UNIVERSITÉ DU QUÉBEC EN ABITIBI-TÉMISCAMINGUE

EFFET DU CLIMAT ET DE LA COMPÉTITION SUR LA CROISSANCE DES FEUILLUS TEMPÉRÉS ET SUR LEUR CAPACITÉ À COLONISER DES PEUPLEMENTS DE LA FORÊT BORÉALE MIXTE

THÈSE
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PAR
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- Chapitre I: Soubeyrand, M., Gennaretti, F., Blarquez, O., Bergeron, Y., Taylor, A. R., D'Orangeville, L., et Marchand, P. (2023). Competitive interactions under current climate allow temperate tree species to grow and survive in boreal mixedwood forest. *Ecography*. https://onlinelibrary.wiley.com/doi/10.1111/ecog.06525
- Chapitre II: Soubeyrand, M., Gennaretti, F., Blarquez, O., Bergeron, Y., Grondin, P., et Marchand, P. Effect of climate and competition on future temperate tree species colonization of mixedwood boreal stands.
- Chapitre III: Soubeyrand, M., Marchand, P., Duchesne, L., Bergeron, Y., et Gennaretti, F. Interactions between climate, soil and competition drive tree growth in Quebec forests. *Forest Ecology and Management*, https://doi.org/10.1016/j.foreco.2024.121731.

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Bal. Fir: Balsam Fir

BF-PB: Balsam fir – paper birch

BF-YB: Balsam Fir – Yellow Birch

CEC: Cation-exchange capacity

CMI: Climate Moisture Index

CMI JJA: Climate Moisture Index of June, July and August

DBH: Diameter at Breast Height

DBHI: Diameter at Breast Height Increment

DD5: Growing Degree Day

ELPD: Expected Log Pointwise Predictive Density

Eq: Equation

FERLD: Forêt d’Enseignement et de Recherche du Lac Duparquet

Fig: Figure

GLI: Global Light Index

LOO: Leave One Out

MAT: Mean Annual Temperature

MaxPotGrowth: Maximum Potential Growth

MFFP: Ministère des Forêts, de la Faune et des Parcs

MRNF: Ministère des Ressources Naturelles et des Forêts

MSP: Mean Summer Precipitation

NCI: Neighbourhood Competition Index

Pap. Bir.: Paper Birch

PCA: Principale Component Analysis

PPT: Precipitation

SBB: Sapinière à bouleau blanc

SDM: Species Distribution Models

SSP: shared socioeconomic pathways

TAVE: Average Temperature

RESEF: Réseau d'Etude et de Surveillance des Ecosystèmes Forestiers

RCP: Representative Concentration Pathway

Tre. Asp.: Trembling Aspen

Whi. Ced.: White Cedar

Whi. Spr.: White Spruce

LISTES DES SYMBOLES ET DES UNITÉS

°C: degrés Celsius

cm: centimètre

cm.yr^{-1} : centimètre par an

trees.ha^{-1}: Nombre d’arbres par hectare

ha: hectare

m^2: mètre carré

m^2.ha^{-1}: mètre carré par hectare

mm: millimètres

mm.y^{-1}: mètre par an

log: logarithme

log_{10}: logarithme base 10

RÉSUMÉ

Les changements climatiques et l'aménagement forestier pourraient perturber la croissance et la répartition des espèces, notamment dans les hautes latitudes et les écotones où certaines espèces atteignent leur limite méridionale ou septentrionale de leur distribution. C'est le cas des feuillus tempérés, l'érable à sucre, l'érable rouge et le bouleau jaune, qui sont supposés migrer vers le nord dans la forêt boréale mixte du Québec avec le relâche de certaines contraintes climatiques. Cependant, d'autres facteurs non climatiques régissent la croissance et la distribution des espèces tels que la compétition entre les différents arbres, les facteurs édaphiques et aussi les interactions entre ces facteurs.

Cette thèse de doctorat visait à mieux comprendre les conditions qui favorisent ou limitent la croissance et la survie des feuillus tempérés au nord de leur aire de répartition, dans la forêt boréale mixte du Québec, en prenant en compte des facteurs tels que la compétition entre les espèces, les changements climatiques, et les dynamiques de succession forestière afin d'évaluer la possibilité de migration de ces feuillus tempérés. Nous voulions aussi comprendre quels étaient les impacts de l'interaction entre les facteurs climatiques, du sol et de la compétition (intra- et interspécifique) sur la croissance des feuillus tempérés pour identifier des possibles stratégies d'adaptation pour la gestion forestière.

Le premier chapitre avait pour objectif de paramétriser et valider le modèle SORTIE-ND afin de considérer les interactions entre les feuillus tempérés et les espèces de la forêt boréale mixte. Nous avons ensuite utilisé ce modèle pour déterminer la capacité des feuillus tempérés à croître et survivre dans les peuplements de la forêt boréale mixte à partir du stade de semis. Nous montrons que les feuillus tempérés peuvent croître et survivre dans tous les peuplements, excepté les peuplements récemment coupés qui ont une intense régénération de peuplier faux-tremble. Nous avons aussi montré que lorsque les semis de feuillus tempérés sont introduits en densité moyenne (5000 semis par hectare) ou élevée (10000 semis par hectare), les feuillus tempérés pouvaient dominer le peuplement après 110 ans.

Le chapitre II avait pour objectif de déterminer le potentiel de colonisation des feuillus tempérés dans la forêt boréale mixte si un petit peuplement de feuillus tempérés matures est présent à proximité. De plus, nous avons évalué l'impact des changements climatiques sur ce potentiel de colonisation en modifiant la croissance en réponse à différents scénarios de forçage climatique. Nous avons montré que les feuillus

tempérés pouvaient coloniser les peuplements boréaux mixtes avec une plus grande capacité dans les peuplements les plus jeunes. Nous montrons aussi que l'effets des changements climatiques n'augmentaient pas la capacité des feuillus tempérés à coloniser les peuplements boréaux mixtes, même si la croissance des feuillus tempérés augmentait. Ces résultats témoignent de comment la gestion forestière en rajeunissant les forêts peut faciliter la migration des espèces tempérées vers le nord.

Dans le chapitre III, nous avons utilisé les données du réseau d'étude et de surveillance des écosystèmes forestiers (RESEF) pour modéliser la croissance des feuillus tempérés et des espèces d'arbres de la forêt boréale mixte en incluant les effets du climat, du sol, de la compétition et de l'interaction entre ces variables. Après avoir sélectionné le meilleur modèle, nous avons démontré que c'est l'ombrage des arbres compétiteurs qui serait le meilleur prédicteur de la croissance radiale des arbres. Les interactions entre le climat, le sol et la compétition ont joué un rôle crucial dans les modèles de croissance, mais les effets avaient des intensités et des directions différentes en fonction des espèces. Pour l'érable à sucre et l'épinette noire, la compétition intraspécifique aurait un effet plus délétère que les relations interspécifiques et serait particulièrement modulée par les effets climatiques, et notamment les variables en relation avec la température. D'ici à 2100, les conditions climatiques prédites au Québec, même dans les scénarios les plus optimistes, ne seront plus adaptées à certaines espèces, par exemple, l'épinette noire dans le sud du Québec.

Cette thèse de doctorat a démontré que la limite nord de répartition des feuillus tempérés n'est pas contrôlée par les normales climatiques de la région. En outre, elle a mis en évidence que la survie et la croissance des jeunes arbres sont les processus les plus importants à considérer dans la modélisation des feuillus tempérés au sein des peuplements de la forêt boréale mixte. Par conséquent, les futurs modèles devraient intégrer des facteurs tels que les caractéristiques du sol et les conditions météorologiques sur la survie et la croissance des juvéniles pour obtenir une vision plus complète de l'ensemble des effets en jeu dans la forêt boréale mixte.

Les implications de cette thèse de doctorat sont principalement axées sur l'aménagement forestier. Le chapitre III nous a permis de démontrer que diminuer les interactions de compétition intraspécifique en augmentant la diversité au sein des peuplements pourrait augmenter la croissance des arbres les plus commercialisés. Cela impliquerait d'augmenter la complexité de la structure interne des peuplements après récolte. L'établissement des feuillus tempérés pourrait participer à ce processus et rendrait la forêt boréale mixte plus résistante et résiliente face aux changements climatiques et aux perturbations mais impliquerait des changements pour l'industrie forestière qui n'exploite pas encore ces essences.

INTRODUCTION GÉNÉRALE

0.1 Contexte

Les forêts québécoises, situées dans la partie est du Canada, se composent de deux biomes distincts: la forêt tempérée nordique au sud et la forêt boréale au nord (Saucier et al. 1998; 2003, Fig. 0.1). Ces écosystèmes forestiers fournissent une diversité de services écosystémiques importants au fonctionnement global de la planète et de notre économie, tels que le stockage de grandes quantités de carbone atmosphérique, des habitats pour de nombreuses espèces, ainsi que la fourniture de matière première pour l'industrie du bois qui est un pilier de l'économie québécoise (Brandt *et al.*, 2013 ; Mack *et al.*, 2021). La forêt mixte, située à l'interface des biomes tempérés et boréaux, se caractérise par une coexistence complexe entre les espèces feuillues tempérées et les conifères typiques de la forêt boréale et c'est dans cette zone que les espèces tempérées atteignent la limite nord de leur répartition (Saucier *et al.*, 1998, 2003). Ces espèces incluent l'érable à sucre (*Acer saccharum* Marsh.), le bouleau jaune (*Betula alleghaniensis* Britt.) et l'érable rouge (*Acer rubrum* L.) qui sont les trois feuillus tempérés faisant l'objet de cette thèse de doctorat. Ces trois espèces emblématiques des forêts d'Amérique du Nord sont d'une importance capitale au niveau économique (bois d'œuvre, fabrication de contreplaqué, pâte, ou sirop d'érable pour l'érable à sucre) et contribuent à la diversité des forêts québécoises favorisant la résilience aux perturbations naturelles et anthropiques ainsi que la biodiversité.

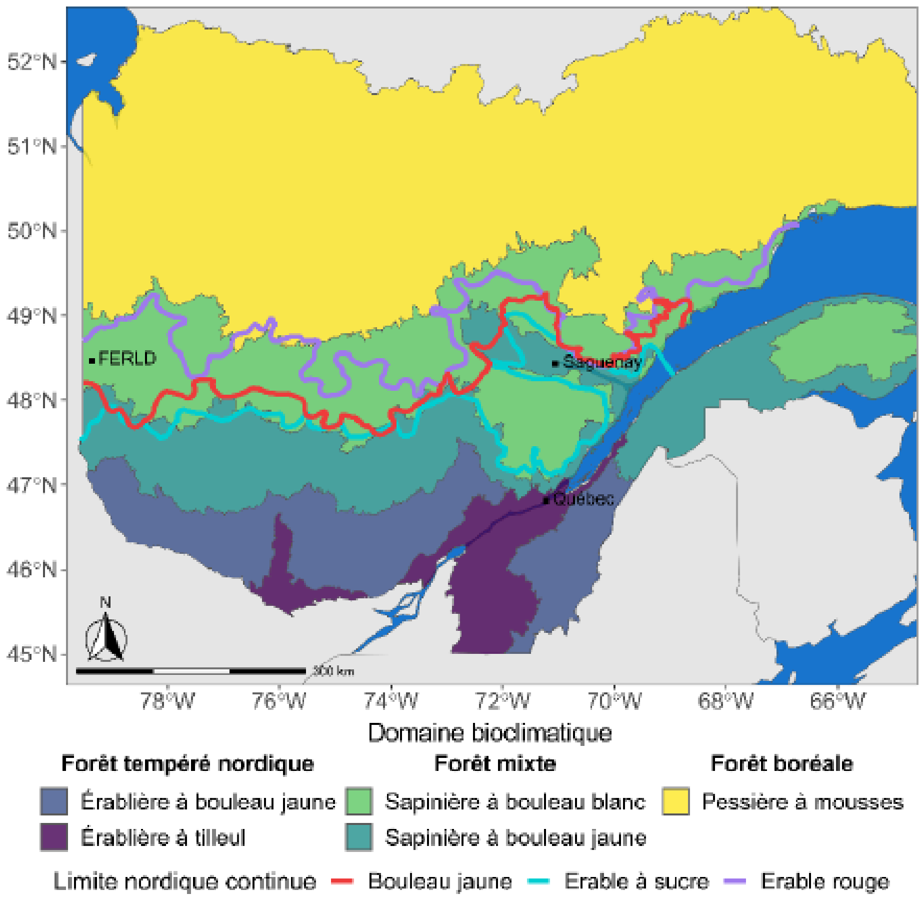

Figure 0.1: Carte des domaines bioclimatiques du Québec au sud de la pessière à mousse et limites nordiques continues des espèces de feuillus tempérés. Ces limites nordiques continues ont été communiqué personnellement par Claude Morneau (Ministère des Ressources naturelles et des Forêts). Ces limites ont été déterminées basée sur des données d'occurrences récoltées par le Ministère des Ressources naturelles et des Forêts. La sapinière à bouleau jaune et la sapinière à bouleau blanc correspondent respectivement à la forêt tempérée mixte et la forêt boréale mixte.

L'impact combiné de l'augmentation des températures (de 2 à 8°C d'ici 2100) et de l'aménagement forestier dans la forêt boréale mixte pourrait modifier la performance, les dynamiques de succession et la distribution des espèces (Coates *et al.*, 2003 ; D'Orangeville *et al.*, 2018 ; Molina *et al.*, 2021 ; Boulanger *et al.*, 2022). Cette transformation pourrait être profonde, car les espèces de feuillus tempérés, actuellement à leur limite nord de répartition sous forme de populations marginales, pourraient migrer et devenir des espèces dominantes au sein des peuplements de la forêt boréale mixte (Boulanger *et al.*, 2017, 2019).

Un tel changement dans la composition forestière de la forêt boréale mixte pourrait entraîner des conséquences majeures pour l'industrie forestière, les régimes de perturbations naturelles et la biodiversité associée aux espèces dominantes des peuplements. Cependant, les études ne tiennent pas toujours compte de certains facteurs cruciaux pour le succès de l'établissement des feuillus tempérés dans la forêt boréale mixte, tels que les interactions de compétition entre les feuillus tempérés et les espèces des peuplements hôtes, ou bien l'effet de la structure interne des peuplements sur l'accès des arbres à la lumière (Carteron *et al.*, 2020 ; Evans *et al.*, 2020 ; Evans et Brown, 2017). L'incertitude entourant l'impact de ces facteurs sur le succès de l'établissement et de la croissance des feuillus tempérés dans la forêt boréale mixte reste considérable. Il est essentiel de comprendre comment la croissance et la capacité d'établissement des feuillus tempérés au sein des peuplements de la forêt mixte sont influencées par des facteurs tels que le climat, les caractéristiques du sol et les interactions de compétitions pour obtenir une vision complète de l'avenir de la forêt boréale mixte (Oboite et Comeau, 2020 ; Henneb *et al.*, 2020).

La zone d'étude du chapitre I et II est située dans la Forêt de Recherche et d'Enseignement du Lac Duparquet (FERLD) dans la région de l'Abitibi au Québec. Le territoire de la FERLD fait partie de la forêt boréale mixte de l'ouest du Québec. Le paysage d'étude est fragmenté en raison de plusieurs incendies historiques et d'épidémies successives de la tordeuse des bourgeons de l'épinette (*Choristoneura fumiferana* Clemens) survenant à différents moments et endroits, ce qui crée une mosaïque de compositions de peuplements variées (Harvey *et al.*, 2002 ; Bergeron *et al.*, 2014). Nous avons choisi cette zone d'étude car elle est intensément étudiée depuis plus de 30 ans, nous donnant accès à des nombreuses données et présente une diversité de compositions de peuplements qui est représentative de la forêt boréale mixte du

Québec (Bergeron, 2000). Plusieurs inventaires et suivis forestiers issus de placettes permanentes ont été mis en place depuis les années 1990 pour étudier les dynamiques de succession forestière. Ces données sont régulièrement mises à jour et rendues disponibles (Maleki *et al.*, 2021). De plus, sur le territoire de la FERLD, on retrouve des populations marginales d'érable rouge sur les pentes et en haut des collines des monts Hébécourt qui pourraient être un des possibles points de départ de l'expansion de l'érable rouge (Zhang *et al.*, 2015b).

0.2 Populations marginales des feuillus tempérés en forêt boréale mixte

Les populations marginales des feuillus tempérés sont des peuplements au-delà de la limite nord continue de l'aire de répartition de ces espèces. La limite nord continue de l'érable à sucre et du bouleau jaune correspond à la limite entre la forêt tempérée mixte et la forêt boréale mixte (Fig. 0.1). L'érable rouge est présent un peu plus au nord que l'érable à sucre et le bouleau jaune, surtout à l'est du Québec, dû à sa plus grande tolérance aux faibles températures, sa plus grande capacité à vivre dans des sols argileux et dans des substrats pauvres en nutriments (Collin *et al.*, 2016 ; Jain *et al.*, 2021). En effet, l'érable rouge présente une grande adaptabilité à une diversité de types de sols, allant des sols sableux aux sols argileux, et peut prospérer dans des conditions de pH particulièrement acides jusqu'à légèrement basique, généralement compris entre 4 et 8 (St Clair et Lynch, 2005). L'érable à sucre préfère les sols allant de sableux à limoneux avec un pH compris entre 5,5 et 7,3 et est une espèce exigeante en éléments nutritifs tels que le calcium, le magnésium et le manganèse (Long *et al.*, 2009). Enfin, le bouleau jaune peut s'installer sur les podsols ou les fluvisols mais performe mieux sur des sols bien drainés; la présence de bois mort favorise aussi sa germination (Lorenzetti *et al.*, 2008 ; Drobyshev *et al.*, 2014 ; Lambert *et al.*, 2016).

Les populations marginales de feuillus tempérés dans la forêt boréale mixte se retrouvent souvent en haut et dans les pentes des collines, là où les conditions climatiques et édaphiques sont un peu plus optimales (Goldblum et Rigg, 2002). En effet, les températures au printemps peuvent être plus élevées dû à des phénomènes d'inversion des couches d'air. En absence de vent, l'air chaud à tendance à remonter au-dessus de la couche d'air froide plus dense qui est drainée en bas de pente (Chung *et al.*, 2006 ; Lindkvist et Lindqvist, 1997). Ainsi, la température du haut et des pentes des collines peut être un peu plus élevée (jusqu'à +4°C) et cela est parfois suffisant pour échapper à un gel tardif qui affecte la survie des juvéniles (Marquis *et al.*, 2021). De plus, les microsites du sol au sommet des collines ont tendance à être plus favorables à la germination et à la croissance des espèces d'arbres tempérés en raison de sols mieux drainés (Goldblum et Rigg, 2002). Ainsi, ces populations marginalement distribuées sont capables de se maintenir dans la forêt boréale mixte et pourrait jouer un rôle d'avant-poste pour la colonisation des feuillus tempérés dans la forêt boréale mixte dans un contexte de relâchement des contraintes climatiques (Vogel *et al.*, 2023).

La limite nord continue de répartition du bouleau jaune serait surtout influencée par les facteurs de recrutement incluant des éléments tels qu'une faible quantité de graines viables, l'absence de bois mort qui est un substrat favorable à la germination des graines (Bolton et D'Amato, 2011 ; Lambert *et al.*, 2016 ; Marx et Walters, 2008) et l'absence d'ouvertures dans la canopée (Gauthier *et al.*, 2016). Cela s'ajoute à la présence de sols humides et argileux typiques de la forêt boréale mixte de l'ouest du Québec qui défavorisent le bouleau jaune (Drobyshev *et al.*, 2014). En revanche, la croissance des arbres matures ne semble pas être un facteur affectant la limite nord de son aire de répartition (Drobyshev *et al.*, 2014). De manière similaire, les températures froides caractéristiques de la forêt boréale mixte ne sembleraient pas limiter la croissance de l'érable rouge à la limite nord continue de son aire de répartition (Zhang *et al.*, 2015b). Cependant, d'autres facteurs tels qu'une faible réserve de graines et les perturbations pourraient jouer un rôle plus important (Tremblay *et al.*, 2002). Les perturbations comme les feux pourraient favoriser la migration de l'érable rouge vers le nord, étant donné sa capacité à se régénérer par rejets mais des feux trop intenses pourraient constituer un frein, car de tels feux pourraient endommager les racines de l'arbre (Zhang *et al.*, 2015b). En revanche, l'érable à sucre est plus sensible aux climats froids, et aux dépôt acides et argileux qui caractérisent les sols de la forêt boréale mixte (Carteron *et al.*, 2020 ; Collin *et al.*, 2016 ; Jain *et al.*, 2021). Les gels tardifs diminuant la survie des semis et la capacité de régénération des arbres, semblent aussi jouer un rôle dans la détermination de la limite nord de répartition de toutes ces trois espèces de feuillus tempérés (Hufkens *et al.*, 2012).

Cependant, d'autres facteurs pourraient également exercer une influence déterminante sur la colonisation et l'établissement des feuillus tempérés au sein de la forêt boréale mixte. Ces facteurs incluent leur capacité de dispersion, les interactions biotiques, la topographie du terrain, ainsi que les régimes de perturbations (Paillard *et al.*, 2023). Les caractéristiques du sol de la forêt boréale mixte pourraient également jouer un rôle essentiel dans la capacité des feuillus tempérés à s'établir, en particulier dans la région de la FERLD où le sol présente une texture argileuse et où les mycorhizes associés aux feuillus tempérés, essentielle à la germination, est en grande partie absente (Carteron *et al.*, 2020 ; Collin *et al.*, 2017a, 2018 ; Solarik *et al.*, 2020).

La compétition pour l'accès à la lumière avec les espèces des peuplements hôtes pourrait également jouer un rôle clé dans la limitation de l'expansion des espèces tempérées au sein de la forêt boréale mixte. Par exemple, l'érable à sucre est mieux adapté à l'ombre que l'érable rouge et le bouleau jaune, même si sa croissance augmente avec une plus grande disponibilité de lumière (Beaudet et Messier, 1998). Par conséquent, la capacité de survie et de croissance des espèces tempérées, en particulier l'érable rouge et le bouleau jaune, pourrait varier en fonction de la composition de la canopée. En effet, la quantité de lumière atteignant le sol diffère selon la composition de la canopée en raison de l'interception variable de la lumière par les espèces d'arbres dominantes (Messier *et al.*, 1998). Par exemple, les peuplements purs de peuplier faux-tremble laissent moins de lumière atteindre le sol que les peuplements mixtes ou dominés par des conifères.

De plus, il est impératif de considérer les interactions de compétition pour l'accès à l'espace et aux nutriments, car ces facteurs peuvent jouer un rôle déterminant dans l'établissement des feuillus tempérés au sein de la forêt boréale mixte (Cleavitt *et al.*, 2021 ; Collin *et al.*, 2017a). En général, la compétition intraspécifique est souvent plus intense que la compétition interspécifique en raison de la similarité des niches entre les individus de la même espèce (Adler *et al.*, 2018 ; Aussenac *et al.*, 2019). Cependant, il existe des cas où la compétition interspécifique peut également s'avérer particulièrement délétère. Par exemple, la compétition entre les espèces boréales et les espèces tempérées peut restreindre la croissance des feuillus tempérés en raison de mécanismes biotiques spécifiques, tels que le développement de substrats acides défavorables favorisé par la décomposition des aiguilles et du bois des conifères (Evans *et al.*, 2020 ; Solarik *et al.*, 2020 ; Cleavitt *et al.*, 2021).

Ainsi, la composition en espèces du peuplement hôte s'avère essentielle pour déterminer la capacité de colonisation des feuillus tempérés au sein de la forêt boréale mixte, à la fois en ce qui concerne la compétition pour l'accès à la lumière et celle pour l'espace et les nutriments. Or, la composition en espèces dépend du stade de succession des peuplements, et donc l’intensité de la compétition pourrait être différente selon le stade de succession du peuplement. Au début de la succession dans la région proche de la FERLD, les peuplements sont principalement composés de feuillus tels que le peuplier faux-tremble (*Populus tremuloides* Michx.) et de bouleaux à papier (*Betula papyrifera* Marsh.). Ces peuplements évoluent vers des stades de succession composé de sapin baumier (*Abies balsamea* Mill.), d'épinette blanche et noire (*Picea glauca* Voss et *Picea mariana* Mill.) et de thuya occidental (*Thuja occidentalis* L.) (Bergeron, 2000 ; Chen et Popadiouk, 2002).

Des études à l'échelle du peuplement et du paysage ont montré que l'aménagement forestier, combiné à l'effet des changements climatiques et les perturbations naturelles pourrait améliorer la capacité des espèces tempérées, notamment l'érable à sucre et l'érable rouge, à persister et coloniser de nouveaux peuplements mixtes boréaux, en particulier dans les coupes totales (Boulanger *et al.*, 2019 ; Brice *et al.*, 2019 ; Fisichelli *et al.*, 2014 ; Steenberg *et al.*, 2013). Ces études ont souligné que dans les peuplements en régénération après une coupe, les espèces tempérées ont plus de chances de persister dans la forêt boréale mixte avec un climat plus favorable à leur croissance en raison des changements climatiques. Cependant, Boulanger *et al.* (2019) ont montré que même sous le scénario RCP 8.5 (c'est-à-dire un changement climatique significatif), l'abondance des peupliers faux-tremble sera très élevée dans la forêt boréale mixte après une coupe, réduisant ainsi la capacité des espèces tempérées à croître et à survivre. De plus, Jain *et al.* (2021) ont identifié environ 5% de nouvelles aires potentiellement favorables à l'établissement de l'érable rouge et l'érable à sucre par rapport à leur aire de répartition actuelle dans la région du Saguenay-Lac-Saint-Jean dans un scénario d'augmentation de la température de 2°C. Néanmoins, le rôle de la compétition, de la structure interne des peuplements et des propriétés du sol dans le potentiel de colonisation des feuillus tempérés reste encore mal compris, nécessitant davantage de recherches pour démêler la complexité des facteurs en jeu.

0.3 La modélisation pour comprendre l'évolution temporelles des peuplements forestiers

La modélisation est un élément fondamental de la recherche en écologie forestière, offrant un moyen puissant pour comprendre l'évolution et le devenir des peuplements forestiers (Botkin *et al.*, 1972 ; Cook et Kairiukstis, 1990). Modéliser et prédire comment les peuplements forestiers évolueront au fil du temps en réponse à divers facteurs environnementaux, tels que le climat, le sol, la compétition entre les espèces, et les perturbations naturelles ou anthropiques apparaît primordial dans un contexte de changements climatiques. Dans cette thèse, nous avons exploré deux approches de modélisation distinctes. La première repose sur une analyse statistique pour évaluer la croissance des arbres selon les gradients environnementaux. La seconde est une modélisation mécaniste centrée sur l'individu, permettant de simuler chaque arbre au sein d'un peuplement, avec son établissement, sa croissance et sa mortalité pris en compte. La modélisation mécaniste intègre de façon dynamique la structure du peuplement, ajustant par exemple l'effet des conditions de peuplement sur la compétition au fil du temps. Bien que ces approches diffèrent, elles se complètent en offrant une vision des dynamiques forestières à deux échelles : celle de l'arbre et celle régionale.

0.3.1 Modélisation de la croissance d'un arbre

Dans un contexte de changements climatiques, la modélisation de la croissance des arbres est d'une importance capitale pour comprendre comment les espèces d'arbres évoluent au fil du temps en réponse à divers facteurs environnementaux. Elle consiste à déterminer des gammes de tolérance des espèces en fonction du climat ainsi que d'autres facteurs tels que le sol et la présence d'espèces compétitives. La croissance diamétrale des arbres est un indicateur de performance très utilisés en paléoclimatologie puisqu'il y existe une forte interconnexion entre la croissance radiale des arbres et leur environnement (Copenheaver *et al.*, 2020 ; Moreau *et al.*, 2020a ; Stangler *et al.*, 2016 ; Zhang *et al.*, 2015b). La croissance d'un arbre est généralement maximale au milieu des gradients environnementaux occupés par son espèce et moindre aux extrémités de ces gradients. Par exemple, chaque espèce a une plage de température optimale pour sa croissance (Ryan, 2010).

Pour obtenir des données sur la croissance des arbres, plusieurs méthodes peuvent être employées. La méthode la plus efficace consiste à prélever une carotte ou une tranche transversale du tronc, permettant ainsi la mesure directe de la largeur des cernes ou de la quantité de bois créé par l'arbre. Une autre approche courante consiste à mesurer de manière successive le diamètre des arbres au sein d'une placette permanente, puis à calculer l'accroissement annuel moyen entre deux inventaires. Pour modéliser la croissance des arbres en fonction des gradients environnementaux, nous devons disposer de données environnementales, telles que les conditions climatiques, la composition du sol et la topographie du terrain. Les données climatiques peuvent être collectées sur le terrain à l'aide de stations météorologiques pour caractériser le climat de la placette, ou être estimées à partir de modèles climatiques basés sur les stations météorologiques les plus proches de la placette. Les données relatives au sol et à la topographie proviennent principalement de relevés sur le terrain, bien qu'il existe des cartes des propriétés et de la texture du sol à partir de données de télédétection (Sylvain *et al.*, 2021).

Afin de prédire la croissance d'une espèce, nous avons recours à des modèles qui représentent généralement l'ensemble des courbes de croissance diamétrale en fonction de gradients environnementaux (Cook et Kairiukstis, 1990). Différents modèles statistiques sont disponibles, chacun adapté en fonction des types de données et de la complexité présumée des courbes de réponse (Litton et Zainodin, 1991). L'objectif de ces modèles est de déterminer un jeu de paramètres qui permettent au modèle de s'ajuster au mieux aux observations terrain. Ces paramètres, une fois estimés, influencent la forme des courbes de croissance en fonction des gradients environnementaux. Pour obtenir des courbes en forme de cloche, typiques de la réponse de la croissance des arbres à un gradient environnemental, on transforme la croissance sur une échelle logarithmique puis on intègre des effets quadratiques, c'est-à-dire l'effet de la variable élevée au carré. La combinaison des effets des variables explicatives sélectionnées par le modèle peut être utilisée pour projeter géographiquement les croissances des arbres dans un environnement différent, par exemple dans le futur en utilisant différents scénarios de forçage climatique, ou dans de nouvelles aires en cas de colonisation d'espèces (Goldblum et Rigg, 2005). Cependant cela implique des extrapolations dans des nouvelles conditions qui engendrent des incertitudes considérables.

Certains des facteurs environnementaux utilisés pour modéliser la croissance des espèces peuvent interagir entre eux (Chavardès *et al.*, 2022 ; Coates *et al.*, 2013 ; Oboite et Comeau, 2020). Ces interactions peuvent être complexes et nécessitent une compréhension approfondie de l'écologie des espèces d'arbres modélisées. Par exemple, une augmentation des températures peut stimuler la croissance d'une espèce, mais lorsque cette augmentation de la température est couplée à une diminution de la disponibilité des nutriments dans le sol, l'augmentation de la température peut avoir un effet inhibiteur sur la croissance (Kreuzwieser et Gessler, 2010 ; Mainiero et Kazda, 2006). De même, la compétition entre les arbres au sein d'un peuplement peut varier en fonction des facteurs du sol, du climat ou de la topographie du terrain (Coates *et al.*, 2013 ; Oboite et Comeau, 2020). Par conséquent, la modélisation de la croissance des arbres doit tenir compte de ces interactions pour fournir des prédictions précises.

Parmi les modèles qui peuvent être utilisés pour estimer les courbes de réponses des arbres aux gradients environnementaux, les modèles bayésiens sont de plus en plus utilisés et constituent une alternative aux statistiques fréquentistes (Ellison, 2004). Les modèle baysésiens ont besoin d'une distribution *a priori* sur chaque paramètre du modèle à estimer, cela permet de poser des contraintes sur les valeurs des paramètres à estimer basées nos connaissances antérieures (Etz *et al.*, 2018). Les inférences bayésiennes utilisent des algorithmes de Monte Carlo qui permettent d'échantillonner la distribution *a priori* conjointe des paramètres pour estimer la distribution *a posteriori* des paramètres en considérant les observations (Ellison, 2004). Ces distributions permettent d'obtenir des statistiques descriptives sur les paramètres (moyenne, écart type, médiane, quartile, intervalle de confiance, etc) et ainsi déterminer des incertitudes sur les prédictions, ce qui constitue un réel avantage comparé aux modèles fréquentistes (Wintle *et al.*, 2003).

Souvent, seules les conditions climatiques sont prises en compte dans les modèles environnementaux, alors que la croissance des arbres est également influencée par d'autres facteurs, tels que la compétition intra- et interspécifique, les perturbations naturelles et anthropiques, ainsi que d'autres mécanismes de la dynamique des peuplements forestiers, comme la structure interne des peuplements et la proportion de lumière captée par les arbres voisins. Par conséquent, parallèlement à l'évolution des nouvelles méthodes de modélisation de la croissance des arbres, des modèles à l'échelle du peuplement centrés sur l'individu ont été développés.

0.3.2 Modélisation des facteurs intrinsèques des peuplements

Les modèles de trouée, qui ont été largement développés en foresterie depuis l'étude pionnière de Botkin, Janak et Wallis en (1972), jouent un rôle essentiel dans la modélisation des facteurs intrinsèques aux peuplements forestiers qui influence la croissance, la mortalité et la régénération des arbres. Ces facteurs intrinsèques se réfèrent aux éléments internes aux peuplements, indépendants des conditions extérieures telles que le climat et le sol (Shugart *et al.*, 2018). Les facteurs intrinsèques aux peuplements sont liés aux interactions de compétition entre les arbres qui dépendent de la structure et de la composition du peuplement. La compétition revêt une importance capitale, car ces modèles reposent sur l'hypothèse selon laquelle les interactions de compétition entre les individus constituent les mécanismes prédominants des successions forestières (Watt, 1947). La compétition entre les espèces se manifeste sous diverses formes, allant de la compétition pour l'accès à la lumière à la compétition pour les nutriments du sol (Canham *et al.*, 2004). Ces modèles permettent de simuler les dynamiques de succession des cohortes en prenant en compte la croissance, la reproduction et la mortalité de chaque individu au sein des peuplements. Ainsi, une espèce peut remplacer une autre au sein de la canopée (Shugart et West en 1980, Shugart et al. 2018).

À l'origine, les modèles de compétition n'étaient pas spatialement explicites, principalement en raison de la complexité de la paramétrisation de modèles plus élaborés. De plus, ces modèles ne modélisaient que de petites surfaces (0,01 ha), les ressources informatiques disponibles dans les années 1970 étant limitées. Les interactions de compétition pour l'espace et la lumière se fondaient principalement sur la densité et la hauteur des arbres voisins au sein du peuplement modélisé (Larocque *et al.*, 2016). Par la suite, des modèles spatialement explicites ont été développés. Ces modèles intègrent directement la distribution spatiale des arbres au sein du peuplement (Pacala *et al.*, 1993). En d'autres termes, la position des individus est utilisée pour modéliser les interactions de compétition entre les arbres pour l'accès à l'espace, à la lumière disponible, ou aux ressources du sol, par exemple (Shugart et West, 1977 ; Pastor et Post, 1986 ; Pacala *et al.*, 1993 ; Fischlin et Gyalistras, 1997). Les pressions de compétition exercées par les arbres voisins influencent directement la croissance des arbres, la mortalité et la régénération. La mortalité et la régénération dépendent aussi de processus aléatoires pour les modéliser (Fox, 1993). Les modèles spatialement explicites sont particulièrement adaptés pour étudier les interactions spatiales et les effets de la structuration des peuplements forestiers en fonction du temps.

0.3.3 Le modèle SORTIE-ND

Nous avons utilisé le modèle SORTIE-ND (ci-après SORTIE) pour simuler l'établissement des feuillus tempérés au sein de la matrice boréale mixte, en particulier pour simuler les interactions de compétition entre les feuillus tempérés et les espèces de la forêt boréale. Nous voulions déterminer si la compétition jouait un rôle déterminant dans leur capacité à s'implanter dans cet environnement (Murphy, 2011 ; Pacala *et al.*, 1996). SORTIE-ND est un modèle spatialement explicite à l'échelle de l'individu qui permet de simuler les facteurs intrinsèques aux peuplements. Il calcule la croissance des arbres en fonction d'une croissance potentielle maximale restreinte par l'effet du diamètre des arbres, la quantité de lumière disponible, la compétition pour l'espace et la lumière, ainsi que des effets climatiques, de la même manière que les modèles de croissance. Nous avons choisi le modèle SORTIE pour sa capacité à reproduire efficacement les interactions de compétition entre les arbres et à modéliser l'ensemble du cycle de vie des arbres, de l'état semis jusqu'aux arbres matures et finalement aux chicots. Cette sélection s'est également justifiée par l'adaptabilité du modèle, permettant de représenter de manière réaliste des phénomènes tels que l'allométrie, la croissance, la dispersion et la mortalité des arbres (Benson *et al.*, 2022 ; Bose *et al.*, 2015 ; Maleki *et al.*, 2019).

Dans le modèle SORTIE, chaque arbre est représenté comme une entité discrète dotée de divers attributs tels que le diamètre, la hauteur, la taille de la couronne et l'âge. La croissance diamétrale des arbres est l'équation centrale du modèle SORTIE. En effet toutes les relations allométriques calculés par SORTIE dépendent du diamètre des arbres et donc de l'accroissement diamétrale. Par exemple, la quantité de lumière reçu par les arbres dépend de la dimension de la couronne des arbres adjacents qui dépend du diamètre des arbres (Sattler et LeMay, 2011). Les processus écologiques, comme la croissance, la mortalité et le recrutement des arbres, sont simulés par le biais de modules spécifiques au sein du modèle.

Les caractéristiques des modules, la liste des espèces d'arbres, les valeurs de paramètres, le placement des arbres dans le peuplement comme conditions initiales, les paramètres du peuplements (tels que la taille, la latitude et l'azimut) ainsi que le pas de temps (unités de temps minimales simulées) sont tous définis dans un fichier de paramètres. A chaque pas de temps, SORTIE exécute chacun des processus biophysiques considérés dans un ordre préétabli: calcul de l'exposition lumineuse pour chaque arbre, croissance en diamètre de l'arbre, production de graines, distance de dispersion de ces graines, et mortalité pour les semis et les arbres adultes. Les sorties habituellement utilisé avec SORTIE sont la liste des arbres au cours du temps avec la position des arbres dans le peuplement simulé, le diamètre des arbres, la croissance, la quantité de lumière reçu par les arbres ou la compétition qu'exerce les arbres voisins.

Développer un tel fichier de paramètres requiert beaucoup de données détaillées pour estimer les paramètres de dispersion, de croissance et de mortalité des espèces considérées (Astrup *et al.*, 2008). Un fichier de paramètres a été créé en 2008 pour le territoire de la FERLD qui se trouve dans la forêt boréale mixte de l'ouest du Québec (Poulin et al. 2008; Fig. 0.1). Ce fichier a été majoritairement compilé sur la base de résultats d'études antérieurs pour la paramétrisation de SORTIE dans d'autres zones bioclimatiques mais aussi à partir d'expériences menées à la FERLD (Beaudet *et al.*, 2002, 2011 ; Canham *et al.*, 2004 ; Pacala *et al.*, 1993). Ce fichier de paramètres a été validé et utilisé dans différents contextes tels que l'effet de différentes coupes sur la régénération des peuplements de la FERLD, ou l'impact de la tordeuse de bourgeons d'épinette sur les trajectoires de la dynamique de successions des peuplements de la FERLD (Bose *et al.*, 2015 ; Maleki *et al.*, 2019, 2020). Cependant, certains paramètres pour les arbres tempérés étaient inconnus et ont été calculés grâce à mon travail. De plus, mon travail a permis de considérer des dépendances climatiques plus complexes et réalistes sur la croissance des espèces d'arbre étudiées.

0.4 Objectifs

L'objectif général de ce doctorat était de caractériser les facteurs qui pourraient faciliter ou contraindre la croissance, la survie et l'établissement des feuillus tempérés au nord de leur aire de répartition, en forêt boréale mixte, en considérant spécifiquement la compétition intra- et interspécifique, le climat dans un contexte de réchauffement climatique, le sol et les dynamiques de successions forestières. Le chapitre I avait pour but de paramétriser et de valider le modèle SORTIE-ND pour pouvoir simuler les interactions de compétition entre les feuillus tempérés et les espèces de la forêt boréale. Pour le chapitre II, nous avons inclue les effets de scénarios de changements climatiques sur la croissance des arbres et nous avons évalué la capacité de colonisation des feuillus tempérés à partir d'arbres marginaux en peuplements boréaux. Dans ces deux premiers chapitres, nous avons aussi déterminé le potentiel de persistance des espèces feuillues tempérées lorsqu'elles sont introduites au stade de semis (chapitre I) et leur potentiel de colonisation à partir d'arbres tempérés matures (chapitre II), ainsi que les changements de composition dans les peuplements boréaux mixtes suite à la colonisation d'espèces de feuillus tempérés. L'objectif du chapitre III était de déterminer comment la compétition, la fertilité du sol, le climat et l'interactions entre ces facteurs affectent la croissance des espèces d'arbres communes au Québec, incluant les trois espèces de feuillus tempérés étudiées précédemment et le bouleau blanc, le sapin baumier et l'épinette noire.

CHAPITRE I COMPETITIVE INTERACTIONS UNDER CURRENT CLIMATE ALLOW TEMPERATE TREE SPECIES TO GROW AND SURVIVE IN BOREAL MIXEDWOOD FOREST

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1.1 Résumé en français [Ajout à l'article original]

Avec les changements climatiques, les optima climatiques se déplacent vers les pôles plus rapidement que les processus de migration des arbres, ce qui entraîne une inadéquation entre la répartition des espèces et les enveloppes bioclimatiques. Les espèces d'arbres feuillus tempérés pourraient profiter du relâchement des contraintes climatiques et de la gestion forestière pour migrer vers la forêt boréale. Ici, nous utilisons le modèle de simulation forestière SORTIE-ND pour déterminer le potentiel de persistance de trois espèces tempérées (érable à sucre, érable rouge et bouleau jaune) lorsqu'elles sont introduites au stade de semis dans des peuplements typiques du domaine bioclimatique de la sapinière à bouleau blanc de l'Est du Canada (SBB), en quantifiant les conséquences sur la composition des espèces indigènes. SORTIE-ND est un modèle de peuplement forestier spatialement explicite et individuel qui simule la croissance, la régénération et la mortalité des arbres. Nous avons effectué une nouvelle paramétrisation de l'équation de croissance des arbres de SORTIE-ND permettant l'inclusion de modificateurs climatiques sur la croissance des arbres. Après avoir validé notre modèle avec des données provenant de parcelles d'inventaire forestier permanent, nous avons modélisé la dynamique de peuplements non récoltés à différents stades de succession, ainsi que de peuplements post-récolte, après l'ajout de semis d'érable à sucre, d'érable rouge et de bouleau jaune à différentes densités. Nos résultats montrent que les conditions climatiques actuelles du domaine de la SBB ne limitent pas la croissance et la survie des espèces tempérées dans les peuplements boréaux. Parmi les espèces tempérées introduites, l'érable à sucre avait la plus faible capacité de croissance et de survie à la fin de la simulation. Les assemblages d'espèces des peuplements hôtes ont été affectés par la présence d'espèces tempérées lorsque l'ajout de semis était supérieur à 5 000 semis tempérés par hectare au début de la simulation. Dans les peuplements récemment coupés à blanc, les semis d'espèces tempérées étaient incapables de se développer en raison de la concurrence intense de la régénération des trembles. Nos résultats suggèrent que le climat actuel et les interactions compétitives entre les espèces tempérées et les espèces boréales ne devraient pas empêcher les espèces tempérées de se développer et de survivre dans le domaine de la SBB.

Mots-clés: Simulateur SORTIE-ND, *Acer saccharum*, *Acer rubrum*, *Betula alleghaniensis*, gestion forestière, effet de compétition.

1.2 Abstract

With climate change, climatic optima are shifting poleward more rapidly than tree migration processes, resulting in a mismatch between species distributions and bioclimatic envelopes. Temperate hardwood tree species may take advantage of the release of climate constraints and forest management to migrate into the boreal forest. Here, we use the SORTIE-ND forest simulation model to determine the potential for the persistence of three temperate species (sugar maple, red maple and yellow birch) when introduced at seedling stage in typical balsam fir-paper birch bioclimatic domain stands of Eastern Canada (BF-PB), quantifying the consequences on the native species composition. SORTIE-ND is a spatially explicit, individual-based forest stand model that simulates tree growth, regeneration and mortality. We performed a novel calibration of the SORTIE-ND tree growth equation allowing for the inclusion of climate modifiers on tree growth. After validating our model with data from permanent forest inventory plots, we modeled the dynamics of unharvested stands at different successional stages, as well as post-harvest stands, after the addition of sugar maple, red maple and yellow birch seedlings at different densities. Our results show that current BF-PB domain climate conditions do not limit growth and survival of temperate species in boreal stands. Of the temperate species introduced, sugar maple had the lowest ability to grow and survive by the end of the simulation. Species assemblages of host stands were impacted by the presence of temperate species when the addition of seedlings was above 5 000 temperate seedlings per hectare at the beginning of the simulation. For stands that were recently clear cut, temperate seedlings were unable to grow due to intense competition from aspen regeneration. Our results suggest that both current climate and competitive interactions between temperate species and boreal species should not impede temperate species to grow and survive in BF-PB domain.

Keywords: SORTIE-ND simulator, Acer saccharum, Acer rubrum, Betula alleghaniensis, forest management, competition effect

1.3 Introduction

Global climate change is expected to produce complex impacts on forest ecosystems and tree species distributions (Boulanger *et al.*, 2019; Brice *et al.*, 2019; Brice *et al.*, 2020). Under a warming climate, tree species are projected to migrate poleward, tracking their optimal climatic niche, as temperature and precipitation are known to shape the geographical range of tree species at the global scale (Morin *et al.*, 2008 ; Lee-Yaw *et al.*, 2016). At the local scale, other factors influence tree species distributions, including edaphic conditions, biotic mechanisms, and dispersal abilities (Fisichelli *et al.*, 2012; Solarik *et al.*, 2019). Consequently, we observe a lag between shifts of bioclimatic envelopes and occupancy of these envelopes through migration. In particular, tree species with limited dispersal and late sexual maturity may be at greater risk of not keeping pace with high climate change velocity (Aitken *et al.*, 2008 ; Boisvert-Marsh *et al.*, 2014 ; Solarik *et al.*, 2016).

The Canadian boreal mixedwood forest ecotone is composed of two distinct bioclimatic domains: the balsam fir-yellow birch (BF-YB) bioclimatic domain at the south and the balsam fir-paper birch (BF-PB) bioclimatic domain at the north (Saucier et al., 1998, Fig 1.1). The BF-PB domain corresponds with the northern limit of the temperate species sugar maple (*Acer saccharum* Marsh.) and yellow birch (*Betula alleghaniensis* Britt.)(Saucier *et al.*, 1998, 2003). The northern limit of red maple (*Acer rubrum* L.) is in the spruce-moss forest, further north (Tremblay *et al.*, 2002). In the BF-PB domain, only marginal stands of these temperate species can be found on the top of hills where, due to frequent temperature inversions, climatic conditions are more favorable than in lower elevation plains and valleys (Jin *et al.*, 2008). In addition, soil microsites on hilltops tend to be more favorable for the germination and growth of temperate tree species because of better drained soils (Goldblum et Rigg, 2002). All three temperate species can maintain and reproduce in these marginal stands, but severe spring frost and low temperature during the growing season are known to affect their reproductive capacity (Tremblay *et al.*, 2002 ; Drobyshev *et al.*, 2014 ; Graignic *et al.*, 2014). These marginal and isolated stands could act as seed sources, facilitating the colonization of temperate species from the BF-YB domain into the northern prevalent conifer matrix.

Even though the future climate may promote a northward expansion of temperate species into BF-PB domain (Fisichelli *et al.*, 2014; Evans and Brown, 2017; Boulanger *et al.*, 2017; Taylor *et al.*, 2017), other edaphic and biotic factors, natural disturbances, and forest management activities could influence their migration success and rate (Lee-Yaw *et al.*, 2016; Boulanger *et al.*, 2018; Solarik *et al.*, 2020; Carteron *et al.*, 2020). For instance, competition of boreal species with temperate species may limit their northward expansion due to specific biotic mechanisms, such as the development of unfavorable acidic substrate with the decay of conifer needles and wood (Solarik *et al.*, 2020; Evans *et al.*, 2020; Cleavitt *et al.*, 2021). Light competition could also be a limiting factor for temperate species expansion. Sugar maple is more shade tolerant than red maple and yellow birch, but its growth still increases with light availability (Beaudet and Messier, 1998). Therefore, the ability of temperate species to grow and survive, especially red maple and yellow birch, may vary under different canopy compositions due to variability in canopy light interception (Messier *et al.*, 1998). Temperate species could take advantage of gap dynamics created by natural disturbances or forest management in stands of the BF-PB domain due to the reductions in competitive pressure for light and space (Kellman, 2004; Gasser *et al.*, 2010; Bannon *et al.*, 2015).

Modeling species distributions under climate change is an important and challenging task for understanding and predicting the fate of future ecosystems and natural resources. The most widely used tools to predict future species distribution are Species Distribution Models (SDMs), largely based on bioclimatic envelope modeling (Guisan et Thuiller, 2005). They are used to derive probabilities of occurrence in current and new geographical areas with climate change. Although SDMs can model species distributions at large-scales, SDMs are criticized because they generally only consider climatic variables and neglect biotic interactions, natural disturbances and other mechanisms of forest stand dynamics (Pellissier *et al.*, 2012; Heads, 2015). Some of these shortcomings can be mediated using process-based stand simulation models. Such models, which simulate the demographics of individual trees in a stand, are capable of simulating forest succession by considering competitive interactions for resources between trees (e.g., light and space) (DeAngelis and Grimm, 2014; Maleki *et al.*, 2019). Spatially explicit stand simulators model direct interactions between trees by considering their specific spatial positions, thus directly accounting for competition for light and space among trees. Further, these models simulate tree seed dispersal, recruitment and mortality using probabilistic approaches to evaluate changes in stand demography (Shugart and West, 1977; Pacala *et al.*, 1993; Shugart *et al.*, 2018).

In this study, we use a forest stand simulation model to estimate the ability of temperate tree species to grow and survive under current climate conditions in Western Quebec BF-PB domain stands where they are currently absent. We simulated stand dynamics of the BF-PB domain along a gradient of stands characterized by different ages and composition, from young pure aspen stands to older coniferous dominated stands, representative of the regional landscape. Within each stand we "added-in" different seedling densities of our target study species, i.e., sugar maple, red maple, and yellow birch. We estimated the specific impact of initial seedling density on the resultant species assemblages (based on basal area) over 110 years duration simulations (1991 to 2100) keeping constant climate. The main objectives of this study were threefold: (1) to assess if current climatic conditions in the BF-PB domain may inhibit the growth and survival of temperate tree species; (2) to determine the role of intra- and interspecific competition on the resultant basal area of temperate trees through time (2.a) considering different successional stages and (2.b) stands that have been harvested or not; and (3) to determine the impact of the introduction of temperate tree species on native boreal tree communities.

1.4 Material and methods

1.4.1 Study area

The simulated study area is located in the Lake Duparquet Research and Teaching Forest (FERLD) in the Abitibi region of western Quebec, Canada. The growing season (May to September) is characterized by a mean temperature of 14°C and cumulative precipitation of 447 mm (mean from 1970 to 2019). The FERLD is located within the BF-PB domain (Fig. 1.1). The study landscape is fragmented by multiple past fire events staggered through time and space resulting in a mosaic of different stand compositions from shade-intolerant species to late successional coniferous stands. Early succession stands are primarily composed of trembling aspen (*Populus tremuloides* Michx.), paper birch (*Betula papyrifera* Marsh.) and jack pine (*Pinus* *banksiana* Lamb.), and are replaced by balsam fir (*Abies balsamea* Mill.), white spruce (*Picea glauca* V.) in mid-successional mixedwood stands and white cedar (*Thuja occidentalis* L.) in late successional stands (Bergeron, 2000; Chen and Popadiouk, 2002). Spruce budworm (*Choristoneura fumiferana* Cle.) outbreaks affect coniferous species, especially balsam fir and create gaps that early succession species may colonize (Kneeshaw and Bergeron, 1998; Bergeron *et al.*, 2014). Concerning the three studied temperate species, red maple was scarcely present in the area, and sugar maple and yellow birch were absent.

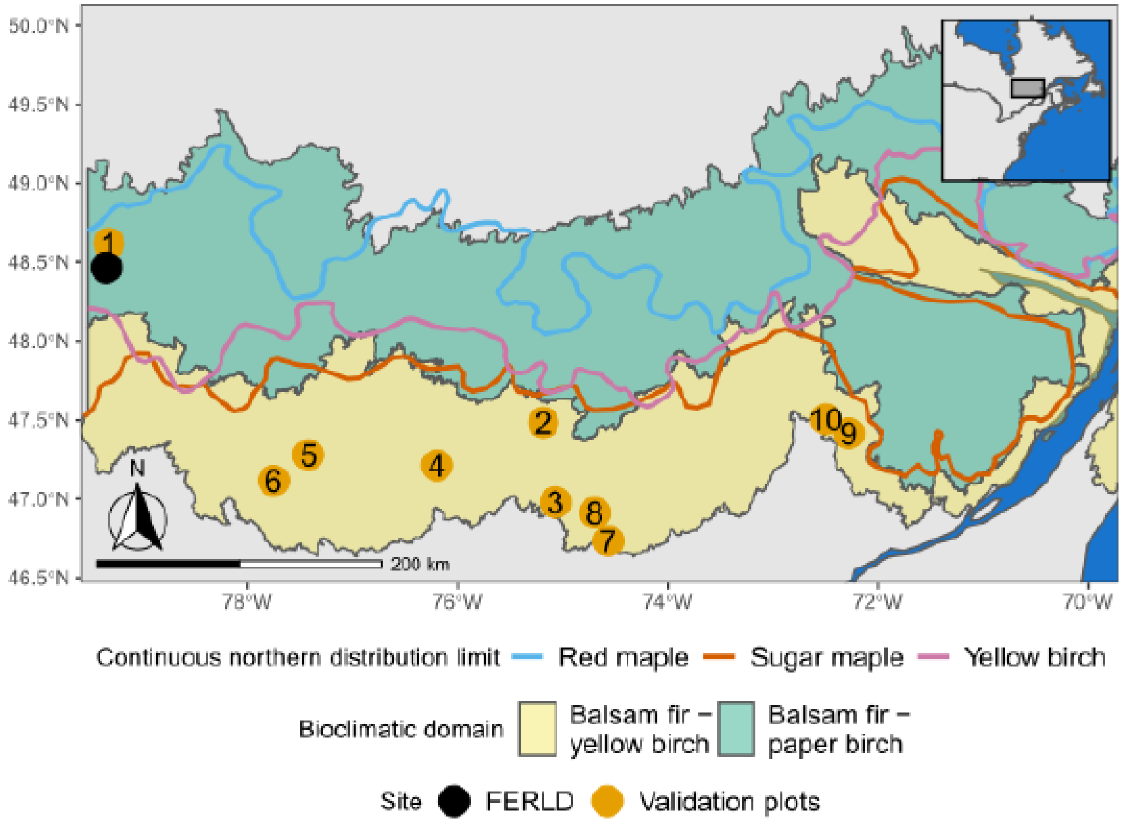


Figure 1.1: Map of the study area with points representing the location of the Lake Duparquet Teaching Research Forest (FERLD, in black) and the government permanent forest inventory plots used to validate the model (in orange). Numbers within dots correspond to the validation plots in Fig. 1.1. Bioclimatic domains and distribution limits of the temperate tree species are depicted as polygons and lines respectively (C. Morneau, personal communication, 2022).

1.4.2 Model description and general application

The simulations were conducted with the SORTIE-ND model (hereafter SORTIE; version 7.05; Pacala *et al.*, 1996; Murphy, 2011). SORTIE is a spatially explicit, individual-based model that simulates stand dynamics by modeling the whole life cycle of trees within a stand (i.e., seedling, sapling, adult, and snag). Each tree is modeled as a discrete object with different attributes such as diameter at breast height (DBH), height, crown dimension and age. Ecological processes, such as tree growth, mortality and recruitment are simulated by specific modules within the main model. Modules, tree species lists, parameter values, tree initial conditions, local conditions (plot size, latitude, azimuth) and time step (minimal time units simulated) are specified in a parameter file. Time steps in SORTIE are generally one year, but can be longer. Within a timestep, SORTIE executes each biological-physical process considered in a predefined order: calculation of light received by each tree, diametrical tree growth, the number of seeds produced, their dispersal distance, and mortality for both seedlings and trees. Initial conditions can be set in the SORTIE parameter file by indicating the number of trees per hectare for each 2cm DBH class and species. SORTIE then randomizes tree positioning in the simulated plot. Alternatively, the position of each tree can be specified. We consider SORTIE is a good candidate model to address our research objectives as it is flexible, permitting us to capture more realistically tree allometry, growth, dispersion and mortality using non-linear relationships and stochastic processes (Bose *et al.*, 2015; Maleki *et al.*, 2019; Benson *et al.*, 2022).

Supporting Information A.1 and A.2 describe the SORTIE submodels and our implementations. In Supporting Information C and D, parameter values for yellow birch, red maple and sugar maple can be found along with six additional boreal tree species composing the BF-PB domain: trembling aspen, paper birch, balsam fir, white spruce, jack pine and white cedar. Tree allometry parameters, as well as those describing tree mortality and recruitment modules, were obtained from previous studies using SORTIE for those species (see references in Supporting Information D). To account for climatic effects on the tree growth of each species, as well as interspecific competition between temperate and boreal species, we produced a new parameterization of the adult growth modules of those species. We then validated our SORTIE parameterization by comparing simulations with independent data. Finally, we used the model to simulate the persistence of introduced temperate species seedlings in current climate conditions, with initial conditions based on a successional chronosequence of BF-PB domain stands at FERLD (Fig. 1.1). In each initial conditions, we added different densities of temperate seedlings at the beginning of each simulation. Each of these steps is described in detail in the following sections.

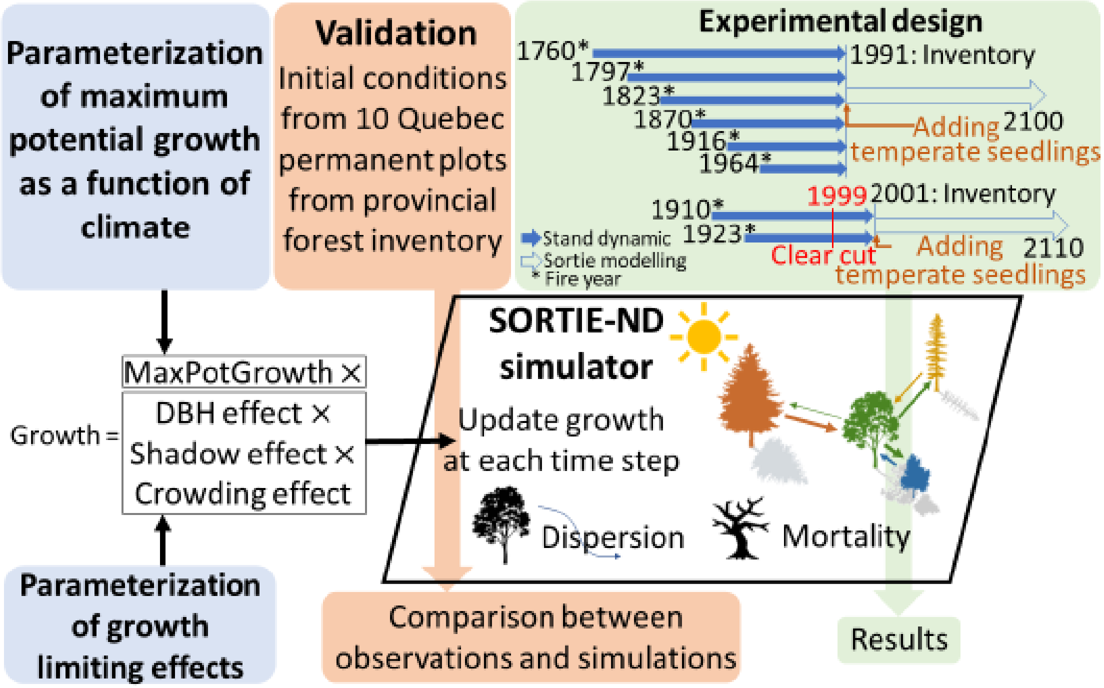


Figure 1.2: Conceptual framework of the model and the experimental design used in this study. The model has been parameterized in two steps represented by the two blue frames. Validation process is represented in orange frame, a map of the validation sites can be found in Fig. 1.1. The experimental design is represented in the green frame, where a timeline of the FERLD forest stands used for initial modeling is represented.

In each stand, different densities and combinations of temperate species has been added in the BF-PB domain stands.

1.4.3 Parameterization of the SORTIE growth model

We used the growth module in SORTIE, based on a Neighborhood Competition Index (NCI), to represent the growth of adult trees, i.e, trees ≥10cm DBH. This module simulates tree growth through time (diameter at breast height increment in cm·yr^{-1}, DBHI) as a proportion of maximum potential growth (*MaxPotGrowth*), which may be achieved under optimal growing conditions. In our study, *MaxPotGrowth* parameter varies as a function of climate to account for differences in tree growth between plots and inventory years, and simulate more accurately the tree growth across different forest domains. The realized growth were obtained by multiplying this potential growth by different limiting effects taking values between 0 and 1, representing the effects of tree size, shading from other trees, and non-light-based competition or "crowding" effects (Canham et al., 2004; Equation 1).

$$DBHI\,(cm.yr^{-1}) = MaxPotGrowth \times size\,effect \times shading\,effect \times crowding\,effect \tag{1}$$

We parameterized Eq.1 in two steps. First, we parameterized the effect of tree size, shading and crowding on tree growth with a hierarchical Bayesian model, using data from the RESEF Quebec forest monitoring network ("Réseau d'Étude et de Surveillance des Écosystèmes Forestiers"), which is a network of 1-ha plots across Quebec where trees were inventoried every 5 years from 1986 to 2020, and where the position and DBH of all trees in the plot is known. In this study, we retained 37 RESEF plots where temperate tree species coexisted with boreal tree species. We also added to the RESEF data 6 additional mapped 1-ha plots located in the FERLD, which have been inventoried 5 times since 1991 (Maleki *et al.*, 2021). The full parameterization dataset for our growth model thus included 43 plots, 19 184 different trees, for a total of 72 964 DBH observations. In this final dataset, all possible couples of species interactions were represented, so that SORTIE could adequately be parameterized.

Secondly, we estimated *MaxPotGrowth* as a function of four climate variables: mean annual temperature (MAT), growing degree days (DD5), mean summer precipitation (MSP) and summer climate moisture index (CMI). Because the RESEF plots are only located in Quebec and because the bioclimatic distributions of the considered species also lie outside of Quebec, we used an extensive network of inventory plots located across eastern North America to capture the whole species bioclimatic range. We used tree growth measurements from 4067 permanent forest inventory plots located across eastern North America including 21 647 trees. We modeled tree growth as a function of climate using quantile Bayesian regression with the 95th percentile of observed growth as a substitute for the mean expected growth in the absence of competition. This second step also served to assess whether current climate conditions would be a limiting factor to tree growth affecting the performance of temperate species in the studied boreal stands (Objective 1; see Supporting Information B for additional information).

In our parameterization of SORTIE, seedling and sapling growth only depends on the amount of received light which is computed based on the crown space of neighboring trees. The species-specific sensitivity of seedling and sapling growth to light was parameterized previously (Pacala *et al.*, 1994; Poulin *et al.*, 2008). The resulting growth rate also determines their mortality probability.

1.4.4 Validation of the SORTIE model

Before executing our simulation experiments, we first verified if SORTIE, with the new tree growth parameterization, was able to reproduce observed stand dynamics. To do so, we used data from the permanent forest inventory network provided by the Quebec Ministry of Forests, Wildlife and Parks (MFFP; Fig. 1.1). These comprise of 400-m^2 circular plots sampled on average every 10 years from the 1970s onwards. At each inventory date, various data are collected on trees and saplings (e.g., composition, DBH) and of environmental attributes (e.g., soil conditions, topography, understory composition). We extracted the species and size distribution ($trees \cdot ha^{-1}$ for each species and size class) of trees and saplings of 10 permanent plots with repeated measurements for the validation process. The plots were selected according to the following criteria: they must be located within the boreal mixedwood forest in western Quebec (BF-PB and BF-YB domains); the studied species were present (i.e., sugar maple, red maple, yellow birch, paper birch, trembling aspen, jack pine, balsam fir, white spruce and white cedar); temperate tree species co-existed with boreal tree species; and did not experience any major disturbances such as wildfires, logging or insect outbreak between the first and last inventory.

The first inventory date in each plot were used as initial conditions for the SORTIE simulations, with the position of each individual trees randomized respecting the DBH distribution of each species by SORTIE. This step was done automatically as an option in SORTIE if x-y coordinates of each tree are not available. The length of the simulation was equal to the number of years between the first inventory and the last inventory, so that the simulation ended at the last inventory of the plot. We recorded tree DBH, growth and spatial coordinates over time in the simulations and we extracted results only for the years where an inventory took place. For this validation exercise, the size of the simulated plots was 4 ha (200 m x 200 m) and they were divided into

100 subplots of 400 m^2 to obtain 100 replicates at the same size of the observed plots. It was important to get replicates inside the simulation plots because SORTIE randomized the position of trees in the plot. Each replicate had different initial tree composition that may lead to different results at the end of the simulations. All these results were compared with the observation.

We evaluated SORTIE model performance by assessing the ability of the model to reproduce species assemblages observed in the validation plots using the following steps. We first performed a principal component analysis (PCA) of the adult basal area per hectare of each species (multivariate response) across all validation plots (observations and simulations). PCA was used to characterize stand species assemblages by deriving the position of each plot (observations and simulations) in multivariate space. For each simulation, we extracted the Euclidean distance between the observation position or the simulated subplots, and the centroid of the corresponding simulated subplots. We considered the simulations consistent with the observed data if the distance between the observation and the centroid was within the nearest 95% of the distances between simulated subplots and their centroid.

1.4.5 Simulation experiment design

For our simulation experiment, we obtained initial conditions for the SORTIE simulations from plots in the FERLD territory where tree DBH was sampled in a 400 m^2 area (Maleki *et al.*, 2021). These plots were unharvested post-fire stands and harvested stands representing different successional forest stages and tree compositions (Maleki *et al.*, 2021). Unharvested post-fire stands included plots with the following years of last fire: 1760, 1797, 1823, 1870, 1916 and 1964 (Fig. 1.2). Plots were inventoried in 1991 following a spruce budworm outbreak. We considered dead balsam fir, which is the primary host of the spruce budworm in that area, as alive in our initial conditions to remove the potential effect of spruce budworm outbreak (Bergeron *et al.*, 1995). Two post-harvest stands that underwent clearcutting in 1999 were inventoried two years later, representing our initial conditions for harvested stands (Brais *et al.*, 2013). These post-harvested stands originated by previous fires in 1910 and 1923. We extracted the mean density per species and DBH class of 153 available plots to initialize 8 stands for the SORTIE simulations (6 unharvested regenerated after specific fire years and 2 harvested in 1999; Supporting Information Table A.8).

At the beginning of each simulation for each initial stand, we added a variable number of temperate seedlings of sugar maple, red maple, yellow birch or all three species. Three seedling densities were considered: a low-density experiment (500 seedlings per hectare), a medium-density experiment (5 000 seedlings per hectare), and a high-density experiment (10 000 seedlings per hectare). The number of seedlings for the high-density corresponds to one seedling per m^2; we note that the density of temperate seedlings could be higher, i.e., more than 100 000 seedlings per hectare in particular conditions (Henry *et al.*, 2021). However, such a high density leads to a very high seedling mortality and unnecessarily prolongs simulation times. For the medium- and low-density, we choose to have two times less the higher density and twenty times less, respectively. For the "all species" scenario, the density levels above are applied to each temperate species, leading to an overall seedling density three times higher than the single species scenario. A simulation without introduced temperate seedlings was also executed as a control. For the simulation experiments, the size of the simulated plot was 1 hectare and we let the model randomize the position of trees at the beginning of the simulation. Because we used the option of SORTIE that randomized tree positions, we divided the simulated 1 ha plot into 25 subplots of 400 m^2 to have a range of plausible simulated results to analyze. We set the timestep as one year but recorded tree coordinate, DBH, and growth every 5 years to reduce memory requirement.

Basal areas at the last timestep (after 110 years of simulations, i.e., from 1991 to 2100 with constant climate) were extracted to assess the capacity of temperate trees to grow and survive in stands of the BF-PB domain. We compared these basal areas under the different conditions simulated, i.e., with different initial seedling densities (Objective 2), at different stages of BF-PB stand dynamics (Objective 2.a) and in harvested and unharvested stands (Objective 2.b). To investigate the effect of temperate species establishment, growth and survival, on native assemblages of the BF-PB domain (Objective 3), we built a multivariate space using PCA analysis with the simulated basal area of all species in all simulations and time steps. For each simulation, we then extracted the position of each timestep in multivariate space and plotted the trajectory through time of the different simulations in the multivariate space, defined by the first two principal components. We compared the level of departures of these trajectories to that of the control group to assess the impact of temperate trees presence on the species assemblages in the stands.

1.5 Results

1.5.1 Climate effect on temperate species growth

MaxPotGrowth were equal to 0.66 $cm \cdot yr^{-1}$ for sugar maple, 0.50 $cm \cdot yr^{-1}$ for red maple and 0.85 $cm \cdot yr^{-1}$ for yellow birch in the current FERLD climate, north of their continuous distribution range. Those parameter values were high enough to allow them to grow and survive in BF-PB domain (Supporting Information Fig. A.7 and Fig. A.8). Consequently, current climate conditions were not an important limiting factor.

Growing degree days (DD5) was the climate variable with the major influence on MaxPotGrowth for all species (Fig. 1.3).

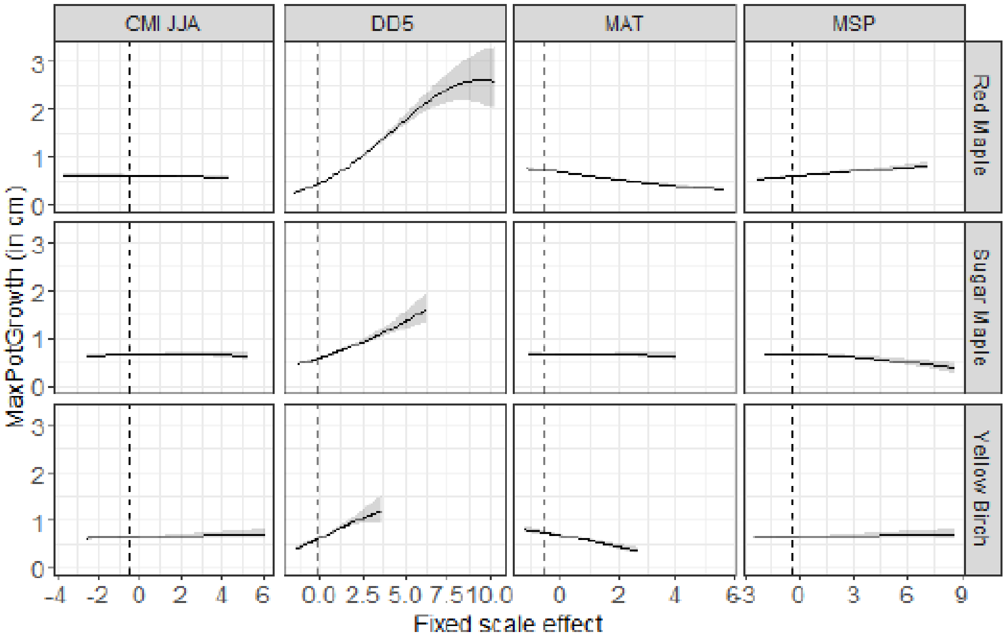


Figure 1.3: Climatic effects of the quantile Bayesian regression used to find maximum potential growth for temperate species. Values of the X axes correspond to the standardized climate variables (see panel column name). CMI JJA: Climate moisture index for the month of June, July and August, DD5: annual growing degree days, MAT: mean annual temperature and MSP: mean summer precipitation. The dashed vertical line represents present climate at the FERLD study site.

1.5.2 Model validation

SORTIE simulations of species assemblages by basal area were consistent with observations given that species assemblages were included in the 95% simulated interval for 9 out of 10 observed plots (Fig. 1.4). Plot 9 deviated from observations as the simulated basal area of balsam fir was slightly overestimated (Fig. 1.4.a, Supporting Information Fig. A.4). The simulations did not reproduce the full range of variability in observed tree growth, which is to be expected since SORTIE does not include all sources of stochasticity on tree growth, but the comparison of simulated and observed growth of each species showed no systematic under- or overestimation of growth (Supporting Information section F).

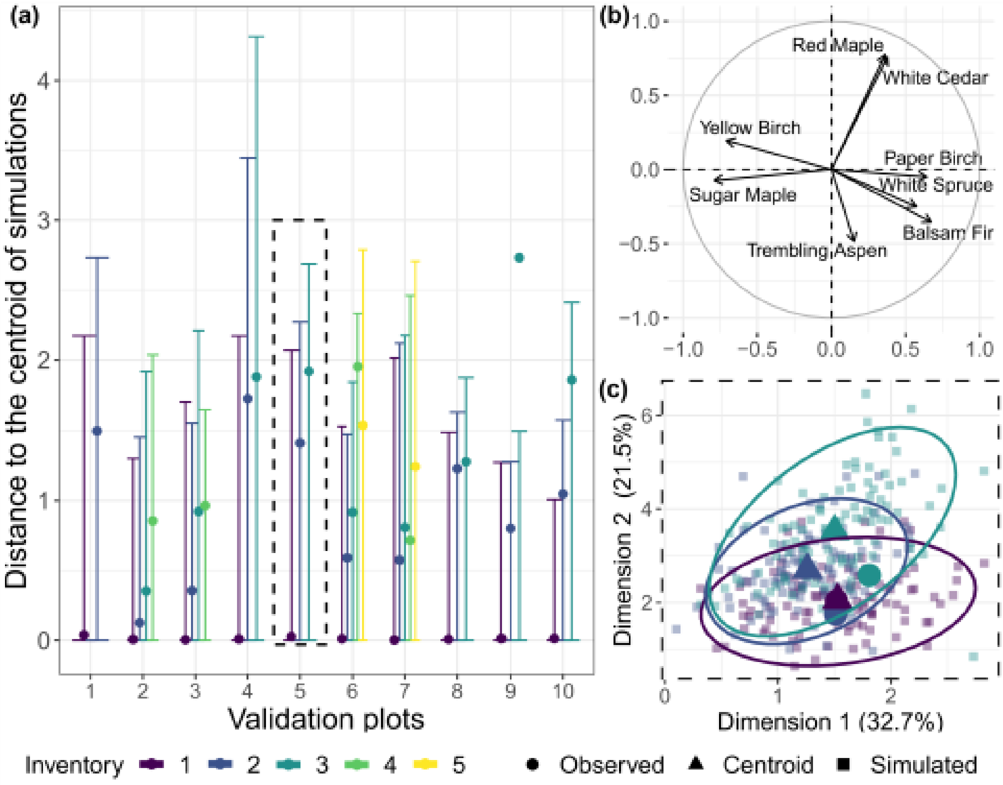


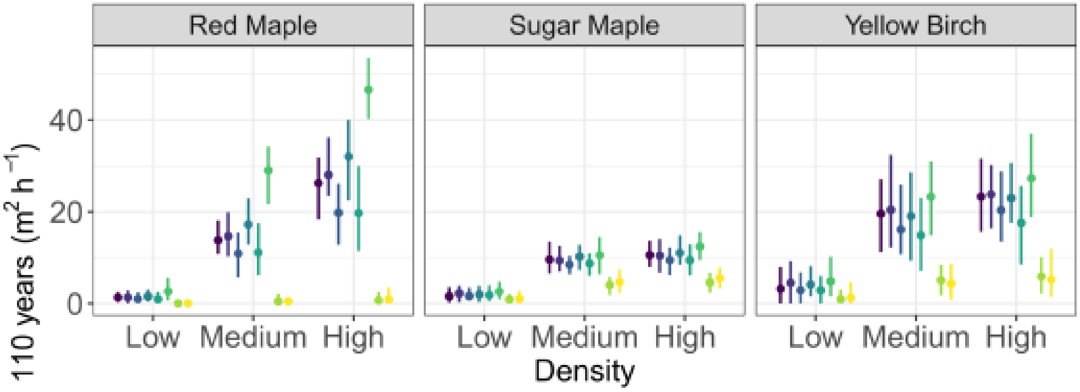
Figure 1.4: (a) Distance of the observed plot composition (point) and of the simulated subplot compositions (error bar, encompassing 95% of the simulations) to the centroid of simulated subplot compositions for the same plot and inventory date. The multivariate space was constructed by PCA with the simulated basal area ($m^2.ha^{-1}$) of all species in the validation plots located in the BF-YB stands. (b) Arrows showing the contribution of the basal area of each species on the main two axes of the PCA. (c) An example of the construction of the metrics presented in (a). First, the simulated basal area across replicated subplots is projected for each inventory (squared colored points). Second, the centroid of simulated points is computed by inventory (triangle points). Third, the observation points for each inventory are projected in the multivariate space (round points). Finally, the Euclidean distances between the centroid of the simulated subplots and the observation are calculated for each inventory. In (c), the orange triangle and the circle are superimposed since the centroid of the simulations

corresponds to the observation at the beginning of the simulation, i.e., for the first inventory.

1.5.3 Growth and survival of temperate tree species in BF-PB stands

The simulated adult basal area of temperate tree species at the last time step (110 years) indicated that all temperate species can grow and survive in the stands of the BF-PB domain under most simulated conditions (Fig. 1.5). Yellow birch displayed a higher basal area than sugar maple and red maple, indicating that yellow birch would be the most suitable species to grow and survive in the simulated stands. In harvested stands, yellow birch and sugar maple showed a lower basal area than in unharvested stands, while red maple did not survive in harvested stands after 110 years.

(a) Adding **one** temperate tree species



(b) Adding **all** temperate tree species

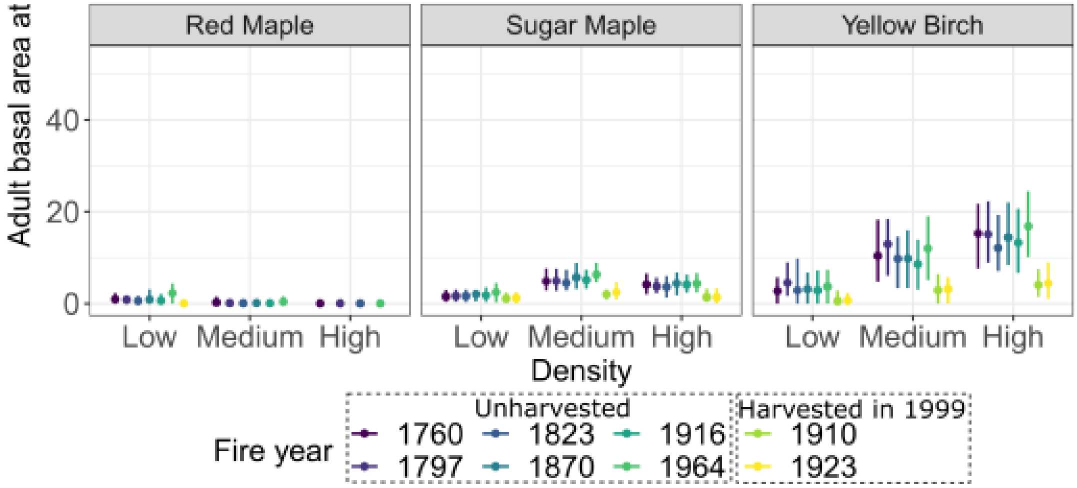


Figure 1.5: Simulated adult basal area at the last simulation timestep (110 years) for temperate tree species in stands of the BF-PB domain. Simulations consider different initial conditions relative to time since stand-replacing fire, harvesting, and density of added temperate seedlings (one species at a time (a) or all species together (b)). Low, medium and high densities seedlings correspond to 500, 5 000 and 10 000 seedlings per hectare respectively. Error bars are intervals containing 95% of the subplots in each simulation.

When temperate trees were simulated separately in unharvested stands, their basal area after 110 years increased according to their initial seedling from low- to medium-density. However, when going from a medium- to a high-density, only the basal area of red maple increased, whereas the two other species remained constant (Fig. 1.5 and Fig. 1.6). In harvested stands, the basal area of yellow birch and sugar maple increased between low- and medium-density, but not between medium- and high- seedling densities whereas red maple basal area remained constant with increasing density.

The adult basal area of temperate species was lower when they are added altogether than alone in harvested and unharvested stands (Fig. 1.5.b). In these conditions, yellow birch basal area increased with density; sugar maple basal area increases from low- to medium-density, but remained constant for higher density; and the basal area of red maple decreased with increasing seedling density up to extinction under high initial densities (Fig. 1.5.b).

The basal area of temperate trees did not vary with the successional stage of the stand at the beginning of the simulation (time since last fire). However, for the younger stand (fire of 1964), basal area for red maple was higher than other stands (Fig. 1.5.a).

1.5.4 Effect of temperate tree introduction on native BF-PB assemblages

The presence of temperate species had an impact on the native species composition of BF-PB domain stands, except under low temperate seedling densities (Fig. 1.6). Time trajectories of the control simulations move in the multivariate space from stands with high presence of aspen towards stands with abundant white cedar and balsam fir typical of old forests in the study region. When adding a low-density of temperate seedlings in the unharvested stands, the trajectories shifted in the same direction as the control group, which means that the stand assemblages remained similar between the control group and the low-density group. In contrast, we observed important differences between control stands and stands with medium to high seedling densities. The trajectories of stands with medium to high seedling densities shifted towards regions of the multivariate space that are correlated with high basal areas for the temperate species, indicating that temperate species have persisted in these stands. Furthermore, when adding red maple and yellow birch seedlings, the assemblages of stands at medium to high densities were similarly distributed in the multivariate space, indicating that an increase in density from medium to high did not further alter the species composition of the stands.

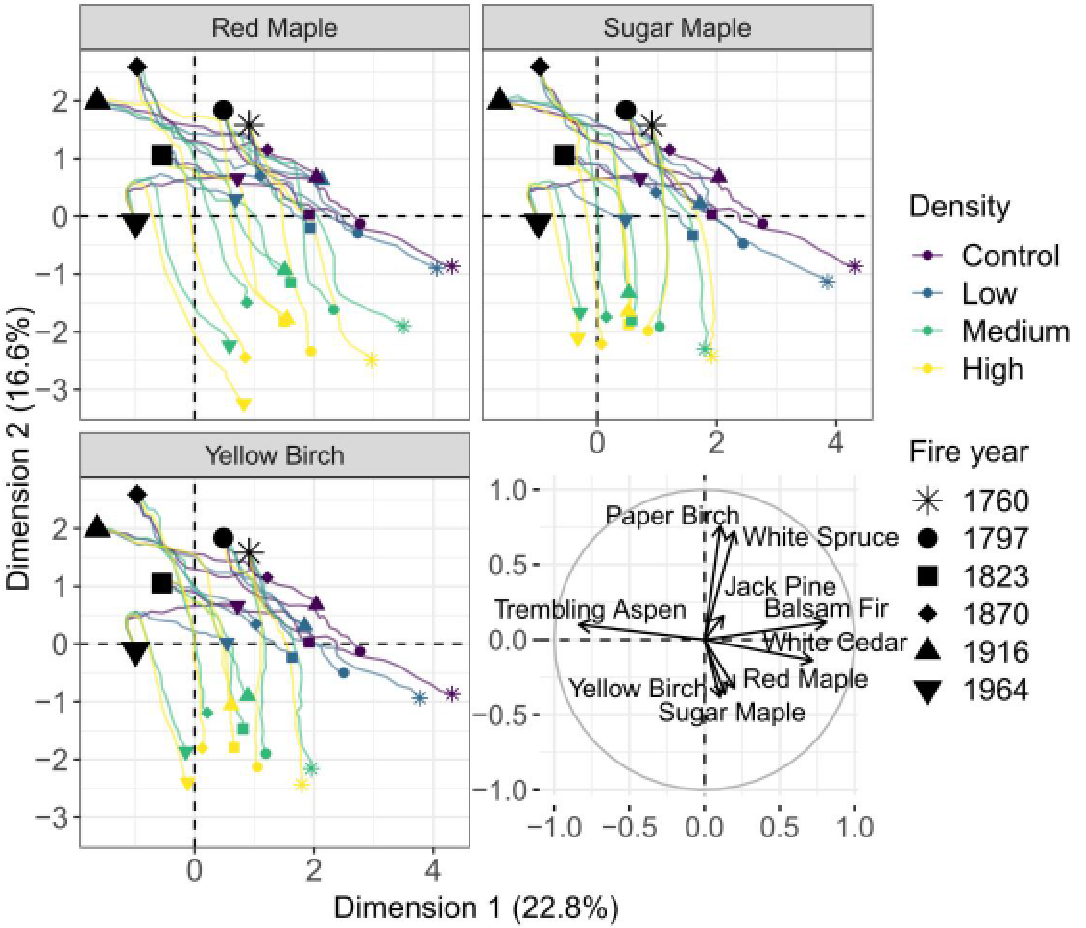


Figure 1.6: Simulated trajectories of stands assemblage in a multivariate space. The principal component analysis (PCA) is based on the basal area of adult trees across all simulation results. In each panel, various trajectories represent the chronology of the stands depending on the density of seedlings added in the BF-BP stands. The control group corresponds to simulations with no temperate tree species. Black dots correspond to the position of initial conditions in the multivariate space, and colored dots correspond to the results of the simulation at the last time step (110 years). This figure only displays unharvested stands given the low ability of temperate tree species to grow and survive in recently harvested stands.

1.6 Discussion

In this study, we proposed a new parameterization of the SORTIE stand simulation model that allowed us to account for climate effects on growth as well as spatial interactions between trees in growth calculations. We aimed to assess whether sugar maple, red maple and yellow birch could grow and survive in stands of the balsam fir-paper birch bioclimatic domain (BF-PB) and what effect this would have on native species that currently dominate these stands. After parameterizing and validating the model, we showed that temperate tree species could grow in current climate conditions of the BF-PB domain and persist in most stands we simulated after introduction.

1.6.1 Persistence of temperate species introduced in boreal mixedwood stands

The *MaxPotGrowth* parameter values of all temperate species were sufficiently high to allow them to grow in the current climate conditions of studied stands in the BF-PB domain (Supporting Information Fig. A.7; Leites et al., 2019; Brice et al., 2020). Maximum stand density is influenced in SORTIE by the impact of inter- and intraspecific competition on the mortality, i.e., the more the stand is crowded, the more the competition is intense for light and space with higher juveniles and adults mortality rate (Bergeron *et al.*, 2014). We showed that increasing temperate seedling density at the beginning of the simulation does not vary linearly with the basal area at the end of the simulation. When adding sugar maple and yellow birch in medium- and high-density, stands reached the maximum density for those species that can be supported. The addition of extra seedlings did not lead to higher final basal area.

Red maple has the lowest *MaxPotGrowth* parameter value but the highest capacity for growth and survival in stands with medium- and high- seedling density, indicating the importance of competitiveness, and its low mortality and high regeneration rates (Supporting Information Fig. A.8; Power *et al.*, 2019). Yellow birch was the temperate species with the higher ability to persist when introduced in unharvested and low-density stands with its higher growth rate and thus higher basal area at the end of the simulation. In medium- and high-density stands, self-thinning of red maple was lower than that of sugar maple and yellow birch (supporting information Fig. A.7 and Fig. A.8), resulting to greater ability for red maple to persist when introduced in these stands as reported by other studies (Andrews *et al.*, 2018; Boulanger *et al.*, 2019). Except for the younger stand, initial composition of stands seems to have little effect on the temperate tree species performance in unharvested stands indicating that the establishment of seedlings on appropriate seedbeds is probably the most critical process in the mixedwood boreal forest (LePage *et al.*, 2000; Charron and Greene, 2002; Solarik *et al.*, 2020).

1.6.2 Implications for forest management and native boreal species assemblages

Unexpectedly, temperate species had a lower performance in harvested stands, despite more favourable light conditions and the absence of adult trees (Boulanger *et al.*, 2019). On clay soils like those at the FERLD site, trembling aspen colonize harvested stands and any gaps rapidly after disturbances through root suckering (Landhäusser *et al.*, 2010). The high-density and growth of trembling aspen in harvested stands leads to a high level of seedling competition with neighboring trees (Bergeron *et al.*, 2014). This high competition intensity from trembling aspen leads to high seedling mortality for the temperate trees, reducing their basal areas in harvested stands.

When temperate seedlings were added to the younger stand, i.e. the stand re-initiated in 1964, temperate species could persist better than in older stands, especially red maple. This stand had a lower initial total basal area (all species combined) since the stand was 27 years old when sampled. In this stand, temperate seedlings do not suffer from as much competition by trembling aspen seedlings and saplings, since the aspen cohort is already mature. The ability of temperate species to persist in stands may be higher in managed forests if temperate species colonize a sufficiently mature stand. Modeling studies at stand and landscape scales have shown that forest management coupled with climate change improved the ability of temperate species, particularly sugar maple and red maple, to persist when introduced in boreal mixedwood stands, especially in clearcuts (Steenberg *et al.*, 2013; Fisichelli *et al.*, 2014; Boulanger *et al.*, 2019; Brice *et al.*, 2020). These studies emphasized that in stands regenerating from forest management, temperate species are more likely to persist in the boreal mixedwood forest with a climate favorable to their growth due to climate change. Boulanger *et al.* (2019), however, showed that even under RCP 8.5 (i.e. significant climate change), aspen abundance will remain very high in the boreal mixedwood forest after clearcutting, reducing the ability of temperate species to grow and survive.

According to our simulations, when medium and high seedling densities of a single temperate species are added to the stands, their survival has major consequences for the native species assemblage. Temperate species co-exist with the other species in the stands at the detriment of late-successional boreal species such as white cedar and balsam fir (Fisichelli *et al.*, 2014; Frelich *et al.*, 2021). In medium- and high- seedling density simulations, stands were at the maximum density they could attain, and high mortality rate occurred for boreal tree species.

1.6.3 Other potential impediments on the northward expansion of temperate species

Our results show that current climatic conditions and interaction with boreal species may permit temperate species to grow and survive in the simulated BF-PB domain stands. However, these results do not indicate that all BF-PB domain will be dominated by temperate species by 2100, as our study was not designed to estimate future species distributions. Temperate species are currently present only as marginal stands. Additional constraints may therefore limit their northward migration such as dispersal, edaphic conditions, and disturbances (Tremblay *et al.*, 2002; Drobyshev *et al.*, 2014; Graignic *et al.*, 2014). These constraints could be the subject of improvements to the simulations presented in this study.

In our study, temperate seedlings were only added at the initial step of our simulations, but if a seed source exists near a stand, a continuous flow of seeds should arrive in the stands. We did not model this potential constant seed flow, because we were interested in assessing the ability of temperate species to persist as a function of initial density of added temperate seedling. Caspersen *et al.* (2005) demonstrated that inappropriate substrates limit more than seed dispersal the abundance of yellow birch and sugar maple at the northern limit of their distribution. In addition, at a broader spatial scale, the demographic characteristics of temperate species, such as late sexual maturity, reproductive strategies with cycles of 3 to 7 years and their seed dispersal, will constrain their poleward migration even with the projected shift of their potential bioclimatic range with the current rate of climate change (Aitken *et al.*, 2008; Hossain *et al.*, 2017; Boisvert-Marsh *et al.*, 2022).

The substrate of coniferous stands is generally more acidic and drier than that of hardwood forests, limiting temperate species recruitment (Collin *et al.*, 2018). Acidic and drier soil affects the uptake of nutrients by temperate species in coniferous stands and affects the probability of germination and growth of temperate juveniles (St.Clair *et al.*, 2008; Caspersen *et al.*, 2011; Solarik *et al.*, 2018). However, the presence of temperate trees in stands was demonstrated to increase the recruitment of temperate species when not too dense to compete with temperate seedlings (Solarik *et al.*, 2020). Thus, adding a substrate-modifying effect on recruitment in future model simulations could improve the plausibility of establishment rates in specific stands.

Although our results suggest that competition with boreal trees was not a critical determinant of the northern limit of temperate tree species, competition is not the only biotic factor that could influence their distribution (Evans et Brown, 2017). Other biotic factors may also influence temperate species migration northwards. For instance, seed predation has been shown to reduced maple regeneration in northern Quebec (Brown and Vellend, 2014). Presence or absence of pathogens, insect outbreak cycles, and mycorrhizal facilitation might also be involved in supporting or limiting the northward migration of temperate species (Frelich *et al.*, 2012; Cleavitt *et al.*, 2011, 2014; Carteron *et al.*, 2020; Evans *et al.*, 2020).

In this study, we did not consider projected climate change and disturbances such as stochastic climate extreme events, or insect outbreaks. These may represent future improvements to this study. With projected climate change, the growing season will possibly be longer consistent with the temperature increase and higher growth of temperate species in BF-PB domain may be observed (Taylor *et al.*, 2017; Reich *et al.*, 2022). With higher growth, temperate species have even a higher ability to persist when introduced in stands of the BF-PB domain (Boulanger *et al.*, 2017, 2019). Meteorological events such as late frost, windthrow, flood or drought can directly affect the growth and mortality of the tree species we have considered, which could facilitate or hinder the performance of temperate species in boreal mixedwood stands (Leithead *et al.*, 2010; Moreau *et al.*, 2020a). The spruce budworm is the major defoliating insect in the study area (Bergeron *et al.*, 2014). This insect causes mortality of balsam fir and spruce with a 30-year cycle during outbreaks that are expected to be more intense with climate change (Pureswaran *et al.*, 2019). The gaps created by the spruce budworm will lead to more light and space for the temperate tree species to grow and survive in stands (Kellman, 2004; Gasser *et al.*, 2010; Bannon *et al.*, 2015). In the long term, the presence of temperate species may mitigate the intensity of the outbreaks, as spruce budworm host species will decrease in the stands (Cappuccino *et al.*, 1998).

1.7 Conclusion

Our study shows that temperate tree species seedlings may grow and survive within mixedwood boreal tree species communities currently to the north of their geographic distribution under a range of native stand compositions, densities, loggings and under current climate conditions. More specifically, both current climate and competitive interactions between temperate and boreal species were not factors impeding temperate species persistence when introduced in stands of the BF-PB domain. Forest management had antagonistic effects on temperate tree species performance. Competition from trembling aspen seedlings limited the persistence of introduced temperate species in recently harvested stands, while temperate species had a higher ability to persist in later successional mature aspen stands. This study provides a new framework for investigating the abilities of temperate tree species to growth and survive in novel stand at the northernmost limit of their distributional range.

1.8 Acknowledgments

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Permanentes datasets. This research was enabled in part by computer resources provided by Compute Canada (www.computecanada.ca). We thank anonymous reviewers from Corrige-moi UQAT students' group for critical revision and suggestions on the manuscript. We thank the two anonymous reviewers for their constructive feedback.

1.9 Data accessibility

Data used in this study has been archived on GitHub and can be found at https://doi.org/10.5281/zenodo.6819495 (Soubeyrand *et al.* 2022); some data that was obtained under license from governmental organizations will be published with a one-year embargo.

CHAPITRE II EFFECT OF CLIMATE AND COMPETITION ON FUTURE TEMPERATE TREE SPECIES COLONIZATION OF MIXEDWOOD BOREAL STANDS

Maxence Soubyerand, Fabio Gennaretti, Olivier Blarquez, Pierre Grondin,

Yves Bergeron, Philippe Marchand

2.1 Abstract

Temperate hardwood tree species may take advantage of climate change to migrate northward tracking their optimal growth and survival niches. Other factors than climate could constrain or facilitate their establishment north of their actual range, such as competitive interactions, their ability to disperse, or forest management. The objectives of this study were to quantify the ability of temperate tree species to colonize boreal mixedwood stands from a few temperate tree species seeders, to determine which life processes of temperate tree species are important in their ability to colonize stands, and to determine the impact of temperate tree species colonization on native boreal mixedwood communities. We used the individual based forest model SORTIE-ND to simulate natural succession dynamics in an age gradient of stands in the boreal mixedwood forest of Eastern Canada considering four different projected climate change scenarios. To mimic the natural colonization of temperate trees from marginal populations eventually established by long-distance migration, we replaced a patch in the center of the simulated stands with temperate tree species, i.e., red maple, sugar maple or yellow birch. We then performed a sensitivity analysis on the parameters determining the growth, dispersal, and mortality of temperate tree species to determine which of these processes was critical to their expansion. All three temperate tree species were able to colonize the boreal stands with higher performance in younger stands, and greater colonization skills for yellow birch. The impact of the climate scenarios on the growth of adult temperate tree species was not sufficient to obtain major changes in their final basal area. Dispersal, mortality, and juvenile growth were the most important processes for the colonization capacity of the temperate tree species. Our results suggest that temperate tree species expansion would not be limited/accelerated by climate change and that forest management could promote temperate tree species expansion by rejuvenating the forest landscapes.

Keywords: SORTIE-ND, Acer saccharum, Acer rubrum, Betula alleghaniensis, marginal populations, forest management, competitive effect

2.2 Résumé

Les espèces d'arbres feuillus tempérés pourraient profiter des changements climatiques pour migrer vers le nord en suivant leurs niches optimales de croissance et de survie. D'autres facteurs que le climat pourraient limiter ou faciliter leur établissement au nord de leur aire de répartition actuelle, comme les interactions compétitives, leur capacité de dispersion ou l'aménagement forestier. Les objectifs de cette étude étaient de quantifier la capacité des feuillus tempérés à coloniser les peuplements de forêts mixtes boréales à partir de quelques semenciers de feuillus tempérés, de déterminer quels processus de vie des feuillus tempérés sont importants dans leur capacité à coloniser les peuplements, et de déterminer l'impact de la colonisation des feuillus tempérés sur les communautés natives de forêts mixtes boréales. Nous avons utilisé le modèle forestier individuel SORTIE-ND pour simuler la dynamique de la succession naturelle dans un gradient d'âge de peuplements de la forêt boréale mixte de l'est du Canada en considérant quatre scénarios climatiques différents. Pour imiter la colonisation naturelle des feuillus tempérés à partir de populations marginales éventuellement établies par une migration à longue distance, nous avons remplacé une parcelle au centre des peuplements simulés par des feuillus tempérés, c'est-à-dire l'érable rouge, l'érable à sucre ou le bouleau jaune. Nous avons ensuite effectué une analyse de sensibilité sur les paramètres déterminant la croissance, la dispersion et la mortalité des feuillus tempérés afin de déterminer lesquels de ces processus étaient essentiels à leur expansion. Les trois feuillus tempérés ont été capables de coloniser les peuplements boréaux mixtes, avec une performance plus élevée dans les peuplements plus jeunes, et de plus grandes capacités de colonisation pour le bouleau jaune. L'impact des scénarios climatiques sur la croissance des feuillus tempérés adultes n'était pas suffisant pour obtenir des changements majeurs dans leur surface terrière finale. La dispersion, la mortalité et la croissance juvénile étaient les processus les plus importants pour la capacité de colonisation des feuillus tempérés. Nos résultats suggèrent que l'expansion des feuillus tempérés ne serait pas limitée ni accélérée par le changement climatique et que l'aménagement forestier pourrait promouvoir l'expansion des feuillus tempérés en rajeunissant les paysages forestiers.

Mots-clés: SORTIE-ND, *Acer saccharum*, *Acer rubrum*, *Betula alleghaniensis*, populations marginales, aménagement forestier, effet compétition

2.3 Introduction

Temperature and precipitation normals have an important role on tree species distribution ranges at the continental scale (D'Orangeville *et al.*, 2016). Consequently, tree species are projected to migrate poleward or at higher elevations under a warming climate, tracking their optimal climatic niche (Morin *et al.*, 2008; Lee-Yaw *et al.*, 2016). However, the speed of this process may vary according to many other factors operating at more regional and local scales, including species migration ability, climatic and edaphic conditions of microsites, and biotic factors such as species competition, seed predation, fires, insect outbreaks and forest management (Fisichelli *et al.*, 2012; Canham et Murphy, 2016a; Evans and Brown, 2017). The extent to which biotic factors interact with climate to shape tree species distributions remains an important unresolved issue (Oboite and Comeau, 2020).

The Quebec mixedwood ecotone is composed of two distinct forest: the southern temperate mixedwood forest and the northern boreal mixedwood forest (Saucier *et al.*, 1998, 2003). The high abundance of temperate tree species such as sugar maple (*Acer* *saccharum* Marsh.), red maple (*Acer rubrum* L.) and yellow birch (*Betula alleghaniensis* Britt.) in the temperate mixedwood forest is the main difference between the two forests (Saucier *et al.*, 2003). Red maple can also be found in hilltops of the boreal mixedwood forest where soil microsites and climatic conditions are more favourable than in the bottom of hills (Marquis *et al.*, 2021). With climate change, the marginal populations of these three species are expected to expand northward, i.e. in the boreal mixedwood forest, and eventually colonize the bottom of hills due to the release of climate constraints (Boulanger *et al.*, 2022). However, site conditions of the boreal mixedwood forest may not be favourable for their establishment because of poor nutriment substrates, high tree density in the native stands or lack of facilitating microorganisms (St.Clair *et al.*, 2008; Collin *et al.*, 2017a, 2018; Carteron *et al.*, 2020; Solarik *et al.*, 2020).

Multiple models with a different degree of complexity and spatial and temporal resolutions may be used to simulate future migrations from current tree species distribution ranges. Species distribution models (SDMs), based on the statistical relationship between current distribution and climate, were used to project the potential temperate tree species migration northward in the mixedwood boreal forest (McKenney *et al.*, 2011). Although SDMs have been improved taking into account migration aspects, they do not consider some important local processes such as interspecific competition, stand density or edaphic factors (Boisvert-Marsh *et al.*, 2022). Alternatively, process-based landscape model were used to project future boreal and temperate tree species performance and biomass, but also this type of large-scale model does not include factors operating at the stand level, such as tree-specific competition for light and space (Boulanger *et al.*, 2017, 2018). Conversely, spatially explicit stand models consider direct interactions between trees in a stand using their spatial positions to compute competition for light and space among trees including potential interspecific facilitation-exclusion (Pacala *et al.*, 1993; Shugart and West, 1977; Shugart *et al.*, 2018). These models can be used in a context of species migration to assess the ability of a species to colonize a specific stand considering interaction with existing trees, recruitment and mortality processes.

In this study, we use a spatially explicit forest stand model to study compositional changes in various stands of the boreal mixedwood forest after addition of a patch of temperate trees in the center of the stand, i.e., sugar maple, red maple, and yellow birch. This set up emulates the potential spread of temperate trees from northern marginal populations eventually established by long-distance migration. We thus determine whether temperate tree species may colonize boreal mixedwood stands considering inter-tree competitive interactions and different climate scenarios. Our objectives are threefold: (1) assess temperate tree growth in mixedwood boreal forests under different climate scenarios; (2a) determine the colonisation potential of temperate tree species from already established marginal population in boreal mixedwood stands, (2b) ranking the limiting impact of dispersal, mortality and growth processes; and (3) determine potential composition shifts in boreal mixedwood stands following the colonization of temperate tree species.

2.4 Methods

2.4.1 Study area

The study area is located at the Lake Duparquet Research and Teaching Forest (FERLD) in the Abitibi region of western Quebec, Canada. The growing season (May to September) is characterized by a mean temperature of 14°C and cumulative precipitation of 447 mm (mean from 1970 to 2019). The FERLD territory is within the boreal mixedwood forest western Quebec and is located in the clay belt characterize by glaciolacustrine clay deposits (Fig. 2.1, Saucier *et al.*, 1998; Roy *et al.*, 2015). The study landscape is fragmented by multiple past fire events and spruce budworm outbreak (*Choristoneura fumiferana* Clem.) staggered through time and space resulting in a mosaic of different stand compositions (Bergeron *et al.*, 2014). Early succession stands are composed of trembling aspen (*Populus tremuloides* Michx.), paper birch (*Betula papyrifera* Marsh.) and jack pine (*Pinus banksiana* Lamb.), and are replaced by balsam fir (*Abies balsamea* Mill.), white and black spruce (*Picea glauca* V. and *Picea mariana* Mill.), white cedar (*Thuja occidentalis* L.) in mid and late successional stands (Bergeron, 2000; Chen and Popadiouk, 2002). Marginal red maple stands are scarcely present in the area mainly in the slope and top of the hills (Tremblay *et al.*, 2002). Sugar maple and yellow birch are absent.

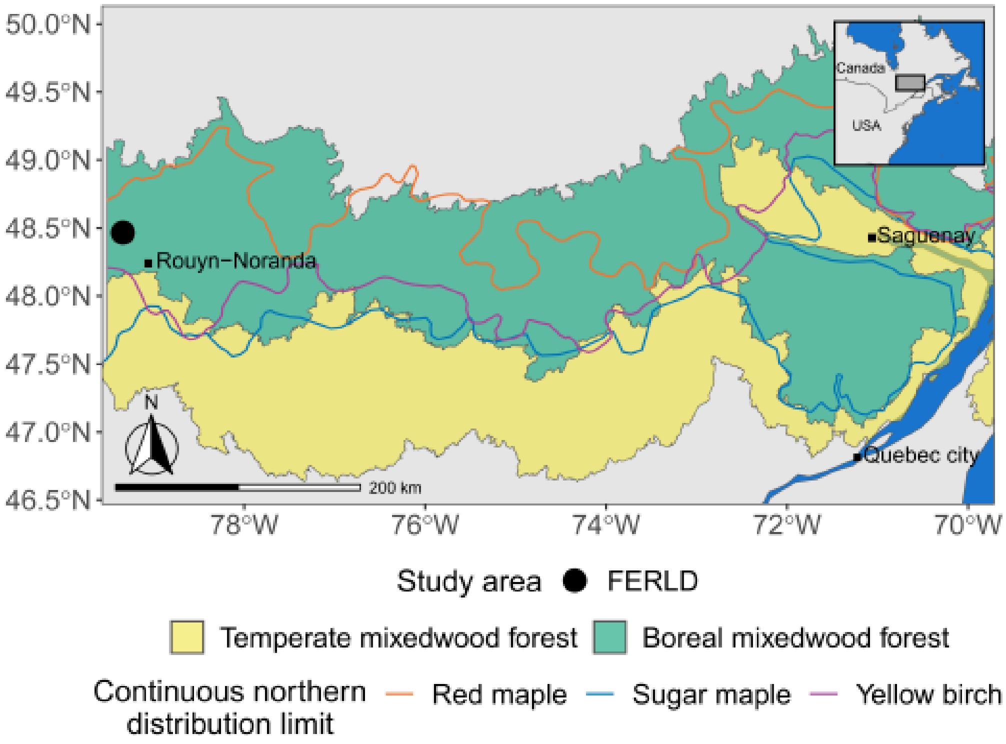


Figure 2.1: Map of the study area with points representing the location of the Lake Duparquet Teaching Research Forest (FERLD, in black). The two forests and northward continuous distribution limits of the three studied temperate tree species are depicted as polygons and solid lines, respectively (Saucier *et al.*, 2003; Morneau, 2022).

2.4.2 Overview of the model and of the simulation experiments

We performed the simulations using the spatially explicit and individual based SORTIE-ND model (hereafter SORTIE; version 7.05; Pacala *et al.*, 1996; Murphy, 2011). SORTIE simulates stand dynamics by modeling the whole life cycle of trees within a stand (i.e., seedling, sapling, adult, and snag). Each tree is modeled as a discrete object with different attributes such as diameter at breast height (DBH), height, crown dimension and age. At each timestep, usually one year, SORTIE simulates the interactions between trees, calculates their growth considering the impact of competition for light and space of neighboring trees, and updates tree attributes. Simultaneously, SORTIE computes the number of seeds produced and their dispersal distance and determines the mortality of both seedlings and trees.

Soubeyrand *et al.* (2023) described a new SORTIE parameterization procedure to include the impact of climate change, the validation strategy of model simulations, as well as the parameter values that are used in this study for yellow birch, red maple and sugar maple and for six additional boreal tree species composing the studied forest stands: trembling aspen, paper birch, balsam fir, white spruce, jack pine and white cedar. Tree allometry parameters, as well as those describing tree mortality and recruitment modules, were obtained from previous studies (Poulin *et al.*, 2008; Maleki *et al.*, 2019).

We modeled the diameter at breast height increment of trees as a function of time (DBHI; in $cm.y^{-1}$) with the "Neighboring Competition Index (NCI) growth" module. This module calculates growth as a fraction of the maximum potential growth (*MaxPotGrowth*) that can be achieved under optimal growth conditions. In our study, the *MaxPotGrowth* parameter varied with climate to account for differences in tree growth between climate scenarios. The potential growth-climate relationships were computed in Soubeyrand et al. (2023) using a large network of inventory data spanning

Northeastern North America and considering four climate variables: climate moisture index of June, July and August (CMI JJA), growing degree day (DD5), mean annual temperature (MAT) and mean summer precipitation (MSP). We then obtained the realized growth by multiplying *MaxPotGrowth* by various limiting effects with values between 0 and 1, representing the effects of tree size, shading from other trees, and non-light-based crowding effect including potential interspecific competition between trees, competition for space, nutrients and water accessibility (Canham et al., 2004; equation 1).

$$DBHI\ (cm.yr^{-1}) = MaxPotGrowth \times size\ effect \times shading\ effect \times crowding\ effect \qquad (3.1)$$

Here, we used the model to simulate the colonisation of temperate tree species in 4 boreal mixedwood stands used as initial conditions. Such stands belong to a successional chronosequence of inventoried plots (Maleki *et al.*, 2021). In each of those stands, we added various size of temperate tree subplots at their center at the beginning of the simulations. Each simulation was carried on with a specific climate scenario until 2100. We then performed a sensitivity analysis on important parameters to analyze the processes controlling the speed of the invasion of temperate trees in boreal mixedwood stands. The final simulations were compared in terms of growth and final basal area of temperate trees and of trajectories of composition changes. Each of these steps is described in detail in the following sections and is illustrated in Fig. 2.2.

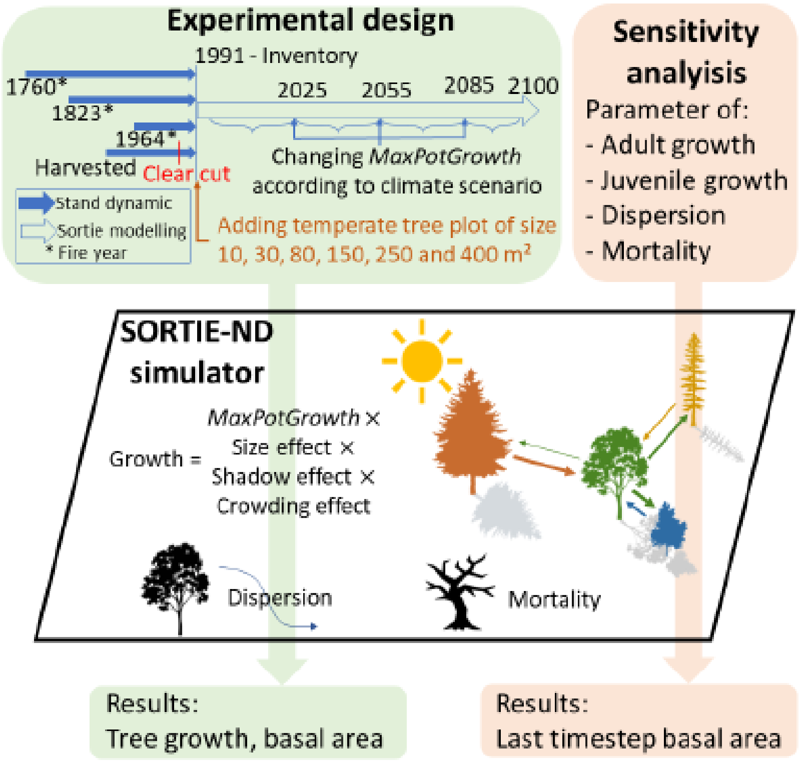


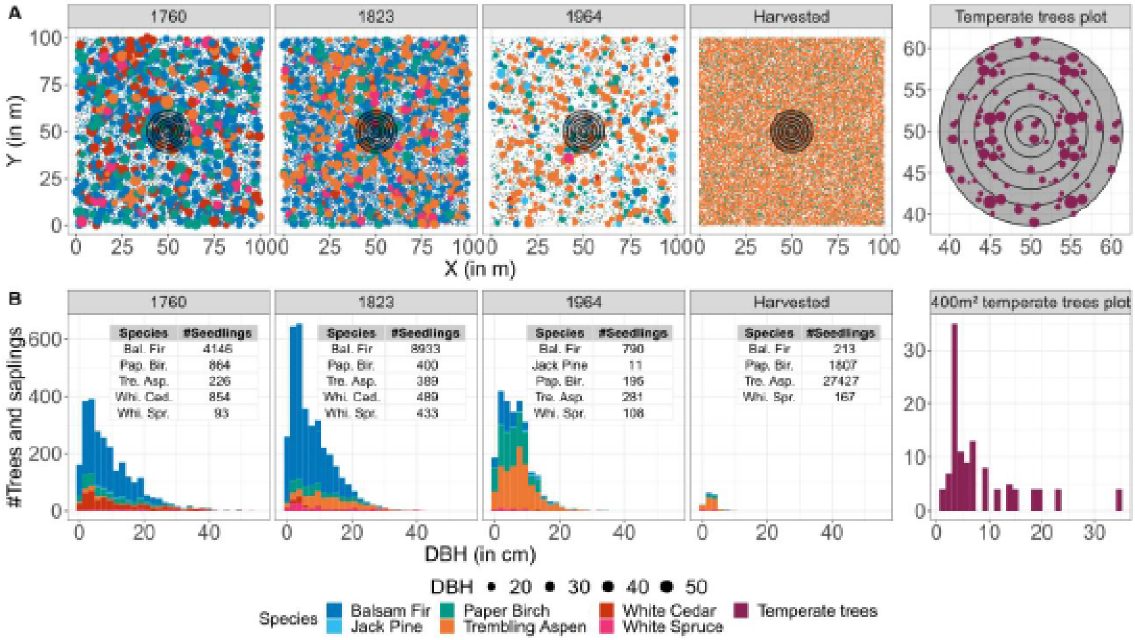
Figure 2.2: Conceptual framework of the simulation experiments. We performed the sensitivity analysis only using the stand reinitiated in 1964.

2.4.3 Stand initial conditions

Tree DBH by species was sampled in 173 plots of 400 m^2 in stands previously burned during different fire years (Maleki *et al.*, 2021). Such inventories provided 4 successional forest stages with different stand compositions to be used as initial conditions for our simulations (Fig. 2.3). The three unharvested stands burned in 1760, 1823 and 1964 and were inventoried in 1991 following a spruce budworm outbreak, which affected balsam fir trees. We considered dead balsam fir as alive to remove the potential effect of the spruce budworm outbreak in our simulation results. One fourth stand originated by a fire in 1923 and was harvested in 1999 (Brais *et al.*, 2013). This stand was inventoried two years after the clearcut offering the possibility to consider recently harvested stands. We extracted the mean density per species and per DBH class of all available plots in each stand to initialize the SORTIE simulations by indicating the number of trees per hectare per each 2cm DBH class by species. SORTIE then randomized tree positioning in the simulated plot.

At the beginning of each simulation, we replaced a round subplot at the center of the stands by a plot composed of temperate trees: sugar maple, red maple or yellow birch (Fig. 2.3). We extracted tree position and DBH from a pure sugar maple stand from the RESEF Quebec forest monitoring network ("Réseau d'Étude et de Surveillance des Écosystèmes Forestiers") to produce the replacement plots. We considered the same tree position and DBH for the red maple and yellow birch experiments to allow the comparison of the results between the tree temperate tree species. Six plot size were considered: 10, 30, 80, 150, 250 and 400 m² to account for different sizes of the marginal population. A simulation without introduced temperate plots was also executed as a control (Fig. 2.3).

These initial conditions allowed us for modelling the colonization of temperate tree species in the adjacent mixedwood boreal stands from the added patch of temperate trees. Such central patches are intended to emulate a long-distance migration event from which colonization of the boreal mixedwood forest could begin (Graignic *et al.*, 2018).



1760

Species	#Seedlings
Bal. Fir	4146
Pap. Bir.	864
Tre. Asp.	226
Whi. Ced.	854
Whi. Spr.	93

1823

Species	#Seedlings
Bal. Fir	8933
Pap. Bir.	400
Tre. Asp.	389
Whi. Ced.	489
Whi. Spr.	433

1964

Species	#Seedlings
Bal. Fir	790
Jack Pine	11
Pap. Bir.	196
Tre. Asp.	281
Whi. Spr.	108

Harvested

Species	#Seedlings
Bal. Fir	213
Pap. Bir.	1807
Tre. Asp.	27427
Whi. Spr.	167

Figure 2.3: Representation of the initial conditions used in the simulation. (A) Tree positioning in a one-hectare plot according to the year of the last fire. Initial conditions for the harvested plot correspond to two years following a clear-cut in a stand natural regenerated after a 1923 fire event. Each species is represented by a color and the size of the circle indicates its diameter class. Circles in plots correspond to the sizes of temperate tree plots added in different simulations: 10, 30, 80, 150, 250, and 400 m² in area. The right panel represents the position of temperate trees in the patch at different sizes. (B) Histograms of the number of saplings and adult trees according to their DBH in the stands (the number of seedlings is also written) and in the 400m² temperate tree species plot added in the simulations.

2.4.4 Inclusion of climate scenarios

Downscaled future climate projections were extracted using the software climateNA (Wang *et al.*, 2016) generating a mean ensemble from 13 general circulation models' simulations with a resolution of 16 km². We selected three representative concentration pathways (RCPs) scenarios, (1) the optimistic RCP 2.6, (2) the plausible RCP 4.5 and (3) the pessimistic RCP 8.5. Mean climate data were extracted for 4 periods for the mean model ensemble: 1991-2025, 2025-2055, 2055-2085 and 2085-2100. We also used a climate scenario with no climate change, i.e., the climate from 1991 unchanged.

In each of SORTIE simulations, we considered the time-dependent effect of climate warming on tree growth by updating the value of the parameter *MaxPotGrowth* at years 2025, 2055 and 2085 according to the simulated climate. To do this, we stopped the simulations at each year where *MaxPotGrowth* had to be modified, then updated the value of the *MaxPotGrowth* parameter according to the new climatic conditions and restarted the simulation with the final tree positions and DBHs of the previous timestep.

2.4.5 Comparison and assessment of simulated results

To determine if temperate trees can grow in boreal mixedwood stands, we extracted the realized growth of each tree from the simulations. We decomposed tree growth to retrieve the average impacts of each growth effect of equation 1 (objective 1).

We extracted temperate tree basal areas at last timestep (after 110 years of simulation, i.e., from 1991 to 2100) to assess the capacity of temperate trees to colonize boreal mixedwood stands. The central temperate tree plots were removed to consider only the basal area of temperate tree that invaded the adjacent stands. We compared these basal areas under the different conditions we simulated, i.e., with different initial temperate trees central plot size, in different climate scenarios, at various stages of boreal mixedwood stands at initial condition and in harvested and unharvested stands (objective 2a).

To determine potential composition shifts in boreal mixedwood stands following the colonization of temperate tree species, we performed Principal Component Analysis (PCA) to investigate the effect of the temperate tree species invasion on the boreal mixedwood stands under different climate scenarios (objective 3). We used the tree species basal area of all boreal and temperate tree species across all timesteps of all simulations as basis for the PCA. We displayed the time trajectory of each simulated scenarios over the two first axes of the PCA. We then compared the extent to which the time-dependent trajectories were different from the control trajectories, i.e., without temperate trees.

2.4.6 Sensitivity analysis

We performed a sensitivity analysis by varying parameters of four important modules of SORTIE to evaluate their influences on the invasion of temperate trees in boreal mixedwood stands: juvenile diametrical growth, adult diametrical growth, seed dispersal and mortality (objective 2b; Table 2.1). We choose these parameters because dispersion, mortality and growth process are directly implicated in the ability of temperate tree species to colonize mixedwood boreal forest (Urli *et al.*, 2016 ; Solarik *et al.*, 2016 ; Putnam and Reich, 2017).

In SORTIE, juvenile growth is simulated as:

$$Y = log_{10}(radial\ growth + 1) = \frac{A \times GLI}{\frac{A}{S} + GLI} \qquad (3.2)$$

where Y is the juvenile growth in cm.year^{-1}, A is the maximum diameter growth on the log scale, S is the slope of the diameter growth response and GLI is the amount of light received by the tree which takes 1 when the tree received full light and 0 when the tree received no light.

The adult growth is defined by the equation (3.1) and depends by the size effect simulated as:

$$DBH\ effect = exp\left(-0.5 \times \left(\frac{ln\left(\frac{DBH}{X_0}\right)}{X_b}\right)^2\right) \qquad (3.3)$$

where DBH is the DBH of the tree in cm, X_0 is the DBH corresponding to maximum growth in cm and X_b determines the width of the Gaussian effect of ln DBH on growth.

The adult growth (Eq. 3.1) also depends by the shading effect simulated as:

$$Shading\ effect = exp(-m \times S) \qquad (3.4)$$

here m is the shading effect coefficient, S is the shading measurement, or the fraction of light intercepted by neighbors, as calculated by the "sail light" module in SORTIE.

The adult growth (Eq. 3.1) finally also depends on the crowding effect simulated as:

$$Crowding\ effect = exp(-C \times DBH \times NCI), \qquad (3.5)$$

where C is the crowding effect coefficient. The neighbor competition index (NCI) for each tree i is simulated by:

$$NCI_i = \sum_{j=1}^{N} \lambda_{ik} \left(\frac{DBH_j{}^{\alpha}}{dist_{ij}^{\beta}}\right) \qquad (3.6)$$

where λ_{ik} strength of competition for different species pairs, k is the species of the neighbor j, α expresses the effect of the DBH of the neighbor tree, $dist_{ij}$ is the distance in meters of the neighbor j from the tree i and β is the exponent of the effect of distance on the NCI.

The density of dispersed seeds (R_i, in seeds.m^{-2}) is calculated as

$$R_i = \frac{STR}{n} \times \sum_{j=1}^{T} \left(\frac{DBH_j}{30}\right) \times e^{-d \times m_{ij}} \tag{3.7}$$

where R_i is the seed density produced per m² at a point i, *STR* is the number of seeds produce by a tree of 30 cm DBH, *n* is a normalizing factor, *d* is the Weibull canopy gap dispersal parameter that controls the probability of the presence of a seed at a distance *m* in meters of the seed maker.

The seeds of sugar maple and red maple are samaras, small winged seeds that typically fall near the seed tree. However, they can also be carried by lateral winds to disperse over longer distances. Generally, most maple seeds are found within a radius of 100 meters around the seed tree (Ribbens *et al.*, 1994). In contrast, yellow birch seeds are not samaras and tend to disperse farther than those of maples. Additionally, yellow birch can produce a greater number of seeds than the two maple species (Caspersen and Saprunoff, 2005). Thus, although each of these species has distinct dispersal strategies, they are all adapted to spread and effectively colonize forest habitats.

Juvenile mortality occurs from two sources: a stochastic constant mortality rate, and a mortality for seedlings and saplings based on their growth rate (depending on light availability, see eq. 3.2):

$$P(mortality|growth) = 1 - e^{-\,e^{-M_2 \times G}} \tag{3.8}$$

where G is the growth of the tree (in cm.year^{-1}) and M_2 is a parameter for the light dependent mortality.

Adults can die from three independent causes: a stochastic mortality rate, a senescence-based mortality rate and a competition-based mortality rate. Senescence based mortality rate was not included in this sensitivity analysis because, temperate trees that colonize the stands didn't reach the senescence. Competition mortality depends on the ratio between the maximum growth the tree can attain relative to its DBH and the actual growth of the tree. The higher the shading effect and crowding effect, the higher the probability of mortality.

$$P(mortality|competition) = Z^{\frac{\frac{growth}{MaxPotGrowth \times size\ effect}}{max}} \qquad (3.9)$$

where Z is the competition mortality shape parameter, growth is the actual growth of the tree (in cm.year^{-1}) and max is the competition mortality maximum parameter, which indicates the maximum relative increment ($\frac{growth}{MaxPotGrowth \times size\ effect}$) at which mortality may occur.

In the sensitivity analysis, we set the 16 selected parameters at 0.1, 0.2, 0.4, 0.6, 0.8, 1.2, 1.4, 1.6, 1.8 and 2 times the optimal parameter values (Table 2.1). In addition, for each species and each parameter, we assigned the parameter value of the other two species to know if specific parameter values allowed a species to better invade the stands. In the analysis, only one parameter varied iteratively while the others remain constant at their optimal value (480 simulations = 3 species x 16 parameters x 10 parameters values). The sensitivity analysis was done for the stand regenerated in 1964 with the RCP 4.5 climate change scenario and using the 150 m^2 central patch of temperate trees.

Table 2.1: List of the parameters used in the sensitivity analysis with the associated optimal parameter values for sugar maple, red maple and yellow birch.

Module	Parameter	Sugar maple	Red maple	Yellow birch
Juvenile growth	A	0.34	0.43	0.43
	S	0.68	0.11	0.58
Adult growth: Maximum potential growth	*MaxPotGrowth*	Changed according to climate scenario and time		
Adult growth: Size Effect	X_0	21.65	20.19	16.18
	X_b	1.18	1.84	1.07
Adult growth: Shading Effect	m	1.16	0.56	0.8
Adult growth: Crowding Effect	c	$6.51.10^{-4}$	0.044	0.018
	α	1.24	0.081	0.088
	β	0.32	0.71	0.53
Dispersion	STR/n	1.32	0.54	21
	d	$5.81\text{x}10^{-4}$	$3.62\text{x}10^{-5}$	$6.30\text{x}10^{-5}$
Juvenile mortality	M_2	4.79	6.64	2.67
	Random	0.01	0.01	0.01
Adult mortality	z	$3\text{x}10^{-6}$	$3\text{x}10^{-6}$	$4.33\text{x}10^{-6}$
	max	0.17	0.17	0.25
	Random	0.01	0.01	0.01

2.5 Results

Climate at the FERLD should be warmer with more precipitations by the end of the century. More particularly, the mean annual temperature should increase of 2.1 (rcp 2.6) – 6.47 (rcp 8.5) °C and growing degree day should increase of 347 – 1098°C according to the climate scenario by 2100 (Fig. 2.4.A). On the other hand, the mean summer precipitation should increase of 447 (rcp 2.6) — 493 (rcp 8.5) mm. The additional precipitation generated by climate change is not expected to be sufficient to compensate the increase in temperature because the future summer climate moisture index should drop from -0.301 to -0.4 (rcp 2.6) — -3.41(rcp 8.5) by 2100, inducing a deficit a water and therefore droughts.

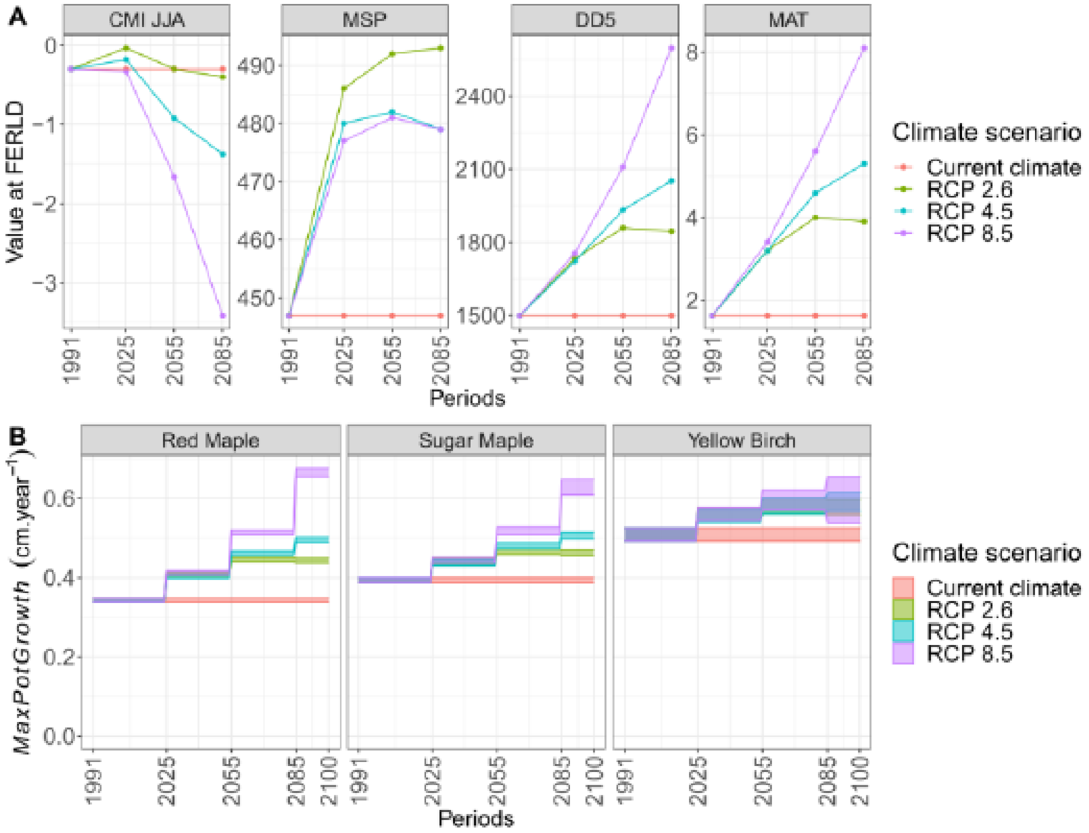


Figure 2.4: (A) The future climate in the FERLD territory through the June-July-August climate moisture index (CMI JJA), the growing degree days (DD5), the mean annual temperature (MAT) and the mean summer precipitation (MSP) according to four climate scenarios. (B) MaxPotGrowth values estimations as a function of time and depending on the species and on the climate scenarios. Error areas correspond to the 5th and the 95th quantile Bayesian confidence intervals of *MaxPotGrowth*.

The updated *MaxPotGrowth* according to the climate scenario showed that all temperate tree species should take advantage of climate change, increasing their potential growth in the FERLD territory (Fig. 2.4.B). In the RCP 2.6 scenario, *MaxPotGrowth* increased with time but reached a plateau in 2055, whereas in the RCP 4.5 and RCP 8.5 scenarios, *MaxPotGrowth* increased over time over the entire simulated period. Yellow birch is less sensitive to climate change than sugar maple and red maple but showed higher *MaxPotGrowth* value in no climate change and RCP 2.6 climate scenarios.

The realized growth of yellow birch was higher than those of sugar maple and red maple (average growth was 0.288 cm.yr^{-1} for yellow birch, 0.147 cm.yr^{-1} for red maple and 0.148 cm.yr-1 for sugar maple). We observed that overall realized growth was lower in the 1760 stand than in the three others for red maple and sugar maple whereas for yellow birch the growth remained constant across stands (Fig. 2.5). For red maple and sugar maple, the realized growth was more dependent on the initial species composition of the colonized stand than on the climate scenario. The realized growth of sugar maple and red maple increased over time especially in the 1823 and 1964 stands, while for yellow birch, the realized growth had a bell-shape with a maximum around 2070. This bell-shape was due to an increasing negative impact of the size of the trees on their growth after 2070 because the crowding effect and the shading effect remained almost constant for yellow birch over time and in different stands. Conversely, for maple trees, the crowding effect was higher in older stands (regenerated in 1760) than in younger ones (in 1964).

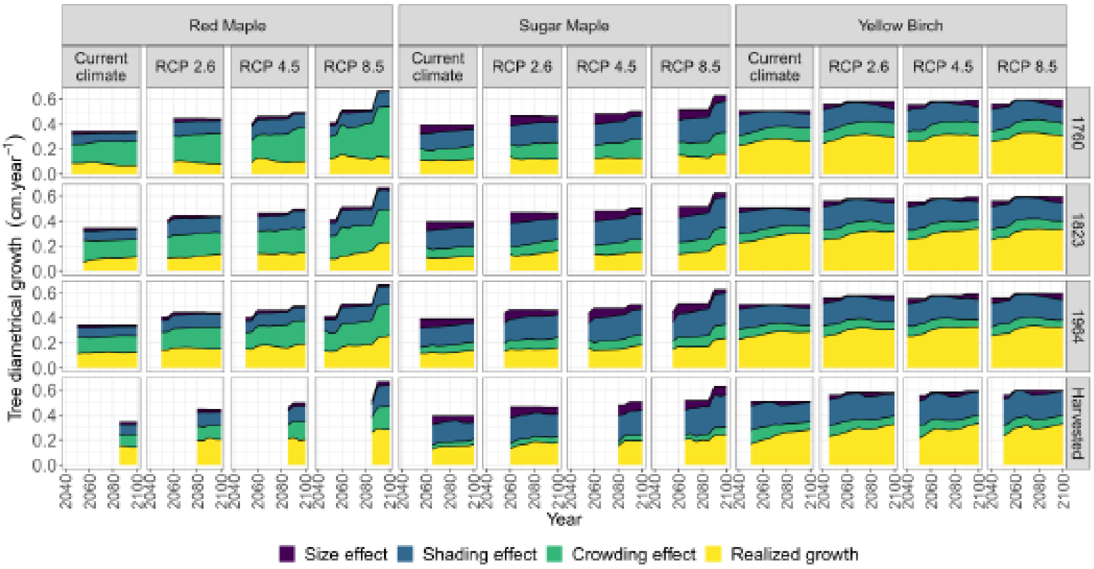


Figure 2.5: Mean decomposition of the tree growth as a function of time depending on the temperate tree species, the considered stand, and the climate scenario. Simulations were performed with a 400m² central patch. The sum of the realized growth and the three effects correspond to the MaxPotGrowth value. Tree growth decomposition does not begin at the start of the simulation (1991) because trees are juveniles before (DBH less than 10 cm), and the growth of juvenile is computed with another module.

Sugar maple and yellow birch could establish in all stand conditions whereas red maple could establish only in the harvested and 1964 stands (Fig 2.6). Yellow birch displayed the highest basal areas at last timestep (mean basal area of 1.23 m²/h for yellow birch, 0.264 m²/h for sugar maple, and 0.180 m²/h for red maple). Temperate tree species invasion increased with the size of the central patch of temperate tree species. Younger and harvested stands were more easily invaded although this effect was less evident in the case of sugar maple. Climate scenarios did not appear to affect the invasiveness of temperate trees in boreal mixedwood stands.

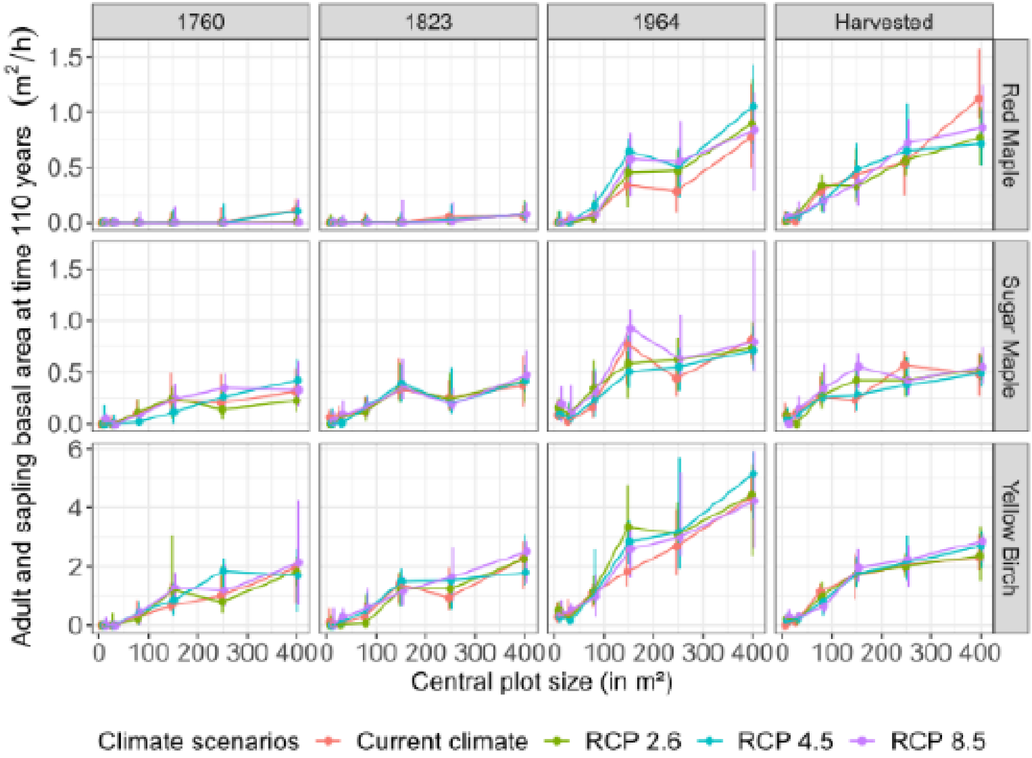


Figure 2.6: Simulated adult basal area at the last simulation timestep (109 years corresponding to 2100) for temperate tree species in boreal mixedwood stands. Simulations consider different initial conditions relative to time since stand-replacing fire, harvesting, size of the central patch of temperate trees and climate scenarios. Central patches were removed when determining tree basal area to consider only those trees that have invaded the adjacent stand. 80% error bars are generated considering subplots in each simulation. Note different y-axis scales between rows.

Last timestep basal area of temperate trees was mostly responsive to variations of juvenile growth, juvenile mortality and dispersion parameters (Fig. 2.7, Supporting Information Fig. B.1). We observed strong variations of last timestep basal area when modifying the A parameter of juvenile growth; an increase of two time of the initial value of A causes a 7.16 times increase in last timestep basal area of yellow birch, 6.44 for sugar maple and 2.32 for red maple. The STR/n parameter was also an important parameter since this parameter set the number of seeds created by a tree of 30cm DBH. STR/n percentage increments produced similar percentage increments in the basal area at last timestep. STR/n for yellow birch is 15.9 times higher than sugar maple and 38.9

times higher than red maple, explaining the better colonization performance of yellow birch. If the STR/n parameter value of yellow birch was attributed to the two other tree species, we observed an increase of basal area by a factor of 4.7 for sugar maple and of 20.8 for red maple. Concerning the parameters of the adult growth, c and β had little effect on the last timestep basal area while α and $MaxPotGrowth$ had a strong effect. Basal area in the last timestep also responded to juvenile mortality and especially M_2 which is the parameter that related juvenile tree growth and mortality, with higher growth leading to lower mortality. The parameterized value of M_2 for all temperate tree species was at about the threshold value where a decrease in M_2 would result in a drastic mortality and thus a drop in the species basal area per stand.

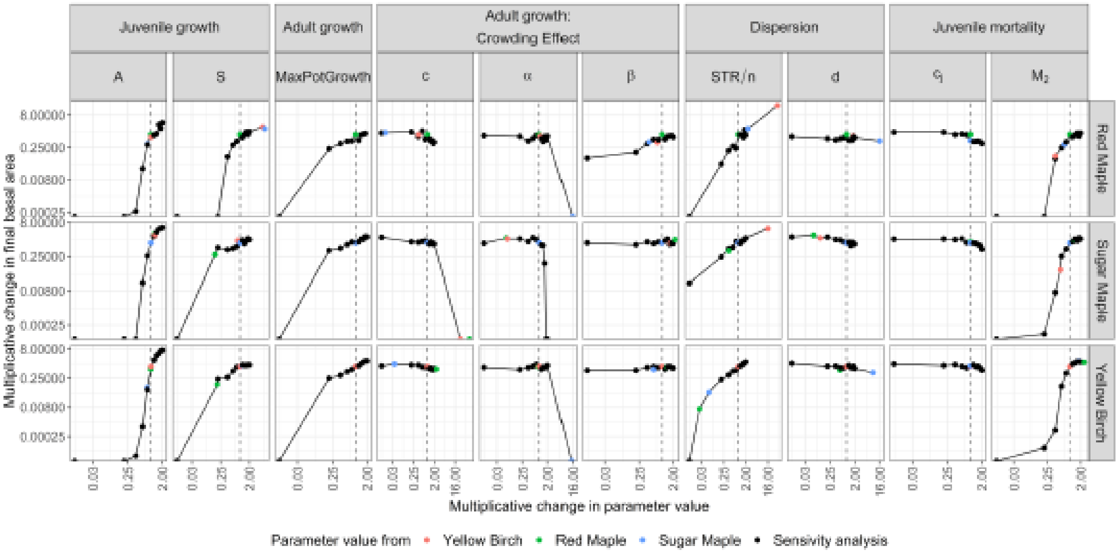


Figure 2.7: Sensitivity analysis on 10 parameters influencing adult and sapling basal area at the last timestep. The sensitivity analysis has been performed on 6 other parameters of adult growth and adult mortality that can be found on the supporting Information Fig. B.1. Only the evaluated parameter varies while the others are fixed at their optimal value. Color points are the results of simulations with the parameter value of the species associated to that color. The vertical gray dashed lines correspond to the parameter value used for the experimental design. Here, we only used the RCP 4.5 climate scenario and a 150m² central patch of temperate trees in the stand reinitialized in 1964. The central plot has been removed to calculate the temperate tree basal areas.

All temporal trajectories moved toward the space correlated with the basal area of white cedar and balsam fir consistent with the observed natural dynamics of stands in the boreal mixedwood forest (Fig. 2.8). Trajectories of the younger stand began in the space correlated with trembling aspen abundance and finished in the space correlated with coniferous species, the trajectories of the other two stands moved from mixed stands to coniferous dominated stands, particularly with high presence of white cedar. The most important deviations from the control trajectories (stands without temperate tree species) occurred in the youngest stand where the temperate tree species had the highest colonization ability. Trajectories were deviated because of the actual presence of temperate tree species, but also because of the consequences of the presence of temperate trees in stands which could affect regeneration, growth and survival of mixedwood boreal species.

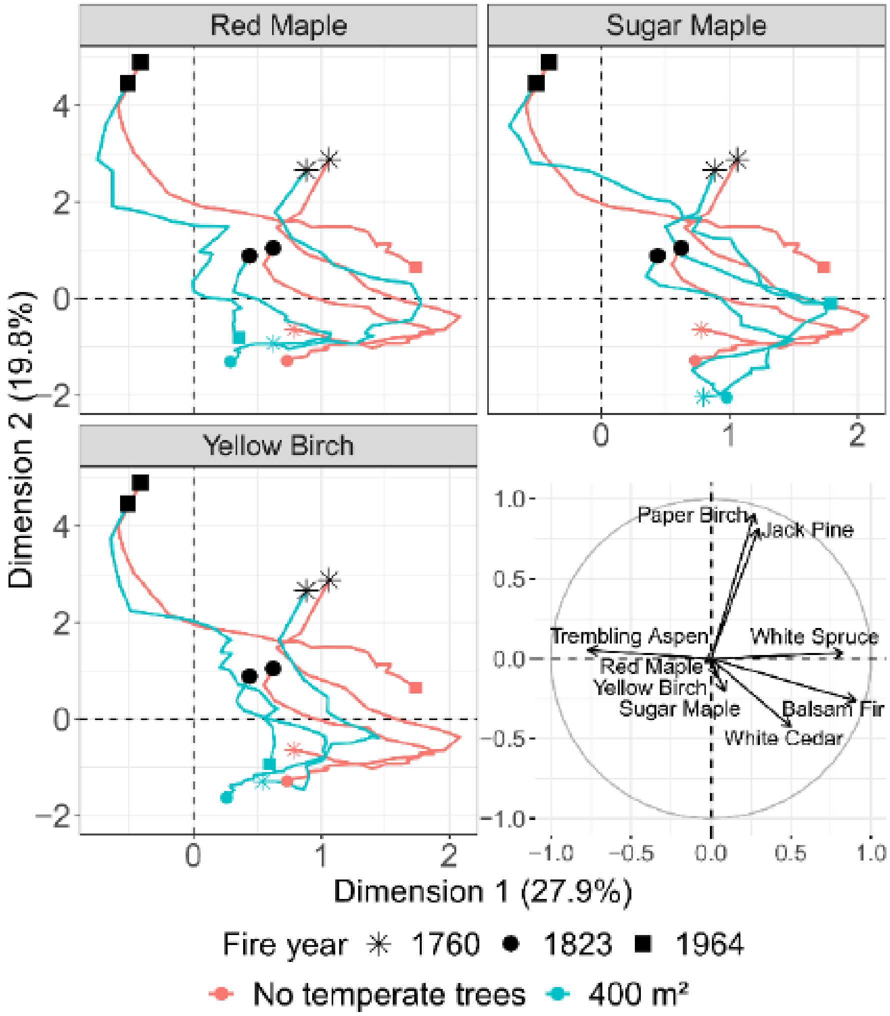


Figure 2.8: Simulated trajectories of stand assemblages in a multivariate space built with a principal component analysis (PCA) based on the basal area of adults and saplings across all simulation results. Trajectories in each panel represent the chronology of the stand's composition depending on the absence (orange lines) or addition (blue lines) of the 400 m² patch of temperate tree species. Black dots correspond to the position at initial conditions in the multivariate space, and colored dots correspond to the results of the simulations at the last timestep (after 110 years). The PCA correlation circle used to generate the trajectories is shown in the lower right panel. The temperate tree species arrows are represented by short vectors located in the central-lower part of the ordination.

2.6 Discussion

2.6.1 Temperate tree traits determining their colonization success of boreal stands

Our study considered three temperate tree species with contrasted auto-ecology and functional traits. Both yellow birch and red maple are considered fast-growing pioneer species although they are moderately shade tolerant (Kobe *et al.*, 1995). Sugar maple is shade-tolerant and slow growing, this species can colonize stands at all stages of the successional dynamic (Beaudet and Messier, 1998). Sugar maple usually regenerates in gaps created by windthrow or insect outbreaks in mature stands and under the canopy, while yellow birch and red maple colonize stands in gaps and after major disturbances such as fire or harvesting (Fei and Steiner, 2009 ; Gasser *et al.*, 2010 ; Duchesne and Prévost, 2013). Yellow birch has also higher ability to disperse far from the seed source because of the reduced mass of the seeds compared of maples (Ribbens *et al.*, 1994; Caspersen and Saprunoff, 2005; Hossain *et al.*, 2017; Evans *et al.*, 2020). In our simulations, these contrasted auto-ecology and functional traits resulted in different colonization performance of mixedwood boreal stands, in accordance with other studies (Boulanger *et al.*, 2022). Yellow birch was the species with higher performance while sugar maple and red maple had similar and lower performance. Yellow birch maximum potential growth and realized growth were higher than the other two species, as expected by its fast growth in empty spaces such as in gaps or in harvested stands (Beaudet and Messier, 1998). Red maple growth was mostly reduced by highly competitive interactions with the other trees in the mixed stands and sugar maple lacked of light to growth enough (see Fig. 2.5 and Beaudet and Messier, 1998).

Our study showed that the number of seed produced per year and the seedling and sapling growth rate and mortality are the most important traits and processes determining the speed of the colonization of temperate trees in boreal stands (see also

Aitken *et al.*, 2008; Bouchard *et al.*, 2019). Yellow birch took advantage of its high juvenile and adult growth, and its ability to disperse its abundant seeds in stands relatively distantly compared to red maple and sugar maple (Caspersen and Saprunoff, 2005; Canham and Murphy, 2016b). Yellow birch was thus able to produce more stems developing faster than those of red maple and sugar maple, leading to higher birch basal area by 2100 (Supporting Information Fig. B.2). Soubeyrand *et al.* (2023) showed that all three studied temperate tree species may easily survive and grow in boreal mixedwood stands. The present study refines these results and shows that seed dispersal and seedling mortality are the prominent processes limiting the actual northward migration of temperate trees.

Marginal populations of temperate tree species located in the top and the slopes of the hills in the mixedwood boreal forest may act as pioneering outposts, facilitating the colonization and spread of temperate trees in the boreal forest in the context of climate change (Vogel *et al.*, 2023). The greater seed dispersal capacity of yellow birch confers a higher potential for rapid migration and subsequent colonization of the mixedwood boreal forest. Yellow birch should colonize new stands and expand its distribution faster compared to the two other studied temperate tree species.

Our findings highlight the significance of juvenile growth in determining the basal area of temperate tree species. According to our model, this growth stage is primarily influenced by the amount of light received by each seedling and sapling, which is the predominant factor driving their development (Godman and Krefting, 1960 ; Pacala *et al.*, 1994 ; Collin *et al.*, 2018). However, the establishment of temperate tree species in boreal mixedwood micro-sites may be limited by specific substrate and local stand conditions (Collin *et al.*, 2017a, 2018; Carteron *et al.*, 2020; Solarik *et al.*, 2020). For instance, yellow birch's seed germination probability is likely to be higher on coniferous dead wood compared to dead deciduous trunks (Marx and Walters, 2008; Bolton and D'Amato, 2011; Lambert *et al.*, 2016) a pattern that does not apply to red maple and sugar maple. Kellman *et al.* (2004) conducted in situ experiments to study sugar maple seed germination in various boreal stands (old conifers, young conifers, stands dominated by birch) and revealed that the probability of germination is not influenced by the dominant species in the stands but is more influenced by site-specific effects. Conversely to seed germination, seedling mortality could be dependent on the dominant tree species in the stand, such as for sugar maple showing high mortality in boreal stands, intermediate mortality in temperate stands, and minimal mortality in mixed stands (Kellman, 2004; Collin *et al.*, 2018; Carteron *et al.*, 2020). This differential mortality pattern highlights that specific tree species composition and micro-site conditions may play crucial roles in the successful colonization and survival of a tree species. This aspect merits further attention in future studies.

2.6.2 Effects of climate change

Our results are consistent with other studies showing that temperate tree species can grow north of their range under current climate, and that their growth should increase by 2100 due to the release of climatic constraints (Ashraf *et al.*, 2015). Temperate tree growth at their northern distributional range and their range expansion northward are not limited by growth, but rather by stand-intrinsic effects such as species pre-existing composition and disturbances (Zhu *et al.*, 2012; Drobyshev *et al.*, 2014; Zhang *et al.*, 2015b). Increased temperature and changes in water regime should not directly influence the performance of temperate tree species but indirectly via changes in disturbance regimes. Red maple and yellow birch should take advantage of stands disturbances increasing light availability such as budworm outbreaks, windthrows, or harvesting (Duchesne and Ouimet, 2008; Leithead *et al.*, 2010; Hart *et al.*, 2012; Duchesne and Prévost, 2013). When established, sugar maple should also be resilient to disturbed environments and increased fire activity, promoting the species expansion in the mixedwood boreal landscapes (Pilon et Payette, 2015; Payette *et al.*, 2018). In addition to the potential increase of gaps caused by an increase in disturbance severity and frequency, temperate tree species may also take advantage of gaps created by tree mortality during natural stand succession (Gasser *et al.*, 2010; Leithead *et al.*, 2010; Hart *et al.*, 2012; Després *et al.*, 2014).

Although the growth of temperate trees increased with time and projected climate, the species composition and density of the receiving stand had the greater effect on the realized growth of temperate tree species in accordance with previous studies (Zhu *et al.*, 2012; Drobyshev *et al.*, 2014; Zhang *et al.*, 2015b; Power *et al.*, 2019). The effects of projected climate on the colonization success were even negligible compared to those related to the receiving stand composition and density. However, we only consider the effects of climate on the adult growth, while such effects may be important at the seedling and sapling stage (Canham and Murphy, 2016a, 2017; Clark *et al.*, 2021). In our study, juveniles growth and mortality only depends on light availability without consideration of short-term meteorological events (Leithead *et al.*, 2010; Moreau *et al.*, 2020a). For example, late-spring frost could highly affect seed production and juvenile growth and mortality of temperate trees, limiting their northward expansion (Godman and Krefting, 1960; Hufkens *et al.*, 2012; Tao *et al.*, 2021; Marquis *et al.*, 2022). Future studies on modeling temperate tree species expansion must focus on including climate and meteorological effects at all life stage of trees, i.e., seed germination, growth, reproduction, and survival. However, at the moment, we lack quantitative field data to properly include these effects in the simulations.

2.6.3 Implication for forest management

Colonization by temperate tree species was different according to the age of the receiving mixedwood boreal stand. Older stands had an higher proportion of coniferous species leading to high competitive interactions for nutrient, light and space (St.Clair *et al.*, 2008; Collin *et al.*, 2017a). High competition level led to high mortality of temperate tree species and reduced growth of juvenile and adult trees in accordance with the results of other studies (Putnam and Reich, 2017). Initial composition of the younger unharvested stands (reinitiated in 1964) was dominated by trembling aspen and had lower overall tree density compared to older stands leading to lower level of competition for light and space and higher colonization success for temperate trees.

Forest fires can have a significant impact on the colonization of temperate tree species in mixedwood boreal stands by rejuvenating the host stands and providing appropriate substrates. As competition constraints for space are released, temperate tree species find favorable conditions to establish (Brice *et al.*, 2020). The study area is also significantly impacted by the spruce budworm, which is a major defoliating insect (Bergeron *et al.*, 2014). The outbreaks of this insect occur on average every 30 years, lead to the mortality of fir and spruce trees, and are expected to increase in severity due to climate change (Pureswaran *et al.*, 2019). Such outbreaks create gaps within the stands, providing an opportunity for temperate tree species to thrive by accessing more light and space (Kellman, 2004; Gasser *et al.*, 2010; Bannon *et al.*, 2015). However, the increased presence of temperate species could potentially help mitigate the severity of future outbreaks by decreasing the abundance of budworm's host species (Cappuccino *et al.*, 1998).

Forest management, by rejuvenating the mixedwood boreal landscapes, could accelerate the migration of temperate tree species northward. Other landscape-scale modeling studies at the temperate-boreal ecotone showed that climate change coupled with forest management could modify the distribution of temperate tree species, especially after clearcuts (Steenberg *et al.*, 2013; Fisichelli *et al.*, 2014; Boulanger *et al.*, 2019; Bouchard *et al.*, 2019). Temperate tree species should have a greater ability to establish in young stands north of their distribution range, with climate change favoring their growth, accelerating transitions to forests dominated by hardwoods (Brice *et al.*, 2019, 2020; Molina *et al.*, 2021). However, our simulations showed that recently harvested or young post-fire stands are less suitable to temperate tree colonization. This is primarily due to high level of competition for space with aspen, which produces abundant root suckers and grows rapidly during its juvenile stages. As a result of this competition, seedlings and saplings of temperate tree species experienced higher mortality rates. Our study refines theses results and shows that the success of temperate tree colonization increases in stands older than 20 years (after the aspen self thinning) and younger than 140 years (where light availability is still high enough). Around the FERLD, 17% of the stands have an age between 20 and 140 due to forest management, and 24% due to fire. This means that 41% could eventually be favorable to colonization by temperate tree species if seed-bearing trees are near enough.

2.7 Conclusion

Our study shows potential colonization success of temperate trees into mixedwood boreal stands if a seed-bearing tree is near enough. Our set-up simulates the expansion from an already existing marginal population established, for example, by long distance migration. Other additional factors could limit the colonization of temperate trees into the lowlands and northward in the boreal forest, such as edaphic factors, fire and insect disturbances or meteorological extremes (Drobyshev *et al.*, 2014; Zhang *et al.*, 2015b). For example, the soil of boreal stands is generally more acidic than that of hardwood forest which could have an impact on temperate tree germination, growth and survival (Collin *et al.*, 2017a). In addition, the clay soils like in the clay belt and those around FERLD territory may be not favourable for the establishment of temperate tree species because of soil properties with high proportion of clay and lack of mycorrhizal symbionts (Carteron *et al.*, 2020). However, our study demonstrates that, when a patch of temperate trees is introduced or already present in a mixedwood boreal stand, the trees can disperse, grow, and colonize the adjacent stand north of their current continuous distribution range. Current and projected climate conditions have low impact in the colonization success. Dispersal ability and juvenile growth and mortality are instead the most sensitive processes. The colonisation success depends on the succession stage of the adjacent mixedwood boreal stand, being maximum in younger stands and mixed stands with gaps dynamics. This study has important implications for adjusting forest management practices in the mixedwood boreal forest in the context climate change and for the northward expansion of the temperate tree species' distributional range.

2.8 Acknowledgements

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2.9 Data accessibility

Data used in this study have been archived on GitHub and can be found at https://zenodo.org/badge/latestdoi/604226721.

CHAPITRE III INTERACTIONS BETWEEN CLIMATE, SOIL AND COMPETITION DRIVE TREE GROWTH IN QUEBEC FORESTS

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3.1 Abstract

Climate, soil, and competition factors jointly drive tree growth variability at local and regional scale. However, the comprehensive interaction of these factors and their combined effects on tree responses within their environment remains poorly explored in current research. Using a detailed forest inventory dataset in Québec, we examined tree growth of red maple (*Acer rubrum* L.), sugar maple (*Acer saccharum* Marsh.), yellow birch (*Betula alleghaniensis* Britt.), white birch (*Betula papyrifera* Marsh.), balsam fir (*Abies balsamea* Mill.), and black spruce (*Picea mariana* Mill.), as a function of competition for light and space with neighboring trees, climate and soil-related variables. Interactions between all these variables were considered in a Bayesian model predicting tree growth. The amount of light received by trees was the main variables explaining tree growth except for black spruce which was influenced mostly by climate variables. Among the studied species, only red maple and white birch exhibited increased growth under warmer conditions. Intraspecific competition had strong species-specific impacts, varying from negative effects for balsam fir, to positive for red maple and yellow birch. Interactions between climate, soil, and competition played a crucial role in shaping growth patterns, especially for sugar maple, balsam fir, and black spruce that strongly responded to a combination of climate and competition factors. In general, tree growth also increased with the soil cation-exchange capacity (CEC), especially when higher CEC is coupled with higher temperatures and precipitation, except for black spruce. While anticipated climate conditions in Quebec, even under the most optimistic scenarios, will have a strong negative impact on the tree growth of most tree species, management can mitigate this impact by promoting tree diversity with more complex stand structures.

Keywords: tree growth, climate, competition, soil, interactions

3.2 Résumé

Les facteurs climatiques, du sol et de la compétition influencent conjointement la variabilité de la croissance des arbres à l'échelle locale et régionale. Cependant, l'interaction de ces facteurs et leurs effets combinés sur les réponses des arbres dans leur environnement restent peu explorés dans les recherches actuelles. En utilisant un ensemble de données détaillé sur l'inventaire forestier au Québec, nous avons examiné la croissance des arbres, notamment de l'érable rouge (*Acer rubrum* L.), de l'érable à sucre (*Acer saccharum* Marsh.), du bouleau jaune (*Betula alleghaniensis* Britt.), du bouleau blanc (*Betula papyrifera* Marsh.), de la sapin baumier (*Abies balsamea* Mill) et de l'épinette noire (*Picea mariana* Mill.), en fonction de la compétition pour la lumière et l'espace avec les arbres voisins, du climat et de variables liées au sol. Les interactions entre toutes ces variables ont été prises en compte dans un modèle bayésien prédisant la croissance des arbres. La quantité de lumière reçue par les arbres était la principale variable expliquant la croissance des arbres, à l'exception de l'épinette noire, qui était principalement influencée par les variables climatiques. Parmi les espèces étudiées, seuls l'érable rouge et le bouleau blanc ont montré une croissance accrue dans des conditions plus chaudes. La compétition intraspécifique a eu des impacts spécifiques pour chaque espèce, variant d'effets négatifs pour le sapin baumier à des effets positifs pour l'érable rouge et le bouleau jaune. Les interactions entre le climat, le sol et la compétition ont joué un rôle crucial dans l'explication de la croissance, en particulier pour l'érable à sucre et l'épinette noire, qui ont fortement réagi à une combinaison de facteurs climatiques et de compétition. En général, la croissance des arbres a également augmenté avec la capacité d'échange cationique du sol (CEC), en particulier lorsque des valeurs de CEC plus élevées étaient associées à des températures et des précipitations plus élevées, à l'exception de l'épinette noire. Bien que les conditions climatiques anticipées au Québec, même dans les scénarios les plus optimistes, auront un impact négatif marqué sur la croissance des arbres de la plupart des espèces, la gestion peut atténuer cet impact en favorisant la diversité des arbres avec des structures de peuplement plus complexes.

Mots-clés: croissance des arbres, climat, compétition, sol, interactions.

3.3 Introduction

Forest management and biodiversity will face multiple challenges in the coming decades due to the climate-change-related rise in temperature and increase in droughts (Molina *et al.*, 2022 ; Girona *et al.*, 2023). Forecasting how forests will respond to these changes requires a good understanding of the factors affecting tree distribution and growth. At global scale, tree distribution and growth are closely linked to climate and soil properties as they influence the length of the growing season and nutrient and water availability (Goldblum and Rigg, 2005; Lafleur *et al.*, 2010). At local scale, such as the stand level, tree growth also depends on competition with other trees for light, soil nutrients and water (Zhang *et al.*, 2015a; Aussenac *et al.*, 2019; Boakye *et al.*, 2021). The influence of competition, climate and soil on tree growth is frequently studied, but we lack understanding on how these factors interact to influence tree responses in their environment (Henneb *et al.*, 2020; Oboite and Comeau, 2020).

Climate has an important effect on tree growth, especially at higher latitude in temperate and boreal forests (Doblas-Reyes *et al.*, 2021). In the boreal forest, tree growth is primarily limited by a short growing season due to cold temperatures and frozen soils in the dormant season (Gennaretti *et al.*, 2017; Wang *et al.*, 2023). However, as the climate warms, the growing season in the boreal zone may become longer and tree growth may increase (Loehle et Solarik, 2019; Moreau *et al.*, 2020b). In temperate forests, water limitations are more important than those linked to direct effect of temperature, and climate change may imply reduced tree growth due to more frequent droughts (Loehle and Solarik, 2019; Moreau *et al.*, 2020a).

Tree survival and growth also tightly depend on soil quality determined by properties such as soil texture, pH, structure or nutrient content. Soil texture, for example, is associated with soil porosity, which regulates the water holding capacity and gaseous diffusion (Upadhyay and Raghubanshi, 2020). Tree responses to soil properties are highly species-specific. In the boreal zone, jack pine performs well on sandy soil with low water retention, whereas spruce trees prefer silty or clay textures (Ste-Marie *et al.*, 2007). Soil pH is also important because it influences the availability of nutrients to the trees. Trees tend to grow well in slightly acidic soil, with a pH between 6 and 7. If the soil pH is too acidic or too alkaline, it can limit the ability of trees to absorb nutrients. Only some tree species are specialized for more acidic soils such as red maple in the temperate zone (Burns and Honkala, 1991). In addition, strong interactions exist between climate and soil properties. For example, lower temperature and higher precipitation can be coupled with soil paludification, resulting in reduced stand productivity (Simard *et al.*, 2007; Paré *et al.*, 2011).

In addition to the above abiotic factors, shade from surrounding trees and the number of surrounding trees determine resource availability and are important to predict tree-scale growth responses (Canham *et al.*, 2004). Competition between trees can be enhanced or mitigated by soil properties (Cavard *et al.*, 2011). Poor quality soils can reduce the availability of nutrients, which can make competition between trees more intense (Coates *et al.*, 2013). In the boreal forest, competition for nutrients is often high due to low soil nutrient availability (Ghotsa Mekontchou *et al.*, 2020). Understanding these interactions is important for predicting how forest may respond in the future and determine site specific management strategies.

In this study, we analyzed tree growth in a variety of temperate and boreal mixed forest stands in Quebec (Canada) covering a large soil fertility and climate gradient and considering competition of neighbouring trees. Our focus is on the interaction between soil, climate, and competition factors to understand which conditions may especially decrease tree growth. We used the data from the RESEF dataset ("Réseau d'Étude et de Surveillance des Ecosystèmes Forestiers") which includes 45 forest stands in Quebec where tree diameters and positions were tracked through successive inventories every 5 years since the 1980s. Soil chemistry and texture were available at the sites. The specific objectives of this study were: (a) determine how competition, soil fertility and climate affect the growth of common tree species in Quebec, (b) determine which interaction effects are more deleterious for the growth of specific tree species in Quebec forests (e.g., low soil fertility combined to high competition; high climate stress combined to high competition) (c) identify future vulnerabilities with climate change for the studied tree species.

3.4 Methods

3.4.1 Study area and study material

The study area encompassed the major vegetation zones of Quebec, ranging from pure deciduous forests in southern Quebec, to temperate and boreal mixedwood stands, and boreal coniferous forests below the northern limit of the commercial forest zone (Fig. 3.1). The mean annual temperature within the study area varies from 6°C to -1°C, while annual precipitation exhibited a gradient from east to west Quebec, ranging from 1050 mm to 650 mm per years. The major perturbations affecting these forests are fire events and insect outbreaks (Aakala *et al.*, 2023). Variations in temperature and precipitation as well as disturbances play a crucial role in shaping the composition and dynamics of the study stands (Brice *et al.*, 2020).

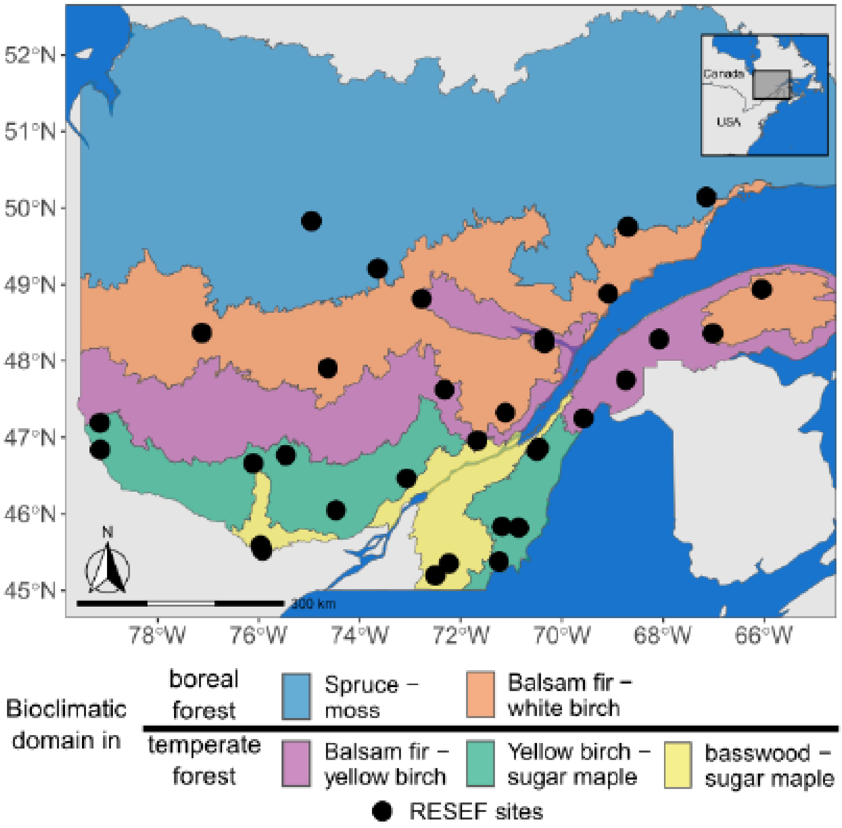

Figure 3.1: Map of the location of the RESEF sites and main bioclimatic domains of Quebec (Canada).

Our study focuses on dominant tree species of Quebec forests, including red maple (*Acer rubrum* L.), sugar maple (*Acer saccharum* Marsh.), yellow birch (*Betula alleghaniensis* Britt.), white birch (*Betula papyrifera* Marsh.), balsam fir (*Abies balsamea* Mill.), and black spruce (*Picea mariana* Mill.). Red maple, sugar maple, and yellow birch are deciduous trees adapted to well-drained, organic-rich soils. They are commonly found in mature temperate forests and exhibit shade tolerance. These species are also frequently encountered in transitional zones between deciduous and coniferous forests (Burns and Honkala, 1991). White birch is less shade tolerant, has greater tolerance to colder climates and is typically found further north in the boreal forest compared to the previous hardwoods. Balsam fir is a coniferous species well-adapted to acidic and humid soils and is frequently observed in Quebec's boreal and sub-boreal forests. Black spruce is a cold-adapted conifer that thrives in peatlands and nutrient-poor soils.

The used data come from the RESEF dataset ("Réseau d'Étude et de Surveillance des Ecosystèmes Forestiers"), which was established in the 1980s to provide fundamental data for comparative analysis, track long-term ecosystem dynamics, evaluate the impact of climate change on forest ecosystems, and analyze the relationships between ecological factors and natural or anthropic perturbations (Fig. 3.1). It includes 45 forest stands spread across all major forested vegetation zones of Quebec but 33 was selected for this study based on soil data availability and the presence of at least two inventories per sites (latitude from 45.20 to 49.83 and longitude from -79.14 to -67.01; Fig. 3.1). In each stand, tree diameters and positions of trees with a DBH (Diameter at Breast Height) greater than 1 cm are measured through successive inventories every 5 years from 1986 to 2020. Stand size range from 0.5 ha in deciduous stands to 0.25 ha squared area in mixed and boreal stands. Diametrical tree growth (mm.y^{-1}) data were computed by subtracting the DBH between two inventories and dividing by the number of growing seasons between the two inventories. This was the response variable of our models once transformed to logarithm. After selection of the species of interest, we only retained healthy trees, trees with a diameter of at least 9.1 cm corresponding to trees of commercial interest, and sites where soils samples were available. The final dataset comprises 33 forest stands, 149 different yearly inventories and 30568 computed growth data (mm.y^{-1}; black spruce: 12158; sugar maple: 11356; balsam fir: 4861; yellow birch: 963; white birch: 713 and red maple: 517).

From the RESEF dataset, we also computed the level of neighbourhood competition experienced by each tree with the following Neighborhood Competition Index (NCI):

$$NCI_i = \sum_{j=1}^{N} \left(\frac{DBH_j{}^{\alpha}}{dist_{ij}^{\beta}} \right),$$

where NCI_i is the effect of competition on the tree i, DBH_j is the diameter at breast height in cm of the neighbor j, α is a parameter expressing the exponential effect of DBH of the neighboring trees, $dist_{ij}$ is the distance in meter between the tree i and the neighbor j, and β is a parameter expressing the exponential effect of distance on the NCI. We selected neighbouring trees within 10 meters from focal trees. NCI_i was computed with individuals of the same species (NCI_{intra}), conifer trees of different species ($NCI_{conifer}$) and deciduous trees of different species ($NCI_{deciduous}$). We used specific α and β parameter values for each study species from Soubeyrand *et al.* (2023).

At each RESEF site, soil properties were measured at most inventory dates, including soil nutrients and texture. From the measured properties, we used the pH, the cation exchange capacity (CEC) and the percentage of clay in the B horizon, which are three variables that may well summarize soil fertility (Duchesne *et al.*, 2002 ; Collin *et al.*, 2016, 2018 ; Hansson *et al.*, 2020 ; Ouimet *et al.*, 2021). For inventories with missing soil samples, we used the mean variable value of all other inventories at the same site.

Light available for each tree at each inventory date was computed with the SORTIE-ND model (Pacala *et al.*, 1996; Murphy, 2011). SORTIE-ND is a spatially explicit, individual-based model that simulates stand dynamics by modeling the whole life cycle of trees within a stand (i.e., seedling, sapling, adult and snag). SORTIE-ND is based on the tree growth calculation including a shading module (GLI light module) that computes the proportion of light received by each tree in the stand according to the height and the crown dimension of the neighboring trees. SORTIE-ND requires tree allometric parameters to compute tree crown dimension and height from tree DBH. We used parameters from Poulin *et al.* 2008 and Soubeyrand *et al.* 2023). When tree species parameters were not available, i.e., neighboring trees out of our target tree species, we used available tree parameters from species with similar biological traits. We provided to SORTIE-ND tree DBH, position and whether trees were dead or alive to create stem maps of all inventories at the RESEF sites. We then ran SORTIE-ND one single timestep to extract the proportion of shadow received by the target trees ranging from 0 (full sun) to 100 (no sun).

3.4.2 Climate data

We obtained historical climate data for each RESEF site using the ClimateNA software (Wang *et al.*, 2016) and extracting data from the first to the last inventory by providing GPS coordinates and elevation. We only used two humidity-related and two temperature-related climate variables known to have high impact on tree growth (Hogg, 1997; St.Clair *et al.*, 2008): the average vapour pressure deficit (VPD), the precipitation sum (PPT), the average temperature (TAVE), and the growing degree days of the summer season (DD5), i.e., June, July and August. To each inventory and corresponding tree growth period, we assigned the average values of the climate variables starting from the previous inventory year.

3.4.3 Bayesian models of tree growth

We modeled tree growth increment (in mm.year^{-1}) as:

$$\log Growth = \alpha + \beta\, size\, effect + \gamma\, shading\, effect + \theta\, crowding\, effect + \rho\, soil\, effect + \varphi\, climate\, effect + interactions + random\, effect \qquad (3.1)$$

In this model, α represents the intercept. $\beta\, size\, effect$ captures the tree size effect modelled as $\beta\, size\, effect = \beta_1\, DBH^2 + \beta_2\, DBH$. $\gamma\, shading\, effect$ captures the influence of the shadows created by neighboring trees. $\theta\, crowding\, effect$ accounts for the crowding effect including intra-species competition (NCI_{intra}), conifer competition ($NCI_{conifer}$), and deciduous competition ($NCI_{deciduous}$) with the following equation $\theta\, crowding\, effect = \theta_1 NCI_{intra} + \theta_2\, NCI_{conifer} + \theta_3\, NCI_{deciduous}$. The soil effect is described by $\rho\, soil\, effect = \rho_1\, CEC^2 + \rho_2\, CEC + \rho_3\, pH_{water}{}^2 + \rho_4\, pH_{water} + \rho_5\, PC_{clay}{}^2 + \rho_6\, PC_{clay}$. Finally, the climate effect is described by $\varphi\, climate\, effect = \varphi_1\, PPT^2 + \varphi_2\, PPT + \varphi_3\, CMI^2 + \varphi_4\, CMI + \varphi_5\, T_{AVE}{}^2 + \varphi_6\, T_{AVE} + \varphi_7\, DD5^2 + \varphi_8\, DD5$. Interactions terms are included between climate and soil, soil and competition as well as climate and competition. A random effect of the site on the intercept is also included. We executed the models using the brms package (Bürkner, 2021) using 2 chains and 2000 iterations on the R software (version 4.2.3; R Core Team, 2023).

The combination of variables used in model 3.1 was selected by removing iteratively variables of the same group at once, i.e., climate, soil, competition and shade variables. We also tested potential interactions between variables. We finally fitted 34 models per species detailed in supporting information B. Models were compared based on a leave-one-out cross-validation approach (LOO Information Criterion; Vehtari et al., 2020). We thus selected the model with the lowest LOO information Criterion.

We also compared the LOO Information Criterion of specific leave-one-out models (i.e., full model without soil constraints, full model without competition, full model without climate, full model without light) and using the full model as a reference baseline to evaluate the relative importance of the 4 groups of variables in explaining tree growth of each species. The larger the difference between one tested model and the full model, the more important the corresponding group of variables was for explaining tree growth of that species.

3.4.4 *A priori* distribution of the parameters

The a priori distributions of the model parameters needed in a Bayesian framework were determined for soils and climate parameters with independent datasets spanning larger geographical regions (determination of priors for climate variables) or including additional sites (determination of priors for soil variables). It was important to get accurate *a priori* distribution for these parameters because only one value per RESEF inventory was available relative to the much higher number of observations for the DBH, the competition and the shading effects corresponding to one observation per tree per inventory. Conversely, for the DBH, shading and competition parameters, we set a scale-centered normal distribution as an uninformative prior.

For the *a priori* distributions of the climate parameters, we used data from an extensive network of government plots in the northeastern United States and the Canadian provinces of Ontario, Quebec and New Brunswick covering most of the distribution range of the studied tree species. This network comprises 42090 DBH measurements in 3757 plots (10685 for balsam fir; 8229 for red maple; 6789 for white birch; 4488 for sugar maple; 3876 for black spruce; 1981 for yellow birch). Using this data, we modeled in a Bayesian framework tree growth per each species as a function of VPD, PPT, TAVE, and DD5. Historical climate values were extracted using climateNA providing GPS coordinates and elevation per each site. The models used scale-centered climate variables and tree DBH and used various combinations of the following explanatory variables, log $growth\ =\ \beta_1\, DBH^2 +\ \beta_2\, DBH +\ \varphi_1\, PPT^2 + \varphi_2\, PPT + \varphi_3\, CMI^2 + \varphi_4\, VPD +\ \varphi_5\, {T_{AVE}}^2 + \varphi_6\, T_{AVE} + \varphi_7\, DD5^2 + \varphi_8\, DD5$. Model selection proceeded with the following rules: (a) the simple and quadratic effect of DBH were necessarily selected, (b) only one between VPD and PPT, and one between TAVE and DD5 could be selected because of their high cross-correlation, and (c) when quadratic term was selected also the linear term was necessarily selected. We selected the model with the lowest LOO Information Criterion. The prior distribution for all parameters followed a standard normal distribution. The posterior distributions of the retained model parameters were used as priors for the model 3.1.

For a more exact determination of the priors of the soil parameters, we used decadal dendrometric and edaphic data from the Quebec government's permanent inventory plots distributed in the commercial forest of Quebec. We extracted tree growth of the study species where the same soil variables used for the model of model 3.1 were available. This represented 17021 tree growth measurement in 961 sites. We scale-centered all soil variables and used the posteriors of the DBH parameters obtained with the preceding climate model. The *priors* for the soil model were also set as normal distributions. We then selected the best combination of the following full model based on the LOO Information Criterion: $\log growth = \beta_1\, DBH^2 + \beta_2\, DBH + \rho_1\, CEC^2 + \rho_2\, CEC + \rho_3\, pH_{water}{}^2 + \rho_4\, pH_{water} + \rho_5\, PC_{clay}{}^2 + \rho_6\, PC_{clay}$. Model selection proceeded with the following rules: (a) the simple and quadratic effect of DBH were necessarily selected, and (2) when the quadratic effects were selected, the related linear effect was necessarily selected. Similarly to the retained climate variables, the posterior distributions of the retained soil model parameters were used as priors for the model 3.1.

3.4.5 Analysis of tree growth responses

For each species, we showed on plots the effects of the retained climate and soil variables on tree growth, including interactions with the competition terms. This procedure allowed for visualizing the influence of the significant variables, while displaying the potential impact of climate change and understanding how forest management may contribute to reduce such impact by modulating competition between trees. For the climate variables, we also extracted the mean climate conditions for the 2100 horizon at all RESEF sites where one species was present and displayed such values on the plots to analyze potential future species-specific responses. We used four different Shared Socioeconomic Pathways (SSP) climate scenario from the IPCC Sixth Assessment Report (SSP1: A future with strong global cooperation, ambitious sustainability policies, and low greenhouse gas emissions; SSP2: Socioeconomic development continues along current trends, with moderate efforts to address climate change; SSP3: Limited global cooperation, high inequality, and fragmented climate change efforts; SSP5: Heavy reliance on fossil fuels, rapid economic growth, and limited climate action; IPCC (2023)). The mean of 13 simulations from models contributing to the Coupled Model Intercomparison Project was used (Wang *et al.*, 2016). For the soil variables, we extracted values from the permanent inventory plots of the Quebec government where one species was present. We displayed the resulting frequency distribution on plots of that species, highlighting the potential future responses of each tree species within its respective edaphic distribution ranges.

3.5 Results

3.5.1 Model selection

The selection of the climate variables differed for the different species. The model for sugar maple only retained DD5, while the other models always retained one temperature-related (TAVE or DD5) and one humidity-related (PPT or VPD) variable (Table 3.1). Among the soil variables, CEC has been consistently selected, but not necessarily with a quadratic effect. Therefore, CEC appeared to be a good indicator of the growth for all the study species. For all species growth increased with CEC, except for black spruce. Maples and conifer trees were also linked to the clay content, and to pH in the case of the two conifer tree species (Table 3.1).

Table 3.1: Climate and soil variables selected with the preliminary analysis on independent datasets.

Species	Selected climate variables	Selected soil properties
Sugar maple	$DD5 + VPD + VPD^2$	$CEC + CEC^2 + PC_{CLAY}$
Red maple	$PPT + PPT^2 + DD5 + DD5^2$	$CEC + PC_{CLAY}$
Yellow birch	$VPD + VPD^2$	CEC
White birch	$VPD + VPD^2 + TAVE + TAVE^2$	CEC
Black spruce	$VPD + VPD^2 + TAVE + TAVE^2$	$CEC + CEC^2 + pH + PC_{CLAY} + PC_{CLAY}^2$
Balsam fir	$VPD + TAVE + TAVE^2$	$CEC + CEC^2 + pH + pH^2 + PC_{CLAY} + PC_{CLAY}^2$

The final models (see eq. 3.1) for sugar maple, black spruce and balsam fir retained all group of variables whereas for red maple and white birch, interactions related with competition have not been selected, and for yellow birch none of the terms related with climate were selected (Table 3.2).

Table 3.2: Group of variables retained in the final models (model 3.1) explaining the radial growth of the tree species and explained variance. The random effect of the site is included in the R².

Species	Model selected with LOO	R^2
Sugar maple	Competition + soil + climate + shading + soil:competition + climate:competition + soil:climate (full model)	0.22
Red maple	Competition + soil + climate + shading + soil:climate	0.30
Yellow birch	Competition + soil + shading + sol:competition	0.22
White birch	soil + climate + competition + shading + soil:climate	0.35
Black spruce	Competition + soil + climate + shading + soil:competition + climate:competition + soil:climate (full model)	0.34
Balsam fir	Competition + soil + climate + shading + soil:competition + climate:competition + soil:climate (full model)	0.49

For sugar maple and yellow birch, shade from surrounding trees and competition for space, water and nutrients were identified as the most influential factors (Fig. 3.2). For the remaining species, the relative importance of the groups of variables is more shared. Nonetheless, shade emerges as a significant factor for white birch growth. Climate appeared to be particularly important for black spruce and balsam fir.

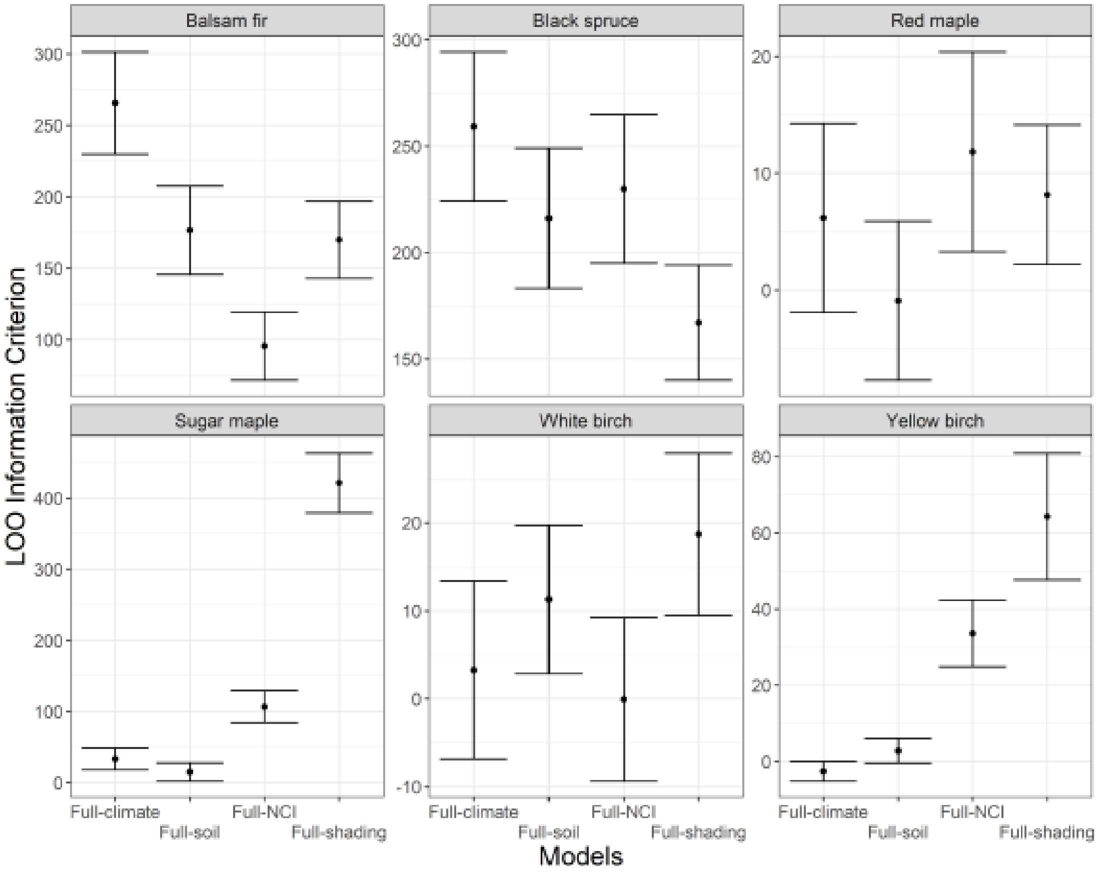

Figure 3.2: Importance of specific groups of variables in the models explaining the growth of each study tree species (log(mm.year^{-1})). The importance is based on the comparison between Loo Information Criterions between the full model and the model without one group. Higher values indicate greater importance of the group in the final model. Conversely, values below zero suggest that the removal of the group improves the model. NCI stands for Neighbourhood Competition Index.

3.5.2 Quality of model fit

The predicted growth curves generally aligned with the actual growth rates for each species, with better performance for balsam fir, black spruce, and white birch (Fig. 3.3,

Table 3.2). However, it is important to note that the models fitted better for high growth rates than for low growth rates and that the model uncertainties were large.

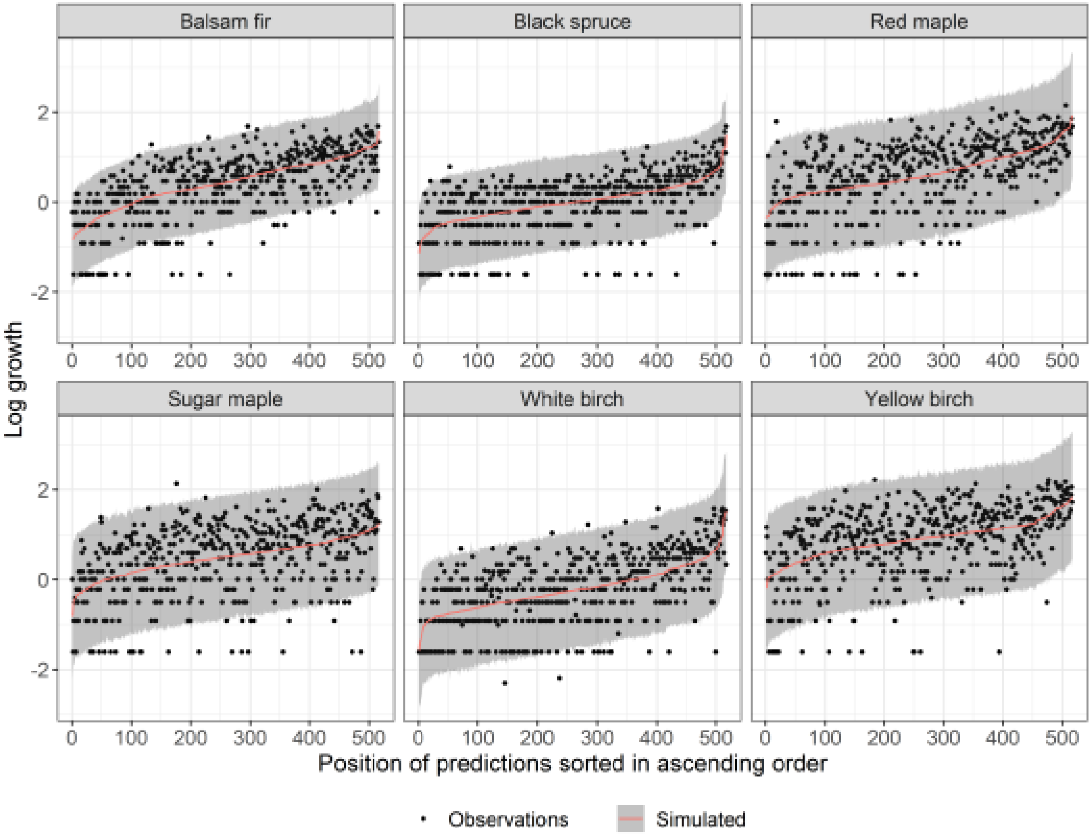

Figure 3.3: Predicted and observed growth sorted by their prediction positions. Simulated growth is represented by the mean line and 95% confidence intervals. The actual growth observations are shown as points. To address the issue of overplotting due to a high number of observations, we randomly selected 517 predictions for each species, which corresponds to the lowest number of observations among the species, namely red maple.

3.5.3 Impact of explanatory variables and of their interactions on tree growth

The model coefficients can be analyzed to interpret tree-growth trends according to ontogenic and environmental conditions. The coefficient of the DBH squared was found to be negative, except for red maple, indicating an increase in growth until an optimal DBH followed by a decrease in growth as DBH increases. The red maple's slightly positive DBH square coefficient indicates the presence of a DBH value where unexplained constrains by our model are maximal (Fig. 3.4). For all species, lower light availability corresponded to lower tree growth. Intraspecific competition had a positive impact on red maple, yellow birch, and white birch but had a negative effect on balsam fir, sugar maple, and black spruce. Especially for balsam fir, intraspecific competition was more detrimental than interspecific competition. Competition from coniferous species had a detrimental effect on red maple, sugar maple, and yellow birch. Black spruce and white birch were instead not significantly affected by any kind of competition. It is important to emphasize that even when the simple of competition effect doesn't have a direct impact on tree growth (see Fig. 3.4), it can significantly modulate the effect of other environmental variables by interaction (see below).

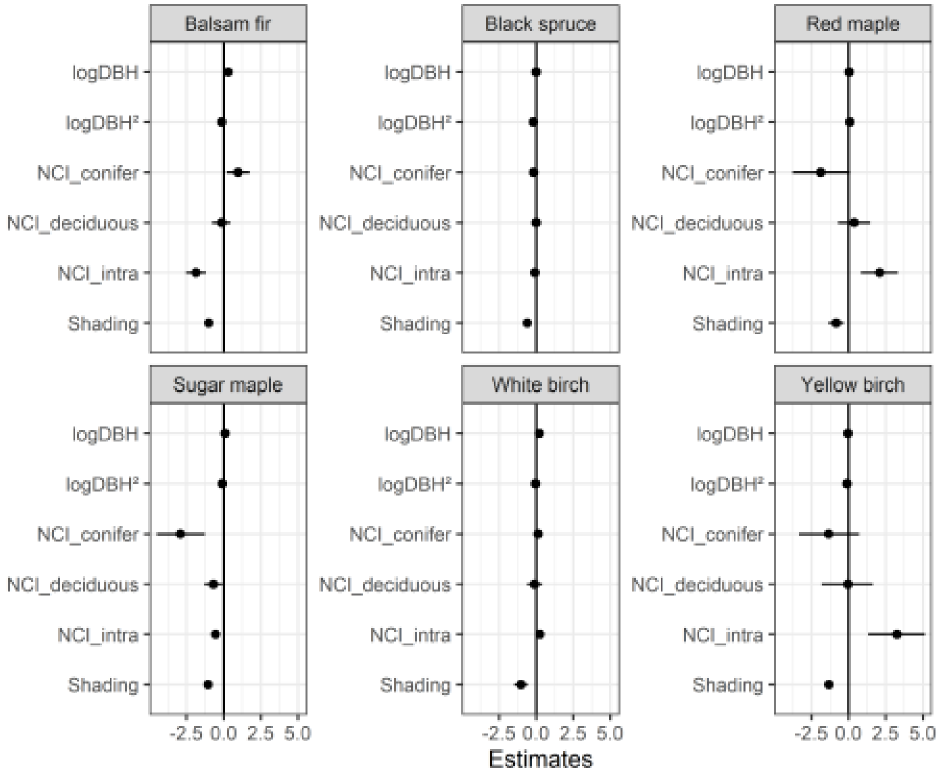

Figure 3.4: Model estimates of DBH, competition and shading effects for each species after model selection. The points represent the median of the estimates, and the error bars indicate the 2.5th - 97.5th quantile range of the posterior distributions. The model was highly constrained for tree DBH, leading to small error bars.

Only red maple and white birch showed increased growth under warmer climate, other species showed a decline in growth. However, several interactions between climate, soil, and competition may modulated tree growth (Fig. 3.5 and Fig 3.6). The growth trends of balsam fir trees appeared to increase with warmer temperatures, although the uncertainties were large. Similar findings were found for black spruce, where higher TAVE values leaded to decrease growth, especially under high intraspecific competition. Tree growth of red maple and yellow birch increased with higher intraspecific competition (NCI intra).

By 2100, tree species will face climate conditions much different than the current ones in Quebec even in the most optimistic climate scenario. These changes may profoundly affect tree growth. For example, black spruce growth in Québec will be limited by the rise in temperatures even under the most optimistic scenario (Fig 3.5).

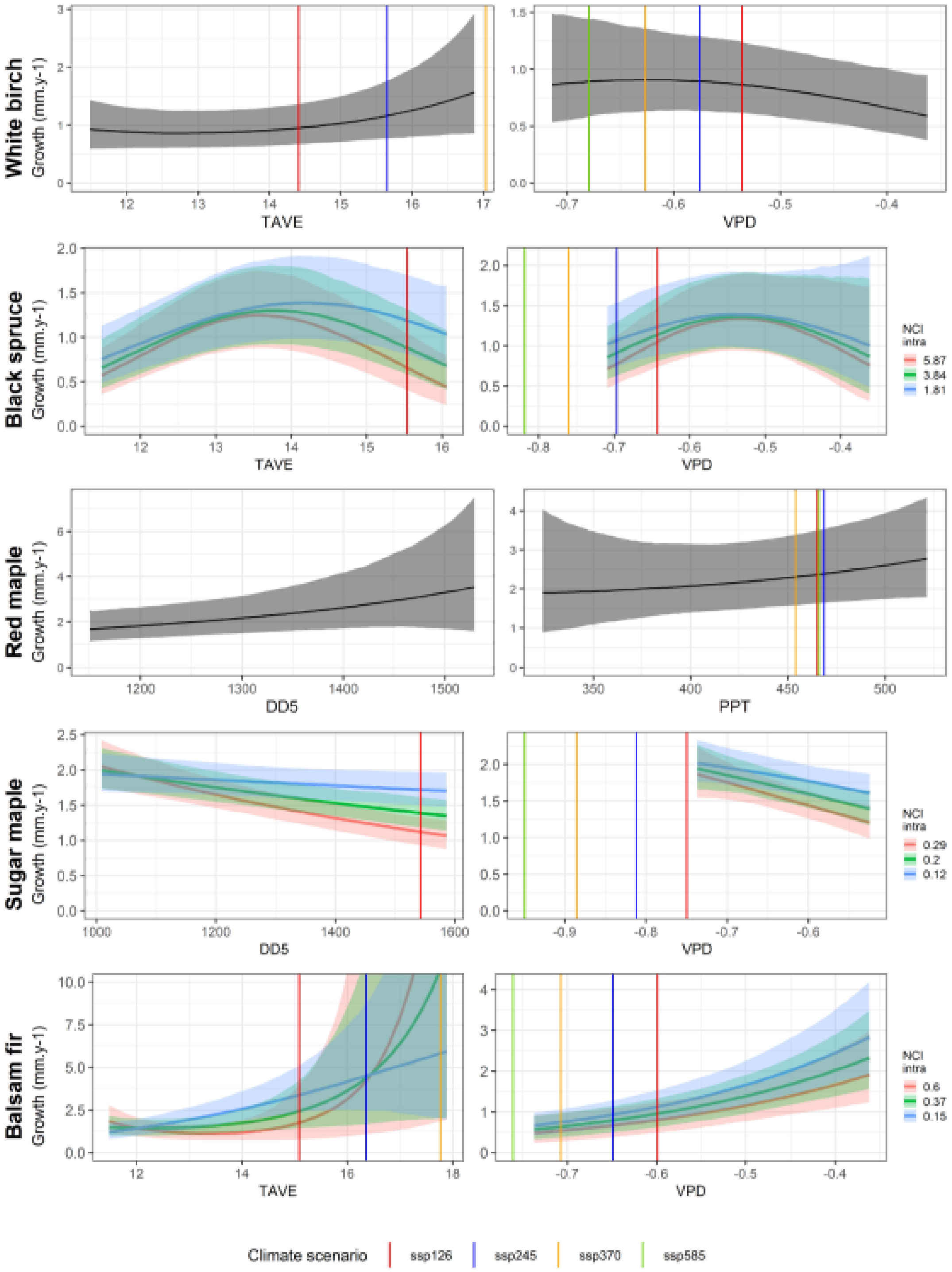

Figure 3.5: Radial growth of tree species in relation to climate variables and interactions with intraspecific competition. The green line corresponds to the mean of the interaction variable, and the red and blue lines correspond to the mean plus and minus one standard deviation, respectively. Error areas correspond to the 5th and the 95th quantile Bayesian confidence intervals. All linear, quadratic and interaction effects can be found in the Supplementary Information. Colored vertical lines represent mean future climate variable values (2100 horizon; four considered climate scenarios) at the RESEF sites where the species are present. Only future climate values inside our prediction range are shown.

Tree growth responses to soil variables were found to be influenced by climate conditions and competition of neighbouring trees (Fig. 3.6). Tree growth increases with CEC, except for yellow birch especially with null intraspecific competition and for black spruce and balsam fir only with low temperature. White birch and red maple showed a stronger positive response to higher CEC, modulated by temperature and precipitation levels. Both sugar maple and balsam fir exhibited increased growth with higher CEC, with a low interaction effect of competition. Black spruce growth was inversely related to CEC and soil acidity, especially with lower temperature values. Sugar maple growth was negatively affected by the proportion of clay, and the negative impact was further amplified under lower intraspecific competition.

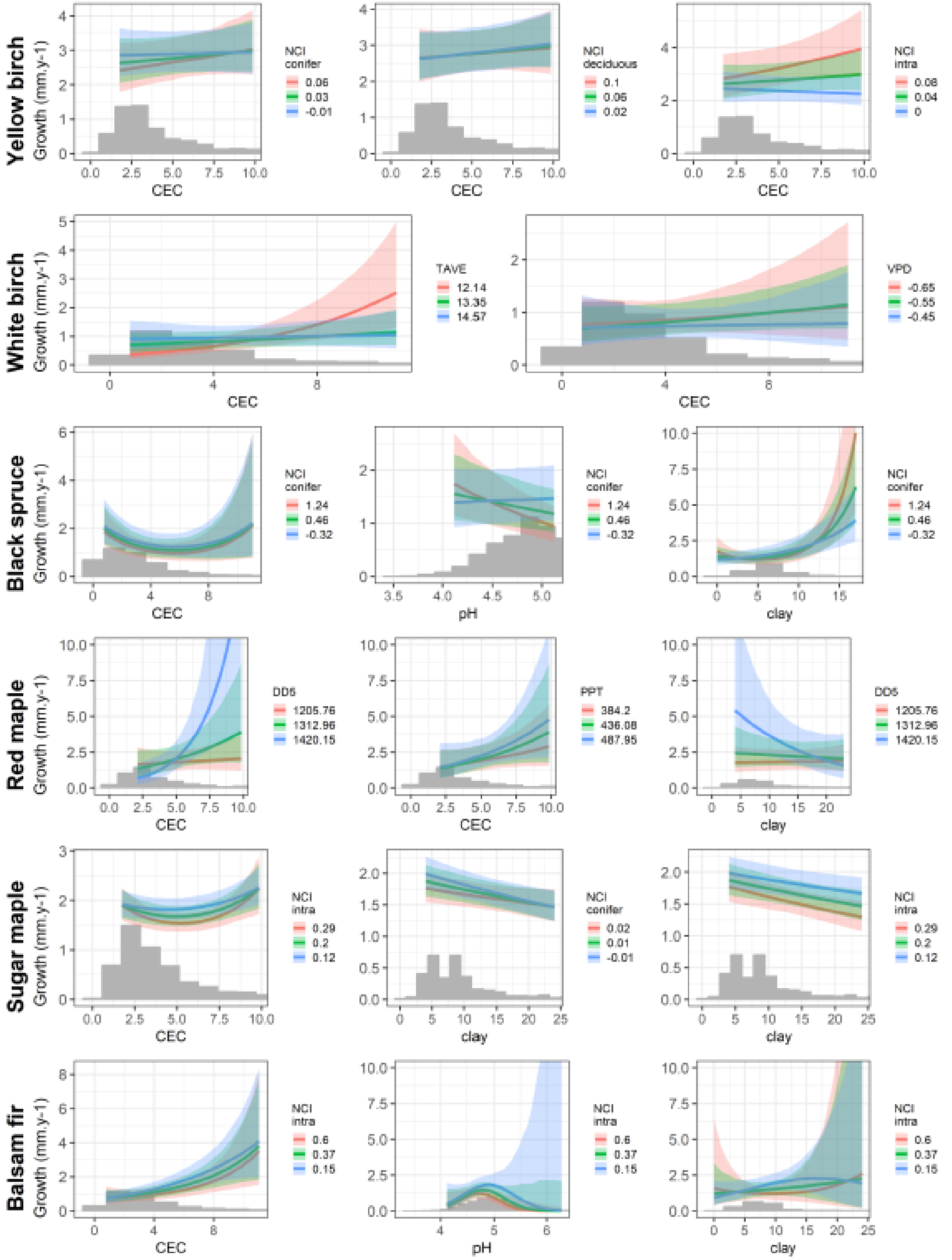

Figure 3.6: Growth of the selected tree species in relation to soil properties and interactions with competition and climate variables. The green line corresponds to the mean of the interaction variable, and the red and blue lines correspond to the mean plus

and minus one standard deviation, respectively. Error areas correspond to the 5th and the 95th quantile Bayesian confidence intervals. All linear, quadratic and interaction effects can be found in Supplementary Information. We also displayed histograms depicting the frequency distribution of soil properties in the permanent plot of Quebec where the species is present.

3.6 Discussion

3.6.1 How tree species growth responses to climate and soil properties are modulated by competition?

In this study, we investigated the interplay of tree species growth responses with climate, soil properties, competition, and the amount of light received by the trees in mixed forest stands of Quebec. A large dataset was used including temperate and boreal forest stands where the position of each tree is monitored at each inventory date. We find that tree growth was regulated by each of these factors individually and by the interactions among them. Our findings highlight the critical role of competition in shaping tree growth responses within climate and soil gradients but were highly species-specific, i.e., the direction and strength of these effect varied with tree species as suggested by other studies (Ford *et al.*, 2017). It is worth noting that the shading effect emerged as a key factor influencing the growth of all examined tree species.

The contrasting results of competition interactions with climate and soil properties for different tree species is shown by the negative effects (i.e. higher intraspecific competition corresponds to increased sensitivity of tree growth to climate or soil variables with growth reductions becoming more plausible) observed for balsam fir, sugar maple, and black spruce and the positive effects for red maple and yellow birch. These results feed the ongoing debates between the Stress Gradient Hypothesis and the CSR (competitive, stress-tolerant, ruderal) Strategy Theory (Coates *et al.*, 2013).

According to the Stress Gradient Hypothesis, in stressful environmental conditions like drought or low nutrients availability, competition among species may decrease (Lortie and Callaway, 2006; Maestre *et al.*, 2009). This could explain why some tree species that compete for resources in less stressful environments are less sensitive to competition during drought periods (Aussenac *et al.*, 2019). For example, red maple and yellow birch may be better suited to exploit available resources in a competitive environment when conditions are stressful. On the other hand, the CSR Strategy Theory focuses on species life strategies (Tilman, 1985). According to this theory, competition for resources is a key factor explaining tree communities especially in challenging environmental conditions such as drought or low nutrient availability where tree competitions should be exacerbated (Tilman, 1985). During prolonged drought periods, water availability decreases, intensifying competition among species (Ford *et al.*, 2017; Castagneri *et al.*, 2022; Kulha *et al.*, 2023). With increasingly hotter summers and reduced precipitation, soil water availability is expected to become a problematic factor for tree growth, and intraspecific competition could further deteriorate growth (Magalhães *et al.*, 2021). Thus, species like balsam fir, sugar maple, and black spruce, which are less stress-tolerant, might be disadvantaged in competitive environments such as dryer conditions.

Other studies have demonstrated that the interactions between competition and environmental variables can shape tree growth responses. Coates *et al.* (2013) also illustrated that the growth of dominant tree species in the sub-boreal spruce region of the Canadian boreal forest was influenced by interactions between tree competition and soil fertility, and this interaction was specific to each species and environmental context. Oboite and Comeau (2020) suggested that an increase in intraspecific competition would likely lead to reduced tree growth among dominant species in western Canada and Alaska as the climate warms. They also observed that the effects of interactions between interspecific competition and a warmer climate was species-specific. Chavardès *et al.* (2022) demonstrated that the growth responses of black spruce and jack pine (*Pinus banksiana Lamb.*) in the mixedwood boreal forests of western Quebec generally exhibited a negative correlation with temperature, particularly when intraspecific competition was higher. Our results precise these competition-environment interactions for the dominant tree species in Québec by taking advantage of a large and detailed forest inventory dataset that includes the precise coordinates of each tree.

3.6.2 Importance of climate-soil interactions on tree growth rate

Among the considered variables, only CEC has been consistently selected in all models for all tree species. This variable is a robust proxy for soil fertility (Weil. and Brady, 2016). In addition to the positive effect of CEC on tree growth (except for black spruce), we observed that the interaction between CEC and climate is important, especially in the case of red maple, black spruce, and white birch. For example, the growth of red maple was positively influenced by higher temperatures, and decreased when soil fertility was low and the proportion of clay in the soil was high.

Our findings suggest that optimal sugar maple growth is associated with specific soil conditions such as nutrient-rich soils with low clay content (Schaberg *et al.*, 2006). Since the 1970s, sugar maple has been experiencing a decline in growth and regeneration due to multiple factors (Bishop *et al.*, 2015). The primary factor contributing to this decline is likely the soil acidification resulting from atmospheric pollution and associated to a decrease of nutrient availability (Duchesne *et al.*, 2002; Sullivan *et al.*, 2013; Collin *et al.*, 2016). Although soil acidity was not selected in our model for sugar maple, it includes CEC showing the importance of nutrient concentration in soils. Another factor that may have contributed to the sugar maple's growth decline is the invasive behaviour of American beech (*Fagus grandifolium*

Ehrh.), which can establish rapidly and compete with sugar maple (Duchesne *et al.*, 2005; Gravel *et al.*, 2011). Our model was built with data from mature stands, and competition between sugar maple and other deciduous was less intense than with conifers. However, the species was highly sensitive to the amount of light intercepted by other trees confirming the results of other studies focussing on the beech-maple interactions (Beaudet *et al.*, 1999; Nolet *et al.*, 2015). This increased competition can exert significant pressure on sugar maple growth, mitigating the beneficial effects of nutrient-rich soils (Collin *et al.*, 2017b).

3.6.3 Implications for forest management

By the year 2100, it is anticipated that certain tree species will face climates that are currently outside their current distribution range (McKenney *et al.*, 2011). For instance, the black spruce southern distribution range is located in southern Quebec. Under the most favorable climate scenario, we found that black spruce will be already approaching the upper threshold of its current temperature niche in our study region. Girardin *et al.* (2016) found that the growth and productivity of black spruce may be compromised in the future, potentially leading to a decline in growth rates due to a lack of soil water availability especially in the southern part of its distribution range. On the other hand, the climate may increase the growth of this species farther north, with the release of climate constraints such as an extended growing season and higher summer temperatures (D'Orangeville *et al.*, 2016; Pedlar and McKenney, 2017; Gennaretti *et al.*, 2017; Moreau *et al.*, 2020b). These results may have profonde implications for the forest sector in Quebec which currently depend on black spruce logging. It is imperative that alternative and sustainable management options are thoroughly explored and implemented to ensure the resilience and long-term viability of the forestry industry in Quebec.

Our study highlights the crucial importance of considering interactions between soil, climate, and competition when modeling tree growth, especially in the context of assessing the impacts of climate change. We observed that, with the anticipated climate warming trend, the growth of black spruce, balsam fir, and sugar maple is expected to decrease. This decline should be exacerbated by high levels of competition, particularly intraspecific competition. Therefore, to achieve high productivity in stands containing these species, it is essential to mitigate intraspecific competition by diversifying tree species composition. Indeed, greater species diversity in forest stands may imply complementary niches and interactions, and may result in improved resistance to drought (Aussenac *et al.*, 2019) and insect infestations (Chavardès *et al.*, 2022). Tree diversity is often advocated to enhance the resistance and resilience of forest ecosystems to various environmental constrains (Cappuccino *et al.*, 1998; Paquette andMessier, 2011; Charnley *et al.*, 2017).

Conversely, other species such as red maple and yellow birch may better tolerate intraspecific competition, especially in favorable micro-site conditions with nutrient-rich soils, low clay content and higher air temperatures (Collin *et al.*, 2016). Considering the high performance of red maple in a warmer climate and the decline of sugar maple since the 1970s in Quebec (Boakye *et al.*, 2023), it is advisable for the forest industry to increase the exploitation of red maple even in the boreal zone where it is currently present only in marginal populations. This will be particularly possible if the wood quality of red maple at the northern limit of its distributional range will be high enough under future climate conditions (Havreljuk *et al.*, 2013).

3.7 Acknowledgments

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3.8 Conflict of interest statement

We have no conflict of interest to declare.

3.9 Funding statement

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CONCLUSION GÉNÉRALE

La multiplicité des facteurs régissant la croissance et la répartition des espèces d'arbres complique les estimations concernant leur évolution de leur aire de répartition dans un contexte de changements climatiques et d'aménagement forestier intense. Cette complexité est particulièrement marquée aux latitudes élevées, où les changements climatiques sont plus prononcés, ainsi que dans les écotones, dans lesquels certaines espèces atteignent leur limite de répartition. C'est le cas des trois espèces d'arbre feuillu tempéré qui ont fait l'objet d'étude de cette thèse de doctorat, l'érable à sucre, l'érable rouge et le bouleau jaune. Plus particulièrement, l'objectif général de cette thèse était de déterminer quels étaient les facteurs qui pouvaient faciliter ou contraindre la colonisation, la croissance et la survie des feuillus tempérés dans la forêt boréale mixte du Québec. Nous avons considéré les effets de la compétition, du climat dans un contexte de réchauffement climatique, du sol et des dynamiques de successions forestières.

4.1 Colonisation des peuplements boréaux mixtes par les feuillus tempérés

L'équation centrale du modèle SORTIE-ND traite de la croissance des arbres adultes. L'équation que nous avons utilisée se décompose en trois éléments distincts: l'effet du diamètre de l'arbre, l'effet de l'ombre des arbres voisins captant la lumière, et l'effet de la compétition pour les ressources avec ces mêmes arbres voisins (Canham *et al.*, 2004). Grâce à ces trois éléments, le modèle SORTIE-ND est capable de reproduire fidèlement les dynamiques de succession des peuplements en forêt tempérée et en forêt boréale mixte ce qui a permis l'étude de scénarios de coupes, de perturbation de la forêt boréale mixte par la tordeuse des bourgeons de l'épinette ou des dynamiques de succession (Bose *et al.*, 2015; Maleki *et al.*, 2019). En revanche, aucune étude de modélisation avec SORTIE-ND ne s'était intéressée au cas dans lequel les feuillus tempérés et les espèces de la forêt boréale mixte puissent co-exister. Nous avons donc paramétrisé le modèle de manière que les feuillus tempérés et les espèces de la forêt boréale mixte puissent interagir ensemble dans la composante de compétition du modèle. Pour cela nous avons paramétrisé l'équation de la croissance grâce aux données du réseau d'étude et de surveillance des écosystèmes forestiers au Québec (RESEF). Nous avons ensuite validé avec succès cette paramétrisation en utilisant les placettes permanentes du gouvernement du Québec qui se trouvaient dans la forêt tempérée mixte (chapitre I).

Avec cette nouvelle paramétrisation, nous avons déterminé si les feuillus tempérés pouvaient s'établir dans des peuplements boréaux mixtes à travers deux plans d'expérience différents avec leurs avantages et inconvénients respectifs mais présentant des résultats similaires. Dans le premier chapitre, nous avons introduit les feuillus tempérés sous forme de semis aléatoirement répartis dans les peuplements avec différentes densités (500, 5000 ou 10 000 semis par hectare). Dans le deuxième chapitre, nous avons remplacé une placette centrale du peuplement hôte par une placette de feuillu tempéré au stade d'arbre mature. Introduire les feuillus tempérés sous forme de semis permettait de contrôler directement le nombre de semis rajoutés dans le peuplement, ainsi nous avons pu suivre la survie des semis au cours du temps. Cependant, il est important de noter que ce plan expérimental ne reflète pas nécessairement la réalité, car il est hautement improbable que de nombreuses graines d'arbres puissent arriver simultanément en grande quantité dans un peuplement pour ensuite cesser d'arriver. Le deuxième plan expérimental en revanche reflète un peu mieux comment les feuillus tempérés pourraient coloniser la forêt boréale mixte. En effet, une placette comprenant une dizaine d'arbres matures au milieu d'un peuplement pourrait résulter de migrations longue distance. Ce scénario se présente effectivement sur le terrain, notamment dans le territoire de la FERLD, sur les collines Hébécourt, où on peut observer la présence de quelques dizaines d'érable rouge, entourés de sapins baumiers, d'épinettes blanches et de bouleaux blancs. Dans notre plan expérimental, ce réservoir de feuillus tempérés disperse alors ses graines avec un flux constant dans le peuplement adjacent et peut le coloniser.

Nous avons pu montrer que les feuillus tempérés pouvaient s'établir et persister dans les peuplements boréaux mixtes lorsqu'ils sont introduits au stade de semis (chapitre I) et au stade mature (chapitre II). En effet, les interactions de compétition entre les feuillus tempérés et le climat actuel ne seraient pas des facteurs qui contraindraient leur établissement, leur survie et leur croissance dans la forêt boréale mixte. Lorsque les feuillus tempérés sont introduits sous forme de semis dans le peuplement, c'est l'érable rouge qui aurait la meilleure capacité à croître et survivre (surface terrière après 110 ans de simulations), suivi du bouleau jaune et de l'érable à sucre. En revanche, lorsque les feuillus tempérés sont introduits au milieu du peuplement, c'est le bouleau jaune qui colonise le mieux le peuplement adjacent profitant de sa grande capacité à se disperser suivi de l'érable à sucre et de l'érable rouge.

Nous avons considéré plusieurs stades de succession des peuplements de la forêt boréales mixtes pour déterminer si la capacité des feuillus tempérés était modifiée en fonction de la composition et de la densité en arbre des peuplements. En effet, les changements d'intensité de la compétition entre les arbres dans les différents stades de successions pourraient avoir un impact sur leur capacité à coloniser les peuplements. La capacité de l'érable à sucre et du bouleau jaune à croître et survivre était légèrement plus élevée dans le peuplement le plus jeune, mais elle était indépendante de la composition des autres peuplements dans lesquels ils ont été introduits. Cela signifie que ces espèces sont affectées de la même manière, quelle que soit la composition des espèces du peuplement hôte. Ces résultats sont en accord avec leur autoécologie, car ces espèces sont tolérantes à l'ombre et bien adaptées à la régénération sous le couvert forestier (Burns et Honkala, 1991). En revanche, l'érable rouge est moins tolérant à l'ombre s'établie abondamment seulement dans les peuplements les plus jeunes.

Dans le cas particulier où les semis étaient introduits dans des peuplements récemment coupés, les feuillus tempérés ne parvenaient pas à se maintenir en raison de la forte compétition induite par la régénération excessive des peupliers faux-trembles. En revanche, lorsque les feuillus tempérés étaient introduits depuis une placette au centre du peuplement, ils avaient la capacité de coloniser le peuplement récolté. En effet, cette placette centrale sert de refuge pendant la phase de régénération intensive des peupliers faux-trembles, ce qui permet aux feuillus tempérés de coloniser le peuplement successivement après l'éclaircissage naturel des peupliers faux-trembles.

L'introduction de feuillus tempérés dans la forêt boréale mixte aurait un impact significatif sur les dynamiques de succession de cette forêt avec des conséquences potentielles pour les espèces hôtes. En effet, nous avons montré que les trajectoires de dynamique de succession seraient déviées des trajectoires sans feuillu tempéré. Les espèces tempérées s'établissent dans les peuplements au détriment des espèces boréales de stade de succession plus tardif, telles que le thuya occidental et le sapin baumier qui pourraient être remplacés par les feuillus tempérés. La proportion de feuillus devrait ainsi augmenter dans les peuplements au détriment des espèces de conifères avec des conséquences potentielles sur les régimes de perturbations, pour l'industrie forestière mais aussi pour la biodiversité à cause des changements de composition spécifique des peuplements de la forêt boréale mixte (Vanderwel *et al.*, 2011).

4.2 Effet des changements climatiques sur la croissance des espèces de la forêt boréale mixte

Bien que SORTIE-ND soit hautement adaptable aux situations que nous souhaitions modéliser, SORTIE-ND ne considère le climat qu'à travers des variables climatiques simples telles que la température et les précipitations annuelles moyennes. Or, la caractérisation des effets des changements climatiques sur la croissance des arbres apparait beaucoup plus complexe que ces deux indicateurs seulement. Pour le chapitre I et II, nous avons alors pris en compte, dans l'étape de la paramétrisation de la croissance des arbres, l'influence du climat à travers d'autres indicateurs de la croissance des arbres en relation avec la température, les précipitations pendant la saison de croissance, mais aussi de sécheresse.

Nous avons démontré que la croissance des feuillus tempérés était particulièrement influencée par la variable DD5 (degrés-jours de croissance) (chapitre I et chapitre III). Nos résultats ont montré que les conditions climatiques actuelles de la forêt boréale mixte sont favorables à la croissance des feuillus tempérés, signifiant que ce n'est pas le climat qui contraint l'établissement des feuillus tempérés au nord de leur aire de répartition (chapitre I; Drobyshev *et al.* 2014; Zhang *et al.* 2015). Les changements climatiques devraient rendre les conditions de croissance des feuillus tempérés encore plus favorable dans la forêt boréale mixte, mais nos résultats montrent que la capacité des feuillus tempérés à s'établir dans la forêt boréale mixte n'est pas augmentée, même sous le scénario de forçage climatique le plus intense (chapitre II). Alors que la croissance réalisée des feuillus tempérés augmente avec l'intensification des changements climatiques, d'autres facteurs que nous modélisons avec SORTIE-ND, tels que la régénération et la mortalité, influencent beaucoup plus la capacité des feuillus tempérés à s'établir dans la forêt boréale mixte. Les effets des changements climatiques étaient donc négligeables par rapport à ceux liés à la composition et à la densité du peuplement hôte.

En revanche, pour d'autres espèces de la forêt boréale mixte, les impacts des changements climatiques pourraient être délétères à leur croissance et leur survie. Dans le chapitre III, nous montrons que la croissance du sapin baumier, de l'épinette noire et de l'érable à sucre pourrait diminuer au Québec d'ici 2100, même sous le scénario climatique le plus optimiste alors que la croissance du bouleau blanc resterait stable. Par exemple, l'épinette noire, actuellement présente dans le sud du Québec, pourrait connaître une baisse de croissance due à un manque d'eau dans le sol au sud de son aire de répartition, mais une croissance accrue plus au nord en raison d'une saison de croissance prolongée et de températures estivales plus élevées. D'ici 2100, il est prévu que certaines espèces d'arbres occuperont des zones climatiques qui se trouvent en dehors de leur aire de répartition actuelle.

4.3 L'importance des interactions climat-sol-compétition dans la modélisation de la croissance des espèces d'arbres

La compétition pour les ressources est souvent considérée comme un facteur important dans l'étude de la croissance des arbres (Aussenac *et al.*, 2019; Oboite et Comeau, 2020). Les arbres sont en compétition pour l'accès aux ressources telles que les nutriments disponibles dans le sol ou l'eau (Coates *et al.*, 2013). Or, la disponibilité de ces ressources dépend directement de facteurs du sol tels que la concentration en nutriment des sols mais aussi des facteurs climatiques influençant la disponibilité en nutriments et en eau du sol, notamment lors des cas extrêmes de sécheresse et d'inondations (Lévesque *et al.*, 2016). En effet, la solubilité et la mobilité des nutriments diminuent dans un sol trop sec ou saturé en eau, ce qui entrave leur absorption par les racines des arbres (Kreuzwieser et Gessler 2010). De plus, la sécheresse réduit l'activité des racines et la capacité des micro-organismes à rendre les nutriments accessibles aux arbres (Kreuzwieser et Gessler, 2010 ; Mainiero et Kazda, 2006). Ainsi, les facteurs liés au sol, au climat et à la compétition interagissent. Il est important de considérer ces interactions lorsqu'on modélise la croissance des arbres, car ils peuvent compromettre la croissance et la santé des arbres, les rendant plus vulnérables aux épidémies et aux feux (Chavardès *et al.*, 2021, 2022).

La méthodologie des deux premiers chapitres incluait à la fois l'impact du climat et de la compétition sur la croissance des arbres, mais ces deux facteurs n'étaient pas en interaction, c'est-à-dire que l'intensité de la compétition ne dépendait pas du climat. En revanche, dans le chapitre III, nous avons considéré l'interaction entre le climat et différents types de compétition (intra- et interspécifique) ainsi que l'interaction du climat avec le sol, et de la compétition avec le sol. Nous avons montré que ces interactions influençaient la croissance des arbres typiques de la forêt tempérée mixte et de la forêt boréale, et que la direction et l'intensité de ces effets étaient spécifiques à l'espèce. Dans un climat de plus en plus chaud, l'effet de la compétition peut varier, devenant soit plus intense, soit plus faible dépendant de l'espèce considérée. Par exemple, dans le chapitre III, nous montrons que la croissance de l'érable à sucre diminuerait en réponse aux changements climatiques, et cette diminution de la croissance pourrait être plus prononcée en présence d'une pression de compétition accrue. En revanche, la croissance de l'érable rouge augmenterait, et une compétition accrue pourrait encore stimuler davantage sa croissance.

4.4 Implications

Les résultats du chapitre III ont montré que les interactions intraspécifiques ont un impact plus négatif sur la croissance des arbres que la compétition interspécifique pour l'érable à sucre et l'épinette noire, ce qui peut s'expliquer par la compétition pour les mêmes nutriments. Une réduction de la compétition intraspécifique est souvent associée à une augmentation de la diversité des espèces, ce qui conduit à des taux de croissance plus élevés, une meilleure résistance à la sécheresse et aux épidémies d'insectes (Aussenac *et al.*, 2019; Chavardès *et al.*, 2022). Cela souligne l'importance de la diversité des arbres pour renforcer la stabilité des écosystèmes forestiers face aux défis environnementaux actuels. Par conséquent, les gestionnaires forestiers pourraient promouvoir une structure de peuplement plus complexe afin d'optimiser les effets de compétition entre les arbres, ce qui pourrait entraîner une productivité plus élevée et une meilleure adaptation aux changements climatiques.

L'établissement des feuillus tempérés dans la forêt boréale mixte pourrait accroître la complexité et la diversité dans les peuplements, renforçant ainsi la résistance et la résilience de la forêt boréale mixte face aux perturbations. Cela provoquera une augmentation de la proportion de feuillu dans le paysage contribuant au phénomène d'enfeuillement de la forêt boréale mixte observé depuis les 100 dernières années, principalement dû à l'aménagement forestier. La présence des feuillus tempérés en forêt boréale mixte pourrait atténuer les épidémies de tordeuse des bourgeons de l'épinette car la proportion de sapin et d'épinette serait plus faible et ces arbres plus dispersés dans le peuplement, ce qui limiterait la propagation de l'épidémie (Cappuccino *et al.*, 1998). Cependant, l'épidémie de livrée des forêts pourrait être plus sévère, car l'érable à sucre et le bouleau jaune sont des hôtes de l'insecte. Avec une proportion plus élevée de feuillus, les épidémies pourraient également affecter davantage les espèces déjà présentes, telles que le peuplier faux-tremble et le bouleau blanc, en raison d'une plus grande proportion des peuplements de feuillus dans le paysage menant à une propagation rapide de l'épidémie. Les régimes de feux de forêt pourraient aussi être modifiés par les différences d'inflammabilité des feuillus et des conifères (Blarquez *et al.*, 2015).

Nous avons démontré que la capacité d'établissement des feuillus tempérés dans la forêt boréale mixte était plus élevée dans les peuplements les plus jeunes, ainsi que dans les peuplements récoltés (chapitre II). Par conséquent, l'aménagement forestier et les feux de forêts, en rajeunissant les paysages de la forêt mixte boréale, pourraient accélérer la migration des espèces d'arbres tempérés vers le nord. De plus, des études à l'échelle des peuplements et des paysages ont montré que la combinaison de l'aménagement forestier, des changements climatiques et des régimes de perturbations naturelles pourrait renforcer la capacité des espèces tempérées, notamment l'érable à sucre et l'érable rouge, à coloniser et à persister dans des peuplements mixtes boréaux (Boulanger et Pascual Puigdevall, 2021 ; Brice *et al.*, 2020).

Cette thèse de doctorat démontre aussi l'importance des vastes bases de données mise à disposition par le gouvernement du Québec. Pour atteindre nos objectifs, nous avons utilisé le réseau des placettes-échantillons permanentes pour la validation de la paramétrisation du chapitre I, et pour déterminer les distributions *a priori* du modèle du chapitre III. Ce réseau comprend plus de 12 000 placettes-échantillons permanentes de 400 m², échantillonnées en moyenne tous les 10 ans depuis les années 1970, et répertorie des variables liées aux arbres, au sol et à la topographie du terrain, couvrant la quasi-totalité du territoire au sud du 52e parallèle. Nous avons également utilisé les données du RESEF pour la paramétrisation du modèle du chapitre I et II, et pour modéliser la croissance des arbres pour le chapitre III. Ce réseau comprend 31 placettes rééchantillonnées tous les 5 ans depuis les années 1990, fournissant des informations précises telles que la position des arbres, ce qui nous a permis de calculer des indices de compétition dépendant de la distance et des données détaillées sur les sols et la topographie. Ces données se révèlent d'une importance cruciale pour l'analyse des écosystèmes forestiers au Québec, notamment pour évaluer les répercussions des changements climatiques sur la croissance et la répartition des espèces.

4.5 Perspectives

Les résultats des chapitres I et II suggèrent que les feuillus tempérés puissent coloniser, croître et survivre dans les peuplements de la forêt boréale mixte si les peuplements ne sont pas trop vieux (entre 20 et 140 ans après une perturbation majeure). Cependant, d'autres facteurs devraient être pris en compte pour affiner ces résultats, tels que l'inclusion des effets du sol sur la germination et la croissance des feuillus tempérés. Le substrat des peuplements de conifères est généralement plus acide et plus sec que celui des forêts de feuillus, ce qui limite le recrutement des espèces tempérées (Collin *et al.*, 2018). Les sols acides et plus secs affectent l'absorption des nutriments par les espèces tempérées dans les peuplements de conifères et influent sur la probabilité de germination et de croissance des semis de feuillus tempérés (St.Clair *et al.*, 2008 ; Caspersen *et al.*, 2011 ; Solarik *et al.*, 2018). Cependant, la présence de feuillus tempérés dans les peuplements boréaux en faible densité faciliterait le recrutement de nouveaux feuillus tempérées (Solarik *et al.*, 2020). Ainsi, l'établissement de l'érable à sucre pourrait être facilité dans les populations marginales d'érable rouge qui se trouvent plus au nord (Pilon et Payette, 2015). L'ajout d'un effet de modification du substrat sur le recrutement dans les futures simulations de modèles pourrait améliorer la plausibilité du succès de colonisation des feuillus tempérés dans des peuplements plus nordiques.

Une autre approche consisterait à élargir l'échelle spatiale de notre modélisation en étudiant la colonisation des feuillus tempérés à l'échelle du paysage, par exemple en utilisant le modèle Landis II. Dans cette approche, la croissance et la probabilité d'établissement des feuillus tempérés pourraient être dérivées du modèle SORTIE-ND, en tenant compte des améliorations précédentes du modèle, telles que l'inclusion des données sur le sol et les gelées tardives. Cette approche nous permettrait de modéliser l'expansion/contraction des peuplements marginaux de feuillus tempérés en prenant en considération la topographie du terrain, notamment la structuration du territoire en collines, où on retrouve actuellement ces peuplements. Cela nous permettrait également de prédire la future distribution des feuillus tempérés, ainsi que celle d'autres espèces de la forêt boréale mixte tout en intégrant l'influence des perturbations naturelles et de l'aménagement forestier (Seidl *et al.*, 2023).

ANNEXE A INFORMATIONS SUPPLÉMENTAIRES CHAPITRE I

A.1 Model description and equations

A.1.1 Plot

The plot is the space of a given size where trees are located, and the model behaviors are simulated. The shape of the plot is squared with 200 meters length for validation plots and 100 meters length for plots used for the experimental design. Toroidal boundary conditions are used so that trees at opposite edges of the plots are neighbors.

A.1.2 Allometry

Allometry relationships govern the tree size and shape attributes such as the diameter, the height and the crown of trees in relationship to the tree diameter. These attributes are used to calculate shading and crowding effects in the growth computation. The tree diameter is expressed in centimeters, and the tree height and crown size are expressed in meters.

A.1.2.1 DBH – diameter at 10 cm relationship for sapling

$$DBH = (diam10 \times R) + I$$

where *diam10* is the diameter at 10 cm height, R and I are the slope and intercept, respectively, of the relationship between DBH (diameter at breast height) and $diam10$. Here the intercept is fixed at 0.

A.1.2.2 Standard diameter-height relationship for adult trees

$$Height = 1.35 + (H_1 - 1.35) \times \left(1 - e^{-(B \times DBH)}\right)$$

where H_1 is the average maximum height the species can reach and B is the initial slope of the height – DBH relationship.

A.1.2.3 Crown radius and height

$$Crown\,radius = C_1 \times DBH^{a}$$

where C_1 is the crown radius for a DBH of 1 m and a is the crown radius exponent.

$$Crown\ height = C_2 \times height^{b}$$

where C_2 is the crown height for a tree height of 1 m and b is the crown height exponent.

A.1.3 Global Light Index (GLI)

The availability of light for each individual tree is calculated based upon the Sun position and movements during the growing season; more specifically, it is based upon the azimuth angles and the solar altitude.

A.1.4. Growth sub-models

A.1.4.1 Non-limited absolute growth for seedlings and saplings

$$Y = log_{10}(radial\ growth + 1) = SF \times \frac{A \times GLI}{\frac{A}{S} + GLI}$$

where *Y* is the juvenile growth in cm, *SF* is a suppression factor (fixed to 1), *A* is the asymptotic diameter growth, *S* is the slope of the diameter growth response and *GLI* is the amount of light received by the trees.

A.1.4.2 Neighborhood Competition Index (NCI) growth for adult trees

We used the "NCI growth" module in SORTIE to represent the growth of adult trees (section B.4.2). This module models tree growth through time (diameter at breast height increment in cm·yr^{-1}, DBHI) as a proportion of a maximum potential growth (*MaxPotGrowth*), which may be achieved under optimal growing conditions. The realized growth is obtained by multiplying this potential growth by different limiting effects taking values between 0 and 1, representing the effects of tree size, shading from other trees, and non-light-based competition or "crowding" effects (Canham et al., 2004). We use NCI growth for all species except jack pine, for which we lacked data to estimate competition interactions with each of the other species (Poulin *et al.*, 2008).

$$Growth\ = MaxPotGrowth\ \times size\ effect\ \times shading\ effect\ \times crowding\ effect$$

with $DBH\ effect = exp\left(-0.5 \times \left(\frac{ln\left(\frac{DBH}{X_0}\right)}{X_b}\right)^2\right)$, where DBH is the DBH of the tree in cm, X_0 is the DBH corresponding to maximum growth in cm and X_b determines the width of the Gaussian effect of log DBH on growth;

$Shading\ effect = exp(-m \times S^n)$, where m is the shading effect coefficient, S is the shading measurement, or the fraction of light intercepted by neighbors, as calculated by the "sail light" module in SORTIE and n the shading effect exponent (the latter set to 1 in this model);

$Crowding\ effect = exp(-C \times DBH^{\gamma} \times NCI^{D})$, where C is the crowding effect coefficient, γ represents the sensitivity of competition as a function of DBH (set to 0 in this model), D the NCI effect exponent (set to 1 in this model). The NCI for each tree i as the sum of crowding effects applied by each neighbor j is calculated by:

$NCI_i = \sum_{k=1}^{N} \lambda_{ik} \left(\frac{\frac{{DBH_k}^{\alpha}}{q}}{dist_{ik}^{\beta}}\right)$, where λ_{ik} strength of competition for different species pairs, q and α express the effect of the DBH of the neighbor tree (q is set to 1 in this model), $dist_{ik}$ is the distance in meters of the neighbor k from the tree i and β is the exponent of the effect of distance on the NCI. Neighbors up to 10 m from the focal trees are considered in the NCI calculation.

A.1.4.2. Constant radial growth for jack pine

Due to lack of data to fit the full NCI growth model, jack pine growth has been considered constant at 0.659 cm·year^{-1}.

A.1.5. Mortality sub-models

A.1.5.1. Juvenile mortality

Juvenile mortality occurs at random, with a probability of mortality for seedlings and saplings at each annual time step based on growth:

$$P(mortality|growth) = 1 - e^{-M_1 \times e^{-M_2 \times G}}$$

where M_1 is the mortality at zero growth (fixed to 1), G is the growth of the tree (in cm) and M_2 is the coefficient for the light dependent mortality.

A.1.5.2. Adult mortality

Adults can die at random from three independent causes: a stochastic (constant) mortality rate, a senescence-based mortality rate and a competition-based mortality rate. The probability of mortality due to senescence is given by:

$$m_s = \frac{e^{\alpha + \beta \times (DBH - DBH_s)}}{1 + e^{\alpha + \beta \times (DBH - DBH_s)}}$$

where α and β are coefficients expressing the relationship of mortality and DBH. DBH is the current DBH of the focal tree and DBH_s is the DBH corresponding to the onset of senescence both in cm.

Competition mortality depends on the ratio between the maximum growth the tree can attain relative to its DBH and the actual growth of the tree. The higher the shading effect and crowding effect, the higher the probability of mortality.

$$P(mortality|competition) = Z^{\frac{\frac{growth}{MaxPotGrowth \times size\ effect}}{max}}$$

where Z is the competition mortality shape parameter, growth is the NCI growth of the tree (in cm) and *max* is the competition mortality maximum parameter, which indicates the maximum relative increment ($\frac{growth}{MaxPotGrowth \times size\ effect}$) subject to mortality. All trees with a relative increment greater than or equal to *max* will live.

A.1.6. Substrate and establishment

Substrates are what seedlings germinate on. SORTIE consider six types of substrates for which species-specific suitability parameters are incorporated into the model: forest floor litter, forest floor moss, scarified soil, tip-up mounds, decayed logs and fresh logs.

A.1.7. Gap spatial dispersal and substrate seed survival

The density of seeds (R_i, in numbers.m^{-2}) is calculated as

$$R_i = \frac{STR}{n} \times \sum_{k=1}^{T} \left(\frac{DBH_k}{30}\right)^{\beta} \times e^{-D \times m_{ik}^{\theta}}$$

Where R_i is the seed density produced per m^2 at a point i, *STR* is the number of seeds produce by a tree of 30 cm DBH, *n* is a normalizing factor, β is the Weibull canopy gap beta parameter (fixed to 2 to make the seedling quantity proportional to the basal area of the seedmaker), *D* is the Weibull canopy gap dispersal parameter that controls the probability of the presence of a seed at a distance m in meters of the seed maker, and θ is the the Weibull canopy theta parameter, fixed to 3.

A.1.8. Output

Every 5 timesteps, we extract the position, the status (seedling, sapling, adult or snag) and the diameter of each tree, which allows us to compute many indicators of the stands and trees, for example density, basal area, regeneration, mortality and growth.

A.2 Model parameterisation

A.2.1 Estimating the effects of tree size, shading and crowding on growth

Tree growth is calculated by the "Neighborhood Competition index (NCI) growth" module in SORTIE using the following equation (see details in section B.4.2):

$$DBHI = MaxPotGrowth \times \exp\left(-0.5\left(\frac{\log DBH - \log X_0}{X_b}\right)^2\right) \times \exp(-m\,S) \times \exp(-c\,NCI)\,, (\mathrm{B.1.1})$$

with

$$NCI_i = \sum_j \lambda_{ij} \frac{DBH_j^{\alpha}}{dist_{ij}^{\beta}} \ . (\mathrm{B.1.2})$$

Either c (in Eq. B.1.1) or one of the λ_{ij} (in Eq. B.1.2) for a given species i must be set constant for the parameters to be identifiable. In practice, we do not estimate c by itself, but we set it to the largest estimated λ_{ij} for each species i, and then rescale the λ_{ij} by dividing by c (so that the largest λ_{ij} is always 1).

A logarithmic transformation of equation B.1.1 allows the log DBHI to vary quadratically with the log DBH and linearly with S and NCI.

$$\log DBHI = \log MaxPotGrowth - 0.5\left(\frac{\log DBH - \log X_0}{X_b}\right)^2 - m\,S - c\,NCI\,.\,(\mathrm{B.1.3})$$

To estimate the parameters in Equation (B.1.2) and (B.1.3) – *MaxPotGrowth*, X_0, X_b, m, c, α, β and λ_{ij}, we used data from the Quebec forest monitoring network RESEF ("Réseau d'Étude et de Surveillance des Écosystèmes Forestiers"), which are a network of 1-ha plots where trees were inventoried every 5 years from 1986 to 2020, and where the position and DBH of all trees in the plot is known. In this study, we retained 37 RESEF plots where temperate tree species coexist with boreal tree species. We also added data from 6 mapped 1-ha plots located in the Lake Duparquet Research and Teaching Forest (FERLD), which have been inventoried 5 times since 1991 (Maleki *et al.*, 2021). The full parameterization dataset for our growth model thus included 43 plots, 19 184 different trees, for a total of 72 964 DBHI observations. The shading measurement S was determined by inputting the spatial configuration of each plot in SORTIE and calculating S using the SORTIE sail light module for this initial tree map.

To estimate the required parameters from equation B.1.3, we used a statistical model where the mean of log DBHI depends on the fixed effects of tree size, shading and crowding (i.e. eqs. B.1.2 and B.1.3), as well as random effects of the tree and the inventory (the latter being a unique combination of plot and sampling year):

$$\mu_{\log DBHI} = a + b_1 \log DBH + b_2\,(\log DBH)^2 - m\,S - c\,NCI + \nu_{tree} + \nu_{inv}.\,(\mathrm{B.1.4})$$

In equation B.1.4, the variables ν represent normally distributed random effects of trees and inventory identities, and the parameters *MaxPotGrowth*, X_0, and X_b in equation B.1.3 can be derived algebraically from estimates of a, b_1 and b_2.

We fitted Equation B.1.4 as a hierarchical Bayesian model using RStan (Stan Development Team, 2021), with the following priors placed on the model coefficients: a followed a normal distribution with a mean equal to -1 and standard deviation to 1; b_1, b_2, m followed a standard normal distribution; α, β and λ_{ij} followed an exponential distribution of parameter 1; the standard deviation of ν_{tree} and ν_{inv} followed a standard normal distribution and residuals followed a standard normal. Some distributions were truncated to half-normal priors based on constraints: b_2 was constrained to be less or equal to zero to obtain a bell-shaped response curve in accordance with Equation B.1.3; m was constrained to be less or equal to zero to have a negative effect of shading on tree growth; standard deviations were constrained to be greater or equal to zero.

The statistical model was fit separately for each species. For each species, we considered two versions of the statistical distribution of the DBHI observations: either log DBHI is normally distributed around its mean (lognormal model), or the DBHI itself is normally distributed around the exponentiated mean of log DBHI (normal model). We also considered two versions of the NCI species effects λ_{ij}: in the more complex one, λ varies for each species pair; in the simpler model, λ takes 3 different values for competition with individuals of the same species, conifer trees of different species and temperate trees of the same species. We selected the best model among the 4 model versions (2 residual distributions x 2 models for species competition) based on the approximate leave-one-out cross-validation process (PSIS-LOO method) with the R package loo (Vehtari *et al.*, 2017, 2020).

A.2.2 Estimating the maximum potential growth as a function of climate

When estimating the effects of tree size, shading and crowding in the previous section, we used random effects to account for differences in tree growth between plots and inventory years. However, if some of these differences can be explained by known factors such as climate, it would be useful to model this relationship explicitly. By varying the maximum potential growth parameter in SORTIE to reflect climatic conditions at the simulated site, we could more accurately predict the growth of a species across different bioclimatic zones.

To estimate the climate-maximum potential growth relationship, we used annual growth increments from plots covering the bioclimatic envelope of the studied tree species. We used tree growth measurements (DBH increments) on 21 647 trees from 4 067 permanent forest inventory plots located across eastern North America, with an average of 6 trees of our species of interest per plot (Table A.8). Annual and seasonal climate data for each plot were obtained from climateNA (Wang *et al.*, 2016). To estimate tree growth as a function of climate, we chose climate variables that are known to have strong effects on tree growth. We selected two temperature-related climate variables: mean annual temperature (MAT) and growing degree days (DD5); and two precipitation-related climate variables: mean summer precipitation (MSP) and annual climate moisture index (CMI).

Similar to the size effect in equation B.1.4, we assumed that climate variables have a quadratic effect with negative curvature on the scale of log DBHI, representing symmetric reduction in growth around an optimum:

$$\mu_{\log DBHI} = a + \beta_1 MAT + \beta_2 MAT^2 + \gamma_1 MSP + \gamma_2 MSP^2 + \delta_1 DD5 + \delta_2 DD5^2 + \phi_1 CMI + \phi_2 CMI^2 + b_1 \log DBH + b_2 (\log DBH)^2 - m\,S - c\,NCI. \tag{B.2.1}$$

Given that we did not have the necessary information to estimate *S* and *NCI* from this North American dataset, we used Bayesian quantile regression to estimate the effect of climate variables on the 95th percentile of log DBHI, as an approximation of the maximum growth achievable with no shading or crowding:

$$Q_{\log DBHI}(0.95) = a + \beta_1 MAT + \beta_2 MAT^2 + \gamma_1 MSP + \gamma_2 MSP^2 + \delta_1 DD5 + \delta_2 DD5^2 + \phi_1 CMI + \phi_2 CMI^2 + [b_1 \log DBH + b_2 (\log DBH)^2]. \quad (B.2.2)$$

As before, we fitted the model B.2.2 separately for each tree species. As we assumed that the model in the previous section could provide a more accurate estimate of b_1 and b_2, by separating the effect of size from that of competition from other trees, we do not re-estimate these parameters here. Instead, the term in square brackets in equation B.2.2 is added as a fixed offset to the regression model.

We used the R package brms working with RStan to fit the quantile Bayesian regression (Bürkner, 2021 ; R Core Team, 2023 ; Stan Development Team, 2021). The prior distribution for all parameters estimated in the Bayesian framework followed a standard normal distribution, with quadratic term coefficients constrained to be less or equal to zero. The fitted model B.2.2 was used to set the maximum potential growth parameter in SORTIE for the different sites considered in this study, by replacing the climate variables with the appropriate values for the site and setting DBH equal to the DBH of optimal growth (X_0) for each species.

As described above, we used the 95th percentile of observed tree growth for each species as a substitute for the mean expected growth in the absence of competition. For each species in the dataset, this may result in a positive or negative bias when using the maximum potential growth estimated from model B.2.2. On the one hand, trees in the 95th percentile may still experience competition; on the other hand, greater than average growth may be due to non-measured local conditions other than competition, for example, soil conditions and topography. To estimate that bias, we compared the estimates of maximum potential growth at the RESEF sites, the same sites used to fit

Equation (B.1.4), to the maximum potential growth predicted from fitted Equation B.2.2 using the climate variables at those sites. The bias was defined as the mean across those sites of the difference between the estimate of log *MaxPotGrowth* from model B.2.2 and that of model B.1.4. This bias was then subtracted from the estimates produced from model B.1.4.

A.3 Parameterization results

Table A.1: Model selection results for the parameterization of the growth effect equation. ELPD stands for expected log pointwise predictive density. The full model is the model when considering all species-specific interactions whereas the grouped model is the model with species grouping (conifers, deciduous, intra) for competition parameter estimations.

Species	Model	Error distribution	ELPD difference	Standard error difference	ELPD	Standard error ELPD
Yellow Birch	Grouped	Normal	0	0	772.81	38.91
	Full	Normal	-6.18	2.46	766.64	38.6
	Grouped	Logarithmic	-380.72	39.12	392.09	38.83
	Full	Logarithmic	-382.88	39.06	389.93	38.78
Red Maple	Grouped	Normal	0	0	500.97	25.99
	Full	Normal	-1.32	1.79	499.65	25.97
	Grouped	Logarithmic	-137.53	27.73	363.44	27.21
	Full	Logarithmic	-139.6	27.75	361.38	27.34
Sugar Maple	Grouped	Normal	0	0	9730.27	337.98
	Full	Normal	-27.32	5.27	9702.95	337.62
	Grouped	Logarithmic	-830.08	327.42	8900.18	109.93
	Full	Logarithmic	-834.63	327.63	8895.64	109.85
Balsam Fir	Grouped	Normal	0	0	10100.85	208.28
	Full	Normal	-4.96	20.65	10095.89	194.15
	Full	Logarithmic	-1817.2	204.84	8283.65	112.62
	Grouped	Logarithmic	-1832.61	205.11	8268.24	112.69

Table A.1 (continued)

Trembling Aspen	Grouped	Logarithmic	0	0	2143.16	75.77
	Full	Logarithmic	-5.15	8.22	2138.01	75.92
	Grouped	Normal	-289.3	121.96	1853.86	135.67
	Full	Normal	-289.84	120.82	1853.32	134.49
Paper Birch	Full	Logarithmic	0	0	3016.06	56.4
	Grouped	Logarithmic	-3.33	3.24	3012.73	56.18
	Full	Normal	-724.07	150.99	2291.99	160.88
	Grouped	Normal	-741.55	152.25	2274.5	162.13
White Spruce	Full	Normal	0	0	1131.23	99.95
	Grouped	Normal	-5.29	3.79	1125.94	101.45
	Full	Logarithmic	-26.7	94.5	1104.53	46.4
	Grouped	Logarithmic	-29.97	94.41	1101.26	46.64
White Cedar	Grouped	Logarithmic	0	0	2069.6	68.8
	Full	Logarithmic	-6.63	2.61	2062.97	68.94
	Full	Normal	-2970.91	1156.29	-901.31	1185.22
	Grouped	Normal	-2971.69	1159.09	-902.09	1188.01

Table A.2: Parameter values obtained in the growth effect equation parameterization. Values in each cell are the posterior median with the 95% credible interval in parentheses. Full models are noted with *, the other ones are grouped models.

Species	X_0	X_b	m	C	α	β
Yellow Birch	16 (13, 18)	1.1 (0.9, 1.3)	0.8 (0.57, 1)	0.018 (0.0019, 0.066)	0.088 (0.0067, 0.38)	0.53 (0.12, 1)
Red Maple	20 (0.97, 52)	1.8 (1.1, 5.7)	0.56 (0.17, 0.96)	0.044 (0.0042, 0.23)	0.081 (0.0065, 0.36)	0.71 (0.18, 1.4)
Sugar Maple	22 (20, 23)	1.2 (1.1, 1.3)	1.2 (1, 1.3)	0.00065 (0.00025, 0.0017)	1.2 (0.95, 1.5)	0.32 (0.17, 0.43)
Balsam Fir	14 (13, 14)	0.75 (0.7, 0.82)	0.7 (0.57, 0.84)	0.00044 (1e-04, 0.0022)	1.6 (1, 2.2)	0.74 (0.55, 0.89)
Trembling Aspen	45 (38, 64)	1 (0.9, 1.3)	0.84 (0.64, 1)	0.012 (0.0043, 0.024)	0.12 (0.0076, 0.47)	0.27 (0.028, 0.62)
Paper Birch*	16 (13, 18)	0.91 (0.73, 1.3)	0.73 (0.44, 1)	0.12 (0.029, 0.25)	0.022 (0.0014, 0.095)	0.6 (0.47, 0.69)
White Spruce*	16 (14, 18)	0.81 (0.67, 1)	0.83 (0.48, 1.2)	0.54 (0.083, 0.94)	0.035 (0.0027, 0.15)	1.2 (0.94, 1.5)
White Cedar	100 (32, 3.9e+12)	2.9 (1.6, 11)	0.42 (0.15, 0.69)	0.0084 (0.0011, 0.028)	0.49 (0.047, 1.2)	0.59 (0.47, 0.68)

Table A.3: Estimated λ parameter values for competition strength between species. Full models are noted with *, the other ones are grouped models. Bold values represent intraspecific competition. Values in each cell are the posterior median with the 95% credible interval in parentheses. For SORTIE modeling, we rescaled λ parameters by dividing λ_{ij} by the largest λ_{ij} for each species and c take the value of the largest λ_{ij} (see Table A.4).

Effect of on	Yellow Birch	Red Maple	Sugar Maple	Balsam Fir	Jack Pine	Trembling Aspen	Paper Birch*	White Spruce*	White Cedar
Yellow Birch	**0.0047** (0.00033, 0.02)	0.018 (0.0019, 0.066)	0.018 (0.0019, 0.066)	0.01 (0.0013, 0.033)	0.01 (0.0013, 0.033)	0.018 (0.0019, 0.066)	0.018 (0.0019, 0.066)	0.01 (0.0013, 0.033)	0.01 (0.0013, 0.033)
Red Maple	0.044 (0.0042, 0.23)	**0.015** (0.001, 0.058)	0.044 (0.0042, 0.23)	0.041 (0.0094, 0.1)	0.041 (0.0094, 0.1)	0.044 (0.0042, 0.23)	0.044 (0.0042, 0.23)	0.041 (0.0094, 0.1)	0.041 (0.0094, 0.1)
Sugar Maple	0.00043 (4.7e-05, 0.0015)	0.00043 (4.7e-05, 0.0015)	**0.00065** (0.00025, 0.0017)	0.00057 (2e-04, 0.0016)	0.00057 (2e-04, 0.0016)	0.00043 (4.7e-05, 0.0015)	0.00043 (4.7e-05, 0.0015)	0.00057 (2e-04, 0.0016)	0.00057 (2e-04, 0.0016)
Balsam Fir	0.00042 (7.9e-05, 0.0026)	0.00042 (7.9e-05, 0.0026)	0.00042 (7.9e-05, 0.0026)	**0.00044** (1e-04, 0.0022)	1.5e-05 (6.4e-07, 0.00021)	0.00042 (7.9e-05, 0.0026)	0.00042 (7.9e-05, 0.0026)	1.5e-05 (6.4e-07, 0.00021)	1.5e-05 (6.4e-07, 0.00021)
Trembling Aspen	0.0059 (0.0012, 0.016)	0.0059 (0.0012, 0.016)	0.0059 (0.0012, 0.016)	0.0012 (7.6e-05, 0.0062)	0.0012 (7.6e-05, 0.0062)	**0.012** (0.0043, 0.024)	0.0059 (0.0012, 0.016)	0.0012 (7.6e-05, 0.0062)	0.0012 (7.6e-05, 0.0062)
Paper Birch*	0.12 (0.029, 0.25)	0.1 (0.0067, 0.37)	0.023 (0.0023, 0.078)	0.027 (0.012, 0.042)	0.03 (0.0024, 0.11)	0.079 (0.05, 0.11)	**0.04** (0.021, 0.06)	0.05 (0.011, 0.096)	0.015 (0.0013, 0.05)
White Spruce*	0.32 (0.035, 0.89)	0	0.54 (0.083, 0.94)	0.056 (0.021, 0.1)	0.039 (0.0031, 0.17)	0.071 (0.019, 0.16)	0.015 (0.00074, 0.071)	**0.18** (0.099, 0.31)	0.098 (0.034, 0.21)
White Cedar	0.0044 (0.00042, 0.022)	0.0044 (0.00042, 0.022)	0.0044 (0.00042, 0.022)	0.0061 (0.00061, 0.029)	0.0061 (0.00061, 0.029)	0.0044 (0.00042, 0.022)	0.0044 (0.00042, 0.022)	0.0061 (0.00061, 0.029)	**0.0084** (0.0011, 0.028)

Table A.4: Estimated rescaled λ parameter values for competition strength between species and c parameter. Full models are noted with *, the other ones are grouped models. Bold values represent intraspecific competition.

Effect of on	Yellow Birch	Red Maple	Sugar Maple	Balsam Fir	Jack Pine	Trembling Aspen	Paper Birch *	White Spruce *	White Cedar	c
Yellow Birch	**0.254**	1	1	0.564	0.564	1	1	0.564	0.564	0.0184
Red Maple	1	**0.334**	1	0.945	0.945	1	1	0.945	0.945	0.0437
Sugar Maple	0.659	0.659	**1**	0.884	0.884	0.659	0.659	0.884	0.884	0.000651
Balsam Fir	0.95	0.95	0.95	**1**	0.0348	0.95	0.95	0.0348	0.0348	0.000442
Trembling Aspen	0.495	0.495	0.495	0.0988	0.0988	**1**	0.495	0.0988	0.0988	0.0120
Paper Birch*	1	0.854	0.189	0.219	0.249	0.647	**0.325**	0.41	0.125	0.122
White Spruce*	0.598	0	1	0.105	0.0722	0.133	0.0285	**0.331**	0.183	0.538
White Cedar	0.53	0.53	0.53	0.732	0.732	0.53	0.53	0.732	**1**	0.00839

Table A.5: Estimated parameter estimations for the maximum potential growth model as a function of climate. Values in each cell are the posterior median with the 95% credible interval in parentheses.

Species	a	β_1	β_2	γ_1	γ_2	δ_1	δ_2	ϕ_1	ϕ_2
Sugar Maple	-0.37 (-0.39,-0.35)	0.0013 (-0.051,0.054)	-0.0031 (-0.012,-7.2e-05)	-0.0035 (-0.034,0.025)	-0.0074 (-0.015,-0.00081)	0.18 (0.13,0.24)	-0.0048 (-0.016,-1e-04)	0.0084 (-0.023,0.042)	-0.0032 (-0.011,-1e-04)
Red Maple	-0.69 (-0.71,-0.67)	-0.11 (-0.14,-0.079)	-0.0046 (-0.015,-0.00014)	0.049 (0.028,0.07)	-0.00095 (-0.0031,-2.3e-05)	0.37 (0.33,0.4)	-0.019 (-0.025,-0.014)	-0.0088 (-0.03,0.012)	-0.0021 (-0.0061,-9.3e-05)
Yellow Birch	-0.23 (-0.26,-0.2)	-0.16 (-0.25,-0.07)	-0.031 (-0.082,-0.0016)	0.016 (-0.022,0.054)	-0.00093 (-0.003,-1.8e-05)	0.27 (0.18,0.38)	-0.028 (-0.073,-0.00072)	0.021 (-0.022,0.067)	-0.0014 (-0.0048,-3.5e-05)
Paper Birch	-0.69 (-0.71,-0.67)	-0.15 (-0.18,-0.12)	-0.067 (-0.085,-0.047)	0.03 (0.0036, 0.056)	-0.0013 (-0.0045,-3.9e-05)	0.29 (0.24,0.33)	-0.0045 (-0.015,-0.00011)	0.01 (-0.017,0.037)	-0.017 (-0.024,-0.0091)
Trembling Aspen	-0.074 (-0.093,-0.054)	0.0075 (-0.033,0.046)	-0.023 (-0.039,-0.0056)	-0.062 (-0.087,-0.032)	-0.0082 (-0.018,-0.00056)	0.19 (0.15,0.23)	-0.0054 (-0.016,-0.00023)	0.055 (0.025,0.081)	-0.014 (-0.027,-0.0016)
White Cedar	-0.81 (-0.85,-0.77)	0.00093 (-0.11,0.12)	-0.021 (-0.064,-0.00073)	-0.14 (-0.2,-0.07)	-0.004 (-0.013,-0.00014)	0.2 (0.097,0.3)	-0.0085 (-0.03,-3e-04)	0.19 (0.12,0.26)	-0.014 (-0.039,-0.00056)
White Spruce	-0.18 (-0.21,-0.16)	-0.036 (-0.077,0.005)	-0.1 (-0.12,-0.073)	0.043 (0.0099, 0.076)	-0.0057 (-0.013,-0.00034)	0.19 (0.15,0.24)	-0.017 (-0.041,-0.0012)	-0.0064 (-0.039,0.025)	-0.0012 (-0.0043,-3.9e-05)
Balsam Fir	-0.32 (-0.34,-0.31)	0.12 (0.093, 0.15)	-0.083 (-0.095,-0.07)	0.011 (-0.01,0.033)	-0.0052 (-0.01,-0.00068)	0.17 (0.13,0.2)	-0.054 (-0.07,-0.038)	0.011 (-0.011,0.034)	-0.0018 (-0.0056,-7.4e-05)
Jack Pine	-0.42 (-0.46,-0.39)	0.29 (0.23,0.35)	-0.012 (-0.039,-0.00045)	-0.031 (-0.064,0.0016)	-0.0018 (-0.0067,-5.6e-05)	0.032 (-0.023,0.089)	-0.12 (-0.13,-0.093)	-0.069 (-0.1,-0.033)	-0.0079 (-0.022,-0.00044)

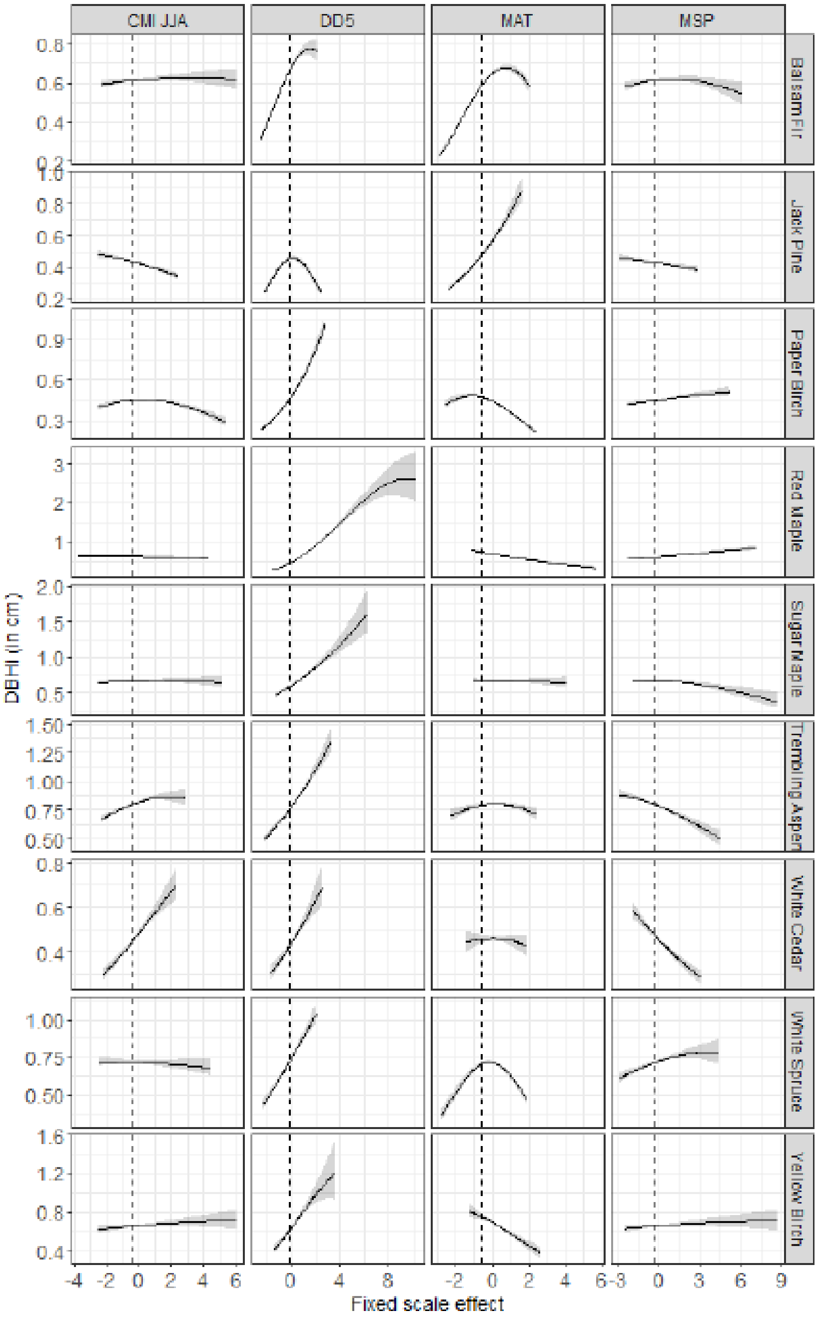

Figure A.1: Maximum potential growth - climate relationship. Climatic effects of the quantile regression used to find maximum potential growth for the studied species. CMI: Climate moisture index, DD5: growing degree days, MAT: mean annual temperature and MSP: mean summer precipitation. The dashed line represents the climate normals at the site where simulations were set (FERLD).

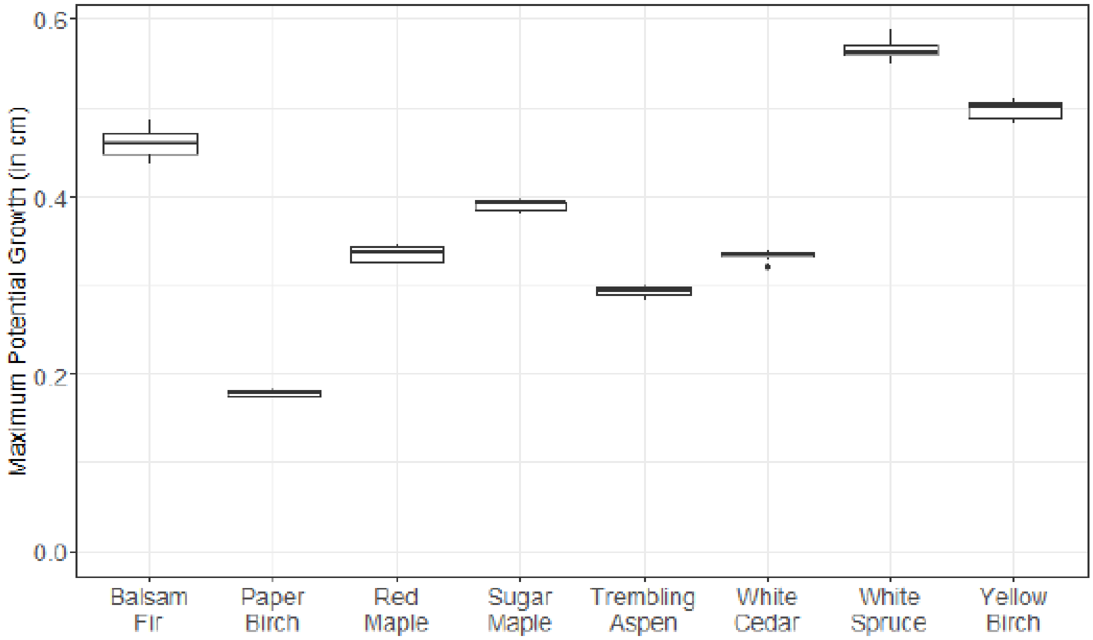

Figure A.2: Maximum potential growth parameter estimated at 15 cm DBH (i.e., for a tree experiencing no shading or crowding). Boxplots correspond to the distribution of the estimates for the 10 validation sites and the FERLD study site, which is due to climatic differences across sites.

A.4 Parameter values from existing literature

Table A.6: Non-adult growth parameter of the SORTIE model used in this study. Index represents the parameter source which are detailed in table A.7. SM: sugar maple, RM: red maple, YB: yellow birch, WC: white cedar, BF: balsam fir, WS: white spruce, JP: jack pine, TA: trembling aspen and PB: paper birch

Submodel	Stage	Parameter	SM	RM	YB	WC[a]	BF[a]	WS[a]	JP[a]	TA[a]	PB[a]
Tree population	Adult	Minimum DHP adult	10	10	10	10	10	10	10	10	10
	Seedling	Slope of height-diameter at 10 cm relationship	0.038[b]	0.032[b]	0.045[b]	0.018	0.015	0.016	0.041	0.031	0.048
	Gaulis	Slope of DBH to diameter at 10 cm relationship	0.7	0.7	0.7	0.594	0.789	0.756	0.791	0.824	0.756
Allometry	Adult	Maximum tree height (m)	25.31[c]	25.7[d]	23.13[c]	18.78	21	34.56	29.1	26.26	20.74
		Slope of asymptotic height	0.0623[c]	0.063[e]	0.063[c]	0.046	0.064	0.03	0.051	0.067	0.084
		Slope of asymptotic crown radius	0.768[c]	0.108[e]	0.602[c]	0.199	0.266	0.262	0.041	0.092	0.22
		Crown radius exponent	0.398[c]	0.491[f]	0.499[c]	0.468	0.366	0.361	0.859	0.761	0.506
		Maximum crown radius	10	10	10	10	10	10	10	10	10
		Slope of asymptotic crown height	0.25[c]	0.49[e]	0.431[c]	0.652	0.345	0.63	1.225	0.262	0.966
		Crown height exponent	1.185[c]	1	0.999[c]	0.982	1.188	1.01	0.581	1.11	0.751
Quadrat-based GLI light	Adult	Amount canopy light transmission (0-1)	0.144[c]	0.134[g]	0.1638[c]	0.144	0.111	0.109	0.124	0.16	0.101
		Snag age class 1 amount canopy light transmission (0-1)	0.722[h]	0.722[h]	0.722[h]	0	0.478	0	0.489	0.65	0.722
		Snag age class 2 amount canopy light transmission (0-1)	0.841[h]	0.841[h]	0.841[h]	0	0.684	0	0.511	0.755	0.841
		Snag age class 3 amount canopy light transmission (0-1)	0.898[h]	0.898[h]	0.898[h]	0	0.9	0	0.74	0.833	0.898
Non-limited absolute growth	Juvenile	Asymptotic diameter growth	0.125[i]	0.167[i]	0.047[i]	0.382	0.567	0.561	6.176	0.828	2.162
		Slope of diameter growth response	0.157[i]	0.027[i]	0.137[i]	0.339	0.079	0.072	0.006	0.024	0.011

Table A.6 (continued)

Constant radial growth - diam with auto height	Adult	Adult constant radial growth in cm·yr^{-1}							0.659		
Stochastic mortality rate	Juvenile	Background Mortality Rate	0.01[j]	0.01[j]	0.01[j]	0.005	0.01	0.01	0.01	0.01	0.01
	Adult	Background Mortality Rate	0.01[k]	0.01[k]	0.01[k]	0.005	0.02	0.013	0.019	0.016	0.009
BC mortality	Juvenile	Light-dependent mortality	4.79[l]	6.64[l]	2.67[l]	9.15	8.45	6.75	3.74	2.55	3.61
Senescence	Adult	Senescence mortality Alpha	-20[m]	-20[m]	-20[m]	-4	-4.5	-4.1	-3.7	-3.5	-3.1
		Senescence mortality Beta	0.135[m]	0.135[m]	0.135[m]	0.05	0.22	0.04	0.28	0.08	0.12
		DBH at Onset of Senescence (cm)	100[m]	100[m]	100[m]	75	40	40	35	45	30
Competition mortality	Adult	Competition mortality shape parameter	3.00E-06[n]	3.00E-06[n]	4.33E-06[h]	3.00E-06	3.00E-06	3.00E-06		4.33E-04	4.33E-06
		Competition mortality maximum parameter	0.17[n]	0.17[n]	0.25[h]	0.17	0.17	0.2		0.32	0.25
Gap spatial disperse	Adult	Minimum DBH for Reproduction (cm)	10[o]	10[o]	10[o]	10	10	10	10	10	10
		Annual STR	1.32[p]	0.54[p]	21[p]	15.33	10.58	13.57	12.29	20.91	16.04
		Weibull canopy dispersal	5.81E-04[p]	3.62E-05[o]	6.30E-05[p]	8.35E-05	5.45E-05	1.10E-07	2.80E-04	3.80E-05	7.76E-06
		STR for stumps	0	0	0	0	0	0	0	1000	0
		Beta for stumps	0	0	0	0	0	0	0	2	0
Gap subtrate seed survival	Juvenile	Fresh logs	1.00E-04[p]	1.00E-04[q]	0.008[p]	0.04281	0.0033	1.00E-04	0.566	0.017	0.381
		Decayed logs	1[p]	1[q]	0.18[p]	0.9156	0.6197	0.7126	0.155	0.013	0.001
		Tip up	1[p]	1[q]	0.18[p]	0.9156	0.6197	0.7126	0.155	0.013	0.001
		Scarified soil	0.04[p]	0.04[q]	1[p]	1.00E-05	0.8228	0.1002	0.008	0.018	0.1
		Floor litter	0.42[p]	0.42[q]	0.0087[p]	0.2609	0.3933	0.2468	0.462	0.781	0.687
		Floor moss	1.00E-04[p]	1.00E-04[q]	0.12[p]	3.00E-05	0.04085	1.90E-04	0.004	0.01	0.12

Table A.7: Parameter source of table A.6.

Index	Parameter source
a	Poulin et al. (2008)
b	Personnal data
c	Lefrançois et al. (2006 ; 2008)
d	Pacala et al. (1993)
e	Russell and Weiskittel (2011)
f	Pacala et al. (1996)
g	Canham et al. (1994)
h	Same parameter value as paper birch
i	Pacala et al. (1994)
j	Same parameter value as other species
k	Same parameter value as juveniles
l	Kobe et al. (1995)
m	Parameter values were set to add no more mortality than the stochastic mortality
n	Same parameter value as white cedar and balsam fir
o	Ribbens et al. (1994)
p	Caspersen et al. (2005)
q	Same parameter value as sugar maple

A.5. Data description

Table A.8: Description of datasets used for parameterization, validation and initial conditions of the experimental design.

Task	Data	Number of plots selected	Observations	Extent	Source
Parameterization of maximum potential growth	PSP	4067	49309	Eastern North America	Personnal communication
Parameterization of growth limitations to potential growth	RESEF and FERLD (spatialized data)	43	72964	Quebec	MFFP and Maleki et al., 2021
Model validation	PEP	12	10369	BF-YB and BF-PB forests	MFFP
Initial conditions	FERLD (non spatialized data)	153	11770	FERLD	Maleki et al., 2021

Table A.9: Correspondence between the identification used in this study for the validation process and the identification used in the permanent forest inventory plots from the Quebec's Ministry of Forests, Wildlife and Parks (MFFP) dataset.

ID_{STUDY}	ID_{PEP}
1	1219611102
2	7100813401
3	7109503802
4	7209406201
5	7209606102
6	7209904001
7	7601505301
8	7608804302
9	7609507102
10	7609509002

Table A.10: Adult and saplings absolute basal area m^2.ha-1 and number of seedlings per hectare of species in the unharvested and harvested sites (used as initial conditions for simulations). The first value in cells of the balsam fir column correspond to basal area of pre-spruce budworm outbreak (considering dead balsam-fir as alive) used for initial conditions.

Perturbation	Year of last fire	Stage	Balsam Fir	Jack Pine	Paper Birch	Trembling Aspen	White Cedar	White Spruce
Unharvested	1760	Adult	11.42; 2.05	0.28	5.4	2.44	7.3	1.72
		Sapling	2.62; 0.99	0.03	0.41	0.09	0.58	0.03
		Seedling	4146; 4074	0	864	226	854	93
	1797	Adult	8.39; 1.03	0.46	6.23	0.48	2.66	1.43
		Sapling	2.77; 1.28	0.02	0.59	0.05	0.21	0.09
		Seedling	6028; 5855	32	790	108	530	271
	1823	Adult	9.93; 2.42	0	3.23	7.72	0.63	1.8
		Sapling	3.71; 2.13	0	0.45	0.61	0.09	0.16
		Seedling	8933; 8422	0	400	389	489	433
	1870	Adult	5.92; 2.03	0.26	5.24	11.81	0.02	3.92
		Sapling	2.22; 1.49	0	0.45	0.67	0.01	0.19
		Seedling	2532; 2240	0	97	97	0	195
	1916	Adult	4.98; 2.53	0	6.32	16.53	0.98	1.53
		Sapling	3.63; 2.5	0	1.54	0.1	0.04	0.53
		Seedling	5459; 5425	0	17	459	102	408
	1964	Adult	0.72; 0.62	0.54	1.45	4.63	0.08	0.09
		Sapling	0.65; 0.65	0.06	1.76	2.55	0.05	0.05
		Seedling	790; 703	11	195	281	0	108
Harvested	1910	Adult	0	0	0	0	0	0.03
		Sapling	1.25	0	0	0.03	0	0.03
		Seedling	30607	0	2790	38813	0	1180
	1923	Sapling	0.02	0	0.02	0.07	0	0
		Seedling	213	0	1807	27427	0	167

A.6. Validation

We validated our model with the 10 permanent forest inventory plots from the Quebec's Ministry of Forests, Wildlife and Parks (MFFP) dataset (further details in the main text). We used tree species and DBH distribution of the first inventory as initial condition for the SORTIE simulations with randomized positions of trees in plots. Each 4 ha plots were divided in 100 subplots of 400 m² each according to the size of the observed plots where the basal area and tree growth were tracked over time. The comparison between simulations and observations for each year where the validation plots were subsequently inventoried were threefold. We first directly compared species basal area through time and tree species growth between simulations and observations. Second, we determined the rank of the observations among simulations. Finally, we compared plots species assemblages between simulations and observations (further details and results in the main text).

Simulations of tree basal area were consistent with observations although in some plots, simulated basal area may differ with observations (Fig. A.3 and Fig. A.4). For example, in plot 9, SORTIE overestimates the basal area of balsam-fir and causes a shift in species assemblages (more details in the main text). This mismatch could be due to balsam fir regeneration problems or disturbances, for instance, insect outbreaks. Moreover, the intervals of the simulations of tree basal area are large because SORTIE randomly positions the trees and the division of the plot into 400 m² subplots leads to a high variability between subplots for basal area results.

The simulated tree growths also show good agreement with the observed growths (Fig. A.5 and Fig. A.6). However, we note that the observed growths are more variable than the simulated growths because SORTIE cannot include all sources of variability that determine tree growth. In accordance with the higher variability of observations, tree basal area ranks of the observation vs. simulations showed that observations are often in the lowest and highest ranks, but no systematic under- or over-estimates of species basal area were detected.

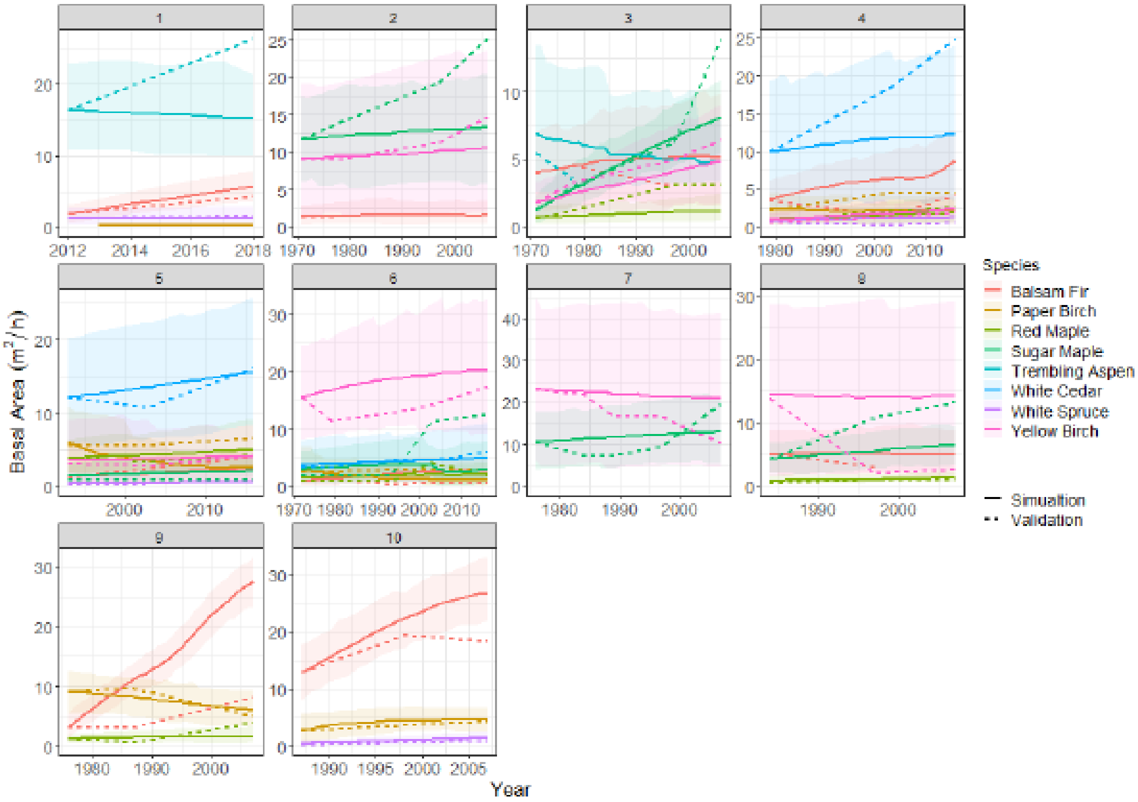

Figure A.3: Direct comparison between simulated basal area (solid lines) and observed basal area (dashed lines) in the 10 plots selected for the validation process. Results of 90% of the simulations in the 100 subplots of size comparable with the observed plots are present in the interval.

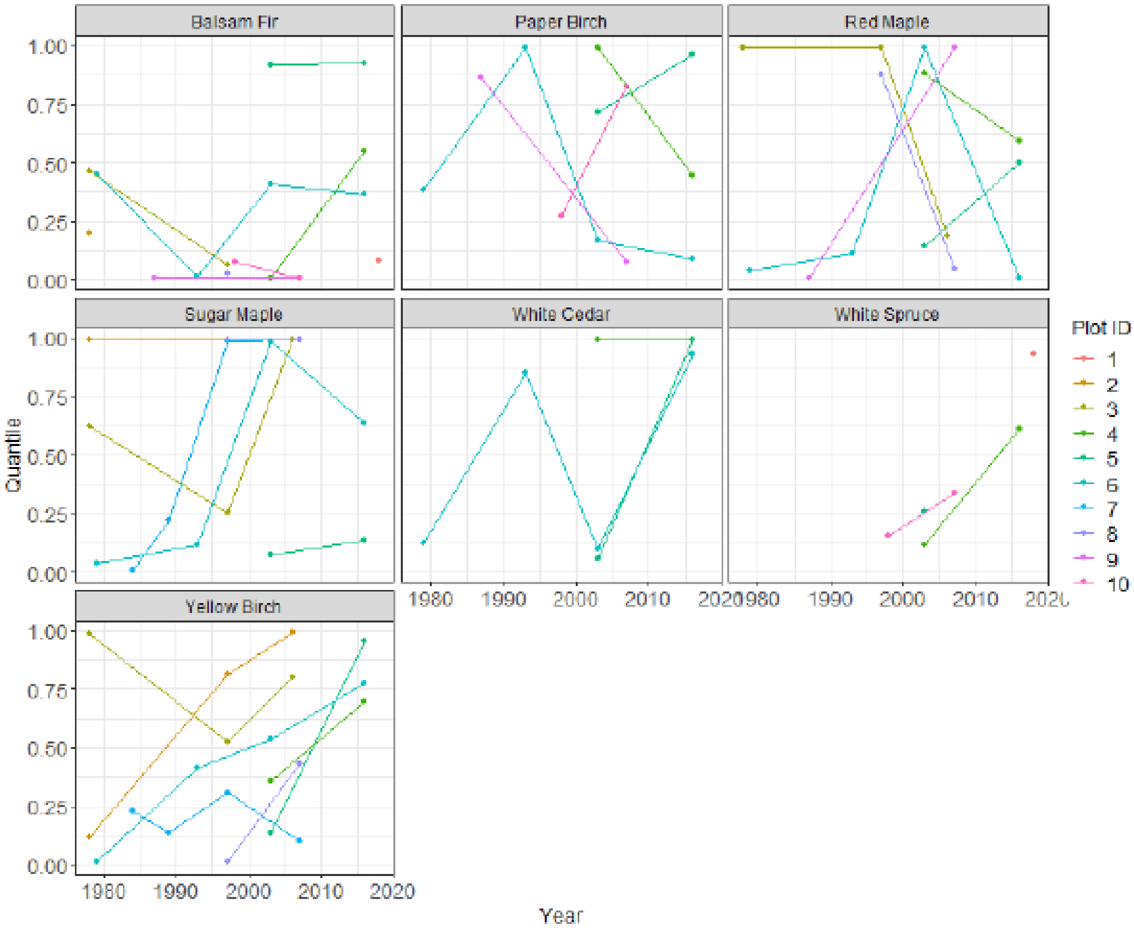

Figure A.4: Quantile of observed basal area rank among simulated subplots basal areas for each species and inventory.

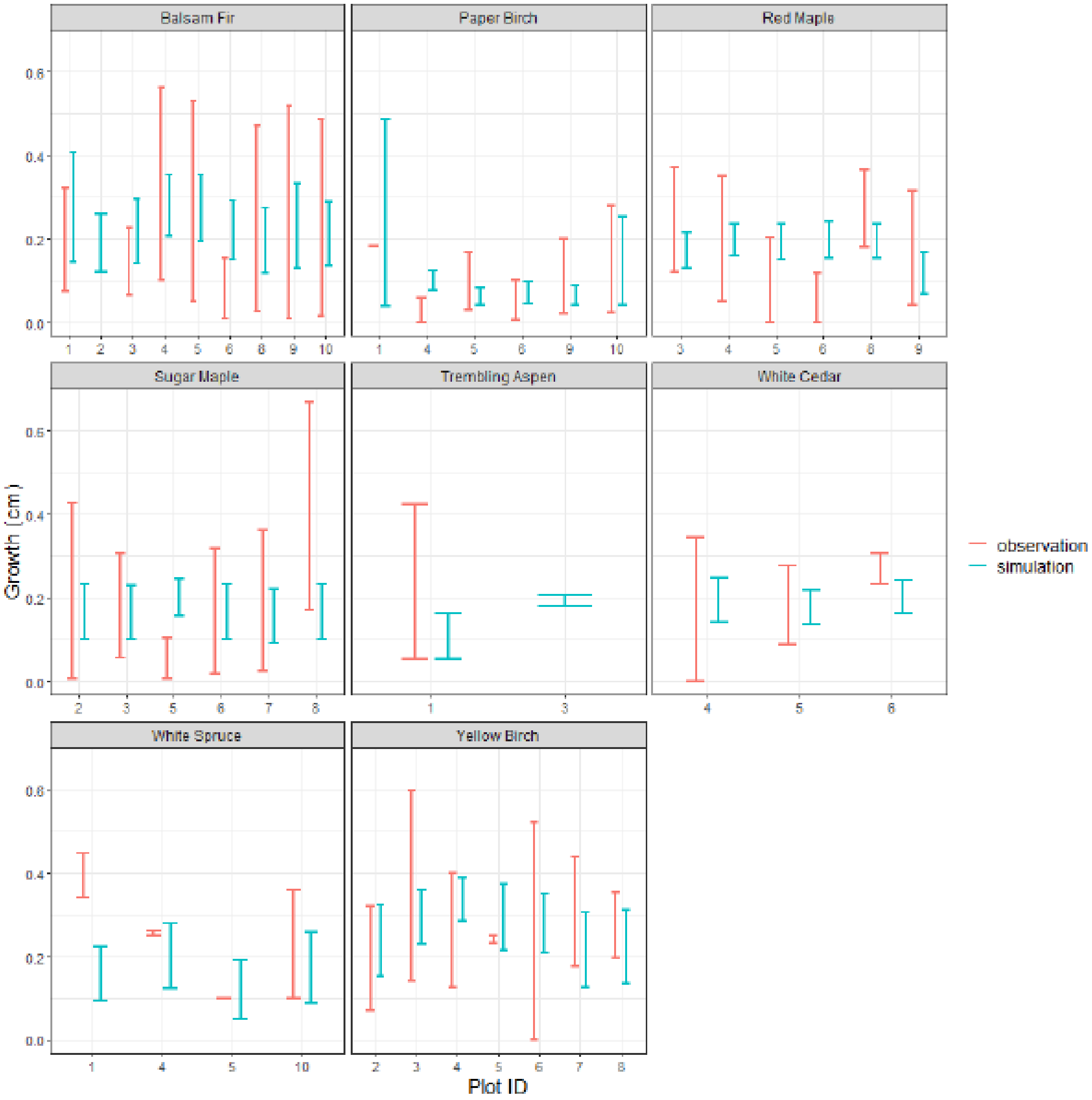

Figure A.5: Direct comparison between simulated growth (blue intervals) and observed basal area (red intervals) in the 10 plots selected for the validation process. 90% of the simulated and validated growths are included in the intervals.

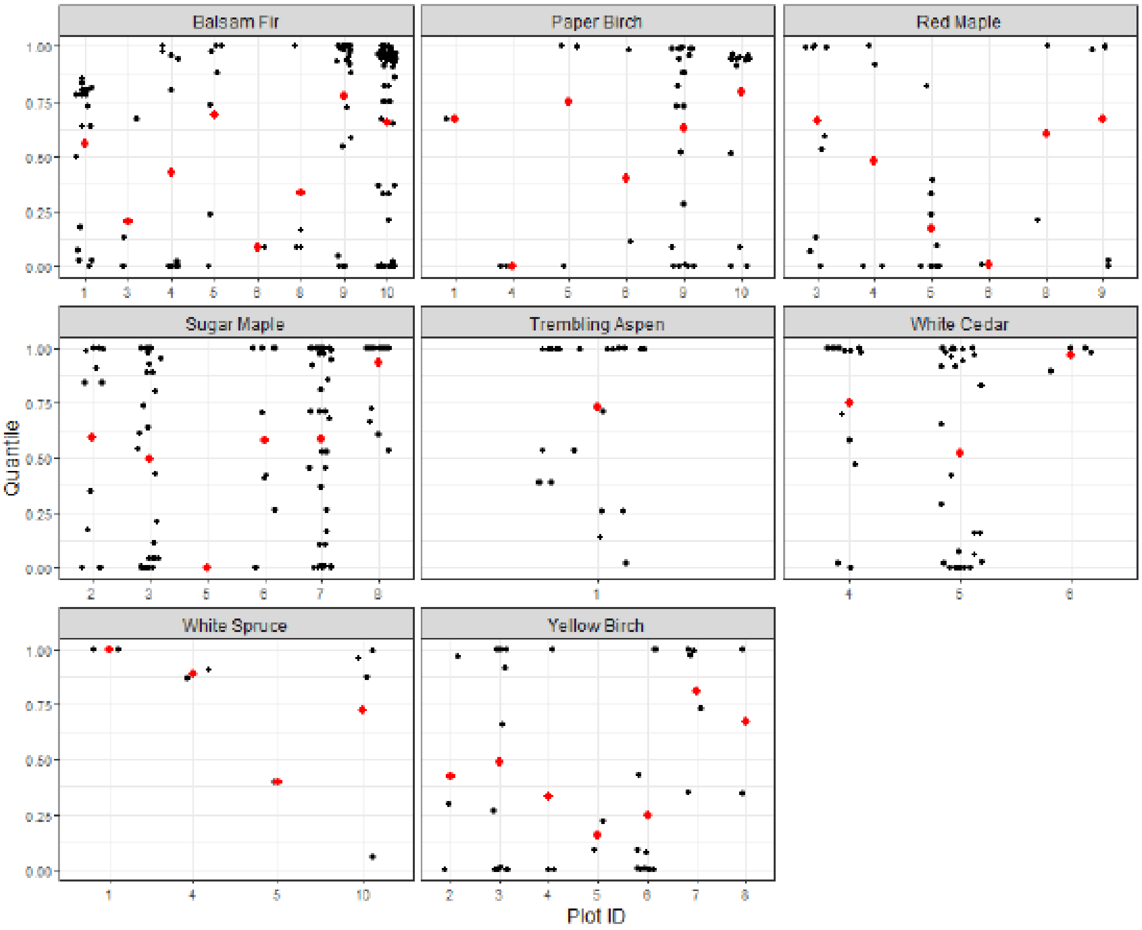

Figure A.6: Quantile of observed growth ranks among simulated growths for each species and inventory (black dots), with their mean shown as a red dot.

A.7 Additional results

The realized growth of yellow birch was higher than the growth of red maple and sugar maple (average growth of red maple: 0.11 cm·year^{-1}; yellow birch: 0.29 cm·year^{-1}; and sugar maple: 0.14 cm·an^{-1}). The density of temperate species seedlings added at the beginning of the simulation had little influence on the growth of temperate species, however, we note that growth was slightly lower for low densities in the unharvested stands (Fig. A.7). Stand age and thus the species composition of the simulated stands had little influence on growth (Fig. A.7).

The total number of stems (seedlings + saplings + adults) dropped at the beginning of the simulations regardless to the initial density of temperate seedlings indicating high seedlings mortality at the beginning of the simulation (Fig. A.8). This mortality was more pronounced in the harvested stands than unharvested stands. Sugar maple was the species that persists most successfully at low added seedling density and in harvested stands. Red maple had the highest number of stems in stands at medium and high densities indicating that red maple had greater resistance to intra- and interspecific competition, except in harvested stands (Fig. A.8).

In unharvested stands, yellow birch was the species with the lowest number of stems (Fig. A.8), whereas at medium and high densities, yellow birch had the highest basal area in the stands. This is due to the higher growth of yellow birch in BF-PB stands, therefore yellow birch was less abundant but larger than the other two temperate species. The number of stems were similar in medium and high density for sugar maple and yellow birch whereas for red maple, the number of stems were higher in high density than in medium density. This last result is consistent with the findings in the main text, where it was noted that an increase in seedling from medium to high density resulted in an increase in basal area for red maple but not the other two species (Fig. 2.5 in the main text).

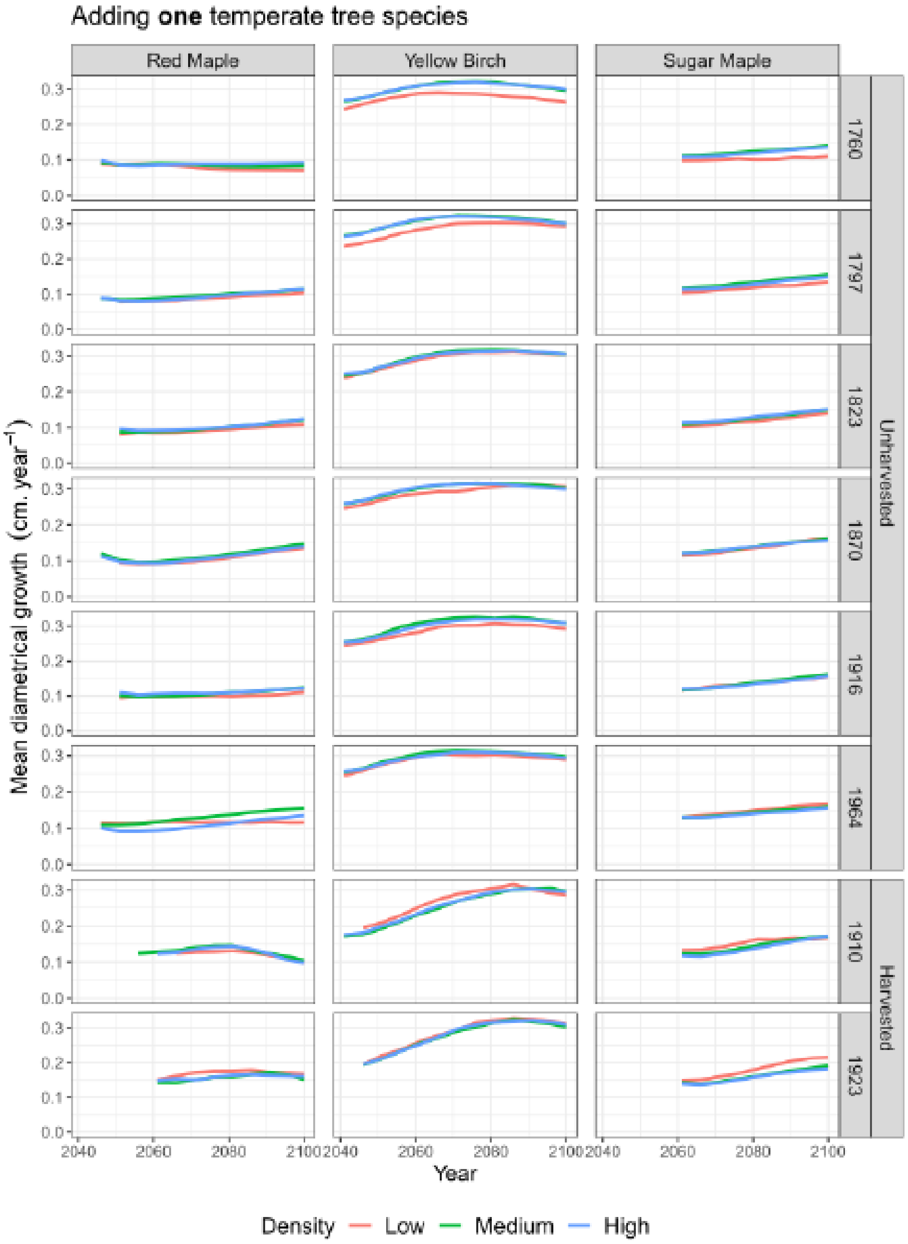

Figure A.7: Simulated average growth of temperate tree species over time per stand and number of temperate seedlings added at the beginning of the simulation. Low, medium and high densities seedlings correspond to 500, 5 000 and 10 000 seedlings per hectare, respectively.

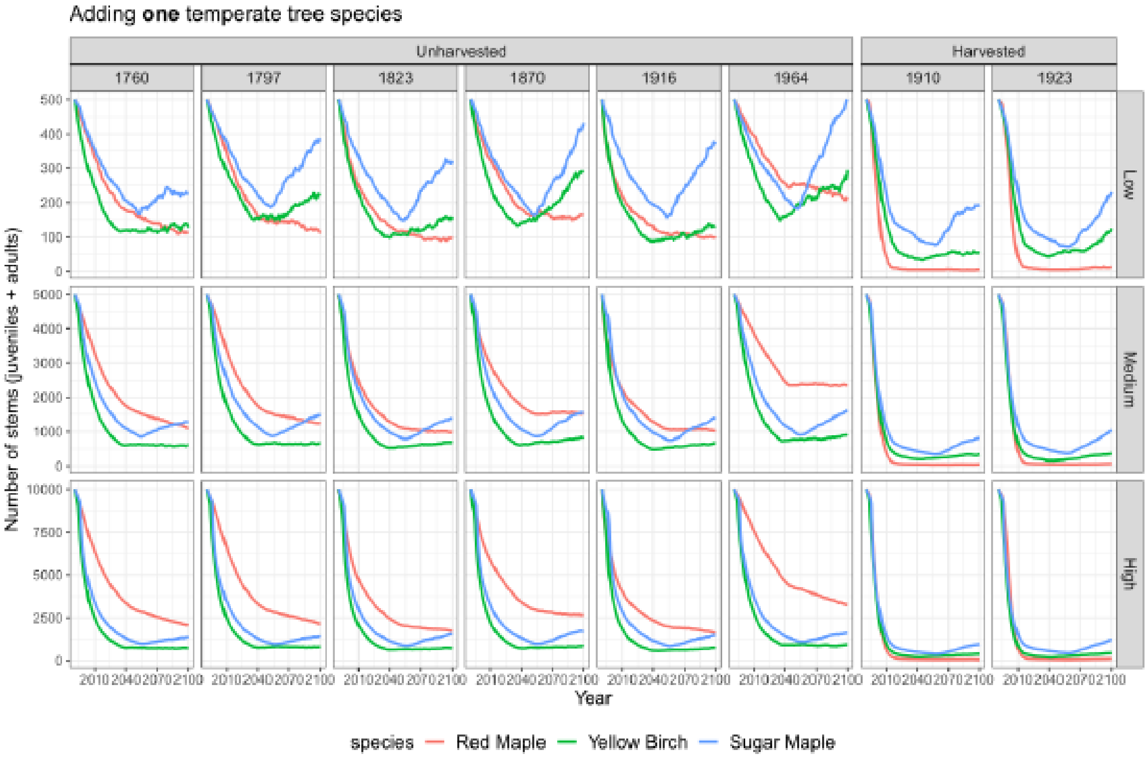

Figure A.8: Simulated number of temperate tree stems (seedlings + saplings + adults) over time per stand and density of temperate seedlings added at the beginning of the simulation. Low, medium and high densities seedlings correspond to 500, 5 000 and 10 000 seedlings per hectare, respectively. Note different y-axis between rows.

ANNEXE B INFORMATIONS SUPPLÉMENTAIRES CHAPITRE II

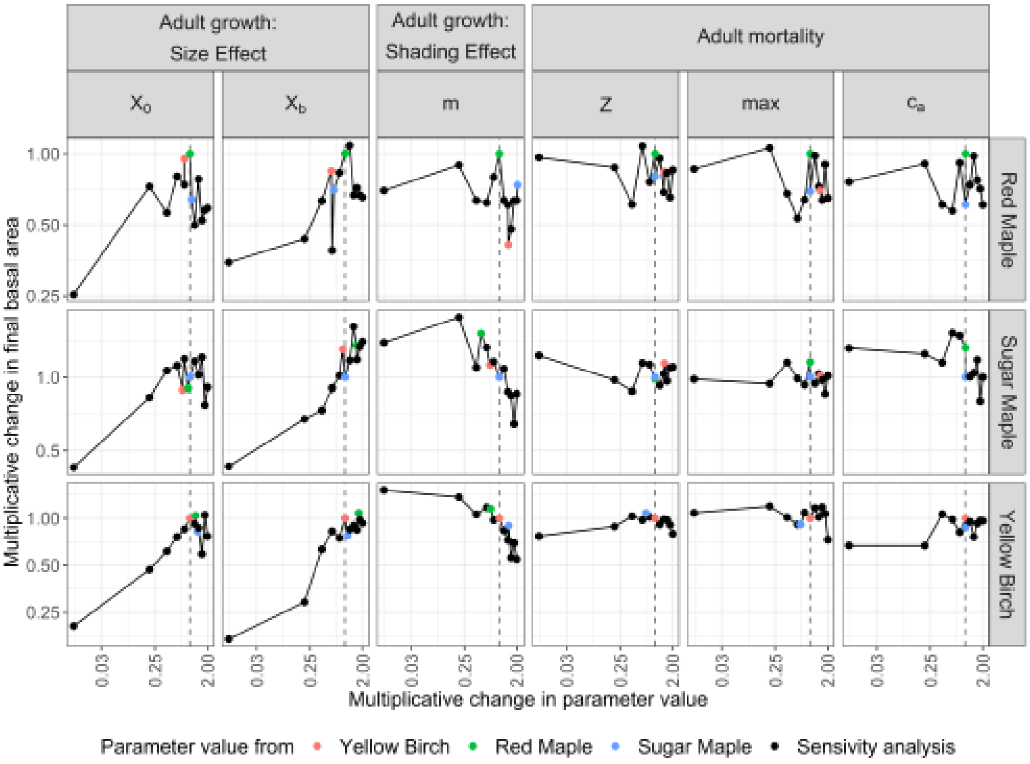

Figure B.1: Sensitivity analysis on 6 parameters influencing adult and sapling basal area at the last timestep. The sensitivity analysis has been performed on 10 other parameters of adult and juvenile growth, dispersion and juvenile mortality that can be found in the main document Fig. 2.7. Only the evaluated parameter varies while the others are fixed at their optimal value. Color points are the results of simulations with the parameter value of the species associated to that color. The vertical gray dashed lines correspond to the parameter value used for the experimental design. Here, we only used the RCP 4.5 climate scenario and a 150m^2 central patch of temperate trees in the stand reinitialized in 1964. The central plot has been removed to calculate the temperate tree basal areas.

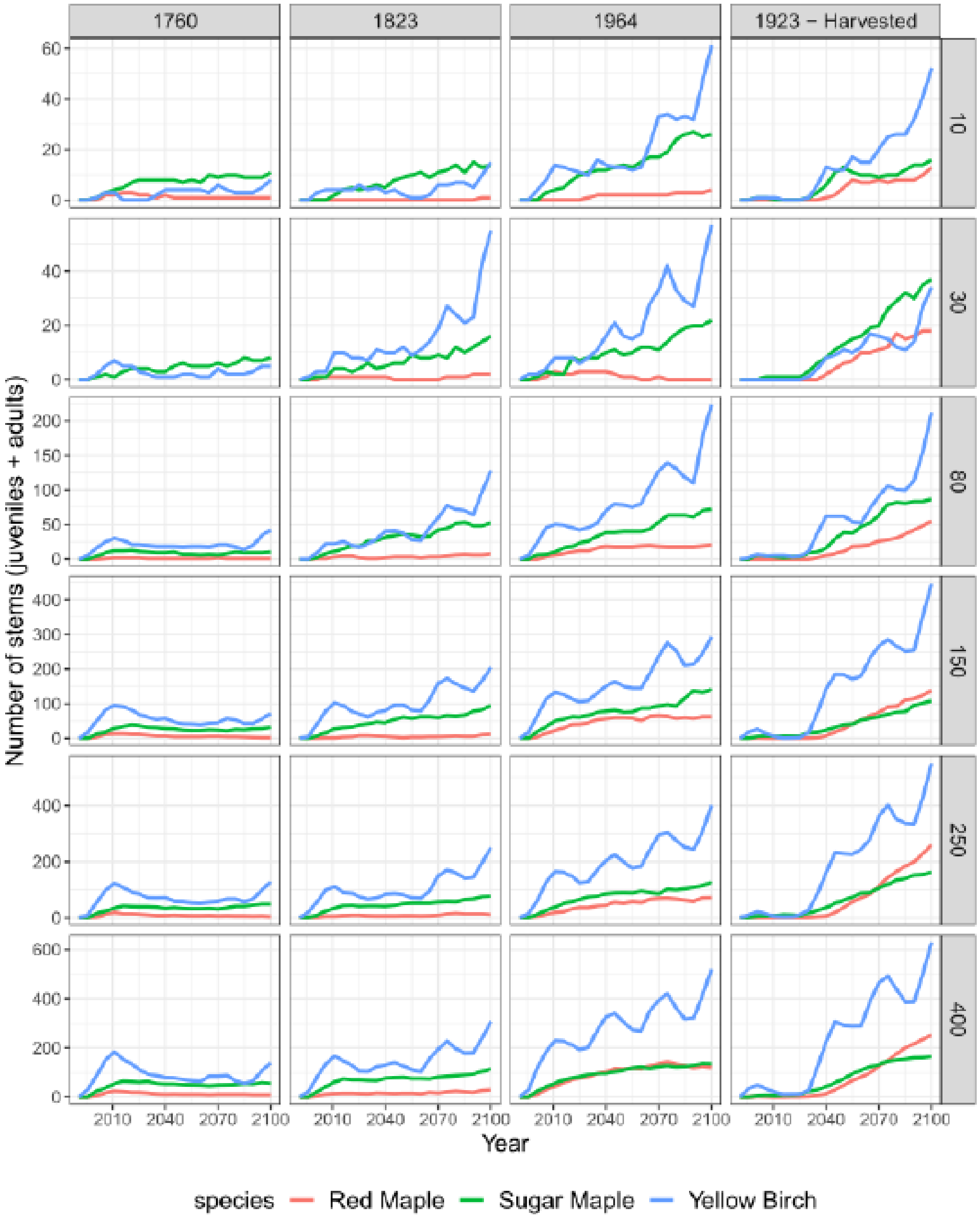

Figure B.2: Simulated number of temperate tree stems (seedlings + saplings + adults) over time per stand and patch size of temperate species added at the beginning of the simulation. Note different y-axis between rows.

ANNEXE C INFORMATIONS SUPPLÉMENTAIRES CHAPITRE III

Table C.1: Full model after selection of climate and soil variables.

Species	Formula
Black spruce	log growth rate ~ logDBH + TAVE + VPD + logDBH^2 + TAVE^2 + VPD^2 + pH + clay + CEC + clay^2 + CEC^2 + NCI_conifer + NCI_intra + NCI_deciduous + Shading + TAVE:pH + TAVE:clay + TAVE:CEC + TAVE:clay^2 + TAVE:CEC^2 + TAVE:NCI_conifer + TAVE:NCI_intra + TAVE:NCI_deciduous + VPD:pH + VPD:clay + VPD:CEC + VPD:clay^2 + VPD:CEC^2 + VPD:NCI_conifer + VPD:NCI_intra + VPD:NCI_deciduous + TAVE^2:pH + TAVE^2:clay + TAVE^2:CEC + TAVE^2:clay^2 + TAVE^2:CEC^2 + TAVE^2:NCI_conifer + TAVE^2:NCI_intra + TAVE^2:NCI_deciduous + VPD^2:pH + VPD^2:clay + VPD^2:CEC + VPD^2:clay^2 + VPD^2:CEC^2 + VPD^2:NCI_conifer + VPD^2:NCI_intra + VPD^2:NCI_deciduous + pH:NCI_conifer + pH:NCI_intra + pH:NCI_deciduous + clay:NCI_conifer + clay:NCI_intra + clay:NCI_deciduous + CEC:NCI_conifer + CEC:NCI_intra + CEC:NCI_deciduous + clay^2:NCI_conifer + clay^2:NCI_intra + clay^2:NCI_deciduous + CEC^2:NCI_conifer + CEC^2:NCI_intra + CEC^2:NCI_deciduous + (1 | PLACE)
White birch	log growth rate~ logDBH + TAVE + VPD + logDBH^2 + TAVE^2 + VPD^2 + CEC + NCI_conifer + NCI_intra + NCI_deciduous + Shading + TAVE:CEC + VPD:CEC + TAVE^2:CEC + VPD^2:CEC + (1 | PLACE)
Sugar maple	log growth rate ~ logDBH + DD5 + VPD + logDBH ^{2} + VPD^2 + CEC + clay + CEC^2 + NCI_conifer + NCI_intra + NCI_deciduous + Shading + DD5:NCI_conifer + DD5:NCI_intra + DD5:NCI_deciduous + VPD:NCI_conifer + VPD:NCI_intra + VPD:NCI_deciduous + VPD^2:NCI_conifer + VPD^2:NCI_intra + VPD^2:NCI_deciduous + CEC:NCI_conifer + CEC:NCI_intra + CEC:NCI_deciduous + clay:NCI_conifer + clay:NCI_intra + clay:NCI_deciduous + CEC^2:NCI_conifer + CEC^2:NCI_intra + CEC^2:NCI_deciduous + (1 | PLACE)

Table C.1 (continued)

Balsam fir	log growth rate ~ logDBH + TAVE + VPD + logDBH^2 + TAVE^2 + pH + clay + CEC + pH^2 + clay^2 + CEC^2 + NCI_conifer + NCI_intra + NCI_deciduous + Shading + TAVE:pH + TAVE:clay + TAVE:CEC + TAVE:pH^2 + TAVE:clay^2 + TAVE:CEC^2 + TAVE:NCI_conifer + TAVE:NCI_intra + TAVE:NCI_deciduous + VPD:pH + VPD:clay + VPD:CEC + VPD:pH^2 + VPD:clay^2 + VPD:CEC^2 + VPD:NCI_conifer + VPD:NCI_intra + VPD:NCI_deciduous + TAVE^2:pH + TAVE^2:clay + TAVE^2:CEC + TAVE^2:pH^2 + TAVE^2:clay^2 + TAVE^2:CEC^2 + TAVE^2:NCI_conifer + TAVE^2:NCI_intra + TAVE^2:NCI_deciduous + pH:NCI_conifer + pH:NCI_intra + pH:NCI_deciduous + clay:NCI_conifer + clay:NCI_intra + clay:NCI_deciduous + CEC:NCI_conifer + CEC:NCI_intra + CEC:NCI_deciduous + pH^2:NCI_conifer + pH^2:NCI_intra + pH^2:NCI_deciduous + clay^2:NCI_conifer + clay^2:NCI_intra + clay^2:NCI_deciduous + CEC^2:NCI_conifer + CEC^2:NCI_intra + CEC^2:NCI_deciduous + (1 | PLACE)
Yellow birch	Log growth rate ~ logDBH + logDBH^2 + CEC + NCI_conifer + NCI_intra + NCI_deciduous + Shading + CEC:NCI_conifer + CEC:NCI_intra + CEC:NCI_deciduous + (1 | PLACE)
Red maple	log growth rate ~ logDBH + DD5 + PPT + logDBH^2 + DD5^2 + PPT^2 + clay + CEC + NCI_conifer + NCI_intra + NCI_deciduous + Shading + DD5:clay + DD5:CEC + PPT:clay + PPT:CEC + DD5^2:clay + DD5^2:CEC + PPT^2:clay + PPT^2:CEC + (1 | PLACE)

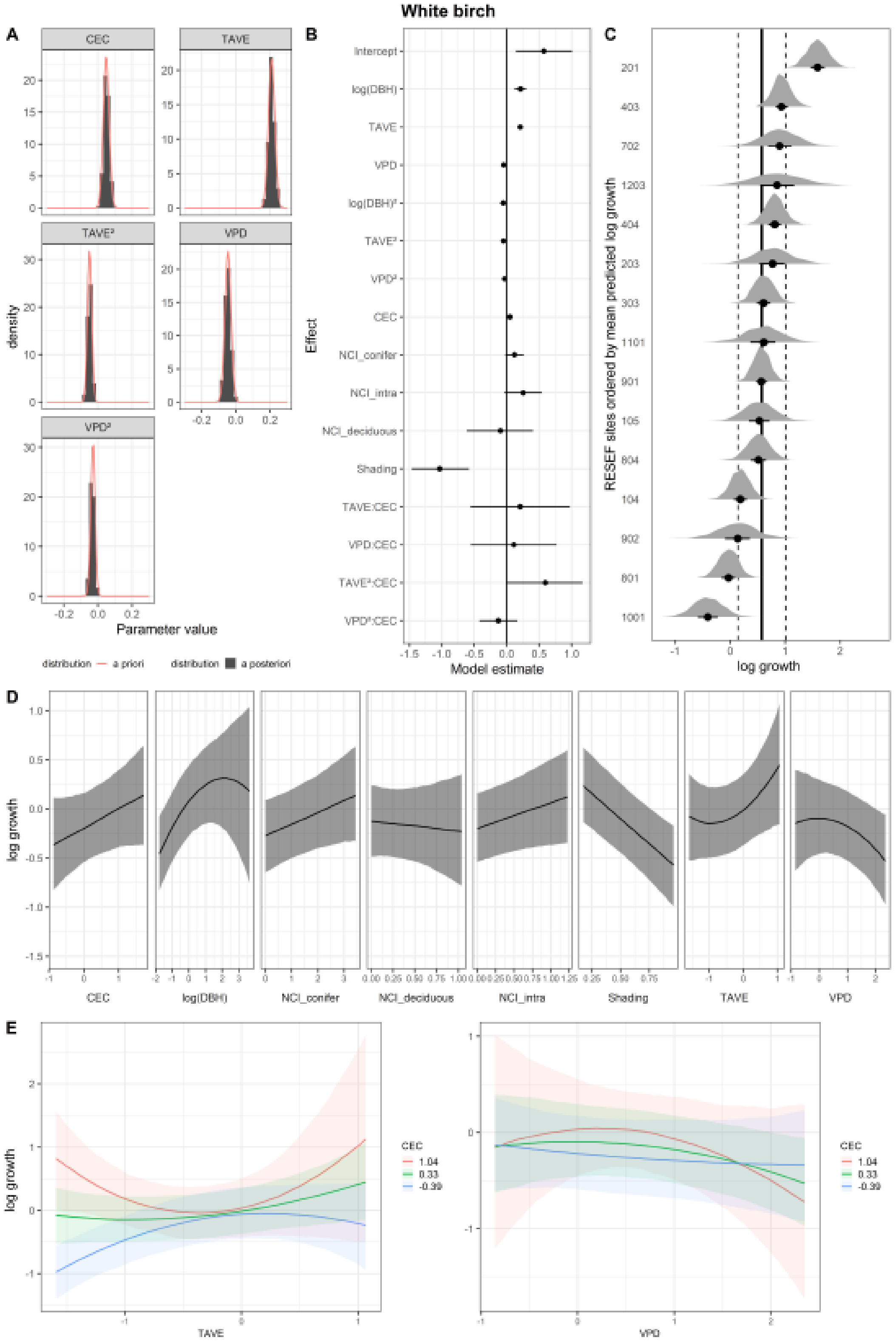
White birch
A
CEC
TAVE
TAVE²
VPD
VPD²
density
Parameter value
-0.2
0.0
0.2
distribution — a priori
distribution ■ a posteriori
B
Effect
Intercept
log(DBH)
TAVE
VPD
log(DBH)²
TAVE²
VPD²
CEC
NCI_conifer
NCI_intra
NCI_deciduous
Shading
TAVE:CEC
VPD:CEC
TAVE²:CEC
VPD²:CEC
Model estimate
-1.5
-1.0
-0.5
0.0
0.5
1.0
C
RESEF sites ordered by mean predicted log growth
201
403
702
1203
404
203
303
1101
901
105
804
104
902
801
1001
log growth
-1
0
1
2
D
log growth
CEC
log(DBH)
NCI_conifer
NCI_deciduous
NCI_intra
Shading
TAVE
VPD
E
log growth
TAVE
VPD
CEC
1.04
0.33
-0.39

Figure C.1: Results of the best model fitted for white birch. A: Comparisons between the *a priori* distribution (in red) and the *a posteriori* distribution. B: The direction and strength of each effect. C: Tree growth organized and ordered by the RESEF sites, with a vertical line denoting the mean growth for all sites, dashed lines indicating the 2.5 and 97.5 quantiles of tree growth for all sites, dots representing the mean growth at each site, and the grey distribution depicting the *a posteriori* distribution of tree growth. D: Response curves illustrating tree growth for each variable in the model. E: Response curves representing the impact of each interaction included in the model. For each of these response curves, we maintained the other variables at their mean values. In this regard, there may be inconsistencies with part B of the figure, which displays the raw coefficients of the model.

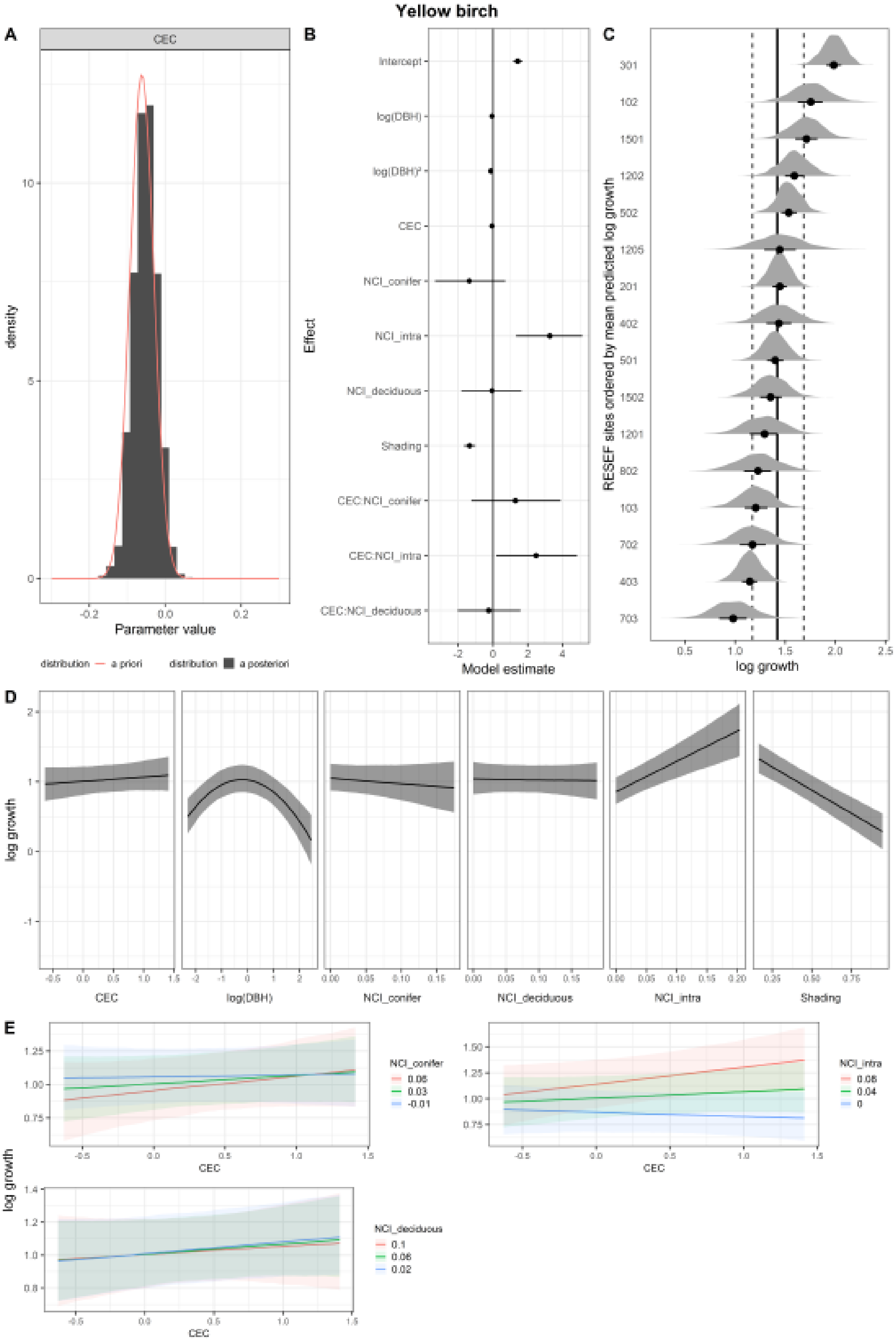
Yellow birch
A
CEC
density
Parameter value
distribution — a priori
distribution ■ a posteriori
B
Effect
Intercept
log(DBH)
log(DBH)²
CEC
NCI_conifer
NCI_intra
NCI_deciduous
Shading
CEC:NCI_conifer
CEC:NCI_intra
CEC:NCI_deciduous
Model estimate
C
RESEF sites ordered by mean predicted log growth
301
102
1501
1202
502
1205
201
402
501
1502
1201
802
103
702
403
703
log growth
D
log growth
CEC
log(DBH)
NCI_conifer
NCI_deciduous
NCI_intra
Shading
E
log growth
NCI_conifer
0.06
0.03
-0.01
NCI_intra
0.08
0.04
0
NCI_deciduous
0.1
0.06
0.02
CEC

Figure C.2: Results of the best model fitted for yellow birch. A: Comparisons between the *a priori* distribution (in red) and the *a posteriori* distribution. B: The direction and strength of each effect. C: Tree growth organized and ordered by the RESEF sites, with a vertical line denoting the mean growth for all sites, dashed lines indicating the 2.5 and 97.5 quantiles of tree growth for all sites, dots representing the mean growth at each site, and the grey distribution depicting the *a posteriori* distribution of tree growth. D: Response curves illustrating tree growth for each variable in the model. E: Response curves representing the impact of each interaction included in the model. For each of these response curves, we maintained the other variables at their mean values. In this regard, there may be inconsistencies with part B of the figure, which displays the raw coefficients of the model.

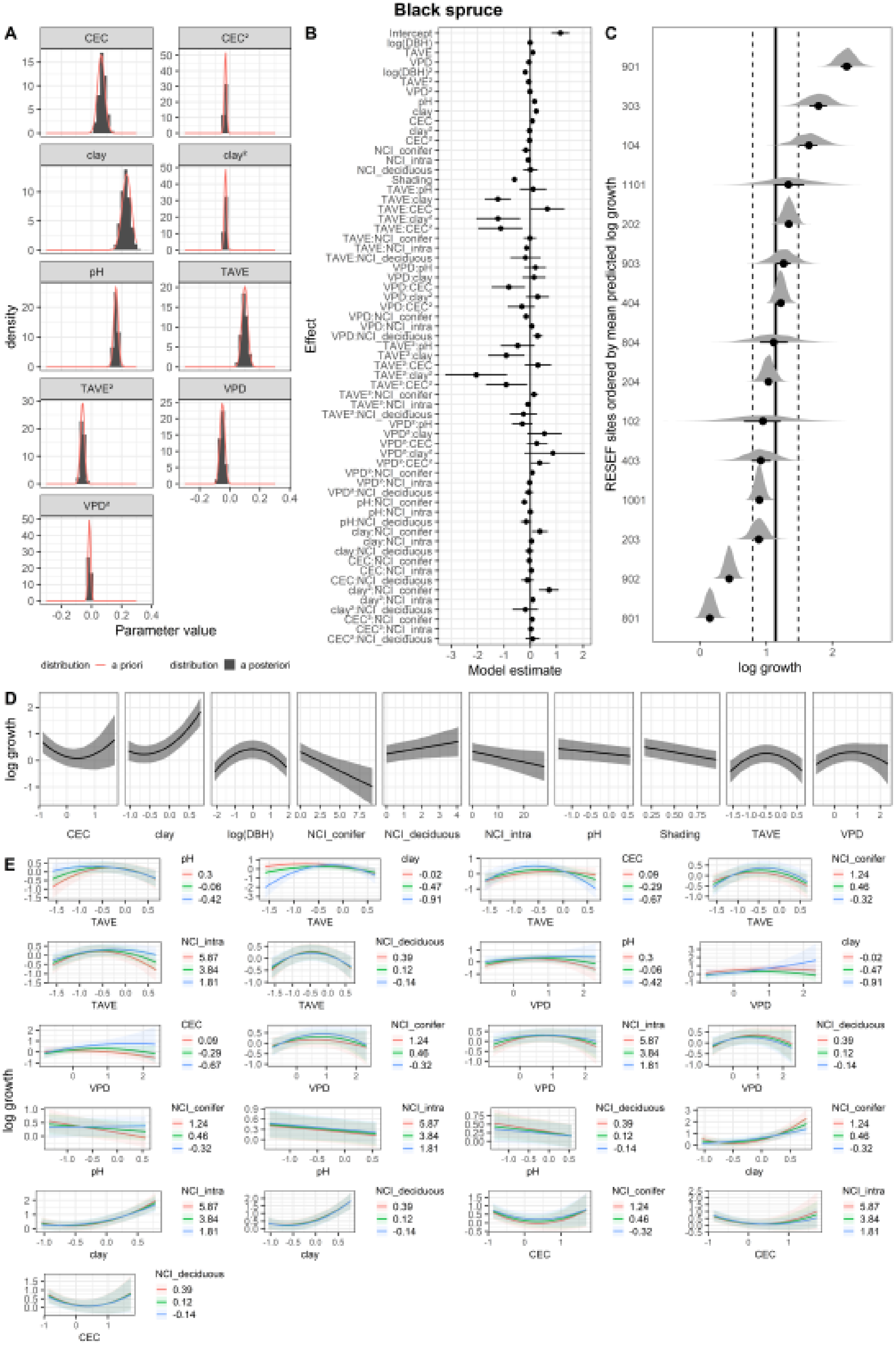
Black spruce
A
B
C
D
E
CEC
CEC²
clay
clay²
pH
TAVE
TAVE²
VPD
VPD²
density
Parameter value
distribution — a priori
distribution ■ a posteriori
Intercept
log(DBH)
TAVE
VPD
log(DBH)²
TAVE²
VPD²
pH
clay
CEC
clay²
CEC²
NCI_conifer
NCI_intra
NCI_deciduous
Shading
TAVE:pH
TAVE:clay
TAVE:CEC
TAVE:clay²
TAVE:CEC²
TAVE:NCI_conifer
TAVE:NCI_intra
TAVE:NCI_deciduous
VPD:pH
VPD:clay
VPD:CEC
VPD:clay²
VPD:CEC²
VPD:NCI_conifer
VPD:NCI_intra
VPD:NCI_deciduous
TAVE²:pH
TAVE²:clay
TAVE²:CEC
TAVE²:clay²
TAVE²:CEC²
TAVE²:NCI_conifer
TAVE²:NCI_intra
TAVE²:NCI_deciduous
VPD²:pH
VPD²:clay
VPD²:CEC
VPD²:clay²
VPD²:CEC²
VPD²:NCI_conifer
VPD²:NCI_intra
VPD²:NCI_deciduous
pH:NCI_conifer
pH:NCI_intra
pH:NCI_deciduous
clay:NCI_conifer
clay:NCI_intra
clay:NCI_deciduous
CEC:NCI_conifer
CEC:NCI_intra
CEC:NCI_deciduous
clay²:NCI_conifer
clay²:NCI_intra
clay²:NCI_deciduous
CEC²:NCI_conifer
CEC²:NCI_intra
CEC²:NCI_deciduous
Effect
Model estimate
901
303
104
1101
202
903
404
804
204
102
403
1001
203
902
801
RESEF sites ordered by mean predicted log growth
log growth
log growth
CEC
clay
log(DBH)
NCI_conifer
NCI_deciduous
NCI_intra
pH
Shading
TAVE
VPD
pH
0.3
-0.06
-0.42
clay
-0.02
-0.47
-0.91
CEC
0.09
-0.29
-0.67
NCI_conifer
1.24
0.46
-0.32
NCI_intra
5.87
3.84
1.81
NCI_deciduous
0.39
0.12
-0.14
TAVE
VPD
pH
clay
CEC
log growth

Figure C.3: Results of the best model fitted for black spruce. A: Comparisons between the *a priori* distribution (in red) and the *a posteriori* distribution. B: The direction and strength of each effect. C: Tree growth organized and ordered by the RESEF sites, with a vertical line denoting the mean growth for all sites, dashed lines indicating the 2.5 and 97.5 quantiles of tree growth for all sites, dots representing the mean growth at each site, and the grey distribution depicting the *a posteriori* distribution of tree growth. D: Response curves illustrating tree growth for each variable in the model. E: Response curves representing the impact of each interaction included in the model. For each of these response curves, we maintained the other variables at their mean values. In this regard, there may be inconsistencies with part B of the figure, which displays the raw coefficients of the model.

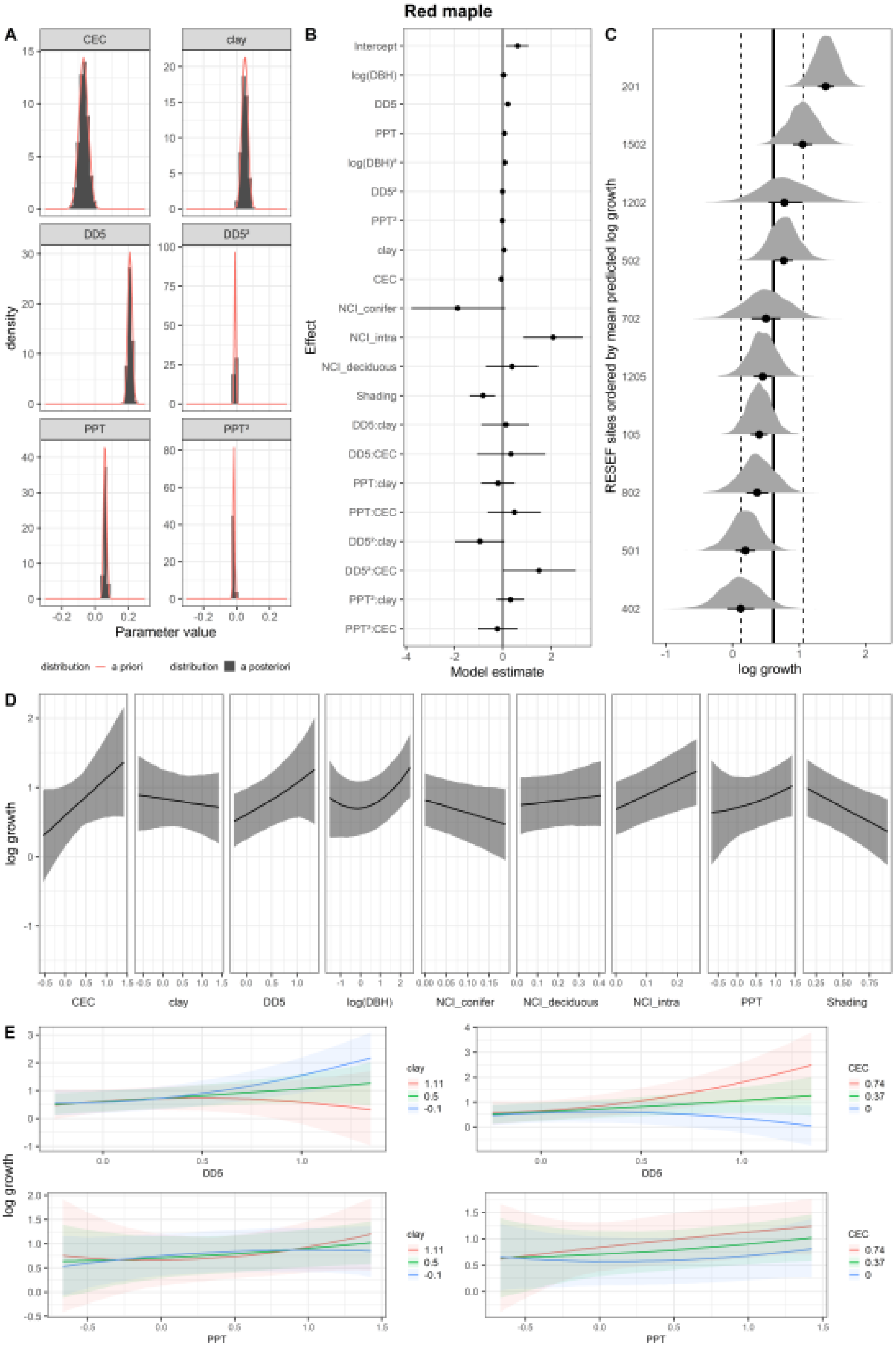
Red maple
A
CEC
clay
DD5
DD5²
PPT
PPT²
density
Parameter value
distribution — a priori
distribution ■ a posteriori
B
Intercept
log(DBH)
DD5
PPT
log(DBH)²
DD5²
PPT²
clay
CEC
NCI_conifer
NCI_intra
NCI_deciduous
Shading
DD5:clay
DD5:CEC
PPT:clay
PPT:CEC
DD5²:clay
DD5²:CEC
PPT²:clay
PPT²:CEC
Effect
Model estimate
C
RESEF sites ordered by mean predicted log growth
201
1502
1202
502
702
1205
105
802
501
402
log growth
D
log growth
CEC
clay
DD5
log(DBH)
NCI_conifer
NCI_deciduous
NCI_intra
PPT
Shading
E
log growth
DD5
PPT
clay
1.11
0.5
-0.1
CEC
0.74
0.37
0

Figure C.4: Results of the best model fitted for red maple. A: Comparisons between the *a priori* distribution (in red) and the *a posteriori* distribution. B: The direction and strength of each effect. C: Tree growth organized and ordered by the RESEF sites, with a vertical line denoting the mean growth for all sites, dashed lines indicating the 2.5 and 97.5 quantiles of tree growth for all sites, dots representing the mean growth at each site, and the grey distribution depicting the *a posteriori* distribution of tree growth. D: Response curves illustrating tree growth for each variable in the model. E: Response curves representing the impact of each interaction included in the model. For each of these response curves, we maintained the other variables at their mean values. In this regard, there may be inconsistencies with part B of the figure, which displays the raw coefficients of the model.

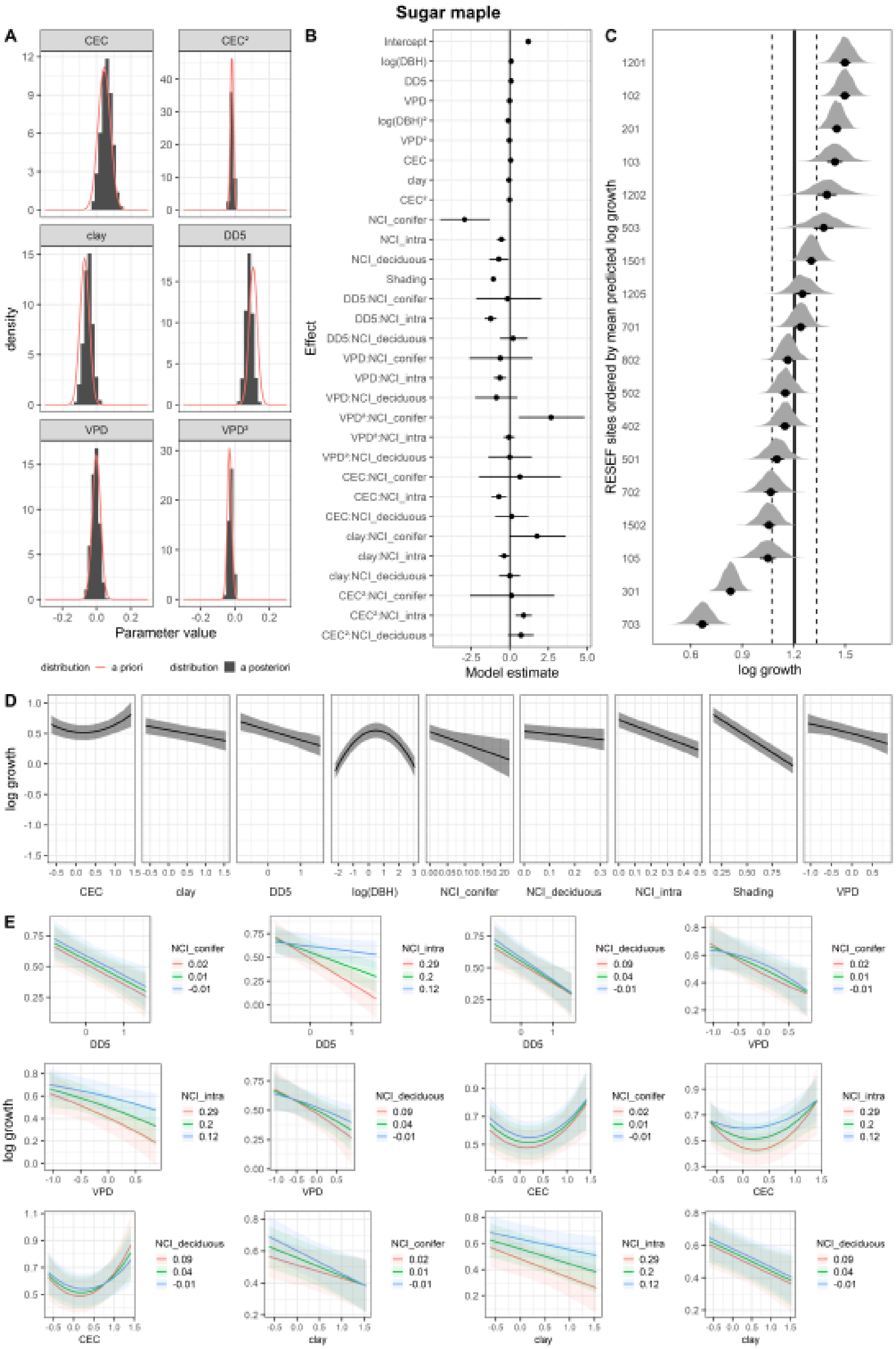
Sugar maple
A
CEC
CEC²
clay
DD5
VPD
VPD²
density
Parameter value
distribution — a priori
distribution ■ a posteriori
B
Intercept
log(DBH)
DD5
VPD
log(DBH)²
VPD²
CEC
clay
CEC²
NCI_conifer
NCI_intra
NCI_deciduous
Shading
DD5:NCI_conifer
DD5:NCI_intra
DD5:NCI_deciduous
VPD:NCI_conifer
VPD:NCI_intra
VPD:NCI_deciduous
VPD²:NCI_conifer
VPD²:NCI_intra
VPD²:NCI_deciduous
CEC:NCI_conifer
CEC:NCI_intra
CEC:NCI_deciduous
clay:NCI_conifer
clay:NCI_intra
clay:NCI_deciduous
CEC²:NCI_conifer
CEC²:NCI_intra
CEC²:NCI_deciduous
Effect
Model estimate
C
1201
102
201
103
1202
503
1501
1205
701
802
502
402
501
702
1502
105
301
703
RESEF sites ordered by mean predicted log growth
log growth
D
log growth
CEC
clay
DD5
log(DBH)
NCI_conifer
NCI_deciduous
NCI_intra
Shading
VPD
E
NCI_conifer
0.02
0.01
-0.01
NCI_intra
0.29
0.2
0.12
NCI_deciduous
0.09
0.04
-0.01
log growth
DD5
VPD
CEC
clay

Figure C.5: Results of the best model fitted for sugar maple. A: Comparisons between the *a priori* distribution (in red) and the *a posteriori* distribution. B: The direction and strength of each effect. C: Tree growth organized and ordered by the RESEF sites, with a vertical line denoting the mean growth for all sites, dashed lines indicating the 2.5 and 97.5 quantiles of tree growth for all sites, dots representing the mean growth at each site, and the grey distribution depicting the *a posteriori* distribution of tree growth. D: Response curves illustrating tree growth for each variable in the model. E: Response curves representing the impact of each interaction included in the model. For each of these response curves, we maintained the other variables at their mean values. In this regard, there may be inconsistencies with part B of the figure, which displays the raw coefficients of the model.

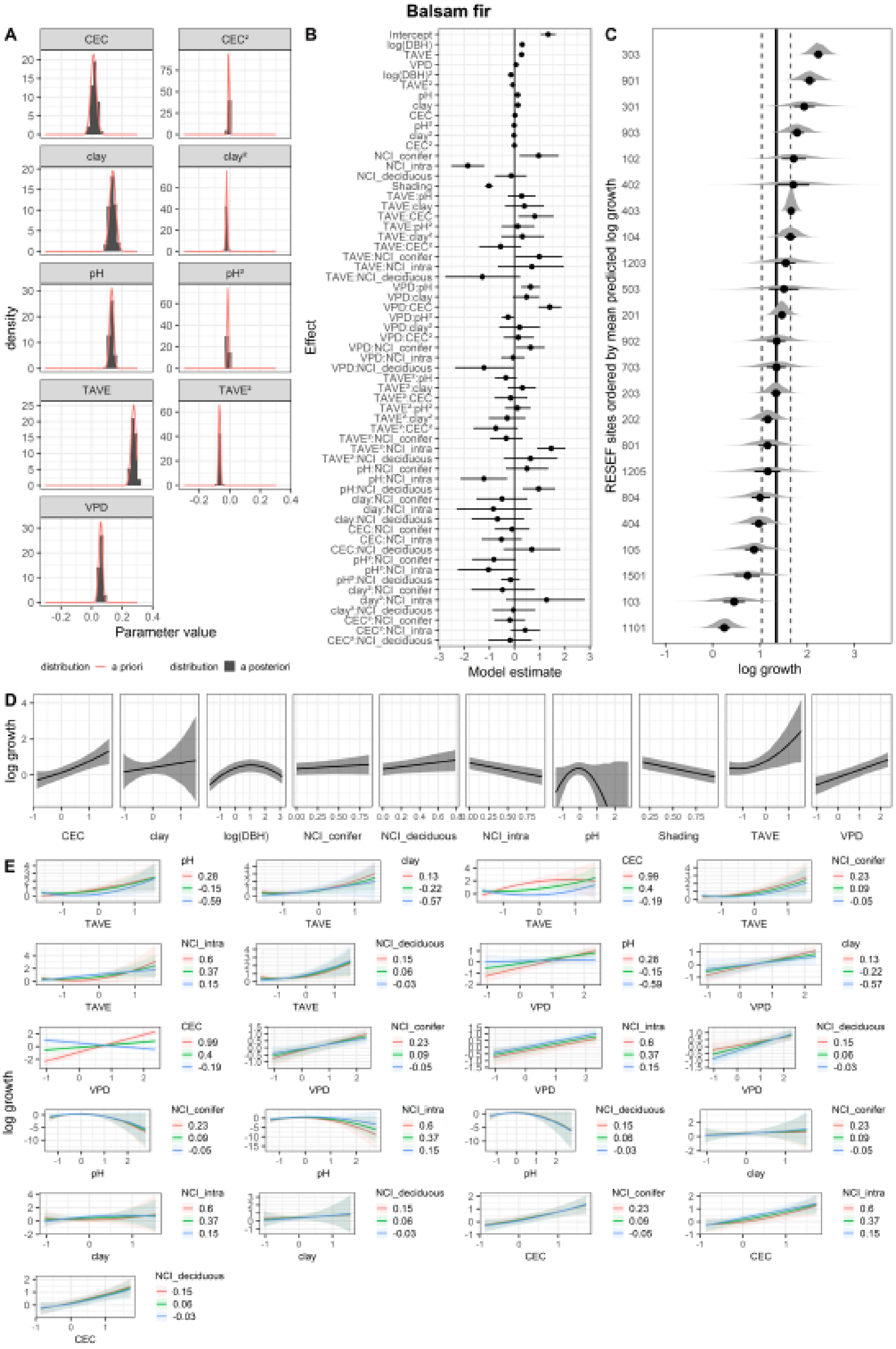
Balsam fir
A
B
C
D
E
CEC
CEC²
clay
clay²
pH
pH²
TAVE
TAVE²
VPD
density
Parameter value
distribution — a priori
distribution ■ a posteriori
Intercept
log(DBH)
TAVE
VPD
log(DBH)²
TAVE²
pH
clay
CEC
pH²
clay²
CEC²
NCI_conifer
NCI_intra
NCI_deciduous
Shading
TAVE:pH
TAVE:clay
TAVE:CEC
TAVE:pH²
TAVE:clay²
TAVE:CEC²
TAVE:NCI_conifer
TAVE:NCI_intra
TAVE:NCI_deciduous
VPD:pH
VPD:clay
VPD:CEC
VPD:pH²
VPD:clay²
VPD:CEC²
VPD:NCI_conifer
VPD:NCI_intra
VPD:NCI_deciduous
TAVE²:pH
TAVE²:clay
TAVE²:CEC
TAVE²:pH²
TAVE²:clay²
TAVE²:CEC²
TAVE²:NCI_conifer
TAVE²:NCI_intra
TAVE²:NCI_deciduous
pH:NCI_conifer
pH:NCI_intra
pH:NCI_deciduous
clay:NCI_conifer
clay:NCI_intra
clay:NCI_deciduous
CEC:NCI_conifer
CEC:NCI_intra
CEC:NCI_deciduous
pH²:NCI_conifer
pH²:NCI_intra
pH²:NCI_deciduous
clay²:NCI_conifer
clay²:NCI_intra
clay²:NCI_deciduous
CEC²:NCI_conifer
CEC²:NCI_intra
CEC²:NCI_deciduous
Effect
Model estimate
RESEF sites ordered by mean predicted log growth
303
901
301
903
102
402
403
104
1203
503
201
902
703
203
202
801
1205
804
404
105
1501
103
1101
log growth
CEC
clay
log(DBH)
NCI_conifer
NCI_deciduous
NCI_intra
pH
Shading
TAVE
VPD
pH 0.28 -0.15 -0.59
clay 0.13 -0.22 -0.57
CEC 0.99 0.4 -0.19
NCI_conifer 0.23 0.09 -0.05
NCI_intra 0.6 0.37 0.15
NCI_deciduous 0.15 0.06 -0.03

Figure C.6: Results of the best model fitted for balsam fir. A: Comparisons between the *a priori* distribution (in red) and the *a posteriori* distribution. B: The direction and strength of each effect. C: Tree growth organized and ordered by the RESEF sites, with a vertical line denoting the mean growth for all sites, dashed lines indicating the 2.5 and 97.5 quantiles of tree growth for all sites, dots representing the mean growth at each site, and the grey distribution depicting the *a posteriori* distribution of tree growth. D: Response curves illustrating tree growth for each variable in the model. E: Response curves representing the impact of each interaction included in the model. For each of these response curves, we maintained the other variables at their mean values. In this regard, there may be inconsistencies with part B of the figure, which displays the raw coefficients of the model.

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