

**Université de Montréal**

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

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

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## Résumé

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...sommaire et mots clés en français...



## **Abstract**

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...summary and keywords in english...



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## Liste des sigles et des abréviations

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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>

## **Remerciements**

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...remerciements...



# **Introduction**

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

L'Homme est aujourd'hui une force prédominante gouvernant les processus écologiques amenant de nombreux chercheurs à suggérer que le système terrestre a basculé dans une nouvelle ère géologique, l'Anthropocène (Crutzen, 2002). Depuis environ un siècle, les activités humaines ont largement perturbé l'équilibre dynamique des cycles naturels. Au cours du siècle dernier, les températures ont augmenté d'environ 1°C et, selon les projections, le 21e siècle assistera à des changements climatiques sans précédent (IPCC, 2014). Avec les changements climatiques, les changements d'utilisation du territoire et la surexploitation des ressources associés à la dégradation et la perte des habitats comptent parmi les plus grandes menaces actuelles pour la biodiversité (IPBES, 2019). 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 peuvent continuer à apparaître sur plusieurs décennies (Bender *et al.*, 1984). 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. 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). L'ampleur, la vitesse et l'intensité de ces menaces mondiales soulignent la nécessité de développer de nouveaux outils d'analyse pour quantifier et détecter 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. Changements climatiques**

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<sub>2</sub>) 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 (entre 1990 et 2014) sur l'état des connaissances relatives au changement climatique. 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<sup>e</sup> 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.*, 2015).

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

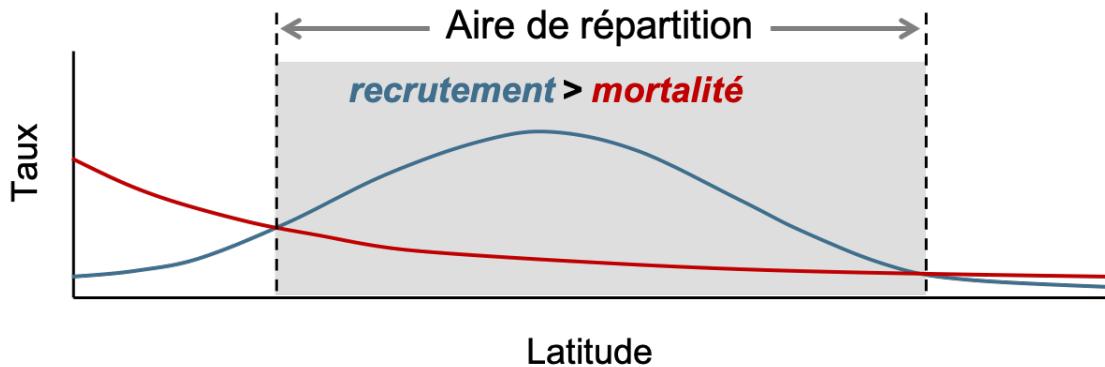
considérables sur les fonctions et les services rendus par les écosystèmes forestiers, tels que le stockage du carbone, le cycle des nutriments, la purification de l'air et de l'eau et le maintien d'habitats pour la faune et la flore (Mitchell *et al.*, 2013; Mori *et al.*, 2017). Ces changements soulèvent 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 de ces changements climatiques sur les écosystèmes forestiers représente donc l'un des grands défis actuels pour la communauté scientifique (Pereira *et al.*, 2010; Garcia *et al.*, 2014).

### 0.3. Distributions géographiques des espèces et niche écologique

L'étude des facteurs qui influencent la distribution des espèces a une longue histoire en écologie (MacArthur, 1972). 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 (Soberón, 2007; Godsoe, 2010), 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 (Maguire 1973 ; Hutchinson 1978). La répartition géographique d'une espèce peut donc refléter la variation spatiale de  $r$  (Fig. 0.1 ; Holt *et al.*, 2005).

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).



**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 surpasse 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).

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). Différents aspects de la dynamique de la métacommunauté peuvent être capturés par quatre grands paradigmes (*species sorting, mass effect, patch dynamic, neutral*; Leibold *et al.*, 2004). Toutes les espèces du pool régional (diversité  $\gamma$ ) sont susceptibles de coloniser les communautés locales. Premièrement, tel que décrit précédemment, la diversité des communautés locales (diversité  $\alpha$ ) peut être influencée par les conditions environnementales et les interactions qui déterminent quelles espèces peuvent survivre localement selon leurs traits (*species sorting*, théorie des niches). Deuxièmement, les espèces d'une communauté “puit” où les conditions sont défavorables peuvent aussi être maintenues par la dispersion répétée d'individus provenant d'une autre communauté “source” (*mass effect*, dynamique source-puit). Cette dynamique source-puit peut donner lieu à des communautés qui contiennent des espèces qui ne sont pas toujours adaptées de manière optimale aux conditions locales. Troisièmement, l'assemblage de la communauté peut être déterminé par une dynamique d'extinction-colonisation à l'échelle régionale (*patch dynamic*), où des extinctions stochastiques permettent de rendre les “patches” disponibles à la colonisation. La diversité locale résulte alors d'un compromis entre les capacités de colonisation et de compétition des espèces sans égard aux conditions locales. Finalement, la communauté peut

être un échantillon aléatoire des espèces du pool régional et ne dépendre que d'événements démographiques et de dispersion stochastiques (théorie neutre).

Le concept de métacommunauté décrit donc un continuum de processus de dynamique d'assemblage de la communauté qui diffèrent sur la base de l'importance relative de la dispersion des espèces, de l'hétérogénéité d'habitat et de l'équivalence entre les espèces selon leur niche écologique et leurs traits (Logue *et al.*, 2011). Ainsi, l'importance relative de ces quatre différents processus influencera la dissimilarité entre les communautés (diversité  $\beta$ ). Alors qu'une grande hétérogénéité environnementale augmente la diversité  $\beta$ , un haut taux de dispersion homogénéise les communautés.

Les perturbations peuvent exercer une influence majeure sur les quatre processus d'assemblage des communautés (Chase, 2005) et sont ainsi un élément clé permettant la co-existence 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 ou les changements climatiques). Selon les cas, les perturbations peuvent libérer des "patches" d'habitat les rendant disponibles pour la colonisation ou encore fragmenter les habitats diminuant ainsi leur connectivité 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, la diversité locale est souvent maximisée à des niveaux intermédiaires de perturbation (Wilkinson, 1999; Connell, 1978; Hastings, 1980) ; 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 l'hypothèse traditionnelle était que leur influence sur la distribution des espèces est spatialement hiérarchisée (Pearson et Dawson, 2003; Diez et Pulliam, 2007). 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 (McGill, 2010; Gotelli *et al.*, 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 à drainage très mauvais ou excessif (Burns et Honkala, 1990).

Mes questions de recherches sont 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 des changements climatiques, complexifiant ainsi les signaux de réponse.

## 0.4. Réponses des communautés forestières aux changements climatiques

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.

### 0.4.1. 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.*, 2015). 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 (van Mantgem *et al.*, 2009; Peng *et al.*, 2011). 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 (van Mantgem *et al.*, 2009; Stephenson *et al.*, 2011).

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 (Sittaro *et al.*, 2017; Boisvert-Marsh *et al.*, 2014; Fisichelli *et al.*, 2014). De façon plus générale, 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 (Fisichelli *et al.*, 2014; Boisvert-Marsh *et al.*, 2019; Grundmann *et al.*, 2011; Bolte *et al.*, 2010). 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 (Peng *et al.*, 2011; Goldblum et Rigg, 2005; Grundmann *et al.*, 2011; Bolte *et al.*, 2010). 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 coniférière à mixte, puis de mixte à feuillue (Fig. 0.2; Boulanger *et al.*, 2019; Price *et al.*, 2013; Chen, 2002; Lindner *et al.*, 2010).



**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.

#### 0.4.2. 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 (Parmesan et Yohe, 2003; Walther *et al.*, 2002; Chen *et al.*, 2011), particulièrement dans les zones de transition où les changements sont plus facilement détectables (Jump *et al.*, 2009; Boulanger *et al.*, 2017). 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; Lenoir *et al.*, 2008; Savage et Vellend, 2015; Kapralov *et al.*, 2006; Gottfried *et al.*, 2012), 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; Fisichelli *et al.*, 2014; Sittaro *et al.*, 2017; Chen *et al.*, 2011; Lindner *et al.*, 2010). 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 présentant une réponse plus rapide que les arbres adultes.

#### 0.4.3. 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 (VanDerWal *et al.*, 2013; Fei *et al.*, 2017). 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  $\alpha$ ) 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  $\beta$ ; McGill *et al.*, 2015; Dornelas *et al.*, 2014). Ces grands remaniements d'espèces pourraient même donner lieu à des associations d'espèces inédites (*no-analog communities*; Williams et Jackson, 2007). Ainsi, en mettant l'accent sur les limites d'aires de répartition, il est possible que l'empreinte des changements climatiques 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, les changements climatiques pourraient transformer la toundra sans arbres en forêt boréale (Danby et Hik, 2007; Kapralov *et al.*, 2006), les forêts tropicales en savane (Hirota *et al.*, 2011) ou les forêts de conifères en forêts de feuillus (Fig. 0.2 ; Boulanger *et al.*, 2019; 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 (Esquivel-Muelbert *et al.*, 2018; Danneyrolles *et al.*, 2019; 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.

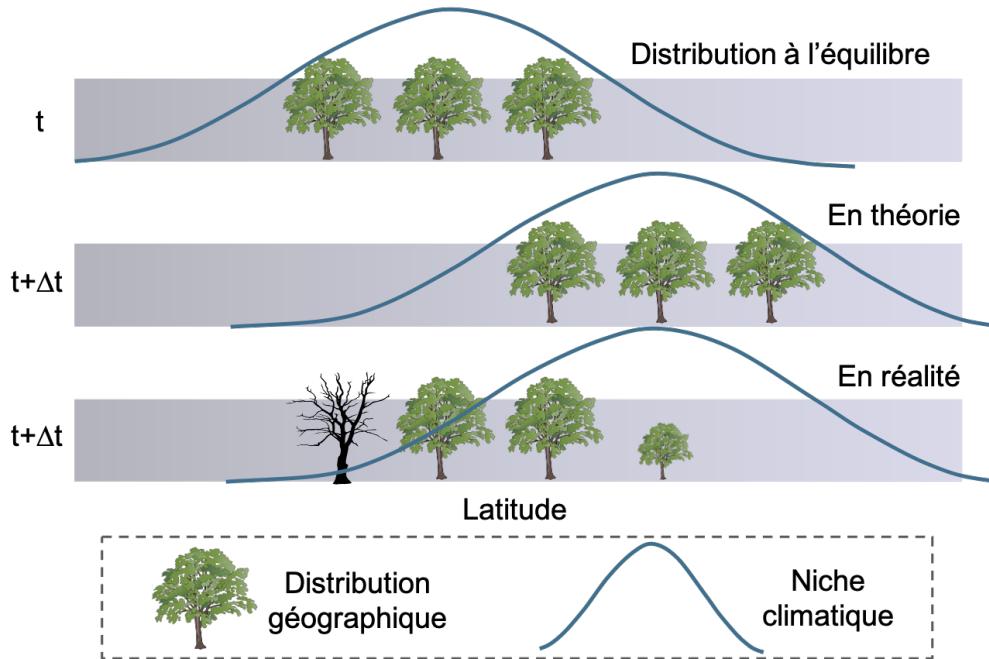
## 0.5. Délais de réponse et déséquilibre

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 ; Zhu *et al.*, 2012; Woodall *et al.*, 2013; Vissault, 2016; Sittaro *et al.*, 2017; Bertrand *et al.*, 2011). 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 des changements climatiques récents (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 (Malcolm *et al.*, 2002; Iverson *et al.*, 2008), 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 aux changements climatiques 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 (Vanderwel et Purves, 2014; Renwick et Rocca, 2015).



**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.

## 0.6. Interaction changements climatiques et 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 (REF ?; Keane *et al.*, 2013; Gauthier *et al.*, 2015; Bergeron *et al.*, 2017; Boulanger *et al.*, 2017). De plus, les forêts sont également soumises à d'importantes pressions anthropiques, tout particulièrement les activités d'exploitation forestière. Depuis plus d'un siècle, les coupes forestières viennent s'ajouter et même se substituer aux perturbations naturelles pour créer un tout nouveau régime de perturbation (Vitousek *et al.* 1997; Frelich 2002).

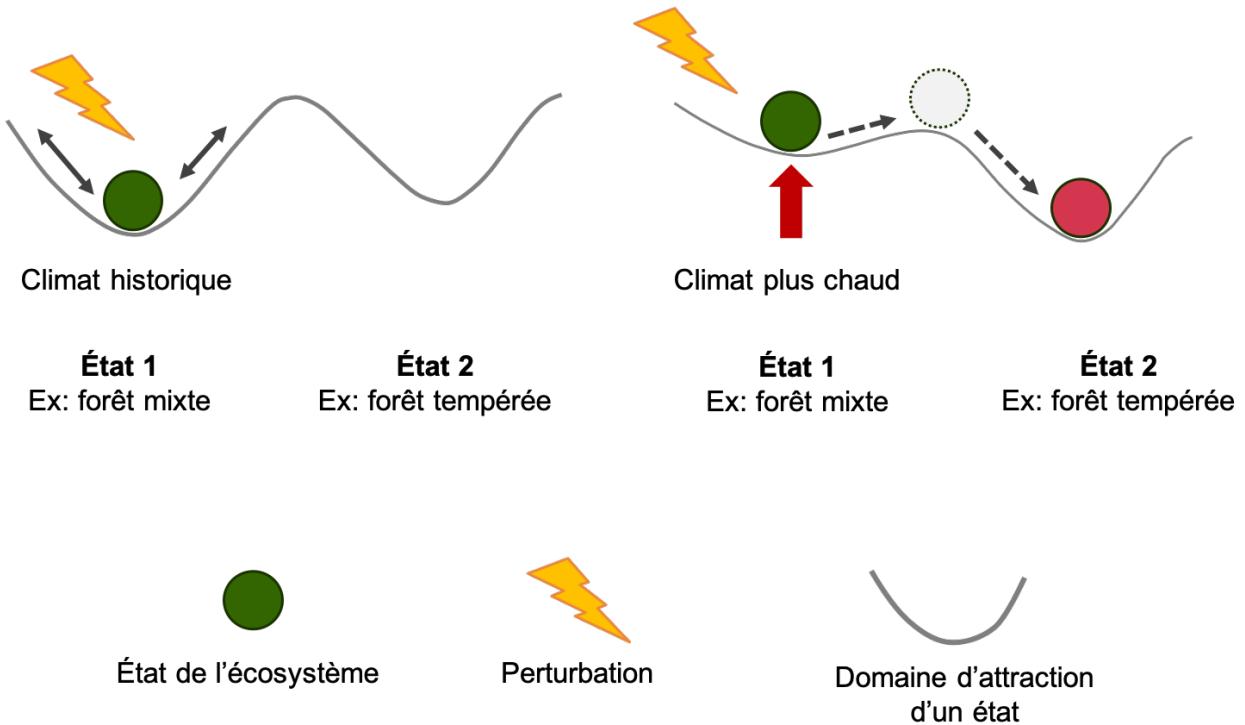
Les perturbations naturelles comme les feux, les épidémies d'insectes, les chablis ou les inondations font partie intégrante de la dynamique des forêts (Attiwill, 1994; Johnstone *et al.*, 2016). Les perturbations éliminent partiellement ou totalement la végétation en place,

rendent disponibles les ressources (e.g., nutriments, lumière), créent des espaces vacants pour la colonisation et peuvent mélanger 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 [REF]. 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 [REF]. Les régimes de perturbations naturelles varient considérablement entre les différents biomes forestiers (Goldblum et Rigg, 2010; Chen et Popadiouk, 2002; 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). De plus, les régimes de perturbations naturelles sont sensibles au climat (Seidl *et al.*, 2020). Ces perturbations se sont déjà intensifiées au cours des dernières décennies (Seidl *et al.*, 2017).

L'exploitation forestière diffère grandement des perturbations naturelles en termes de sévérité, de fréquence, de sélectivité et d'étendue spatiale (Boucher *et al.*, 2006; Schulte *et al.*, 2007; Kuuluvainen, 2009), 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 les paysages forestiers, à simplifier leur structure et à modifier leur composition (Schulte *et al.*, 2007; Boucher *et al.*, 2006; Boucher et Grondin, 2012; McRae *et al.*, 2001; Cyr *et al.*, 2009). 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).

Les perturbations, autant naturelles qu'anthropiques, pourraient moduler la vitesse de réponse des forêts aux changements climatiques. Alors que le changement climatique modifie lentement l'équilibre compétitif entre les espèces, les perturbations diminuent ou éliminent la compétition par les espèces résidentes et créent ainsi des opportunités de colonisation pour les espèces migratrices (Xu *et al.*, 2012; Woodall *et al.*, 2013; Vanderwel et Purves, 2014).

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; *alternative stable state*; Johnstone *et al.*, 2016; Renwick et Rocca, 2015; Turner, 2010). Dans l'écotone boréal-tempéré, les perturbations pourraient potentiellement faciliter le recrutement et l'établissement des espèces tempérées dans les peuplements mixtes et boréaux plus au nord et ainsi agir comme des catalyseurs des changements d'aires de répartition. 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, favorisant plutôt l'expansion des espèces pionnières (Vanderwel et Purves, 2014; Liang *et al.*, 2018).



**Figure 0.4.** Représentation schématique du concept d'états alternatifs stables. 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 cœur 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 aux futurs changements climatiques 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 des changements climatiques 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 les changements climatiques et pour élaborer des stratégies de gestion forestière permettant un aménagement durable des forêts.

## 0.7. Contraintes à la migration

Malgré l'empreinte indéniable des changements climatiques, 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 les changements climatiques 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 les changements climatiques, 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 (Lafleur *et al.*, 2010; Brown et Vellend, 2014; Collin *et al.*, 2017; Carteron *et al.*, 2020; 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 (Fisichelli *et al.*, 2014; Barras et Kellman, 1998; 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 microorganismes 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'érythrina 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.

## 0.8. Problématique et enjeux

La question des effets des changements climatiques 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 des changements climatiques, 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 (Duveneck et Scheller, 2016; Boulanger *et al.*, 2019).

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 des changements climatiques. 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 (Périé et de Blois, 2016; Berteaux, 2014). 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 des changements climatiques 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.

## 0.9. Objectifs et structure de la thèse

La question au coeur de cette thèse est : quel est l'effet combiné des changements climatiques récents 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 *Données*, plus bas).

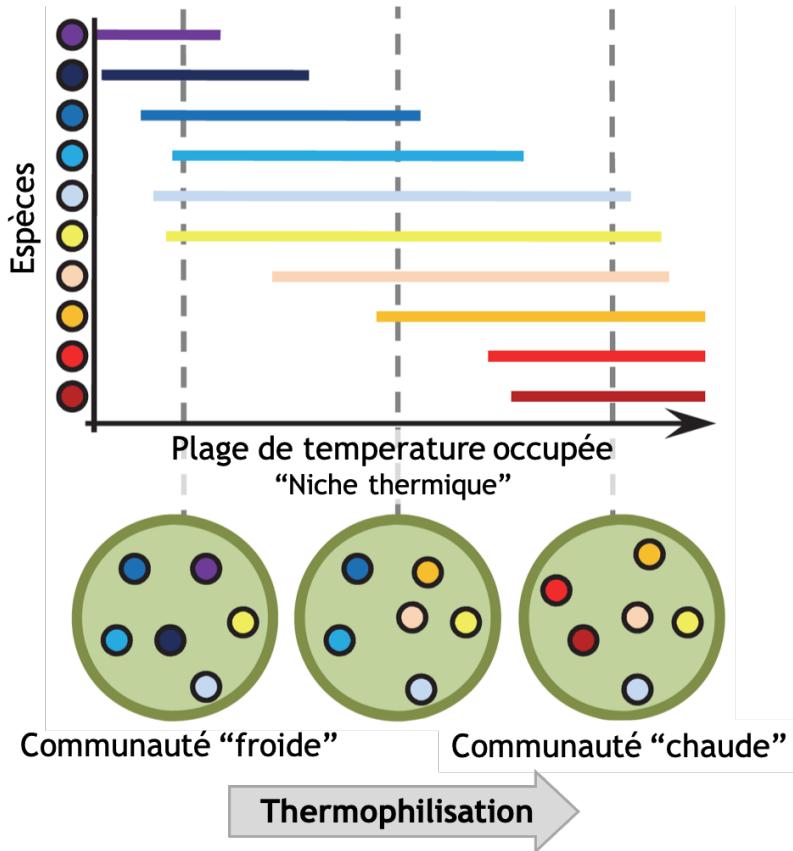
### 0.9.1. Chapitre 1 — Les perturbations amplifient les réponses des communautés forestières au changement climatique dans l'écotone tempéré-boréal

L'objectif du premier chapitre (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  $\beta$  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  $\beta$  temporelle ont été évalués à l'aide de régressions multiples et de partitionnement des variations.

Afin de discerner les effets des changements climatiques 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.



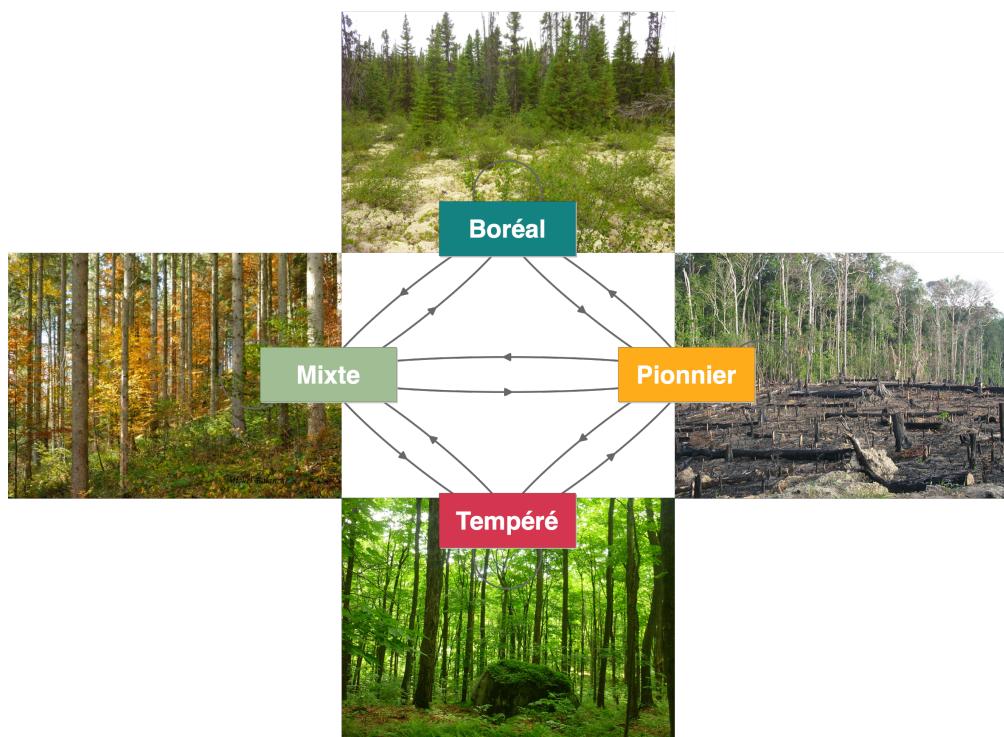
**Figure 0.5.** Représentation schématique du processus de thermophilisation des communautés. Les espèces (cercles de couleur) du pool régional se distribuent le long d'un gradient de température (les bars représentent leur distribution dans l'espace ou leur niche thermique). Les espèces adaptées au 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).

### 0.9.2. Chapitre 2 — Les perturbations modérées accélèrent la dynamique de transition forestière sous l'effet du changement climatique dans l'écotone tempéré-boréal de l'est de l'Amérique du Nord

Dans le chapitre 2 (Brice et al. accepté), 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 (Wootton, 2001; Vissault, 2016) 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.



**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.

### **0.9.3. Chapitre 3 — Tendances et moteurs du recrutement des espèces d'arbres tempérées à leur limite nord**

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.

Dans un premier temps, j'ai comparé la composition entre les arbres et les gaules entre deux périodes d'inventaire (1970-1981 et 2005-2018) pour évaluer si la composition de la régénération s'éloigne de la composition la canopée au fil du temps. Ensuite, les changements de la limite de la répartition latitudinale et altitudinale des gaules ont été comparés entre les différents niveaux de perturbations pour déterminer si les perturbations peuvent accélérer les migrations climatiques.

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 régénérations, des différences importantes pourraient être masquées. En comparant les changements de limite latitudinale ou altitudinale entre les niveaux de perturbations, on peut déterminer si les perturbations peuvent promouvoir ou freiner de nouveaux recrutements au-delà des limites de l'aire de répartition (Woodall *et al.*, 2013).

Et 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).

### **0.9.4. Chapitre 5 — Conclusion**

Dans ce dernier chapitre, je résume mes conclusions et mes nouvelles orientations de recherche. Pris ensemble, les trois chapitres principaux de la thèse fournissent un éventail complémentaire de méthodes et d'approches récentes et nouvelles pour mieux comprendre

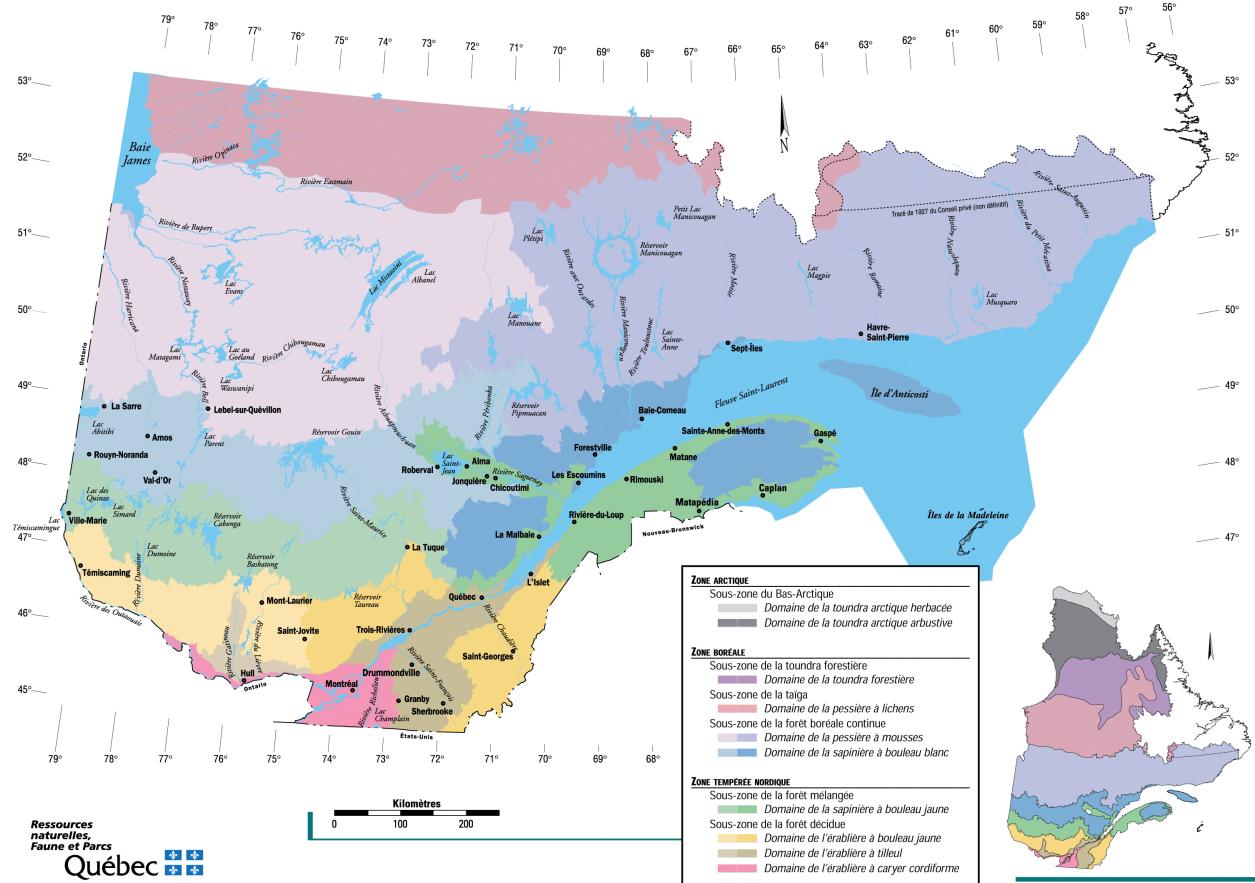
l'effet combiné des changements climatiques et des perturbations sur la dynamique forestière. En accordant une attention particulière aux différents aspects des variations de la diversité et de la composition des communautés forestières, cette thèse apporte des perspectives originales et révèle des changements 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.

### 0.9.5. Données

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 aux changements climatiques, 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 km<sup>2</sup> 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.

# Chapitre 1

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**Les perturbations amplifient les réponses des communautés forestières au changement climatique dans l'écotone tempéré-boréal**



## First Article.

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

by

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**Author contributions** MHB designed the study and performed the analyses with feedback from the other authors. MHB wrote the first and second drafts. All authors substantially contributed to the final version of the manuscript.

## 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  $\beta$  diversity, gains and losses. The effects of climate and disturbances on temporal  $\beta$  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  $\beta$  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; Savage et Vellend, 2015; Lenoir *et al.*, 2008), where ecotones are narrow and well-defined (Jump *et al.*, 2009). Similar evidence is also beginning to emerge for latitudinal shifts (Fisichelli *et al.*, 2014; Sittaro *et al.*, 2017; Boisvert-Marsh *et al.*, 2019). 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 (Talluto *et al.*, 2017; Svenning et Sandel, 2013). 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 (Xu *et al.*, 2012; Vanderwel et Purves, 2014; Leithead *et al.*, 2010; Boisvert-Marsh *et al.*, 2019). 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 (Savage et Vellend, 2015; De Frenne *et al.*, 2013). Conversely, disturbances should increase the prevalence of young forests dominated by shade-intolerant species (Savage et Vellend, 2015; Boucher et Grondin, 2012). 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 (Violle *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 (Devictor *et al.*, 2008; Gaüzère *et al.*, 2015; De Frenne *et al.*, 2013; Feeley *et al.*, 2013; Becker-Scarpitta *et al.*, 2019; Cheung *et al.*, 2013; Danneyrolles *et al.*, 2019). 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  $\beta$  diversity (Legendre, 2019) over 6000 resurveyed communities between a historical (1970–1980) and a contemporary (2000–2016) period. Temporal  $\beta$  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  $\beta$  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.

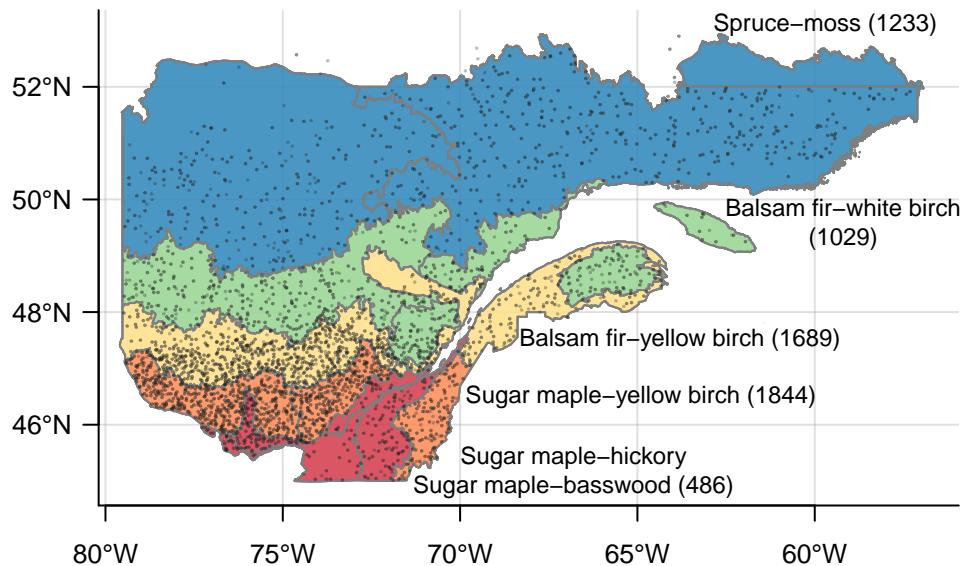
## 2. Methods

### 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 52<sup>nd</sup> 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 ( $400\text{ m}^2$ ), 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  $2\text{ km}^2$  (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. ??).

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. ??). 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.

**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
<b>Baseline conditions</b>	
Temp, Temp <sup>2</sup>	Mean temperature during growing season and its second order polynomial. 10-year average prior to first survey of each plot (°C).
Precip, Precip <sup>2</sup>	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).
<b>Climate change</b>	
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).

Variable name	Variable description
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.
<b>Disturbances</b>	
Age	Stand age (years).
Old harvest	Tree harvesting (clearcutting, partial cutting, selection cutting, etc.) that occurred before the study period. 1. 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).

## 2.3. Analysis

2.3.1.  $\beta$  diversity. For each plot, we computed temporal  $\beta$  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 ( $\beta$ ) was computed using the Ružička coefficient (Fig. ??):

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

$A = \sum_{j=1}^n a_j$  : 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  $\beta$  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. ??). Throughout this paper, gains and losses refer to these relative metrics.

This additive framework allowed us to partition further the different components contributing to  $\beta$  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,  $\beta$  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  $\beta$ , 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 ( $\beta$ , 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  $\beta$ , gains and losses, for each of the three subsets. We also tested relevant interactions between disturbance and climate predictors: Natural (old and recent)  $\times \Delta\text{CMI}$  and Natural (old and recent)  $\times \Delta\text{Temp}$ , because drought and heat stress can increase natural disturbance frequency; Harvest (old and recent)  $\times \Delta\text{Temp}$ , 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  $\alpha$  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

10<sup>th</sup> 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 km<sup>2</sup>, available online <http://worldclim.org/version2>; Fick et Hijmans, 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 10<sup>th</sup> and 90<sup>th</sup> 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 10<sup>th</sup> and 90<sup>th</sup> 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  $\Delta CTI$  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  $\Delta CTI$  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  $\Delta CTI$  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  $\Delta$ CTI by averaging their contributions for plots where they increased and where they decreased.

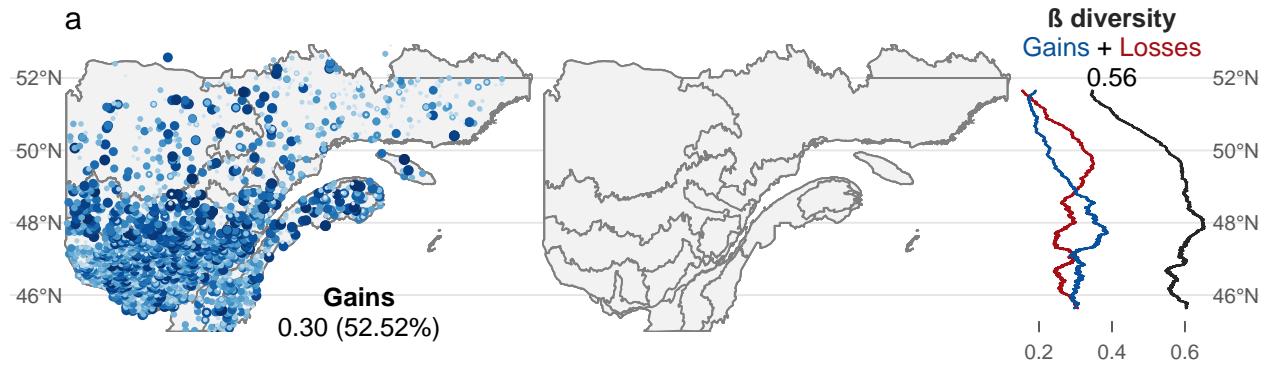
To test the hypothesis that community changes are resulting from post-disturbance succession, we collected traits about species shade tolerance (Species Shade Index, SSI; Niinemets et Valladares, 2006), which represents a species ability to grow in shade conditions. Shade tolerance indices ranged from 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,  $\Delta$ CSI, was computed in the same way as for  $\Delta$ 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 $\beta$ diversity

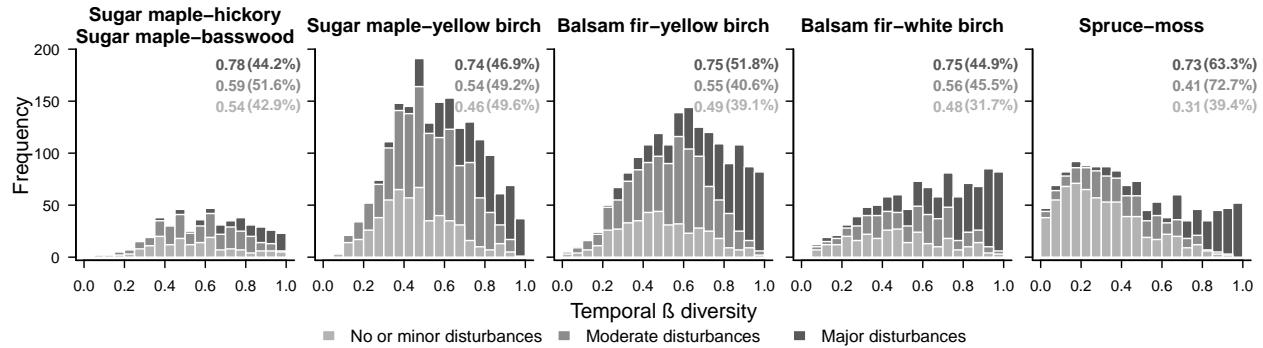
The mean temporal  $\beta$  diversity was 0.56 over all sites in the study area ( $n = 6281$ ), and these temporal changes in composition were attributable to slightly more gains in abundances (52.5%) than losses (47.5%; Fig. 1.2a). Temporal  $\beta$  diversity varied along a latitudinal gradient; it 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  $\beta$  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  $\beta$  (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).



**Figure 1.2.** Maps of gains and losses in tree abundances (a) and latitudinal trends in temporal  $\beta$  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  $\beta$  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.

The magnitude of compositional changes in forests was highly influenced by disturbances (Figs 1.2b-d, 1.3, ??). In each domain, the  $\beta$  diversity values of highly disturbed forests are strongly skewed (Fig. 1.3). The mean temporal  $\beta$  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  $\beta$  diversity (Fig. ??).



**Figure 1.3.** Frequency distributions of temporal  $\beta$  diversity in forests 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  $\beta$  diversity values followed by the percentage of losses in parentheses. The distribution of  $\beta$  diversity values is skewed to the right for higher disturbance levels.

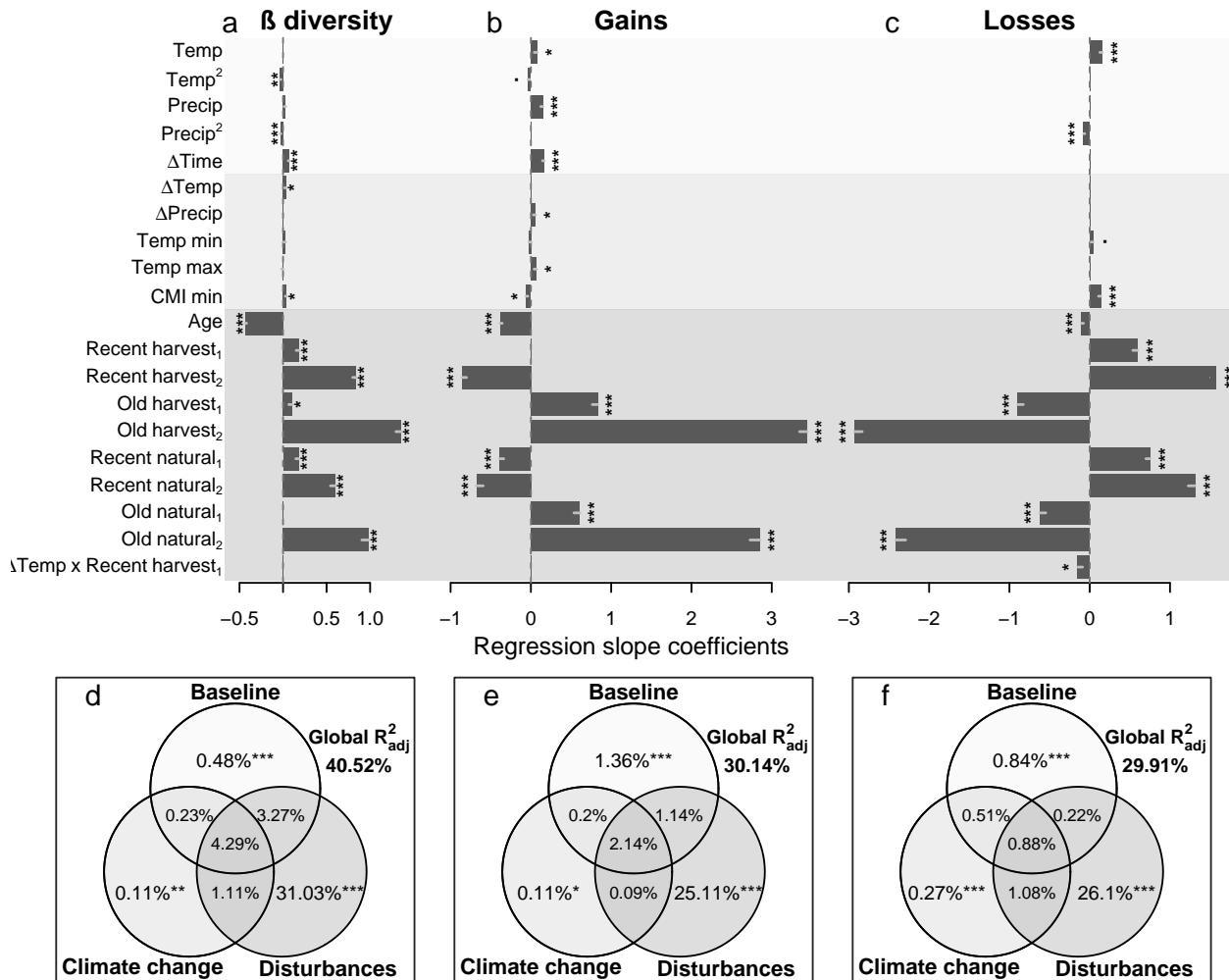
### 3.2. Drivers of temporal changes

Once combined, predictors from the three subsets (baseline, climate change and disturbances; Table 1.1) explained together 40% of the variation of temporal  $\beta$  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  $\beta$ : 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  $\beta$  diversity, with old major harvest (Old harvest<sub>2</sub>) being the most important driver, followed by old major natural disturbances (Old natural<sub>2</sub>; 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 ( $\Delta$ Precip) favoured tree gains. Only one interaction was retained, which indicated that stronger warming ( $\Delta$ Temp) mitigated the effect of recent moderate harvest (Recent harvest<sub>1</sub>) 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 ( $\Delta$ Time) reflects the fact that community change takes time.



**Figure 1.4.** Slope coefficients from multiple regression models for (a) temporal  $\beta$  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

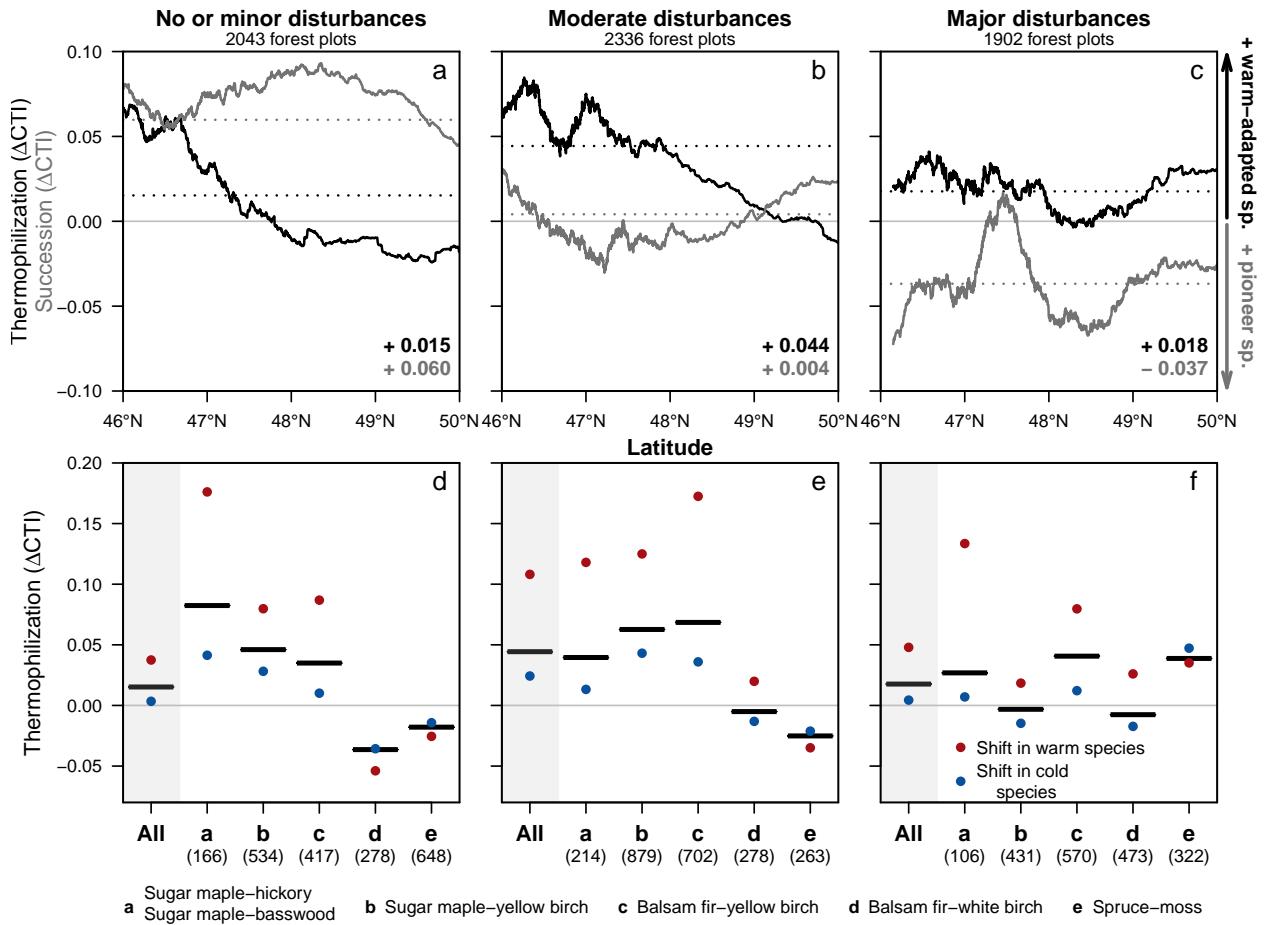
The community temperature index (CTI) increased significantly between the historical and contemporary periods (paired  $t$ -test  $p$ -value  $< 0.001$ ; mean of  $+0.03$  °C/decade for all plots combined, ranging from  $-0.02$  to  $+0.05$  across domains), which indicates a generalised

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  $\Delta\text{CTI}$  at moderate disturbance than at the other levels). Moreover, the latitudinal pattern of  $\Delta\text{CTI}$  varied with the disturbance level: the thermophilization in moderately disturbed forests extended further north than in undisturbed forests, exceeding  $48^{\circ}\text{N}$ , 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  $\Delta\text{CSI}$  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,  $\Delta\text{CTI}$  and  $\Delta\text{CSI}$  were negatively correlated (Pearson  $r = -0.2$ ,  $p\text{-value} < 0.001$ ) indicating that the two ecological processes are intertwined. However,  $\Delta\text{CTI}$  was more strongly correlated to gains in temperate species and losses of boreal species than to gains in pioneer species (Fig. ??), which suggests that thermophilization was not trivially driven by successional processes.

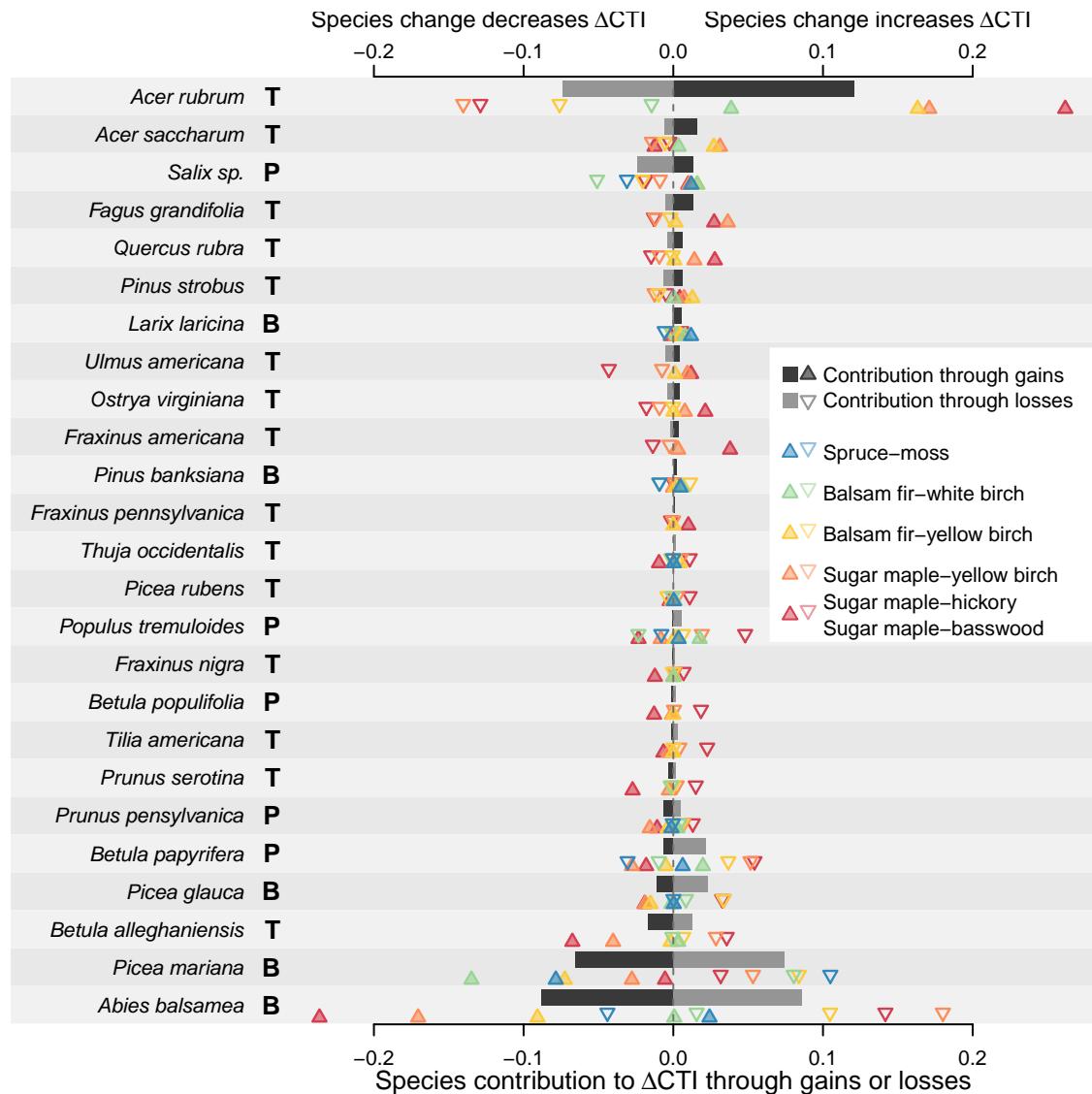
Community thermophilization was asymmetrical and mainly driven by larger gains in warm-adapted species, as indicated by the larger increases in the warm-tail of the temperature distributions than in the cold-tail (Fig. 1.5d-f). Moderate disturbances exacerbated this effect from the sugar maple-yellow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



**Figure 1.5.** Thermophilization (i.e., change in community temperature index,  $\Delta CTI$ ) and successional process (i.e., change in community shade index,  $\Delta CSI$ ) of forests for different levels of disturbance. In the upper panels (a-c), the latitudinal trends in  $\Delta CTI$  (black curve) and  $\Delta CSI$  (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  $\Delta CTI$  (black) and  $\Delta CSI$  (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. ??). 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. ??), 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  $\Delta\text{CTI}$  increased by an average of 0.12 for all plots where \**Acer rubrum*\* has increased in abundance (dark grey bar), whereas the  $\Delta\text{CTI}$  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)boreal 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. ??) 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. Sittaro *et al.*, 2017; Leithead *et al.*, 2010; Fisichelli *et al.*, 2014). 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. ??). 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 (Sittaro *et al.*, 2017; Talluto *et al.*, 2017; Renwick et Rocca, 2015; Svenning et Sandel, 2013). 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 (Leithead *et al.*, 2010; Boucher *et al.*, 2006) and simulation (Wang *et al.*, 2015; Vanderwel et Purves, 2014) 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 (Thompson *et al.*, 2013; Boucher *et al.*, 2006; Danneyrolles *et al.*, 2019) and recently established themselves in boreal forests (Sittaro *et al.*, 2017; Leithead *et al.*, 2010) 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. ??) 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.

## **4.6. 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 code required to repeat the analyses will be made available online on GitHub.

## **Chapitre 2**

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**Les perturbations modérées accélèrent la dynamique de transition forestière sous l'effet du changement climatique dans l'écotone tempéré-boréal de l'est de l'Amérique du Nord**



## 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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**Author contributions** MHB designed the study and performed the analyses with feedback from the other authors. MHB wrote the first and second drafts. All authors substantially contributed to the final version of the manuscript.

## 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 (Parmesan et Yohe, 2003; Chen *et al.*, 2011). 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 (Fisichelli *et al.*, 2014; Reich *et al.*, 2015; Peng *et al.*, 2011; Goldblum et Rigg, 2005; Grundmann *et al.*, 2011; Bolte *et al.*, 2014). 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 (Svenning et Sandel, 2013; Renwick et Rocca, 2015). 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 (Loehle, 2000; Bouchard, 2019) 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 (Serra-Diaz *et al.*, 2015; Boulanger *et al.*, 2019; Bolte *et al.*, 2014). 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 (Peters *et al.*, 2007; Allen, 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 (Lafleur *et al.*, 2010; Brown et Vellend, 2014;

Carteron *et al.*, 2020). 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 (Carteron *et al.*, 2020; Brown et Vellend, 2014). 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 (Lafleur *et al.*, 2010; Barras et Kellman, 1998; Kellman, 2004). 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 (Runkle, 1981; Waggoner et Stephens, 1970; Liénard et Strigul, 2016) 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 (Hill *et al.*, 2004; Boulangeat *et al.*, 2018). 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 (Waggoner et Stephens, 1970; Hill *et al.*, 2004). 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.

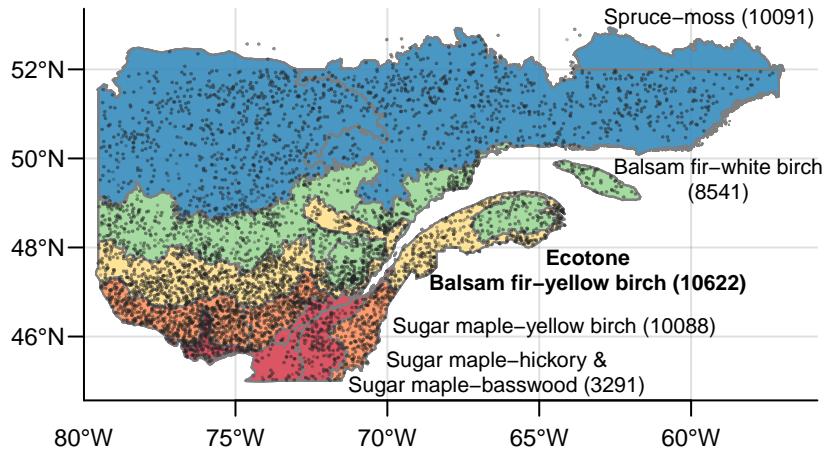
## 2. Methods

### 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 km<sup>2</sup>). 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).

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).

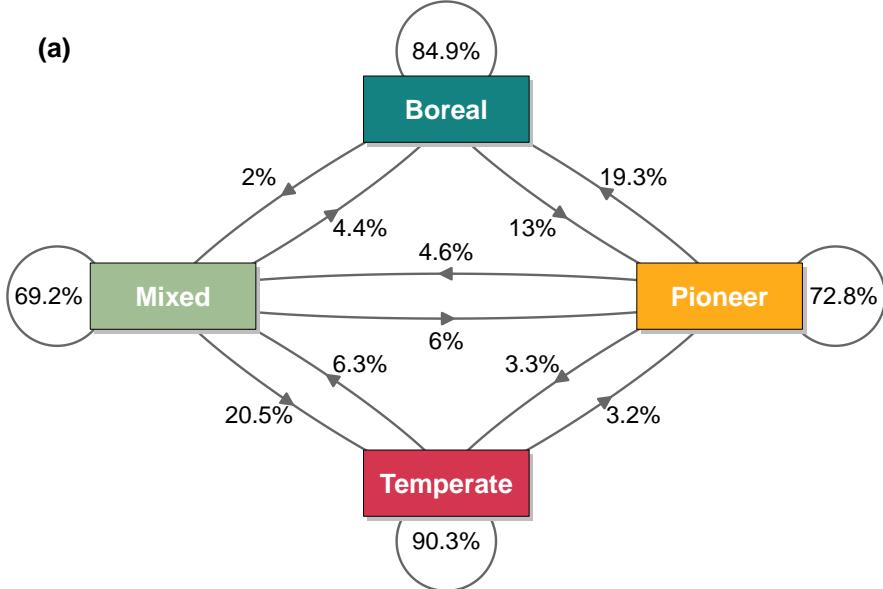


**Figure 2.1.** Locations of the 11,058 forest inventory plots in meridional Québec, Canada. Colours delimit the six bioclimatic domains. The two southernmost domains (red) are here combined. The number of plots in each domain is shown in parentheses. The balsam fir-yellow birch domain (in bold) is the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

## 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 A.2; 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<sup>2</sup>/ha). We analysed state transitions between consecutive plot surveys. Based on this classification, for the 42,633 observations (plots × number of years measured), we recorded 31,690 state transitions, including self-transitions (Fig. 2.2, Table A.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 A.2 and A.2).



(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-km<sup>2</sup> (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 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.

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.

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

Variable name	Variable description
<b>Climate</b>	
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).

Variable name	Variable description
<b>Soil</b>	
pH	pH of the surface horizon
Drainage	6 classes of soil drainage, which range from excessive to very poor, that were treated as numeric.
<b>Disturbances</b>	
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).

## 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; Van Den Hout, 2016; Logofet et Lesnaya, 2000).

In a four-state transition model in continuous time, the Markov process is governed by a  $4 \times 4$  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),  $\beta_{rs}$  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,  $\pi$ . For a regular Markov process, any initial state distribution converges to the same equilibrium as time approaches infinity. The vector of equilibrium  $\pi$  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  $\lambda_{A1}$  and  $\lambda_{A2}$  are the largest and second-largest eigenvalues of  $A$  ( $\lambda_{A1} = 1$  for stochastic  $A$ ), whereas  $\lambda_{Q1}$  and  $\lambda_{Q2}$  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;  $RF_{jk}$ ):

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

**Table 2.2.** Comparisons of the five candidate multi-state models. The number of parameters used in each model corresponds to the number of modelled transitions ( $10 \times$  the number of covariates – 1). The  $\Delta\text{AIC}$  is the difference between the Akaike information criterion of each model ( $\text{AIC}_m$ ) and the minimum of AIC among all models ( $\text{AIC}_{min}$ ):  $\Delta\text{AIC} = \text{AIC}_m - \text{AIC}_{min}$ . Models are presented in decreasing order of their  $\Delta\text{AIC}$ . 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	Number of parameters	-2 Log-likelihood	Delta AIC	LR t
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
<b>Full</b>	<b>All</b>	<b>78</b>	<b>29440.0</b>	<b>0.0</b>	<b>&lt; 0.001</b>

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.2). 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>.

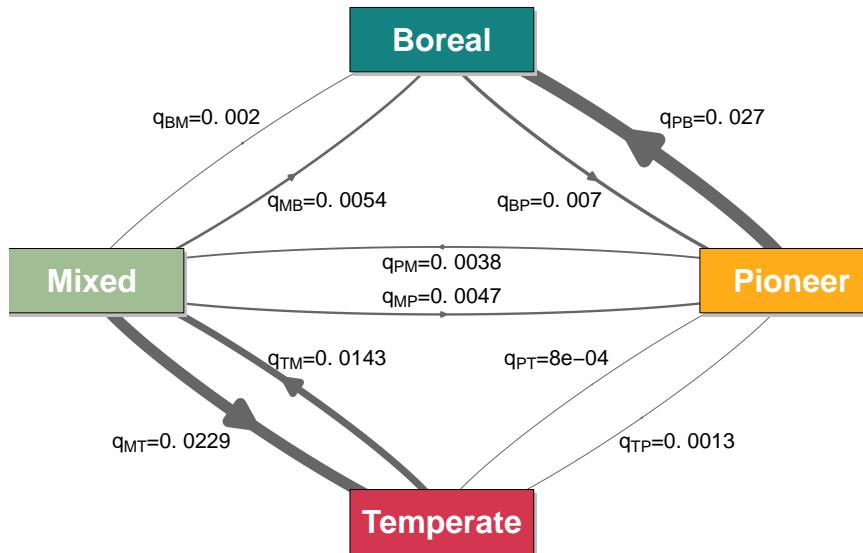
### 3. Results

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,  $p < 0.001$ ; 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.

### 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).

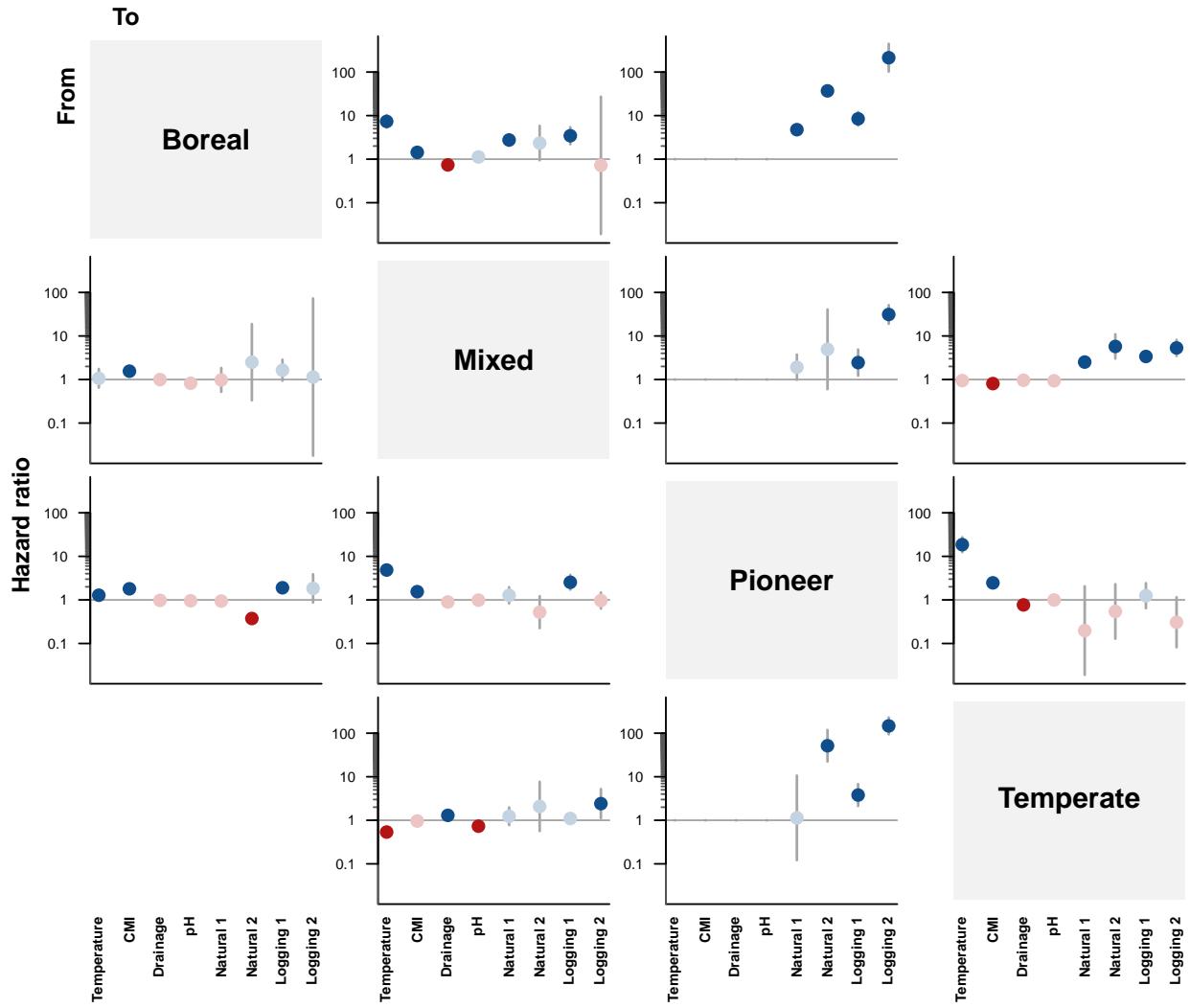
### 3.2. Effect of covariates on transition probabilities

All transitions to Pioneer were highly influenced by disturbances (Fig. 2.4, Table A.2). 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 A.2). 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.



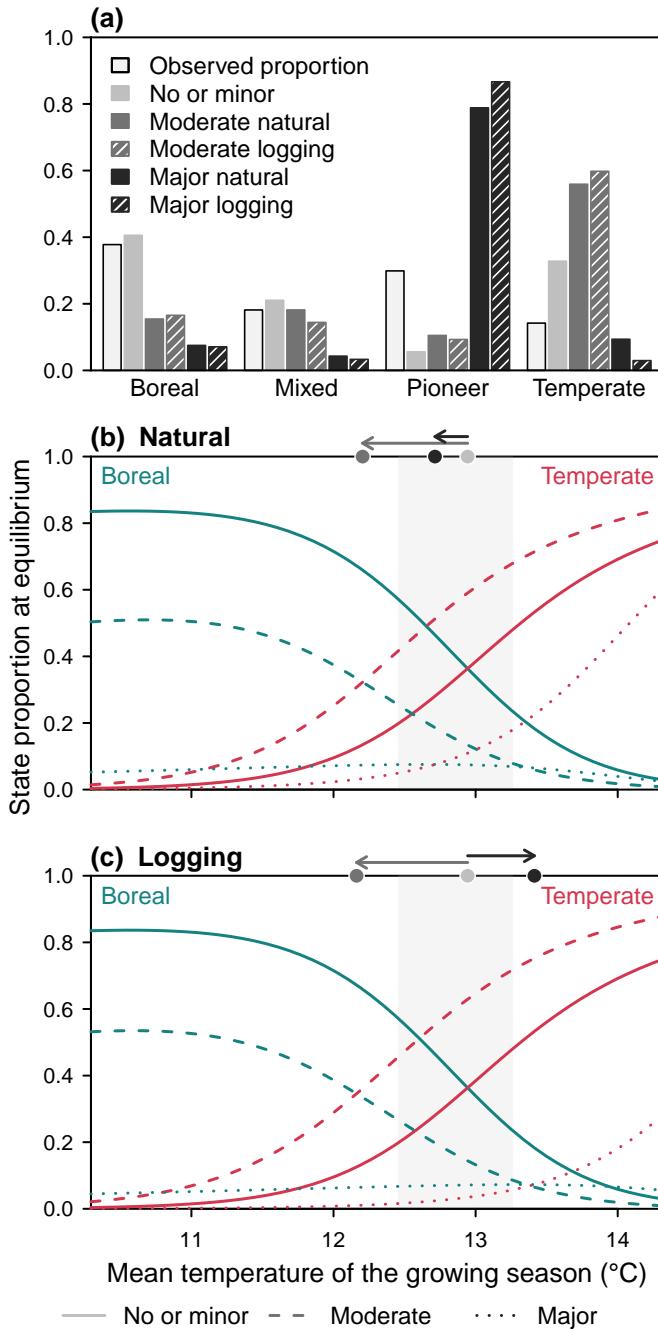
**Figure 2.4.** Hazard ratios (HR) and 95% confidence intervals as estimated from the best multi-state transition model. Each plot represents the estimated HR for transitions from row to column state, e.g., the plot on the first row, second column shows the HR for the Boreal to Mixed transition. The 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.

### 3.3. 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 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).



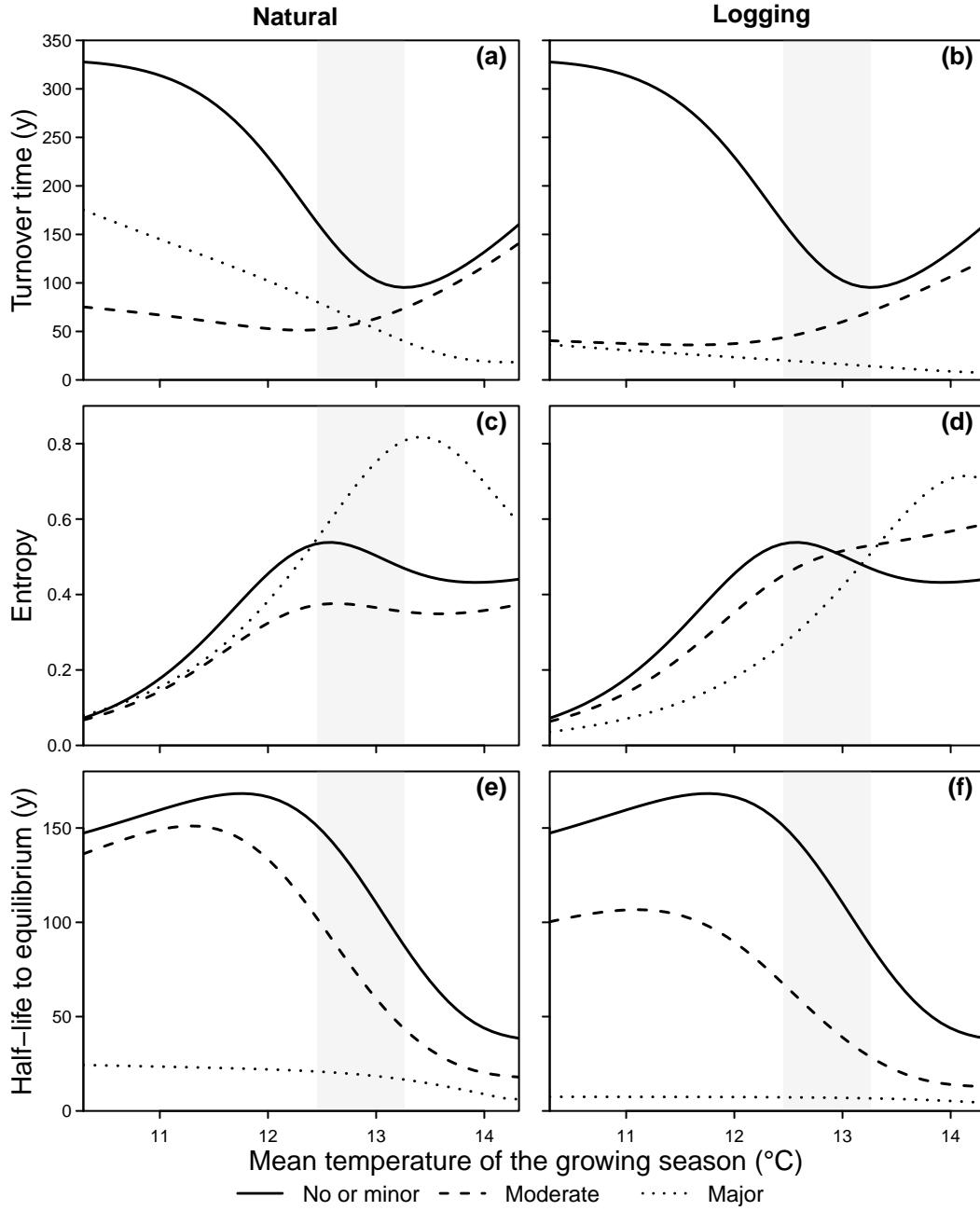
**Figure 2.5.** Changes in forest state proportions at equilibrium for different disturbance types (natural or logging) and intensity (no or minor, moderate, major). The barplot (a) compares the observed state proportion in the ecotone to the potential state proportion at equilibrium for different disturbance 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.

### 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).

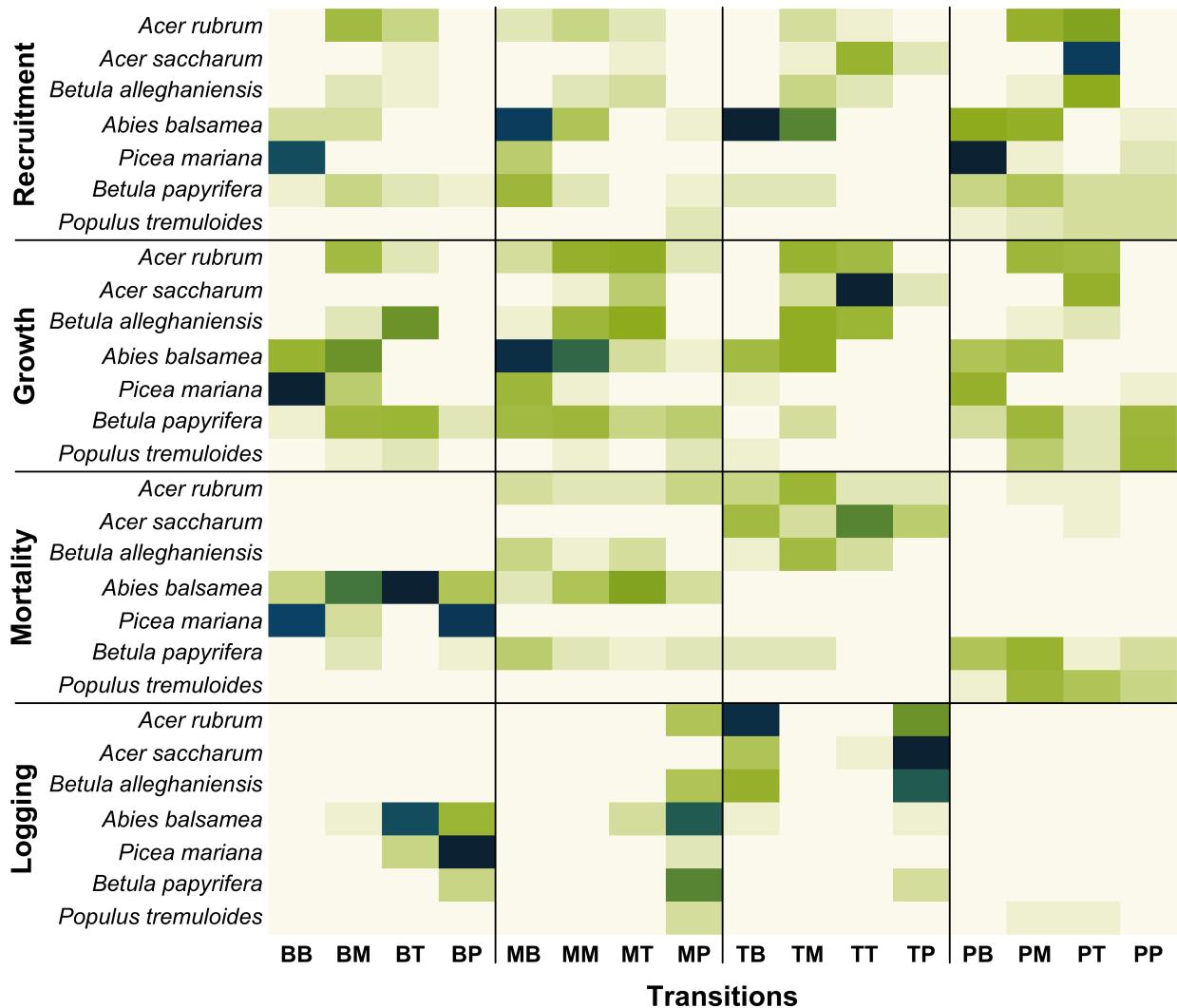
Half-life to equilibrium was the longest at ca. 11.8°C, north of the ecotone, in the balsam fir-white birch domain, while it was the shortest in the southernmost latitudes (Fig. 2.6e,f). Moderate disturbances flattened and shifted this peak to the north and the effect of moderate logging (Fig. 2.6f) 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 2.6.** 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)ooreal, (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 (Johnstone *et al.*, 2016; Renwick et Rocca, 2015; Brice *et al.*, 2019; 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 (Reich *et al.*, 2015; Fisichelli *et al.*, 2014; Boisvert-Marsh *et al.*, 2019; Goldblum et Rigg, 2005; Bolte *et al.*, 2014), 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 (Danneyrolles *et al.*, 2019; Terrail *et al.*, 2019; Boucher *et al.*, 2006). 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; Leithead *et al.*, 2010; Landhäuser *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; Goldblum et Rigg, 2002; Kellman, 2004; Fischelli *et al.*, 2014). 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; Landhäusser *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 (Vissault, 2016; Solarik *et al.*, 2019).

#### 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).

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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>.

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# Appendix C

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

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

## C.1. Supplementary Tables

**Table 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.

Species name	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</i> sp.	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

Species name	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</i> sp.	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</i> sp.	Willow	Pioneer	1.5	13.32
<i>Sorbus</i> sp.	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

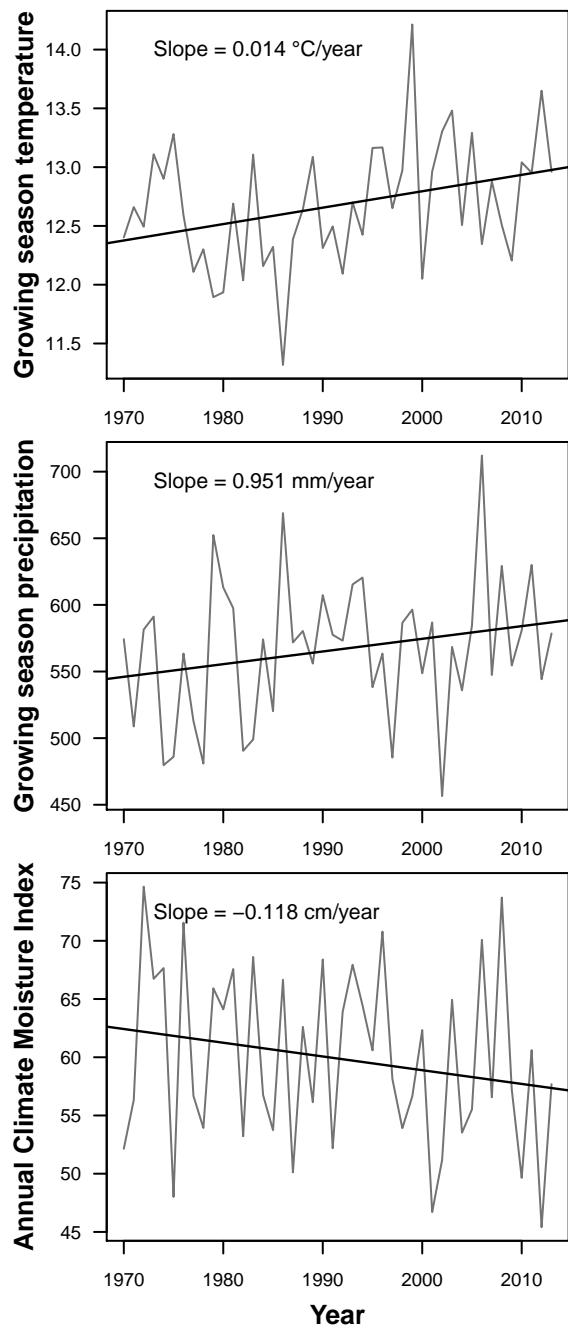
**Table A.2.** 21 original disturbance types and their reclassification into natural disturbances and harvest, with three levels of intensity. Sites with tree planting were excluded from the study.

	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

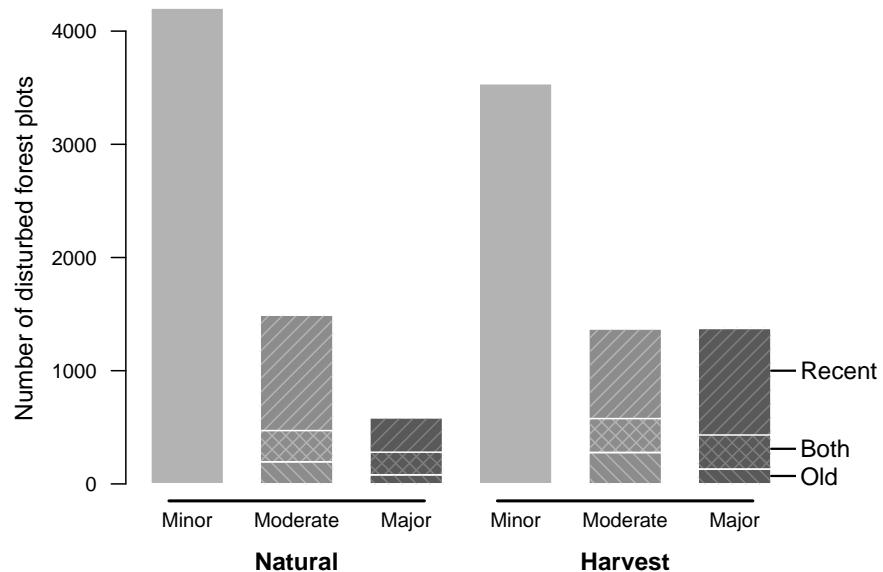
**Table A.3.** List of R packages used for analyses.

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)

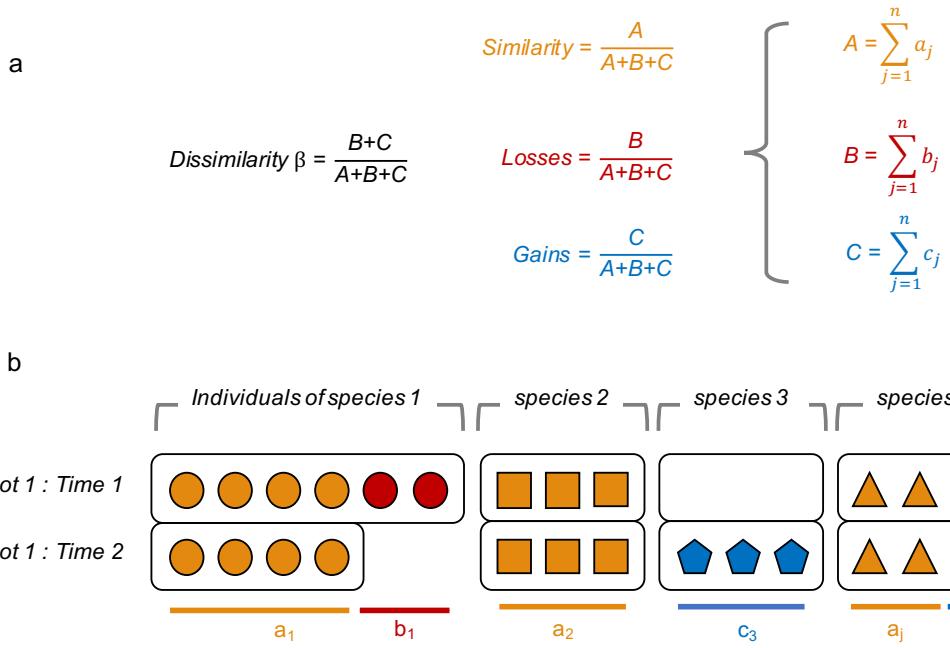
## C.2. Supplementary Figures



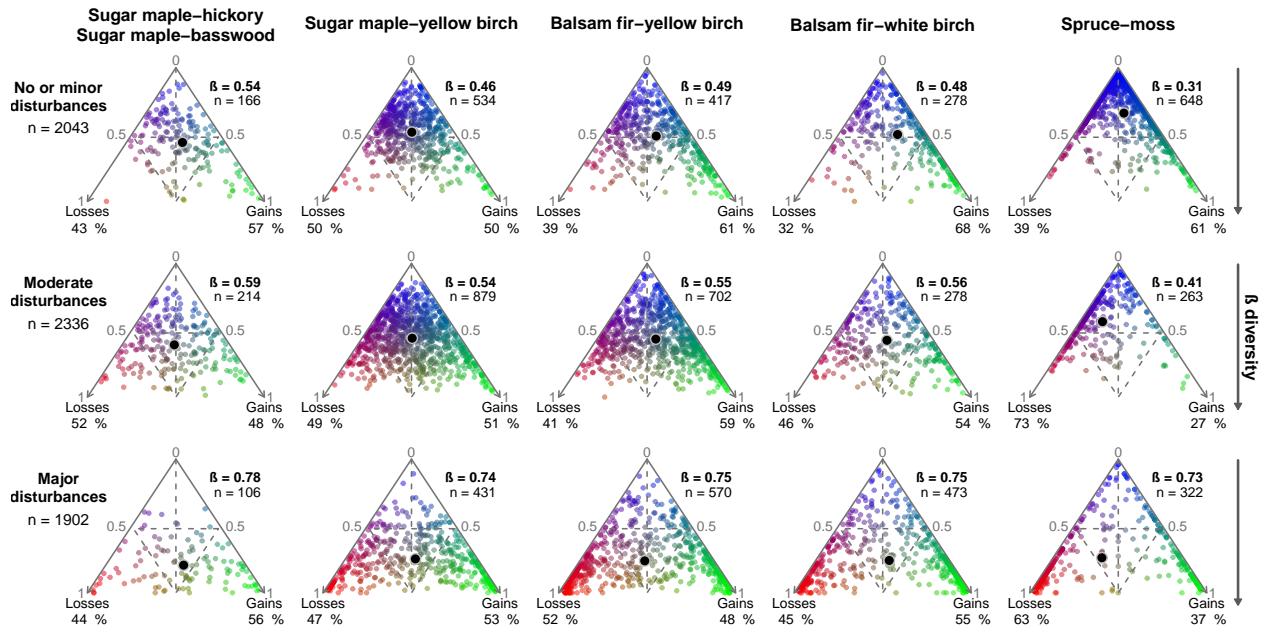
**Figure A.1.** Temporal trends in growing season temperatures (top), total growing season precipitation (middle) and annual climate moisture index (bottom). Grey lines represent averaged climate values across the 6281 studied forest plots. Straight black lines show the fitted least-squared linear regression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



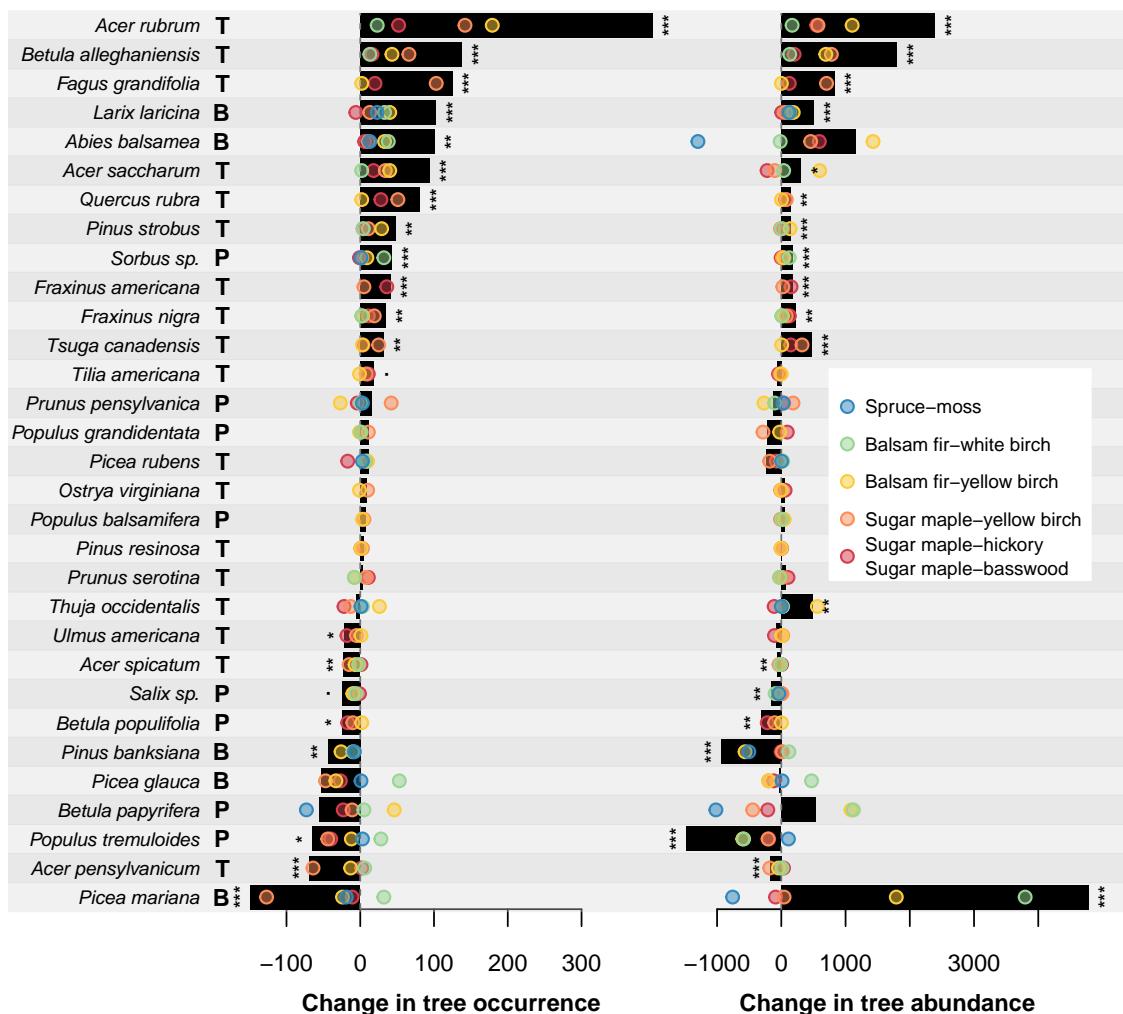
**Figure A.2.** Frequency of forest plots by disturbance type (natural disturbances and harvest), level of intensity (minor, moderate, major) and timing (old refers to disturbances that occurred before the study period whereas recent disturbances occurred during the study period). The three columns in 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.



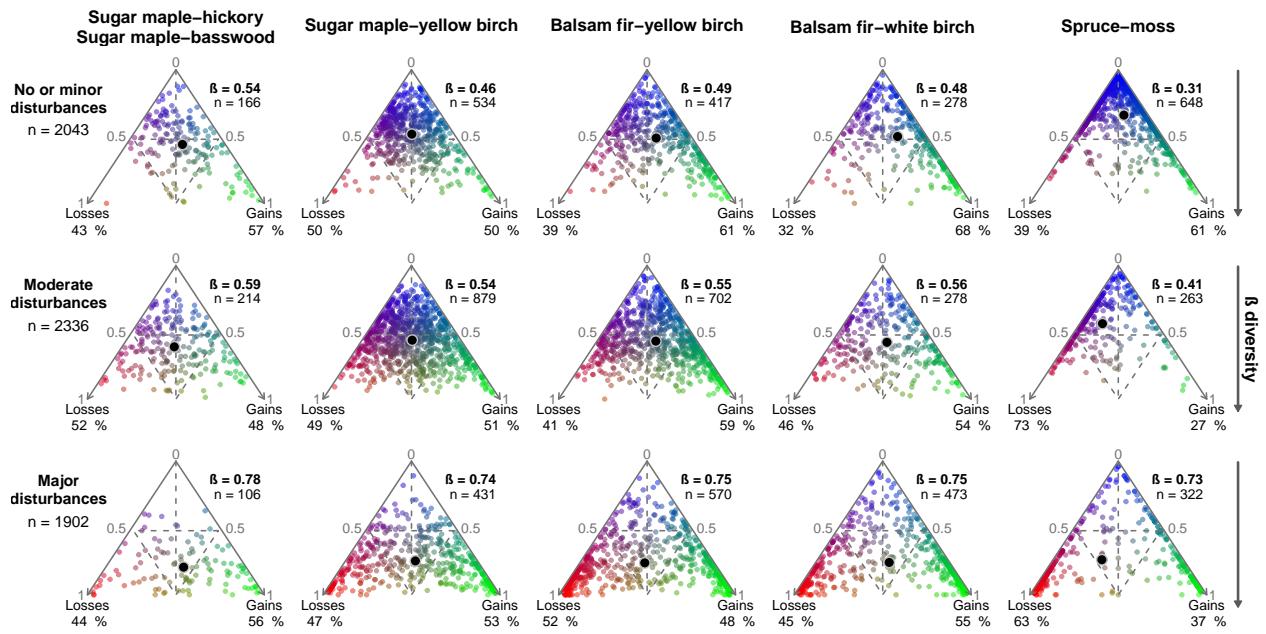
**Figure A.3.** Equations to compute the temporal  $\beta$  diversity index, as well as its components, using the Ružička coefficient for abundance data (a) and an example (b) where the tree composition of a single forest plot is compared between two surveys,  $t_1$  and  $t_2$ . In the example, each 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  $\beta$  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)oreal species.



**Figure A.6.** Relations between change in Community Temperature Index ( $\Delta\text{CTI}$ ) 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.

# Appendix A

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

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Pierre Legendre, Marie-Josée Fortin

## A.1. Supplementary Methods

### A.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  $4 \times 4$  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  $\beta_{rs}$ :

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

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  $\theta$  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:

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

### A.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.

## A.2. Supplementary tables

Table: 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
<b>Boreal</b>		
<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
<b>Pioneer</b>		
<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
<b>Temperate</b>		
<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

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

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

Table: Table of baseline transition intensities ( $q_{rs0}$  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	Natural	Natural2	Logging1	Logging2
<b>Boreal - Boreal</b>	-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)
<b>Boreal - Pioneer</b>	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)
<b>Mixed - Boreal</b>	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)
<b>Mixed - Mixed</b>	-0.033 (-0.037, -0.029)								
<b>Mixed - Pioneer</b>	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)
<b>Mixed - Temperate</b>	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)
<b>Pioneer - Boreal</b>	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)
<b>Pioneer - Mixed</b>	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)	1.28 (0.83, 1.96)	0.52 (0.22, 1.22)	2.54 (1.72, 3.76)	0.97 (0.63, 1.48)
<b>Pioneer - Pioneer</b>	-0.032 (-0.034, -0.029)								
<b>Pioneer - Temperate</b>	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)
<b>Temperate - Mixed</b>	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)
<b>Temperate - Pioneer</b>	0.001 (0.001, 0.002)	1.000	1.000	1.000	1.000	1.13 (0.42, 10.61)	51.54 (22.41, 118.54)	3.8 (2.13, 6.8)	146.94 (94.03, 229.62)
<b>Temperate - Temperate</b>	-0.016 (-0.019, -0.013)								

Table: 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.

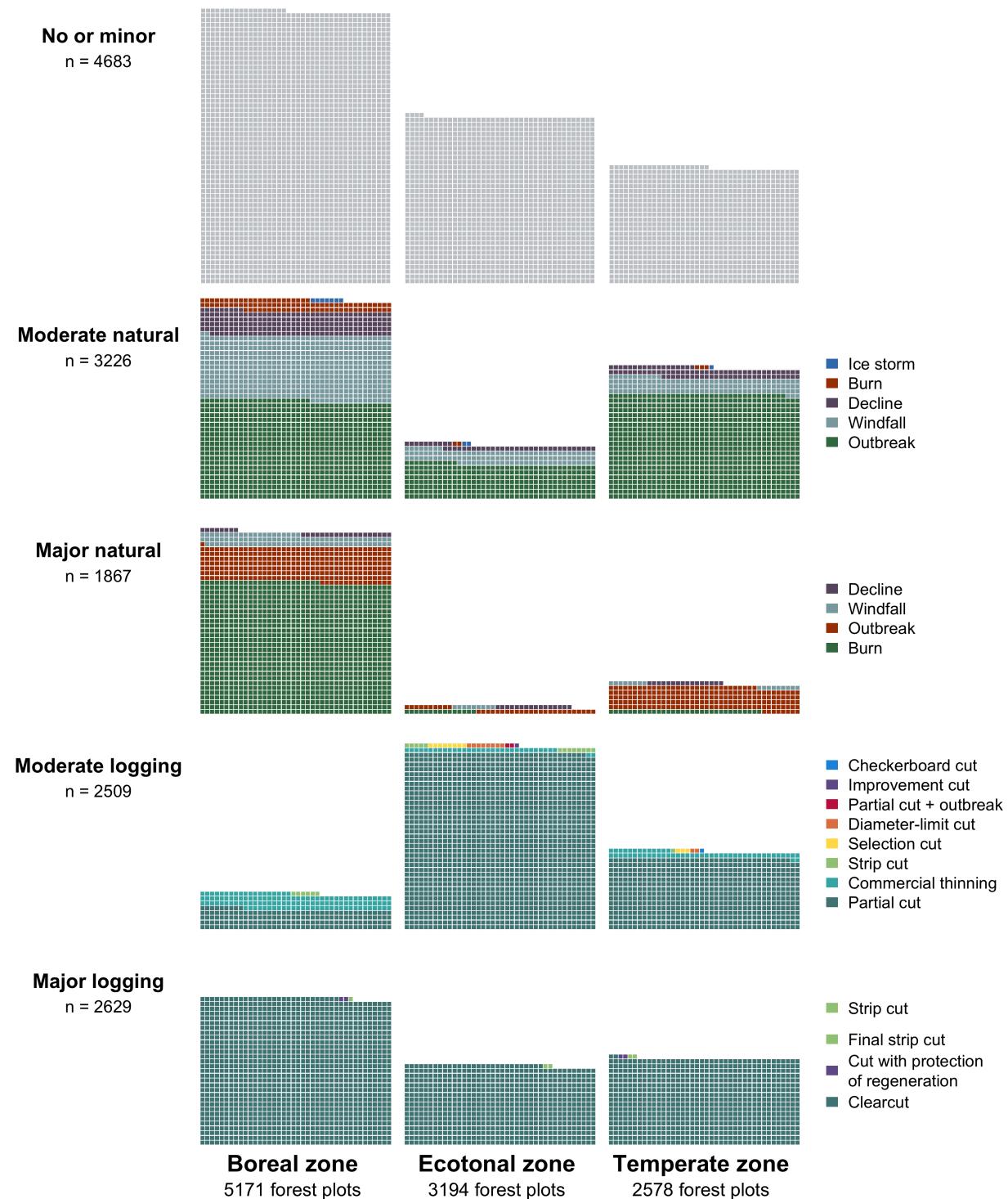
Transitions	Baseline	Temperature	CMI	Drainage	pH	Natural1	Natural2	Logging1	Logging2
Boreal - Boreal	-0.009 (-0.01, -0.008)								
Boreal - Mixed	0.002 (0.001, 0.003)	5.29 (3.58, 7.83)	1.01 (0.73, 1.39)	0.72 (0.62, 0.83)	1.11 (0.94, 1.32)	2.69 (1.92, 3.77)	0.7 (0.05, 9.91)	1.89 (0.87, 4.13)	0.39 (0.01, 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)								

**Table B.2.** List of R packages used.

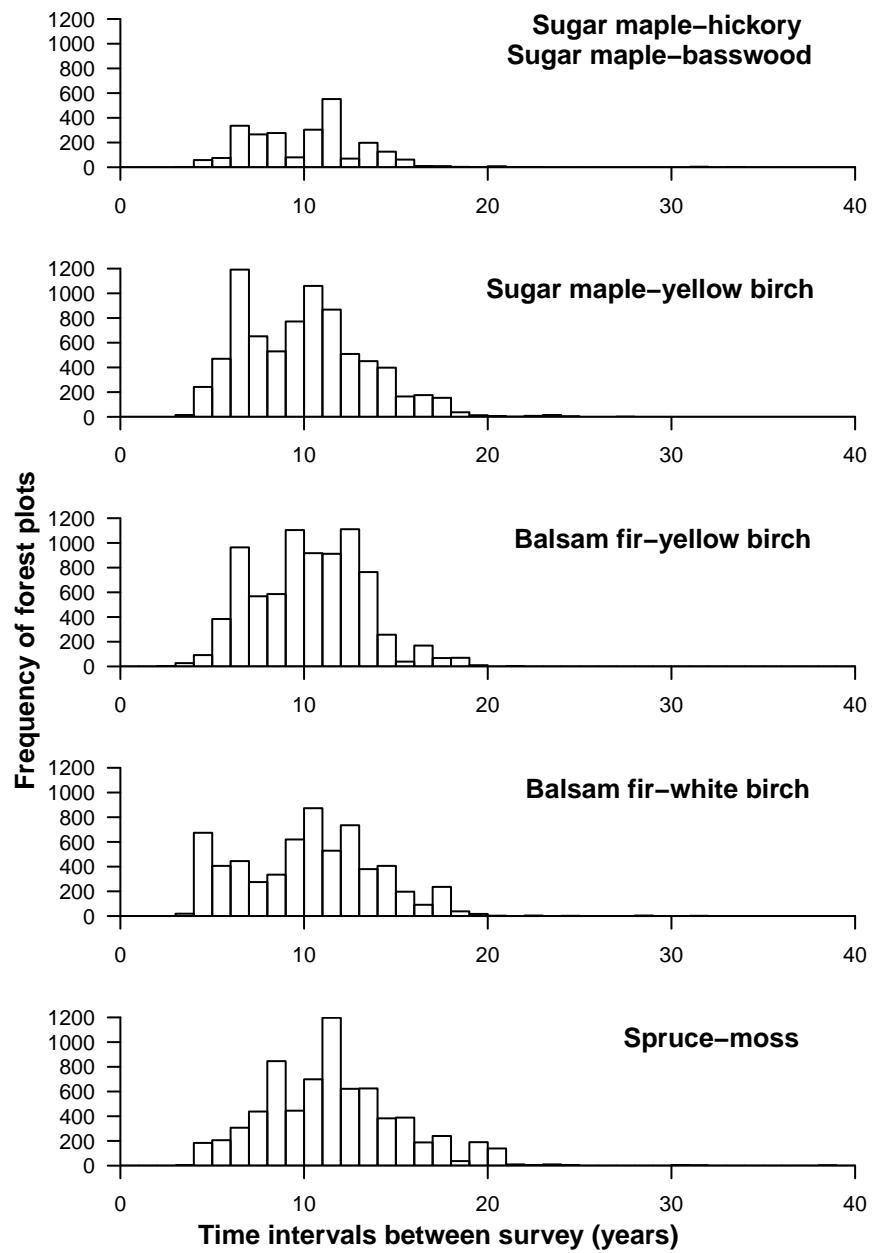
Main			
Packages	functions	Uses	References
msm	msm	Multi-state Markov models in continuous time	Jackson (2011)
	lrtest.msm	Likelihood ratio test	
	pmatrix.msm	Transition probability matrix	
	hazard.msm	Calculate tables of hazard ratios for covariates on transition intensities	
	pnext.msm	Probability 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)



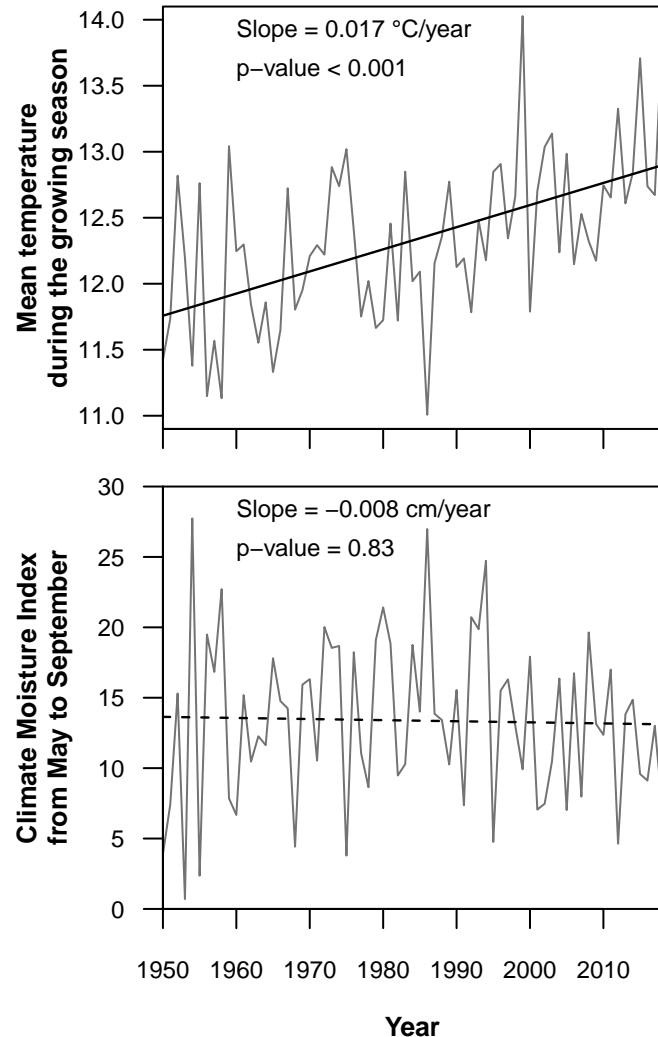
### A.3. Supplementary figures



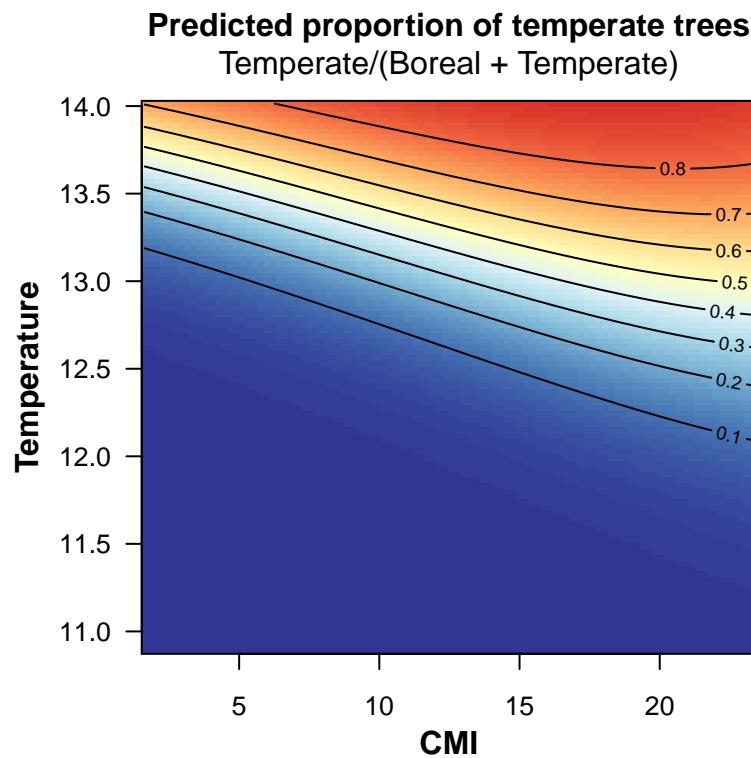
**Figure B.1.** Waffle charts representing the frequency of forest plots by disturbance type (natural disturbances and logging), level of severity (minor, moderate, major) and vegetation zone (boreal, ecotone and temperate). One square is one occurrence of a disturbance in a forest plot (a forest plot 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.



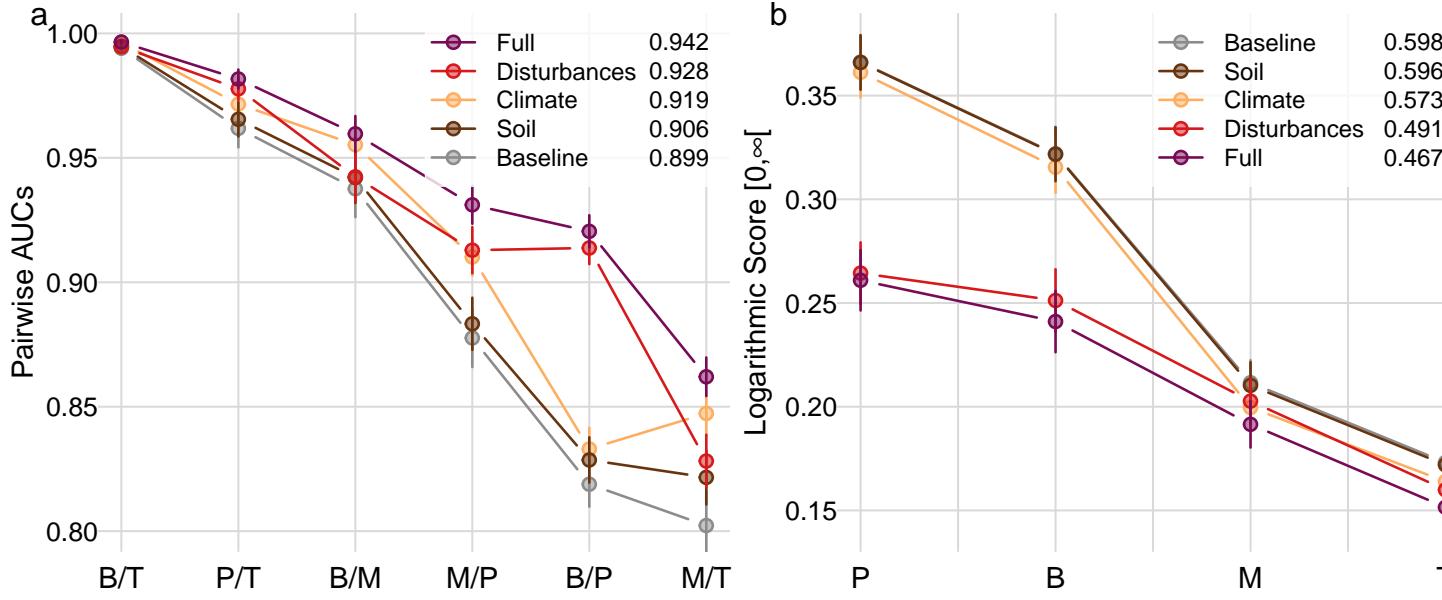
**Figure B.2.** Histograms of time intervals between surveys by bioclimatic domains.



**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.

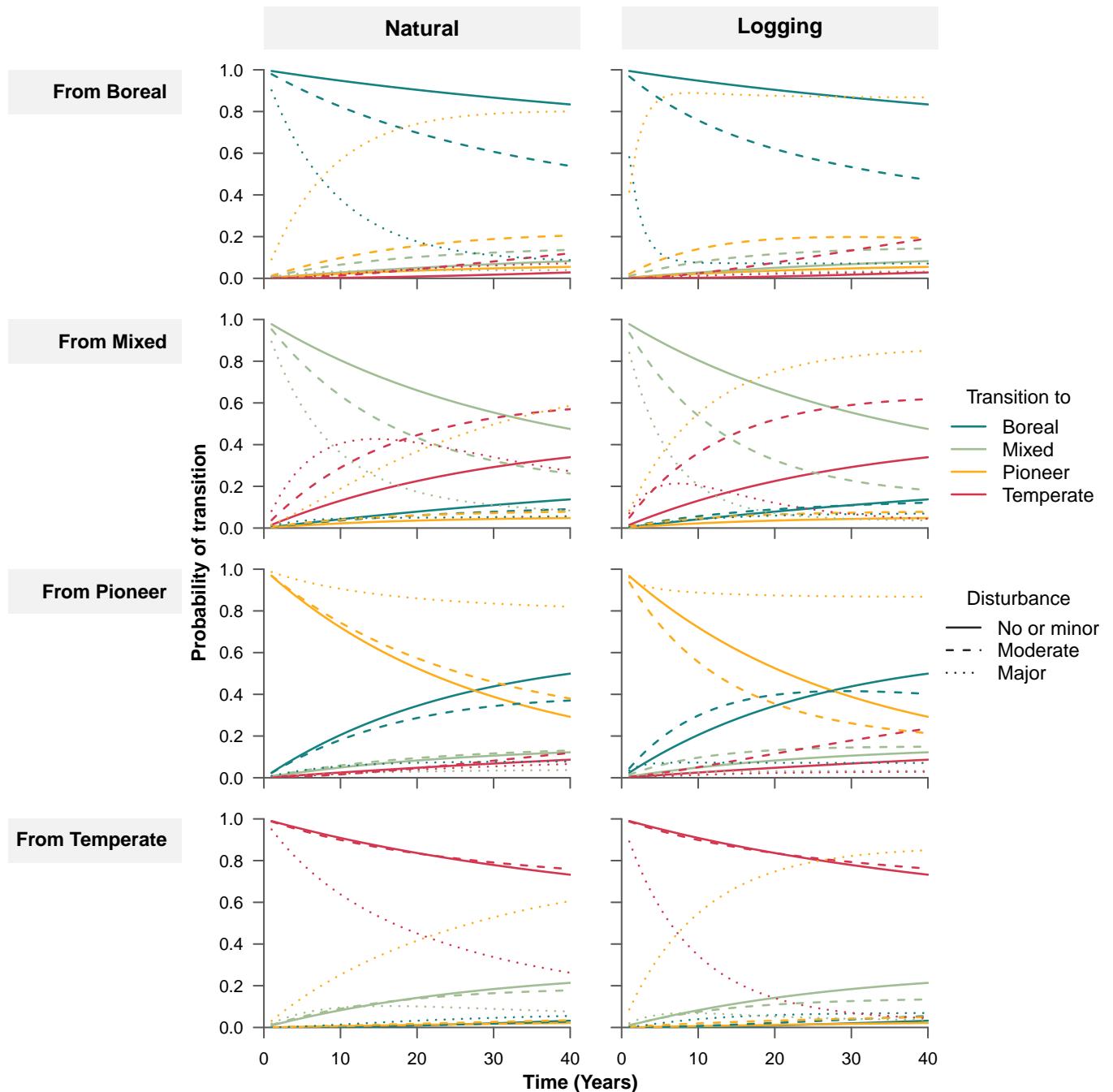


**Figure B.4.** Predicted proportion of temperate species in forest plots (temperate / (boreal + temperate)) measured in basal area using a negative binomial GLM with polynomial terms of two climate variables, temperature and climate moisture index during the growing season ( $R^2 = 50\%$ ).

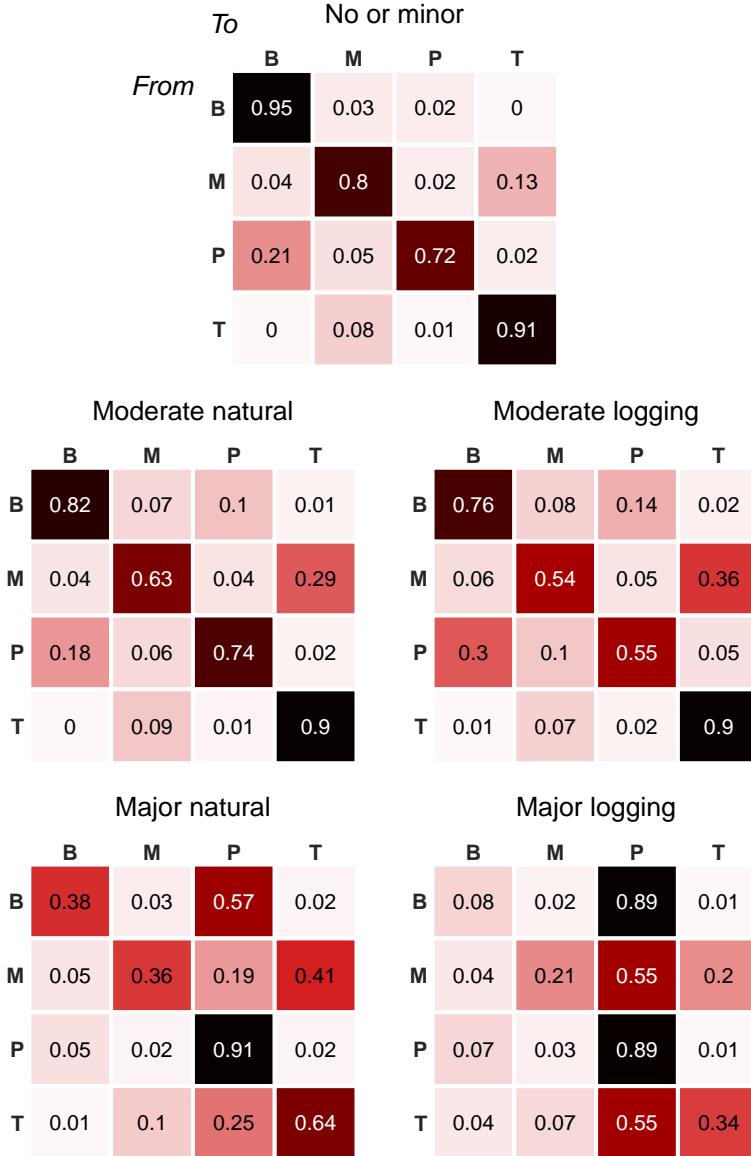


**Figure B.5.** Performance comparisons of the five candidate multi-state models using multi-class area under the curve (mAUC; a) and logarithmic skill score (LS; b) obtained through 10-fold cross-validation. Higher values of mean pairwise AUC (a) indicate a better capacity to discriminate between pairs 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.



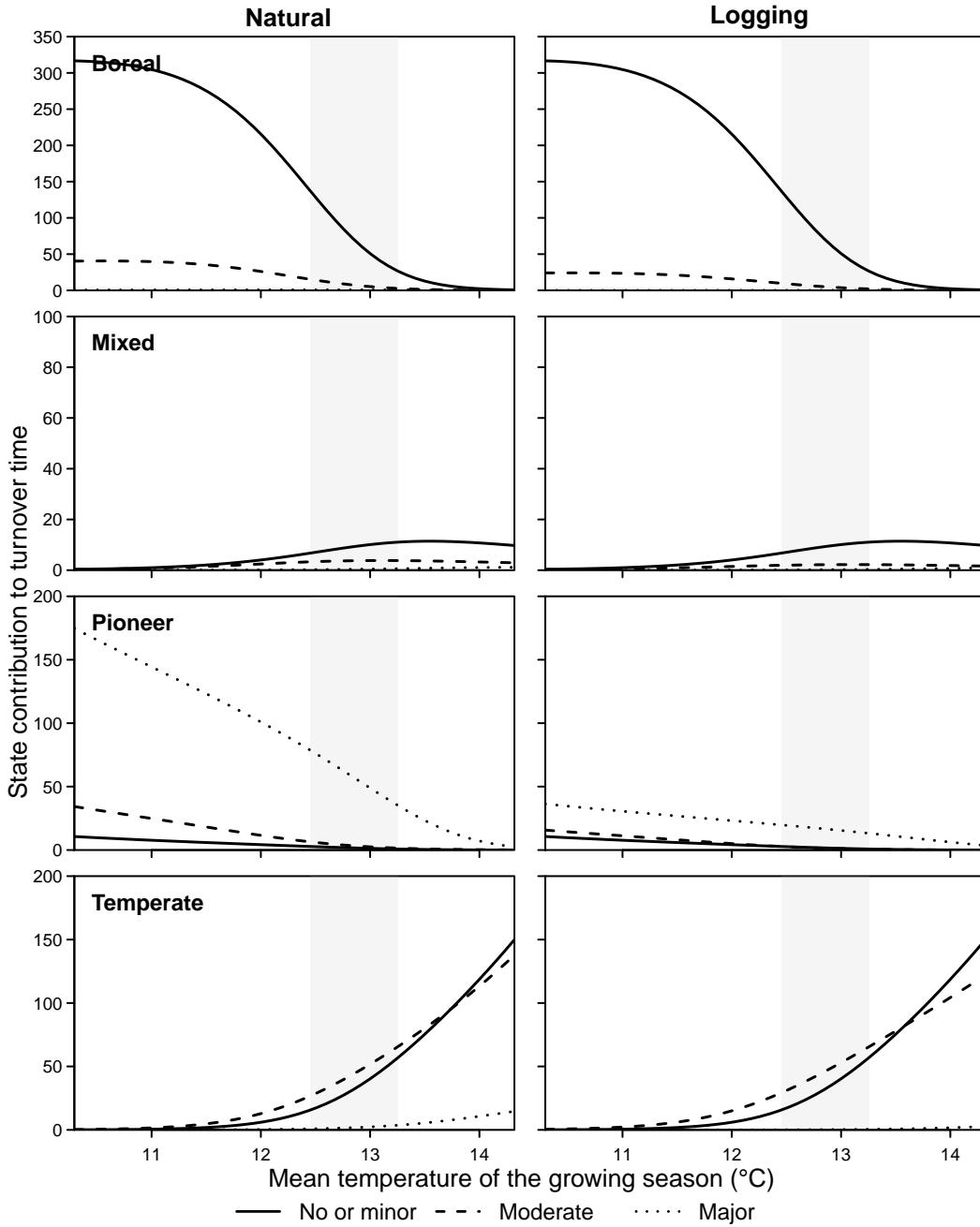
**Figure B.6.** Probability of transition between forest states through time for natural disturbances (left) and logging (right) and for different levels (line type) as predicted by the best multi-state model. All other covariates are fixed at the average conditions found in the ecotone, i.e. the balsam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



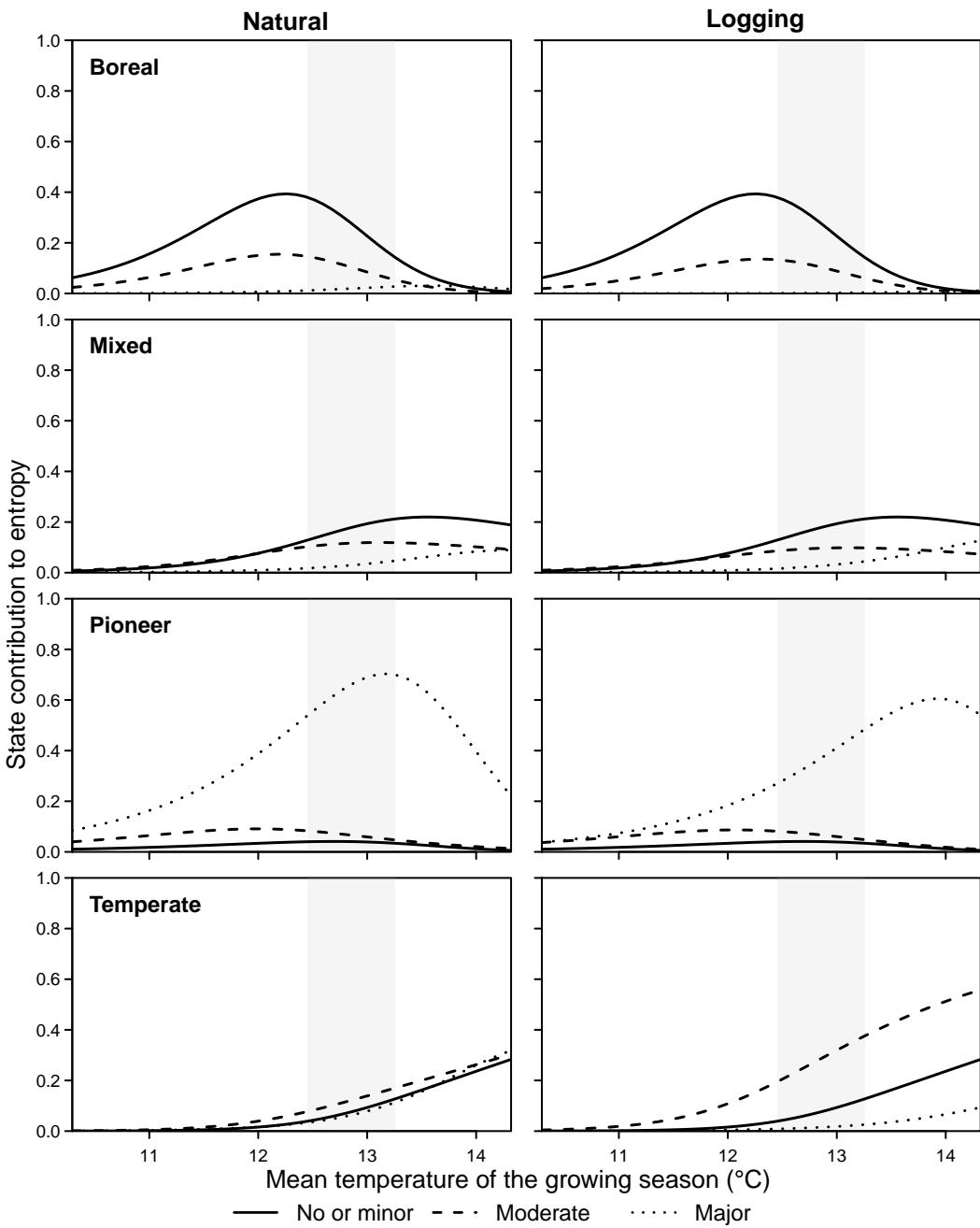
**Figure B.7.** Predicted change in 10-year transition probabilities for different disturbance types and levels. All other covariates are fixed at the average conditions found in the ecotone. Letters correspond to the four forest states: (B)oreal, (M)ixed, (P)ioneer and (T)emperate. Numbers are the modelled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