentage of observed transitions between states ($nb_{rs}/nb_r \times 100$). Instantaneous transition from Boreal to Temperate and vice versa are considered impossible in the model (hence the absence of arrows in the diagram and the zeros in the Q matrix), however rare transitions from Boreal to Temperate and from Temperate to Boreal were observed in the data (less than 0.2%). The Q matrix (b) contains the instantaneous risk to move from one state (row) to another (column), here: (B)oreal, (M)ixed, (P)ioneer and (T)emperate, in that order. Transitions from any other state to Pioneer were modelled as only dependent on disturbances (c).

2.3. Environmental variables

Annual climatic conditions, covering a period from 1960 to 2018, were extracted from a 2-km² (60 arc sec) resolution grid for the entire study area using the ANUSPLIN climate modelling software (<http://cfs.nrcan.gc.ca/projects/3/8>; McKenney *et al.*, 2011). Plot locations were intercepted with two bioclimatic variables hypothesised to influence tree establishment, survival and growth: the mean temperature during the growing season and the

climate moisture index (CMI; difference between precipitation and potential evapotranspiration) from May to September (Table 2.1). To reduce the effect of inter-annual climate variability, each climate variable was averaged over a 10-year period prior to the plot measurement. From 1950 until the present day, growing season temperatures have increased by 0.17 °C/decade in the plots, while CMI have shown no trends (Fig. B.3).

We also collected information pertaining to natural and anthropogenic disturbances that have affected the forest plots during the study period (Table 2.1; Fig. B.1). At each plot, the type of disturbances (21 types) and their level of severity were recorded during field surveys (see Fig. B.1 for details; MFFP, 2016). For our multi-state model, we differentiated two main types of disturbances: natural disturbances and logging, with three levels of severity each (0, no or minor; 1, moderate; 2, major). The MFFP defined major disturbances as events that have resulted in a loss of more than 75% of the total tree basal area, whereas moderate disturbances have caused between 25 and 75% of loss. When the loss in basal area is less than 25%, it is considered to be minor.

Finally, at each plot, several edaphic characteristics were recorded (MFFP, 2016). We selected drainage and pH because they largely affect nutrient availability, soil structural properties and vegetation development (Tan, 2009), and also because they captured most of the variance in soil characteristics in our plots.

Table 2.1. Description of the explanatory variables used in the multi-state models.

Variable name	Variable description
Climate	
Temperature	Mean temperature during growing season, 10-year average prior to plot measurement (°C).
CMI	Mean Climate Moisture Index from May to September, 10-year average prior to plot measurement (cm).
Soil	
pH	pH of the surface horizon
Drainage	6 classes of soil drainage, which range from excessive to very poor, that were treated as numeric.
Disturbances	
Logging	Tree harvesting, including clearcutting, selection cutting, shelterwood cutting, seed-tree cutting, etc. None or minor (0), moderate (1) or major (2).
Natural	Natural disturbances, including forest fires, insect outbreaks, windfall, etc. No or minor (0), moderate (1) or major (2).

Climate and disturbances were included as time-varying explanatory variables (often called covariates in survival models), while soil variables were considered as static. Climate variables at time t were used to model transitions during the interval t and $t + \Delta t$. Disturbances that occurred during the interval t and $t + \Delta t$ were used to model transitions during the same time period.

Note that we solely focused on a parsimonious set of variables that allowed us to determine how climate, disturbances and soils influence transition dynamics. We decided not to include an index of propagule availability, even though it is known to affect tree range shifts (Pearson, 2006), as forest composition is already very strongly correlated with our climate covariates (Fig. B.4; Goldblum et Rigg, 2010; Vissault, 2016). Our model is therefore well-suited for our research goals; however it is not designed to make future range shift projections.

2.4. Analysis

2.4.1. Continuous-time multi-state Markov model

We formalised forest dynamics with a continuous-time multi-state model (Jackson, 2018; Van Den Hout, 2016) in which transitions among states depend upon the current state, time interval, climate, disturbances and soil characteristics (Fig. 2.2). This type of model takes into account the fact that (1) time intervals between surveys were irregular, (2) multiple transitions were possible during an interval, and (3) the exact moments of transitions were not observed (i.e. observations are interval-censored; Logofet et Lesnaya, 2000; Van Den Hout, 2016).

In a four-state transition model in continuous time, the Markov process is governed by a 4×4 transition intensity matrix, Q , where rows are the current states and columns are the future states (Fig. 2.2b). For each state $r,s \in B, M, P, T$, the transition intensity (q_{rs}) represents the instantaneous risk that a plot transitions from state r to state s . Because the states were defined based on stand basal area, instantaneous transitions from Boreal to Temperate (q_{BT}) or from Temperate to Boreal (q_{TB}) were impossible without disturbance; there is a necessary transition through Mixed or Pioneer. For this reason and the fact that these transitions were very rare in the data, we fixed q_{BT} and q_{TB} at 0 (Fig. 2.2b). However, all states can transition directly to Pioneer when disturbed (Fig. 2.2).

The intensities $q_{r,s}$ can be modelled as follows:

$$q_{rs}(t|x(t)) = q_{rs,0}(t)\exp(\beta'_{rs}x(t)),$$

where $x(t)$ is the matrix of explanatory variables (surveys as rows, covariates as columns), β_{rs} are coefficients to be estimated, and $q_{rs,0}(t)$ is a baseline hazard that describes the risk when environment $x(t) = 0$. Hence, $\exp(\beta'_{rs}x(t))$ is the relative increase or decrease in risk associated with a set of characteristics $x(t)$. In this model, time-dependent variables, such as

climate and disturbances, are assumed to be piecewise-constant, i.e., the hazard is constant within a time interval $[t, t + \Delta t]$ and depends on the variable value at t , but can change between the intervals. The inclusion of time-dependent variables in the model allows one to fit a non-homogeneous Markov process. Estimation of model parameters were obtained by maximising the log-likelihood (see Supplementary Methods for details).

We built five models: one baseline model that solely includes the $q_{rs,0}$, one model for each category of covariates independently (climate, soil and disturbances), and one full model, which combines all covariates (Table 2.1). Because multiple state transitions are estimated in a single model (all q_{rs} in Fig. 2.2b), the number of parameters increases rapidly with the number of covariates (number of modelled transitions (here 10) \times (number of covariates + 1)). Thus, to reduce the number of parameters, we assumed that transitions from any state to Pioneer were only determined by disturbances, while climate and soil variables should not directly influence these transitions. All quantitative variables were standardised ($\mu = 0$, $\sigma = 1$) prior to running the models.

2.4.2. Model evaluation

We first evaluated the goodness-of-fit of each model containing covariates (climate, soil, disturbances and full) against the baseline model using likelihood ratio tests (Jackson, 2018), which evaluate if the addition of one or more new parameters significantly increases the likelihood of the model. We also compared and ranked the models using the Akaike information criterion (AIC; Burnham *et al.*, 2002). The model with the lowest AIC was considered to be the best model and thus used in further analyses.

2.4.3. Model baseline and hazard ratios

We first evaluated the trends in recent forest transition dynamics. We used the baseline hazards ($q_{rs,0}$) estimated by our best model as indicators of the underlying forest response. For each pair of states, the baseline hazard describes the risk to make a transition for a mean forest plot (when all covariates are set to 0). We then investigated how environmental covariates influenced the transition dynamics (question 1) by comparing the estimated hazard ratios derived from our best model ($\exp(\beta_{rs})$).

2.4.4. Transient dynamics and equilibrium

We further investigated how disturbances modify the long-term equilibrium (question 2) and the forest transient dynamics (question 3). We computed different properties on the Markov transition matrix along the latitudinal temperature gradient and compared them among five disturbance scenarios defined by disturbance type and severity: (1) no or minor disturbances, when the covariates logging and natural were both fixed at 0; (2) moderate natural, with the covariate natural fixed at 1 and logging fixed at 0; and (3) vice versa for moderate logging; (4) major natural, with the covariate natural fixed at 2 and logging fixed

at 0; and (5) vice versa for major logging. The temperature covariate was also allowed to vary from its lower 10th to its upper 90th percentile, whereas all other covariates were fixed at the average conditions found in the ecotone, the balsam fir-yellow birch domain (Fig. 2.1), to focus solely on the effect of disturbances along the temperature gradient.

An extensive literature describes the multiple properties of discrete-time Markov transition matrices (Caswell, 2008; Hill *et al.*, 2004) which can be adapted to continuous-time models. We chose four informative and complementary properties that fully characterise both the short and long-time scale dynamics of our modelled system: (1) the steady-state distribution, which corresponds to the potential long-term proportion of forest states at equilibrium; (2) the half-life to equilibrium, which evaluates the time of convergence to the steady-state and the length of the transient period; (3) the turnover time, which measures the rate of transient successional changes; and (4) the entropy, which captures the uncertainty regarding the next transitions. While their absolute values should be interpreted with caution, their comparison under various disturbance scenarios can highlight essential features of the dynamics.

First, to measure the potential direction of forest dynamics under a given scenario, we estimated the steady-state distribution, π . For a regular Markov process, any initial state distribution converges to the same equilibrium as time approaches infinity. The vector of equilibrium π can be obtained by taking the left eigenvector of the intensity matrix Q , which has an eigenvalue of 0, normalised to sum to 1, or the left eigenvector of the transition probability matrix A , which has an eigenvalue of 1, normalised to sum to 1 (Norris, 1997).

Then, the convergence rate to the equilibrium distribution can be measured using the damping ratio (Hill *et al.*, 2004):

$$\rho = \lambda_{A1}/\lambda_{A2} = \exp(\lambda_{Q1} - \lambda_{Q2}),$$

where λ_{A1} and λ_{A2} are the largest and second-largest eigenvalues of A ($\lambda_{A1} = 1$ for stochastic A), whereas λ_{Q1} and λ_{Q2} are the largest and second-largest eigenvalues of Q ($\lambda_{Q1} = 0$ for stochastic Q). The convergence time was approximated using the half-life to equilibrium:

$$t_{1/2} = \log(2)/\log(\rho).$$

We also measured the turnover time in each forest state, also called the sojourn time in multi-state models, which corresponds to the time spent in one state before transitioning to a different state. The turnover time can be estimated by $Turnover_r = -1/q_{rr}$, where q_{rr} is the r^{th} entry on the diagonal of the estimated Q matrix. The turnover of the whole system is given by the average of each state turnover time over the steady-state distribution:

$$Turnover = - \sum_r \pi_r \times Turnover_r.$$

Finally, Hill *et al.* (2004) proposed to use the entropy of a discrete-time transition matrix as an index of the incertitude of successional changes. It measures how uncertain we are about the next new state of a site knowing its current state. For a continuous-time process, the entropy can be measured using the jump matrix (Spencer et Susko, 2005), which contains the probabilities that the next state after state r is state s :

$$j_{rs} = -q_{rs}/q_{rr}.$$

The entropy of state s is then:

$$H(j_{.s}) = - \sum_r j_{rs} \times \log(j_{rs}).$$

The normalised entropy of the whole system is the average of the entropies over the steady state, divided by $H_{max} = \log(n_{state} = 4)$:

$$\text{Entropy} = \frac{- \sum_r \pi_r \times H(j_{.s})}{H_{max}}.$$

Values of entropy closer to zero indicate more deterministic transition dynamics whereas values closer to one indicate more random dynamics.

2.4.5. Demographic processes

We finally decomposed the transition dynamics into its underlying demographic components (question 4) for the most abundant species (i.e., three temperate, *Acer rubrum*, *Acer saccharum* and *Betula alleghaniensis*; two boreal, *Abies balsamea* and *Picea mariana*; two pioneer, *Betula papyrifera* and *Populus tremuloides*). The transitions between states can result from various combinations of increases in basal area through tree recruitment and growth and decreases in basal area through mortality and logging. We measured recruitment as the increase in basal area from new trees that had reached or exceeded the threshold diameter of 9.1 cm. Growth was measured as the increase in tree basal area between consecutive surveys. During the surveys, tree vitality was characterised. We used this information to separate mortality as either due to harvesting or to any other causes and measured the loss in basal area that resulted from each of these two mortality processes.

Next, we used an indicator value analysis to quantify the contribution of each demographic process and species to each of the sixteen forest transitions (Dufrêne et Legendre, 1997). The indicator value (IV_{jk}), which measures the exclusiveness of a process j to a transition k , is given by the product of the relative abundance (specificity; RA_{jk}) and the relative frequency (fidelity; RF_{jk}):

$$IV_{jk} = 100 \times RA_{jk} \times RF_{jk}.$$

All analyses were performed using the R programming language version 3.6.1 (R Core Team, 2019). The list of R packages that were used to carry out the analyses is provided in the Supporting Information (Table B.5). All the data used in the study, in addition to R scripts to reproduce the analyses and the figures, can be found online at <https://github.com/mhBrice/transition>.

3. Results

During the study period, a large fraction of Mixed forests transitioned to Temperate forests (20.5%) but few did the opposite (6.3%). There were many transitions from Boreal to Pioneer (13.0%), and more from Pioneer to Boreal (19.3%). Temperate and Boreal forests were generally more persistent (90.3 and 84.9%, respectively, did not transition during the study period) than Mixed and Pioneer forests (69.2 and 72.8%, respectively; Fig. 2.2a).

Overall, the full model, which includes climate, soil and disturbance variables, had the best fit and predictive performances for the observed data (Table 2.2; Fig. B.5). The second-best model was the disturbance model, but it was far behind with a difference in AIC of almost 1500 units from the full model (Table 2.2). All variable subsets improved significantly the likelihood of the model (all likelihood ratio tests were highly significant, $p \ll 0.001$; Table 2.2). Model performance was also evaluated using a 10-fold cross-validation (see Supplementary Methods); it revealed that including climate and disturbances improved overall model predictive performance, while soil variables had a negligible effect (Fig. B.5). Thereafter, all inferences about transition probabilities were derived from the full model.

Table 2.2. Comparisons of the five candidate multi-state models. The number of parameters (Nb of par.) used in each model corresponds to the number of modelled transitions ($10 \times$ the number of covariates – 1). The ΔAIC is the difference between the Akaike information criterion of each model (AIC_m) and the minimum of AIC among all models (AIC_{min}): $\Delta\text{AIC} = \text{AIC}_m - \text{AIC}_{min}$. Models are presented in decreasing order of their ΔAIC . Each model containing covariates was compared to the baseline model using a Likelihood Ratio (LR) test. The best model is the one in bold with $\Delta\text{AIC} = 0$.

	Covariates	Nb of par.	-2 Log-likelihood	ΔAIC	LR test
Baseline	Intercept	10	37874.4	8298.4	—
Soil	Drainage, pH	24	37713.7	8165.7	< 0.001
Climate	Temperature, CMI	24	36288.8	6740.8	< 0.001
Disturbances	Natural, Logging	50	30993.5	1497.5	< 0.001
Full	All	78	29440.0	0.0	< 0.001

3.1. Baseline transition intensities

The baseline transition intensities of the full model provide insights about the background rate of forest changes (Fig. 2.3). Forest dynamics over the whole study area was largely dominated by transitions from Pioneer to Boreal ($q_{PB} = 0.0270$) and from Mixed to Temperate ($q_{MT} = 0.0229$; Fig. 2.3). Mixed forests were 1.6 times (q_{MT} / q_{TM}) more likely to transition to Temperate than the reverse, indicating an increase in proportion of temperate species relative to boreal species in mixedwoods during the study period. For Boreal forests, regeneration from Pioneer to Boreal was 3.9 times (q_{PB} / q_{BP}) more likely than transition from Boreal to Pioneer.

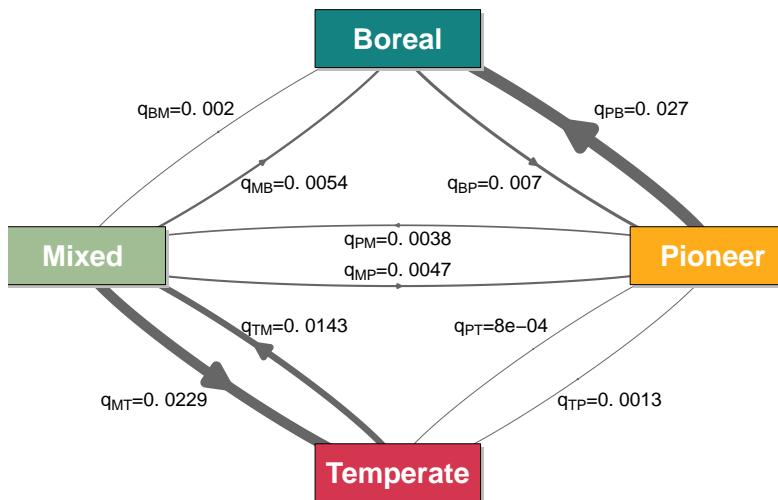


Figure 2.3. Baseline transition intensities as estimated from the best multi-state transition model. Arrows depict the direction of transitions between states. The numbers represent the estimated baseline hazards ($q_{rs,0}$), i.e., the instantaneous risk of moving from one state to another when all covariates are set to 0 (i.e., the means of standardised covariates and disturbance level 0).

3.2. Effect of covariates on transition probabilities

All transitions to Pioneer were highly influenced by disturbances (Fig. 2.4, Table B.3). As could be expected, major disturbances exert stronger effects than moderate disturbances (for both natural and logging), but, for each level of severity, logging had stronger effects than natural disturbances. For example, the risk of transition from Boreal to Pioneer has surged up to 213 times higher for plots that suffered major logging (logging 2) and 37 times higher for plots that suffered major natural disturbances (natural 2) compared to undisturbed plots (minor). Disturbances of all types and severities favoured transitions from Mixed to Temperate forests. Moderate disturbances (natural and logging) doubled the risk of this

type of transition, whereas major disturbances increased it by ca. 5 times (Hazard Ratio (HR) = 5.76 and 5.32, for natural and logging, respectively). Although the effect of major disturbances on the instantaneous risk of transition from Mixed to Temperate was stronger than for moderate disturbances, the probability of this event decreased with time (Fig. B.6). Moderate disturbances also favoured transitions from Boreal to Mixed (HR = 2.76 and 3.45, respectively), while major disturbances had no significant effect on this type of transition. Overall, the effects of disturbances are well reflected by the radical change of structure of the 10-year transition probability matrix (Fig. B.7).

Climate variables also had a significant influence on most transitions (Fig. 2.4). Warmer summer temperature (higher temperature) and higher humidity (higher CMI) favoured transitions from Boreal to Mixed as well as from Pioneer to Mixed and Pioneer to Temperate. Interestingly, warmer temperature did not significantly influence the risk of transition from Mixed to Temperate and higher CMI had a negative effect.

State transitions were also influenced by soil variables (Fig. 2.4, Table B.3). Holding the other covariates constant, the instantaneous risk of transition from Boreal to Mixed and from Pioneer to Temperate decreased by 27% and 23%, respectively, on poorer drainage (more humid), but the risk of transition from Temperate to Mixed increased by 30% (HR = 0.73, 0.77 and 1.30, respectively). Higher pH (acidic soil) had a negative effect on the transitions from Temperate to Mixed (HR = 0.73). These changes in risk ratios associated to soil variables appear almost irrelevant compared to the effect of disturbances, but a slight increase in drainage can dampen the positive effect of disturbances. For instance, under moderate natural disturbances, the instantaneous risk of transition from Boreal to Mixed is 0.007 at moderate drainage but decreases to 0.003 when increasing drainage by 1 point.

3.3. Effect of disturbances on long-term equilibrium

The potential state proportion at equilibrium was strongly influenced by disturbances (Fig. 2.5a). For the undisturbed scenario (minor), the predicted equilibrium at the ecotone was relatively close to the initial observed proportions, with signs of regeneration from Pioneer to Boreal states and slight increases in Mixed and Temperate states. The steady-state proportion of Temperate almost doubled with moderate disturbances (minor: 33%; moderate natural: 56%; moderate logging: 60%), while the boreal state was more than halved. At major disturbances, Pioneer forests dominated the equilibrium landscape, while the other states collapsed.

The steady-state proportion also changed as expected along the temperature gradient (Fig. 2.5b,c). The Boreal state dominates at low temperature (high latitude) and the Temperate state dominates at high temperature (low latitude), highlighting the position of the boundary between these two biomes at a growing season temperature of about 12.9°C,

which is found in the actual ecotone. Moderate disturbances (both natural and logging) displaced the temperate-boreal boundary at lower temperatures (ca. 12.2°C), hence further north of the current ecotone (Fig. 2.5b,c). Because of the dominance of the Pioneer state, the boundary modestly moved north with major natural disturbances (12.7°C), while it retreated to the south with major logging (13.4°C).

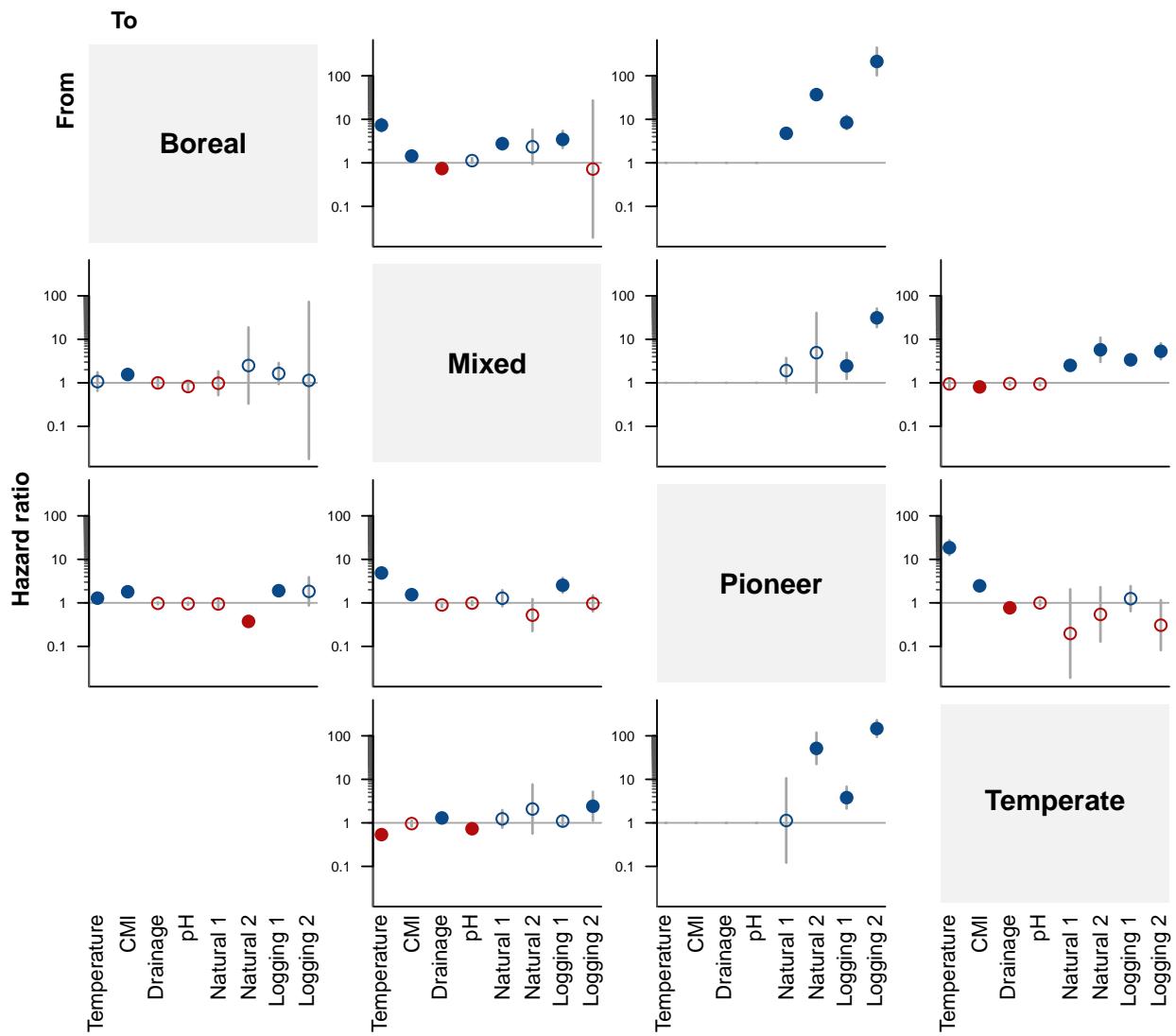


Figure 2.4. Hazard ratios (HR) and 95% confidence intervals as estimated from the best multi-state transition model. Each plot represents the estimated HR for transitions from row to column state, e.g., the plot on the first row, second column shows the HR for the Boreal to Mixed transition. The ordinate is in log scale. The HR of predictors are interpretable as multiplicative effects on the hazard, where values above 1 (in blue) indicate that the predictor is associated with a greater risk of state transition, whereas values below 1 (in red) indicate a lower risk of transition. Predictors statistically different from 1 are shown in dark blue or red. Numbers following disturbance predictors indicate their levels of intensity: 1 = moderate and 2 = major.

3.4. Effect of disturbances on transient dynamics

Disturbances affected forest transient dynamics with greater impact for higher disturbance severity (Fig. 2.6). In the minor disturbance scenario, turnover time was generally longer at low temperature, indicating slower transition dynamics in northern forests (Fig. 2.6a,b). The turnover time then rapidly declined to reach a minimum at ca. 13.25°C, at the southern limit of the ecotone, and went back up after this point. This trough, where transition dynamics is the fastest, is located just a little south of the boundary between Boreal and Temperate dominances found in Figure 5. Major disturbances accelerated transition dynamics all along the temperature gradient, while moderate disturbances also decreased turnover time but more strongly in the northern boreal region (Fig. 2.6a,b). The effect on turnover time was similar for both disturbance types, except that the effect of major logging was much stronger in northern boreal forests than natural disturbances (Fig. 2.6a,b). These spatial patterns reflect the turnover time of the dominant state at each point along the temperature gradient (Fig. B.8).

At minor disturbances, the entropy of the system generally increased from north to south and peaked at ca. 12.6°C, at the northern end of the ecotone (Fig. 6c,d). This peak illustrates where the transition dynamics is most uncertain (transition to all states are possible at this point), while it is very predictable in northern boreal forests (Boreal stays Boreal until it transitions to Pioneer later on). The peak can be mainly attributed to the entropy of the Boreal state at the ecotone, and the generally high values at low latitudes can be principally attributed to the Temperate state (Fig. B.9). This latitudinal pattern of entropy is modified by disturbances. Moderate natural disturbances decreased the entropy throughout the gradient, but especially where the peak is found (Fig. 2.6c). With moderate logging, the peak disappeared, and entropy increased monotonically from north to south (Fig. 2.6d). The peak of entropy was displaced to the south when major disturbances were included, whether natural or logging (Fig. 2.6c,d), where it was dominated by the entropy of the Pioneer state (Fig. B.9).

Half-life to equilibrium was the longest at ca. 11.8°C, north of the ecotone, in the balsam fir-white birch domain, while it was the shortest in the southernmost latitudes (Fig. 2.6e,f). Moderate disturbances flattened and shifted this peak to the north and the effect of moderate logging (Fig. 2.6f) was stronger than natural disturbances (Fig. 2.6e). In the balsam fir-white birch, the half-life to reach equilibrium distribution was reduced almost by half by moderate logging. With major disturbances, forests all along the temperature gradient can reach very quickly their steady-state distribution (maximum of about 8 years for major logging and 25 years for major natural disturbances).

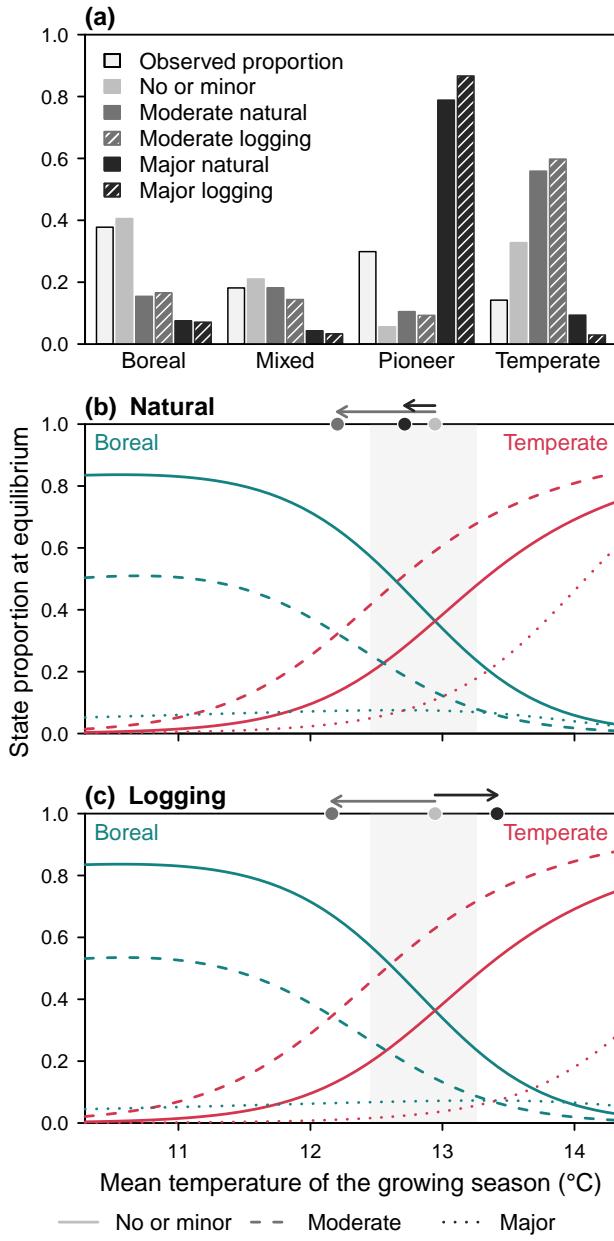


Figure 2.5. Changes in forest state proportions at equilibrium for different disturbance types (natural or logging) and intensity (no or minor, moderate, major). The barplot (a) compares the observed state proportion in the ecotone to the potential state proportion at equilibrium for different disturbance scenarios with all other covariates fixed at the average conditions found in the ecotone. The curved lines (b,c) show the proportions of Boreal (blue) and Temperate forests (red) at equilibrium along the temperature (latitudinal) gradient for no or minor (solid), moderate (dashed) and major (dotted) disturbances, with all other covariates fixed at the average conditions found in the ecotone. The light (no or minor), medium (moderate) and dark (major) grey circles indicate the positions of the boundary between dominance of Boreal and Temperate forests (i.e. the advancing front) while the corresponding arrows show how moderate and major disturbances move the boundary. The polygon approximates the position of the ecotone along the temperature gradient.

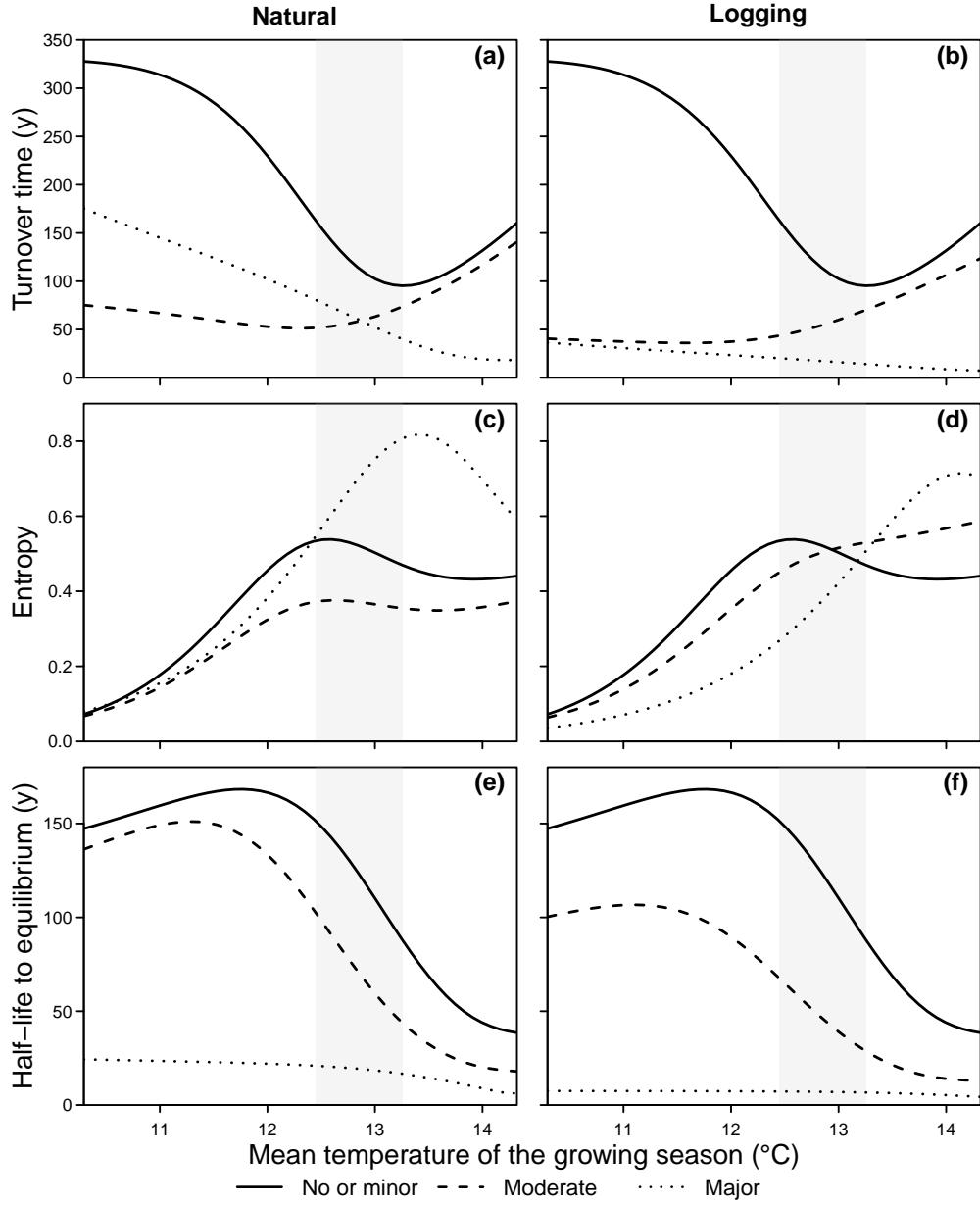


Figure 2.6. Changes in the characteristics of the forest transient dynamics along the temperature (latitudinal) gradient for different disturbance scenarios: no or minor (solid), moderate (dashed) and major (dotted) disturbances for both natural (a,c,e) and logging (b,d,f). All other covariates are fixed at the average conditions found in the ecotone to focus solely on the effect of disturbances along the temperature gradient. The turnover of the whole system (i.e. whole transition matrix) (a,b) corresponds to the time spent in a state before transitioning to the next and is given by the average of each state turnover time over the steady-state distribution. The entropy of the whole system (c,d) corresponds to the uncertainty of the next transition and is given by the average of each state entropy over the steady-state distribution. The half-life to equilibrium (e,f) is the time taken to reach 50% of the steady-state distribution, i.e. when the first eigenvalue becomes twice as large as the contribution of the second eigenvalue. The polygon approximates the positions of the ecotone along the temperature gradient.

3.5. Contribution of demographic processes

Only the demographic processes of a few species contributed substantially to the observed transition dynamics (Fig. 2.7). The importance of some processes were expected. For example, transitions from Boreal to Pioneer were dominated by mortality and logging of *Picea mariana*, while the transitions from Pioneer to Boreal were characterised by recruitment and growth of *Picea mariana* and *Abies balsamea*. Most interestingly, the transitions from Mixed to Temperate were determined by the mortality of *Abies balsamea* and the growth of temperate species, mainly *Acer rubrum* and *Betula alleghaniensis*, and to a lesser extent *Acer saccharum*. The recruitment of temperate species was not indicator of the Mixed to Temperate transitions, but rather of the transitions from Pioneer to Temperate.

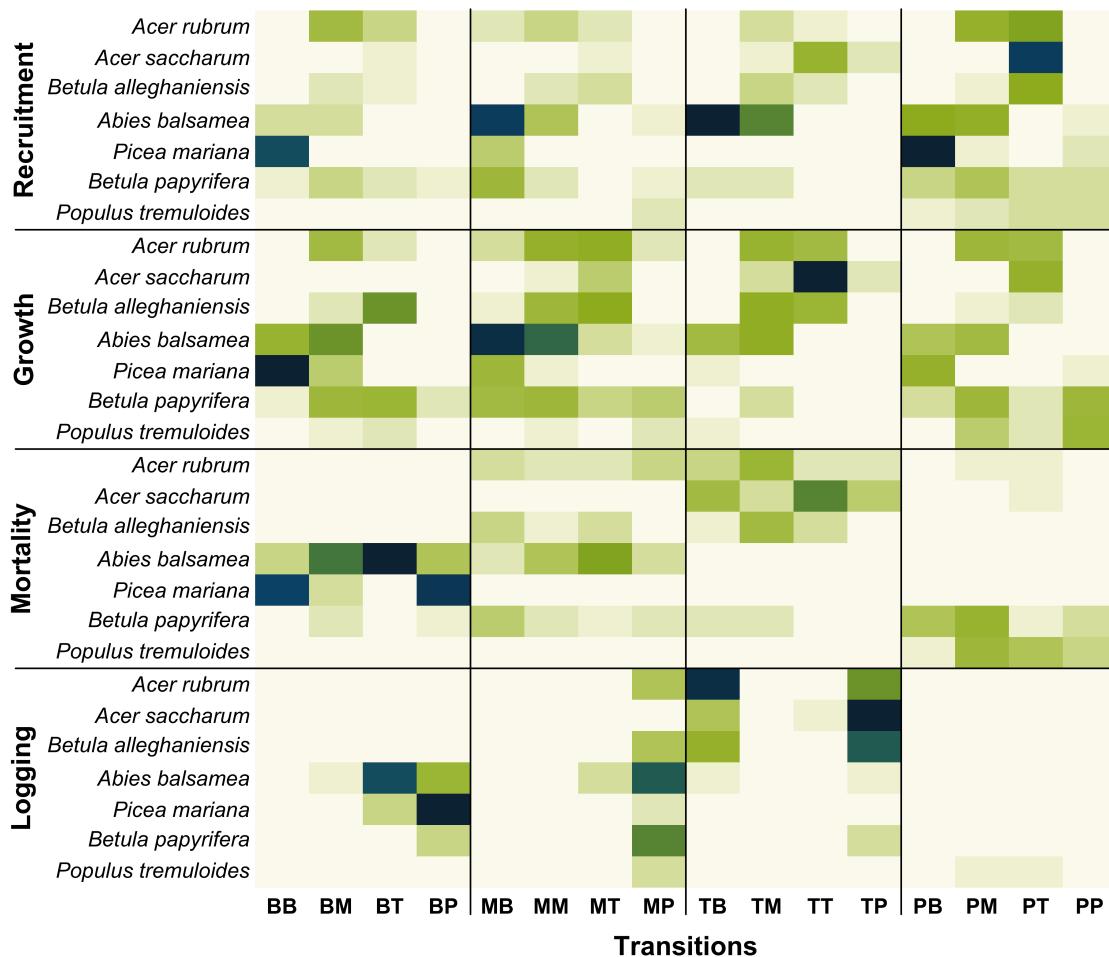


Figure 2.7. Species and demographic process contribution to all observed state transitions across the study area. Letters on the x axis correspond to the four forest states: (B)oreal, (M)ixed, (P)ioneer and (T)emperate. Each pair of letters denotes a transition from one state (first letter) to the next (second letter), e.g., BB is Boreal to Boreal. The darker colours indicate higher indicator value.

4. Discussion

Our study reveals that forest transition dynamics in the temperate-boreal ecotone was predominantly controlled by natural and anthropogenic disturbances and secondarily by climate, whereas local soil conditions exerted relatively minor constraints. While major disturbances only promoted transitions to the pioneer state, moderate disturbances increased the probability of transition from mixed to temperate states. Our analysis of the equilibrium further highlights that the long-term forest dynamics under moderate disturbances favours an increased proportion of temperate forests and thereby a northward shift of the temperate-boreal ecotone. Disturbances also modify the forest transient dynamics, accelerating both the turnover and convergence time and making the dynamics more predictable. Contrary to our expectation, transitions from mixed to temperate forests were not driven by recruitment but mostly by mortality and growth. In accordance with the hypothesis formulated in previous studies (Brice *et al.*, 2019; Johnstone *et al.*, 2016; Renwick et Rocca, 2015; Turner, 2010), our findings show that moderate disturbances catalyse transitions to the alternate, temperate-dominated forest state and could therefore promote regime shifts. Moreover, our results emphasise that forest dynamics are affected by multiple factors operating across different spatial and temporal scales. Predicting range shifts under climate change will thus require approaches that integrate multi-scale patterns and processes (Allen, 2007).

4.1. Trends in recent forest transition dynamics in Québec

Forest dynamics in Québec during the last 48 years was dominated by transitions from pioneer to boreal and from mixed to temperate stands. The important regeneration of boreal forests could be attributed to past natural disturbances, notably the last spruce budworm outbreak. Indeed, the last outbreak, which occurred during the 1970s, has caused major mortality in coniferous species followed by important recruitment pulses and growth releases (Bouchard et Kneeshaw, 2006).

Although we did not directly evaluate the impact of climate change, our results suggest that recent climate warming may contribute to the forest transition dynamics. The high baseline transition rate from mixed to temperate is consistent with the expectation of a northward range shift of temperate trees into the mixed and boreal forests. In our study, these transitions were caused by the concomitant high mortality of an abundant boreal species, *Abies balsamea*, and the increased growth of temperate species. Accordingly, the warming trend of the last decades (Fig. B.3) has been shown to increase growth and reproductive rates of temperate species at their northern limit (Boisvert-Marsh *et al.*, 2019; Bolte *et al.*, 2014; Fisichelli *et al.*, 2014; Goldblum et Rigg, 2005; Reich *et al.*, 2015), thus providing a competitive advantage to temperate over boreal species.

The increased transition rate to temperate forests is likely also a response to historical disturbances and climate change. Comparisons of pre-settlement and present-day forested landscapes of North America have highlighted an important deciduous encroachment in response to historical human activities (Boucher *et al.*, 2006; Danneyrolles *et al.*, 2019; Terrail *et al.*, 2019). Historical legacies and recent climate change are presumably mutually non-exclusive explanations. Indeed, simulations by Boulanger *et al.* (2019) showed that the future climate-induced expansion in temperate species to the detriment of boreal species would amplify the already ongoing trend since preindustrial times.

4.2. Disturbances catalyse forest state transition

Our study highlighted that moderate disturbances favour Mixed to Temperate transitions following climate warming, whereas major disturbances merely promote the Pioneer state. Disturbances directly remove trees, which leads to immediate and substantial changes in forest composition (Brice *et al.*, 2019). Forests are expected to be resilient to normally experienced disturbances and should thus return to their preceding states (Gunderson, 2000). However, climate change alters the conditions that initially supported the persistence of a given state, making forests susceptible to transition to other states (Johnstone *et al.*, 2016).

Following a disturbance, three mechanisms can contribute to the observed changes in tree cover: (1) the loss of a dominant species; (2) the growth release of advanced regeneration of co-occurring species; and (3) the pulse recruitment of new species. Our results show that the first two mechanisms may operate simultaneously, whereas the third had a limited influence.

In the study area, both natural and anthropogenic disturbances disproportionately affected *Abies balsamea*, which has suffered significant mortality due to spruce budworm outbreaks and was also intensively harvested (Duchesne et Ouimet, 2008). The canopy gaps created by the loss of this ubiquitous and abundant boreal species probably allowed for the growth release of co-occurring temperate species. These findings are in line with a study in the temperate-boreal ecotone of Scandinavia where a boreal tree, *Picea abies*, was particularly affected by a drought and an insect outbreak which then favour the growth of a temperate species, *Fagus sylvatica* (Bolte *et al.*, 2014). Combined effects of selective disturbances and climate warming may thus initiate a shift in the competitive balance between boreal and temperate species (Bolte *et al.*, 2014). We only found a weak contribution of temperate tree recruitment to the Mixed to Temperate transitions, likely because our analyses were based on tree basal area. However, other studies analysing abundance data suggest that moderate disturbances may also facilitate colonisation and establishment by opportunistic temperate species under warmer conditions (Brice *et al.*, 2019; Landhäuser *et al.*, 2010; Leithead *et al.*, 2010). Moreover, it is possible that, in the long run, the increased proportion of

temperate species in forest communities could alter soil properties and ultimately facilitate the recruitment of even more temperate species.

In contrast to moderate disturbances, severe disturbances, primarily clearcutting but also large fires in the study area (Fig. B.1), may result in large forest dieback and create openings of very large extent. These newly opened landscapes can be colonised swiftly by early-successional species that benefit from a long-distance seed dispersal and a fast growth, such as *Populus tremuloides* and *Betula papyrifera* (Boucher *et al.*, 2017; Grondin *et al.*, 2018). In contrast, temperate species may be slower to come back following major disturbances because they dispersed over shorter distances (maximum of ca. 200 m for *Acer* compared to 5000 m for *Populus*; Boulanger *et al.*, 2017). Due to the increase in large-scale logging during the last century, the proportion of young recently disturbed forests have been found to have increased in North America (Boucher *et al.*, 2006; Danneyrolles *et al.*, 2018; Thompson *et al.*, 2013). The expected increase in frequency and severity of climate-induced disturbances in combination with clearcuts may further promote the expansion of young pioneer forests in the future.

Compared to the catalysing effect of disturbances, local soil characteristics do not appear to represent a large impediment to state transitions, but transitions may be slower on some soil types. Poor drainage constrained climate-related transitions from Boreal to Mixed states, but not from Mixed to Temperate. This indicates that temperate species can readily colonise soils found in mixedwoods but may have more difficulty in colonising hydric boreal soils. Thus, local soils may be important in explaining the low transition rate from Boreal to Mixed. Very poor drainage, often associated with peatland and thick organic layer, is usually thought to be improper for the regeneration of temperate species (Lafleur *et al.*, 2010). Several studies found that *Acer saccharum* regenerates well across the ecotone because of its large tolerance to various soil conditions (Barras et Kellman, 1998; Fisichelli *et al.*, 2014; Goldblum et Rigg, 2002; Kellman, 2004). At their northern range limit, *A. saccharum* and *A. rubrum*, the species contributing most to compositional changes in Québec (Brice *et al.*, 2019), are hypothesised to be mostly limited by cold soil temperature (Barras et Kellman, 1998; Goldblum et Rigg, 2002).

Moreover, disturbances may counteract any effect of soil properties. Indeed, disturbances, such as logging and fire, often remove the surface organic layers and expose mineral soil. They can, consequently, provide an appropriate seedbed for temperate species recruitment (Archambault *et al.*, 2006; Landhäuser *et al.*, 2010). In combination with climate warming, disturbances may also facilitate temperate migration by increasing understory air and soil temperatures (Stevens *et al.*, 2015).

4.3. Changes in long-term equilibrium and biome boundary

Our model highlights the potential role of disturbances in influencing the position of the temperate-boreal boundary as well as the proportion of temperate and boreal biomes at equilibrium. As a result of the increased replacement of Mixed by Temperate states and a decline of Boreal to Pioneer states, the equilibrium temperate-boreal boundary shifts northward with moderate disturbances. While our results should not be interpreted as projections for the future, they are useful to highlight the direction of forest dynamics under different disturbance scenarios and underscore that short-term changes in the transition probabilities can impact long-term regional forest patterns. Our findings also support the simulations of Boulanger *et al.* (2019) where harvesting under future climate warming was projected to promote further invasions of pioneer species, such as *Populus*, and temperate species, such as *Acer* and *Fagus*, in mixedwoods of Québec.

Based on their simulations, Vanderwel et Purves (2014) concluded that logging would primarily accelerate the expansion of pioneer forests but would not promote extensive biome shifts over the next century in eastern United States. In contrast to their results, we found a clear range shift of the Temperate state under moderate disturbances, whereas the Pioneer state would have the advantage and become dominant at equilibrium only under major disturbances. We hypothesise that the northern shift of the Temperate state induced by moderate disturbances was mainly the result of the increased dominance of temperate species in areas where they are already present. Indeed, the current disturbance regime in our study area contributed to the decline of one boreal species in particular, *Abies balsamea*, which in turn benefited the growth of co-occurring temperate species. Moreover, because of its positive response to past (Danneyrolles *et al.*, 2019), recent (Brice *et al.*, 2019) and future (Boulanger *et al.*, 2019) disturbances in Québec, *Acer rubrum* is likely to play a disproportionate role in the temperate biome shift. However, the low probability of transition from Boreal to Mixed suggests, like other studies, that migration of temperate trees into pure boreal forest will be a much slower process (Solarik *et al.*, 2019; Vissault, 2016).

4.4. Disturbances accelerate the transient dynamics

Beyond their impacts on the equilibrium, disturbances may substantially affect forest transient dynamics. We found that disturbances increased the rate of tree species replacement (reduced turnover time) and induced a convergence of the dynamics (reduced entropy), thereby accelerating transition dynamics toward a new equilibrium (reduced half-life). While disturbances are known to accelerate stand-scale forest succession (Abrams et Scott, 1989; Bolte *et al.*, 2014), here we provided evidence that their effects could translate into an acceleration of regional-scale biome shifts.

In the continuous boreal zone (spruce-moss domain), forests dominated by *Picea mariana* are usually characterised by dynamics of stand self-replacement with minimal compositional changes across disturbance cycles (Goldblum et Rigg, 2010). Consistent with this dynamics, the turnover time of undisturbed northern boreal forests was very long and the entropy very low in our results. The turnover was shortened by disturbances, but the entropy remained low, indicating that the dynamics was still very predictable (back and forth transitions between Boreal and Pioneer states) and that there was no directional shift associated with disturbances. Hence, boreal forests lose their persistence when moderately disturbed but remain resilient as they return to their previous boreal state. Under major disturbances, boreal forests collapsed to Pioneer state and reached this new equilibrium swiftly (short half-life). This observation is consistent with previous studies suggesting that boreal forests can easily shift into an alternative treeless state in response to severe or repeated disturbances (Payette et Delwaide, 2003).

In contrast, the ecotone is characterised by a rapid turnover and high entropy indicating abrupt compositional shift which can go in any direction. Compared to northern boreal forests, the short turnover time implies a low persistence of the forest states in this region even under minor disturbances. This result corroborates the predictions made by Vissault (2016), where mixed forests would undergo a swift conversion to temperate forests in the next decades, whereas boreal forests would present a large inertia presumably because of dispersal limitation. The dynamics of the ecotone appears unstable because it is caught between two stable states, i.e. Boreal to the north and Temperate to the south. Under moderate disturbances, the probability of transitioning to Temperate increases to the detriment of the other possible states, hence the entropy is decreased, and the dynamics becomes more predictable. Such a clear directional shift strongly indicates non-equilibrium dynamics in this region. Although turnover is fast, half-life to equilibrium is long because a forest may not move towards equilibrium and may undergo multiple transitions.

4.5. Ecological and management implications

A common assumption is that factors determining species distributions are hierarchical, such that climate would govern the distributions at regional scale while soil conditions would be more important at local scale (Pearson et Dawson, 2003). However, our study provides empirical evidence that, through their effect on demography, landscape disturbances and, to a lesser extent, local soil factors may interact with global warming to influence regional shifts in forest types. Specifically, natural and anthropogenic disturbances cause a widespread mortality of a dominant boreal species, while climate warming likely increases the growth of co-occurring temperate species in the newly formed canopy gaps, thus altering post-disturbance successional trajectories and catalysing regional forest transitions.

A shift in dominant forest cover from conifer to deciduous broadleaf species entails large changes in tree species diversity and composition (Berteaux *et al.*, 2010) that can accumulate through time and space and induce a complete transformation of regional forest dynamics and functions (Peters *et al.*, 2007). In the long term, this regime shift could increase carbon sequestration (Thurner *et al.*, 2014), modify disturbance regimes (reduced flammability of broadleaf species Terrier *et al.*, 2013; and reduced sensitivity to current outbreak-prone pest MFFP, 2018), alter soil microbial activity (Laganière *et al.*, 2010) and affect wildlife distribution (Mizel *et al.*, 2016).

Such regime shifts will impact strongly on forest management strategies in area where silvicultural practices are tailored to the regional disturbance regimes and rely on natural regeneration. In Québec, ecosystem-based forest management seeks to maintain the composition and structure of a reference state, defined as the preindustrial forest conditions (Pinna, 2009). Yet, Boulanger *et al.* (2019) showed that such management would fail to restore historical forest conditions under future climate change, and that disturbances would only exacerbate the gap. While trying to maintain a historical state is likely impractical, our results emphasise that management should not only anticipate change, but should acknowledge that current forests have already undergone changes and are in the process of further transformation. Moreover, our study suggests that partial cutting could be used to increase temperate tree growth in mixedwoods. However, natural recruitment of temperate trees might not be sufficient. Thus, assisted migration could be necessary to facilitate range expansion, thereby increasing forest resilience to future climate warming (Duveneck et Scheller, 2016). The synergistic effects between climate change and disturbances are likely to further increase future uncertainty by fostering abrupt non-linear changes. In the face of this growing uncertainty, the role of forest management will be critical in building resilience and adaptative capacity of forest ecosystems (Messier *et al.*, 2013).

5. Acknowledgements

The authors declare no conflict of interest.

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6. Data Accessibility Statement

The complete forest inventory dataset used in this study is available online at <https://www.donneesquebec.ca/recherche/fr/dataset/placettes-echantillons-permanentes-1970-a-aujourd'hui>. All the data used in the study, in addition to R scripts to reproduce the analyses and the figures, can be found online at <https://github.com/mhBrice/transition>.

Third Article.

Northern range shifts of temperate tree saplings in Québec: the role of climate, stand composition, soils and disturbances on recruitment dynamics

by

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ABSTRACT.

1. Tree recruitment is a critical step to initiate species range shifts in forest under climate change. While non-climatic factors may slow down sapling establishment, canopy disturbances may promote episodic recruitment pulses of migrating species. Yet, our understanding of the factors controlling tree recruitment dynamics at range margins remains limited.

2. We used permanent forest inventory plots sampled from 1970 to 2018 in Québec, Canada, to examine potential climate-induced shifts in the distribution of saplings (diameter 1-9 cm), with particular attention to four temperate species at their northern range limits (*Acer rubrum*, *Acer saccharum*, *Betula alleghaniensis* and *Fagus grandifolia*). We compared latitudinal shifts in sapling distribution over time (from 1970-1981 to 2005-2018) among different disturbance levels as well as altitudinal shifts among regions. Then, for each of the four species, we fitted a hurdle model to quantify the role of climate, disturbances, as well as abiotic and biotic stand characteristics.

3. Saplings of the four species increased in occurrences across Québec, except for *A. saccharum* which declined in the southern portion of the study area. We found significant northward shifts in sapling distributions in undisturbed forest plots for *Acer spp.* and *Betula*, as well as in moderately disturbed plots for *Acer spp.* only, but no shift at major disturbances. Downslope shifts of temperate saplings at their northern margins, albeit not significant, may signal the onset of a migration from marginal populations found on hilltops. Our results highlight that, although moderate logging can promote sapling recruitment, it was largely constrained by local forest composition (abundance of conspecific and boreal trees), as well as topographic position and drainage.

4. *Synthesis* Temporal patterns of sapling recruitment provided an early signal of northward migrations of temperate tree species and indicated that important compositional changes are underway. However, disturbances can influence the magnitude of range shifts and should therefore be taken into account when projecting future species distributions. While moderate logging may promote recruitment pulses of temperate species at their northern margins, dispersal limitation, priority effect from boreal trees, as well as topographic and edaphic conditions may greatly reduce potential northward shifts of temperate species.

Keywords: Climate change, Disturbances, Logging, Northward range shifts, Québec forest inventory, Temperate-boreal ecotone, Topographic and edaphic conditions, Tree migration, Tree sapling recruitment.

1. Introduction

Spatiotemporal changes in tree recruitment may provide early signals of shifts in species distributions under climate warming (Anderson-Teixeira *et al.*, 2013, Boisvert-Marsh *et al.* (2014); Sittaro *et al.*, 2017; Zhu *et al.*, 2012). While adult trees may survive for a long time in suboptimal conditions, the regeneration process involves a sequence of several important climate-sensitive steps, i.e., flowering, pollination, seed production and germination, and seedling establishment and survival (Bykova *et al.*, 2012). Hence, compared to adult trees, the distribution and composition of young recruits can change rapidly in the face of environmental changes (Copenhaver-Parry *et al.*, 2020). Since species northern range limits are substantially controlled by their physiological tolerances to minimum temperature (Arris et Eagleson, 1989), tree species are expected to shift their distributions toward higher latitudes in response to climate warming. Consistent with these hypotheses, temperate tree species in Québec have shifted their range limits northward and these shifts were larger for saplings than for adult trees (Boisvert-Marsh *et al.*, 2014; Sittaro *et al.*, 2017). However, Sittaro *et al.* (2017) reported that these latitudinal shifts were poorly correlated with climate warming and Boisvert-Marsh *et al.* (2019) showed both positive and negative effects of climate change variables on sapling recruitment at their range margins. This apparent contradiction between the expected northward shifts and the underlying driver may indicate that trees are responding to a complex suite of environmental drivers (Boisvert-Marsh *et al.*, 2019; Carteron *et al.*, 2020; Leithead *et al.*, 2010; Solarik *et al.*, 2019). Because tree migration ultimately depends upon successful recruitments in new locations beyond their current range limits (Renwick et Rocca, 2015), determining what conditions can facilitate or impede sapling establishment is a milestone in predicting future tree species distributions (Copenhaver-Parry *et al.*, 2020) and vulnerability (Aubin *et al.*, 2016).

Seed dispersal limitation is likely one of the primary constraints to tree recruitment at range margins (Caspersen et Saprunoff, 2005; Renwick et Rocca, 2015). Many species typically dispersed their seeds close to the parent trees, from a few metres to a few hundred metres (Scheller et Mladenoff, 2005). As such, many studies have found that recruitment is highly dependent on the abundance of conspecific trees (Caspersen et Saprunoff, 2005; Drobyshev *et al.*, 2014; Graignic *et al.*, 2014; Solarik *et al.*, 2019). Hence, migration at the leading edge may not appear as a moving front following climate warming; recruitment may occur episodically through rare long dispersal events or locally through the expansion from isolated northern populations (Pearson, 2006). Marginal populations at northern range limits (i.e. cryptic refugia) have likely played a key role in postglacial tree migration and they may be as important in future range shifts (McLachlan *et al.*, 2005). In the transition zone of eastern North America, several temperate tree species are spatially constrained on hilltops at their northern limits (Blouin et Berger, 2008; Gosselin, 2002) likely due to warmer

microclimate created by cold air drainage, i.e. cold air flowing downslope and getting trapped into valleys and depressions (Barras et Kellman, 1998; Goldblum et Rigg, 2002). Hence, contrary to the most common predictions of shifts towards higher elevations (Beckage *et al.*, 2008), these northern populations could possibly migrate downslope with climate warming (Goldblum et Rigg, 2002). Although this phenomenon could contribute to the northward range shifts, it has not yet been documented.

In addition to species dispersal limitations, several other biotic and abiotic factors could influence recruitment. For instance, resident boreal populations could constrain establishment and survival of temperate species at their northern margins potentially through direct competition and indirect alteration of substrate quality (Solarik *et al.*, 2019). Indeed, several local-scale studies found that the survival of seedlings of *Acer saccharum* was reduced in boreal forests, principally because their soils have low pH, nutrient availability and microbial activity, as well as high needle cover and different mycorrhizal composition than soils of temperate forests (Brown et Vellend, 2014; Carteron *et al.*, 2020; Collin *et al.*, 2017; Solarik *et al.*, 2019). It is unclear however how these local constraints are translated to regional-scale recruitment patterns. Observed regeneration patterns in the temperate-boreal ecotone of eastern Canada failed to support the idea that there were strong barriers to potential temperate tree recruitment into boreal forest patches (Barras et Kellman, 1998; Fisichelli *et al.*, 2014). Given these uncertainties, regional-scale studies modelling the influence of sub-optimal soil conditions on the recruitment process can provide useful information to predict future forest dynamics.

Disturbances are essential processes to initiate natural forest succession and regeneration by promoting tree recruitment in canopy gaps (Attieill, 1994); it was therefore suggested that they could accelerate tree range shifts (Brice *et al.*, 2020; Renwick et Rocca, 2015; Serra-Diaz *et al.*, 2015; Turner, 2010). Indeed, disturbance events that cause mortality of persistent boreal trees could reduce competition and increase resource availability, thus facilitating the establishment of migrating species. Dendrochronological studies have reported that the recruitment of many tree species during the last century was strongly synchronised with canopy disturbances (recruitment pulse), such as insect outbreak (Bouchard et Kneeshaw, 2006; Duchesne et Prévost, 2013), fire (Bergeron, 2000) and logging (Angers *et al.*, 2005). The type, severity and size of disturbances influence which species are able to establish depending on several characteristics, such as shade-tolerance, dispersal ability and vegetative reproduction (Bergeron, 2000; Brisson *et al.*, 1988). For instance, moderate outbreaks in mixedwoods may favour the regeneration of the mid-tolerant species, such as *Acer rubrum* and *Betula alleghaniensis*, whereas shade-tolerant species, such as *Abies balsamea*, may recruit continuously in small canopy gaps (Duchesne et Prévost, 2013).

Although a recruitment pulse following a disturbance is a common pattern in forest succession (Bouchard et Kneeshaw, 2006), there is little evidence whether this process could

accelerate broad-scale species range shifts under climate change (Renwick et Rocca, 2015). Previous work in Québec showed that both natural and anthropogenic disturbances of moderate severity (i.e., disturbances that removed between 25–75% of the tree basal area) have led to an increased proportion of warm-adapted tree species (thermophilization) in forests (Brice *et al.*, 2019) and promoted transitions from mixed to temperate forests (Brice *et al.*, 2020). However, most of these compositional changes were associated with the high mortality of a dominant boreal species at its trailing edge followed by the growth release of co-occurring temperate species, while the contribution of tree recruitment was marginal (Brice *et al.*, 2020). Some simulation studies have concluded that disturbances are unlikely to drive extensive biome shifts in the coming decades perhaps because they would favour mainly the rapid recovery of resident species (Liang *et al.*, 2018) or the invasion by early-successional species (Vanderwel et Purves, 2014). Empirical studies have reached conflicting conclusions. On the one hand, canopy gaps have been shown to locally facilitate establishment of temperate species in mixed forests of Ontario (Leithead *et al.*, 2010). On the other hand, disturbances had little or no effect on the northern range shifts of tree saplings in the United States (Woodall *et al.*, 2013). Boisvert-Marsh *et al.* (2019) also found a modest and generally negative effect of disturbances on new colonisations of temperate species at their northern range limits. Given that forests are increasingly subject to human disturbances, more empirical evidence is essential to disentangle their role on forest regeneration dynamics under climate change.

Our understanding of the factors controlling recruitment within the temperate-boreal ecotone remains limited, where few broad-scale empirical studies have assessed the influence of a large array of environmental conditions on regeneration dynamics at range margins. This study investigates sapling recruitment dynamics of four dominant temperate broadleaf species (*Acer rubrum*, *Acer saccharum*, *Betula alleghaniensis* and *Fagus grandifolia*) at their northern range limits in Québec, Canada. These four focal species have recently experienced modest to large shifts in their northern range limits (Boisvert-Marsh *et al.*, 2014; Boisvert-Marsh *et al.*, 2019; Sittaro *et al.*, 2017). Specifically, we examine the following questions: (i) How did the spatial distribution of sapling occurrence and abundance changed between a historical and a recent survey? (ii) Do disturbances influence the northward (in latitude) shifts of tree saplings? (iii) Are tree saplings of northern marginal populations migrating downslope? (iv) How do stand composition, topo-edaphic characteristics, climate and disturbances influence tree recruitment at their northern range limits? To address these questions, we assessed regional changes in sapling occurrence and abundance across and compared shifts in latitudinal distributions of saplings among different disturbance severity levels. We also test for shifts in altitudinal distributions among regions. We then investigated the relative importance of a series of environmental factors on tree sapling recruitment (measured as the number of tree individuals that reached a diameter at breast height (DBH) between 1–9 cm

during a time interval): climate, topo-edaphic factors, plot and neighbourhood composition, and disturbances.

2. Methods

2.1. Study area and forest inventory data

We analysed recruitment of temperate tree species using forest inventory plots in Québec, Canada. From 1970 to 2018 (and ongoing), the *Ministère des forêts, de la Faune et des Parcs* (MFFP, 2016) surveyed permanent forest plots approximately every 10 years across the forested portion of Québec in order to document changes in forest productivity and growth. During the same period, a complementary network of temporary forest plots was also put in place in which each plot was surveyed only once principally to inform the timber supply analysis.

The region surveyed by the inventory program extends from approximately 45° to 52° North latitude and covers six bioclimatic domains (Saucier *et al.*, 2009). The present study focuses on the western portion of Québec forests, from the Sugar maple-basswood domain (in the deciduous zone) to the Balsam fir-white birch domain (in the mixed boreal zone; Fig. 3.1) where there is a strong linear climatic gradient from south to north (Fig. C.1) and where climate warming is strongest in meridional Québec (Yagouti *et al.*, 2006). The natural disturbance regimes vary considerably along the latitudinal gradient of the study area, with frequent large-scale insect outbreaks in the northern mixedwood forests, and small windthrows and treefall gaps in the southernmost deciduous forests. Similarly, clearcuts are more frequent in northern regions, while in southern regions partial cuts are more common (Fig. C.2).

Permanent and temporary plots are circular with a radius of 11.28 m and an area of 400 m². Within each plot, trees larger than 9 cm in DBH are identified to species, measured and their vitality noted. In our analysis, we refer to these individuals larger than 9 cm as adults. In permanent plots, saplings (DBH between 1 and 9 cm) were identified and numbered within a smaller subplot (40 m²).

To study recruitment of temperate tree species, we first selected all permanent inventory plots in the study area that had been sampled at least twice. We then disregarded plots that were subjected to active reforestation by plantation during the study period because we were interested in natural recolonisation processes. Finally, we kept plots for which all studied environmental predictors were measured (see below; Table 3.1). This yielded a total of 4099 permanent plots considered (Fig. 3.1).

In the analyses on shifts distribution, we compared a historical (1970-1981) and a recent (2005-2018) inventory periods in order to maximise time interval between measurements and

detect long-term changes. The mean time interval between the historical and the recent surveys was 39.6 years ($sd = 5.3$). To model recruitment at their northern range margins, we subset the northernmost bioclimatic domain where each species is found: the recruitment of *A. rubrum* was analysed in the Balsam fir-yellow birch and the Balsam fir-white birch domains, *A. saccharum* and *B. alleghaniensis* were analysed in the Balsam fir-yellow birch domain, and *F. grandifolia* was analysed in the Sugar maple-yellow birch domain (Fig. 3.1). Unlike the previous analysis, for the recruitment model, we used all available plot measurements and analysed recruitment between consecutive plot surveys to take into consideration multiple recruitment events. The time intervals between plot surveys varied from 4 to 32 years, with a mean interval of 10.88 years ($sd = 3.48$).

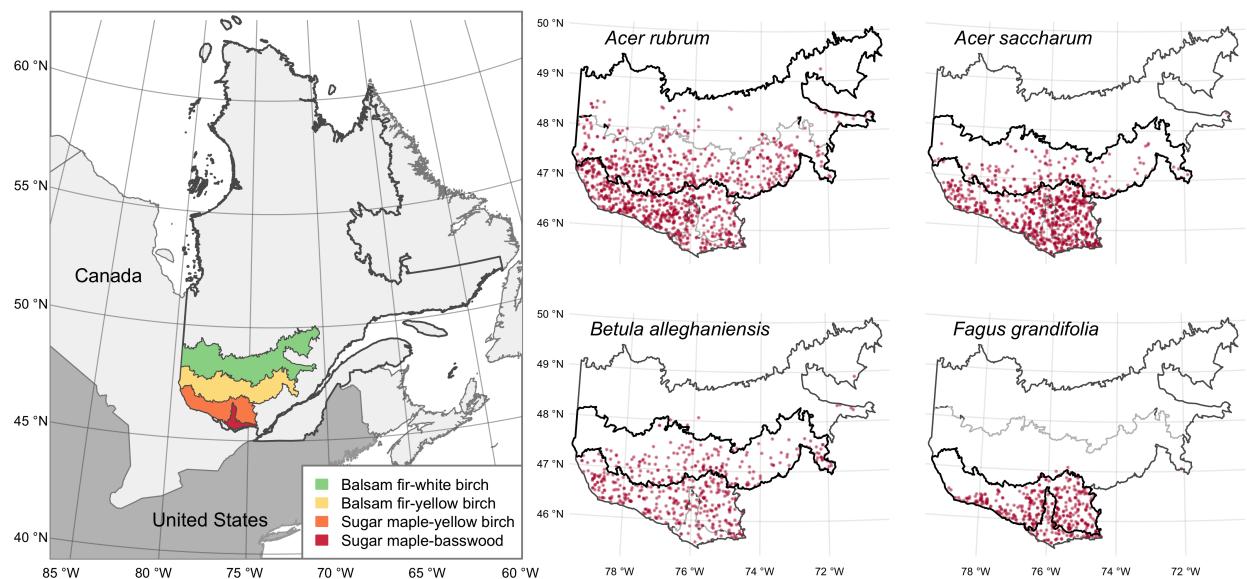


Figure 3.1. Maps of the 4099 permanent inventory plots with sapling recruitment for each of the four temperate tree species. The regions used for the recruitment models (hurdle) are highlighted in black. The coloured map represents the whole study area.

2.2. Environmental variables

Annual climatic conditions from 1960 to 2018, were extracted from a 2-km² (60 arc sec) resolution grid over the entire study area using the ANUSPLIN climate modelling software (<http://cfs.nrcan.gc.ca/projects/3/8>; McKenney *et al.*, 2011). Plot locations were intercepted with two bioclimatic variables hypothesised to influence tree establishment, survival and growth: the mean temperature during the growing season and the climate moisture index (CMI) from May to September (Table 3.1). To account for inter-annual climatic variability and lag in vegetation response to climate, climate variables were averaged over a 10-year period prior to the plot measurement. Climate change in each forest plot was measured as the slope between the climate variable over time from 1950 to 2018. During this period,

growing season temperatures have increased by 0.17 °C/decade in the plots, while CMI have shown no significant trend (Fig. C.3), but the magnitude of climate change varies across the study area (Fig. C.1).

We also collected information pertaining to natural and anthropogenic disturbances that have affected the forest plots during the study period (Table 3.1; Fig. C.2). At each plot, the type of disturbances (21 types) and their levels of severity were recorded during field surveys (see Fig. C.2 for details; MFFP, 2016). For our analyses, we differentiated two main types of disturbances: natural disturbances and logging. Three levels of severity were originally defined by the MFFP (minor, moderate or major) depending on the proportion of basal area affected (Table 3.1). We kept all three levels of logging, but for natural disturbances, we combined the major and moderate levels together because not enough major disturbances affected the studied species, hence their effect could not be estimated.

Core samples were also collected on selected trees deemed representative of the forest plot during surveys to measure their age (MFFP, 2016). Stand age was estimated as the mean of these measures to account for forest succession processes after disturbances.

At each plot, several topographic and edaphic characteristics were recorded (MFFP, 2016). To capture topographic conditions, we selected plot altitude and position along the slope (lower, middle or upper slope). We also selected drainage (xeric, mesic, hydric) and pH (low, medium, high) because they largely affect nutrient availability, soil structural properties and vegetation development (Tan, 2009).

We measured the total tree basal area of all adult trees ($DBH \geq 9\text{cm}$) of boreal species (here, *Abies balsamea*, *Larix laricina*, *Picea glauca*, *Picea mariana* and *Pinus banksiana*) to compute an approximate index of local competition and priority effect on soil conditions (Solarik *et al.*, 2019). Similarly, we computed the basal area of conspecific adult trees of the focal species (i.e. one of the four temperate species under investigation) to approximate local seed availability; when conspecific trees are abundant in the plot, we expect higher seed availability. We used the temporary inventory plots to describe neighbourhood forest composition and account for potential seed sources from surrounding populations. Around each permanent forest plot, we extracted the 100 nearest temporary plots located within a 10-km buffer zone. We chose a radius of 10 km as a compromise between a realistic dispersal distance and the assurance of finding a sufficient number of temporary plots in the buffer zone. Within the buffer, we computed the mean basal area per hectare of the focal tree species, weighted by a negative exponential kernel distance to the given permanent forest plot. This kernel makes it possible to grant a monotonously decreasing importance to the populations that are located further away.

Table 3.1. Description of the explanatory variables used in the hurdle models of tree recruitment.

Variable name	Variable description
Climate	
Temperature	Mean temperature during growing season, 10-year average prior to plot measurement ($^{\circ}\text{C}$).
CMI	Mean Climate Moisture Index (difference between precipitation and potential evapotranspiration) from May to September, 10-year average prior to plot measurement (cm).
ΔTP	Slope between TP and year, from 1950 to 2018 ($^{\circ}\text{C}/\text{year}$).
ΔCMI	Slope between CMI and year, from 1950 to 2018 (cm/year).
Physical	
pH	3 classes pH of the surface horizon: low (<4.0), medium (4.1-4.4), high (≥ 4.4)
drainage	3 classes of soil drainage: hydric, mesic, xeric.
altitude	Altitude of the forest plot (m).
slope	3 classes of slope positions: lower slope, mid slope, upper slope.
Biotic	
$\text{conspe}_{\text{plot}}$	Total basal area of conspecific adult trees (dhp ≥ 9 cm) in a forest plot at t .
$\text{conspe}_{\text{neigh}}$	Total basal area of conspecific adult trees (dhp ≥ 9 cm) in a 10km buffer around a forest plot.
$\text{boreal}_{\text{plot}}$	Total basal area of boreal adult trees (dhp ≥ 9 cm) in a forest plot at t .
Disturbances	
Logging	3 levels of logging severity: None or minor ($\leq 25\%$ of basal area removed); moderate, mainly partial cuts (25-75%); or major, mainly clearcuts ($\geq 75\%$).
Natural	2 levels of natural disturbance severity, mainly insect outbreaks, as well as windfall and few forest fires: None or minor ($\leq 25\%$), moderate or major ($> 25\%$).
age	Stand age (in years).

2.3. Analyses

2.3.1. Changes in sapling latitudinal and altitudinal distribution

We investigated in details the temporal change in the sapling spatial distributions of the four most abundant temperate deciduous species that reach their northern limit in the study area: *Acer rubrum*, *Acer saccharum*, *Betula alleghaniensis* and *Fagus grandifolia*. We examined whether the latitudinal and altitudinal distributions of saplings of these four focal

species changed between a historical (1970-1981) and recent (2005-2018) inventory period. For each time period and each tree species, we selected all plots containing at least one sapling occurrence and extracted the latitude and the altitude of the plots. We then tested for latitudinal and altitudinal shifts between time periods for all selected plots using Wilcoxon-Mann-Whitney tests (Siegel et Castellan, 1988). This nonparametric test quantifies the shift in location (median) between the distributions of two samples. The before-after distributions are not paired because saplings may occur in different plots during the two time periods. We compared the latitudinal shifts among disturbance levels and the altitudinal shifts among bioclimatic domains using the same tests.

2.3.2. Recruitment model

To identify environmental drivers of sapling recruitment, we analysed recruitment between consecutive plot surveys of the selected study area (not only the historical and recent surveys, but all measurements in between) for each of the four temperate species independently. Hence, for any focal species, we modelled recruitment counts observed between t and $t + \Delta t$. Explanatory variables related to climate change (ΔTP and ΔCMI) and physical characteristics (altitude, pH, drainage and slope position) were considered as static (their value for a given plot does not change through time). Climate (TP and CMI) and disturbances (logging, natural and age) were included as time-varying explanatory variables. Climate variables at time t were used to model recruitment events between t and $t + \Delta t$. Disturbances that occurred during the interval t and $t + \Delta t$ were used to model recruitment events during the same time period. The probability of observing recruitment events in a forest plot depend on the time interval between surveys. Because of the variation in time intervals in the dataset, we included an exposure variable in the hurdle models (i.e., an offset on the logarithm of time interval). All quantitative explanatory variables were standardised to mean 0 and standard deviation 1 prior to running the models.

Recruitment is usually represented as a count variable, i.e. number of recruits. Because of the nature of the regeneration process, recruitment data often present a large amount of zero records, i.e. inventory plots with no recruits. The Québec data showed that a very large number of plots had zero counts (between 80 and 90% of zero counts). This implies that the number of zeros is higher than expected at random from conventional distributions, such as Poisson and negative binomial (Zuur, 2009).

We therefore chose to use a hurdle model to include excess zeroes in the modelling process (Zeileis *et al.*, 2008; Zuur, 2009). A hurdle model has the following two parts: first, the zero hurdle part models a right-censored outcome variable indicating plots without ($Y = 0$) or with recruits ($Y = 1$, where all counts larger than 0 are censored, that is, given a value of 1). This part can be fully modelled as a binomial process (logistic regression), including covariates or not. Second, the truncated count part models the number of recruits for those

forest plots with recruits (for those with $Y > 0$). The counts can be modelled with a truncated Poisson or truncated negative binomial model, including covariates or not. We used a negative binomial to model the counts to allow for extra overdispersion in the positive (non-zero) part of the data. The model allows for a set of predictors for the probability of a zero response and a different set for the mean of nonzero responses.

Ecologically, it is relevant to consider these two processes separately because predictors that determine the presence-absence of recruits can be different from those predicting their abundance. Therefore, the zero hurdle part can be interpreted as a regular logistic model, while the count part can be interpreted as a truncated negative binomial model (Zuur, 2009).

Using a binomial distribution to model the presence and absence of recruitment $f_{binomial}$ and a negative binomial to model the number of recruits f_{negbin} , the probability function of the hurdle model f_{hurdle} is given by:

$$f_{hurdle}(Y = y|X, Z, \beta, \gamma) = \begin{cases} f_{binomial}(0|Z, \gamma) & \text{if } y = 0 \\ \frac{1-f_{binomial}(0|Z, \gamma)}{(1-f_{negbin}(0|X, \beta))} \times f_{negbin}(y|X, \beta) & \text{if } y > 0 \end{cases},$$

where Y is a random variable representing the observed number of recruits and y is the outcome variable, Z and X are matrices of predictor variables in the zero part and count part, respectively, and γ and β are the corresponding vectors of coefficients (Zeileis *et al.*, 2008).

We can model the probability of zeros $P(Y = 0) = \pi_i$ and the mean μ_i of positive count data in a forest plot i using the predictor variables Z_i and X_i with the following logistic and log-linear regressions:

$$\text{logit}(\pi_i) = \ln\left(\frac{\pi_i}{1 - \pi_i}\right) = \gamma_0 + \gamma_1 \times Z_{1i} + \dots + \gamma_n \times Z_{ni},$$

$$\log(\mu_i) = \beta_0 + \beta_1 \times X_{1i} + \dots + \beta_n \times X_{ni}.$$

In our model, we tested the same initial set of predictors in Z and X (all variables in Table 3.1). We then performed stepwise backward selection procedures based on Akaike information criterion (AIC; Zuur, 2009) on each part of the hurdle models independently to reduce the number of predictors and keep the most relevant ones. The full hurdle models were then run with the selected predictors. Regression coefficients were estimated by maximum likelihood. We evaluated the goodness-of-fit of the four models (one for each species) against the baseline model using likelihood ratio tests (Zeileis *et al.*, 2008), which evaluate if the addition of one or more new parameters significantly increases the likelihood of the model. We also compared and ranked the importance of each tested predictor using a likelihood ratio test. Starting with a full model containing all the selected predictors, we removed each of the terms one after the other to understand their contribution to the likelihood.

All analyses were performed using the R programming language version 3.6.1 (R Core Team, 2019). The list of R packages that were used to carry out the analyses is provided in the Supporting Information (Table C.1). All data used in the study, in addition to R scripts that reproduced the analyses and figures, will be made available online on GitHub upon manuscript acceptance.

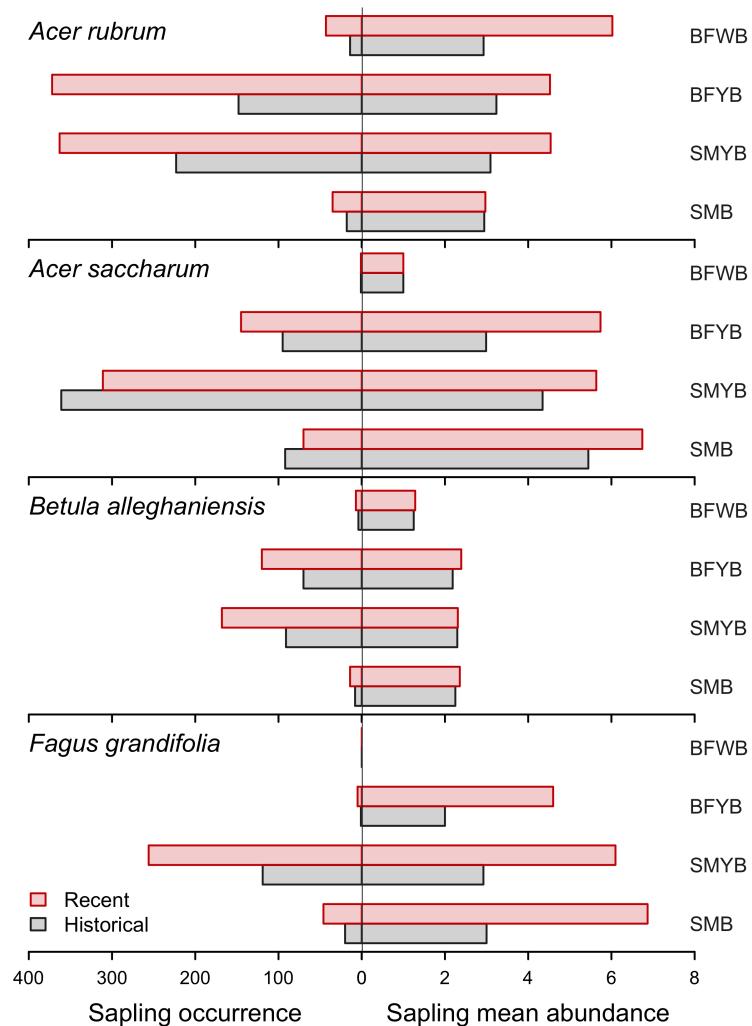


Figure 3.2. Changes in sapling occurrence (number of plots; left portion of the graph) and mean abundance (right) between the historical (1970-1981, in grey) and recent (2005-2018, in red) time periods for each bioclimatic domain. The letters are acronyms for the bioclimatic domains, from north to south: Balsam fir-white birch, BFWB; Balsam fir-yellow birch, BFYB; Sugar maple-yellow birch, SMYB; Sugar maple-Basswood, SMB.

3. Results

3.1. Temporal changes in sapling occurrence and abundance

All four studied species experienced increases in their occurrence and their mean abundance throughout the study area, except for *Acer saccharum*, which experienced occurrence losses in the two southernmost bioclimatic domains (Fig. 3.2). The number of plots with *A. rubrum* saplings increased in all domains and more than doubled in the two northernmost domains; its abundance within these plots also increased, particularly at its northern limit, in the Balsam fir-white birch domain. Occurrences of *Betula alleghaniensis* increased across its range, but its mean abundance did not change much. Occurrences of *Fagus grandifolia* doubled in both Sugar maple domains and new occurrences appeared at its northern range limit, located in the Balsam fir-yellow birch domain. *F. grandifolia* also doubled in abundance throughout its range.

3.2. Latitudinal shifts in sapling distributions

When considering all forest plots together, sapling latitudinal distributions shifted significantly northward through time only for the two *Acer* species (shifts in distribution medians were: $\Delta_{50} = +19.3$ and $+13.2$ km for *A. rubrum* and *A. saccharum*, respectively; Fig. 3.3), whereas we did not observe significant shift for *B. alleghaniensis* and *F. grandifolia*.

Latitudinal shifts were, however, influenced by disturbance severity. We found northward shifts in distributions for *A. rubrum*, *A. saccharum* and *B. alleghaniensis* in undisturbed forest plots (minor; $+18.0$, $+27.0$ and $+26.5$ km, respectively). At moderate disturbances, only the two *Acer* species experienced significant shifts. For *A. rubrum*, the shifts were similar for moderate or major natural disturbances ($+20.1$ km) and moderate logging ($+23.7$ km). For *A. saccharum*, the shift was larger under natural disturbances ($+20.3$ km) than under moderate logging ($+9.8$ km). No significant shift was found for both species at major logging. For *B. alleghaniensis*, the latitudinal shift was only significant at minor disturbances and was hindered at higher disturbance levels. We found no significant shift for *F. grandifolia* for all disturbance levels.

Species latitudinal distributions do not strictly parallel the temperature gradient because it is also influenced by topography. Hence, part of species distributional shifts may not be captured by latitudinal shifts. We thus examined species shifts based on their temperature distributions (mean temperature of the growing season during the historical period) and observed similar patterns for all four species (Fig. C.4) which confirm our previous results (Fig. 3.3).

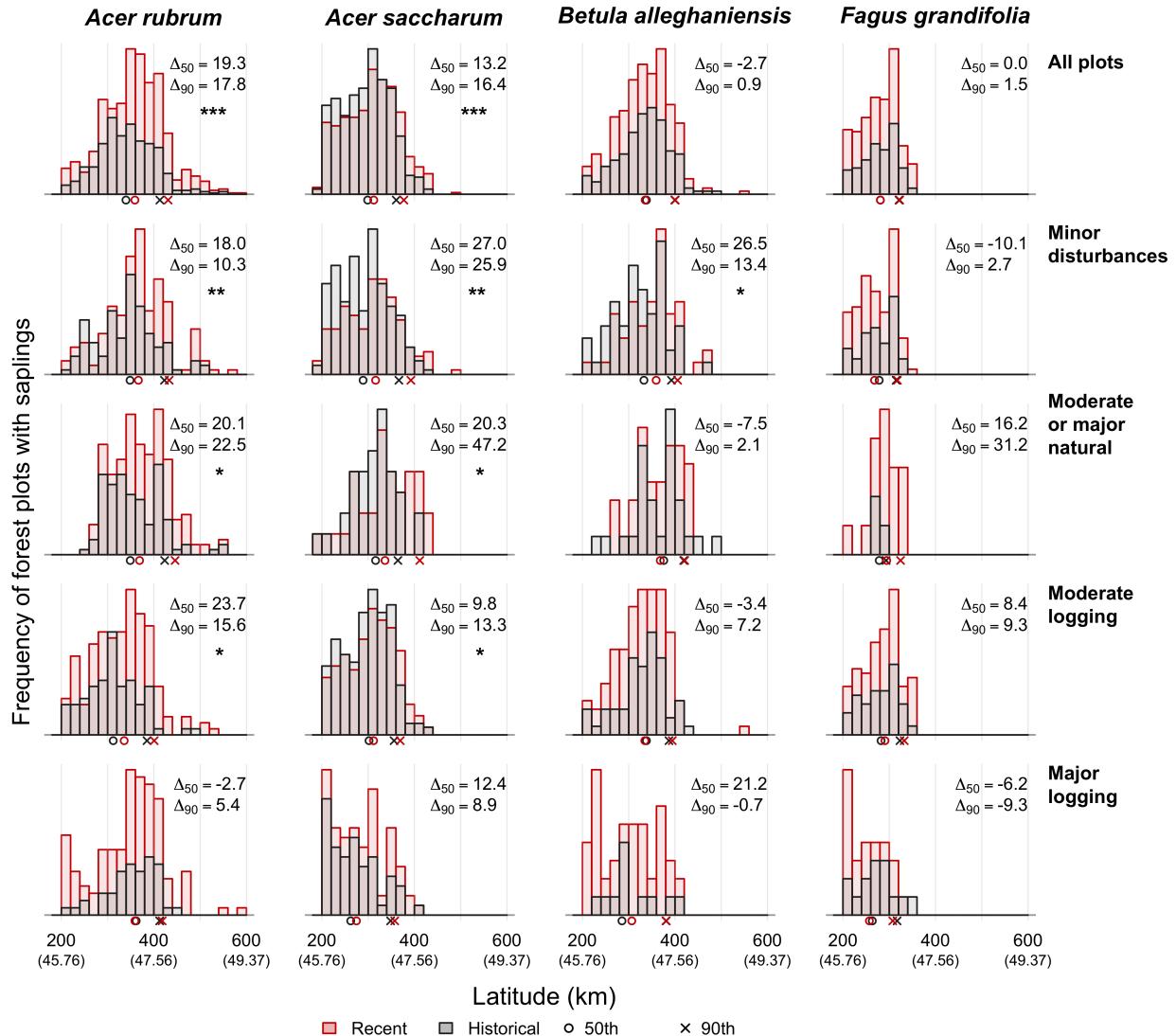


Figure 3.3. Frequency distributions of forest plots containing saplings of each of the four species (column headings), as a function of latitude (abscissa), in the historical (1970–1981; in grey) and the recent (2005–2018; in red) surveys. From top to bottom, distribution of all forest plots combined (first row); plots that have experienced minor disturbances (second row); moderate or major natural disturbances (but no logging; third row); moderate logging (but no natural disturbances; fourth row); and major logging (but no natural disturbances; fifth row). The Δ_{50} and Δ_{90} indicate shifts in kilometres for the 50th (median) and the 90th percentile, respectively, of the latitudinal distribution between the two time periods. The latitudes on the x-axis are projected coordinates in km (NAD83, Quebec Lambert) and the numbers in parentheses correspond to the geographic coordinates in degree. The stars correspond to P -value from Wilcoxon tests comparing the median locations between the historical and recent distributions (. $P \leq 0.10$, * $P \leq 0.05$, ** $P \leq 0.01$, *** $P \leq 0.001$).

3.3. Altitudinal shifts in sapling distributions

We observed no significant shifts in altitudinal distribution for all four species across bioclimatic domains (Fig. 3.4). However, the distributions of all four species presented trends towards downslope shifts, especially at their northern range margins. For example, the median distribution of *A. rubrum* shifted downslope by -64.5 m of altitude.

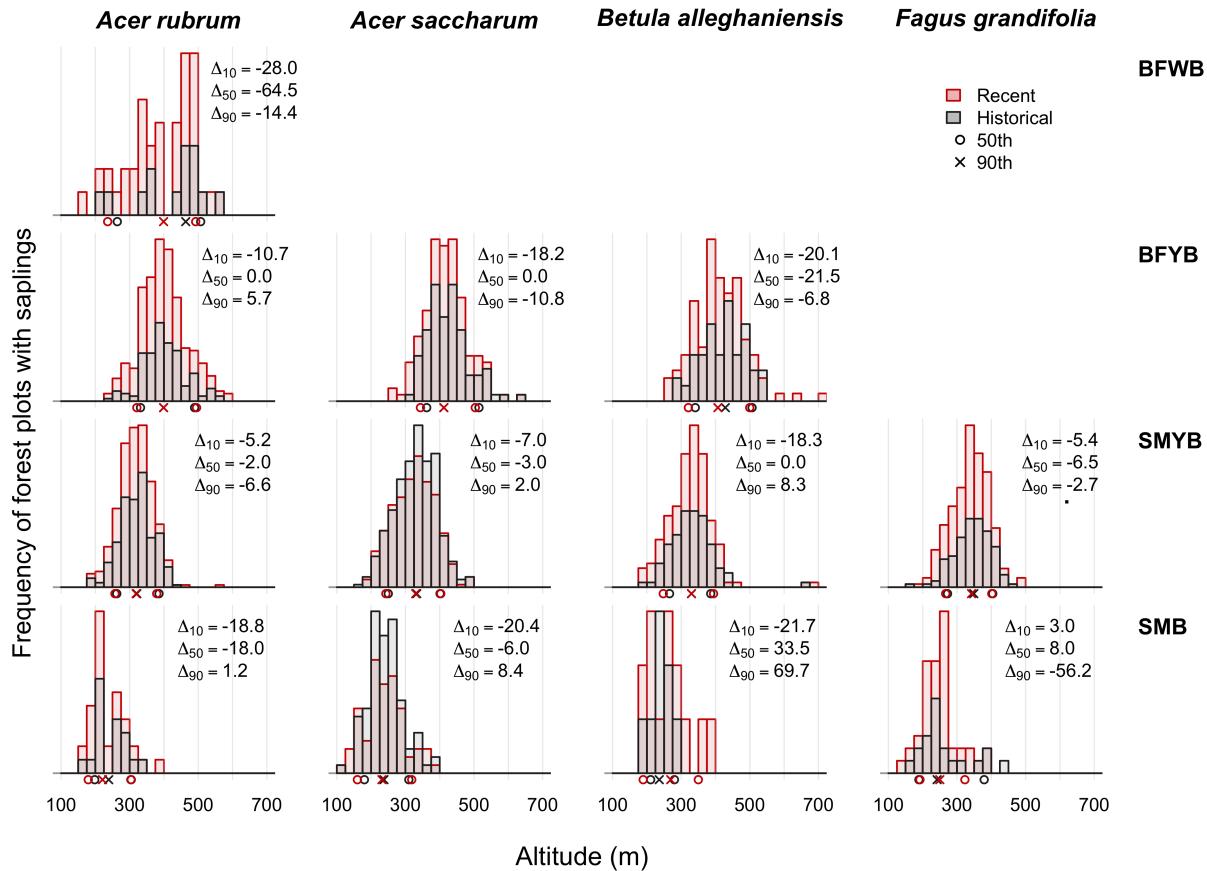


Figure 3.4. Frequency distributions of forest plots containing saplings of each of the four species (column headings), as a function of altitude (abscissa), in the historical (1970–1981; in grey) and the recent (2005–2018; in red) surveys. From top to bottom, distribution of all forest plots in the Balsam fir-white birch (BFWB), Balsam fir-yellow birch (BFYB), Sugar maple-yellow birch (SMYB) and Sugar maple-Basswood (SMB). The Δ_{10} , Δ_{50} and Δ_{90} indicate the shifts in metres for the 10th, 50th (median) and 90th percentiles, respectively, of the altitudinal distribution between the two time periods. Wilcoxon tests were used to compare the median locations between the historical and recent distributions, but none of them were significant.

3.4. Drivers of sapling recruitment

Sapling recruitment of each of the four temperate tree species at their northern margins was influenced by a different set of environmental factors (Fig. 3.5). The explanatory power

was much higher for the zero part (McFadden Pseudo-R² from 20 to 45%) than the count part of the hurdle models (2 to 5%) indicating that we can adequately explain where and when a recruitment event occurred, but not how many did occur. For all species, the biotic variables were the most important, especially the predominance of conspecific adult trees in the plot ($focal_{plot}$), followed by the physical variables, whereas the importance of the other variables varied across species (Fig. 3.5, C.5). The hurdle regression models were all statistically significant (i.e., likelihood ratio tests compared to an intercept only model were all highly significant with $p \leq 0.001$) and showed a good fit to the data (i.e., rootograms indicate a good match between the expected and observed frequencies; Fig. C.6).

The basal area of conspecific trees in the plot ($conspe_{plot}$) and in the neighbourhood ($conspe_{neigh}$) had a strong positive effect on the presence (zero part) and number of recruits (count part) for all species (Fig. 3.5), except for *B. alleghaniensis*, for which conspecific trees in the plot had a negative effect on the number of recruits. The predominance of conspecific trees in the plot was particularly determinant for *A. saccharum* and *F. grandifolia* compared to other variables (Fig. C.5). The total basal area of boreal trees in the plot ($boreal_{plot}$) had a strong negative effect on all species.

Physical variables were also very important to predict the presence and number of recruits, especially for *A. rubrum* and *B. alleghaniensis* (Fig. 3.5, C.5). For all four species, probability of recruitment was higher on hilltops (upper slope, and less so mid slope, compared to lower slope). Altitude influenced *B. alleghaniensis* (negative) and *F. grandifolia* (positive). Poor drainage (hydric compared to mesic soils) had a strong negative effect on all species, while excessive drainage (xeric soils) only affected *F. grandifolia*. The number of recruits of *A. rubrum* and *F. grandifolia* were also lower on hydric soils. Soils with low pH appear beneficial for saplings of *B. alleghaniensis* (compared to medium pH). Soils with high pH had positive effect on both *Acer* species and negative on *F. grandifolia*.

Among the climate variables, temperature always had a positive effect on both the presence and the number of recruits, while CMI had a positive effect on *B. alleghaniensis* only and a negative effect on *A. rubrum* (Fig. 3.5). The effect of climate change varied across species; increased humidity (ΔCMI) was associated with higher probability of recruitment of *A. saccharum*, *B. alleghaniensis* and *F. grandifolia*, but a lower probability for *A. rubrum*. Climate warming (ΔTP) had a positive effect on the presence of *B. alleghaniensis* and negative on *F. grandifolia*. Moreover, climate warming had a positive effect on the number of *A. rubrum* recruits, but a negative effect on *A. saccharum*.

Finally, all disturbances promoted the recruitment of *A. rubrum* (Fig. 3.5). Moderate logging generally increased the presence and number of recruits for all species. Major logging decreased the probability of recruitment of *B. alleghaniensis* and, to a lesser extent, of *A. saccharum* and *F. grandifolia*. Interestingly, the number of recruits of all four species strongly increased with major logging and, less so, with moderate logging. Natural disturbances had a

negative effect on the presence and number of recruits of *A. saccharum* and *B. alleghaniensis*. Recruitment of *A. saccharum* and *F. grandifolia* was more likely to take place in older forest plots (age), whereas more *A. rubrum* recruits were found in younger forests.

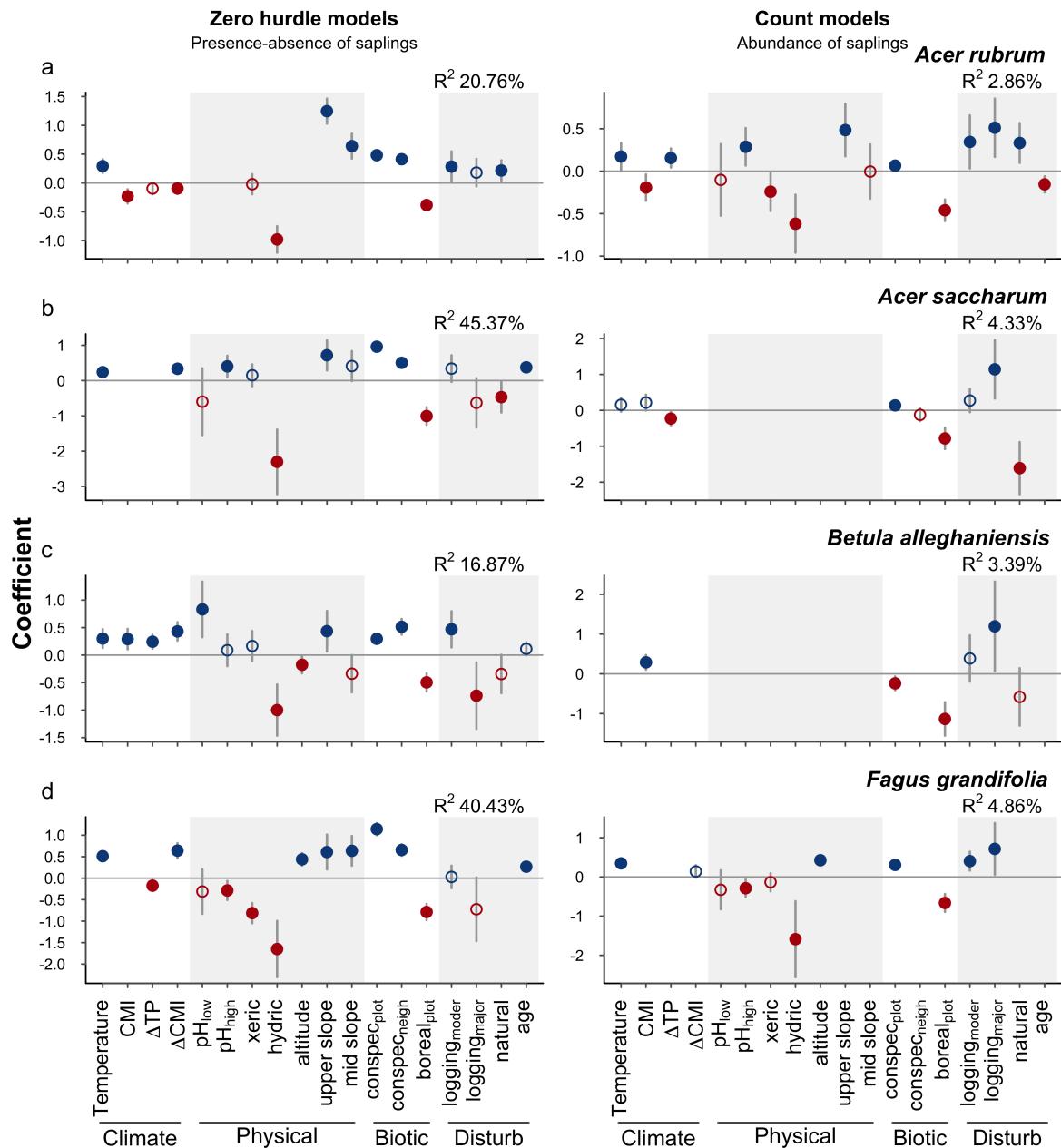


Figure 3.5. Slope coefficients and their 95% confidence intervals estimated by the recruitment models for the four temperate tree species. On the left are the zero parts and on the right are the count parts of the hurdle models. Predictors coloured in blue have a positive effect on the probability of having recruitment (zero part) or the number of recruits (count part), whereas predictors coloured in red have a negative effect. Significant predictors are represented by solid points. McFadden pseudo- R^2 statistics were computed against the null model ($1 - LL_{full}/LL_{null}$). For a description of the predictor variables, see Table 3.1.

4. Discussion

In this study, we used the Québec forest inventory data to examine the distributional shifts in forest regeneration resulting from climate change and to disentangle the underlying environmental drivers of recruitment processes. First, our results showed important changes in the spatial distribution of temperate species recruitment. We observed large increases in the occurrence and abundance patterns of the four studied species, except for *A. saccharum* which declined in the southern portion of the study area. Secondly, we provided evidence of significant northward distribution shifts, but these were affected by disturbances. Saplings of *A. rubrum*, *A. saccharum* and *B. alleghaniensis* experienced northward shifts in undisturbed plots. However, only the two *Acer* species shifted at moderate disturbances (natural or logging). There was no significant shift at major logging. Thirdly, our results may signal the onset of a migration from marginal populations found on hilltops as temperate saplings at their northern margins tended to shift downslope, although this trend was not significant. Finally, we analysed the effect of a large array of environmental conditions on species recruitment to assess how they could control the observed distribution shifts. The hurdle models highlighted that sapling recruitment at species range margins is primarily constrained by stand composition, as well as topo-edaphic characteristics, and facilitated by partial logging. Together, our results suggest that moderate logging may promote recruitment pulses of temperate species, but its catalysing effect on northward shifts may be limited due to other abiotic and biotic constraints.

4.1. Temporal changes in composition and abundance

Forests of the temperate-boreal ecotone are expected to undergo dramatic compositional and structural shifts in response to climate warming (Evans et Brown, 2017). The current distribution of adult trees is mainly a response to past conditions (i.e. climate, disturbances, management, etc.), while the presence and abundance of saplings reflect a response to more recent changes in environmental conditions. Here, we showed important changes in sapling occurrences and abundances of the studied tree species. Saplings of *A. rubrum*, *B. alleghaniensis* and *F. grandifolia* experienced large increases in occurrences in all domains where they are found, indicating colonisation of new habitats. The extensive expansion of *A. rubrum* has been observed across eastern North America (Fei et Steiner, 2007). In contrast, *A. saccharum* experienced a loss in the number of occupied plots over time in the southern portion of its range (i.e. in the two sugar maple domains), but a gain at its northern limit. While the mean abundance of *B. alleghaniensis* was relatively stable over time, the mean abundance of the other three species increased strongly, particularly *F. grandifolia*. The recent decline occurrence of *A. saccharum* and the concomitant expansion of *F. grandifolia* in the forest understory of southern Québec has been previously reported and has been related

to differential responses to disturbances and atmospheric acid depositions (Bal *et al.*, 2015; Nolet *et al.*, 2008a), discussed in more details below.

4.2. Northward shifts

The regional changes in sapling occurrences entailed a northward shift in the distributions of *A. rubrum* and *A. saccharum*, whereas the shift in *B. alleghaniensis* was significant only in undisturbed plots (minor; Fig. 3.3). These shifts in latitudinal distributions provide further support for the hypothesis of climate-induced migration. Despite some differences in the study area and the methodology, our results are qualitatively similar to those of previous studies in the same region (Boisvert-Marsh *et al.*, 2019; Sittaro *et al.*, 2017), with large and significant northward shifts for the two *Acer* species, but no or weak shift for *B. alleghaniensis* and *F. grandifolia*.

Temperate species such as *A. rubrum* and *A. saccharum*, whose limits fall in the southern part of the boreal forest and the northern part of the temperate forest, respectively, have been shown to establish in northern mixedwoods and boreal forests (Fisichelli *et al.*, 2014; Goldblum et Rigg, 2002; Leithead *et al.*, 2010). *A. rubrum* is a recognised “super-generalist” and opportunist species (Abrams, 1998; Burns et Honkala, 1990; Fei et Steiner, 2009). *A. saccharum* is generally categorised as a shade-tolerant late-successional species (Burns et Honkala, 1990), but Nolet *et al.* (2008b) suggested that it should also be considered a generalist trans-successional species, as it is well adapted to different successional stages. Their broad environmental tolerance, combined with warmer temperature in the last decades (Fig. C.3), probably allowed colonisation of new sites at their northern margins and facilitated their northward range shifts. Besides, although we did not test it, it is possible that the presence of *A. rubrum* in northern sites facilitates the migration of *A. saccharum* through arbuscular mycorrhizal associations.

Importantly, our results show that disturbances did not promote larger range shifts but can influence differentially the migration of temperate species. Indeed, both moderate and major disturbances clearly hindered the northward migration of *B. alleghaniensis*, which could explain why it was not detected in previous studies in the same region (Boisvert-Marsh *et al.*, 2014; Boisvert-Marsh *et al.*, 2019). In contrast, both *Acer* species experienced northward shifts of similar magnitude at minor and moderate disturbances (natural or logging), but did not shift at major disturbances. Hence, it appears that only major disturbances could impede their migrations. Our findings provide further insight into the conclusions of Woodall *et al.* (2013). During a 5-year study in the northeastern United States, they compared seedling and adult range margins and reported that disturbances either had no effect or induced a tendency towards range retreat for some species (Woodall *et al.*, 2013). Together, these findings highlight that future tree range shifts may depend upon species

tolerance to disturbances and disturbances should therefore be taken into account in future studies of range shifts. As we only investigated four dominant species, it is highly likely that the distributions of other tree species, as well as understory plants, are similarly altered by disturbances.

4.3. Downslope shifts

Although the altitudinal shifts that we identified are not statistically significant, some interesting regional patterns are beginning to emerge: at their northern range limits, saplings of the four tree species presented slight (albeit not significant) downward trends (Fig. 3.4). Contrary to most predictions regarding temperate tree migration along elevation gradients (e.g., Beckage *et al.*, 2008), this downslope migration is not surprising as the studied species are spatially constrained on hilltops at their northern limits (Blouin et Berger, 2008; Gosselin, 2002). Accordingly, our models indicated that recruitment was generally higher on upper and middle slope, compared to lower slope, especially for *A. rubrum*. Topographic position is known to influence forest microclimates, notably through cold air drainage (Zellweger *et al.*, 2019). This phenomenon was hypothesised to explain the presence of isolated populations of *A. saccharum* on hilltops at its northern range limit (Barras et Kellman, 1998; Goldblum et Rigg, 2002); it could also contribute to explaining the distribution of the other three species. Our results suggest that temperate species could be starting to expand their ranges from existing isolated populations on hilltops to nearby habitats downslope.

4.4. Drivers of sapling recruitment

Our hurdle model first highlighted that the presence of recruits in a site and their abundance are two distinct processes that are controlled by different environmental factors. Moreover, the high of explanatory power of the zero part relative to the count part of the model suggests that the occurrence of a recruitment event is strongly controlled by the biotic and abiotic drivers whereas their abundance is more random.

4.4.1. Biotic conditions

The best single predictor of tree sapling occurrence and abundance across species was the basal area of conspecific adult trees within forest plots (Figs 5, C.5). The predominance of conspecific trees, mainly in the plot but also in the neighbourhood, may reflect a reliable source of seeds and the possibility of vegetative reproduction. It may also correlate with the appropriateness of the environmental conditions for the species. This finding is consistent with other studies that emphasised high positive conspecific density dependence for tree recruitment (Caspersen et Saprunoff, 2005; Drobyshev *et al.*, 2014; Graignic *et al.*, 2014; Solarik *et al.*, 2019).

Many studies have shown that recruitment is limited by seed supply and all the more so at the northern distribution limit (Caspersen et Saprunoff, 2005; Tremblay *et al.*, 2002). For instance, Tremblay *et al.* (2002) showed that northern populations of *A. rubrum* are maintained essentially through vegetative reproduction with occasional sexual recruitments which, in combination, allow this species to colonise recently disturbed sites. In Ontario, Caspersen et Saprunoff (2005) reported an elevated recruitment failure for *F. grandifolia* which was mainly due to low seed fecundity. This species regenerates abundantly by root suckers or by stump sprouts and these have a better survival rate than seedlings (Beaudet *et al.*, 2007; Beaudet et Messier, 2008; Morris *et al.*, 2014). Its reliance on vegetative reproduction may explain the disproportionate importance of conspecific tree cover for *F. grandifolia* recruitment (Fig. 3.5, C.5) as well as the absence of range shift (Fig. 3.3). The production of vigorous root sprouts may also contribute to its competitive advantage over *A. saccharum* in the shared portion of their range (Beaudet *et al.*, 2007; Beaudet et Messier, 2008), where *A. saccharum* recruitment was found to decline (Fig. 3.2). Beaudet *et al.* (2007) suggested that where *F. grandifolia* reproduces predominantly vegetatively, it might maintain a growth advantage over *A. saccharum* under both shade and light conditions. In the northern part of its range, *A. saccharum* is increasing, presumably because it is escaping competition by *F. grandifolia*.

The basal area of boreal species in the forest plots exerted a large negative effect on the recruitment of all species. The cover of boreal trees may be indicative of several environmental conditions unsuitable for temperate tree recruitment (Collin *et al.*, 2017; Solarik *et al.*, 2019). For instance, high boreal cover is negatively correlated with temperate cover and mean temperature, hence it may partly account for the effect of a latitudinal temperature gradient. Boreal tree cover could also impede early sapling recruitment through the direct competition for nutrients, light and water. Moreover, boreal species create poor and acidic soils with high needle cover which can ultimately impede the recruitment of temperate tree species through an inhibitory priority effect (Collin *et al.*, 2017; Solarik *et al.*, 2019). Similarly, under boreal canopy, the insufficiency of arbuscular mycorrhizal fungi may strongly constrain temperate species recruitment (Carteron *et al.*, 2020). Although we do not have the data to test it, lack of suitable substrates for establishment may partly explain the limited range shift of *B. alleghaniensis*. Several studies suggested that microsite variables and competing vegetation may greatly limit recruitment of *B. alleghaniensis*, which preferentially colonises coarse till, decayed logs and bare soil (Caspersen et Saprunoff, 2005; Drobyshev *et al.*, 2014).

4.4.2. Physical variables

Local topographic and edaphic characteristics also largely influenced the probability of sapling presence, but less so their abundance. At their northern margins, lowlands with

poor soil drainage could represent a substantial impediment to temperate tree migration. Lafleur *et al.* (2010) had previously suggested that soil factors should not represent a major constraint for species northward shift except in waterlogged conditions which could prevent or slow down tree migration. All four species generally prefer mesic well-drained soils and only *A. rubrum* is known to tolerate poor soil drainage (Burns et Honkala, 1990; Niinemets et Valladares, 2006). Waterlogged conditions affect oxygen and nutrient availability (St Clair *et al.*, 2008) and could thus reduce seedling and sapling survival. Species tolerance to unfavourable soil conditions could also decrease at their northern range margins where they are already under temperature stress. Similar changes in tolerance were found for *Abies balsamea* at the boundary between mixedwood and coniferous forests where its preference for mesic soils was stronger closer to its northern margin (Messaoud *et al.*, 2007). Moreover, as discussed above, a warmer microclimate associated to cold air drainage could further contribute to the preference of saplings for mesic uplands.

Acidic soils were favourable for the presence of *B. alleghaniensis* saplings, while basic soils were favourable for *A. saccharum* and unfavourable for *F. grandifolia*. Although the presence of *A. rubrum* was not affected by soil pH, its abundance was greater on basic soils. Such species-specific preferences for soil pH have been previously reported and are associated with variations in nutrient availability, such as calcium (Kobe *et al.*, 2002; St Clair *et al.*, 2008). As supported here, seedlings of *A. saccharum*, prefers alkaline calcium-rich soils (DRF, 2017; Kobe *et al.*, 2002; St Clair *et al.*, 2008), whereas *F. grandifolia* grows poorly, little or not at all on calcareous or alkaline soils (DRF, 2017). *B. alleghaniensis* and *A. rubrum* are generally considered tolerant to a wide range of pH (Kobe *et al.*, 2002). Decreasing soil calcium levels in northeastern America, in part due to high atmospheric acid depositions, has been associated with the decline in regeneration and growth of *A. saccharum* and the concomitant expansion of *F. grandifolia* (Bal *et al.*, 2015). Such a phenomenon could contribute to the changes in occurrence patterns we observed for the two species in the southern portion of Québec. Although *A. saccharum* and *A. rubrum* preferred high soil pH, we did not find significant negative effects of low soil pH. And the recruitment of *B. alleghaniensis* was even favoured by low soil pH. Therefore, acid soils common in northern mixed and boreal forests might not be a major barrier to their recruitment and allowed their northward migration.

4.4.3. Disturbance

Recruitment of all species was generally favoured by moderate logging, while the effect of natural disturbances (here mostly insect outbreak and windfall, Fig. C.1) was mainly negative (except for *A. rubrum*, for which the effect was positive). In contrast, major logging decreased the probability of finding at least one recruit (except for *A. rubrum*), but, when there was successful recruitment, the number of recruits was high for all species. This corroborates the results of other studies showing larger recruitments of temperate species in

canopy gaps near their northern margins (Kneeshaw et Prévost, 2007; Leithead *et al.*, 2010; Zhang *et al.*, 2015b). Indeed, many tree species of various shade tolerances can exhibit pulsed recruitment patterns following discrete disturbance events (Bouchard et Kneeshaw, 2006). Furthermore, compared to natural disturbance regime, logging has been shown to favour the increases in temperate tree proportion in mixed forests (Boucher *et al.*, 2009). As logging is a selective disturbance that primarily affects *Abies balsamea* in the study area (Brice *et al.*, 2020; Duchesne et Ouimet, 2008), partial logging may give a competitive advantage to sapling recruitment of the co-occurring temperate species. Moreover, logging can promote strong vegetative reproduction of temperate species (Fei et Steiner, 2009). The effects of natural disturbances on tree regeneration may differ from that of logging. The main natural disturbances in the study area are insect outbreaks caused by the spruce budworm which also predominantly attacks *A. balsamea*. Thanks to an extensive seedling bank, *A. balsamea* can recruit abundantly after an outbreak (Morin, 1994). In contrast, the machinery used for logging could cause damage to the seedling bank.

In our study, recruitment of *A. rubrum* benefited the most from all types of disturbance events (logging and natural) and was favoured in young forests. This species' capacity to regenerate abundantly after disturbances and remain dominant in the canopy is thought to explain its widespread increase across eastern North America (Abrams, 1998; Fei et Steiner, 2009; Tremblay *et al.*, 2002). Moreover, *A. rubrum* can thrive after logging, which promotes strong vegetative regeneration from stump sprouts (Fei et Steiner, 2009; Tremblay *et al.*, 2002).

The observed range shifts of *A. rubrum* and *A. saccharum* may also be partly ascribed to historical disturbances. Expansion of *Acer* species has been documented for all of north-eastern North America since preindustrial times (Danneyrolles *et al.*, 2018; Terrail *et al.*, 2019; Thompson *et al.*, 2013). Their success has been attributed to their ability to thrive in a wide range of soil and light conditions combined with their abundant and efficient regeneration which allows them to quickly colonise recently disturbed sites (Barras et Kellman, 1998; Fei et Steiner, 2009; Nolet *et al.*, 2008b; Zhang *et al.*, 2015b). As such, it is very likely that in our study area *A. saccharum* and particularly *A. rubrum* benefited from both recent and historical human disturbances. Furthermore, both *Acer* species may be continuing their expansion driven by the extensive human disturbances that took place since preindustrial times; thus, their current northern distribution limits may not be at equilibrium with the current climate.

Contrary to our expectations and that of others (Johnstone *et al.*, 2016; Renwick et Rocca, 2015), the positive effect of moderate logging on recruitment did not translate into larger northward range shifts; the shifts observed here were either similar (*Acer spp.*) or reduced (*B. alleghaniensis*) in disturbed forests. In light of these results, we hypothesise that disturbances may not displace range limits *per se* because of other limiting factors, mainly

dependence on conspecific trees for dispersal, priority effect from boreal trees and edaphic conditions. Yet, they could promote recruitment in already occupied sites, thus increasing their relative proportion, as well as in new sites in the neighbourhood and downslope thus increasing their occupancy at their northern range margins, but not beyond.

4.4.4. Climate

Climate has a determinant role in forest dynamics and in constraining species range, and thus we expected to find a larger direct influence of climatic variables on sapling recruitment at the species northern limits. Temperature of the growing season had a positive effect on all species. Consequently, we would expect an overall positive effect of climate warming, but its effect varied widely across species. Climate warming had a positive influence on the presence of *B. alleghaniensis* and the abundance of *A. rubrum*, but a negative effect on the presence of *F. grandifolia* and *A. saccharum* was not affected at all. These disparate signals are consistent with previous work that concluded that the range limits of these four temperate species are not directly controlled by their climatic tolerances, but by fecundity, soil factors or disturbances (Drobyshev *et al.*, 2014; Graignic *et al.*, 2014; Tremblay *et al.*, 2002; Zhang *et al.*, 2015b). These non-climatic and local drivers may modulate or mask any broad-scale climatic effects (Drobyshev *et al.*, 2014; Serra-Diaz *et al.*, 2015; Zhang *et al.*, 2015b) and transform a unidirectional signal of regeneration shift into a more complex set of signals with localised areas of relatively high regeneration. Time lags in tree responses may also explain why range shifts are poorly correlated with the warming trends (Sittaro *et al.*, 2017). Besides, climate extremes, such as droughts and heat waves, as well as variations in early- and late-season climate, may be more important for several tree life cycle events than gradual changes in mean climate conditions (Boisvert-Marsh *et al.*, 2019; Neumann *et al.*, 2017).

5. Conclusions

Tree sapling recruitment is an important process in forest ecosystems. The rate and magnitude of tree range shifts under climate warming will likely depend strongly upon successful tree recruitment at range limits. Integrating tree demographic processes is therefore fundamental for accurately forecasting species range shifts and adapting management strategies, but this will likely be challenging as there is not a single broad-scale response of recruitment dynamics. Saplings of three out of four temperate species experienced northward range shifts in the last decades. However, disturbances may sometimes impede these shifts, as we observed for *B. alleghaniensis*, and they should therefore be taken into account in future studies on range shifts. Moreover, downslope trends in sapling distributions at their northern margins may indicate the onset of an expansion from marginal populations found on hilltops. Overall, our findings suggest that tree recruitment was only weakly related to

broad-scale climate change and was instead controlled by local factors and disturbances. Although moderate disturbances may promote episodic recruitment pulses of temperate species at their northern margins, they did not catalyse larger northward shifts likely because sapling recruitment was constrained by their dependence on conspecific trees for dispersal, the inhibitory priority effect of boreal cover, as well as the unsuitability of lowland hydric soils.

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7. Data Accessibility Statement

The complete forest inventory dataset used in this study is available online at <https://www.donneesquebec.ca/recherche/fr/dataset/placettes-echantillons-permanentes-1970-a-aujourd-hui>. All the data used in the study, in addition to R scripts to reproduce the analyses and the figures, can be found online at <https://github.com/mhBrice/recruitment>.

Conclusion

4.5. Vers une meilleure compréhension des dynamiques forestières en réponse aux changements globaux

De nombreuses études utilisent les données d'inventaire forestier pour tenter de prédire l'avenir sous les changements climatiques (Boulanger *et al.*, 2017; Chen, 2002; Iverson *et al.*, 2008; Meier *et al.*, 2012; Périé et de Blois, 2016; Vissault, 2016). Mais, s'il est possible de faire des prédictions de grands changements pour 2050, soit dans 30 ans, ne devrait-on pas déjà commencer à percevoir les premiers signes de ces changements dans les données cumulées depuis 1970, il y a 50 ans ? Quelles informations pouvons-nous tirer de ces changements récents ? Par ailleurs, les projections des effets du changement climatique sur les forêts ont généralement mis l'accent sur la capacité des espèces à tolérer les augmentations de température et les sécheresses et à se disperser, mais ils ont rarement intégré les effets des perturbations. Étant donné l'importance des perturbations naturelles et de celles générées par l'exploitation forestière dans la dynamique des forêts (Turner, 2010), ces projections du futur basées seulement sur le changement climatique sont-elles réalistes ou trompeuses ? Si les perturbations interagissent avec le changement climatique et exacerbent la mortalité des arbres, les nouvelles politiques d'aménagement du territoire et de la forêt qui reposent sur des modèles incomplets risquent d'être mal adaptées.

À travers ma thèse de recherche, j'ai tenté d'apporter des éléments de réponses à ces questionnements. Ses trois chapitres ont permis de d'analyser en détail les multiples aspects de la dynamique des forêts au cours des dernières décennies afin de mieux comprendre la réponse aux effets combinés du changement climatique et des perturbations. Dans l'ensemble, mes résultats soulignent le rôle central des perturbations dans la réponse des forêts face au changement climatique. En effet, la composition et la structure (Chapitre 1), la dynamique de transition (Chapitre 2), ainsi que la dynamique de régénération (Chapitre 3) des forêts de l'écotone boréal-tempéré au Québec sont principalement contrôlées par les perturbations et leurs effets semblent interagir avec ceux des changements climatiques. J'ai montré comment les perturbations accélèrent la réponse des communautés forestières aux changements climatiques, révélant des synergies qui ont le potentiel de modifier l'avenir de nos forêts.

4.5.1. Réorganisation des communautés

Dans le chapitre 1, je me suis intéressée aux moteurs des changements de composition dans les communautés forestières. Au cours des dernières décennies, les perturbations (par exemple, les coupes à blanc, les épidémies d'insectes, les incendies) ont été les principaux facteurs de changement de composition des communautés forestières, i.e. la diversité β temporelle, dans l'écotone tempéré-boréal. En revanche, les effets uniques du changement climatique sur la diversité β temporelle sont très faibles. Sans approfondir, on aurait pu conclure prématurément que le changement climatique n'a pas influencé la composition des forêts au cours des dernières décennies. L'analyse des changements des traits écologiques de la communauté a permis de révéler un phénomène de thermophilisation des forêts à travers le Québec, i.e. une augmentation des espèces de climat chaud au détriment des espèces de climat froid. En outre, la thermophilisation a été plus grande et s'est étendue plus au nord dans les communautés modérément perturbées que dans celles qui n'ont pas été perturbées ou qui ont subi des perturbations majeures.

Les résultats de ce chapitre ont soulevé d'autres questions importantes : la thermophilisation récentes des forêts indique-t-elle un changement permanent ou bien seulement une dynamique transitoire ? Et, si les perturbations modérées favorisent la thermophilisation, est-ce qu'elles pourraient accélérer des changements d'état permanents ? C'est la question que j'ai creusée dans le second chapitre de ma thèse.

4.5.2. La dynamique des forêts

Dans le chapitre 2, j'ai analysé la dynamique de transition des forêts du Québec en utilisant un modèle à quatre états, soit boréal, mixte, tempéré et pionnier. Encore une fois, les perturbations naturelles et anthropiques ressortent comme les moteurs principaux de la dynamique de transition des forêts au cours des dernières décennies. Alors que les perturbations majeures déclenchent surtout des transitions vers l'état pionnier, les perturbations modérées favorisent les transitions de l'état mixte vers l'état tempéré. De plus, les perturbations modérées accélèrent le taux de renouvellement des forêts et, à long terme, favorisent une augmentation de la proportion de forêts tempérées dans le paysage. Par conséquent, les perturbations modérées ont le potentiel de catalyser un déplacement plus rapide de l'écotone boréal-tempéré vers le nord sous l'effet du changement climatique. Toutefois, contrairement à mes attentes, les transitions des forêts mixtes à tempérées ne découlaient pas d'une hausse du recrutement d'arbres tempérés mais plutôt des processus de mortalité et de croissance.

Si les transitions reposent davantage sur la mortalité et que celle-ci n'est pas équilibrée par le recrutement de nouveaux arbres, les forêts mixtes pourraient en fin de compte dépérir. Alors que les perturbations modérées favorisent la thermophilisation des forêts et la transition de peuplements mixtes à tempérés, comment influencent-elles le recrutement des espèces

tempérées ? Les analyses rapportées dans les deux premiers chapitres étant basées sur les arbres matures seulement, elles ne pouvaient pas bien répondre à cette nouvelle question. Il fallait donc analyser la dynamique des jeunes arbres (i.e. les gaulis).

4.5.3. La régénération des forêts : les premiers pas de la migration

Dans le chapitre 3, j'ai d'abord mis en lumière de grands déplacements de distribution vers le nord pour les gaulis (i.e., jeunes arbres entre 1 et 9 cm de diamètre) de l'érythrine rouge, l'érythrine à sucre et le bouleau jaune dans les forêts non perturbées. Toutefois, sous l'influence des perturbations modérées, seuls les érythrines ont migré et aucune espèce ne s'est déplacée sous l'influence des perturbations majeures. En revanche, la répartition du hêtre à grandes feuilles n'a pas bougé dans tous les cas. Ces résultats soulignent que les futurs déplacements d'aire de répartition des espèces peuvent dépendre de leur réponse aux perturbations. De plus, il y a une légère tendance au déplacement des gaulis vers le bas des pentes, surtout dans les régions proches de leur limite nord. Ces tendances pourraient signaler le début d'une migration des populations marginales vivant au sommet des collines. Mes résultats ont montré que, malgré l'effet positif des coupes partielles sur le recrutement, la prévalence des contraintes locales associées à la composition des peuplements et aux conditions topo-édaphiques risque de freiner la migration des espèces tempérées vers le nord.

4.6. Des forêts en transformation : des individus aux biomes

Les effets des changements environnementaux se répercutent à chaque niveau d'organisation de la biodiversité, se transmettant des individus jusqu'au biome, en passant par les populations, les communautés et les écosystèmes (Bellard *et al.*, 2012; Parmesan et Yohe, 2003). En effet, conformément aux concepts de la science des systèmes complexes, les changements démographiques au bas de la hiérarchie peuvent faire émerger, par des processus d'organisation autonome, des réorganisations massives à l'échelle régionale (Fig. 4.1 ; Filotas *et al.*, 2014; Messier *et al.*, 2013). Les résultats de ma thèse permettent de bien illustrer ces processus ascendants et en interaction par lesquels les forêts de l'écotone boréal-tempéré sont en train de se transformer. L'interprétation de mes résultats sous la perspective des systèmes complexes permet de mieux comprendre la réponse des forêts sous l'effet combiné du changement climatique et des perturbations ainsi que les conséquences écologiques qui en découlent.

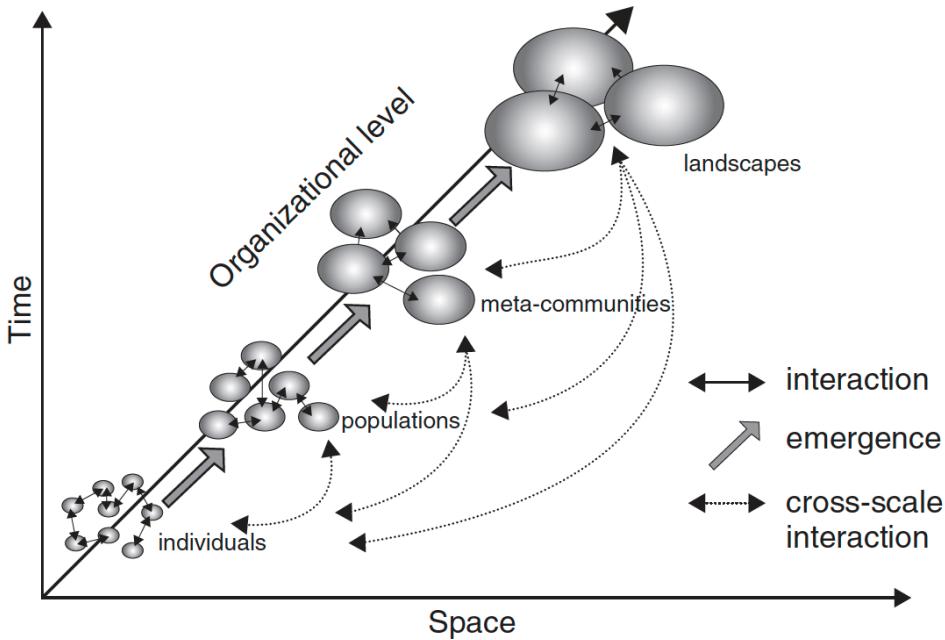


Figure 4.1. Représentation conceptuelle des effets des changements environnementaux sur les forêts sous l’angle d’un système complexe. Les changements dans la dynamique des forêts sont transférés de façon ascendante entre les différents niveaux d’organisation de la biodiversité. Des interactions et des rétroactions ont lieu entre les entités à l’intérieur et à travers les échelles spatiales, temporelles et hiérarchiques. Les entités qui interagissent à un niveau donnent naissance à des entités émergentes de niveau supérieur, dont l’existence, à son tour, affecte le comportement des entités de niveau inférieur. Schéma tiré de Messier *et al.* (2013).

4.6.1. Changements démographiques

Dans un premier temps, le réchauffement climatique favorise le recrutement, la survie et la croissance des espèces tempérées à leur limite nord (Boisvert-Marsh *et al.*, 2019; Bolte *et al.*, 2014; Fisichelli *et al.*, 2014; Goldblum et Rigg, 2005; Grundmann *et al.*, 2011), ce qui leur confère un avantage compétitif par rapport aux espèces boréales. Mais, en l’absence de perturbations, les arbres poussent lentement, leurs taux de mortalité et de recrutement sont faibles et la compétition pour l’espace et la lumière est intense.

Des perturbations peuvent cependant éliminer les individus des espèces résidentes. Dans la zone d’étude, les perturbations naturelles et anthropiques ont provoqué une mortalité disproportionnée d’une espèce dominante dans les forêts mixtes (Chapitre 2). En effet, le sapin baumier a subi une mortalité massive suite aux grandes épidémies de tordeuse des bourgeons de l’épinette dans les années 1967-1992 (Duchesne et Ouimet, 2008). De plus, cette espèce est aussi la plus coupée au Québec. Suite à une perturbation modérée (p. ex., épidémie légère, coupe partielle), les trouées dans la canopée résultant de la perte de cette espèce boréale ubiquiste et abondante ont probablement permis de réduire la compétition

et de libérer des ressources, favorisant ensuite la croissance rapide des espèces tempérées compagnes, telles que les érables rouge et à sucre ainsi que le bouleau jaune (Chapitre 2). De plus, alors que les perturbations naturelles semblent avoir un effet plutôt délétère, les coupes partielles favorisent une hausse du recrutement de ces espèces tempérées à leur limite nord (Chapitre 3). En cas de perturbations majeures (p. ex., grand feu, coupe totale), la majorité des arbres en place meurent ce qui crée des ouvertures de très grande superficie. Ces paysages nouvellement ouverts sont colonisés rapidement par des espèces pionnières telles que le peuplier faux-tremble et le bouleau blanc (Chapitre 2) qui peuvent disperser leurs graines sur de longues distances et croître rapidement en conditions lumineuses (Boucher *et al.*, 2017; Grondin *et al.*, 2018). Suite à une perturbation majeure, les espèces tempérées peuvent être plus lentes à revenir parce qu'elles se dispersent sur des distances plus courtes (Scheller et Mladenoff, 2005).

4.6.2. Dynamique des populations

Le réchauffement et les perturbations peuvent donc exercer leur influence sur la dynamique des populations des espèces par le biais de plusieurs processus démographiques, notamment la reproduction, le recrutement, la croissance et la mortalité. Ces changements à l'échelle des individus et des sites s'accumulent dans le temps et dans l'espace pour altérer l'abondance et l'aire de répartition des populations (Holt *et al.*, 2005). Lorsque les effets sur les individus d'une espèce sont généralement négatifs, le taux de croissance de la population diminu ; certaines populations pourraient être amenées à disparaître localement et, dans le pire des cas, régionalement. À l'inverse, lorsque les effets sur les taux démographiques d'une espèce sont positifs, le taux de croissance de la population augmente, ce qui peut entraîner une augmentation locale de l'abondance et une expansion régionale de l'aire de répartition.

Ces effets sur les taux démographiques des espèces ne sont pas aléatoires, mais sont déterminés par leurs tolérances physiologiques, leurs stratégies d'histoire de vie et leurs capacités de dispersion (Aubin *et al.*, 2016; Estrada *et al.*, 2015). La diversité des caractéristiques écologiques spécifiques est sans doute à l'origine de la grande variabilité dans les réponses des arbres face aux multiples stresseurs environnementaux (Serra-Diaz *et al.*, 2015). Alors que le réchauffement peut favoriser le taux de croissance des populations d'espèces qui sont limitées par les températures très froides, les perturbations devraient promouvoir les espèces opportunistes, intolérantes à l'ombre, avec une bonne capacité de dispersion et de reproduction végétative (Chapitre 3 ; Danneyrolles *et al.*, 2019; De Frenne *et al.*, 2013). Par exemple, l'érable rouge, dont la distribution au nord est en partie limitée par un faible niveau de reproduction sexuée (Tremblay *et al.*, 2002), est reconnue comme une espèce super-généraliste et opportuniste, capable de coloniser rapidement des sites variés après une perturbation

(Abrams, 1998; Fei et Steiner, 2009). Ces caractéristiques pourraient donc expliquer l'expansion rapide qu'a connue l'érythrine rouge au Québec sous l'effet combiné du réchauffement et des perturbations (Chapitres 1, 2 et 3). En revanche, certaines espèces limitées par la dispersion comme le tilleul d'Amérique, ou limitées à un habitat spécifique comme l'érythrine argenté, ou encore intolérantes aux perturbations comme la pruche du Canada, pourraient ne pas profiter des opportunités de recrutement et de croissance suivant des perturbations, et ce même si le climat est devenu plus favorable pour ces espèces.

La sensibilité au climat peut varier entre les différents processus démographiques (Niinemets, 2010). Par exemple, comme la régénération est souvent plus sensible que la survie des adultes aux stress hydrique ou thermique (Niinemets, 2010), une population peut persister pendant des décennies ou des siècles sur un site donné, même si les conditions climatiques sont devenues défavorables à sa régénération (Talluto *et al.*, 2017). Pour cette raison, Jump *et al.* (2009) ont suggéré que l'expansion à la limite nord de la distribution d'une espèce sera plus rapide que les changements à la limite sud puisque la reproduction et le recrutement sont plus sensibles aux changements environnementaux que la mortalité des individus établis. Dans les forêts du Québec, les données montrent effectivement une augmentation rapide de l'abondance (Chapitre 1) et du recrutement des espèces tempérées dominantes (Chapitre 3). Toutefois, la perte des espèces boréales a sans doute été tout aussi importante sinon plus puisque la mortalité n'était pas contrôlée par un stress climatique mais surtout par des perturbations directes comme les coupes, les feux et les épidémies (Chapitres 1 et 2). Ainsi, contrairement à l'hypothèse avancée par Jump *et al.* (2009), les perturbations risquent d'accélérer la contraction de l'aire de répartition des espèces boréales, tandis que l'effet sur l'expansion des espèces tempérées à leur limite nord pourrait être beaucoup plus lent en raison des contraintes au recrutement (Chapitre 3). En effet, le recrutement des espèces tempérées est largement dépendant de la présence des arbres matures conspécifiques pour la dispersion et est freiné par la compétition des espèces boréales de même que par les conditions de mauvais drainage (sites hydriques) dans les bas de pente (Chapitre 3).

4.6.3. Dynamique des communautés

Les changements démographiques des espèces se traduisent donc, à l'échelle locale, en pertes et en gains d'espèces qui influencent la composition et la structure des communautés forestières. Dans l'écotone boréal-tempéré, la thermophilisation des forêts résultait principalement du gain d'une seule espèce tempérée, l'érythrine rouge, combiné à la perte de deux espèces boréales dominantes, le sapin et l'épinette noire, et ce phénomène était accentué par les perturbations modérées (Chapitre 1). Ainsi, sans perturbation, le renouvellement de la communauté est très lent, tandis que celui-ci est accéléré par les perturbations modérées (Chapitres 1, 2 et 3). En revanche, les perturbations majeures détruisent la communauté

en place et réinitialisent la succession à partir du début, ce qui entraîne surtout des gains en espèces pionnières (Chapitres 1 et 2). Au cours de ma thèse, j'ai pu montrer comment ces changements de composition résultent de l'action conjointe de trois mécanismes démographiques qui altèrent la trajectoire de succession après une perturbation modérée : (1) la mortalité d'une espèce dominante ; (2) le relâchement de la croissance des adultes des espèces tempérées compagnes ; et (3) le recrutement accru des gaulis des espèces tempérées compagnes ou présentes dans le voisinage.

Les conséquences au niveau des communautés des changements d'aires de répartition spécifiques aux espèces pourraient mener à la formation de communautés sans analogues, i.e. des communautés dans lesquelles coexistent des espèces dans des combinaisons historiquement rares ou inconnues (Williams et Jackson, 2007). Les modèles de distribution d'espèces sous l'effet du changement climatique prédisent un grand potentiel d'augmentation de la richesse au Québec (Berteaux, 2014). Toutefois, mes résultats soulignent que seule une poignée d'espèces tempérées prospèrent sous ce nouveau régime de perturbations anthropiques. Par conséquent, il est fort probable que les forêts de l'écotone boréal-tempéré ne connaîtront pas un enrichissement, mais plutôt un appauvrissement associé à l'expansion d'une ou de quelques espèces. On prévoit en outre que le déclin des espèces boréales actuellement dominantes, soit le sapin et l'épinette, risque de s'accentuer dans les prochaines décennies dans les domaines de la sapinière en raison du réchauffement climatique (D'Orangeville *et al.*, 2018). Le remplacement de ces espèces résineuses par des espèces feuillues pourrait avoir des conséquences économiques importantes. Par exemple, l'expansion de l'érable rouge pourrait compromettre l'approvisionnement en espèces résineuses à grande valeur commerciale dans la forêt mixte. Les pratiques sylvicoles devront être révisées pour s'adapter à la nouvelle réalité puisqu'elles ont été élaborées en fonction de la composition et de la dynamique naturelle des forêts et dépendent de la régénération naturelle (Pinna, 2009).

4.6.4. Déplacement des grands biomes forestiers

Les effets cumulés des changements à l'échelle des individus, des populations et des communautés peuvent entraîner un déplacement des grands biomes forestiers à l'échelle régionale, notamment une expansion de la forêt tempérée au détriment de la forêt mixte (Chapitre 2). Cette réorganisation régionale de la composition des forêts peut interagir avec le fonctionnement des écosystèmes à l'échelle locale et les processus à l'échelle globale (*cross-scale interactions*; Peters *et al.*, 2007). Ces changements de fonctionnement à l'écotone risquent d'être d'autant plus grands puisque les espèces feuillues et les espèces résineuses présentent des différences importantes sur le plan de leurs caractéristiques et fonctions écologiques (Wardle *et al.*, 2011). L'enfeuillage des forêts mixtes pourrait par exemple influencer localement la qualité de la litière, le taux de décomposition de la matière organique et la composition des

microorganismes du sol (Laganière *et al.*, 2010; Légaré *et al.*, 2005). Les changements dans la composition, la structure d'abondance et la distribution spatiale des forêts affecteront également la survie et la distribution des nombreuses espèces de mammifères, d'oiseaux et d'insectes qui en dépendent pour s'abriter et se nourrir (Friggens *et al.*, 2018). Comme les espèces feuillues sont moins inflammables et moins sensibles aux insectes ravageurs que les conifères, leur augmentation dans le paysage forestier peut modifier le régime régional de perturbations (Terrier *et al.*, 2013; MFFP, 2018). À long terme, l'expansion du biome tempéré au détriment des forêts mixtes et boréales pourrait avoir un effet sur le climat global en augmentant la séquestration du carbone (Thurner *et al.*, 2014) et l'albédo (Anderson *et al.*, 2011).

4.7. Les perturbations — catalyseurs de changements dans les forêts

Les effets combinés du changement climatique et des perturbations peuvent donner naissance à des dynamiques non-linéaires conduisant à un changement de régime écologique (*regime shift*; Fig. 4.1; Harris *et al.*, 2018; Scheffer *et al.*, 2001). Un changement de régime résulte d'une réorganisation rapide de la composition et de la structure d'un écosystème qui entraîne un basculement vers un nouvel état alternatif stable (Scheffer *et al.*, 2001). Par exemple, si la transition des forêts mixtes vers des forêts à dominance tempérée documentée dans le Chapitre 2 persiste, cette transformation pourrait bel et bien s'avérer être un changement de régime.

En théorie, des changements d'état stable peuvent subvenir suivant deux mécanismes : (1) des changements graduels dans les conditions environnementales jusqu'à un niveau critique où le système s'effondre soudainement, et (2) des perturbations trop sévères ou en rafale qui poussent le système hors de son bassin d'attraction (Scheffer *et al.*, 2001). Par exemple, la grande augmentation des taux de mortalité des arbres dans l'ouest des États-Unis en réponse à un stress hydrique grandissant (van Mantgem et Stephenson, 2007) pourrait être le signe avant-coureur d'un dépérissement massif des forêts. Dans un autre cas, Payette et Delwaide (2003) ont montré que les impacts cumulés de la coupe forestière, suivie d'une épidémie d'insectes puis d'un incendie, pourraient avoir des effets catastrophiques sur la régénération des arbres, entraînant la transition d'une pessière dense en un milieu ouvert dominé par le lichen. Bien que les deux mécanismes puissent indépendamment mener à une transition rapide d'état, leurs effets synergiques augmentent le risque de changements rapides de régime écologique (Harris *et al.*, 2018; Scheffer *et al.*, 2001). Mes résultats supportent cette hypothèse et suggèrent que les forêts répondent à l'effet cumulé d'un stress à long terme causé par le changement climatique (i.e., *press disturbance*), en combinaison avec des événements de mortalité aigus (i.e., *pulse disturbance*; Jentsch et White, 2019; Harris *et al.*, 2018). Ainsi,

le réchauffement climatique érode la résilience des forêts mixtes tandis que les perturbations éliminent les espèces boréales en place et accélèrent le processus de succession vers davantage d'espèces tempérées adaptées aux températures plus chaudes (Chapitres 1, 2 et 3).

4.7.1. Résilience, états alternatifs stables et changement de régime

Les résultats issus de ma thèse m'ont amenée à réfléchir en profondeur à la dynamique de changement de régime écologique dans le contexte de l'écotone boréal-tempéré et à redéfinir le paysage conceptuel des états stables de cette région (Fig. 4.2). Le long du gradient latitudinal, la forêt boréale au nord et la forêt tempérée au sud sont les seuls états stables possibles (Fig. 4.2a). Ces états forestiers ont une grande résilience face aux perturbations de type *pulse* qui sont dans la plage de variabilité naturelle de leur région (Grondin *et al.*, 2018) ; une perturbation naturelle ou anthropique peut déplacer le système à l'intérieur du bassin d'attraction, mais le système peut ensuite se rétablir et revenir à son état initial.

Dans la zone de transition entre ces deux grands biomes, on trouve la forêt mixte, un état relativement rare qui change facilement d'un état de dominance à l'autre (Fig. 4.2a). Ceci suggère que la forêt mixte ne serait pas l'état stable de la région, mais que cette communauté représente plutôt un état instable où le système n'est que transitoire. La coexistence des espèces boréales, tempérées et pionnières dans la forêt mixte est maintenue grâce à l'hétérogénéité des perturbations naturelles combinée à des différences dans les stratégies de cycle de vie des espèces (Bouchard et Kneeshaw, 2006; Kneeshaw et Prévost, 2007) sous un climat donné.

En plus des perturbations de type *pulse*, le climat global change graduellement et de façon persistante, ce qui peut altérer la forme du paysage des états stables (Fig. 4.2b). À mesure que le climat se réchauffe, les forêts peuvent perdre leur capacité à se rétablir puisque les espèces en place ne sont plus aussi bien adaptées au climat (Johnstone *et al.*, 2016). Mon interprétation est que le réchauffement modifie surtout le bassin d'attraction de l'état mixte et abaisse le seuil critique à franchir pour se rendre à l'état tempéré (Fig. 4.2b). De plus, le réchauffement peut rendre le bassin de l'état tempéré plus large et profond, donc plus attractif, et, inversement, celui de l'état boréal moins profond. Ces modifications de la courbe des états alternatifs stables fragilisent la forêt mixte, mais, en l'absence de perturbation, la grande inertie des forêts cache la perte de résilience de l'état mixte. Parce qu'ils ont une longue durée de vie, les arbres peuvent faire paraître les forêts inébranlables face aux changements environnementaux alors même que la niche de régénération est en train de se déplacer (Boisvert-Marsh *et al.*, 2019; Sittaro *et al.*, 2017). Toutefois, une perturbation peut facilement faire basculer le système vers un nouvel état ; la composition des forêts mixtes peut donc se déplacer rapidement vers une dominance en espèces tempérées qui sont mieux adaptées aux températures plus chaudes.

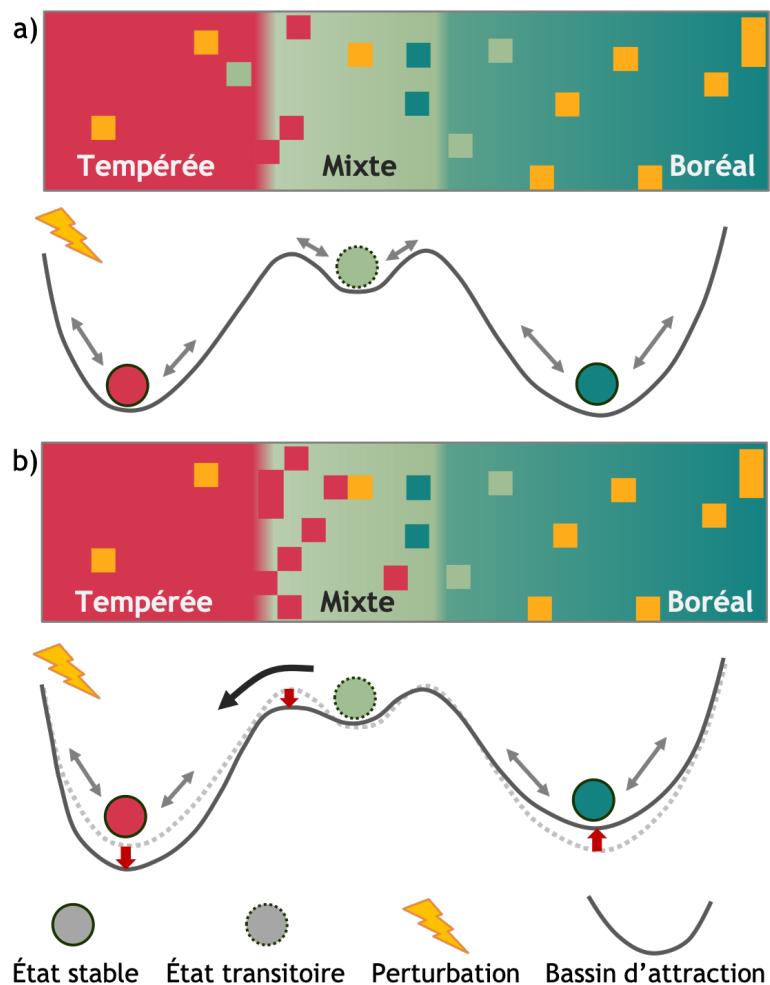


Figure 4.2. Nouvelle représentation conceptuelle des états alternatifs stables le long du gradient latitudinal (a) sans changement climatique et (b) avec changement climatique. Dans ce schéma, la bille caractérise l'état de l'écosystème à un instant donné, le long de la courbe ; les vallées sont les bassins d'attraction des équilibres stables et les sommets des collines sont les équilibres instables. Le schéma rectangulaire représente le paysage correspondant. Au sud du gradient latitudinal de température, un seul état stable existe, la forêt tempérée (en rouge). Au nord du gradient, l'état stable dominant est la forêt boréale (en turquoise). Ce sont des états stables dynamiques ; les perturbations peuvent faire déplacer la boule dans son bassin d'attraction et elle peut même passer par l'état pionnier (un état transitoire non représenté le long de la courbe, mais représenté par des carrés jaunes dans le paysage). La forêt étant habituellement résiliente aux perturbations, elle retourne ensuite vers son état initial. Au centre, dans l'écotone, la forêt mixte (en vert) serait un état transitoire entre les deux états stables dominants ; cet état peut être maintenu grâce à la dynamique naturelle des perturbations. Dans le panneau (b), le changement du climat peut provoquer un changement de la forme du paysage de différentes façons : (1) en abaissant le seuil pour passer de l'état mixte à tempéré, (2) en creusant et en élargissant le bassin d'attraction de l'état tempéré et (3) en rendant moins profond le bassin d'attraction de l'état boréal. Ces modifications font en sorte que la bille dégringole plus souvent de la vallée mixte vers la vallée tempérée sous l'effet d'une perturbation.

Contrairement aux perturbations modérées, les perturbations majeures détruisent toutes la communauté en place et poussent le système vers l'état pionnier, i.e. des peuplements dominés par des espèces intolérantes à l'ombre ou bien avec pas ou très peu d'arbres (Chapitre 2). Leur effet à long terme est difficile à prévoir à partir des données d'inventaire puisque les systèmes n'ont sans doute pas eu le temps de revenir à un état stable dans la période couverte par cette étude (1970 à 2018). En effet, l'état pionnier est en général un état transitoire. Il est donc fort probable que la majorité des forêts soient encore en train de se déplacer vers leur état d'équilibre. Toutefois, il se pourrait que certaines forêts se soient transformées définitivement. Par exemple, les peuplements de peuplier faux-tremble dans les pessières noires représentent normalement un état de transition, mais, sous l'effet des coupes forestières, ces peuplements sont en expansion et semblent se maintenir (Grondin et Cimon, 2003). Pour évaluer la trajectoire des forêts sévèrement perturbées, il faudra attendre encore quelques années.

La fréquence et la sévérité des perturbations naturelles, telles que les incendies, les épidémies d'insectes, les sécheresses et les vagues de chaleur, devraient augmenter dans de nombreuses régions du monde (Bergeron *et al.*, 2006; Seidl *et al.*, 2017). À la lumière de mes résultats, cela pourrait conduire à des changements majeurs dans la composition des forêts au cours des prochaines décennies et potentiellement à des modifications permanentes des états forestiers. Cependant, si les perturbations deviennent trop fréquentes et trop intenses, les forêts pourraient basculer vers une dominance en espèces pionnières de début de succession. Des comportements non-linéaires dans les réponses des écosystèmes forestiers impliquent que de nombreuses projections sous-estiment probablement l'ampleur des changements futurs de la biodiversité (Scheffer *et al.*, 2001). Une telle conclusion souligne l'importance de tenir compte de l'effet synergique des perturbations et du changement climatique dans les stratégies de gestion forestière ainsi que dans les modèles de prédiction.

4.8. L'aménagement forestier dans un monde en changement et incertain

Les effets multiples des changements globaux sur la dynamique forestière soulèvent un défi majeur pour l'aménagement de nos forêts. Face à la rapidité et à l'incertitude de ces changements, nos pratiques visant à contrôler et à prédire précisément l'évolution de nos forêts risquent d'être contre-productive (Puettmann *et al.*, 2009). Étant donné que les coupes forestières ont une influence majeure sur la composition (Chapitre 1), la dynamique (Chapitre 2) et la régénération des forêts (Chapitre 3) et interagissent avec le changement du climat, il est évident que les futures politiques d'aménagement auront un rôle fondamental à jouer pour maintenir ou développer la capacité des forêts à s'adapter rapidement face aux changements globaux.

Le réchauffement que nous avons connu jusqu'à présent n'est que mineur par rapport aux projections faites pour la fin du siècle (IPCC, 2014). Néanmoins, tel que mis en évidence dans l'ensemble de ma thèse, de grandes transformations sont déjà évidentes à toutes les échelles de l'organisation écologique. Avec l'accélération des changements environnementaux et l'inertie inhérente de la dynamique forestière, le déséquilibre ne pourra que s'accentuer et les réponses des forêts dépendront des dynamiques transitoires déjà en cours. En ce moment au Québec, l'estimation de la productivité des peuplements forestiers repose sur des taux de mortalité et de croissance prévisibles sous un climat constant. En aménagement forestier, on simplifie et on présume que le climat est stable et que les forêts sont à l'équilibre. À court terme, ces hypothèses sont valables, alors qu'à long terme elles sont particulièrement problématiques dans le contexte du changement climatique. En effet, comme la dynamique forestière n'est pas à l'équilibre (Talluto *et al.*, 2017), la trajectoire de succession et la niche de régénération sont facilement altérées sous l'effet combiné du réchauffement et des perturbations (Chapitres 2 et 3). Les prédictions issues de calculs qui supposent l'équilibre pourraient à la fois sur-estimer la capacité de régénération et de croissance de certaines espèces et sous-estimer la mortalité associée à des extrêmes climatiques, menant ainsi à une planification mal adaptée. Par conséquent, les activités de gestion doivent non seulement anticiper le changement, mais aussi reconnaître que les systèmes actuels ont déjà été transformés et sont en train de se transformer davantage. L'importance de ce point a été bien exprimée par Seastedt *et al.* (2008) :

«*In managing novel ecosystems, the point is not to think outside the box but to recognize that the box has moved, and in the 21st century, the box will continue to move more rapidly.* »

4.8.1. Évolution des concepts d'aménagement forestier au Québec

Une importante volonté de gestion durable des forêts s'est développée dans les dernières décennies à travers le monde. Jusqu'à la fin du XX^e siècle, les modèles de gestion étaient basés une vision utilitariste de la forêt et étaient centrés sur la production de bois (Kuuluvainen et Grenfell, 2012). Depuis les années 1990, la foresterie a évolué vers un objectif d'aménagement qui intègre davantage de critères écologiques et sociaux (Messier *et al.*, 2013). Au Québec, dans la foulée du documentaire *L'erreur boréale* de Richard Desjardins et Robert Monderie, sorti en 1999, une grande réflexion s'est amorcée sur l'exploitation de la forêt publique. Pour répondre aux inquiétudes de la population, la Commission d'étude sur la gestion de la forêt publique québécoise fut formée en 2003 et a déposé en 2004 un rapport qui faisait état de la situation et formulait de nombreuses recommandations pour améliorer et moderniser la gestion des forêts (Commission d'étude sur la gestion de la forêt publique québécoise, 2004). En réponse à ces recommandations, le Québec s'est doté de la Loi sur l'aménagement

durable du territoire forestier, en vigueur depuis 2013, qui promeut un aménagement écosystémique. L'aménagement écosystémique s'inspire des patrons spatio-temporels générés par les perturbations naturelles, qui servent d'états de référence, afin de maintenir les écosystèmes dans leur plage de variabilité naturelle historique et ainsi réduire les écarts entre les forêts naturelles et aménagées (Attiwill, 1994; Vaillancourt *et al.*, 2009).

L'aménagement écosystémique représente une grande avancée car il intègre un ensemble d'objectifs sociaux et écologiques plus larges et reconnaît l'importance de la biodiversité et des processus écologiques qui influencent la dynamique forestière (Kuuluvainen, 2009; Messier, 2019). Cette nouvelle approche de gestion présente néanmoins une lacune majeure : ces pratiques de gestion ne sont pas conçues pour faire face au rythme rapide des changements globaux et à l'incertitude croissante qui en découle (Messier *et al.*, 2016; Millar *et al.*, 2007). En effet, des pratiques de gestion qui visent à maintenir la composition et la structure des forêts historiques de référence vont devenir de plus en plus difficiles à mettre en œuvre (Boulanger *et al.*, 2019; Duvaneck et Scheller, 2016) et ne permettent pas nécessairement d'améliorer la capacité des écosystèmes à s'adapter à un nouvel ensemble de conditions environnementales (Seastedt *et al.*, 2008). Bien que le retour vers des conditions de référence historiques deviendra sans doute insoutenable dans le futur, les informations historiques documentant la dynamique naturelle des écosystèmes forestiers seront essentielles pour mieux appréhender les dynamiques du futur (Harris *et al.*, 2006).

4.8.2. Perspective : aménager les forêts pour augmenter leur résilience et leur capacité adaptative

La solution privilégiée pour faire face au changement climatique est d'accroître la résilience et la capacité adaptative des forêts (Messier *et al.*, 2013; Seastedt *et al.*, 2008). Alors que la résilience permet à une forêt de retrouver sa structure et ses fonctions d'origine, la capacité adaptative lui permet de diverger d'un état antérieur qui était mal adapté aux conditions environnementales (Filotas *et al.*, 2014). Les perturbations naturelles et les variations climatiques sont inévitables mais en développant une grande diversité, les forêts auront la possibilité de se réorganiser et de s'adapter à des conditions climatiques sans analogues (Messier *et al.*, 2016). S'appuyant sur l'hypothèse d'assurance (de l'anglais *insurance hypothesis*; Yachi et Loreau, 1999), l'idée est de favoriser la diversité génétique, spécifique, fonctionnelle et structurale dans les forêts afin d'augmenter les chances que certaines espèces continueront à assurer principaux services écosystémiques même si d'autres disparaissent.

Pour favoriser la capacité adaptative des forêts, il faut avant tout maintenir la diversité naturelle que l'on trouve à toutes les échelles spatiales, du peuplement jusqu'au biome, de manière à conserver les options d'adaptation qui existent déjà. Par exemple, bien que peu résilientes, les forêts mixtes du Québec ont montré une bonne capacité adaptative face au

changement climatique puisqu'elles ont réussi à se réorganiser de manière à ajuster leur composition aux nouvelles conditions environnementales. En effet, suite à une perturbation, des trajectoires diversifiées peuvent émerger dans les peuplements mixtes puisqu'ils présentent une hétérogénéité en termes de structure, d'âge, de tolérance physiologique et de stratégies d'histoire de vie.

Dans d'autres cas, il sera peut-être nécessaire de cultiver activement la capacité adaptive des écosystèmes grâce à l'aménagement. Ce principe pourrait devenir important dans les forêts boréales étant donné leur composition très homogène et leur très grande inertie face au changement climatique. En effet, alors qu'il y a eu très peu de transitions vers l'état mixte et pas de thermophilisation des communautés, on a plutôt observé une dynamique de remplacement entre les états pionnier et boréal (Chapitres 1 et 2). Comme les forêts du nord du Québec sont très pauvres en espèces, étant largement dominées par l'épinette noire et le sapin baumier, elles ont moins de ressources que les forêts mixtes pour faire face aux changements récents et futurs, ce qui pourrait limiter leur capacité à s'ajuster et à s'éloigner d'un état parfois mal adapté. De plus, selon les scénarios d'émissions de gaz à effet de serre élevés, le climat de la forêt boréale de l'est de l'Amérique du Nord devrait ressembler à celui de la forêt tempérée d'ici la fin du siècle (Gauthier *et al.*, 2015b). Toutefois, la migration des espèces tempérées dans ces régions semble limitée par plusieurs facteurs non-climatiques, notamment leur capacité de dispersion, la compétition par les espèces boréales, ainsi que les conditions édaphiques (Chapitre 3 ; Carteron *et al.*, 2020; Solarik *et al.*, 2019). Des plantations d'enrichissement pourraient alors s'avérer nécessaires pour faciliter la migration des espèces tempérées vers le nord et assurer la résilience des forêts (Duveneck et Scheller, 2016). Par exemple, et comme cela a été suggéré pour la migration postglaciaire des arbres (McLachlan *et al.*, 2005), les populations aujourd'hui marginales pourraient jouer un rôle très important dans la migration future des arbres en réponse au changement climatique (Chapitre 3). Ainsi, la création d'îlots de forêts mixtes sur les sommets de collines dans les forêts boréales assurerait la présence de semenciers de différentes espèces capables de coloniser rapidement les sites après perturbation lorsque les conditions climatiques seront adéquates. Finalement, étant donné les interactions entre échelles, les changements de régime écologique, la variabilité des réponses des espèces ainsi que l'importance des événements stochastiques dans la trajectoire des forêts, il devient de plus en plus clair qu'on ne peut forcer un peuplement à se développer dans une direction prédéterminée précise en fonction de nos besoins en bois (Puettmann *et al.*, 2009). Des recherches récentes encouragent donc à revoir la planification de façon à avoir des objectifs plus larges et plus flexibles qui permettent un ensemble de différentes trajectoires futures à l'échelle régionale (Messier *et al.*, 2016; Puettmann *et al.*, 2009).

L'idée de favoriser la diversité pour assurer la résilience est déjà prise en compte dans l'aménagement écosystémique et constitue donc une porte d'entrée au concept d'adaptation

au changement climatique (Samuel, 2011). Toutefois, il faut éviter de mettre tous nos œufs dans le même panier. Les projections climatiques nous ont informé d'un risque croissant de vagues de chaleur et de sécheresse (IPCC, 2014). Par conséquent, il apparaît logique de mettre l'accent sur la promotion des espèces qui résistent à la sécheresse. Mais, dans un contexte d'incertitude, cette stratégie ne suffit pas puisqu'il est possible que ce ne soit pas la sécheresse qui causera le plus grand stress aux forêts, mais plutôt l'augmentation de la fréquence des feux, l'arrivée de nouveaux insectes ravageurs ou encore les variations des températures printanières. De plus, comme je l'ai montré dans cette thèse, tous ces facteurs de risque peuvent interagir entre eux et mener à des changements rapides et inattendus des écosystèmes forestiers. La grande incertitude associée aux prédictions des effets attendus des changements climatiques doit être intégrée dans la gestion forestière de façon à prendre en compte un large éventail de vulnérabilités des arbres (Messier *et al.*, 2016). Pour permettre à l'écosystème de résister ou de s'adapter à ces multiples facteurs de stress, on pourrait profiter des coupes à rétention variable ou des plantations pour promouvoir les mélanges d'espèces, définies en fonction du domaine bioclimatique, ayant des caractéristiques fonctionnelles diverses, allant des tolérances physiologiques (aux feux, aux ravageurs, à la sécheresse), aux différents modes de régénération (p. ex., banque de graines, cônes sérotineux, reproduction végétative ; Messier, 2019; Puettmann *et al.*, 2009).

4.9. Au-delà des forêts — Aplanir la courbe du changement climatique

Au cours des dernières décennies, l'ouest du Canada a subi une épidémie sans précédent de dendroctone du pin ponderosa, une grave sécheresse (2001–2003) et des saisons de feux extrêmes. Les effets synergiques de ces perturbations ont entraîné un déprérissement rapide et extensif des forêts (Williamson *et al.*, 2009). De telles catastrophes naturelles en rafales montrent que la capacité des gouvernements à s'adapter et à contrôler les dommages peut rapidement être excédée. Or, les prédictions annoncent une accélération de la fréquence et de la sévérité des événements climatiques extrêmes (IPCC, 2014). Si nous n'agissons pas maintenant pour décarboniser notre économie et changer la trajectoire dangereuse dans laquelle nous sommes engagés, le climat mondial continuera de se dérégler et la multiplication des événements climatiques extrêmes dépassera la capacité des systèmes naturels et humains à se rétablir après les perturbations (IPCC, 2018). Ainsi, sans mesures d'atténuation du changement climatique, les stratégies d'aménagement visant à augmenter la résilience et la capacité adaptative des écosystèmes risquent de s'avérer vaines. Le récent rapport spécial du GIEC a conclu que limiter le réchauffement climatique à 1.5 °C est possible mais exigera des transitions rapides et radicales dans tous les aspects de la société (IPCC, 2018).

Au cours des premiers mois de 2020, la planète entière a fait face à la pandémie de la COVID-19 et les gouvernements ont adopté des mesures draconiennes pour tenter d'en atténuer les conséquences. Le message a été clair : il fallait ralentir le rythme de propagation de la maladie pour "aplanir la courbe" et éviter de dépasser la capacité des hôpitaux à traiter les malades. Ce même concept s'applique également à la crise climatique : limiter le réchauffement climatique permettrait de ne pas dépasser la capacité de support de la Terre et donnerait aux sociétés et aux écosystèmes une plus grande marge de manœuvre pour s'adapter. La réponse des gouvernements et de la population à la pandémie de la COVID-19 nous a montré que nous pouvons agir rapidement et mettre la santé des individus devant celle de l'économie. Cette crise sanitaire souligne également qu'il serait préférable d'adopter des mesures préventives afin d'atténuer le changement climatique plutôt que d'attendre passivement de frapper un mur et d'être forcés à vivre dans l'état d'urgence. Maintenant que nous comprenons mieux les conséquences de l'inaction, la priorité est d'utiliser l'ensemble de nos connaissances scientifiques pour construire un scénario positif et durable pour l'avenir (Bennett *et al.*, 2016). Ainsi, comme l'a écrit Antoine de Saint-Exupéry (1948) dans *Citadelle* :

«Pour ce qui est de l'avenir, il ne s'agit pas de le prévoir, mais de le rendre possible. »

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Annexe A

Disturbances amplify tree community responses to climate change
in the temperate-boreal ecotone

Marie-Hélène Brice, Kevin Cazelles, Pierre Legendre, Marie-Josée Fortin

A.1. Supplementary Tables

Tableau A.1. List of species included in the analyses and their traits. The species groups were defined using their trait values and knowledge of species ecology. Temperate species have temperature indices above 4.25, and boreal species below 4.25. Pioneer species have shade tolerance below 2.6 and are generally found in disturbed habitats.

<i>Species name</i>	Vernacular name	Group	Shade tolerance	Temperature index
<i>Abies balsamea</i>	Balsam fir	Boreal	5.0	3.16
<i>Acer pensylvanicum</i>	Striped maple	Temperate	3.5	5.22
<i>Acer rubrum</i>	Red maple	Temperate	3.4	9.28
<i>Acer saccharinum</i>	Silver maple	Temperate	3.6	9.97
<i>Acer saccharum</i>	Sugar maple	Temperate	4.8	6.93
<i>Acer spicatum</i>	Mountain maple	Temperate	3.3	4.52
<i>Alnus incana</i>	Speckled alder	Boreal	1	1.22
<i>Amelanchier sp.</i>	Serviceberry	Temperate	3.4	9.40
<i>Betula alleghaniensis</i>	Yellow birch	Temperate	3.2	4.49
<i>Betula papyrifera</i>	White birch	Pioneer	1.5	3.69
<i>Betula populifolia</i>	Grey birch	Pioneer	1.5	5.58
<i>Carpinus caroliniana</i>	Blue beech	Temperate	4.6	15.90
<i>Carya cordiformis</i>	Bitternut hickory	Temperate	2.1	11.06
<i>Fagus grandifolia</i>	American beech	Temperate	4.8	8.46
<i>Fraxinus americana</i>	White ash	Temperate	2.5	9.54
<i>Fraxinus nigra</i>	Black ash	Temperate	3	4.92
<i>Fraxinus pennsylvanica</i>	Red ash	Temperate	3.1	11.86

<i>Species name</i>	Vernacular name	Group	Shade tolerance	Temperature index
<i>Juglans cinerea</i>	Butternut	Temperate	1.9	8.10
<i>Larix laricina</i>	Tamarack	Boreal	1	3.92
<i>Malus sp.</i>	Crab apple	Temperate	2.2	7.96
<i>Ostrya virginiana</i>	Ironwood	Temperate	4.6	8.91
<i>Picea glauca</i>	White spruce	Boreal	4.2	3.08
<i>Picea mariana</i>	Black spruce	Boreal	4.1	1.68
<i>Picea rubens</i>	Red spruce	Temperate	4.4	4.26
<i>Pinus banksiana</i>	Jack pine	Boreal	1.4	2.99
<i>Pinus resinosa</i>	Red pine	Temperate	1.9	5.54
<i>Pinus strobus</i>	Eastern white pine	Temperate	3.2	6.85
<i>Populus balsamifera</i>	Balsam poplar	Pioneer	1.3	4.25
<i>Populus deltoides</i>	Cottonwood	Pioneer	1.8	8.12
<i>Populus grandidentata</i>	Large tooth aspen	Pioneer	1.2	6.14
<i>Populus tremuloides</i>	Trembling aspen	Pioneer	1.2	4.22
<i>Prunus pensylvanica</i>	Pin cherry	Pioneer	1	4.01
<i>Prunus serotina</i>	Black cherry	Temperate	2.5	4.69
<i>Prunus virginiana</i>	Chokecherry	Temperate	2.6	7.79
<i>Quercus alba</i>	White oak	Temperate	2.9	12.95
<i>Quercus bicolor</i>	Swamp white oak	Temperate	3	9.51
<i>Quercus macrocarpa</i>	Bur oak	Temperate	2.7	6.72
<i>Quercus rubra</i>	Red oak	Temperate	2.8	9.67
<i>Salix sp.</i>	Willow	Pioneer	1.5	13.32
<i>Sorbus sp.</i>	Mountain-ash	Pioneer	2.6	2.31
<i>Thuja occidentalis</i>	White cedar	Temperate	3.5	4.30
<i>Tilia americana</i>	Basswood	Temperate	4	5.34
<i>Tsuga canadensis</i>	Eastern hemlock	Temperate	4.8	6.87
<i>Ulmus americana</i>	American elm	Temperate	3.1	10.67
<i>Ulmus rubra</i>	Red elm	Temperate	3.3	12.37
<i>Ulmus thomasii</i>	Rock elm	Temperate	3.2	7.80

Tableau A.2. 21 original disturbance types and their reclassification into natural disturbances and harvest, with three levels of intensity. Sites with tree planting were excluded from the study.

	Original disturbance types	Reclassification	Disturbance level
1	Improvement cutting	Harvest	Moderate
2	Strip cutting	Harvest	Moderate
3	Checkerboard clear-cutting	Harvest	Moderate
4	Diameter-limit cutting	Harvest	Moderate
5	Selection cutting	Harvest	Moderate
6	Partial cutting	Harvest	Moderate
7	Diameter-limit cutting with crop tree release	Harvest	Moderate
8	Commercial thinning	Harvest	Moderate
9	Partial cutting with light outbreak	Harvest	Moderate
10	Partial burn	Natural	Moderate
11	Light outbreak	Natural	Moderate
12	Partial windfall	Natural	Moderate
13	Partial ice storm	Natural	Moderate
14	Partial decline	Natural	Moderate
15	Final strip cutting	Harvest	Major
16	Harvesting with protection of regeneration	Harvest	Major
17	Clearcutting	Harvest	Major
18	Total burn	Natural	Major
19	Severe outbreak	Natural	Major
20	Total windfall	Natural	Major
21	Total decline	Natural	Major
-	Seeding	Plantation	x
-	Planting	Plantation	x
-	Planting bare-rooted seedlings	Plantation	x
-	Container planting	Plantation	x

Tableau A.3. List of R packages used for analyses.

Packages	Uses	References
adespatial	Forward selection (<code>forward.sel</code>), temporal beta diversity (<code>tbi</code>)	Dray <i>et al.</i> (2018)
FD	Functional composition (<code>functcomp</code>)	Laliberté <i>et al.</i> (2014)
raster	Manipulation of spatial data	Hijmans (2018)
sf	Manipulation of spatial data	Pebesma (2018)
stats	Linear regressions (<code>lm</code>)	R Core Team (2018)
vegan	Variation partitioning (<code>varpart</code>)	Oksanen <i>et al.</i> (2019)
zoo	Rolling average (<code>rollmean</code>)	Zeileis et Grothendieck (2005)

A.2. Supplementary Figures

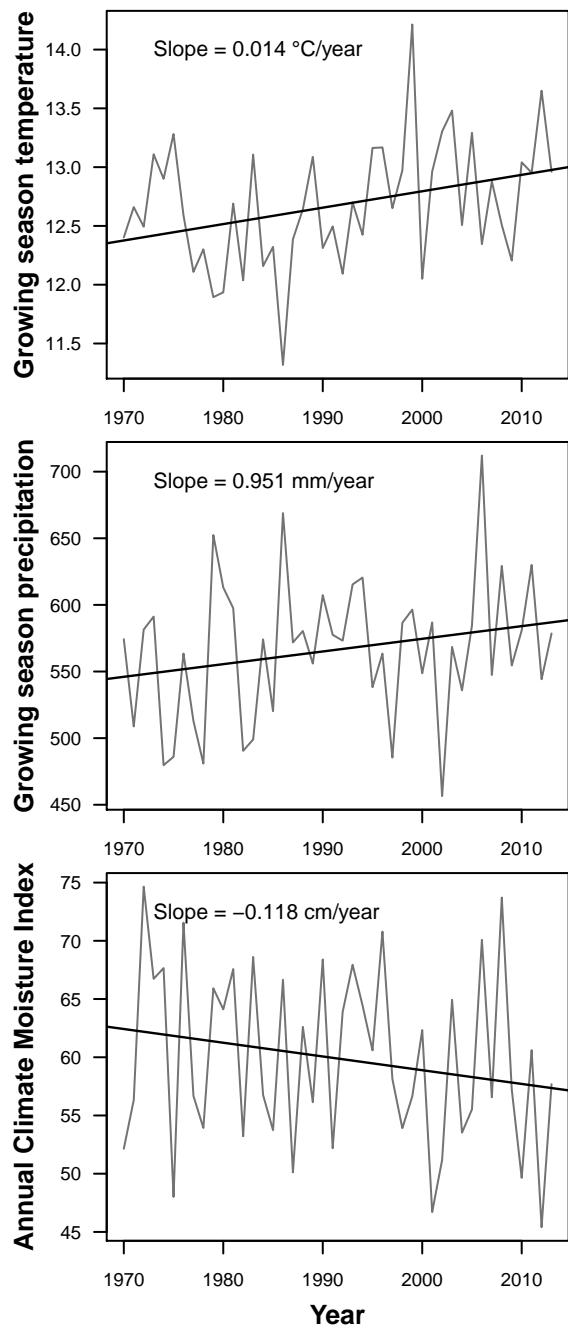


Figure A.1. Temporal trends in growing season temperatures (top), total growing season precipitation (middle) and annual climate moisture index (bottom). Grey lines represent averaged climate values across the 6281 studied forest plots. Straight black lines show the fitted least-squared linear regression lines.

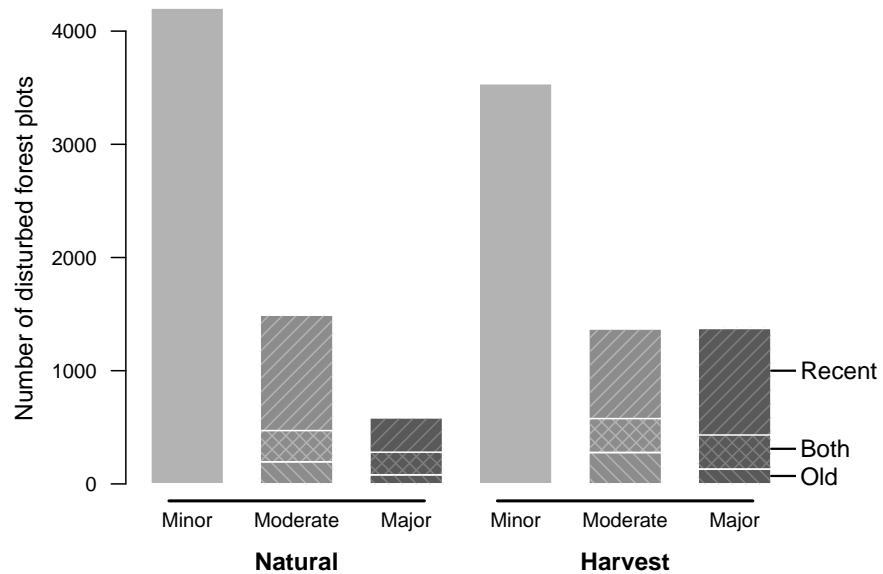


Figure A.2. Frequency of forest plots by disturbance type (natural disturbances and harvest), level of intensity (minor, moderate, major) and timing (old refers to disturbances that occurred before the study period whereas recent disturbances occurred during the study period). The three columns in each disturbance type sum to $n = 6281$ forest plots, but many forest plots have been disturbed by more than one type of disturbance during the study period.

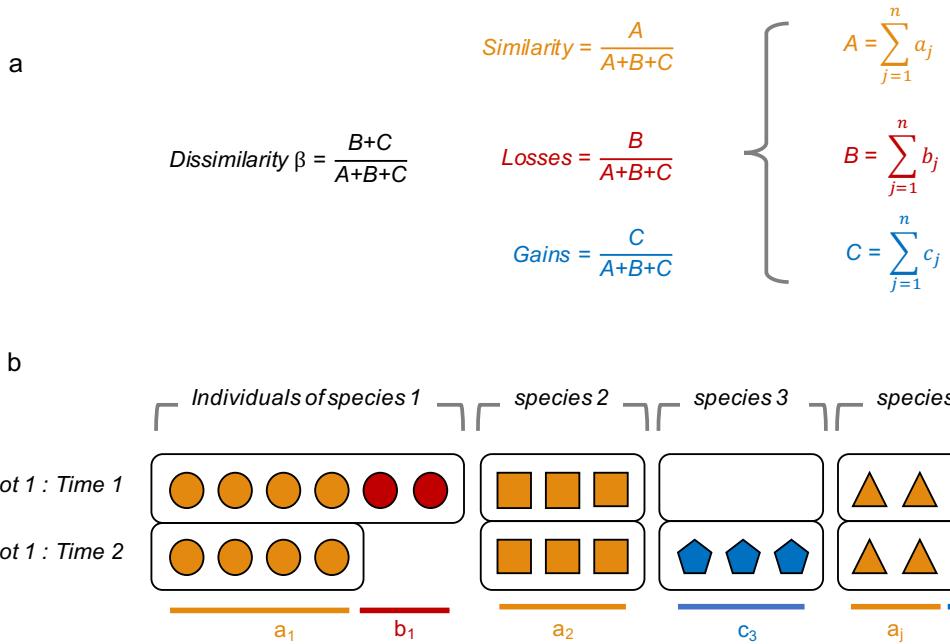


Figure A.3. Equations to compute the temporal β diversity index, as well as its components, using the Ružička coefficient for abundance data (a) and an example (b) where the tree composition of a single forest plot is compared between two surveys, t_1 and t_2 . In the example, each of the n species is represented by a symbol. The symbols in yellow represent the abundance of a species that is common to the two survey (component A ; note that it can be different individuals of the same species). The symbols in red represent the abundance of a species that is lost between t_1 and t_2 (component B). The symbols in blue represent the abundance of a species that is gained between t_1 and t_2 (component C). In this example, $A = 4 + 3 + 2 = 9$, $B = 2$, and $C = 3 + 1 = 4$, therefore $\beta = 2 + 4/(9 + 2 + 4) = 0.4$.

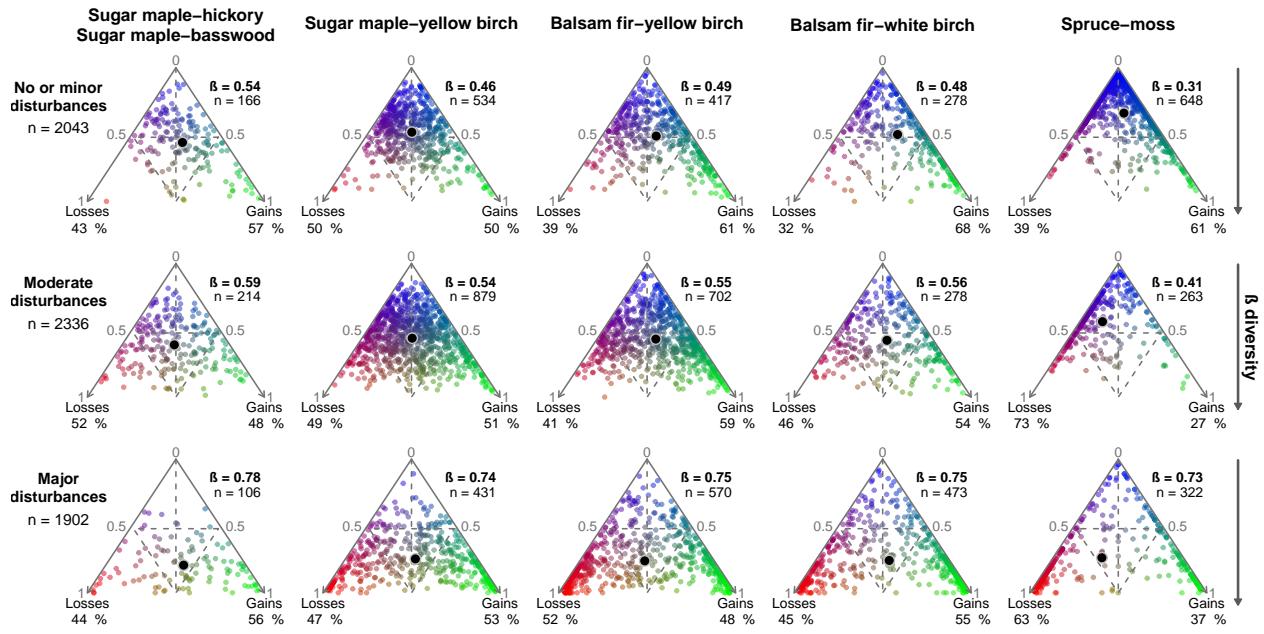


Figure A.4. Triangular diagrams of gains and losses in tree abundance by bioclimatic domains and disturbance levels. Each point represents a forest plot and the large black point represents the centroid. At the upper tip of the triangle, similarity is high ($\beta = 0$; blue colors). At the base of the triangle, dissimilarity is high ($\beta = 1$). On the left, forests in red are dominated by losses, while on the right, forests in green are dominated by gains. The similar distributions of gain and loss values in the ternary diagrams suggests that there is no major difference in temporal β diversity patterns among domains.

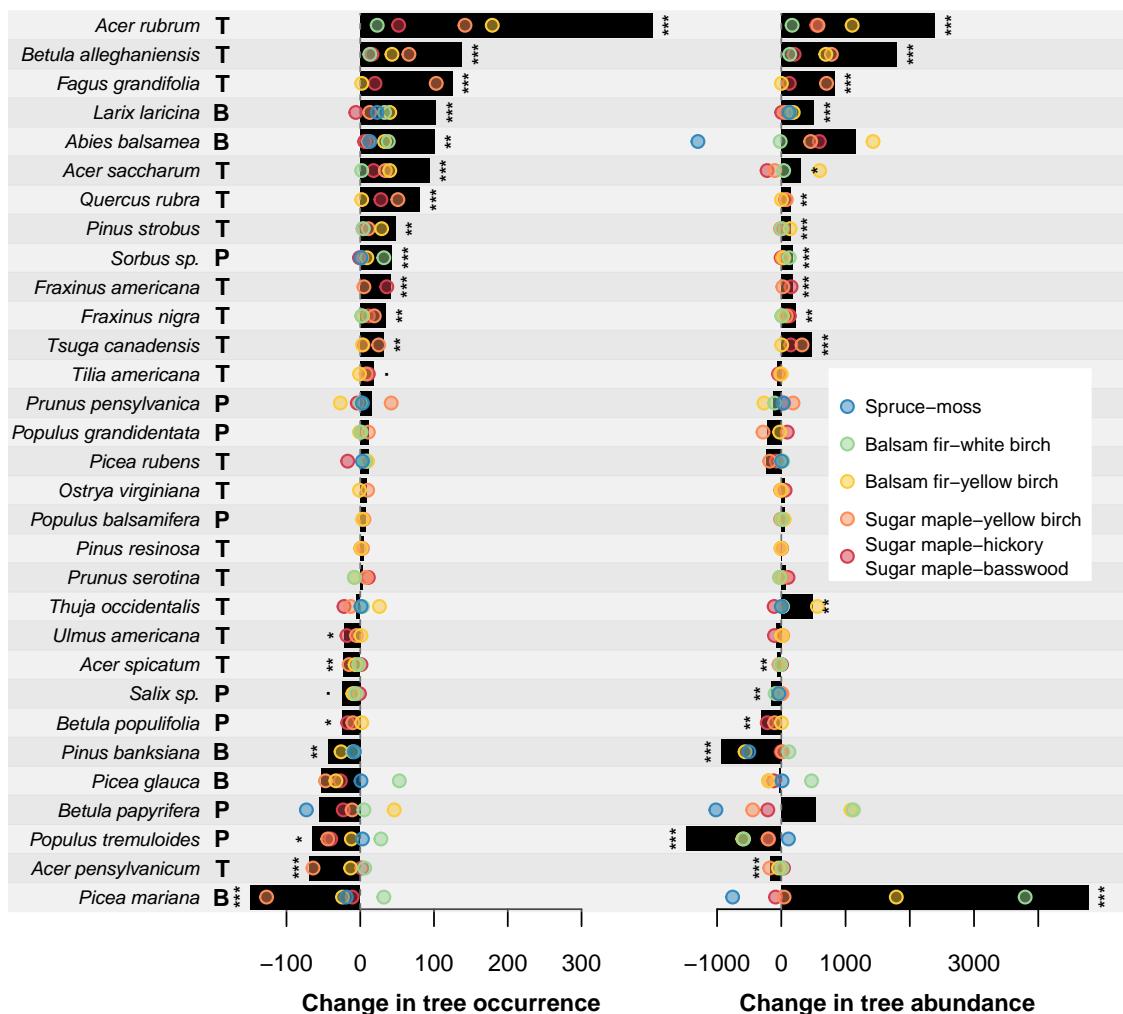


Figure A.5. Species temporal changes for Québec forests and for each bioclimatic domain. Changes in species occurrence (left) and species abundance (right). Only the species occupying more than 20 plots are shown. The bars represent the mean changes across the study area, while the colored points represent the mean changes by bioclimatic domain. Stars represent the levels of the significance of the $*p*$ -value ($*p < 0.05$; $**p < 0.01$; $***p < 0.001$) associated with Wilcoxon signed-rank tests used to determine whether individual species changes in occurrence and abundance were significant. An increase in occurrence indicates that the species has spread regionally, while an increase in abundance indicates that the species has spread locally and/or regionally. Letters next to species names correspond to (T)emperate; (P)ioneer and (B)boreal species.

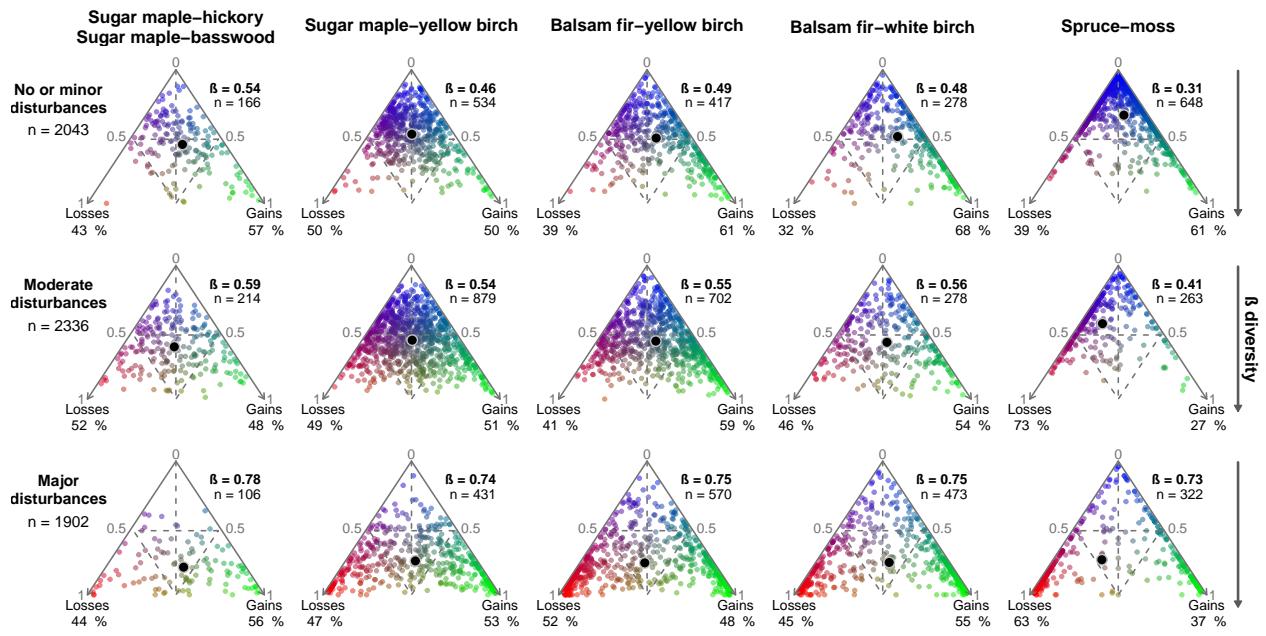


Figure A.6. Relations between change in Community Temperature Index (Δ CTI) and gains in temperate (top), gains in pioneer (middle) and losses in boreal species (bottom). In each panel, the slope and adjusted R^2 of a linear regression model are shown.

Annexe B

Moderate disturbances accelerate forest transition dynamics under climate change in the temperate-boreal ecotone of eastern North America

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B.1. Supplementary Methods

B.1.1. Multi-state models

For states $r, s \in B, M, P, T$ and time $t, \Delta t >= 0$, transition probabilities (a_{rs}) are defined as the probability that a plot in state r at time t is in state s at time $t + \Delta t$ and can be written as :

$$A_{r,s}(t + \Delta t) = A(S_{t+\Delta t} = s | S_t = r).$$

In a four-state transition model, the transition probability matrix $P(t + \Delta t)$, hereafter simplified to $A(t)$, is a 4×4 matrix, where the rows are the current states and the columns the future states, containing the transition probabilities $a_{rs}(t)$ for a specified time interval. For a time-homogeneous model, $A(t)$ is solved by taking the matrix exponential of the intensity matrix Q scaled by the time interval :

$$A(t) = e^{tQ}.$$

The intensity matrix Q contains transition intensities $q_{r,s}$ which represent the instantaneous risk of moving from state r to state s :

$$q_{r,s} = \lim_{\Delta \rightarrow 0} \frac{P(Y_{t+\Delta} = s | Y_t = r)}{\Delta}, \text{ on off-diagonal elements,}$$

$$q_{r,r} = - \sum_{s \neq r} q_{rs}, \text{ on diagonal elements.}$$

We can define transition-specific hazard regression models for those states $r,s \in B,M,P,T$ between which a direct transition is possible according to the specified multi-state process (Fig. 2.2 in main text). The intensities q_{rs} can be modelled as a product of a baseline hazard $q_{rs,0}$ and a log-linear effect of the explanatory variables $x(t)$ and their coefficients β_{rs} :

$$q_{rs}(t) = q_{rs}(t|x(t)) = q_{rs,0}(t)\exp(\beta'_{rs}x(t)).$$

In this model, $q_{rs,0}(t)$ is a baseline hazard function that describes the risk for a reference plot i with environment $x_i(t) = 0$, and $\exp(\beta'_{rs}x(t))$ is the relative increase or decrease in risk associated with the set of characteristics $x_i(t)$. This model allows one to include the effect of time-dependent covariates on transition intensities and therefore to relax the time homogeneity assumption of Markov models. Time-dependent covariates, such as climate and disturbances, are assumed to be piecewise-constant, i.e., the hazard is constant within a specified time interval $[t, t + \Delta t]$ and depends on the covariate value at t , but is allowed to change between the intervals.

Estimation of model parameters can be obtained by maximising the log-likelihood function using the transition probability matrix. The contribution of plot i at time j to the likelihood is given by :

$$LL_i(\theta|s,x) = \prod_{j=1}^J A(S_j = s_j | S_{j-1} = s_{j-1}, \theta, x),$$

where θ is the vector with all model parameters, x denotes the vector with the covariate values, and s denotes the observed state trajectory s_1, \dots, s_J at times t_1, \dots, t_J . The full likelihood function is the product of the contributions of all N plots :

$$LL(\theta) = \prod_{i=1}^N LL_i(\theta|s,x).$$

B.1.2. Performance of candidate models

We fitted all models on the full data sets but also used cross-validation to estimate the predictive performance on held-out data. We used two statistics, the area under the receiver operating characteristic (ROC) curve (AUC) and the logarithmic scoring rule (LS), to assess the agreement between the observed state and the models' predictions. The AUC is a popular performance metric for binary classifiers that measures the probability that a randomly drawn member of state s has a lower estimated probability of belonging to state r than a randomly drawn member of state r . The AUC ranges from 0 to 1, where a score of 1 indicates perfect discrimination, while a score of 0.5 is as good as random. Hand et Hill (2001) has extended the AUC method to multi-class problems. For any pair of states r and s , we can compute $\hat{A}(r|s)$, the probability that a randomly drawn member of state s has a lower estimated probability of belonging to state r than a randomly drawn member of state r . We can measure the discrimination rate between all pairs of states by computing the pairwise AUC :

$$\hat{A}(r,s) = [\hat{A}(r|s) + \hat{A}(s|r)]/2.$$

Averaging the pairwise AUC gives the overall multi-class AUC (hereafter mAUC) of the model :

$$mAUC = \frac{2}{c(c - 1)} \sum_{r < s} \hat{A}(r,s).$$

The LS was proposed by Good (1952) and is often used in weather forecasts (Gneiting et Raftery, 2007). While AUC is a function of different classification thresholds, LS measures the degree to which predicted probabilities are close to the observed outcomes. We computed a global score for each model :

$$LS = \frac{1}{N} \sum_{i=1}^N -\log(P(S_i = s_i)),$$

where S_i is the random variable describing the state of the forest in the i^{th} plot and s_i is the observed state. So, LS only depends upon the predicted probability of the realised state and not on the probabilities assigned to the other possible states. The score is very sensitive to incorrect predictions : if a model predicted the observed state with a probability of 100%, the score for that plot would be 0, while if a probability of zero was assigned to the observed state, the score would go to infinity. Hence, this sensitivity emphasises the differences between model predictions and strongly penalises a model that only gives high probabilities to self-transitions.

To assess the quality of prediction for the four states individually, we computed LS for each state r where we summed the predicted probabilities $P(S_i = r)$ if the observed state is indeed r and $1 - P(S_i = r)$ otherwise.

We evaluated and compared the predictive performance of our five models using the overall mAUC and the pairwise AUCs, as well as the overall LS and the state-specific LS. These metrics were estimated using stratified K -fold cross-validation (Burnham *et al.*, 2002). We first stratified the data set by bioclimatic domains to ensure that each fold was representative of the plot geographical distribution and randomly split the data set in $k=10$ folds. The cross-validation process was repeated k times, during which $k - 1$ folds were used to train the models and the remaining fold was used to validate the model predictions against the observed state transitions. The cross-validated performance metrics were then averaged for each model.

B.2. Supplementary Tables

Tableau B.1. List of the 46 species included in the analyses, their frequency and their corresponding group. The frequency corresponds to the number of forest plots in which they were observed. The species groups were defined using their trait values and knowledge of species ecology (see Brice *et al.* 2019 for details).

<i>Species name</i>	Vernacular name	Frequency
Boreal		
<i>Abies balsamea</i>	Balsam fir	7870
<i>Larix laricina</i>	Tamarack	551
<i>Picea glauca</i>	White spruce	4181
<i>Picea mariana</i>	Black spruce	6082
<i>Pinus banksiana</i>	Jack pine	1339
Pioneer		
<i>Betula papyrifera</i>	White birch	5863
<i>Betula populifolia</i>	Grey birch	226
<i>Populus balsamifera</i>	Balsam poplar	216
<i>Populus deltoides</i>	Cottonwood	2
<i>Populus grandidentata</i>	Large tooth aspen	582
<i>Populus tremuloides</i>	Trembling aspen	2504
<i>Prunus pensylvanica</i>	Pin cherry	1495
<i>Salix sp.</i>	Willow	499
<i>Sorbus sp.</i>	Mountain-ash	515
Temperate		
<i>Acer negundo</i>	Manitoba maple	1
<i>Acer nigrum</i>	Black maple	3
<i>Acer pensylvanicum</i>	Striped maple	719
<i>Acer rubrum</i>	Red maple	3273
<i>Acer saccharinum</i>	Silver maple	23
<i>Acer saccharum</i>	Sugar maple	2190
<i>Acer spicatum</i>	Mountain maple	206
<i>Amelanchier sp.</i>	Serviceberry	33
<i>Betula alleghaniensis</i>	Yellow birch	2582
<i>Carpinus caroliniana</i>	Blue beech	6
<i>Carya cordiformis</i>	Bitternut hickory	10
<i>Fagus grandifolia</i>	American beech	928

(continued)

<i>Species name</i>	Vernacular name	Frequency
<i>Fraxinus americana</i>	White ash	261
<i>Fraxinus nigra</i>	Black ash	465
<i>Fraxinus pennsylvanica</i>	Red ash	33
<i>Juglans cinerea</i>	Butternut	16
<i>Ostrya virginiana</i>	Ironwood	493
<i>Picea rubens</i>	Red spruce	861
<i>Pinus resinosa</i>	Red pine	131
<i>Pinus rigida</i>	Pitch pine	2
<i>Pinus strobus</i>	Eastern white pine	762
<i>Prunus serotina</i>	Black cherry	243
<i>Quercus alba</i>	White oak	9
<i>Quercus bicolor</i>	Swamp white oak	8
<i>Quercus macrocarpa</i>	Bur oak	14
<i>Quercus rubra</i>	Red oak	453
<i>Thuja occidentalis</i>	White cedar	1269
<i>Tilia americana</i>	Basswood	395
<i>Tsuga canadensis</i>	Eastern hemlock	472
<i>Ulmus americana</i>	American elm	228
<i>Ulmus rubra</i>	Red elm	9
<i>Ulmus thomasii</i>	Rock elm	3

Tableau B.2. Frequency of all observed transitions between the four forest states during the study period. Transitions are from rows to columns.

	Boreal	Mixed	Pioneer	Temperate	Sum
Boreal	9760	203	1454	3	11420
Mixed	82	4996	393	682	6153
Pioneer	1539	678	6460	198	8875
Temperate	2	488	168	4584	5242
Sum	11383	6365	8475	5467	31690

Tableau B.3. Table of baseline transition intensities ($q_{rs,0}$ in first column) and Hazard ratios (HR) and their 95% confidence intervals as estimated from the best multi-state transition model. The HR of covariates are interpretable as multiplicative effects on the baseline hazard, where values above 1 indicate that the predictor is associated with a greater risk of state transition, whereas values below 1 indicate a lower risk of transition. Covariates statistically different from 1 are coloured in grey.

Transitions	Baseline	Temperature	CMI	Drainage	pH	Natural1	Natural2	Logging1	Logging2
Boreal - Boreal	-0.009 (-0.01, -0.008)								
Boreal - Mixed	0.002 (0.001, 0.003)	7.36 (5.28, 10.28)	1.43 (1.11, 1.85)	0.74 (0.65, 0.84)	1.12 (0.98, 1.29)	2.76 (2.03, 3.75)	2.34 (0.94, 5.82)	3.45 (2.2, 5.42)	0.72 (0.02, 27.18)
Boreal - Pioneer	0.007 (0.006, 0.008)	1.000	1.000	1.000	1.000	4.76 (3.88, 5.84)	37.01 (30.67, 44.66)	8.45 (5.89, 12.12)	213.52 (102.4, 445.24)
Mixed - Boreal	0.005 (0.003, 0.008)	1.07 (0.65, 1.75)	1.56 (1.18, 2.06)	1 (0.8, 1.25)	0.82 (0.65, 1.04)	0.98 (0.52, 1.85)	2.5 (0.33, 18.8)	1.64 (0.94, 2.86)	1.14 (0.02, 72.72)
Mixed - Mixed	-0.033 (-0.037, -0.029)								
Mixed - Pioneer	0.005 (0.004, 0.006)	1.000	1.000	1.000	1.000	1.91 (0.98, 3.73)	4.94 (0.6, 40.6)	2.45 (1.22, 4.91)	31.22 (19.07, 51.11)
Mixed - Temperate	0.023 (0.02, 0.026)	0.95 (0.76, 1.18)	0.81 (0.7, 0.92)	0.96 (0.88, 1.05)	0.94 (0.87, 1.01)	2.52 (2.04, 3.11)	5.76 (3.02, 10.98)	3.39 (2.79, 4.11)	5.32 (3.46, 8.16)
Pioneer - Boreal	0.027 (0.025, 0.029)	1.28 (1.17, 1.41)	1.8 (1.65, 1.96)	0.98 (0.93, 1.02)	0.96 (0.9, 1.01)	0.94 (0.77, 1.15)	0.38 (0.29, 0.49)	1.9 (1.55, 2.33)	1.84 (0.87, 3.89)
Pioneer - Mixed	0.004 (0.003, 0.004)	4.86 (3.7, 6.39)	1.55 (1.25, 1.91)	0.9 (0.8, 1.01)	0.99 (0.89, 1.1)	0.99 (0.83, 1.96)	0.52 (0.22, 1.22)	2.54 (1.72, 3.76)	0.97 (0.63, 1.48)
Pioneer - Pioneer	-0.032 (-0.034, -0.029)								
Pioneer - Temperate	0.001 (0.001, 0.001)	18.57 (12.5, 27.6)	2.46 (1.88, 3.23)	0.77 (0.65, 0.91)	1 (0.88, 1.13)	0.2 (0.02, 2.05)	0.54 (0.13, 2.3)	1.25 (0.64, 2.42)	0.31 (0.08, 1.15)
Temperate - Mixed	0.014 (0.012, 0.017)	0.54 (0.41, 0.7)	0.96 (0.83, 1.12)	1.3 (1.15, 1.47)	0.73 (0.65, 0.82)	1.24 (0.78, 1.97)	2.08 (0.57, 7.65)	1.1 (0.84, 1.44)	2.41 (1.12, 5.21)
Temperate - Pioneer	0.001 (0.001, 0.002)	1.000	1.000	1.000	1.000	1.13 (0.12, 10.61)	51.54 (22.41, 118.54)	3.8 (2.13, 6.8)	1.46.94 (94.03, 229.62)
Temperate - Temperate	-0.016 (-0.019, -0.013)								

Tableau B.4. Table of baseline transition intensities and hazard ratios as estimated from a full multi-state model ran on forest states defined with a different threshold than in the main manuscript. Here, plots are assigned to Boreal or Temperate states using a threshold of >85% (instead of >75%) of species dominance of the plot basal area. See Table S5 for details about the interpretation of the table.

Transitions	Baseline	Temperature	CMI	Drainage	pH	Natural1	Natural2	Logging1	Logging2
Boreal - Boreal	-0.009 (-0.01, -0.008)								
Boreal - Mixed	0.002 (0.001, 0.003)	5.29 (3.58, 7.83)	1.01 (0.73, 1.39)	0.72 (0.62, 0.83)	1.11 (0.94, 1.32)	2.69 (1.92, 3.77)	0.7 (0.05, 9.91)	1.89 (0.87, 4.13)	0.39 (0.01, 27.18)
Boreal - Pioneer	0.007 (0.006, 0.008)	1.000	1.000	1.000	1.000	4.61 (3.73, 5.68)	37.5 (31, 45.38)	8.81 (6.08, 12.77)	197.37 (110.34, 353.04)
Mixed - Boreal	0.002 (0.001, 0.004)	0.8 (0.41, 1.56)	1.61 (1.1, 2.35)	1.08 (0.79, 1.48)	0.69 (0.45, 1.07)	0.88 (0.33, 2.33)	1.19 (0.04, 38.52)	1.05 (0.41, 2.68)	0.76 (0, 201.91)
Mixed - Mixed	-0.021 (-0.024, -0.019)								
Mixed - Pioneer	0.005 (0.004, 0.006)	1.000	1.000	1.000	1.000	3.2 (2.04, 5.04)	12.6 (6.22, 25.5)	2.7 (1.61, 4.54)	46.45 (33.21, 64.97)
Mixed - Temperate	0.015 (0.013, 0.017)	0.89 (0.71, 1.11)	0.76 (0.66, 0.88)	1.02 (0.94, 1.12)	0.95 (0.88, 1.02)	2.38 (1.92, 2.96)	3.07 (1.6, 5.88)	3.14 (2.61, 3.78)	4.71 (3.02, 7.34)
Pioneer - Boreal	0.025 (0.023, 0.027)	1.21 (1.1, 1.33)	1.8 (1.64, 1.96)	0.98 (0.94, 1.03)	0.95 (0.9, 1.01)	0.96 (0.78, 1.17)	0.37 (0.28, 0.49)	1.85 (1.5, 2.28)	1.7 (0.94, 3.08)
Pioneer - Mixed	0.005 (0.005, 0.006)	5.31 (4.29, 6.58)	1.82 (1.55, 2.14)	0.89 (0.81, 0.98)	0.99 (0.91, 1.08)	1.13 (0.8, 1.59)	0.48 (0.25, 0.9)	2.42 (1.82, 3.21)	0.8 (0.57, 1.12)
Pioneer - Pioneer	-0.031 (-0.033, -0.029)								
Pioneer - Temperate	0 (0, 0.001)	22.53 (14.08, 36.06)	2.48 (1.82, 3.38)	0.7 (0.57, 0.85)	1.04 (0.91, 1.2)	0.1 (0, 5.96)	0.57 (0.14, 2.31)	1.05 (0.46, 2.38)	0.34 (0.09, 1.28)
Temperate - Mixed	0.017 (0.014, 0.021)	0.55 (0.42, 0.71)	0.88 (0.76, 1.02)	1.35 (1.2, 1.52)	0.79 (0.71, 0.87)	1.78 (1.16, 2.74)	1.61 (0.53, 4.91)	1.32 (1.04, 1.67)	4.35 (2.38, 7.93)
Temperate - Pioneer	0.001 (0.001, 0.002)	1.000	1.000	1.000	1.000	0.54 (0.01, 46.28)	37.81 (13.25, 107.92)	3.41 (1.76, 6.62)	142.39 (85.95, 235.89)
Temperate - Temperate	-0.018 (-0.022, -0.015)								

Tableau B.5. List of R packages used.

Main			
Packages	functions	Uses	References
msm	msm	Multi-state Markov models in continuous time	Jackson (2011)
	lrtest.msm	Likelihood ratio test	
	pmatrix.msm	Transition probability matrix	
	hazard.msm	Calculate tables of hazard ratios for covariates on transition intensities	
	pnext.msm	Probability of each state being next	
	sojourn.msm	Mean sojourn times from a multi-state model	
sf		Manipulation and mapping of spatial data	Pebesma (2018)
pROC	multiclass.roc	Compute multi-class AUC	Robin <i>et al.</i> (2011)
scoring	logscore	Compute logarithmic score	Merkle et Steyvers (2013)
labdsv	indval	Calculates the indicator value	Roberts (2019)

B.3. Supplementary Figures

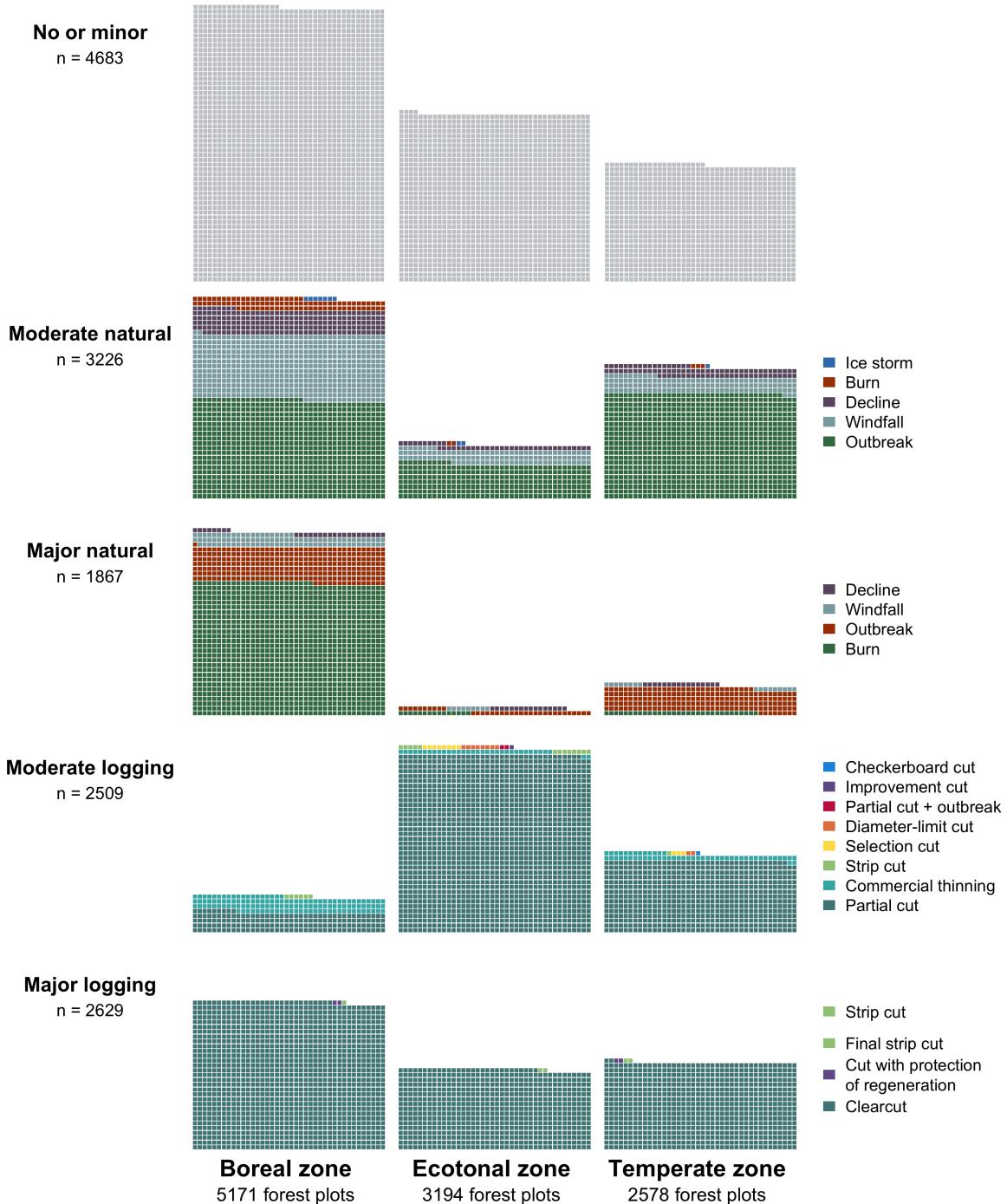


Figure B.1. Waffle charts representing the frequency of forest plots by disturbance type (natural disturbances and logging), level of severity (minor, moderate, major) and vegetation zone (boreal, ecotone and temperate). One square is one occurrence of a disturbance in a forest plot (a forest plot can be disturbed more than once). In each chart (except for the no or minor disturbances), the colours represent the 21 original disturbance types recorded in the field surveys.

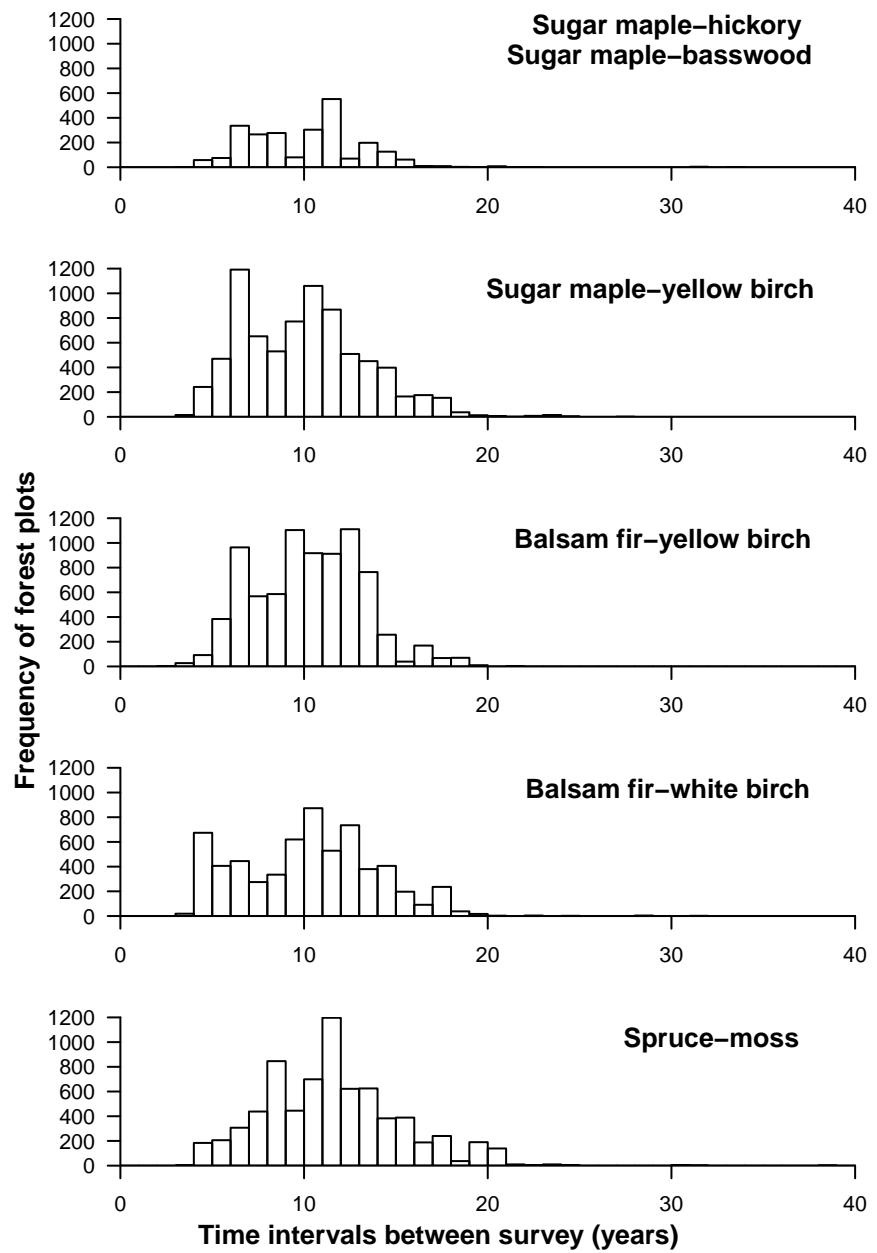


Figure B.2. Histograms of time intervals between surveys by bioclimatic domains.

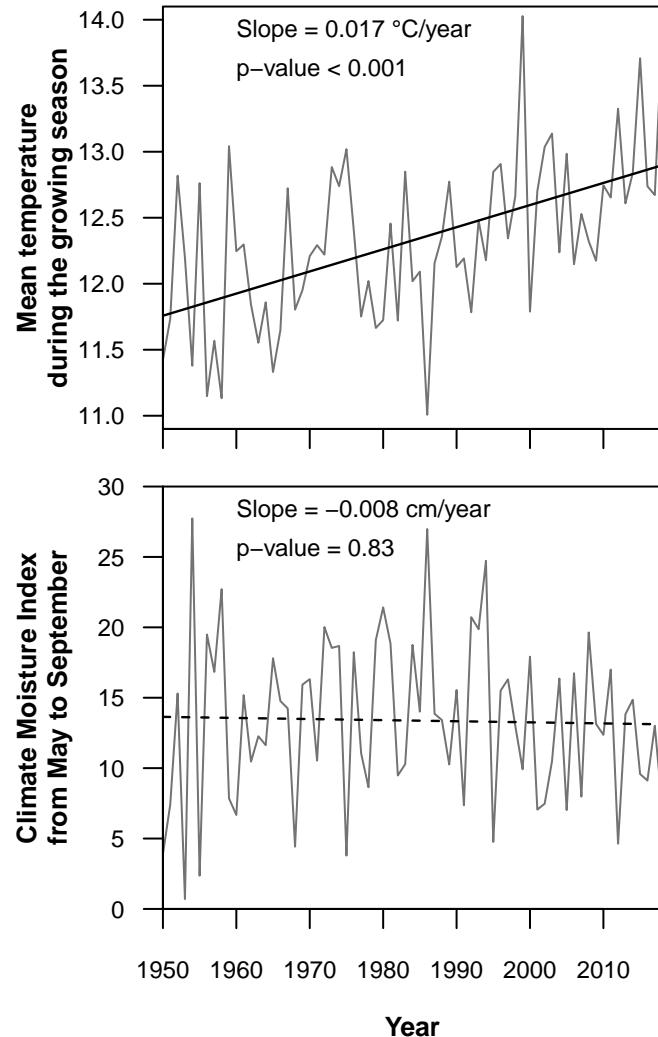


Figure B.3. Temporal trends in growing season temperatures (top) and annual climate moisture index (bottom). Grey lines represent averaged climate values across the 11,058 studied forest plots. Straight black lines show the fitted least-squared linear regression lines.

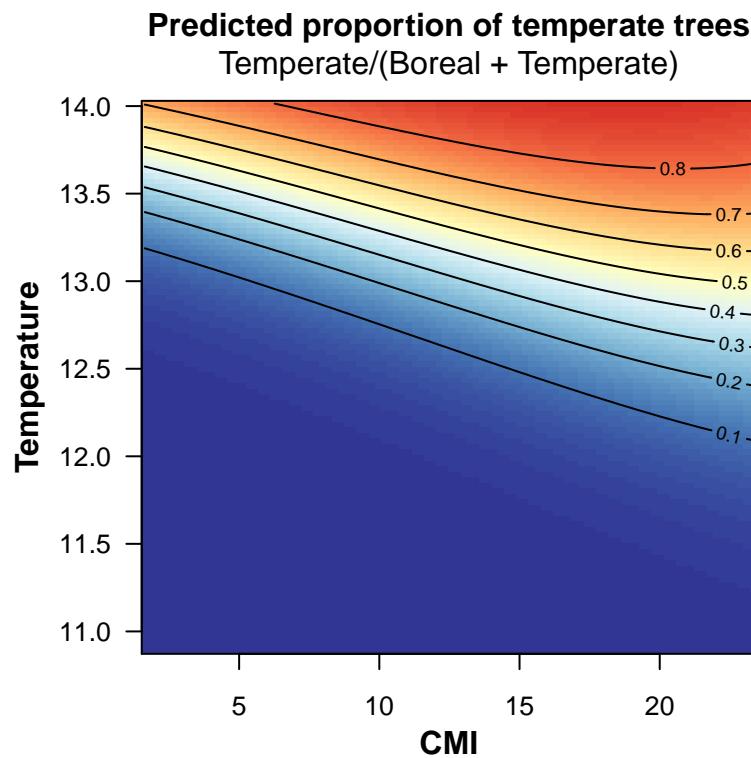


Figure B.4. Predicted proportion of temperate species in forest plots (temperate / (boreal + temperate)) measured in basal area using a negative binomial GLM with polynomial terms of two climate variables, temperature and climate moisture index during the growing season ($R^2 = 50\%$).

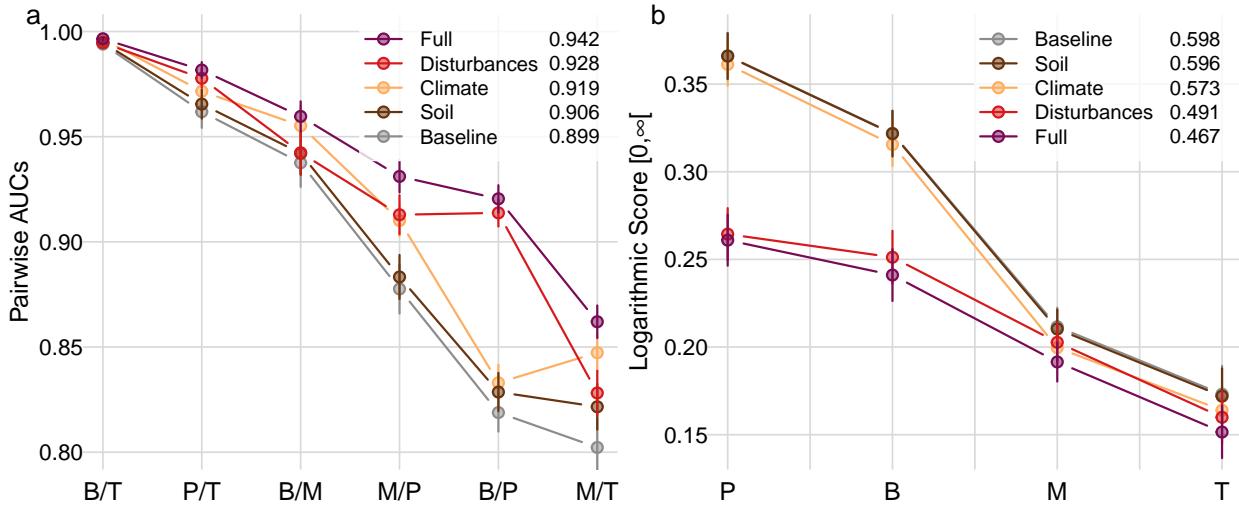


Figure B.5. Performance comparisons of the five candidate multi-state models using multi-class area under the curve (mAUC; a) and logarithmic skill score (LS; b) obtained through 10-fold cross-validation. Higher values of mean pairwise AUC (a) indicate a better capacity to discriminate between pairs of the four forest states : (B)oreal, (M)ixed, (P)ioneer and (T)emperate. The overall mAUC of each model is given next to the legend. Lower values of mean state-specific logarithmic scores (b) indicate better prediction accuracy for each of the four forest states. The overall logarithmic score of each model is given next to the legend.

Model evaluation using 10-fold cross-validation revealed that including climate and disturbances improved overall model predictive performances, while soil variables had a negligible effect. All models were good at distinguishing Boreal from Temperate (high pairwise AUC). Soil variables slightly help to predict Mixed and Temperate states. Including climate variables help to distinguish Mixed from the other states, while including disturbances help to distinguish Pioneer from the other states, especially Boreal.

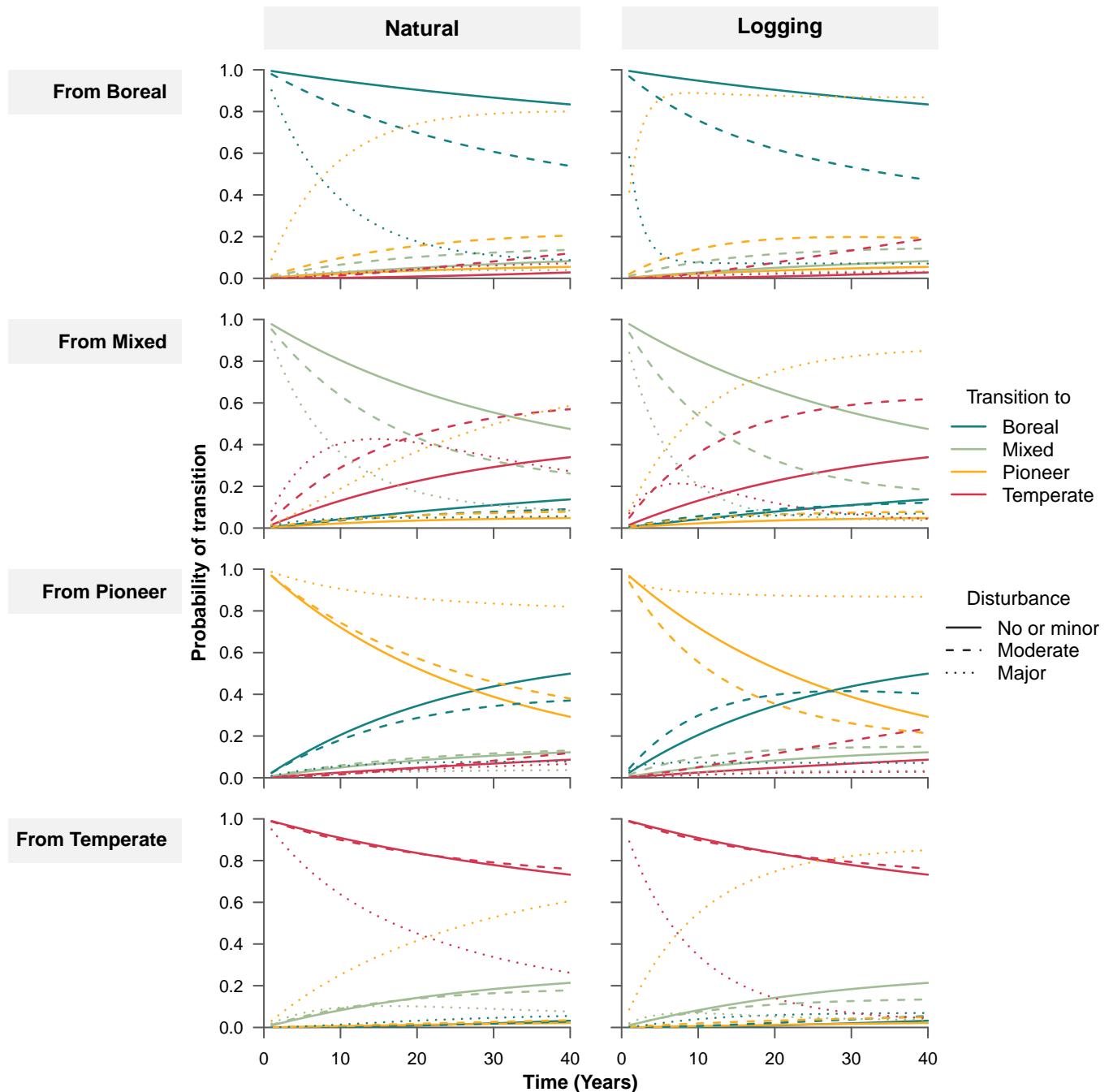


Figure B.6. Probability of transition between forest states through time for natural disturbances (left) and logging (right) and for different levels (line type) as predicted by the best multi-state model. All other covariates are fixed at the average conditions found in the ecotone, i.e. the balsam fir-yellow birch domain.

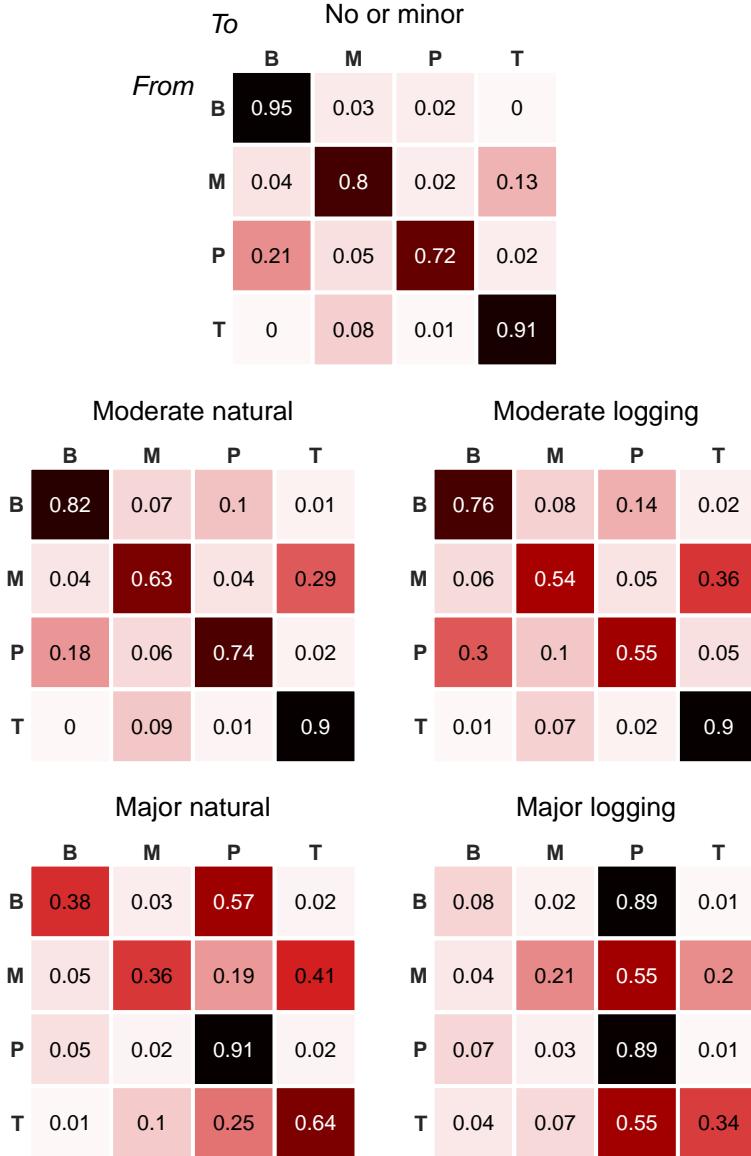


Figure B.7. Predicted change in 10-year transition probabilities for different disturbance types and levels. All other covariates are fixed at the average conditions found in the ecotone. Letters correspond to the four forest states : (B)oreal, (M)ixed, (P)ioneer and (T)emperate. Numbers are the modelled transition probabilities from rows to columns and darker colour indicates higher transition probability.

The largest values across most matrices were generally associated with self-transitions (matrix diagonal), meaning that the vast majority of forest plots remained in the same state after 10 years. At minor disturbances, the self-transitions were very strong but transitions from Pioneer to Boreal and from Mixed to Temperate were also important. At moderate disturbances, probabilities of self-transitions decreased, while transitions from Boreal to Pioneer, and from Mixed to Temperate increased the most. Transitions from Mixed and Temperate

to Pioneer did not increase much at moderate disturbances, likely because such disturbances were less frequent and less severe than in Boreal forests. The difference between natural disturbances and logging was conspicuous only for major disturbances. For both types of major disturbances, the transition probabilities to Pioneer showed a great increase compared to moderate disturbances, but these values exploded in the major logging transition matrix, exceeding self-transitions.

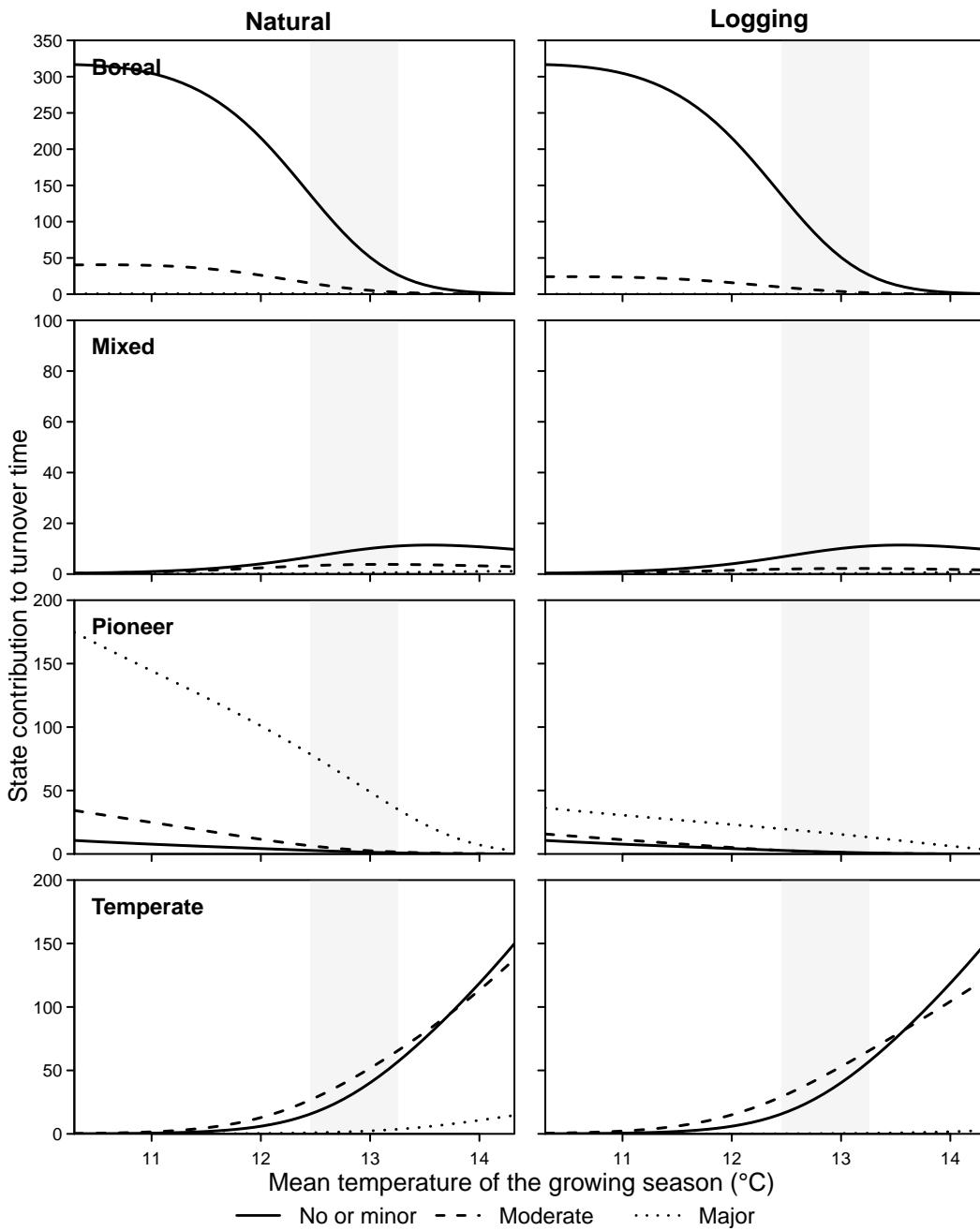


Figure B.8. State contribution to forest turnover (see Fig. 2.7a,b in main text) along the temperature (latitudinal) gradient for different disturbance scenarios : minor (solid), moderate (dashed) and major (dotted) disturbances for both natural (a,c,e) and logging (b,d,f). All other covariates are fixed at the average conditions found in the ecotone, i.e. the balsam fir-yellow birch domain, to focus solely on the effect of disturbances along the temperature gradient. The turnover time of a state (or sojourn time) measures the time spent in this state before transitioning to the next. Long turnover time can translate to large resistance. Here, at any point along the gradient, state turnover time is scaled by the steady state distribution and the sum of all scaled state turnover gives the the turnover time of the transition matrix. The colours at the top of the plots approximate the position of the bioclimatic domains.

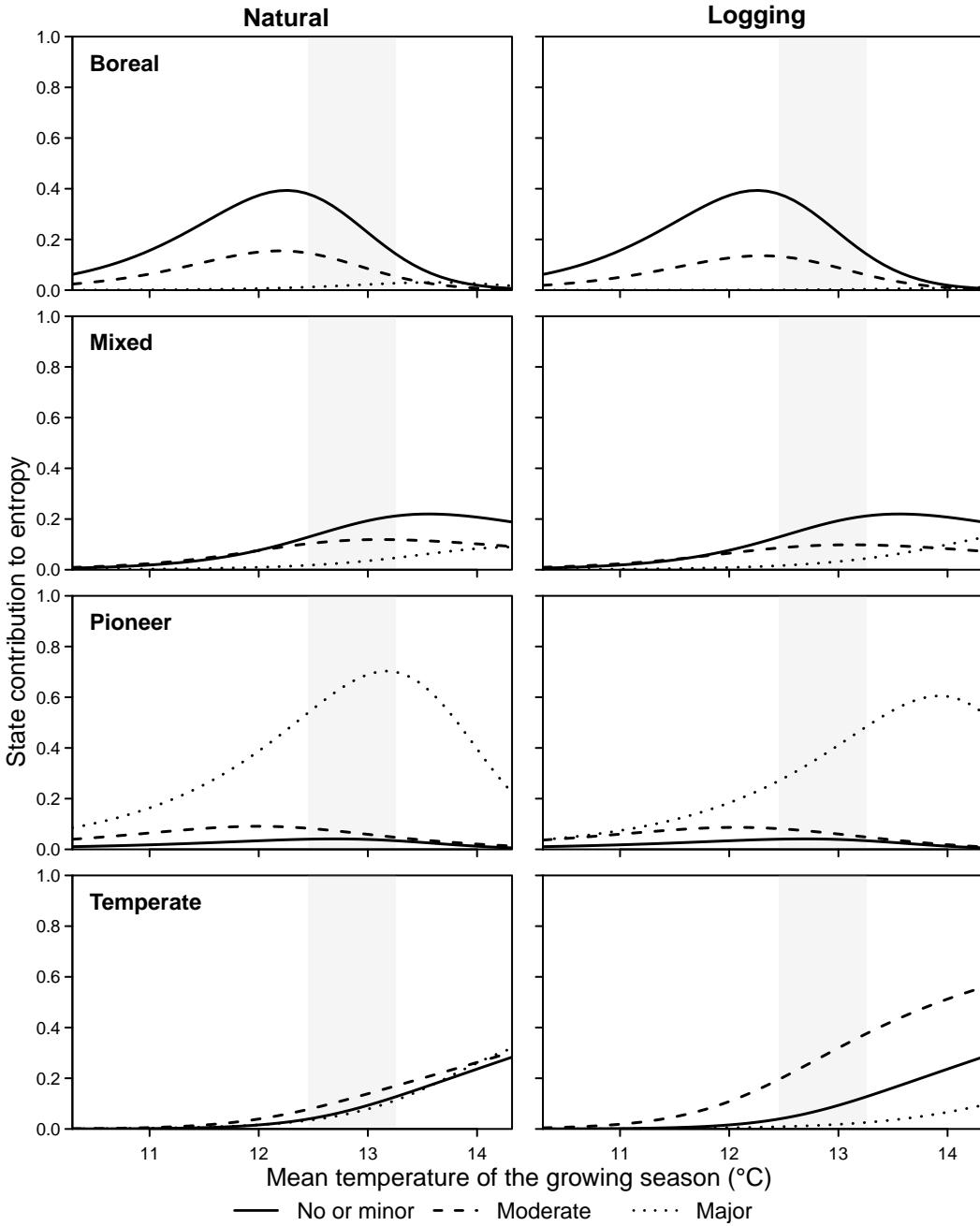


Figure B.9. State contribution to forest entropy (see Fig. 2.7c,d in main text) along the temperature (latitudinal) gradient for different disturbance scenarios : minor (solid), moderate (dashed) and major (dotted) disturbances for both natural (a,c,e) and logging (b,d,f). All other covariates are fixed at the average conditions found in the ecotone, i.e. the balsam fir-yellow birch domain, to focus solely on the effect of disturbances along the temperature gradient. The entropy of a state measures the incertitude of its next transition. Here, at any point along the gradient, state entropy is scaled by the steady state distribution and the sum of all scaled state entropy gives the the entropy of the transition matrix. The colours at the top of the plots approximate the position of the bioclimatic domains.

Annexe C

Northern range shifts of temperate tree saplings in Québec : the role of climate, stand composition, soils and disturbances on recruitment dynamics.

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C.1. Supplementary Table

Tableau C.1. List of R packages used.

Main Packages functions	Uses	References	
countreg	hurdle rootogram zerotrunc	Hurdle model for count data Evaluate model goodness-of-fit Zero-Truncated model for count data	Zeileis <i>et al.</i> (2008)
adespatial	TBI	Paired sample compositional dissimilarity	Legendre (2019)
lmtest	lrtest	Likelihood Ratio Test of Nested Models	Zeileis et Hothorn (2002)
sf		Manipulation and mapping of spatial data	Pebesma (2018)

C.2. Supplementary Figures

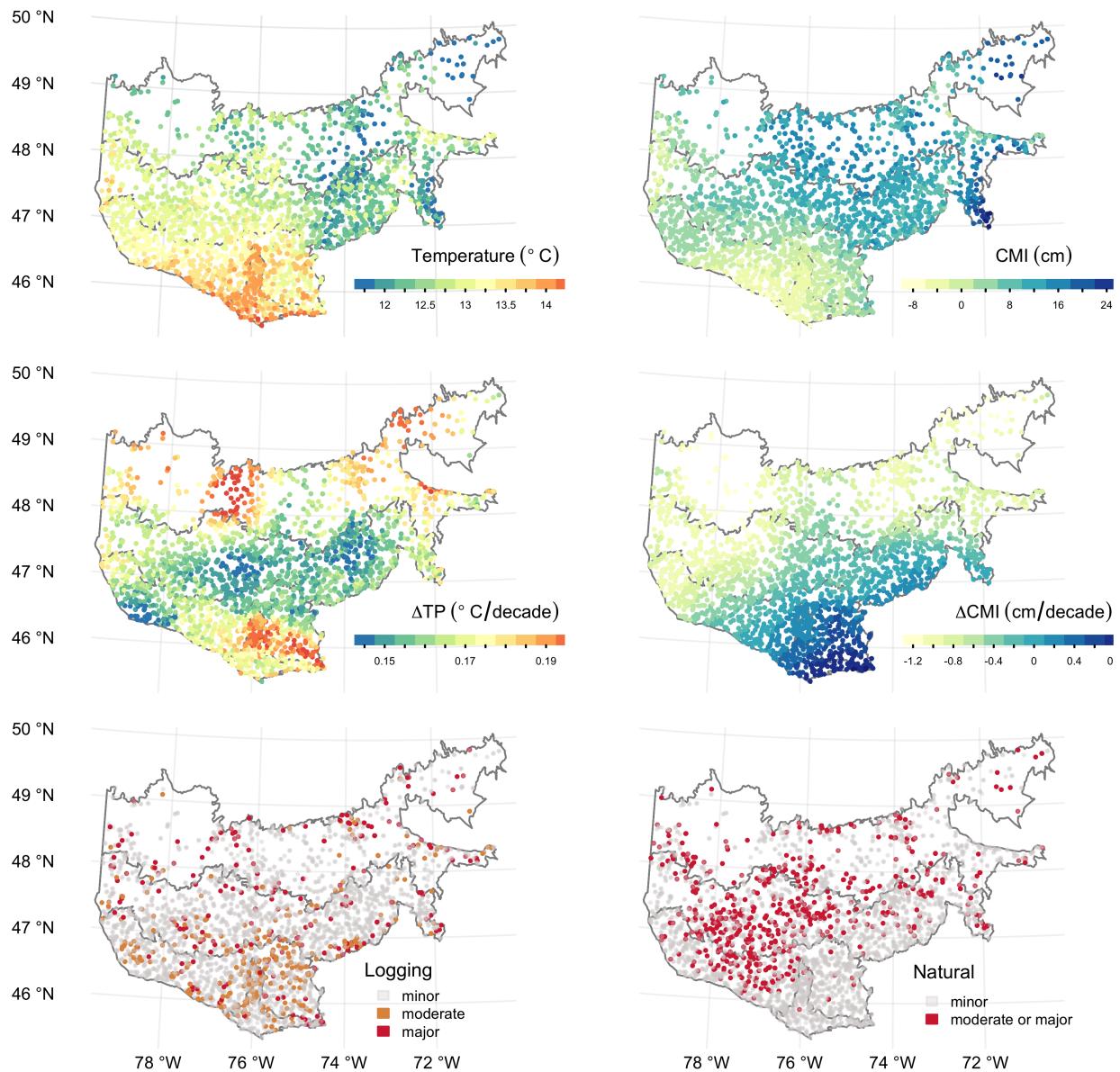


Figure C.1. Maps showing the spatial variation of selected predictor variables.

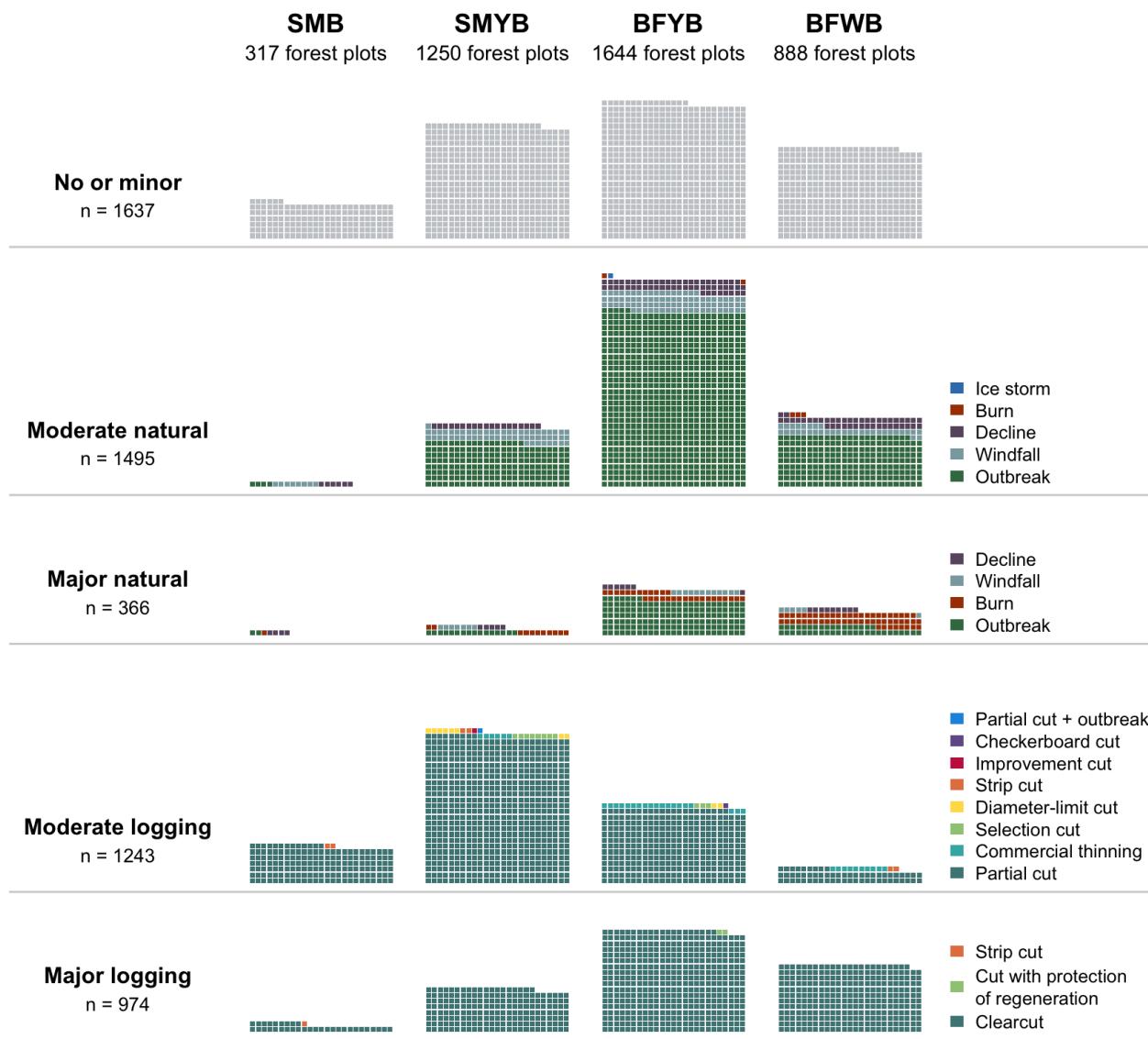


Figure C.2. Waffle charts representing the frequency of forest plots by disturbance type (natural disturbances and logging), level of severity (minor, moderate, major) and studied bioclimatic domains (Sugar maple-Basswood, SMB ; Sugar maple-yellow birch, SMYB ; Balsam fir-yellow birch, BFYB ; Balsam fir-white birch, BFWB). One square is one observation of a disturbance in a forest plot (a forest plot can be disturbed more than once). In each chart (except for the no or minor disturbances), the colours represent the 21 original disturbance types recorded in the field surveys.

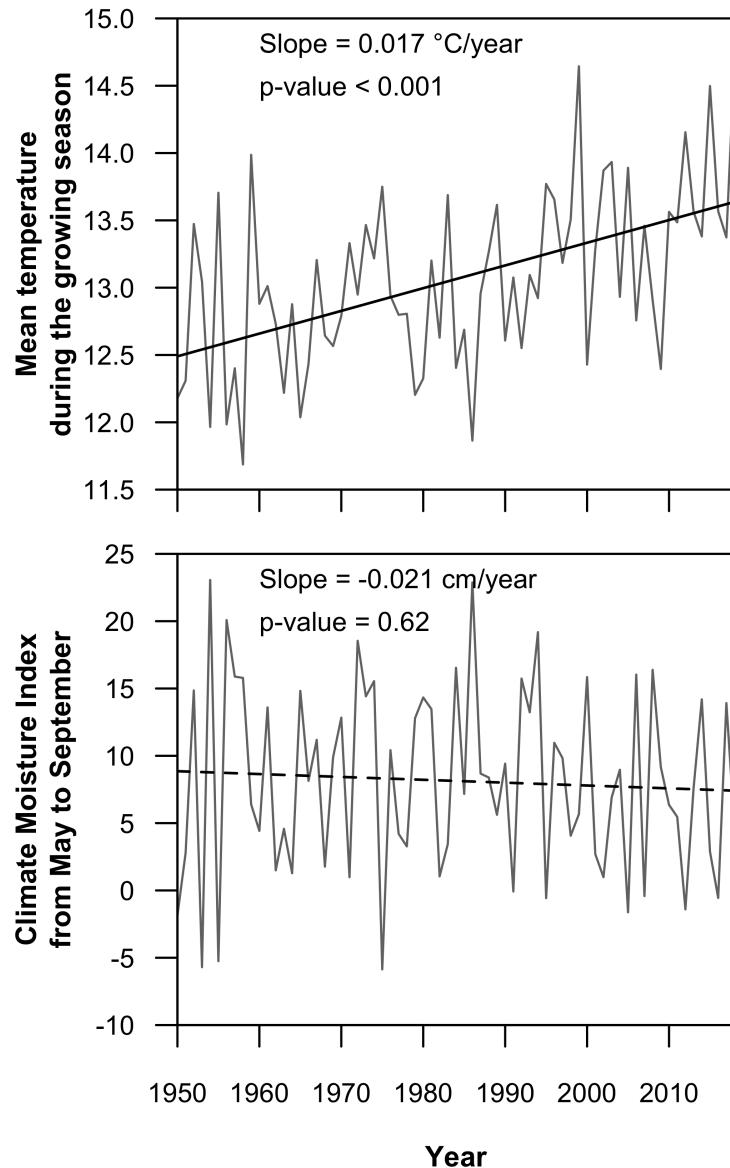


Figure C.3. Temporal trends in growing season temperatures (top) and annual climate moisture index (bottom). Grey lines represent averaged climate values across the 4099 studied forest plots. Straight black lines show the fitted least-squared linear regression lines (dashed line : non-significant relationship).

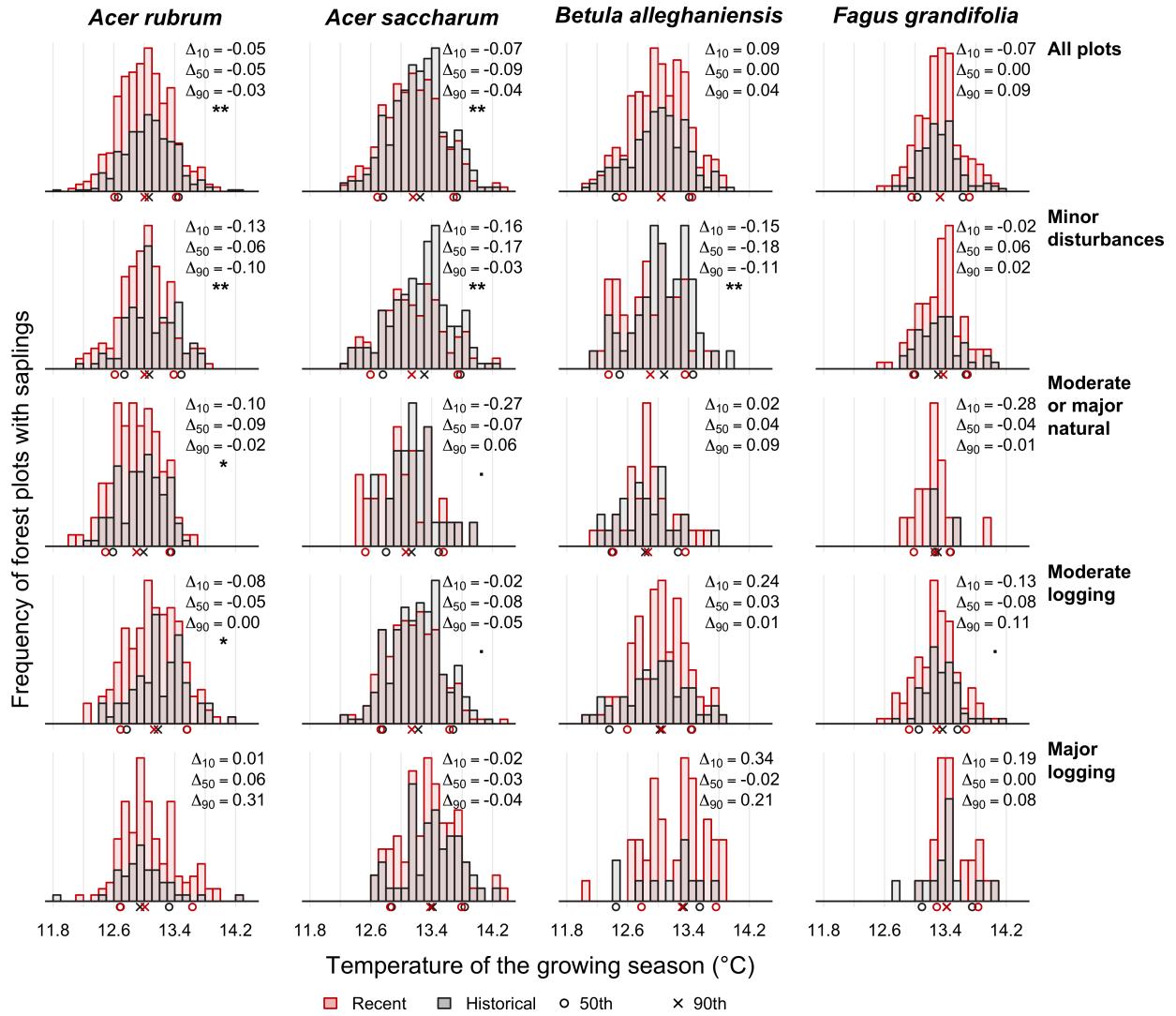


Figure C.4. Frequency distributions of forest plots containing saplings of each of the four species (column headings), as a function of the growing season temperature (abscissa), in the historical (1970–1981; in grey) and the recent (2005–2018; in red) surveys. To assess shift in sapling distributions, we used the mean temperature of the growing season of the historical period. From top to bottom, distribution of all forest plots combined (first row); plots that have experienced minor disturbances (second row); moderate or major natural disturbances (but no logging; third row); moderate logging (but no natural disturbances; fourth row); and major logging (but no natural disturbances; fifth row). The Δ_{10} , Δ_{50} and Δ_{90} indicate the shifts in °C for the 10th, 50th (median) and 90th percentiles, respectively, of the altitudinal distribution between the two time periods. A shift of the distribution to the right indicate a shift toward lower temperature, hence to the north. The stars correspond to P -value from Wilcoxon tests comparing the median locations between the historical and recent distributions (. $P \leq 0.10$, * $P \leq 0.05$, ** $P \leq 0.01$, *** $P \leq 0.001$).

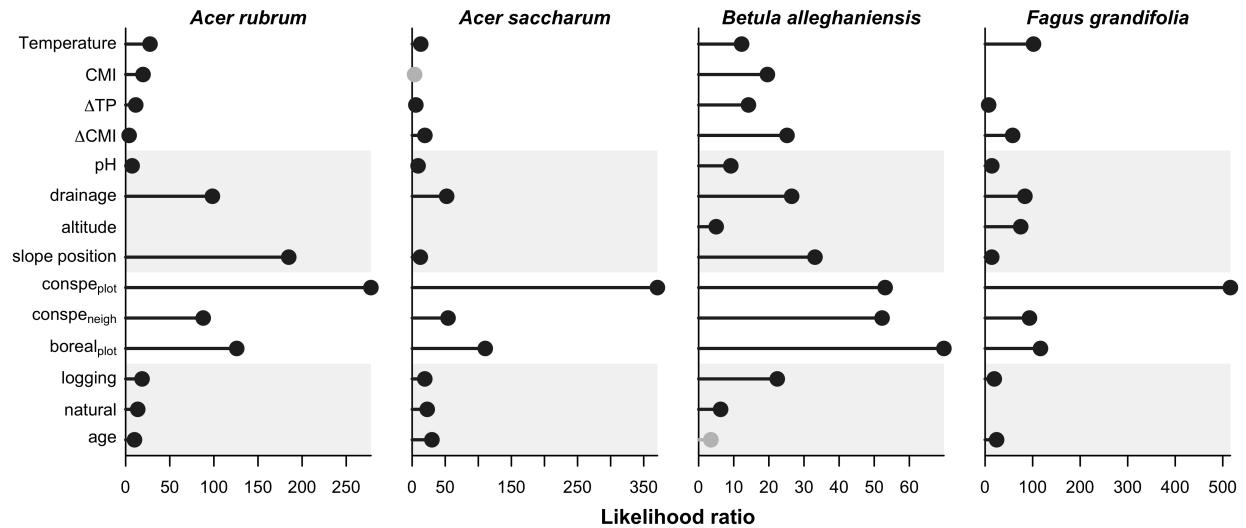


Figure C.5. Variable importance measured by the change in likelihood ratio after their removal from the full hurdle model. Black bars indicate significant predictors and grey ones are not significant according to the likelihood ratio tests.

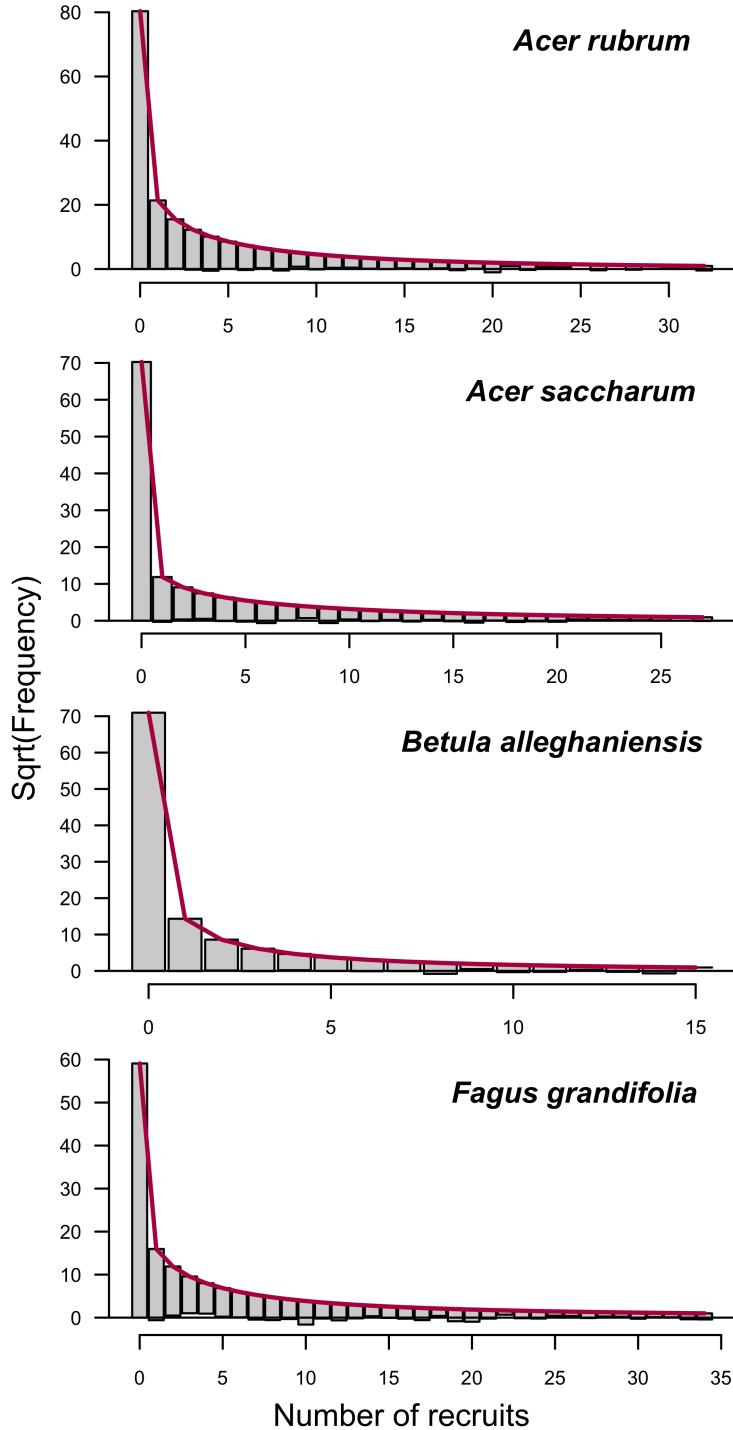


Figure C.6. Diagnostic plots for the hurdle models of sapling recruitment for each of the four temperate tree species. Rootograms (Kleiber *et al.* 2016) comparing the observed and predicted counts of tree saplings. On the x -axis are the count bins ($0, 1, 2, \dots$) and on the y -axis are the square root of the observed or predicted counts. The red curve represents the square root of predicted counts. The bars are the square root of observed counts and they are hanging from the predicted curve; a bar that does not reach the zero line indicate that the model overestimates a particular count bin, and a bar that exceeds the zero line indicate underestimation of sapling counts.