Patterns and processes affecting northward migration of tree species in a changing climate

Laura Boisvert-Marsh

Department of Plant Science
Faculty of Agricultural and Environmental Sciences
McGill University, Montreal

November 2020

A thesis submitted to McGill University in partial fulfillment of the requirements of the degree of DOCTOR OF PHILOSOPHY

Table of Contents

List of Tables

List of Figures

List of Abbreviations

AIC	Akaike Information Criterion
Cgr	Climate gradient
CTA	Classification tree analysis
DBH	Diameter at breast height
$\mathrm{Dist}_{\mathrm{best}}$	Variable with highest absolute Wald z score from best disturbance model
FDA	Flexible discriminant analysis
gdd5	Growing degree days, base 5°C
GAM	Generalized additive models
GLM	Generalized linear models
LDD	Long distance dispersal
$\mathrm{LDD}_{\mathrm{min}}$	Minimum distance of long distance dispersal
$\mathrm{LDD}_{\mathrm{max}}$	Maximum distance of long distance dispersal
LongGroup	Longitudinal band (2° wide)
LRS	Latitudinal range shift
MFFP	Ministère des Forêts, Faune et des Parcs (Québec)
NE	Northward expansion
NT	Northward shift by southern range thinning
$\mathrm{Occ}_{\mathrm{gain}}$	Occupancy gain
P_1	Inventory conducted by MFFP between 1970 and 1977
P_2	Inventory conducted by MFFP between 1992 and 2002
P_3	Inventory conducted by MFFP between 2003 and 2015
RCP 8.5	Representative concentration pathway
RF	Random Forest
ROC	Receiver Operator Curve
SES	Standardized effect size
SF	Southward shift by southern range filling
ST	Southward shift by northern range thinning
<50th	Zone south of a species' 50th percentile of latitudinal distribution
>50th	Zone north of a species' 50th percentile of latitudinal distribution
>90th	Zone north of a species' 90th percentile of latitudinal distribution
$\Delta \mathrm{C}_{\mathrm{best}}$	Variable with highest absolute Wald z score from best climate change model
Δclimate	Difference in values for a given climate variable between conditions observed in P_3 minus P_1 (i.e., climate change)
Δgdd5	Difference in growing degree days, base 5°C
ΔPrecip	Difference in precipitation
ΔTMax	Difference in maximum temperature
ΔTMin	Difference in minimum temperature

Abstract

Northern limits of species distributions are at the 'leading edge' of studies on biological response to climate change, and therefore examining changes in species distributions is a crucial step in quantifying species' potential to track climate through poleward migration. Tracking distributional changes over large geographic areas remains a challenge, however, and the abiotic and biotic contexts under which these changes are occurring are unclear. The overall objective of this thesis is to understand the patterns and processes of range shifts in relation to rapid environmental change, focusing on forest tree species of Eastern North America to inform sustainable forest management. In the first study, I aimed to identify migration pathways from northern temperate to boreal forests for species showing range expansion. In the second study, I focused on climate change and natural and anthropogenic disturbances to assess their relative influence on observed patterns of species range shifts. In the third study, I developed a modelling framework to evaluate the potential for range shift for 10 tree species in response to climate change by integrating information on life history and dispersal ability to improve projections. These three studies improve our knowledge about tree species responses to climate change across time and space, showing how local biotic and abiotic factors translate into responses at broader scales and which processes underlie the observed patterns. Species are showing evidence of migration in response to warming especially toward their northern range limit, with some taking advantage of migration pathways that involve disturbances disrupting priority effects and associated species facilitating establishment in challenging environmental conditions. Species that can benefit the most from novel biotic interactions and disturbances in the boreal forest, and whose dispersal and establishment is relatively effective are likely to expand their range without assistance while others could require some intervention. Developing management strategies that consider the potential for species to track their suitable climate is an important step toward sustainable forest management, and this thesis can help incorporate ecological knowledge into the planning process.

Résumé

Les études portant sur les limites de répartition se trouvent « à l'avant-garde » de la réponse biologique des espèces aux changements climatiques. L'étude des changements de répartition récents démontre le potentiel des espèces à suivre ou non leur niche climatique. L'influence des changements climatiques sur ces déplacements est présumée importante, mais il y a encore peu d'évidence qui supporte cette relation à l'échelle du site. Enfin, une compréhension accrue des processus écologiques sous-jacents à cette dynamique peut améliorer les prédictions de modèles. L'objectif général de cette thèse est de comprendre les patrons et les processus associés au déplacement des limites de répartition des espèces d'arbres dans l'est de l'Amérique du Nord en lien avec les changements globaux en cours afin d'informer les pratiques d'aménagement forestier durable. Pour atteindre cet objectif, trois études ont été menées. La première étude identifie des voies de migration de la forêt tempérée mixte vers la forêt boréale pour des espèces ayant démontrées un déplacement vers le nord de leur limite de répartition. La deuxième étude compare à l'échelle du site l'influence relative des changements climatiques récents versus celle des perturbations sur les changements d'aires de répartition observés. La troisième étude évalue la capacité des espèces à migrer selon des scénarios plus réalistes en se basant sur une plateforme de modélisation qui incorpore les connaissances écologiques sur les arbres. Ces trois études montrent que les espèces migrent en réponse au réchauffement et cette réponse est plus évidente à l'approche de leur limite nordique. De plus, certaines espèces pourraient bénéficier de voies de migration offertes par les perturbations (naturelles ou anthropiques), celles-ci atténuant la compétition avec les espèces boréales résidentes, et par leur association à des espèces pouvant faciliter la colonisation dans des conditions environnementales difficiles. Les espèces ayant une dispersion et colonisation des semences plutôt efficaces et le potentiel de prendre avantage des nouvelles interactions biotiques entres espèces et des perturbations dans la forêt boréale devraient étendre leur répartition sans intervention majeure tandis que d'autres pourraient bénéficier de plan de gestion. L'élaboration de mesures d'aménagement qui tiennent compte des espèces ayant le potentiel de suivre le climat et celles qui éprouveront des difficultés est un aspect important de la gestion durable des forêts et cette thèse peut servir de guide à l'incorporation des connaissances écologiques dans cette planification.

List of Species Studied

Species name	**Abbreviation**	**English name**	**French name**
Abies balsamea (L.) Mill.	ABIBAL	Balsam fir	Sapin baumier
Acer rubrum L.	ACERUB	Red maple	Érable rouge
Acer saccharum Marshall	ACESAC	Sugar maple	Érable à sucre
Betula alleghaniensis Britt.	BETALL	Yellow birch	Bouleau jaune
Betula papyrifera Marshall	BETPAP	Paper birch	Bouleau à papier
Fagus grandifolia Ehr.	FAGGRA	American beech	Hêtre à grandes feuilles
Ostrya virginiana (Mill.) K. Koch	OSTVIR	Eastern hop-hornbeam	Ostryer de Virginie
Picea glauca (Moench) Voss	PICGLA	White spruce	Épinette blanche
Picea mariana (Mill.) BSP	PICMAR	Black spruce	Épinette noire
Pinus strobus L.	PINSTR	Eastern white pine	Pin blanc
Populus tremuloides Michx.	POPTRE	Trembling aspen	Peuplier faux-tremble
Quercus rubra L.	QUERUB	Northern red oak	Chêne rouge
Thuja occidentalis L.	THUOCC	Eastern white cedar	Thuya occidental

Acknowledgements

This thesis would not have been possible without the support of many along the way. I firstly wish to express my immense gratitude to my supervisor, Prof. Sylvie de Blois. Your mentorship over the last 13 years through my undergraduate and graduate studies has been instrumental in getting me to where I am today. Not only have you supervised me through my various academic projects, you have supported me through several major life transitions and have generously provided guidance along the way. Malgré tout ce qui s'est passé dans les dernières années, ton support était immesurable. J'ai beaucoup évolué au fil des années et je n'aurai pas pu arriver à ce point toute seule. Je vous remercie infiniment.

I would also like to acknowledge my collaborators on the various chapters – Dr. Catherine Périé, John Pedlar, Dr. Isabelle Aubin, Dr. Dan McKenney, Charlene Williams and Amaël LeSquin, all of whom were instrumental in getting these projects done. I also wish to thank my committee members, Dr. Catherine Potvin and Dr. Olivia Wilkins as well as the additional members of the examining committee – Dr. Benoit Côté and Dr. Don Smith - for their insightful comments about my project. Additionally, I recognize the funding from the Department of Plant Science in the early stages of the project as well as the funding from le Ministère des Forêts, Faune et des Parcs and the Forest Change project from Natural Resources Canada. I would also like to acknowledge members of Ecolab. We have become physically separated over the years, but our connections have been maintained. I would also like to acknowledge my co-workers at the Canadian Forest Service. You have genuinely cared about the outcome of my project but also, more importantly, my well-being. In particular, I would like to thank Isabelle Aubin. Tu n'as pas hésité quand j'avais besoin du prendre du temps pour m'avancer sur le plan académique. J'apprécie que tu aies reconnu dès le début l'importance pour moi de mener ce projet jusqu'au bout.

I would also like to thank my family, those that have always been there and those I have acquired along the way. Mom, Barron, Joanna, Bonnie, Alex, Charlotte, Peter, Michael, Vicki and Morgan as well as all the nieces and nephews - I could not have got through this without you, even if you did not understand half of what I was talking about. I particularly acknowledge Gérard Boisvert and Bob Marsh - you were always there in spirit. In addition, I would like to thank my wonderful friends. You have feigned enough interest to make it seem like you were

interested in what I was doing and have provided the moral support to get there. Lastly, I recognize the unwavering love and support of my husband, James Buchanan. What a **long**, strange road this has been, but we made it to the other side together. This accomplishment is for both of us. I promise, I am done this time!

Contributions of Authors

This manuscript-based thesis was prepared in accordance to the guidelines of McGill University as provided by Graduate and Postdoctoral Studies.

Laura Boisvert-Marsh (candidate) conceived the studies and conducted the analyses presented in the research chapters, with substantial contributions and guidance from the candidate's supervisor, **Prof. Sylvie de Blois**. LB-M wrote the introduction, literature review and overall thesis summary, discussion, and conclusions. LB-M also benefited from inputs of her collaborators on the research chapters (Chapters 4 and 5); their roles are described below.

In Chapter 3, LB-M and SdB conceived the original study; LB-M designed the methodology and led data analysis with input from SdB; LB-M wrote the initial manuscript draft. LB-M and SdB edited the manuscript.

In Chapter 4, LB-M, CP, and SdB conceived the original study and designed the methodology; LB-M along with SdB led the analysis of the data and the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication and inclusion of the thesis.

In Chapter 5, LB-M designed the methodology under the guidance of John Pedlar, SdB and Isabelle Aubin. Under the direction of LB-M, Amael Le Squin developed the mathematical functions for the dispersal kernels and wrote the R code. Dan McKenney and JP provided the species climate envelope models and Charlene Williams provided paleoecological observations used to estimate migration velocities. LB-M oversaw trait documentation and processed the data, conducted the simulations and ran the post-hoc analyses. LB-M led the writing of the manuscript, with considerable input from JP, SdB and IA. All authors gave final approval for inclusion of the manuscript in the thesis.

Contributions to Knowledge

Chapter 3 - Range shifts in response to climate change will ultimately involve colonisation at previously unoccupied sites, but little is known about the abiotic and biotic conditions that will facilitate tree migration. This research confirms previously detected northward range shifts across a broad area (~761000 km^2) and is among the first studies that examines pathways by which northward range expansion is occurring. Additionally, this is among the few studies that characterize abiotic and biotic factors (climate, soils, disturbance, biotic interactions) that underlie recruitment and migration over broad scales. Similarly, this research identifies species that could facilitate northward migration of other temperate species into the boreal forest.

Chapter 4 – The direct effect of recent climate change on species distribution is often surmised from latitudinal shifts but rarely quantified. This research offers among the first quantitative evidence using repeated broad-scale surveys of the effect of climate change at the site level relative to the effect of disturbance on regeneration patterns that result in latitudinal tree migration. These findings highlight spatially explicit and divergent responses within and between species to climate change and disturbance along a latitudinal gradient. Moreover, the importance of monthly and seasonal climate variables over annual ones points towards biological processes such as reproduction, dispersal and establishment being affected at critical stages of the life cycle.

Chapter 5 – For trees, projected rate of shifts in climatically suitable habitat is expected to far exceed the natural migratory capacity of species but their ability to migrate remains relatively poorly understood. Specifically, dispersal ability has not been fully incorporated into modelling because of the difficulty of obtaining field-based empirical data to calibrate dispersal kernels. This work supports the growing body of knowledge modelling how the rapid rate of projected climate change will influence species persistence in the future. This work overcomes the lack of species-specific dispersal kernels and proposes a novel way to translate observed range shift velocities into usable mathematical functions that can be incorporated into process-based modelling studies, even beyond tree species.

Chapter 1 - INTRODUCTION

Climate change is expected to direct ecosystem dynamics in novel and unexpected ways. Rapid increases in temperature and important, but variable, changes in precipitation patterns will have a profound effect on many of the Earth's processes. Climate warming is not a far off scenario yet to occur; we are within the first projected time period of climate projections (2011-2040). As the effects of climate change become clearer, the consequences of such warming on biodiversity must be considered so that swift but informed decisions can be taken to minimize negative impacts on ecosystems.

Biotic responses, such as northward migration of species or decline in parts of the range, have already been shown in several taxa (Parmesan and Yohe 2003, Root et al. 2003, Wilson et al. 2005, Hickling et al. 2006, Devictor et al. 2008, Harsch et al. 2009, Chen et al. 2011, Comte and Grenouillet 2013, Alofs et al. 2014). For trees, climate variables are strong predictors of site occupancy (Canham and Thomas 2010), correlate with recruitment patterns (Elliott 2012), and determine northern range limits (Morin et al. 2007). Early correlative distribution models relating tree species observations to temperature and precipitation (Guisan and Zimmermann 2000, Iverson et al. 2008, McKenney et al. 2011, Périé et al. 2014) project that suitable bioclimatic conditions for most species will shift northward hundreds of kilometers by the end of the century. It is highly doubtful, however, that trees will establish at new sites fast enough to track changing climate conditions (Boisvert-Marsh et al. 2014, Nadeau et al. 2015). Most projections do not take into account constraints on dispersal and establishment which are likely to mediate actual shifts (Clark et al. 1998, Hampe and Jump 2011). Studies that do include dispersal and colonization suggest large discrepancies between where tree species can grow and where they could end up if migrating with assistance (Iverson et al. 2005, Morin and Thuiller 2009, Périé et al. 2014, Talluto et al. 2016, Aubin et al. 2018), with important implications on forest community composition (Davis and Shaw 2001).

Given that trees cannot simply pick up their roots and move themselves, understanding the patterns and processes involved in shifting geographic ranges is essential to detect whether trees are responding to warming and able to successfully move northward. Range expansion results from short and/or long-distance dispersal of individuals (or propagules), with these individuals finding favorable conditions for survival and reproduction at leading edges. The net sum of these individual movements will shift the frequency of species occurrence in space and ultimately range boundaries. For plants, range expansion implies successful colonization and establishment at sites previously unoccupied, and so changes in occurrence patterns in time and space can provide an early concrete signal of range shift. Therefore, examining the range or distribution changes that have already taken place is a crucial step in quantifying species' potential to track climate and can help improve both model predictions and ultimately our understanding of ecological processes in the face of rapid ecological shifts.

1.1 – Objectives and hypotheses

The overall objective of the proposed research is to understand patterns and processes of range shifts in relation to rapid environmental change focusing on forest tree species of Eastern North America to inform sustainable forest management practices. This objective was addressed with three studies, of which the specific objectives are briefly described below.

Study 1 – Unravelling potential northward migration pathways for tree species under climate change

Northern limits of species distributions are at the 'leading edge' of studies on biological response to climate change. However, characterizing species' range dynamics linked with warming and tracking distribution changes over large geographic areas remains a challenge. Evidence of broad-scale latitudinal changes in plant species distributions is still limited compared to altitudinal changes (Lenoir and Svenning 2015). My previous research provided rare direct evidence of latitudinal range shifts between 1970 and 2002 for five tree species over broad spatial scales in Quebec (Boisvert-Marsh et al. 2014). For trees, climate-induced range expansion ultimately implies successful colonization and establishment at previously unoccupied sites by the species. In this study, I reanalyse inventory data for eight tree species to assess whether northward trends detected previously are sustained in the contemporary period (2003-2015). I then focus on putative migration sites to investigate the biotic and abiotic context under which range shifts are taking place for tree species.

Specific objectives

1.1. – Quantify changes in range limits for eight tree species between 1970 and 2015 in Quebec, Canada and identify potential migration sites.

1.2. – Assess abiotic and biotic conditions at these migration sites and compare these conditions to those found at sites occupied by a species in the reference period (1970-1977).

Hypotheses

1.1.1 - The latitudinal distribution of saplings will shift northward with time.

1.1.2 – The northward shifts will be driven by increased recruitment in northern parts of the range.

1.2.1 – Recruitment will occur at previously unoccupied sites (i.e., migration sites) that are classified as unsuitable (edaphic and/or climatically) based on the reference period.

1.2.2 – Migration sites will be largely associated with disturbances (natural and/or anthropogenic).

1.2.2 - Northward migrating species will form novel or uncharacteristic associations at migration sites.

This chapter has been resubmitted to Journal of Biogeography for peer review following minor revisions: **Boisvert-Marsh, L.** and de Blois, S. Unravelling potential northward migration pathways for tree species under climate change.

Study 2 - Divergent responses to climate change and disturbance drive recruitment patterns underlying latitudinal shifts of tree species

While climate factors are assumed to drive recent observations of range shifts (Evans and Brown 2017), there is very little evidence of a direct relationship between patterns of range shifts and climate change at the site level. Even if trees are responding to warming conditions, climatic influences can be hard to discern from the effect of other environmental changes such as logging or natural disturbances. In most parts of the world, land-use and natural disturbances have modified species composition, creating opportunities for juvenile recruitment and community redistribution. If natural or anthropogenic disturbances are spatially structured (such as forestry activities in Quebec), their effect can be confounded with that of climate change. I investigated spatially explicit patterns of sapling recruitment in Quebec, Canada and related these patterns to observed range shifts. I carried these analyses out on four tree species that showed northward expansion in the first study and for which we had sufficient observations for statistical analysis. I then estimated the probability of observing a recruitment event in response to changes in climate, disturbance and their interaction in different parts of the study area using a multimodel selection approach.

Specific objectives

2.1. – Assess the relative influence of observed climate change vs. disturbance on patterns of tree sapling occupancy dynamics that drive range shifts.

2.2. – Determine whether the relative importance of climate and/or disturbance varies along a spatial gradient.

Hypotheses

2.1.1. – The probability of sapling recruitment will increase with warming, especially at high latitudes, but that relationship can change in space.

2.2.1. – Given the prevalence of disturbances in the study area, the disturbance signal will be more important than the climate one.

This chapter has been published: **Boisvert-Marsh, L.**, Périé, C. and de Blois, S. 2019. Divergent responses to climate change and disturbance drive recruitment patterns underlying latitudinal shifts of tree species. Journal of Ecology 107(4), 1956-1959.

Study 3 - Dispersal-based scenarios for Canadian trees show limited range tracking under climate change

At northern latitudes, species distribution models in Eastern Canada project that suitable climate for tree species will shift by hundreds of kilometers by the end of this century. Even in the northern parts of their range, not all areas remain suitable and some native tree species may be susceptible to warming-induced decline (D'Orangeville et al. 2016, Girardin et al. 2016, Périé and de Blois, 2016, D'Orangeville et al. 2018). Developing more realistic migration scenarios that take into account species traits will help assess how the projected rate of shift of suitable climate matches or not the migratory capacity of species (Corlett and Westcott 2013, Boisvert-Marsh et al. 2014, Périé et al. 2014, Sittaro et al. 2017, Aubin et al. 2018). Ten forest species native to eastern Canada were modelled based on empirical data that characterise life history, observed migration rates and dispersal ability. These models were applied across eastern Canada over 90 years at a resolution relevant to dispersal processes (25m resolution, ~14 billion raster cells). Climatic envelopes based on 3 time periods (2011-2040, 2041-2070, 2071-2100) were included to determine whether habitat remains suitable for species over the entire time period. In addition to considering species traits, this study also proposes a novel method to improve projections of future range shifts by incorporating observed tree migration rates from my previous research.

Specific objectives

3.1 – Develop a framework to assess realistic migration capacity of tree species in Eastern Canada.

3.2. – Quantify the difference between changes in range limits based on dispersal scenarios taking into account species' traits and changes in range limits determined by models of suitable climate.

Hypotheses

3.1.1 – Dispersal constraints limit the ability of species to fill the range projected to become suitable with climate change.

3.2.1 – Given the constraints on species' ability to disperse, the discrepancy between tree range limits and limits of suitable climate will accelerate over this century.

This chapter is currently in revision at Diversity and Distributions: **Boisvert-Marsh, L.**, Pedlar, J., de Blois, S., Le Squin, A., McKenney, D., Williams, C., Aubin, I. Dispersal-based scenarios for Canadian trees show limited range tracking under climate change.

Chapter 2 – LITERATURE REVIEW

2.1 - Climate trends, past and projected

Temperature increases have already been observed since the start of the 20th century (Hansen et al. 2006). Global average land and ocean temperatures have increased by 0.95°C since 1880, with 18 of the 19 warmest years on record since 2000, and the second hottest in 2019 (NOAA National Centers for Environmental Information 2020). Climate warming is particularly strong at northern latitudes (Xu et al. 2013) and is projected to amplify through this century. Looking at trends over the last 70 years, there has been a general increase in mean annual temperature across Canada, with the greatest warming observed in Northern Canada (Zhang et al. 2019). Warming patterns vary also across the seasons; winter temperatures have been increasing faster than summer temperatures, with over 4°C warming in some areas since the late 1940s. In the area encompassing Quebec forests currently managed for commercial purposes (south of ~53°N, the area covered by this thesis), mean annual temperature climbed by 0.48°C on average for the 37 years between 1965 (five years before forest inventories were initiated in Quebec) and 2002 (Boisvert-Marsh et al. 2014), accelerating to +1.14°C up to 2014 (year of the most recent forest inventory available, Boisvert-Marsh et al. 2019).

Climate change is expected to bring much warmer conditions in Canada by the end of this century. Across the Canadian Boreal Forest (see Baldwin et al. 2018 for vegetation classification), winter temperature changes are projected to increase by 7-9°C by the 2100 time horizon according to RCP 8.5[1], while the increases in the Eastern Temperate Forest are expected to be slightly less but still of large magnitude (+5-7°C) (Zhang et al. 2019). Projected temperature increases in the summer are more uniform across forest types, falling in the order of 5-7°C (Zhang et al. 2019). For areas of Quebec with commercially important forests, climate models project an increase of +3.2-7.7°C in the summer and +4.4-9.9°C in the winter by 2100, as compared to 1971-2000 (Ouranos 2015). Projections of precipitation patterns are more variable,

---

[1] Representative Concentration Pathways, or RCPs, are scenarios of climate change based on emission concentrations (i.e. volume of emissions) and land use changes. Each scenario (RCP2.6, 4.5, 6 and 8.5) are expressed as units of radiative forcing (in Watts per meter squared). RCP8.5 considers that population growth will remain high and income growth and improvements to emissions-controlling technology will be modest. Hence, this RCP assumes a high demand for energy and is therefore the highest emissions scenario (i.e. worst case scenario) (Riahi et al. 2011; van Vuuren et al. 2011).

both between seasons and across Canada. Summer is expected to bring drier conditions to southern Canada (Zhang et al. 2019). On the other hand, precipitation in the North is generally expected to increase, with the highest relative increases expected in the winter.

Shifts in temperature and precipitation induce changes to evapotranspiration, soil water balance and annual recharge. For example, areas of the Prairies that already receive lower precipitation should see that trend exacerbated, with annual deficits of precipitation relative to potential evapotranspiration growing by the end of the century (McKenney et al. 2011). In the North, winter warming increases the water holding capacity of the air (Zhang et al. 2019) and hence the potential for increased snowfall and snow depth. In southern Canada, the proportion of total annual precipitation that falls as snow should continue to decrease as warmer winters shift precipitation patterns towards rain. Less snowpack in areas that remain near freezing through the winter as well as colder areas which receive more snow put soils at risk of increased freeze-thaw cycles, which can impact soil processes and water balance later in the year (Henry 2008). In addition, less snowpack and/or earlier spring snowmelt can affect soil water availability later in the season (Adam et al. 2009, Buermann et al. 2013).

2.2 - Plant species' responses to climate and climate change

Responses to climate change vary depending on whether the focus is on individual plant, plant population, or geographical range. At the plant level, the response will depend on the physiological tolerance of that individual in relation to the environmental change (Reed et al. 2011). An individual plant may simply tolerate the new conditions with no evident physiological or ecological response; it may respond favorably through increased survival, including survival of offspring, growth and reproduction; it may show some plasticity, for instance by shifting the timing of reproductive events to increase fitness under shifting environmental conditions, or it may decline and eventually die if climate changes are outside its physiological tolerance or if the ecological changes and changes in biotic interactions are such that the plant is no longer competitive in that environment. Although there are set physiological limits for a species, physiological tolerance will vary within and among populations and in time and space. At the population level, selective pressure from climate can lead to a sorting out of individuals in favor of those with traits best adapted to the new conditions. If these traits are transmitted, there will be a shift in the frequency of traits (and genes coding for these traits) in the population leading to improve fitness under the new climate.

Plants are not like animals and cannot simply move to escape unfavorable conditions, although temporal escape is possible. Range contraction, expansion, or shift can result from all the responses previously mentioned and different processes may act in different parts of the range. Climate change has been linked to range shifts of tree species during the Holocene (Davis and Shaw 2001, Ordonez and Williams 2013), with site factors shown to influence local responses (Schwörer et al. 2017). While climate factors are also assumed to drive recent observations of range shifts (Evans and Brown 2017), there is limited evidence of a direct relationship between patterns of range shifts and climate change. Understanding potential biological, physiological or ecological species responses in relation to geographical location can help predict range shifts in a climate change context.

2.2.1 - What limits a species 'range'?

All species show range limits that can be defined in space (Kirkpatrick and Barton 1997) and populations at their range margins face different constraints than more interior populations. Range limits occur for several reasons (Chardon et al. 2015), but they generally reflect some sort of failure to colonize (refered to in the literature as *dispersal limitation,* but which should be distinguished from seed dispersal, even though it is a component) and inability to recruit due to physiological limitations (*fitness limitation*) (Sexton et al. 2009, Angert et al. 2018). Patterns such as habitat suitability and processes like biotic interactions, dispersal, and adaptability interact to determine limits (Hargreaves et al. 2014). The relative importance of each of these factors dictate whether and how a given species will respond to climate change (Aitken et al. 2008, Chardon et al. 2015, Louthan et al. 2015, Aubin et al. 2016).

Common thinking on patterns of species distribution is that ranges become more disjunct and often show lower abundance toward both extreme ends of the environmental gradient (Brown 1984, Louthan et al. 2015). Related to this, one of the early hypotheses about the causes of range limits was that they were roughly equivalent to climatic niche limits (Kirkpatrick and Barton 1997, Pulliam 2000, Gaston 2009, Sexton et al. 2009). Climate variables tend to be strongly correlated with species occurrences at regional or continental scale (Canham and Thomas 2010) and have been shown to limit species distributions at cold limits (Morin et al. 2007). Constraints placed by climate can limit biological processes that are important for fitness (Morin et al. 2007, Sheth and Angert 2018, Anderegg and HilleRisLambers 2019). Small differences between range limit and niche limit (i.e. extent of realized vs. fundamental climatic niche) suggest climatic limitation in range distributions. Recent work synthesizing results from empirical studies and niche models suggests that this pattern may hold (Lee-Yaw et al. 2016). As such, changes in temperature and precipitation should elicit species-specific responses in fitness and growth at marginal range limits. A recent review conducted by Aubin et al. (2016) outlined plant traits that may respond to such changes, as well as those that can confer migratory success. Similarly, Estrada et al. (2016) found that traits related to movement ability, ecological generalization and competitive ability positively influenced the ability of plants to shift their range.

The assumption that climatic niche limits approximate range limits lies at the heart of future projections of correlative models (Araújo and Peterson 2012). Also known as species distribution models, they associate occurrence with environmental characteristics to better understand the species-climate relationship underlying their observed geographic range (Guisan and Zimmermann 2000). Results from these models give valuable insight into the potential magnitude of shifts in suitable climate conditions for a range of species by the end of the 21st century (Guisan and Zimmermann 2000, Thuiller et al. 2005, Iverson et al. 2008, McKenney et al. 2011, de Blois et al. 2013, Beauregard 2016, Périé and de Blois 2016). What was quickly apparent from these outputs is that many plants and trees species will not track changing climate conditions. For example, in Eastern North America, it was found that the suitable bioclimatic habitat for trees could shift on average by 193km by the end of this century (Berteaux et al. 2014, Périé et al. 2014). Similarly, the suitable habitat for understory plant and shrubs would shift by 628km on average (Beauregard 2016).

In addition to questioning the ability to keep up with the velocity of climate change (Loarie et al. 2009), recent work has also challenged the notion that species are climatically constrained at their apparent harsh range limit. A review of transplant experiments found that the range limits of plants coincided with niche limits in 46% of cases; this was higher in studies reviewing elevational range limits vs. geographic limits (Hargreaves et al. 2014). This suggests that most species are constrained by factors other than climate at their range limits, such as the inability of species to disperse into suitable environments (e.g. habitat fragmentation, edaphic constraints). Oldfather et al. (2020) found that the geographic edge was only weakly correlated with climate limits for 665 tree species in the United States. Moreover, an overview of global studies that quantified tree species latitudinal shifts at the leading edge found that less than one quarter of species had undergone poleward shifts (Renwick and Rocca 2015). In the Estrada et al. (2016) meta-analysis, dispersal ability was positively associated with range characteristics (e.g. range size and proportion of range occupied) in about half the studies examined.

Non-climatic habitat factors and barriers to dispersal can also limit species before they attain their climatic limits. Migration lags (Bohner and Diez 2020), lack of mutualists (Warren and Bradford 2014), shifts in edaphic conditions (Lafleur et al. 2010, Brown and Vellend 2014), negative biotic interactions (Jones and Gilbert 2016) or simply running out of geographic space to expand (Marris 2007) can all define the limits of species even before their biophysical climatic limits are attained. Genetic isolation by distance, where gene flow between populations decreases with increasing distance (Sexton et al. 2014), arises from dispersal issues and can place species at greater risk of migration lags or even localized extirpations if temperature increase outpaces species' tolerance. The association between climate and distribution as well as the drivers of range limits are likely to depend on spatial scale and context (Chardon et al. 2020, Oldfather et al. 2020). This suggests that characteristics other than climate can drive species range dynamics, not to mention how species in movement can be biologically, physiologically and/or ecologically different depending on what area of the range is under examination.

2.2.2 - Characteristics of plant populations at their limits

Understanding whether biological constraints are spatially structured along environmental gradients can reveal whether species are responding to climatic warming (De Frenne et al. 2013, Reich et al. 2015). Biological thresholds of what limits survival, growth and reproduction influence which individuals persist and which ones become maladapted to current conditions. These divergent responses to environment and climate change between individuals and populations can lead to idiosyncratic changes in species geographic ranges. Temperature controls many biological responses, with warming expected to ameliorate many physiological processes up to a point. In a recent synthesis, Hargreaves et al. (2014) found that fitness declines for one or more key vital rate beyond the range limit in 75% of the cases reviewed. Responses to climate gradients can result in differential expression of life history traits and ultimately demographic rates related to survival, fitness and/or reproduction.

Climatic constraints on growth and development are an intuitive way to infer physiological limitations. Incomplete bud/tissue development, lack of tissue hardening, accumulation of non-structural carbohydrates signal that individuals do not quite have enough time to complete developmental milestones that would allow persistence through the winter (Hoch and Körner 2012, Vitasse et al. 2013, Lenz et al. 2014, Körner et al. 2016). In roots, growth is slowed as the northern limit is approached (Schenker et al. 2014, Zadworny et al. 2016), with rates eventually falling to zero coinciding with elevational range limits (Schenker et al. 2014). Yet, biomass and percentage allocated to absorptive fine roots was higher in cold sites than warm sites with more fungal hyphae in colder areas (Zadworny et al. 2016). Along elevational gradients, individuals approaching their cold limits are often shorter than their warmer counterparts (Körner et al. 2016). In support of this, Lenz et al. (2014) found that tree ring growth gradually decreased only near the range limit. Similarly, correlations between mean annual temperature and basal area increment were significant only in the upper elevational reaches of studied tree species (Lenz et al. 2014), suggesting that climate alone becomes limiting for annual growth in non-linear, threshold manner. On the other hand, climate itself is not linear; extreme climate events are becoming more frequent and can shift plant responses at a variety of scales, ranging from individual physiological-based responses (Aubin et al. 2016) to population and range-wide scales (Reyer et al. 2013). When these extremes occur toward the physiological or range limits, they can induce positive shifts (Renwick and Rocca 2015), like increased growth and sporadic seed production (Tremblay et al. 2002, Asselin and Payette 2006, Caccianiga and Payette 2006), or induce negative shifts (increased mortality; van Mantgem et al. 2009, Bussotti et al. 2015).

Differences in phenology and reproductive capacity within a species' range also suggests climatic limitation because producing viable seeds can be biologically costly. At the northern ends of distribution, cold and shorter growing seasons have been found to define plant range extent because of their effects on flowering and fruit production (Morin and Payette 1984, Purves 2009, Sheth and Angert 2018, Hargreaves and Eckert 2019). For example, 300 km north of its range, annual cocklebur survived and grew as well as it did within its range but failed to produce fertile seeds (Griffith and Watson 2005, Griffith and Watson 2006). A study of *Phragmites australis* along a 1200km long transect found that individuals required lower heat sums at their northern limits in the Lac St-Jean area to produce flowers and set seed than more central populations, but did not produce fertile seed (Lovat 2013). Limit of reproduction by seed in *Fallopia japonica* is near Quebec City, despite actual range limits being closer to Rimouski and Rivière du Loup (Groeneveld et al. 2014). Instead, when limited by climate at northern limits, plants can produce fewer or smaller seeds (De Frenne et al. 2013, Carón et al. 2014) or favour reproduction by vegetative means (Caccianiga and Payette 2006, Landhäusser et al. 2010).

At first glance, populations at the rear edge may appear somewhat stable (Hampe and Petit 2005) but can also be limited by climatic factors (Cahill et al. 2014). A commonly invoked reason for tree persistence long after conditions have changed is their longevity; they are adapted to lags in response to climate allowing them to withstand extreme impacts temporarily until conditions moderate (Slaton 2015, Villellas et al. 2015, Sheth and Angert 2018). Inertia to change can arise because deep roots allow species persistence in conditions that are no longer tolerable for their seedlings (Davis et al. 1986). Like at the northern edge, reproductive limitation and recruitment failure can also occur at the warm edge (Matías and Jump 2015, Sheth and Angert 2018, Anderegg and HilleRisLambers 2019). However, demographic compensation can explain apparent population resilience; it is where one vital rate increases as another decreases (Villellas et al. 2015, Sheth and Angert 2018). For example, decreasing reproductive output could be compensated by higher propagule survival rate, counteracting or at least delaying overall changes in the population growth rate. This persistence can delay precipitous changes but also prevent better suited species from becoming established (Urban et al. 2012, Renwick et al. 2016). These mechanisms can only delay the inevitable so long; in absence of other adaptations, population declines are expected as conditions shift outside species physiological range of viability. Extreme events such as disease, invasive species, bad mutations, severe weather events, natural disturbance or habitat loss can rapidly increase mortality rates (Hanski 1998, Holt 2003, van Mantgem et al. 2009, Young et al. 2019).

2.2.3 - Move, adapt or die

As shown in the previous section, marginal conditions affect plants differently depending on what end of the climate gradient is under examination (Angert et al. 2018) and whether or not climate gradients are related to geographic gradients (Oldfather et al. 2020). Both ends of the gradient have potential to show rapid responses to climate (van Mantgem et al. 2009, Renwick and Rocca 2015) or inertia to change (Hampe and Petit 2005, Villellas et al. 2015). How species respond and what rate will determine whether or not range limits shift in space.

2.2.3.1 - Evidence for Adaptation to Climate and Climate Change

Constraints on reproductive output and growth in marginal conditions and stochasticity can select for offspring that may not be the best suited for prevailing conditions (Hargreaves and Eckert 2019). Strong selective pressures and local adaptation can lead to populations with narrow environmental tolerances, thus limiting their ability to adapt (Peterson et al. 2019). However, the impact of such maladaptation may not be completely negative (Brady et al. 2019). Species rarely perform best where they are most climatically suited (Oldfather et al. 2020; for e.g., see Anderson and Wadgymar 2020), for a variety of reasons that have been mentioned. Adaptive responses to climate are species-specific, location-specific and depend on the genetic make-up of species (Sexton et al. 2014, Etterson et al. 2016). Usually, adaptation in trees lags behind rapid, sustain environmental change (Davis and Shaw 2001, Aitken et al. 2008, Sheth and Angert 2018), probably because changes in vital rates to environmental gradients can result in contradictory responses (Villellas et al. 2015). These changes will act on individuals at a variety of time scales, which may or may not scale across populations or ranges (Royer-Tardif et al. In review).

In the short term, changes in phenotype in response to shifting climate will be a first indication of adaptive capacity (Parmesan 2006, Nicotra et al. 2010, Bussotti et al. 2015). One particular phenotypic response of note to range shifts is changes in phenology. Changes to the timing of phenophases in response to environmental cues can provide insight because of their link to phenotypic plasticity and reproduction (Reed et al. 2011, Aubin et al. 2016). In climates with strong seasonality, temperature thresholds trigger many processes such as flowering, bud burst and senescence (Rathcke and Lacey 1985). Warming has rapidly advanced vernal biological events and delayed autumnal ones (Bertin 2008), but the amplitude of change in the timing of spring events is greater than the delay of fall events (Parmesan and Yohe 2003, Bertin 2008, Cook et al. 2012, Panchen et al. 2015, Zohner et al. 2020). Timing shifts are often associated with early spring conditions such as timing of snowmelt and average temperature. These trends are also accentuated with increasing latitude since warming is stronger at high latitudes. In general, species that shifted phenological events earlier in response to warming in recent decades have performed better compared to those that did not exhibit plasticity in their phenological timing (Cleland et al. 2012). Extensions to the growing season that push forward leaf out or delay senescence can initiate primary productivity earlier (Kwit et al. 2010) and extend it later in the season (Gallinat et al. 2015). Senescence, however, generally responds to light-related cues rather than temperature ones (Gill et al. 2015). Like budburst, fruit ripening also seems to have advanced (Gallinat et al. 2015). For some species, earlier fruit maturation and germination could take advantage of fall warming and longer growing seasons (Morin et al. 2007).

The extent of plasticity in trait expression and breadth of genetic diversity will likely dictate a species' capacity to tolerate climatic shifts in the short term (Royer-Tardif et al. In review). However, rapid warming puts populations with strong, localized adaptation at risk of mismatch with observed conditions because of their long life span and their ability to remain on the landscape even when climate is outside their physiological tolerance (Hampe and Jump 2011, Boisvert-Marsh et al. 2014, Aubin et al. 2018, Peterson et al. 2019). Maladaptation is of particular concern for species with a very narrow climatic tolerances or with few populations to favour genetic recombination and adaptive capacity (Aitken et al. 2008, Alberto et al. 2013). Hence, plasticity may not be sufficient for some populations to adjust to rapidly changing environmental conditions (Bussotti et al. 2015).

There is evidence for rapid evolutionary shifts in traits of populations near the edge of their climatic tolerances (Gallien et al. 2016). Colonization of new areas may elicit an adaptive response to changing climate, promoting further colonization (Olivieri et al. 1990). In the Swedish Archipelago, islands with younger populations showed more genetic variability than islands with intermediate aged ones as well as originating from multiple seed sources (Giles and Goudet 1997). The reasons are two-fold; increasing numbers of individuals and enhanced gene flow to peripheral populations increase the chance that adaptation is boosted in novel or underexploited areas (Davis and Shaw 2001, Case et al. 2005, Iverson et al. 2005). Release from climatic stress may lead in this case to range expansion. The degree of gene flow between central and marginal populations seems to be key. Several recent studies suggest that adequate gene flow, leading to less differentiation between populations, can translate into higher ability to respond positively to climate warming (Cavanaugh et al. 2014, Cavanaugh et al. 2015, Kennedy et al. 2017). Sufficient gene flow toward the range edge may promote selection towards characters that favour persistence and even expansion in novel conditions (Kennedy et al. 2017). High mortality in early life stages at the range limit can act as a range shaping mechanism, selecting for adapted alleles that can tolerate novel climates (Bussotti et al. 2015). In situations where the range edge coincides with a fitness limitation, populations may have already adapted to climate variability such that alleviated climate stress may allow them to perform better (Cavanaugh et al. 2014, Castorani et al. 2017, Peterson et al. 2019).

2.2.3.2 - Range Contraction, Expansion or Shift

Regardless of whether biophysical processes or stochastic effects characterise limits, tree ranges change continuously through time as a function of dispersal, colonization, establishment and extinction rates in a given area (Corlett and Westcott 2013). Lags in response put species in a constant push-pull dynamic to keep up with rapid climate warming (Davis and Shaw 2001). Three common, population-level reactions have been observed in response to change, either at the trailing edge, leading edge or both (Holt 2003): 1) Contraction, where metapopulation extinctions cause an edge to recede; 2) Expansion, where newly colonized populations result in an advance in the edge; or 3) Shifts, where one edge expands where another one contracts, resulting from a combination of the previous two reactions and causing no significant change in total distribution area. The processes that influence the patterns described below can also influence within-distribution changes which modulate range shape and changes in extent even when there is no net shift at the edge (Breshears et al. 2008, Maggini et al. 2011, Lenoir and Svenning 2015). Hence, shift is used here to refer to any change in species distribution that may ultimately affect range limits.

Extinction, in a metapopulation framework, implies localized disappearance of subpopulation patches rather than the wholesale extirpation of an entire species (Hanski 1998).

Seen this way, extinction acts as a range shaping mechanism continuously responding to different kinds of deterministic (e.g. habitat loss) and stochastic (e.g. environmental) effects (Brown et al. 1996, Hanski 1998). Climate impacts that affect background rates of mortality increase extinction risk as population levels decrease toward a minimum viable population threshold (Thomas 1994). Population growth rates characterise this risk, where low reproductive output, survival or recruitment can decrease the growth rate. Beyond these thresholds, range contraction occurs when extinction rates exceed colonization rates. Range collapse occurs when extinction rates far exceed colonization in a given time period such that the distribution area retracts rapidly (Holt 2003, Lenoir and Svenning 2015). Even if population growth rates fall, microclimatic refugia and landscape heterogeneity seen in reconstructed distributions from the Quaternary allowed species to persist in disjunct but highly adapted populations that can eventually recolonize the landscape (Hampe and Petit 2005).

Range expansion is another notable response to changing climatic conditions (Davis and Shaw 2001, McLachlan et al. 2005). Range expansion results from concerted small scale processes acting together to produce a detectable, broad scale extension to a boundary. In other words, for a range to expand, population growth in an area must show a notable increase, based on increases in one of the key vital rates (reproduction, survival, and recruitment), and dispersal to a new location. The likelihood that range expansion will occur is likely to be mediated by whether a species is limited at their edge by climatic constraints (Chardon et al. 2015) and the population growth rate mediated by density dependence (Clark et al. 2001), dispersal ability (Aubin et al. 2016), barriers (Caplat et al. 2016) and life history (Corlett and Westcott 2013). On the latter point, detecting range expansion is likely to depend on temporal context (Renwick and Rocca 2015). Hence, trees show a considerable lag between initial colonization, sexual maturity and full reproductive output (Travis et al. 2011), making range expansion a relatively slow process (Corlett and Westcott 2013).

The factors that influence dispersal vary between deterministic and stochastic processes. Given this, it is not surprising that propagule dispersal ability alone has been a poor explanation for observed migration (Angert et al. 2011). Additional parameters are required for each step of the range shift process to fully evaluate a tree species' ability to shift (for example, see Corlett and Westcott 2013, Aubin et al. 2018). Recruitment occurs when propagules are produced and disseminated and subsequently germinate and survive, producing new individuals (Eriksson and Ehrlén 2008). This recruitment can take place where a species already is present, thereby adding to its population. Additionally, effective dispersal can lead to recruitment where a given species was not observed previously, leading to a new colonization event and possibly population establishment. Here, the distinction is that colonization refers to germination success of an individual in a previously unoccupied area, but this may not be sufficient for a population to reach the minimum number of individuals required to be viable (low density stochastic population growth, Louthan et al. 2015). Establishment, on the other hand, is successful when a population exceeds the minimum viability threshold and a population becomes self-sustaining (Harper 1977). Seed production influences both the likelihood that a successful germinant will be produced and disperse an appreciable distance away from its source (i.e. long distance dispersal). Where climate is limiting, low frequency of seed production and high interannual variation in seed production may limit the formation of new populations except in years that are amenable (Brown and Wu 2005, Renwick and Rocca 2015). Areas with low density stochastic population growth rates could likely respond favorably to alleviated climate constraints by increases in seed production, survival and/or recruitment (see discussion above).

Propagule dispersal itself is a stochastic process but certain characteristics will mediate dispersal distance and spatial arrangement of the edge (Chuang and Peterson 2016). Species with mechanisms to disperse long distances, such as those with wind dispersed seeds (e.g., *Acer spp.*) or with specialized structures to float along wind currents (e.g., *Populus spp.*), could be more successful at expanding their ranges. Because dispersal across long distances is more consistently effective for species with these structures, propagule pressure is higher across a broader range of distances, thereby increasing the chances a propagule will successfully land in a suitable spot for germination. In this case, these species would be expected to exhibit a more continuous advancing front (Fig 2, Chuang and Peterson 2016). On the other hand, species with less effective means to disperse via abiotic vectors (seed appendages that are ineffective for wind dispersal or gravity dispersed propagules) will commonly demonstrate low movement distances. They could also be moved by animal agents, but while the latter can be highly effective distance-wise, the probability of successful long distance dispersal from animal vectors is likely quite low and unpredictable, resulting in lower propagule pressure. Consequently, expanding fronts would be rather diffuse and most subsequent range movement would come from filling around these population nodes (Fig 2, Chuang and Peterson 2016). Regardless of whether edges advance cohesively or diffusely, multiple generations are required before an appreciable change is detectable. The "age" of the advancing front here is key (sensu Chuang and Peterson 2016). Life history characteristics such as age to sexual maturity and age of maximum seed production will determine when the next generation of colonizers will start. Here, selection can act to favour shorter generation times, higher reproductive output and stronger dispersal, but may require multiple generations before becoming effective.

As discussed, climate is usually a limiting factor on fitness and population growth rates at broad scales (D'Arrigo et al. 2004, Caccianiga and Payette 2006, Miller et al. 2017). As such, climate is useful to explain distributions. However, species are typically not the most abundant at the center of their distribution nor where they are the most climatically suited (Sagarin and Gaines 2002, Murphy et al. 2006, Beauregard and de Blois 2016, Oldfather et al. 2020). Moreover, the likelihood that range expansion will occur is likely to be mediated by whether a species is limited at their edge by other non-climatic factors that influence colonization and establishment (Sagarin and Gaines 2002, Chardon et al. 2015, Jones and Gilbert 2016). In other words, it is not sufficient for a seed to arrive at a new location; it must land at a site suitable for germination and growth. Given the interplay between random, directional and interspecific processes even within an area, it is unlikely that a single factor will explain range movements (or lack thereof). At fine scales, range shift processes are mediated by biotic controls (Louthan et al. 2015) such as species' dispersal ability (Chuang and Peterson 2016), interspecific competition (Ettinger and HilleRisLambers 2013), predators (Brown and Vellend 2014) and lack of conspecifics (Warren and Bradford 2014). The extent of range filling (proportion of suitable niche occupied by a given species; Svenning and Skov 2004) could suggest *dispersal limitation* (see Sheth and Angert 2018 for example) and offer some insight as to which factors merit consideration.

The balance between adaptation, dispersal, persistence and extirpation (local extinction) amongst populations ultimately determines species' changes in their geographic range. For climate-based migration and range expansion to occur, individuals will first respond to shifting temperature and/or precipitation patterns. At this level, plasticity in response to favorable conditions, such as earlier flowering in the spring or later senescence or fruit ripening in the fall, or increased vital rates linked to growth and fitness, such as higher reproductive output or increased survival at the juvenile stage, signals whether tree species can respond to changing conditions. Understanding how these processes interact at the northern edge and how they are linked to climate can provide crucial insight into how species have already responded and whether they can adapt to continued climate variability.

2.3 – Disturbance and its influence on range dynamics

Undisturbed forests can resist compositional change for a time (e.g., Leak 1996) even when climate suitability has shifted favourably or unfavourably (Davis and Shaw 2001, Hampe and Jump 2011). However, it is expected that climate change will modify the frequency and/or intensity of natural events (Dale et al. 2001) and can also amplify the impacts of human-induced disturbance (Perring et al. 2018). In most parts of the world, land use changes and natural disturbances have modified forest habitats considerably (Dale et al. 2001, Gauthier et al. 2015). Both of these types of disturbances affect recruitment and trigger successional changes, breaking the inertia that inhibits new, possibly better-suited, species from moving in (Urban et al. 2012, Renwick et al. 2016). Disturbances, therefore, have the potential to modify species composition appreciably in combination with climate change, creating opportunities for the redistribution of species (Leithead et al. 2010, Lembrechts et al. 2016).

Post-disturbance successional trajectories are not always well understood, and this is especially true in relation to climate change. Disturbances could act synergistically with climate warming, opening the canopy, reducing competition locally and facilitating species turnover at suitable sites (Thom et al. 2017). Conversely, disturbances could have the opposite effect in areas where warming thresholds for recruitment are reached, precipitating long-term compositional changes and exacerbating the negative impacts of climate change (Young et al. 2019). It is possible that changes in intensity and recurrence of natural disturbance like fire and drought may limit species' ability to migrate and persist in the temperate and boreal forest (Boulanger et al. 2018, Boisvert-Marsh et al. 2020).

Management legacies from forest harvesting have left lasting imprints in forests around the world (Cyr et al. 2009, Venier et al. 2014, Nowacki and Abrams 2015, Perring et al. 2018, Danneyrolles et al. 2019). For example, harvesting activities can favour the formation of a recalcitrant layer, a suite of species favoured by forest practices that inhibits the colonization of other species (Aubin et al. 2014). In fire-dependant ecosystems like the boreal forest, harvesting that does not emulate the effects of fire, i.e., by not removing the organic layer, can create site conditions that favour accumulation of competing species such as *Sphagnum spp*. and ericaceous shrubs (Fenton et al. 2005). Such conditions can delay the return of forests to their pre-disturbance conditions. However, harvesting activities that follow best practices and emulate natural disturbance can facilitate compositional shifts of target species (Leithead et al. 2010, Santala et al. 2019). Land-use and landscape fragmentation also influence the ability of plant species to reach suitable sites. For some species, land use change can facilitate unintentional introductions of species that migrate well via human vectors (de Blois et al. 2013). For other species, land use and fragmentation can act as a barrier to dispersal when unsuitable habitats effectively block plants and trees from expanding their range limits (Liang et al. 2018, Miller and McGill 2018).

2.4 – Some observed evidence to date

Forest ecosystems all over the world are experiencing compositional changes. Disentangling the relative influence of various biotic and abiotic factors will be key to understanding what role climate plays in recruitment and compositional shifts. During the current warming period, doubling mortality rates have been positively correlated with increasing temperature and water deficit in old growth forests in the southwestern United States (van Mantgem et al. 2009). Not all of these changes, however, can be directly linked to climate change and some of the effects may be directly influenced or exacerbated by other factors. Closer to home, Quebec forests are definitely undergoing rejuvenation (Crête and Marzell 2006, Duchesne and Ouimet 2008), largely precipitated by harvesting through the 20th century. While silvicultural practices and policy have evolved through time (Nagel et al. 2017, Messier et al. 2019), the effects of harvesting in the past are still felt today (Crête and Marzell 2006, Duchesne and Ouimet 2008, Cyr et al. 2009, Boisvert-Marsh et al. 2014, Brice et al. 2019, Danneyrolles et al. 2019), with consequences for species composition at temperate and boreal forests and the transitions between these zones.

2.4.1 – Temperate forest

The temperate deciduous forest in eastern Canada is characterised by *Acer saccharum* as the main canopy component (Baldwin et al. 2019b). Within this area, subtypes are distinguished by the relative importance of secondary species components: from south to north, *Carya cordiformis, Tilia americana* and *Betula alleghaniensis*; additionally, *Pinus strobus, Fagus grandifolia, Fraxinus americana, Quercus rubra, Ostrya virginiana* loosely structured in importance from west to east (Saucier et al. 2003, Ontario Government 2007, Baldwin et al. 2019b). While human settlements have existed in this area long before European colonization, species composition of northern temperate forests in the last few centuries has been heavily influenced by European settlers (Nowacki and Abrams 2015). In southern portions of Quebec and Ontario, logging and conversion for agriculture as well as urban sprawl have isolated forests, fragmenting them into patches (Elliott 1998, Brisson and Bouchard 2003, Butt et al. 2005, Domon and Bouchard 2007, Cheng and Lee 2008, Jobin et al. 2010, Jobin et al. 2014). Large intact areas of forest exist at the northern edge of the temperate zone (i.e. *Acer saccharum-Betula alleghaniensis* according to the ecological classification in Quebec), while in the south, large areas are typically limited to protected areas.

In addition to land conversion and logging, recruitment failure and decline of *Acer saccharum* have been recorded across the Canada's eastern temperate forests and into the United States in recent years (Duchesne and Ouimet 2008, Boisvert-Marsh et al. 2014, Bishop et al. 2015, Bose et al. 2017, Fei et al. 2017). Gap dynamics are an important part of forest dynamics and ecological succession in *Acer saccharum* dominated stands (Canham 1988). Regeneration failure of *Acer saccharum* has been observed in areas where there is considerable *Fagus grandifolia* recruitment (Beaudet et al. 1999, Gravel et al. 2011). Extensive, dense thickets of *Fagus grandifolia* saplings can form in the understory in response to damage from disturbance or pathogens (i.e. Beech bark disease Cale et al. 2013, Giencke et al. 2014). Although, *Fagus grandifolia* and *Acer saccharum* are both shade tolerant species, *Acer* is somewhat less so (Burns and Honkala 1990) and these thickets decrease light levels below what is required for *Acer*.

Additionally, the 1998 ice storm in northeastern United States, eastern Ontario and southern Quebec caused considerable damage to forests, with the most damage occurring in southern Quebec (Hopkin et al. 2003). Extensive damage to tree crowns resulted in impacts on mature stems (e.g., growth; Pisaric et al. 2008) and induced changes in light availability (Beaudet et al. 2007). In some cases, *Acer saccharum* regeneration failure was noted where canopy openings from ice damage were smaller and hence light conditions changed relatively less, favouring instead *Fagus grandifolia* (Beaudet et al. 2007, Nolet et al. 2008).

Atmospheric deposition of nitrogen and sulfur through the 1990s resulted in soil acidification that leached out nutrients like calcium. *Acer saccharum* is a relatively nutrient demanding species (Beaudet et al. 1999, St.Clair et al. 2008), and this loss of calcium reduced *Acer* growth throughout southern Quebec, particularly on non-calcareous soils (Duchesne et al. 2002). These drivers of composition change, among others, and their relative influence on *Acer saccharum* are a matter of debate (Moore and Ouimet 2006, Nolet et al. 2015), but could ultimately confound or interact with the effects of climate change (St.Clair et al. 2008).

2.4.2 – Boreal-temperate ecotone

The ecotone by nature is an area subject to considerable spatial variation in habitat and, consequently, species composition (Messaoud et al. 2007, Beckage et al. 2008, Leithead et al. 2012, Fisichelli et al. 2014, Solarik et al. 2018). The transition between the temperate and boreal forests is no exception (Evans and Brown 2017). In eastern Canada, the temperate zone transitions from being mainly deciduous (described above) to mixed deciduous- (mainly *Acer rubrum*, *Betula papyrifera*, *B. alleghaniensis*, *A. saccharum*) conifer forests (*Abies balsamea* with some *Picea glauca*) (Baldwin et al. 2019a) to predominantly conifer forests (mostly *A. balsamea*, *Picea mariana*) with a deciduous component of *Populus tremuloides* and *Betula papyrifera* (Baldwin et al. 2016). Conifers become increasingly prevalent and dominant as temperate species become increasingly limited by boreal conditions; boreal soils are colder with lower nutrient cycling so they tend to accumulate litter, have lower pH and nutrient status and can be waterlogged (Lafleur et al. 2010, Beauregard and de Blois 2014). Recent evidence shows that changes in occupancy and abundance patterns are occurring at the ecotone (Crête and Marzell 2006, Messaoud et al. 2007, Duchesne and Ouimet 2008, Leithead et al. 2012, Boisvert-Marsh et al. 2014, Fisichelli et al. 2014, Boisvert-Marsh et al. 2019, Brice et al. 2019). Species ranges are constantly shifting, such that ecotones are zones of continuous tension (Gaston 2009, Sexton et al. 2009).

Species whose range limits fall within this area of tension would be expected to show range contraction and expansion based on fitness, growth, and survival, particularly if they are influenced by limiting climate. Our 2014 study of range limit shifts found that three species whose northern limit falls within the ecotone – *Acer rubrum*, *Acer saccharum*, and *Betula alleghaniensis* - show patterns consistent with northward migration (Boisvert-Marsh et al. 2014). Various field studies show these species can migrate into sites near their northern limit where typical boreal species are present (Barras and Kellman 1998, Tremblay et al. 2002, Kellman 2004, Leithead et al. 2012, Fisichelli et al. 2014), but factors limiting their colonization are not well understood at broad scales. Soils and climate are important influences on the current distributions of these species and could limit further expansion for certain ones (Lafleur et al. 2010, Collin et al. 2017, Solarik et al. 2018). It is unclear though whether northward migrating temperate species are co-occurring with more northerly distributed species, such as *Abies balsamea* or *Picea mariana*, or are pushing them out. Crête and Marzell (2006) found that the proportion of old stand age classes (>100 years) had decreased in the *Abies balsamea* - *Betula alleghaniensis* forest domain (as defined by Quebec's ecological classification, Saucier et al. 2003) over the last few decades. A likely cause of this change is the increasing occurrence of moderate to major disturbances in this area, which is accelerating species turnover particularly in the southern boreal forest where *Abies balsamea* is frequent (Brice et al. 2019). The relative importance of factors such as climate, disturbance and soil constraints will be important to understand at broad scales as the climate continues to warm and provides newly suitable climatic habitat.

2.4.3 – Boreal forest

The boreal forest in eastern Canada is dominated by *Abies balsamea* and *Picea mariana* with *Picea glauca* and *Pinus banksiana* as secondary components depending on whether fire has occurred recently or not (Baldwin et al. 2016). In Quebec, *Picea mariana* becomes increasingly dominant from south to north within the continuous boreal forest and persists as the main tree species right up to the transition where forest cover becomes discontinuous (Saucier et al. 2003). The deciduous species, *Betula papyrifera* and *Populus tremuloides*, are also important secondary species, mainly where disturbance has occurred (Baldwin et al. 2016). Natural disturbance from fire, insects and windthrow is an important component of forest dynamics here (Gauthier et al.

2015). Disturbance dynamics vary from west to east and tend to correspond with precipitation gradients which influence the fire return interval. In the west, fire is more common and intense fires can initiate stand replacement (Gauthier et al. 2015, Baldwin et al. 2016). As climate becomes increasingly maritime eastward, fires become less frequent and intense; there, insect outbreaks play a greater role in the disturbance regime (Baldwin et al. 2016).

Many researchers have postulated that the rates of change in climate warming, precipitation patterns, and soil processes may modulate species ability to migrate into the boreal landscape, at least in the short term (Lafleur et al. 2010, Evans and Brown 2017). Climate can alleviate biological and physiological constraints on species in the boreal forest which influence seed production, seedling establishment and growth. As warming continues, species and populations limited by cold temperatures could respond favorably to warming. When conditions permit, increases in seed production of *Pinus banksiana* (Houle and Filion 1993) and germination success in *Picea mariana* (Gamache and Payette 2005) have been shown in areas in Quebec where climate has recently warmed to a point that alleviates biological constraints. A study near the treeline in northern Quebec found a recent shift in dominant reproductive mode of *Picea mariana* from clonal reproduction via layering to reproduction by seed (Caccianiga and Payette 2006). Over the past ~60 years in boreal forests of Canada, tree growth rates have demonstrated strong region- and species-specific trends, linking lower growth to increasing temperature and higher growth to increasing precipitation, but no spatially consistent response to climate change at the national scale (D'Orangeville et al. 2016, Girardin et al. 2016).

For wholesale replacement of boreal to temperate species to occur, modification of biogeochemical cycles would need to take place. Compositional shifts are unlikely to happen rapidly within the heart of the *Picea mariana*-dominated part of the boreal forest. In the absence of human-mediated disturbance in this area, most of the changes in composition for now are likely to be driven by species that are already present locally. The southern boreal forest, on the other hand, faces different pressures, both from climate and disturbances. For *Picea mariana*, any benefit of warming on growth may be temporary as climate projections show that the species' current bioclimatic tolerances will be exceeded by the end of the century (D'Orangeville et al. 2016, Périé and de Blois 2016, Boulanger et al. 2017). Conversely, a study in northwestern Quebec that examined key biophysical determinants of the latitudinal transition between the

Abies balsamea to *Picea mariana* forest found that seed production for *Picea glauca* and *Abies balsamea* was lower in the latter forest (Messaoud et al. 2007). This study also found that years of good seed production of *Picea glauca* and *Abies balsamea* coincided with the number of degree days in a growing season and the maximum temperature of the warmest month in the preceding year.

Forestry activities in Quebec have generally progressed from south to north over time (Boisvert-Marsh et al. 2014, 2019, Brice et al. 2019) and are expected to continue northward in the coming years (Jobidon et al. 2015, Boudreault 2016). If natural or anthropogenic disturbances are spatially structured, their broad scale effects can be confounded with that of climate change (Lenoir et al. 2017, Liang et al. 2018). Another study in Quebec observed an increase in the number of deciduous saplings in the *Abies balsamea* - *Betula papyrifera* and *Picea mariana* - feathermoss domains in Quebec between 1970 and 2000 (Crête and Marzell 2006). While this finding reflects common post-disturbance dynamics in the boreal forest, successional pathways could be influenced by greater deciduous presence. Litter from deciduous broadleaved species decompose more quickly than litter comprised of conifer needles and a greater component should promote the availability of macronutrients that can be limited in boreal soils (Bauhus et al. 1998, Laganière et al. 2010, Nagati et al. 2018). Improved nutrient conditions and higher pH through improved decomposition and nutrient cycling should benefit *Abies balsamea* (Lafleur et al. 2010). As the climate continues to warm, any growth benefits of *Picea mariana* could be negated and juvenile stages could be outcompeted by other species, particularly at the ecotone.

2.5 - Detecting distribution shifts

Poleward migration of tree species is one possible response as suitable climate conditions shift northward. To assess distributional changes and better understand how they link to demographic processes, studies have employed two general techniques: comparison of composition over time (direct or indirect) and correlative modelling.

2.5.1 – Direct comparisons of changes in composition over time

Despite emerging research into distribution changes, studies of historical or ongoing range limit shifts are still relatively rare for plant species (Lenoir and Svenning 2015). Sessile organisms like plants require multiple generations of dispersal and successful establishment at sites previously unoccupied by a given species before sustained range shifts can be detected. Hence, recent occupancy changes should provide the most direct evidence of range dynamics (Lenoir and Svenning 2015), if the shift is in the direction predicted by bioclimatic models (Beckage et al. 2008, Lenoir et al. 2008, Chen et al. 2011) and if the rate of shift is sufficient to keep up with rapid climate changes (Corlett and Westcott 2013, Aubin et al. 2018).

Consistent growth and fitness responses can elicit a population level response, such that spatial patterns within a region may be detectable. An example of one such spatial pattern is compositional change in a plot, which can be assessed by a number of field inventory methods such as species' presence/absence or abundance (e.g., percent cover, relative abundance, or count). Transects and quadrats are standard field designs for many contemporary studies of range dynamics. As such, they may or may not directly quantify shifts, depending on the extent and purpose of the study. Many studies have compared current observed species' distributions with published historical trends. In California, Kelly and Goulden (2008) resampled a transect at specific intervals along a wide elevational gradient that was established 30 years earlier. They calculated a mean elevation weighted by cover which accounted for relative species abundance, for each time period sampled (1977 and 2007). A study in alpine systems (Pauli et al. 2007) looked at species composition and habitat preferences at the transition between the alpine - tundra ecotone with particular interest of new arrivals to the area. One drawback of these studies is that it is difficult to reproduce studies exactly as previously designed when methods are somewhat unclear (Woodall et al. 2008).

One approach to detect range shifts is the percentile method, which links changes in species presence to latitude (Lenoir et al. 2009). This method can provide evidence of range shifts when combined with broad spatial assessments of plot occupancy (gain, loss vs. unchanged). In addition to consistent surveys through time, analyzing such latitudinal shifts across broad geographic areas requires precise recording of survey locations (Tingley and Beissinger 2009) and extensive data coverage (Shoo et al. 2006). A rare example of this method used both latitudinal shifts and occupancy patterns for 11 tree species in Quebec over 30 years (Boisvert-Marsh et al. 2014) to assess recent migration at northern limits. It showed patterns consistent with northward migration for five temperate species, while another three showed some evidence of northward shift. These analyses were based on a dataset provided by the *Quebec Ministère des Forêts, Faune et des Parcs* (MFFP), which established an extensive network of inventory plots south of 53°N in Quebec for the purposes of characterizing forest resources for commercial purposes in the province. Four inventories have been completed (1970-1981, 1977-1992, 1992-2002, 2003-2015) across more than 6200 permanent plots spread out over 761,000km2. The fifth inventory is underway and expected to be completed by 2025. Long-term broad scale monitoring programs such as the ones conducted by the MFFP are uncommon and resource intensive to implement, but also invaluable in studies of range dynamics.

2.5.2 – Indirect comparisons

When direct resampling is not possible, ecological models, notably generalized linear/additive models, have been employed to interpret how species respond to specific gradients and how those gradients have shifted through time. In ecological modelling, statistical models are most commonly used to associate presence or abundance with a specific response variable, such as latitude or altitude. Lenoir et al. (2008) and Lenoir et al. (2009) used a modelling approach to interpret both spatial and temporal changes in elevation. They obtained species data from surveyed plots along an elevational gradient in mountainous regions of western France. In their 2008 study, they evaluated the difference in a species' optimum elevation between two time periods (1905-1985 and 1986-2005). They did this by evaluating species response curves and outputs of logistic regression (type of generalized linear model for presence/absence response variables; Guisan et al. 2002) to assess their response to elevation. Lenoir et al. (2009) used contemporary data (1986-2006) to evaluate the altitudinal difference in optima between seedlings and trees of a given species. This was done using generalized additive modelling (GAM) and generalized linear modelling (GLM; Guisan et al. 2002) and then the outputs were compared. GAM and GLM calculate the probability that a species may occur at a given location. Thus, the optimum altitude for trees or seedlings of a given species was computed as the location of maximum likelihood of occurrence, following the abundant core hypothesis (Murphy et al. 2006). If the response was unimodal, then the relative probability of occupancy was calculated between seedlings and trees to assess whether there were any changes in the range dynamics. More recently, Harsch and HilleRisLambers (2016) used quantile regression between observed altitude and sampling year to assess the rate of elevational range shift of a given species at the 5th (lower), 50th (median) and 95th (upper) limits between 1970 and 2009. To account for uneven sampling efforts between time periods, a null model was constructed to estimate the baseline velocity for the dataset.

To circumvent the lack of temporal data, recent studies have also compared the spatial distribution of juvenile trees (e.g. seedlings or saplings) with that of mature trees of the same species for a given time period (Woodall et al. 2009, Zhu et al. 2012, Woodall et al. 2013, Boisvert-Marsh et al. 2014, Zhu et al. 2014). In these studies, the underlying hypothesis is that the distributions of juvenile trees are indicative of recent and possibly future migration trends, whereas mature trees are indicative of past conditions. Contradictory patterns have been revealed by these studies depending on the species or the portion of the range examined (Zhu et al. 2012, Boisvert-Marsh et al. 2014). In the 2014 study, Boisvert-Marsh et al. also found that the northernmost limit (defined as the 90th percentile of latitude) for the saplings of eight of 11 species was south of that of trees in the first time period (1970-1977). However, when comparing trends through time, the saplings of those same species demonstrated northward shifts. Hence, it is not clear if the spatial position of juveniles relative to trees actually translates into sustained range extension (or contraction) through time (Boisvert-Marsh et al. 2014, Máliš et al. 2016).

A possible explanation for the different spatial patterns between studies is that the regeneration niche of juvenile life stages may differ from the adult niche (Grubb 1977, Dobrowski et al. 2015). Based only on climate, species tolerance can vary considerably depending on life stage, making seedling and sapling life stages particularly sensitive to climate extremes and variation (Munier et al. 2010, Kueppers et al. 2017) with important implications for recruitment success (Young et al. 2019). When conditions are marginal at the leading edge, current populations can result from pulse recruitment, successful recruitment that is limited only to the most favorable years (Brown and Wu 2005, Renwick and Rocca 2015, Copenhaver-Parry et al. 2020). Long-term monitoring data are invaluable in this context as they can validate observed spatial trends from the relative positions of trees and juveniles, as well as those predicted from species distribution models (Périé and de Blois 2016) or patterns of tree abundance (Murphy et al. 2010).

2.5.3 – Correlative modelling and species distribution models

Based on the assumption that the relationship between species distribution and climate remains stable through time, current and future climate scenarios can be used to infer where species could find suitable habitat conditions in the future. The most popular method has been correlative modelling, also known as species distribution modelling (Guisan and Zimmermann 2000, Thuiller et al. 2005, Iverson et al. 2008, McKenney et al. 2011, de Blois et al. 2013, Périé and de Blois 2016), which associates environmental variables, such as climate (McKenney et al. 2011) or climate and edaphic variables (Beauregard and de Blois 2014, Périé and de Blois 2016), with species occurrence.

Different response variables have been used to model distributions. Presence/absence models like generalized linear models, generalized additive models, regression trees, or Random Forest, can be used when a species' distribution has been sampled enough to fully capture the range of conditions a species can occupy (Thuiller et al. 2005, Iverson et al. 2008). Each model carries its own assumptions, each with their own strengths and weaknesses. One way to account for differing modelling abilities is consensus modelling, with the original platform BIOMOD (Thuiller et al. 2009) and the newer BIOMOD2 (Gallien et al. 2016) by far being the most popular tools. Species abundance models have been employed to model tree distributions in eastern North America (Chambers et al. 2013), but model performance was considerably lower than for other models that were performed using only presence/absence in the same area (Périé et al. 2014, Périé and de Blois 2016). The choice of abundance metric (counts vs. percent cover vs. relative species importance) and its ability to reflect gradients can play an important role in how well the model performs, but could be related to differences in maximum probability of occurrence across a species range (Chambers et al. 2013, Van Couwenberghe et al. 2013). This is likely because determinants of species abundance in a given area relate more directly to local effects such as spatial autocorrelation, soil conditions or competition than to climate (Canham and Murphy 2016, Gomes et al. 2018). Maxent (Elith et al. 2011) has also been used for modelling species presence when data on absence are less readily available, such as for modelling occurrence based on herbarium records.

Results from models such as these give insights into the magnitude at which shifts in suitable conditions could occur, and where species could be vulnerable, with projections often extending to the end of the 21st century. While some taxa (e.g. birds) could keep pace, what has been quickly apparent from these models was that many plants and trees species will not be able to keep pace with estimated shifts in suitable climate conditions projected to be in the order of several hundred kilometers. For example, in eastern North America, the suitable bioclimatic habitat for trees will shift on average by 193km by the end of this century while for understory herbs and shrubs the shift is 628km (Périé et al. 2014; Beauregard 2016). Species distribution models have been heavily criticized, mostly based on the nature of the species-climate relationship (Araújo and Peterson 2012). As mentioned previously, climate may not be the only or even the main limiting factor for some species (Hargreaves et al. 2014, Chardon et al. 2015). As well, models based on long-term averages of broad-level variables (e.g., long-term averages of annual variables) may not reflect the species-specific responses that can dictate how species are structured along certain climatic gradients, whether the climate/species relationships change in space (Cavanaugh et al. 2015, D'Orangeville et al. 2016, Girardin et al. 2016, Boisvert-Marsh et al. 2019) and how species could eventually respond (Morin et al. 2007, Cleland et al. 2012). Despite these shortcomings, correlative models can provide valuable insight on the degree to which species are likely to be exposed to climatic changes (i.e., exposure, Iverson et al. 2008, McKenney et al. 2011, Périé and de Blois 2016). Integrating different types of model response (Stahl et al. 2014) and life history information (Engler et al. 2012) or combining different approaches (Talluto et al. 2016, Zurell et al. 2016) could help refine model outputs and provide more realistic predictions.

2.6 - General remarks

As shown in this literature review, research into the breadth of possible biological responses to climate change is advancing rapidly. The importance of assessing range response to climate change is well acknowledged, but the general lack of data over large latitudinal gradients and relatively long time periods has limited research into these aspects. Moreover, there is a need to assess the role of climate versus other drivers in determining range response to climate change. In spite of increased knowledge about ecological and physiological processes that characterize species response to climate, linking the broad scale of range patterns to the fine scale of population processes to predict range dynamics remains a major challenge. This thesis aims to narrow the gap between pattern and process in range dynamics in relation to climate change.

Chapter 3 - UNRAVELLING POTENTIAL NORTHWARD MIGRATION PATHWAYS FOR TREE SPECIES UNDER CLIMATE CHANGE

Authors : Laura Boisvert-Marsh[1], Sylvie de Blois[1, 2]

Affiliations

[1]Department of Plant Science, Macdonald Campus of McGill University, 21111 Lakeshore, Ste-Anne-de-Bellevue, Québec, H9X 3V9, Canada.

[2]McGill School of Environment, McGill University, 3534 University St., Montreal, Quebec, H3A 2A7

This manuscript is under review at Journal of Biogeography (Resubmitted after Minor revisions).

3.1 - Abstract

Aim: Climate-induced range expansion ultimately implies recruitment at sites that were previously unoccupied by a species (i.e., occupancy gains). Using evidence on abiotic conditions and biotic interactions at these migration sites, we aimed to identify migration pathways from northern temperate to boreal forests for species showing northward range expansion.

Location: Quebec, Canada

Taxon: Trees of northern temperate/boreal forests

Methods: Using past (1970-1977) and recently updated (2003-2015) forest inventories across 761100 km^2, we first quantified latitudinal shifts for saplings of eight tree species and investigated occupancy gains at migration sites. We used field evidence and a consensus modelling approach to determine environmental suitability and identify edaphic, climatic and disturbance conditions, as well as species co-occurrence patterns, characterising recent occupancy gains. The results were interpreted in relation to novel species associations facilitating species migration in unsuitable landscapes.

Results: All species showed northward latitudinal shifts driven by increased recruitment and occupancy gains northward. Occupancy gains occurred largely at historically unsuitable sites. Migration sites showed a shift towards humus types characteristic of the boreal forest and not typically found in the core range of most temperate species. Climatic conditions at migration sites were initially colder than at occupied sites, but warming suggests recent climatic suitability. A decrease in conifer basal area at migration sites following disturbances reduced priority effects that possibly constrained deciduous species establishment. Co-occurrence patterns pointed to deciduous species tolerant of boreal edaphic conditions, leading the way for other temperate species.

Main conclusions: Temperate tree species can recruit into sites typical of boreal forests, even under environmentally challenging conditions. Warming and disturbances open up the way for some novel species associations that have in turn the potential to facilitate the recruitment of temperate species into the boreal forest, revealing migration pathways.

Keywords: Range shift; Tree migration; Edaphic variables; Disturbance; Long-term forest monitoring; Climate change; Forest dynamics; Quebec, Canada

3.2 - Introduction

Understanding the spatial and ecological dynamics at the leading edge of species distribution is fundamental to understand range shifts under climate change (Lenoir and Svenning 2015). At northern latitudes, the magnitude of climate warming is particularly strong (IPCC 2014, Zhang et al. 2019) and there is pressure on species to migrate to track suitable climatic conditions (Chen et al. 2011, Lenoir et al. 2020). By the end of this century, species distribution models project that suitable climate for tree species in North America will have shifted northward by hundreds of kilometers (McKenney et al. 2011, Périé and de Blois 2016). Even though the pace of climate change exceeds the capacity of many species to keep up with climate, leading to climatic debt (Bertrand et al. 2016), and other types of geographical responses such as westward or downward migrations are possible (Lenoir et al. 2010, Zhu et al. 2012, Fei et al. 2017), most species are expected to expand their range northward or upward and some are already doing so (Boisvert-Marsh et al. 2014, Sittaro et al. 2017, Boisvert-Marsh et al. 2019). For trees, range expansion will ultimately imply successful colonization and establishment at sites previously unoccupied by the species. The conditions under which recruitment of juvenile stages occur at these potential migration sites could reveal various biotic and abiotic factors ultimately facilitating or hindering range shifts and could highlight migration pathways (Ettinger and HilleRisLambers 2013, Fisichelli et al. 2013).

Unlike boreal tree species expanding into the mostly treeless taiga and northern tundra, temperate tree species at their northern limit in North America have to establish into the southern edge of the boreal forest to successfully migrate northwards. In doing so, they will have not only to compete with resident boreal species, but also cope with edaphic conditions that may not be optimal for them. In Canada, the deciduous species that characterise the temperate forest are replaced by coniferous boreal species as the climate becomes colder along a latitudinal gradient, a pattern also found where there is a strong altitudinal gradient. This change in species composition matches a change in ecosystem properties and biogeochemical cycles. Compared to temperate forest soils, boreal soils are colder with slower nutrient cycling, tend to accumulate litter—particularly since conifer litter is slow to decompose —have lower pH and nutrient status, and can be waterlogged (Lafleur et al. 2010). Edaphic conditions, species composition and climate are therefore interrelated (Beauregard and de Blois 2014), and these interrelationships are expected to determine species turnover in time and space, particularly at the transition between the temperate and boreal zones where deciduous and coniferous species mix (Brown and Vellend 2014, Fisichelli et al. 2014, Brice et al. 2020). In the closed canopy of mixed or boreal forests, for instance, resident conifers may also constrain the establishment and growth of temperate migrants (De Frenne et al. 2013, Solarik et al. 2020) through their effect on light, litter and decomposition, influencing in turn nutrient availability, soil pH and soil fungal communities (Hobbie 1996, Fisichelli et al. 2013, Collin et al. 2017, Nagati et al. 2018). Conversely, the presence of deciduous species in the canopy of migration sites could further promote suitable soil conditions for migrating temperate species through increased pH and nutrient mineralization (Bradley and Fyles 1995, Collin et al. 2016) and/or the promotion of favourable soil biota (Brown and Vellend 2014). Such interactions can result in competitive exclusion, release, or facilitation and determine species distribution when propagules are available (Lenoir et al. 2010, Wisz et al. 2013), Hence, biotic interactions may play a more prominent role in setting range limits than previously thought (Louthan et al. 2015, Freeman et al. 2018).

The relationship between edaphic conditions, species composition and climate is also modulated by natural (e.g. insects, fire, windthrow) and anthropogenic disturbances in forests at high latitudes (Gauthier et al. 2015). Depending on their intensity, disturbances can break the inertia that inhibits more temperate species from moving into new communities, while forcing boreal species out (De Frenne et al. 2013). At the community level, disturbance effects are strong and persistent compared to the effect of climate change (Danneyrolles et al. 2019). Greater changes in tree species abundance over time has been observed as disturbances intensify, with moderate disturbances favoring thermophilization of mixed forests (Brice et al. 2019) and major disturbances leading to a shift from boreal forests to forests dominated mainly by deciduous pioneer species (Brice et al. 2020). Openings from disturbances could provide opportunities for range expansion through the colonization of new sites at the cold edge of a species range. When considering tree species individually, the relative contribution of disturbances (natural and forest harvesting) and climate change to the recruitment of saplings varied depending on the species and the portion of the range under consideration (Boisvert-Marsh et al. 2019). In the latter study, warming tended to reduce recruitment probability in the southern part of the study area, but increased it in the north. In any case, the recruitment of deciduous species into mixed forests or deciduous pioneer species into boreal forests could lead the way by modifying conditions and creating positive feedbacks that facilitate the establishment of other temperate species.

Using past (1970-1977) and recently updated (2003-2015) data from forest inventories that cover a 761100 km² area in northeastern North America, we investigated latitudinal patterns indicative of range dynamics for eight target tree species (*Ostrya virginiana, Fagus grandifolia, Acer saccharum, Betula alleghaniensis, Thuja occidentalis, Acer rubrum, Populus tremuloides, Betula papyrifera*). The first six species are temperate trees, whereas the last two are widely distributed pioneer species typical of disturbed boreal forests. First, we quantified the direction and magnitude of their latitudinal shifts focusing on the changes in the latitudinal limits of saplings over space and time. Then, we focused on sites recently colonized by the target species (i.e. sites with occupancy gains) as potential migration sites, examining abiotic and biotic conditions as evidence of potential migration pathways from northern temperate to boreal forests. Here, pathways are inferred in relation to the characteristics of the original habitat and of migration sites, opportunities for recruitment that arose from disturbances, and the presence of co-occurring species potentially facilitating migration (Wilson et al. 2009). We expected 1) the latitudinal distribution of saplings to shift northward with time and 2) this shift to be driven by increased recruitment in northern parts of the range. As species colonize sites previously unoccupied, we also expected 3) increased recruitment on sites classified as unsuitable (edaphic and/or climatically) and 4) disturbances to characterise migration sites. Finally, 5) northward migrating species may form novel or uncharacteristic associations and 6) that these co-occurrence patterns would suggest potential migration pathways through facilitation.

3.3 - Methods

3.3.1 **-** *Study area*

Our study area covers roughly 761100 km² in Québec (Canada), from 45°-53°N and from 61°-80°W. The province encompasses about 2% of all forested areas in the world and a significant proportion of all boreal forests (Ministry of Forests, Wildlife and Parks –MFFP– https://mffp.gouv.qc.ca/the-forests/international/?lang=en). A strong latitudinal climate gradient defines two major vegetation zones (Saucier et al. 2003). The temperate zone includes *Acer* *saccharum*-dominated forests to the south and mixed *Abies balsamea-Betula alleghaniensis* forests to the north. The latter type is considered as a transition zone (ecotone) that includes temperate species, such as B. alleghaniensis, and boreal species, such as *A. balsamea*. Species whose range limits fall within this area are expected to show expansion or contraction as climate changes. The boreal forest zone includes *A. balsamea-Betula papyrifera* forests to the south and vast *Picea mariana*-feathermoss forests to the north. The northern limit of the study area roughly coincides with the ecotone between the continuous boreal forest and the taiga.

Along with changes in climatic and edaphic conditions, the natural disturbance dynamics vary between temperate and boreal forests, with windthrows and small treefall gaps in the former and large-scale insect outbreaks (especially *Choristoneura fumiferana*) and fire in the latter (Seidl et al. 2020). Harvesting attempts to mimic the disturbance regime, with partial or selective cuts in the south and clear-cuts towards the north.

3.3.2 - *Data from forest inventories*

We used extensive forest inventories of permanent plots to monitor long-term forest dynamics throughout the study area, ensuring consistency in sampling (Ministère des Forêts, Faune et des Parcs 2015). Data collection started in 1970 and is ongoing. Four inventory campaigns of permanent plots have been completed, each lasting several years. At each sampling location, two permanent plots of 400 m^2 at an average distance of 425 m are usually paired for sampling. Plot density decreases northward, along with tree species diversity (one pair of plots per 26 km^2 in the *Acer saccharum* forest, one pair per 104 km^2 in the *Abies balsamea* forest and one pair per 259 km^2 in the *Picea mariana* forest).

We used tree species data from two of the forest inventories—hereafter called P_1 and P_3 for continuity with Boisvert-Marsh et al. (2014, 2019) —allowing sufficient time for colonisation and establishment. P_1 in this study covers the period 1970-1977, corresponding to the first inventory campaign, and was considered our reference period; P_3 covers 2003-2015 and corresponds to the fourth campaign. We used data from 6309 plots in P_1 resampled in P_3, excluding plots where active reforestation occurred. Analyses focused on eight target tree species reaching or approaching their northern limit in the study area (ordered by their northern limit, from most southerly to northerly): *Ostrya virginiana, Fagus grandifolia, Acer saccharum, Betula alleghaniensis, Thuja occidentalis, Acer rubrum, Populus tremuloides, Betula papyrifera.*

This study focuses on changes in the distribution of saplings over space and time as evidence for latitudinal shifts. For inventory purposes, the MFFP defines a sapling as having a diameter at breast height (DBH) of 1.1-9.0cm DBH, grouped by 2cm DBH classes, and >=1.3m tall. Saplings of the smallest size class (1.1-3.0 cm DBH; hereafter called "saplings") are considered to be indicative of relatively recent recruitment events and were used in this study (and previous studies, Boisvert-Marsh et al. 2014, 2019) when evaluating sapling occurrence. When evaluating species occurrence/occupancy, we referred to all stems with a diameter at breast height greater than 1.1cm for a given species. Sampling methods for saplings were consistent between P_1 and P_3, whereas seedling data collection was not. For each target species, the total number of occupied plots in each inventory was first recorded. Then, for a given species, we recorded all plots with saplings in P_1 and all plots with saplings in P_3.

3.3.3 - Calculating latitudinal shifts and occupancy change ratios

We used the percentile approach to define latitudinal zones for each species based on the recorded presence of saplings in a plot and the associated latitude in P_1 (Boisvert-Marsh et al. 2014). The zones' limits were set at the median (50th) percentile of latitudinal distribution in P_1 and at the 90th percentile of distribution in P_1 using relevant methods for each (see Section 8.1.2). Three latitudinal zones were thus defined: south of the 50th percentile of latitudinal distribution (<50th), north of the 50th percentile (>50th), and north of the 90th percentile (>90th, northernmost limit). Note that, because of the northern location of our study area, the 50th percentile does not reflect the median latitude of the entire north-south range of a species but rather the median within the study area. The changes in the location of latitudinal limits were also computed, using the difference in limits calculated for P_1 and P_3 at both the 50th and 90th. Positive values indicate northward latitudinal shift and negative values southward. The significance level was set to 0.05 using non-parametric methods appropriate for non-independent samples (bootstrap resampling at the 50th percentile, pooled confidence intervals at the 90th percentile).

To understand further how sapling distribution dynamics influence the observed latitudinal shifts, we calculated a 'sapling occupancy change ratio' for each of the three latitudinal zones. For each species, this was recorded as the increase or decrease in the number of plots with saplings between P_1 and P_3 relative to the number of plots occupied by saplings in P_1. We refer to positive ratios as 'filling' (i.e. more plots with saplings than before) and negative ones as 'thinning'. The sign and magnitude of the occupancy change ratio north of a limit relative to the ratio south of a limit determine the direction of latitudinal limit shift between inventories. For instance, proportionally higher filling north than south will result in a northward latitudinal shift. Similarly, substantial thinning south of a limit of interest (50th or 90th) may shift that latitudinal limit to the north. A McNemar's test for paired samples was used to see if the frequency of recorded presence/absence in a latitudinal zone was statistically different ($p <= 0.05$) between the two inventories.

3.3.4 - Occupancy gains and abiotic/biotic conditions at migration sites

For the next step, we focused on sites recently colonized by a target species by identifying 'sapling occupancy gains', i.e., plots where saplings of a species were recorded in P_3 but where the species was not recorded in P_1. We considered these plots as potential migration sites. The proportion of plots with occupancy gains in P_3 relative to all plots with saplings in P_3 was calculated.

To understand how environmental conditions influence the occurrence of a species and to provide context to interpret patterns in migration sites, we first determined habitat suitability in P_1 for each target species and associated species using species distribution models (SDMs). The SDMs were based on presence/absence of all stems >1.1cm DBH in P_1, with climatic (1965-1980, i.e., the climate prior to the most intense warming; Boisvert-Marsh et al. 2019) and edaphic predictors (Section 8.2.2.1). The models were calibrated on the entire study area using a consensus approach (Biomod2, Thuiller et al. 2016). The probability threshold for suitability was determined taking into account the trade-off between model sensitivity (i.e., ability to correctly identify presences) and specificity (i.e., ability to correctly identify absences).

The SDMs provided information on important environmental variables related to species distribution and site suitability/unsuitability for a target species in the reference period (P_1). We extracted information on suitability/unsuitability based on P_1 for all migration sites, and compared migration sites in relation to all sites occupied by the target species in P_1 using growing degree days (base 5ºC), January minimum temperature, humus type, surficial deposit, drainage, depth of humus layer, soil texture and pH of the B horizon to detect trends. Moreover, we examined disturbance history (presence and type of disturbance) at migration sites as recorded from each inventory to determine whether disturbances had a role in species occupancy gains. As an indicator of competition, disturbance impact, and light availability, we also compared basal area in all occupied plots with basal area in migration plots in $P_{1,}$ and calculated the change in basal area between P_1 and P_3. Basal area (m^2/ha) was calculated for stems with a DBH greater than 9.1 cm for all species present, for conifer species only, and for *Picea mariana* and *Abies balsamea* separately.

To further investigate biotic conditions at migration sites and identify species interactions that could influence establishment, we examined pairwise co-occurrence patterns using an adapted metric of co-occurrence (Pellissier et al. 2010). The pair of species considered were each of the eight target species recorded at migration sites in P_3 (i.e., presumedly established between P_1 and P_3) with each of seven species characteristic of the major forest types in the study area as recorded in P_1 (*Acer saccharum, Betula alleghaniensis*, *Betula papyrifera, Abies balsamea, Picea mariana*) or frequent enough to warrant analysis (*Acer rubrum*, *Picea glauca*). The co-occurrence index at migration sites is given in Eq. 3.1:

$$\frac{N(Si_{\mathrm{GainsP3}} \cap Sj_{\mathrm{P1}})}{\mathrm{Min}(Si_{\mathrm{GainsP3},}\, Sj_{\mathrm{P1}})}$$

Equation 3.1

where N $(Si_{\mathrm{GainsP3}} \cap Sj_{\mathrm{P1}})$ is the number of shared plots between those showing occupancy gains in P_3 for a target species S_i , $Si_{\mathrm{GainsP3},}$ and the occurrence of an associated species of interest S_j in $P_{1.}$ $\mathrm{Min}(Si_{\mathrm{GainsP3},}\, Sj_{\mathrm{P1}})$ is the number of occurrences of the least frequent of these two categories (here, always Si_{GainsP3}). This index ranges from 0 (species pair never co-occurs) to 1 (species pair always co-occurs). The co-occurrence index is reported for the two northern latitudinal zones, the same ones used in the occupancy change ratio analysis and that are important for northward range expansion (i.e., >50th percentile of latitude and >90th).

Finally, to provide context for interpreting potentially novel species associations revealed in the previous analysis, we determined how each target species was associated with each of the seven associated species over their range in P_1. In this case, associations were assessed using a

C-score index (Gotelli 2000), which is as a measure of shared occurrences between a pair of species relative to the total number of observations for each. An observed pairwise C-score was calculated using presence/absence in P_1 over the entire study area, and within latitudinal bands (1° wide) for a detailed analysis. The observed C-score was then compared to the expected C-score, a distribution of C-scores obtained from randomising the co-occurrence matrix (n=10000) to produce a simulated null model constrained by the availability of environmental conditions suitable for both species (Peres-Neto et al. 2001). The environmental constraints were included as the raw modelled probabilities of occurrence from the SDMs for all studied species. The difference between the observed and expected C-score was transformed into a **standardized effect size** (SES) value to allow comparison between species and latitudinal bands (methods and equations provided in Section 8.2.2.4).

3.4 - Results

Latitudinal shifts - The dominant patterns for the latitudinal limits of saplings at the 50th and even more so at the 90th is a northward shift (Fig. 3.1, maps in Section 8.2.3). The magnitude of the shifts was generally stronger at the 90th (mean shift = 21.26 km, Table 8.1.1) than at the 50th limit (mean shift = 7.77 km, Table 8.1.2). These shifts were significant for two species at the 50th (*Acer rubrum, Acer saccharum*) and for six species at the 90th (*Acer rubrum, Acer saccharum, Betula papyrifera, Fagus grandifolia, Ostrya virginiana, Populus tremuloides*) (Fig. 3.1). The only southward shift observed was for *P. tremuloides* at the 50th but the species shifted northward at the 90th.

Occupancy change ratios - All species showed an increase in the overall number of plots with saplings between the two time periods. For most species, the northward shifts observed were driven by patterns of increasing positive occupancy change ratios with latitude (Fig. 3.1). Two species, *A. saccharum* and *T. occidentalis,* saw occupancy decrease south of the 50th but increase northward, shifting that limit northward. *B. alleghaniensis* had similar occupancy change ratios across the three latitudinal zones, resulting in the lowest northward shifts of all species. *P. tremuloides* saw larger increases in sapling occupancy south of the 50th relative to north, driving that limit southward. *Fagus grandifolia* had the largest overall change in the number of plots occupied (173%) while *A. saccharum* had the lowest (11%) (Table 8.1.3). Overall, when looking only at significant trends, five species showed patterns consistent with northward expansion through northward latitudinal shifts and higher plot occupancy ratios in the northern part of the study area (Fig. 3.1).

Recruitment patterns in P_1 and P_3 - When averaging across all target species, saplings were observed in 23.9% of the plots in P_1 (Table 8.2.1.1). When considering the latitudinal distribution in P_1 of the proportion of plots showing recruitment, the majority of species showed the highest proportions in the southernmost zone. In P_3, recruitment increased across all plots, with saplings observed in 36.0% of the plots on average. All species showed an increase in the proportion of plots with recruitment over the entire study area between P_1 and P_3 (Table 8.1.3 and Table 8.2.1.1). For some of these species (*F. grandifolia, A. saccharum, A. rubrum*, *B. papyrifera),* this represented a shift from south (<50th), which had the highest proportion of plots with saplings in P_1, to north in P_3 (Table 8.2.1.1).

Occupancy gains as migration sites - On average, 23.4% of plots with saplings of a species in P_3 did not show that species in P_1 (i.e., occupancy gains) (Fig. 3.2; Table 8.2.1.1). *Acer rubrum* had the highest proportion of occupancy gains across the study area (35.0%), while *A. saccharum* had the lowest (13.8%). When considering the latitudinal distribution in P_3 of the plots showing occupancy gains, the majority of species showed greater proportion of gains at their northern limit (>90th), followed by >50th, except for *F. grandifolia* and *B. alleghaniensis* (greater proportional gains <50th followed by >90th). However, the difference between latitudinal zones was not significant (one way ANOVA with zone as factor, F=1.863, p=0.18).

SDM and habitat suitability in P_1 - Species distribution model performance based on area under the receiver operating curve was overall good to very good (0.848-0.984, Table 8.2.2.1.1). Growing degree days (base 5°C) based on the 1965-1980 period had the highest or second highest relative importance for all target species while January minimum temperature was among the top 3 variables for 6 of 8 species. Edaphic factors found to constrain suitability were humus type (one of the top 3 variables for 7 of 8 target species) and/or surface deposit (3 of 8 target species). The majority of sites occupied in P_1 by a target species were found to be suitable according to the SDM, although there were greater proportions of suitable sites that were not occupied in the southern than in the northern portions of the range. The proportion of sites classified as unsuitable tended to increase going northward (Table 3.1), although less so for the southernmost species, *F. grandifolia* and *O. virginiana*. In all portions of the range, occupancy gains occurred at much higher proportions at unsuitable sites compared to patterns for occupied sites in P_1, with proportions increasing from south to north. In the northernmost zone, the proportion of unsuitable sites where occupancy gains were observed varied considerably among species, ranging from 28.6% for *B. alleghaniensis* to 100% for *T. occidentalis*.

Edaphic conditions - Most species tended to occupy an increasing proportion of mor sites going northward in P_1 (Table 3.2). This was even more the case for sites with occupancy gains for all temperate deciduous species, although less so for *B. alleghaniensis*. At migration sites, however, the two pioneer species and *T. occidentalis* tended to shift away from mor to organic soils for the pioneer species and to moder for *Thuja*. The depth of the humus layer at migration sites relative to occupied sites showed contrasting patterns between latitudinal zones, but there was no significant difference (Table 8.2.2.2.3, two-tailed t-test, >50th p=0.343; >90th: p=0.80).

With the exception of *T. occidentalis*, the most common type of soil texture class for the B horizon for occupancy gains was sandy loam or loam, generally reflecting patterns shown for occupied sites in P_1 (Table 8.2.2.2.5). Similar trends between occupied P_1 sites and migration sites were observed for surficial deposits, with most gains in sites with glacial deposits (Table 8.2.2.2.7). The exceptions were *T. occidentalis* and *P. tremuloides*, which showed occupancy gains in sites associated with subsidence for the former and lacustrine deposits for the latter. For drainage class, the majority of occupied sites in P_1 and occupancy gains were in sites with good to moderate drainage, but *O. virginiana*, *A. rubrum* and *B. papyrifera* tended to show higher occupancy gains in sites with slower drainage over occupied P_1 sites (Table 8.2.2.2.9). Despite some differences between suitable and unsuitable sites, pH of the B horizon was mostly similar between occupied P_1 sites and migration sites (Table 8.2.2.2.10).

Climate factors - For temperature-based variables (growing degree days – GDD - and January minimum temperature), five target species showed lower values in the reference period P_1 at migration sites north of the 50th relative to occupied sites in P_1 (Table 3.3; Table 8.2.2.2.12). Patterns in temperature variables were more variable in northern areas, with four target species showing lower values at migration sites above the 90th. In almost all cases, growing degree days and January minimum temperatures in P_1 were lower in unsuitable migration sites than in suitable sites. Across migration sites, growing degree days and January minimum temperatures increased between P_1 and P_3 but these increases varied between species and between suitable and unsuitable sites. For a given species, warming in unsuitable migration sites brought GDD and minimum January temperature within the mean of occupied sites in P_1. There were no appreciable trends in annual precipitation between occupied sites and migration sites among the target species, but migration sites were on average wetter in P_3 than in P_1 (> 50th: 17.43mm ± 14.084; >90th: 11.80mm ±20.046, Table 8.2.2.2.13).

Disturbances - Occupancy gains occurred mostly in disturbed sites north of the 50th and 90th, and in relatively similar proportions (average of 64.5% and 65.5% respectively across target species; Table 8.2.2.2.15). Gains were mostly associated with disturbances recorded in P_3, mainly with harvests (>50th: 20.98% on average across target species; >90th: 19.78% on average). The exceptions were *Acer saccharum* and *Betula alleghaniensis*, which were associated with harvests in P_1.

Basal area - Basal area of conifers, including *Picea mariana* and *Abies balsamea*, increased with increasing latitude in occupied P_1 plots for all target species (Table 3.4). Temperate forest species tended to occupy sites in P_1 with higher basal area of *Abies balsamea* than of *Picea mariana* while the two pioneer species tended to occupy sites with higher basal area of *Picea mariana*. On average, the basal area of these two conifers tended to decrease at migration sites between P_1 and P_3, particularly north of the 90th. Moreover, decreases in basal area between P_1 and P_3 were greater in migration sites that were unsuitable than for the suitable ones, but this varied considerably between species and sites.

Pairwise co-occurrence patterns at migration sites

Co-occurrence index - Pairwise co-occurrence patterns between a target species and an associated species are reported for north of the 50th and the 90th limits in Fig. 3.3. With the exception of *P. mariana*, co-occurrence index values increased from the most southerly to the most northerly associated species. Of the associated species, *A. balsamea* showed the highest overall co-occurrence index values (Fig. 3.3), with significant differences among associated species (Table 8.2.2.3.2).

Occupancy gains in relation to pairwise associations in P_1 – Negative or positive pairwise association patterns across the latitudinal distribution of the target species are reported in Table 8.2.2.4.1. *Ostrya virginiana* tended to show a positive association with *A. saccharum*, but a negative one with *A. rubrum* (Table 8.2.2.4.1), whereas gains of *O. virginiana* north of the 50th and 90th were most often in plots with these two species (Fig. 3.3). In P_1, *F. grandifolia* tended to show a negative association with *A. balsamea*, but a positive one with *A. saccharum* (Table 8.2.2.4.1), despite gains of *F. grandifolia* found most often in plots with these species respectively (Fig. 3.3). *Acer saccharum* tended to show a negative association with *A. balsamea* at all but the northernmost latitudes, whereas both *B. alleghaniensis* and *T. occidentalis* had a positive association with *A. balsamea* (Table 8.2.2.4.1). Despite this, gains for *Acer saccharum* were most often in plots with *A. balsamea*, as were gains for *B. alleghaniensis* and *for T. occidentalis* (Fig. 3.3). *Acer rubrum* tended to have positive association with *B. papyrifera* followed by plots with *A. balsamea* (Table 8.2.2.4.1) while gains for *Acer rubrum* were mostly in plots with these species in P_1 (Fig. 3.3). Although *P. tremuloides* and *B. papyrifera* showed random association patterns (not clearly positive or negative; Table 8.2.2.4.1) with *P. mariana,* they were the only species that commonly showed gains in plots with this species (Fig. 3.3).

3.5 - Discussion

The northward migration of tree saplings observed in a previous time period (Boisvert-Marsh et al., 2014) was largely sustained, suggesting directional changes consistent with those expected from warming at high latitudes (Lenoir and Svenning, 2015), although spatially-structured disturbances can also influence distribution dynamics (Boisvert-Marsh et al., 2019; Brice et al., 2020; De Frenne et al., 2013). The transition from the temperate to boreal forest, however, is particularly challenging for species that will need to cope with strong gradients in soil conditions and competition with boreal species. By investigating baseline conditions at sites with occupancy gains as well as potential interspecific influences on species establishment, our study complements others examining site and/or biotic constraints to migration (Brown and Vellend, 2014; Carteron et al., 2020; Collin et al., 2016; Solarik et al., 2020). Site conditions are important because failure to establish at unsuitable sites will result in species distribution lagging behind suitable climate (i.e., disequilibrium dynamics; Svenning & Sandel, 2013).

Although the evidence is still admittedly scarce and plant migration response is expected to lag behind the rapid pace of climate change (Gaüzère et al. 2018; Lenoir et al., 2020), our results indicate that some species can occupy uncharacteristic conditions by migrating into less than optimal sites and form novel associations at range margins that may ultimately facilitate their migration. Predictors in the SDMs included only abiotic variables, but the distribution being analysed integrates abiotic conditions, biotic interactions and disturbances which interact to define the realised niche. Here, the proportion of sites that were suitable but not occupied by a given species in the reference period tended to be higher in the southern portions of the study area than in the north, suggesting other constraints on site occupancy (e.g., competition, dispersal limitation).

Across the study area, migration sites occupied proportionally much more unsuitable sites than reference ones did, reflecting recent expansion into unfavorable abiotic conditions. The abiotic variables that defined suitability the most were growing degree days, humus type, January minimum temperature, and surface deposit. Migration sites tended to have lower GDDs compared to reference sites, particularly at the northern edge, a pattern we would expect with northern migration and which may have precluded establishment in the past. This was even more true for migration sites that were found to be unsuitable: for all species, these sites tended to have lower GDDs than the average of all migration sites. This implies that unsuitability was partly defined by climatic constraints in the reference period, P_1. Interestingly, however, all sites warmed up since then and the differences we observed for GDDs between P_1 and P_3 likely resulted in migration sites becoming climatically suitable with time. Exploratory analyses (not shown) with the SDMs calibrated on P_1 occurrences and edaphic conditions, but with climate encompassing both time periods (1965-2015) suggest that temperature-related climatic constraints were historically more important, an interesting pattern consistent with our analyses of migration sites.

If releasing the climatic constraints had a positive impact on the demographic processes leading to migration at the leading edge (Sheth and Angert 2018), the newly colonized sites did not necessarily offer optimal edaphic conditions. For instance, reference sites for *Acer saccharum* were largely characterised by moder humus, but for migration sites there were a greater proportion of mor humus characteristic of the acidic soil of the boreal forest. These mor sites were largely classified as unsuitable for *A. saccharum*, highlighting a tendency for the three most temperate species to migrate towards distinct humus types that brought them away from their SDM-calibrated tolerance. It is unclear whether they will be able to persist in these conditions, but evidence from field observations or transplantation experiments can provide some clues. *Acer saccharum* has been shown to establish in boreal sites (Barras and Kellman 1998, Goldblum and Rigg 2002, Kwit et al. 2010, Fisichelli et al. 2014), but migration may have been limited by temperature constraints (Graignic et al. 2014; this study, Collin et al. 2017) or by increased predatory pressure beyond the range (Brown and Vellend 2014). Using soil from beyond its altitudinal range to grow *A. saccharum* within its range resulted in low regeneration, indicating edaphic limitations in boreal soil (Brown and Vellend 2014). Not all tree populations, however, may be constrained equally by edaphic conditions. Seedlings from northern provenances have been shown to establish at and beyond their current range on boreal-like microsites better than southern seedlings did (Solarik et al. 2018), suggesting local pre-adaptations that could facilitate migration. If less than optimal edaphic conditions do not completely filter out species, however, they could still contribute to the mismatch between species distribution and suitable climate conditions. We therefore expect that mismatch to be less important for species like *Acer rubrum* whose distribution is constrained more by climatic than edaphic variables according to the SDMs. *Acer rubrum* indeed showed a large latitudinal shift in our study and others (Tremblay et al. 2002, Leithead et al. 2010, Brice et al. 2019).

The majority of migration sites were disturbed in P_1 or P_3 or both, supporting the claim that disturbances can provide opportunities for recruitment through changes in abiotic (warmer soils, more light, etc.) and/or biotic (species turnover, lower competition, facilitation, etc.) conditions. Not surprisingly, the two pioneer species, *Populus tremuloides* and *Betula papyrifera,* were found in the highest proportion of disturbed migration sites north of the 50th. The latter, in particular, showed relatively rapid northward shifts into the southern boreal and *Picea mariana*-feathermoss forest domains. A spruce budworm epidemic in the boreal forest between 1975 and 1990 likely contributed to the decline of conifers while favouring sapling diversity and abundance (Crête and Marzell 2006). Our migration sites also tended to show a decline in basal area with time, especially a decline in *Abies balsamea* and *P. mariana* for sites colonised by *P. tremuloides* and *B. papyrifera*. As climate becomes unsuitable for conifers in the south (Boisvert-Marsh et al. 2014, Boulanger et al. 2017, D'Orangeville et al. 2018) and as disturbance regimes intensify in response to climate—e.g., forestry activities moving northward (Jobidon et al. 2015), changed fire frequency (Boulanger et al. 2014)—priority effects (Solarik et al. 2020) should weaken and provide opportunities for deciduous pioneer species to establish.

The release from climatic constraints and the establishment of deciduous species tolerant of boreal soil conditions following disturbances could shift dynamics towards more temperate species overall. A warmer climate improves litter decomposition and dries out waterlogged soils, further accelerating changes in soil nutrient status in boreal sites toward conditions favorable for temperate species (Lafleur et al. 2010). Moreover, the presence of deciduous species can further promote deciduous seedling density, possibly through better light availability (Solarik et al. 2020) and changes in edaphic substrates (Laganière et al. 2010). Novel or uncharacteristic species associations at migration sites can further suggest potential migration pathways through facilitation, particularly for species that are limited by edaphic conditions in the boreal forest. The co-occurrence of *A. saccharum* with *A. rubrum* in a significant proportion of occupancy gain plots, for instance, points towards such a pathway. *Acer saccharum* and *A. rubrum* show negative association across their range, implying spatial segregation, but were found to co-occur in up to 52% of migration sites. Field studies at the ecotone have shown that *A. rubrum* seedlings, more so than *A. saccharum*, can tolerate low soil pH at sites where needle litter is abundant while also mobilizing nutrients from the soil better (Collin et al. 2016), characteristics that are important for breaking into the boreal forest. With time, *A. rubrum* could promote suitable soil conditions for a species like *A. saccharum* through increased pH and nutrient mineralization (Collin et al. 2016, Collin et al. 2017) and/or the promotion of favourable soil biota (Brown and Vellend 2014). The observed rapid migration of *A. rubrum* into boreal forests could therefore open up the way for more temperate species to follow. Likewise, species turnover toward *B. papyrifera* in boreal sites will promote the accumulation of its relatively labile litter, which speeds up decomposition and mobilizes higher levels of carbon, nitrogen and other nutrients than those of conifer litter (Bradley and Fyles 1995, Bauhus et al. 1998, Laganière et al. 2010, Nagati et al. 2018). *Acer rubrum*'s positive association with *B. papyrifera* where their range overlap and in migration sites suggests that the latter could lead the way through the boreal forest for the former, which would itself lead the way for more meridional species.

Of course, the species co-occurrence patterns we observed do not tell the whole migration story, and mechanistic interpretations of association patterns are inherently complex (Cazelles et al. 2016). Inferences are based on putative migration sites that become scarcer towards range margins and we focused on pairwise associations with dominant species that could be transient while ignoring other species interactions that could also influence regeneration patterns (Royo and Carson 2006, Werner et al. 2019). But if current species associations at migration sites are any indication of potential migration pathways, we do expect temperate species to recruit into boreal forest types at a rate that will be determined by warming intensity, disturbance frequency, and rate of edaphic change among others. With warming at the temperate-boreal ecotone, boreal coniferous species are projected to decline while temperate broadleaf species are projected to increase. Species turnover is exacerbated by disturbances that open up the canopy, altering competitive interactions and weakening priority effects to the benefit of migrating species (Solarik et al. 2020). The rate of edaphic change may be the most limiting process (Lafleur et al. 2010) and recruitment possibly itself episodic (Graignic et al. 2014, Renwick and Rocca 2015), but our results indicate that some temperate species can at least establish in what appear to be sub-optimal conditions at range margins. Deciduous species better adapted to boreal edaphic conditions can also lead the way for other, more meridional species with which they increasingly associate at range margins. Transplant experiments or assisted migration experiments in a forestry context (Pedlar et al. 2012) could be designed to test various hypotheses about potential migration pathways based on species interactions.

3.6 - Acknowledgements

We acknowledge the Ministry of Forests, Wildlife and Parks (*Ministère des Forêts, de la Faune et des Parcs,* Quebec) for providing initial access to forest inventory data. We also highlight the work of the countless people over the last 45 years who worked on the inventories. The research was supported by grants from the Natural Sciences and Engineering Research Council of Canada to SdB and from the Department of Plant Science (McGill) to LBM. The authors declare no conflict of interest.

3.7 - Data Accessibility

Forest inventory data, including species data and edaphic and disturbance variables, are available from https://www.donneesquebec.ca/recherche/fr/dataset/placettes-echantillons-permanentes-1970-a-aujourd-hui. The BioSIM program used to interpolate climate data used in the species distribution models is available from https://cfs.nrcan.gc.ca/publications?id=34818.

3.8 – Biosketch and Author Contributions

Laura Boisvert-Marsh is a Ph.D. candidate at McGill University under Prof. Sylvie de Blois. LB.-M. is studying the spatial patterns of forest ecosystem response to climate change and their underlying processes. Author contributions**:** L.B.-M and SdB conceived the original study idea; L.B.-M. designed the methodology and led data analysis with input from SdB; LB.-M. wrote the initial manuscript draft. SdB and LB.-M. edited the manuscript.

Table 3.1: Proportion of sites (unoccupied in P_1, occupied sites in P_1, migration sites) that were found to be suitable or unsuitable for each target species using species distribution modelling. Models were calibrated using average climate in P_1 (1965-1980) and edaphic factors. Suitability of a site was determined using model probability at which sensitivity (i.e., ability of model to correctly identify presences) and specificity (i.e., ability to correctly identify absences) is maximized (see Table 8.2.2.1.1 for cutoffs).

	Unoccupied		Occupied			Migration sites		
	Suitable	Unsuitable	n	Suitable	Unsuitable	n	Suitable	Unsuitable
	<50th							
Ostrya virginiana	35.80	64.20	90	100.00	0.00	10	90.00	10.00
Fagus grandifolia	53.94	46.06	215	100.00	0.00	34	88.24	11.76
Acer saccharum	58.66	41.34	620	98.89	1.11	29	89.66	10.34
Betula alleghaniensis	64.92	35.08	716	97.10	2.90	40	75.00	25.00
Thuja occidentalis	39.93	60.07	361	98.63	1.37	9	66.67	33.33
Acer rubrum	82.36	17.64	735	98.40	1.60	101	91.09	8.91
Populus tremuloides	19.64	80.36	647	88.57	11.43	38	19.44	80.56
Betula papyrifera	36.60	63.40	1722	85.81	14.19	94	51.06	48.94
	>50th							
Ostrya virginiana	3.24	96.76	120	99.17	0.83	24	29.17	70.83
Fagus grandifolia	6.78	93.22	223	99.10	0.90	31	58.06	41.94
Acer saccharum	12.60	87.40	666	92.64	7.36	62	69.35	30.65
Betula alleghaniensis	15.54	84.46	811	89.64	10.36	18	77.78	22.22
Thuja occidentalis	8.15	91.85	297	91.58	8.42	16	37.50	62.50
Acer rubrum	11.17	88.83	809	78.62	21.38	200	43.50	56.50
Populus tremuloides	8.69	91.31	506	85.38	14.62	42	21.43	78.57
Betula papyrifera	27.23	72.77	1358	87.04	12.96	120	57.50	42.50
	>90th							
Ostrya virginiana	1.62	98.38	65	100.00	0.00	13	15.38	84.62
Fagus grandifolia	4.49	95.51	109	98.17	1.83	16	43.75	56.25
Acer saccharum	7.40	92.60	209	87.56	12.44	30	60.00	40.00
Betula alleghaniensis	10.71	89.29	314	83.12	16.88	7	71.43	28.57
Thuja occidentalis	3.36	96.64	115	86.96	13.04	7	0.00	100.00
Acer rubrum	3.48	96.52	230	62.61	37.39	75	24.00	76.00
Populus tremuloides	5.00	95.00	213	76.06	23.94	23	26.09	73.91
Betula papyrifera	13.30	86.70	464	70.26	29.74	68	42.65	57.35

n – Number of sites of a given type. Only given for occupied sites in P1 and Migration sites

Table 3.2: Proportions of occupied sites in P_1 and migration sites by humus type. Humus type was noted in the field (see Table 8.2.2.2.1 for descriptions) and are arranged based on prevalence from south to north. For each target species, the number of migration sites where a given humus type was observed relative to the total number of migration sites was calculated (expressed as %). In addition, within each category, the proportion of these migration sites classified as either suitable or unsuitable was also calculated (between 0 and 1). Suitability of migration sites was determined using species distribution modelling based on climatic (1965-1980) and edaphic factors, as defined by the model probability at which sensitivity (i.e., ability of model to correctly identify presences) and specificity (i.e., ability to correctly identify absences) is maximized.

	Mull				Moder				Mor				Organic			
	Occupied P_1	Migration sites			Occupied P_1	Migration sites			Occupied P_1	Migration sites			Occupied P_1	Migration sites		
Species	%	%	Un-suitable	Suitable only	%	%	Un-suitable	Suitable only	%	%	Un-suitable	Suitable only	%	%	Un-suitable	Suitable only
	>50th															
Ostrya virginiana	5.00	8.33	0.00	1.00	82.50	54.17	0.62	0.38	12.50	37.50	1.00	0.00	0	0	--	--
Fagus grandifolia	4.04	3.23	0.00	1.00	73.54	64.52	0.15	0.85	22.42	32.26	1.00	0.00	0	0	--	--
Acer saccharum	3.60	3.23	0.00	1.00	71.02	54.84	0.03	0.97	24.32	40.32	0.68	0.32	1.05	1.61	1	0
Betula alleghaniensis	1.60	0.00	0.00	0.00	52.03	55.56	0.00	1.00	43.40	44.44	0.50	0.50	2.97	0	--	--
Thuja occidentalis	0.67	0.00	0.00	0.00	25.59	31.25	0.80	0.20	61.95	50.00	0.75	0.25	11.78	18.75	0	1
Acer rubrum	0.87	1.00	0.50	0.50	36.34	28.50	0.51	0.49	60.82	67.00	0.57	0.43	1.97	3.5	1	0
Populus tremuloides	2.37	2.38	1.00	0.00	13.44	11.90	0.80	0.20	82.02	80.95	0.76	0.24	2.17	4.76	1	0
Betula papyrifera	0.96	0.83	1.00	0.00	12.08	10.83	0.31	0.69	79.68	69.17	0.33	0.67	7.28	19.17	0.83	0.17
	>90th															
Ostrya virginiana	0.00	7.69	0	1	84.62	53.85	0.86	0.14	15.38	38.46	1	0	0	0	--	--
Fagus grandifolia	8.26	6.25	0	1	70.64	50.00	0.25	0.75	21.10	43.75	1	0	0	0	--	--
Acer saccharum	5.74	3.33	0	1	64.11	60.00	0.06	0.94	29.67	36.67	1	0	0.48	0	--	--
Betula alleghaniensis	2.55	0.00	0	0	38.85	42.86	0	1	55.73	57.14	0.50	0.50	2.88	0	--	--
Thuja occidentalis	1.74	0.00	--	--	17.39	42.86	1	0	63.48	57.14	1.00	0.00	17.39	0	--	--
Acer rubrum	2.17	1.33	1	0	24.78	18.67	0.86	0.14	71.74	78.67	0.73	0.27	1.3	1.33	1	0
Populus tremuloides	1.41	4.35	1	0	8.45	8.70	0.50	0.50	87.32	78.26	0.72	0.28	2.82	8.7	1	0
Betula papyrifera	0.22	0.00	--	--	2.80	5.88	0.75	0.25	87.93	77.94	0.49	0.51	9.05	16.17	0.91	0.09

Table 3.3: Annual growing degree days (base 5°C, GDD) in occupied sites in P_1 and at migration sites. Climate data used in this study covers 1965 to 1980 (encompasses P_1) and 1998 to 2015 (encompasses P_3). At occupied sites in P_1, mean GDD for P_1 was used and averaged across all sites. At migration sites, mean GDD for P_1 was used and averaged across all migration sites as well as the mean difference in GDD between inventory periods (ΔGDD P_3-P_1). Suitability of migration sites was determined using species distribution modelling based on climatic (1965-1980) and edaphic factors, as defined by the model probability at which sensitivity (i.e., ability of model to correctly identify presences) and specificity (i.e., ability to correctly identify absences) is maximized. See Table 8.2.2.1.1 for cut-offs.

	Occupied P_1		Migration sites											
			All				Unsuitable only				Suitable only			
			P_1		ΔGDD P_3-P_1		P_1		ΔGDD P_3-P_1		P_1		ΔGDD P_3-P_1	
	Mean	St. dev	Mean	St. dev	Mean	St. dev	Mean	St. dev	Mean	St. dev	Mean	St. dev	Mean	St. dev
	>50th													
Ostrya virginiana	1554.66	94.721	1540.79	102.597	171.81	38.250	1512.45	101.837	179.27	25.740	1609.61	69.946	153.69	57.451
Fagus grandifolia	1463.26	95.074	1481.42	111.312	156.57	49.941	1429.15	130.661	137.09	49.627	1519.18	78.838	170.65	46.507
Acer saccharum	1418.71	108.346	1391.66	112.677	152.25	45.334	1347.31	75.228	141.69	49.055	1411.27	121.371	156.92	43.369
Betula alleghaniensis	1353.61	116.076	1367.46	122.104	149.59	37.405	1351.36	164.618	139.03	46.205	1372.06	114.633	152.60	35.956
Thuja occidentalis	1408.38	96.407	1408.26	109.897	114.95	65.443	1342.35	60.503	111.13	65.618	1518.10	80.472	121.32	70.853
Acer rubrum	1386.51	109.319	1372.69	102.682	149.00	45.752	1316.29	85.322	153.50	37.570	1445.95	72.852	143.17	54.262
Populus tremuloides	1265.30	122.370	1212.91	125.697	102.06	65.595	1186.38	126.187	104.15	63.740	1310.19	61.076	94.40	75.603
Betula papyrifera	1193.20	161.822	1136.62	186.416	118.64	54.286	1044.56	220.558	128.46	37.372	1204.67	118.282	111.39	63.282
	>90th													
Ostrya virginiana	1522.76	76.123	1505.33	110.806	190.48	23.249	1497.42	117.208	184.56	19.915	1548.82	74.084	223.05	3.752
Fagus grandifolia	1464.66	103.138	1441.31	75.952	140.10	59.654	1419.67	75.016	125.58	54.967	1469.14	72.888	158.77	64.382
Acer saccharum	1362.74	89.309	1346.09	74.422	145.80	54.212	1317.02	59.339	130.81	54.033	1365.47	78.587	155.79	53.478
Betula alleghaniensis	1307.03	93.398	1275.60	99.302	131.90	45.449	1229.44	129.332	122.72	72.147	1294.07	95.488	135.58	41.690
Thuja occidentalis	1359.72	94.141	1331.79	55.431	80.14	49.410	1331.79	55.431	80.14	49.410	--	--	--	--
Acer rubrum	1314.66	87.752	1325.06	88.367	138.55	53.945	1302.54	85.235	153.67	39.806	1396.39	54.502	90.65	65.202
Populus tremuloides	1202.18	132.775	1206.51	138.072	73.94	67.359	1168.86	136.617	73.33	63.090	1313.18	75.378	75.67	84.982
Betula papyrifera	1064.31	156.914	1041.66	166.922	103.42	54.505	966.92	174.476	124.66	34.868	1142.16	84.354	74.86	63.129

Table 3.4: Basal area at occupied sites in P_1 and at migration sites. Basal area (m^2/ha) was calculated in each time period (P_1 and P_3) for all live stems with a DBH >9.1 cm (including other species not assessed in this study), for conifers and for two dominant conifer species in the study area, Abies balsamea and Picea mariana. Additionally, differences in basal area between P_1 and P_3 at migration sites were also calculated. Suitability of migration sites was determined using species distribution modelling based on climatic (1965-1980) and edaphic factors, as defined by the model probability at which sensitivity (i.e., ability of model to correctly identify presences) and specificity (i.e., ability to correctly identify absences) is maximized. See Table 8.2.2.1.1 for cutoffs.

	Occupied P_1		Migration sites							
	BA P_1		BA P_1		ΔBA P_3-P_1					
					All sites		Unsuitable only		Suitable only	
	Mean	St. dev	Mean	St. dev	Mean	St. dev	Mean	St. dev	Mean	St. dev
>50th										
Species Name	Total basal area - All species									
Ostrya virginiana	22.67	7.505	19.44	10.464	2.11	10.71	-0.25	11.225	7.87	7.013
Fagus grandifolia	23.07	6.51	23.15	7.032	-1.05	8.579	-2.99	9.249	0.35	8.035
Acer saccharum	21.36	7.653	19.62	10.966	-0.31	13.096	0.09	13.552	-0.49	13.048
Betula alleghaniensis	20.67	8.409	18.7	6.721	-1.8	9.224	-9.38	3.577	0.36	9.254
Thuja occidentalis	24.22	9.808	12.08	7.965	1.53	9.424	0.71	11.184	2.88	6.146
Acer rubrum	20.5	8.235	19.12	10.282	-3.68	12.636	-3.04	13.013	-4.52	12.153
Populus tremuloides	18	10.204	21.37	12.791	-17.14	15.389	-18.62	15.52	-11.73	14.43
Betula papyrifera	18.98	10.754	16.54	13.448	-5.96	16.737	-8.62	13.316	-4	18.725
	Basal area – All conifer species									
Ostrya virginiana	2.73	4.514	1.85	3.523	0.36	2.452	-0.44	1.822	2.30	2.833
Fagus grandifolia	2.89	4.407	7.31	8.176	-3.77	6.740	-5.06	8.407	-2.83	5.298
Acer saccharum	4.59	5.877	8.20	8.473	-0.61	9.073	0.51	8.308	-1.11	9.442
Betula alleghaniensis	8.32	7.972	8.57	8.644	-4.81	8.361	-9.87	5.056	-3.36	8.682
Thuja occidentalis	16.22	9.821	7.03	4.978	-0.22	7.688	-1.88	8.543	2.55	5.591
Acer rubrum	8.72	7.939	9.85	9.439	-3.08	9.464	-2.72	10.192	-3.55	8.461
Populus tremuloides	8.67	8.879	16.98	12.356	-14.30	14.365	-16.00	14.502	-8.09	12.686
Betula papyrifera	12.62	10.771	15.44	13.415	-6.44	15.687	-8.49	12.614	-4.92	17.554
	Basal area - *Abies balsamea*									
Ostrya virginiana	1.12	2.15	0.97	2.259	-0.19	2.192	-0.72	2.11	1.1	1.949
Fagus grandifolia	1.38	2.4	3.77	4.667	-2.01	3.903	-2.2	4.731	-1.86	3.321
Acer saccharum	2.54	3.674	4.47	4.725	-1.17	5.818	-0.72	8.249	-1.37	4.457
Betula alleghaniensis	4.95	5.57	5.28	7.574	-2.97	8.508	-8.59	9.041	-1.37	7.957
Thuja occidentalis	6.46	5.617	3.6	4.698	-1.9	5.85	-3.02	7.226	-0.05	1.448
Acer rubrum	4.69	5.533	4.44	5.846	-1.78	6.374	-1.64	6.896	-1.96	5.658
Populus tremuloides	2.14	4.047	6.79	9.05	-5.97	9.427	-7.02	9.984	-2.12	5.961
Betula papyrifera	6.37	8.08	7.45	11.074	-3.52	11.365	-2.96	6.934	-3.94	13.794
	Basal area - *Picea mariana*									
Ostrya virginiana	0.01	0.069	--	--	--	--	--	--	--	--
Fagus grandifolia	0.16	0.972	0.08	0.39	-0.08	0.39	-0.02	0.078	-0.12	0.51
Acer saccharum	0.17	0.917	0.41	1.705	-0.29	1.856	-0.04	0.348	-0.4	2.216
Betula alleghaniensis	0.41	1.575	1.2	2.882	-0.89	2.717	-2.4	4.35	-0.46	2.095

Thuja occidentalis	1.25	3.284	1.56	1.977	0.31	2.226	0	1.372	0.82	3.312
Acer rubrum	1.03	2.824	1.46	3.272	-0.28	3.429	-0.17	4.195	-0.42	2.06
Populus tremuloides	3.86	6.791	7.47	10.411	-6.86	10.608	-7.71	11.628	-3.77	4.711
Betula papyrifera	4.41	7.425	6.17	8.557	-2.83	8.843	-4.81	9.721	-1.37	7.89
>90th										
	Total basal area - All species									
Ostrya virginiana	22.44	6.214	20.52	9.033	-0.58	11.9	-2.62	11.663	10.65	6.431
Fagus grandifolia	23	6.537	18.64	8.83	-1.68	7.783	-4.26	11.782	3.64	12.43
Acer saccharum	20.2	7.839	23.79	8.392	0.48	12.599	-2.46	8.034	-0.68	7.955
Betula alleghaniensis	18.9	8.336	18.92	9.228	-4.41	12.591	-8.75	4.913	-2.67	14.784
Thuja occidentalis	23.23	11.344	10.98	8.447	2.41	10.126	2.41	10.126	--	--
Acer rubrum	19.14	8.461	17.38	10.011	-2.41	12.097	-2.63	13.088	-1.72	8.483
Populus tremuloides	17.85	11.637	21.34	11.643	-17.03	14.818	-18.62	15.883	-12.49	11.206
Betula papyrifera	21.14	11.118	18.17	11.95	-8.45	15.037	-9.95	12.72	-6.43	17.722
Basal area – All conifer species										
Ostrya virginiana	2.88	3.779	2.74	4.567	-0.65	2.041	-0.86	2.148	0.53	0.749
Fagus grandifolia	2.70	4.304	5.77	5.662	-3.39	6.041	-1.52	4.609	1.97	9.159
Acer saccharum	4.77	5.471	6.69	8.32	0.58	7.763	-4.21	7.17	-2.33	4.514
Betula alleghaniensis	8.23	7.732	13.70	9.939	-9.43	11.900	-12.56	6.361	-8.18	13.98
Thuja occidentalis	16.96	11.377	6.74	5.63	-0.68	8.658	-0.68	8.658	--	--
Acer rubrum	8.57	8.211	9.29	8.964	-1.94	9.733	-2.57	10.53	0.05	6.449
Populus tremuloides	9.04	9.623	17.30	11.579	-14.41	13.935	-16.59	14.862	-8.24	9.261
Betula papyrifera	16.23	11.103	17.78	11.789	-8.82	14.707	-10.08	11.895	-7.12	17.898
Basal area - *Abies balsamea*										
Ostrya virginiana	1.6	2.628	1.66	2.927	-1.11	2.141	-1.41	2.193	0.53	0.749
Fagus grandifolia	1.17	2.114	4.13	4.521	-2.09	4.443	-3.44	5.564	-0.28	4.502
Acer saccharum	3.08	4.097	4.61	5.84	-1.54	5.11	-2.17	5.241	-1.99	3.566
Betula alleghaniensis	5.68	6.16	9.95	10.522	-6.94	12.723	-14.68	9.587	-3.85	13.34
Thuja occidentalis	7.64	6.385	3.77	5.369	-2.34	6.694	-2.34	6.694	--	--
Acer rubrum	5.33	6.424	4.01	5.94	-1.12	6.949	-1.65	7.517	0.53	4.499
Populus tremuloides	1.48	3.582	6.06	8.574	-5.22	9.017	-6.11	9.566	-2.69	7.385
Betula papyrifera	6.99	8.254	8.34	10.678	-3.62	11.195	-3.57	7.059	-3.69	15.24
	Basal area - *Picea mariana*									
Ostrya virginiana	0.02	0.091	--	--	--	--	--	--	--	--
Fagus grandifolia	0.14	0.604	0.05	0.278	-0.15	0.541	0.05	0.17	-0.08	0.358
Acer saccharum	0.17	0.932	0.15	0.541	-0.03	0.301	-0.03	0.094	-0.31	0.818
Betula alleghaniensis	0.54	1.883	1.46	2.749	-1.36	2.648	-0.35	0.493	-1.76	3.122
Thuja occidentalis	1.1	2.638	1.49	2.488	0.05	1.674	0.05	1.674	--	--

Acer rubrum	0.92	2.583	1.91	3.961	-0.23	4.332	-0.13	4.731	-0.53	2.799
Populus tremuloides	5.33	7.865	9.56	11.219	-8.98	11.458	-10.79	12.598	-3.84	5.19
Betula papyrifera	8.11	9.306	8.45	9.836	-4.85	9.876	-5.87	10.202	-3.48	9.421

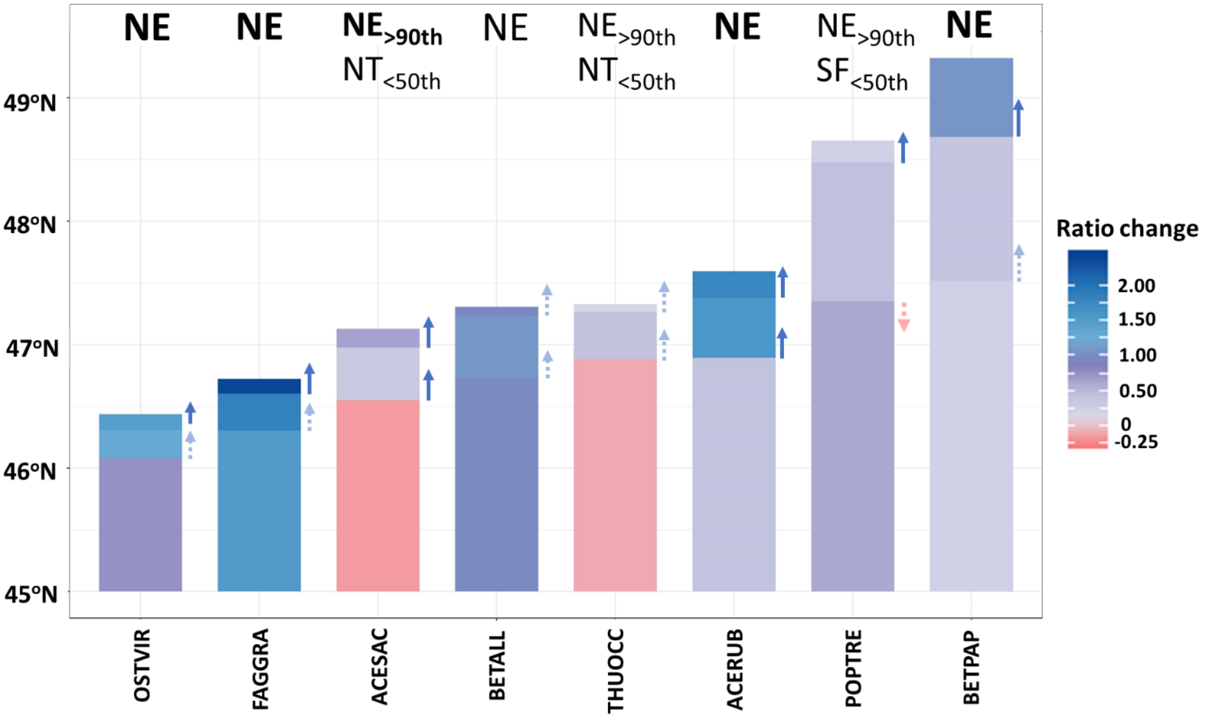


Figure 3.1: Summary of evidence for assessing latitudinal shifts of tree species. Overall response was assessed by combining a) latitudinal range shifts (LRS; as indicated by arrows; upward blue – northward, downward red – southward, significance to 0.05 indicated by solid arrow), b) occupancy changes in the three latitudinal zones (<50th; >50th; >90th); gradient colour (legend on right) indicates increase in the ratio of plots occupied relative to P_1. Ratios indicative of an increase in the number of plots occupied are in purple/blue tones whereas ratios indicative of a decrease in the number of plots are in red tones. Combined range shift pattern for a given species is indicated at the top. Three outcomes were considered: northward range expansion (abbreviated as NE, in combination with increased plot occupancy north of percentile of interest), northward shift by southern range thinning (NT, i.e. with lower plot occupancy south of percentile of interest), southward shift by southern range filling (SF: with higher plot occupancy south of percentile of interest). Bold font indicates that both tests are significant. Species are ordered from left to right according to their 90th percentile latitudinal limit. See Section 8.2.1 for further details.

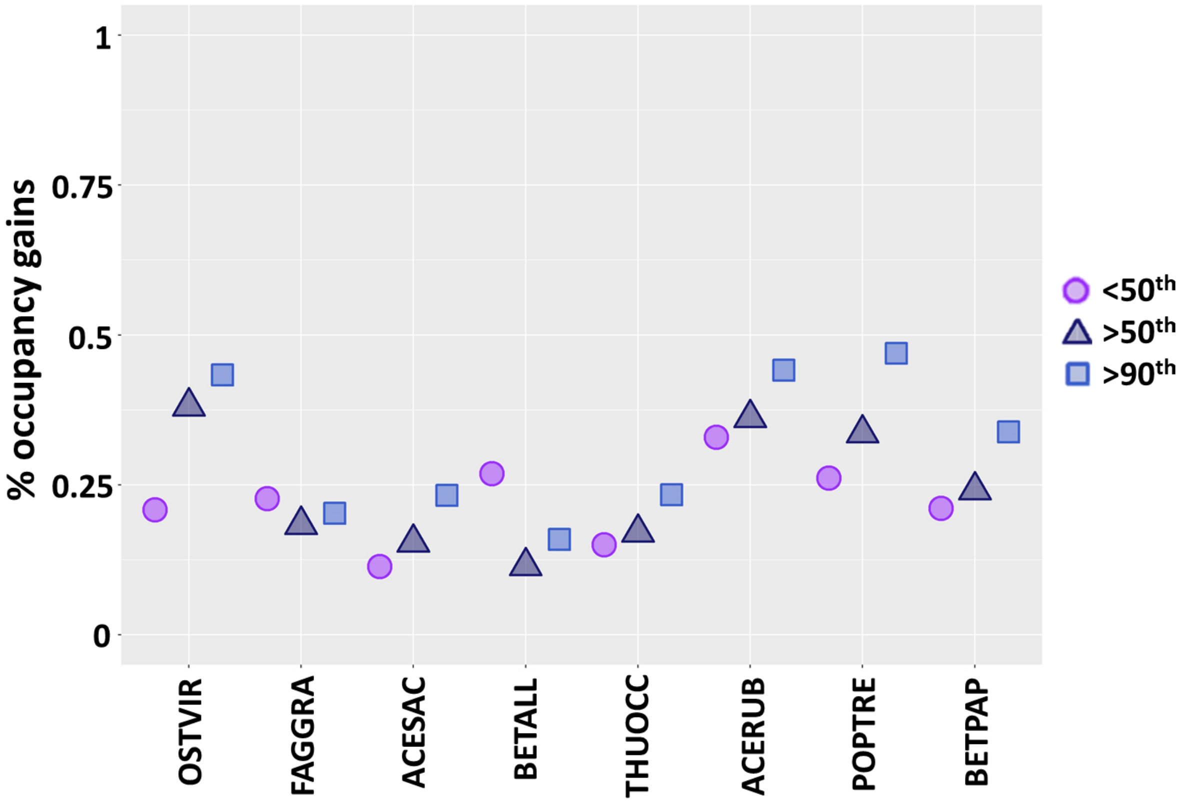


Figure 3.2: Proportion of plots with sapling occupancy gains across latitudinal zones. A gain is recorded when saplings of a target species are observed in a plot in P_3 where that species (regardless of size) was absent in P_1. Three values corresponding to the three latitudinal zones are shown for each target species. Proportion values are relative to the total number of plots with saplings in P_3 and range from 0 (all recruitment occurred where the species was already present in P_1) to 1 (all recruitment resulted in occupancy gains). The three latitudinal zones correspond to those defined by sapling distribution in P_1: south of the 50th latitude (circle), north of the 50th (triangle), and north of 90th (square).

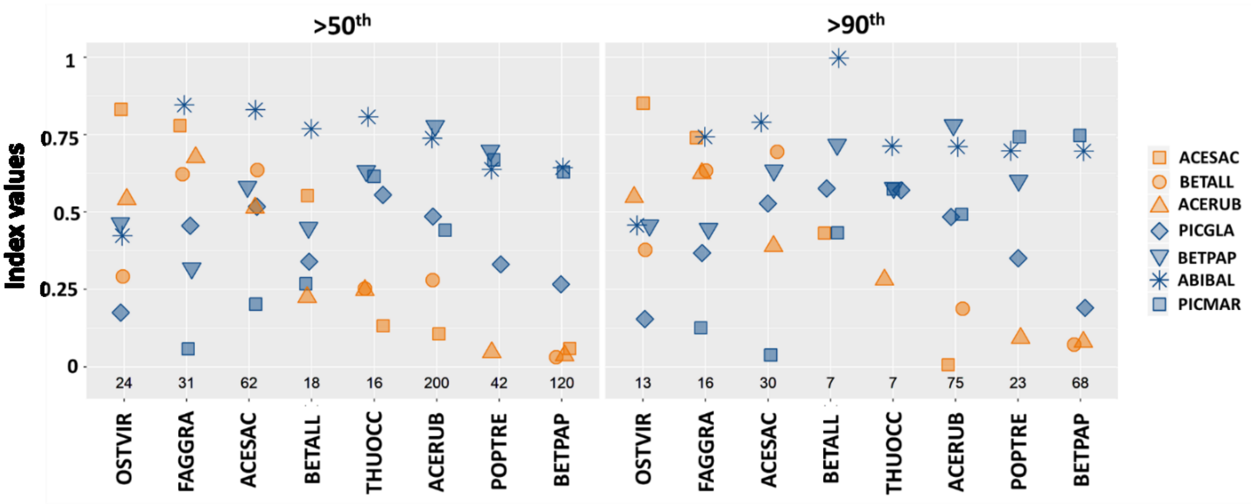


Figure 3.3: Pairwise co-occurrence index values between a target species and an associated species in plots with occupancy gains. For a target species (x-axis), the pairwise co-occurrence index represents the number of shared plots between sites with occupancy gains and an associated species in P_1 (represented by symbols, see legend) relative to the total number of migration sites. The co-occurrence index on the y-axis ranges from 0 (species never co-occur) to 1 (species always co-occur). Two latitudinal zones corresponding to those defined by sapling distribution in P1 are shown: north of the 50th (left), and north of the 90th percentile of latitudinal distribution (right). The total number of observed plots with occupancy gains (i.e., migration plots) for a target species is indicated along the x-axis.

3.9 - References

Barras, N., and M. Kellman. 1998. The supply of regeneration micro-sites and segregation of tree species in a hardwood/boreal forest transition zone. Journal of Biogeography **25**:871-881.

Bauhus, J., D. Paré, and L. Côté. 1998. Effects of tree species, stand age and soil type on soil microbial biomass and its activity in a southern boreal forest. Soil Biology and Biochemistry **30**:1077-1089.

Beauregard, F., and S. de Blois. 2014. Beyond a Climate-Centric View of Plant Distribution: Edaphic Variables Add Value to Distribution Models. PloS one **9**:e92642.

Bertrand, R., G. Riofrío-Dillon, J. Lenoir, J. Drapier, P. de Ruffray, J.-C. Gégout, and M. Loreau. 2016. Ecological constraints increase the climatic debt in forests. Nature Communications **7**:12643.

Boisvert-Marsh, L., C. Périé, and S. de Blois. 2014. Shifting with climate? Evidence for recent changes in tree species distribution at high latitudes. Ecosphere **5**:art83.

Boisvert-Marsh, L., C. Périé, and S. de Blois. 2019. Divergent responses to climate change and disturbance drive recruitment patterns underlying latitudinal shifts of tree species. Journal of Ecology **107**:1956-1969.

Boulanger, Y., S. Gauthier, and P. J. Burton. 2014. A refinement of models projecting future Canadian fire regimes using homogeneous fire regime zones. Canadian Journal of Forest Research **44**:365-376.

Boulanger, Y., A. R. Taylor, D. T. Price, D. Cyr, E. McGarrigle, W. Rammer, G. Sainte-Marie, A. Beaudoin, L. Guindon, and N. Mansuy. 2017. Climate change impacts on forest landscapes along the Canadian southern boreal forest transition zone. Landscape Ecology **32**:1415-1431.

Bradley, R. L., and J. W. Fyles. 1995. Growth of paper birch (*Betula papyrifera*) seedlings increases soil available C and microbial acquisition of soil-nutrients. Soil Biology and Biochemistry **27**:1565-1571.

Brice, M.-H., K. Cazelles, P. Legendre, and M.-J. Fortin. 2019. Disturbances amplify tree community responses to climate change in the temperate–boreal ecotone. Global Ecology and Biogeography **28**:1668-1681.

Brice, M.-H., S. Vissault, W. Vieira, D. Gravel, P. Legendre, and M.-J. Fortin. 2020. Moderate disturbances accelerate forest transition dynamics under climate change in the temperate-boreal ecotone of eastern North America. Global Change Biology **26**:4418-4435.

Brown, C. D., and M. Vellend. 2014. Non-climatic constraints on upper elevational plant range expansion under climate change. Proceedings of the Royal Society B: Biological Sciences **281**. doi:10.1098/rspb.2014.1779

Carteron, A., V. Parasquive, F. Blanchard, X. Guilbeault-Mayers, B. L. Turner, M. Vellend, and E. Laliberté. 2020. Soil abiotic and biotic properties constrain the establishment of a dominant temperate tree into boreal forests. Journal of Ecology **108**:931-944.

Cazelles, K., M. B. Araújo, N. Mouquet, and D. Gravel. 2016. A theory for species co-occurrence in interaction networks. Theoretical Ecology **9**:39-48.

Chen, I.-C., J. K. Hill, R. Ohlemüller, D. B. Roy, and C. D. Thomas. 2011. Rapid range shifts of species associated with high levels of climate warming. Science **333**:1024-1026.

Collin, A., C. Messier, and N. Bélanger. 2017. Conifer Presence May Negatively Affect Sugar Maple's Ability to Migrate into the Boreal Forest Through Reduced Foliar Nutritional Status. Ecosystems **20**:701-716.

Collin, A., C. Messier, B. Côté, M. Fontana, and N. Bélanger. 2016. Contrasting Nutritional Acclimation of Sugar Maple (*Acer saccharum* Marsh.) and Red Maple (*Acer rubrum* L.) to Increasing Conifers and Soil Acidity as Demonstrated by Foliar Nutrient Balances. Frontiers in Ecology and Evolution **4**.

Crête, M., and L. Marzell. 2006. Évolution des forêts québécoises au regard des habitats fauniques: analyse des grandes tendances sur trois décennies. Forestry Chronicle **82**:368-382.

D'Orangeville, L., D. Houle, L. Duchesne, R. P. Phillips, Y. Bergeron, and D. Kneeshaw. 2018. Beneficial effects of climate warming on boreal tree growth may be transitory. Nature Communications **9**:3213.

Danneyrolles, V., S. Dupuis, G. Fortin, M. Leroyer, A. de Römer, R. Terrail, M. Vellend, Y. Boucher, J. Laflamme, Y. Bergeron, and D. Arseneault. 2019. Stronger influence of anthropogenic disturbance than climate change on century-scale compositional changes in northern forests. Nature Communications **10**:1265.

De Frenne, P., F. Rodríguez-Sánchez, D. A. Coomes, L. Baeten, G. Verstraeten, M. Vellend, M. Bernhardt-Römermann, C. D. Brown, J. Brunet, J. Cornelis, G. M. Decocq, H. Dierschke, O. Eriksson, F. S. Gilliam, R. Hédl, T. Heinken, M. Hermy, P. Hommel, M. A. Jenkins, D. L. Kelly, K. J. Kirby, F. J. G. Mitchell, T. Naaf, M. Newman, G. Peterken, P. Petřík, J. Schultz, G. Sonnier, H. Van Calster, D. M. Waller, G.-R. Walther, P. S. White, K. D. Woods, M. Wulf, B. J. Graae, and K. Verheyen. 2013. Microclimate moderates plant responses to macroclimate warming. Proceedings of the National Academy of Sciences of the United States of America **110**:18561-18565.

Ettinger, A. K., and J. HilleRisLambers. 2013. Climate isn't everything: Competitive interactions and variation by life stage will also affect range shifts in a warming world. American Journal of Botany **100**:1344-1355.

Fei, S., J. M. Desprez, K. M. Potter, I. Jo, J. A. Knott, and C. M. Oswalt. 2017. Divergence of species responses to climate change. Science Advances **3**:e1603055.

Fisichelli, N. A., L. E. Frelich, and P. B. Reich. 2013. Climate and interrelated tree regeneration drivers in mixed temperate–boreal forests. Landscape Ecology **28**:149-159.

Fisichelli, N. A., L. E. Frelich, and P. B. Reich. 2014. Temperate tree expansion into adjacent boreal forest patches facilitated by warmer temperatures. Ecography **37**:152-161.

Freeman, B. G., J. A. Lee-Yaw, J. M. Sunday, and A. L. Hargreaves. 2018. Expanding, shifting and shrinking: The impact of global warming on species' elevational distributions. Global Ecology and Biogeography **27**:1268-1276.

Gauthier, S., P. Bernier, T. Kuuluvainen, A. Z. Shvidenko, and D. G. Schepaschenko. 2015. Boreal forest health and global change. Science **349**:819.

Gaüzère, P., L. L. Iversen, J.-Y. Barnagaud, J.-C. Svenning, and B. Blonder. 2018. Empirical Predictability of Community Responses to Climate Change. Frontiers in Ecology and Evolution **6**.

Goldblum, D., and L. S. Rigg. 2002. Age Structure and Regeneration Dynamics of Sugar Maple at the Deciduous/Boreal Forest Ecotone, Ontario, Canada. Physical Geography **23**:115-129.

Gotelli, N. J. 2000. Null model analysis of species co-occurrence patterns. Ecology **81**:2606-2621.

Graignic, N., F. Tremblay, and Y. Bergeron. 2014. Geographical variation in reproductive capacity of sugar maple (*Acer saccharum* Marshall) northern peripheral populations. Journal of Biogeography **41**:145-157.

Hobbie, S. E. 1996. Temperature and Plant Species Control Over Litter Decomposition in Alaskan Tundra. Ecological Monographs **66**:503-522.

IPCC. 2014. Climate Change 2014: Synthesis Report. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change., Geneva, Switzerland.

Jobidon, R., Y. Bergeron, A. Robitaille, F. Raulier, S. Gauthier, L. Imbeau, J.-P. Saucier, and C. Boudreault. 2015. A biophysical approach to delineate a northern limit to commercial forestry: the case of Quebec's boreal forest. Canadian Journal of Forest Research **45**:515-528.

Kwit, M. C., L. S. Rigg, and D. Goldblum. 2010. Sugar maple seedling carbon assimilation at the northern limit of its range: the importance of seasonal light. Canadian Journal of Forest Research **40**:385-393.

Lafleur, B., D. Paré, A. D. Munson, and Y. Bergeron. 2010. Response of northeastern North American forests to climate change: Will soil conditions constrain tree species migration? Environmental Reviews **18**:279-289.

Laganière, J., D. Paré, and R. L. Bradley. 2010. How does a tree species influence litter decomposition? Separating the relative contribution of litter quality, litter mixing, and forest floor conditions. Canadian Journal of Forest Research **40**:465-475.

Leithead, M. D., M. Anand, and L. C. R. Silva. 2010. Northward migrating trees establish in treefall gaps at the northern limit of the temperate-boreal ecotone, Ontario, Canada. Oecologia **164**:1095-1106.

Lenoir, J., R. Bertrand, L. Comte, L. Bourgeaud, T. Hattab, J. Murienne, and G. Grenouillet. 2020. Species better track climate warming in the oceans than on land. Nature Ecology & Evolution **4**:1044-1059.

Lenoir, J., J. C. Gégout, A. Guisan, P. Vittoz, T. Wohlgemuth, N. E. Zimmermann, S. Dullinger, H. Pauli, W. Willner, and J. C. Svenning. 2010. Going against the flow: potential mechanisms for unexpected downslope range shifts in a warming climate. Ecography **33**:295-303.

Lenoir, J., and J. C. Svenning. 2015. Climate-related range shifts – a global multidimensional synthesis and new research directions. Ecography **38**:15-28.

Louthan, A. M., D. F. Doak, and A. L. Angert. 2015. Where and When do Species Interactions Set Range Limits? Trends in Ecology & Evolution **30**:780-792.

McKenney, D. W., J. H. Pedlar, R. B. Rood, and D. Price. 2011. Revisiting projected shifts in the climate envelopes of North American trees using updated general circulation models. Global Change Biology **17**:2720-2730.

Ministère des Forêts, Faune et des Parcs. 2015. Normes techniques, Placettes-Échantillons Permanentes, 4e inventaire écoforetier du Québec méridional. Ministère des Forêts, Faune et Parcs, Direction des Inventaires Forestiers, Québec, Québec.

Nagati, M., M. Roy, S. Manzi, F. Richard, A. Desrochers, M. Gardes, and Y. Bergeron. 2018. Impact of local forest composition on soil fungal communities in a mixed boreal forest. Plant and Soil **432**:345-357.

Pedlar, J. H., D. W. McKenney, I. Aubin, T. Beardmore, J. Beaulieu, L. Iverson, G. A. O'Neill, R. S. Winder, and C. Ste-Marie. 2012. Placing Forestry in the Assisted Migration Debate. BioScience **62**:835-842.

Pellissier, L., K. A. Bråthen, J. Pottier, C. F. Randin, P. Vittoz, A. Dubuis, N. G. Yoccoz, T. Alm, N. E. Zimmermann, and A. Guisan. 2010. Species distribution models reveal apparent competitive and facilitative effects of a dominant species on the distribution of tundra plants. Ecography **33**:1004-1014.

Peres-Neto, P. R., J. D. Olden, and D. A. Jackson. 2001. Environmentally constrained null models: site suitability as occupancy criterion. Oikos **93**:110-120.

Périé, C., and S. de Blois. 2016. Dominant forest tree species are potentially vulnerable to climate change over large portions of their range even at high latitudes. PeerJ **4**:e2218.

Renwick, K. M., and M. E. Rocca. 2015. Temporal context affects the observed rate of climate-driven range shifts in tree species. Global Ecology and Biogeography **24**:44-51.

Royo, A. A., and W. P. Carson. 2006. On the formation of dense understory layers in forests worldwide: consequences and implications for forest dynamics, biodiversity, and succession. Canadian Journal of Forest Research **36**:1345-1362.

Saucier, J.-P., P. Grondin, A. Robitaille, and J.-F. Bergeron. 2003. Zones de végétation et les domaines bioclimatiques du Québec. Direction des inventaires forestiers, Ministère des Ressources naturelles et de la Faune, Québec, Québec.

Seidl, R., J. Honkaniemi, T. Aakala, A. Aleinikov, P. Angelstam, M. Bouchard, Y. Boulanger, P. J. Burton, L. De Grandpré, S. Gauthier, W. D. Hansen, J. U. Jepsen, K. Jõgiste, D. D. Kneeshaw, T. Kuuluvainen, O. Lisitsyna, K. Makoto, A. S. Mori, D. S. Pureswaran, E. Shorohova, E. Shubnitsina, A. R. Taylor, N. Vladimirova, F. Vodde, and C. Senf. 2020. Globally consistent climate sensitivity of natural disturbances across boreal and temperate forest ecosystems. Ecography **43**:967-978.

Sheth, S. N., and A. L. Angert. 2018. Demographic compensation does not rescue populations at a trailing range edge. Proceedings of the National Academy of Sciences **115**:2413.

Sittaro, F., A. Paquette, C. Messier, and C. A. Nock. 2017. Tree range expansion in eastern North America fails to keep pace with climate warming at northern range limits. Global Change Biology **23**:3292-3301.

Solarik, K. A., K. Cazelles, C. Messier, Y. Bergeron, and D. Gravel. 2020. Priority effects will impede range shifts of temperate tree species into the boreal forest. Journal of Ecology **108**:1155-1173.

Solarik, K. A., C. Messier, R. Ouimet, Y. Bergeron, and D. Gravel. 2018. Local adaptation of trees at the range margins impacts range shifts in the face of climate change. Global Ecology and Biogeography **27**:1507-1519.

Svenning, J.-C., and B. Sandel. 2013. Disequilibrium vegetation dynamics under future climate change. American Journal of Botany **100**:1266-1286.

Thuiller, W., D. Georges, R. Engler, and F. Breiner. 2016. biomod2: Ensemble platform for species distribution modeling. R package version 3.3-7. R Foundation for Statistical Computing Vienna, Austria.

Tremblay, M. F., Y. Bergeron, D. Lalonde, and Y. Mauffette. 2002. The potential effects of sexual reproduction and seedling recruitment on the maintenance of red maple (*Acer rubrum* L.) populations at the northern limit of the species range. Journal of Biogeography **29**:365-373.

Werner, C. M., D. J. N. Young, H. D. Safford, and T. P. Young. 2019. Decreased snowpack and warmer temperatures reduce the negative effects of interspecific competitors on regenerating conifers. Oecologia **191**:731-743.

Wilson, J. R. U., E. E. Dormontt, P. J. Prentis, A. J. Lowe, and D. M. Richardson. 2009. Something in the way you move: dispersal pathways affect invasion success. Trends in Ecology & Evolution **24**:136-144.

Wisz, M. S., J. Pottier, W. D. Kissling, L. Pellissier, J. Lenoir, C. F. Damgaard, C. F. Dormann, M. C. Forchhammer, J.-A. Grytnes, A. Guisan, R. K. Heikkinen, T. T. Høye, I. Kühn, M. Luoto, L. Maiorano, M.-C. Nilsson, S. Normand, E. Öckinger, N. M. Schmidt, M. Termansen, A. Timmermann, D. A. Wardle, P. Aastrup, and J.-C. Svenning. 2013. The role of biotic interactions in shaping distributions and realised assemblages of species: implications for species distribution modelling. Biological Reviews **88**:15-30.

Zhang, X., G. Flato, M. Kirchmeier-Young, L. Vincent, H. Wan, X. Wang, R. Rong, J. Fyfe, G. Li, and V. Kharin. 2019. Changes in temperature and precipitation across Canada; Chapter 4. Pages 112-193 *in* E. Bush and D. S. Lemmen, editors. Canada's Changing Climate Report. Governemnt of Canada, Ottawa, Ontario.

Zhu, K., C. W. Woodall, and J. S. Clark. 2012. Failure to migrate: lack of tree range expansion in response to climate change. Global Change Biology **18**:1042-1052.

CONNECTING TEXT

In Chapter 3, I showed that northward migration for temperate species is indeed occurring and examined which biotic and abiotic factors characterize migration pathways. Results suggest that warming and disturbances can open up the way for novel species associations. Specifically, two species that are tolerant of conditions in the boreal forest, *Acer rubrum* and *Betula papyrifera,* may provide migration pathways for other more meridional species. In the following study, I assessed the relative influence of climate change, disturbance and their interaction on species recruitment for four species of the northern temperate forest (*Acer rubrum*, *Acer saccharum*, *Betula alleghaniensis* and *Fagus grandifolia*). I focused on sets of variables within each of these factors that could influence recruitment (climate change – annual, seasonal or monthly variables; disturbance – type and timing). I also evaluated how the relationship between each of these components varies along a latitudinal gradient.

Chapter 4 - DIVERGENT RESPONSES TO CLIMATE CHANGE AND DISTURBANCE DRIVE RECRUITMENT PATTERNS UNDERLYING LATITUDINAL SHIFTS OF TREE SPECIES

Authors : Laura Boisvert-Marsh[1], Catherine Périé[2], Sylvie de Blois[1, 3]

Affiliations

[1]Department of Plant Science, Macdonald Campus of McGill University, 21111 Lakeshore, Ste-Anne-de-Bellevue, Québec, H9X 3V9, Canada.

[2]Direction de la recherche forestière, Ministère des Forêts, de la Faune et des Parcs du Québec, Complexe Scientifique, 2700 rue Einstein, Québec, Québec, G1P 3W8, Canada.

[3]McGill School of Environment, McGill University, 3534 University St., Montreal, Quebec, H3A 2A7

This manuscript was published as:

Boisvert-Marsh, L., Périé, C. and de Blois, S. 2019. Divergent responses to climate change and disturbance drive recruitment patterns underlying latitudinal shifts of tree species. Journal of Ecology 107(4), 1956-1959. It is presented in this thesis with permission of the publisher (Wiley).

4.1 - Abstract

1. Climate change is expected to result in a reorganization of the continental distribution of tree species. Recent shifts in distribution patterns have been reported, but it is not always clear how climate change influences these patterns locally, especially in relation to other disturbances.

2. We investigated latitudinal shifts of four ecologically important tree species between 1970 and 2014 within a study area that encompasses their northernmost range limit in northeastern North America (Quebec, Canada; ~761 000km^2). Changes in latitudinal limits were defined in relation to changes in tree saplings' occurrence patterns within forest plots resampled over two time periods (1970-1977 and 2003-2014). By examining changes in the frequency of occurrences in different portions of the study area along a latitudinal gradient, we were able to identify spatially explicit patterns of loss or gain (sapling recruitment) resulting in the shifts observed. We then estimated the probability of observing a recruitment event in response to changes in climate, disturbance and their interaction, using a multimodel selection approach.

3. Latitudinal limits of all four species shifted northward, but these shifts resulted from different patterns of plot occurrence changes, depending on the species and the location examined. Greater recruitment at northern locations than at southern ones drove shifts for *Acer saccharum* Marsh*.,* *Fagus grandifolia* Ehrh., and *Acer rubrum* L., but less so for *Betula alleghaniensis* Britt. Climate variables indicating changes in early or late growing season conditions were most often selected in models. Warming tended to reduce recruitment probability in the south but increase it in the north, leading to divergent responses for a given species across the study area. Disturbance effects were generally less important than climate change effects, as was their interaction.

4. Synthesis – Spatially explicit and divergent responses to climate change and disturbance drive recruitment patterns underlying latitudinal shifts of tree species. The importance of early- or late-season climate variables points towards biological processes being affected at critical stages of the life cycle. Understanding the factors that influence species' migration capacity in a changing climate is crucial to inform adaptive management and conservation practices.

Keywords: Climate change; forest dynamics; Global change ecology; latitudinal shift; long-term forest monitoring; range shift; tree migration; Quebec, Canada.

4.2 - Introduction

As climate change intensifies, the long-term consequences on biodiversity must be considered to minimize negative impacts on ecosystem productivity and livelihoods. Expected biotic responses to climate change include upward (elevational) or poleward (latitudinal) migration of species, although the former has been documented for plants more than the latter (Lenoir and Svenning 2015, Yalcin and Leroux 2017). Climate tends to change over larger distances along latitudinal gradients than for elevational ones, and tree range displacement involves relatively slow processes of reproduction, dispersal and establishment (Aubin et al. 2018). The magnitude of climate warming is particularly strong at northern latitudes and can put pressure on species to migrate toward more suitable habitats (Chen et al. 2011, Xu et al. 2013). The pressure to shift could result in a long-term reorganization of the continental distribution of species in response to warming, with major consequences for the management of biodiversity and related regulatory frameworks (Berteaux et al. 2018).

For trees, evidence of potential latitudinal (or longitudinal) range shifts is mostly based on the observation of temporal changes in the spatial distribution of occurrence or abundance patterns (Zhu et al. 2012, Boisvert-Marsh et al. 2014, Sittaro et al. 2017). Range shifts can result from a variety of site- and species-specific processes that lead to new occurrences or increased abundance at some locations and declines at others. For instance, a northward shift in latitudinal range limits for a species can result from increased recruitment in the northern portion of the range and/or from decreased site occurrence in the south (Lenoir and Svenning 2015). A better understanding of changing distribution patterns in different portions of the range can therefore reveal important processes driving species responses at broad scales.

Climate change has been linked to range shifts of tree species during the Holocene (Davis and Shaw 2001), with site factors shown to influence local responses (Schwörer et al. 2017). While climate factors are also assumed to drive recent observations of range shifts (Evans and Brown 2017), there is limited evidence of a direct relationship between patterns of range shifts and climate change. The availability of suitable data, such as repeated surveys of forest trees of North America over time periods at which climate change is usually considered (~30 years) and from longer chronologies established from tree rings, has begun to provide valuable insights into the spatially explicit responses of species to climate. For instance, whereas poleward shifts driven by increases in temperature were expected at high latitudes, westward shifts in species abundance associated with changes in moisture availability were also documented for trees in the eastern United States (Fei et al. 2017). These westward shifts were larger (median rate 15.4 km per decade) than the latitudinal ones (11.0 km per decade) and resulted from increased stem density at the leading edge. The rate and direction of range shifts were shown to vary by region and species traits. Over the past ~ 60 years in boreal forests of Canada, tree growth rates demonstrated strong region- and species-specific trends, linking negative growth responses to increasing temperature and positive responses to increasing precipitation, but no consistent boreal-wide response to climate change (Girardin et al. 2016). Interestingly, in eastern North America, correlations between *Picea mariana* (Mill.) B.S.P. growth and temperature in Quebec, Canada differed across the study area, from negative south of 49°N to positive north of that latitude (D'Orangeville et al. 2016). Evidence from these recent studies points to spatially explicit processes that control tree growth or abundance and which cannot easily be averaged over the entire range of a species. Studies on the response of tree growth or abundance to changes in climate provide valuable information within the range, but range shift will ultimately result in the recruitment of juveniles at sites previously unoccupied or where recruitment had been previously unsuccessful, and so recruitment patterns must be examined. Juvenile stages tend to be more sensitive to climate stress than adult stages (Munier et al. 2010, Kueppers et al. 2017), therefore the spatial dynamics of juveniles (i.e. saplings) both within the range and at range edges can provide an early signal to evaluate the potential for range expansion (Boisvert-Marsh et al. 2014). Recruitment patterns offer evidence of successful reproduction and establishment or, conversely can suggest constraints, including climatic ones, on life cycle events (Smithers et al. 2018).

In most parts of the world, land use and natural disturbances have modified species composition, creating opportunities for juvenile recruitment and community redistribution (Leithead et al. 2010, Lembrechts et al. 2016). If natural or anthropogenic disturbances are spatially structured, their broad scale effect can be confounded with that of climate change (Lenoir et al. 2017, Liang et al. 2018). For instance, forestry activities in our study area (Quebec, Canada) tend to show a progression from south to north over time. Disturbance resulting from logging could match (or not) northward range shifts expected from climate change, highlighting the importance of taking disturbance into account in range shift studies. Also, climate change can modify the frequency and/or amplitude of natural (Dale et al. 2001) or human-induced disturbance (Perring et al. 2018), suggesting an important role for the interaction between climate change and disturbances in explaining range shifts (Lembrechts et al. 2016, Dainese et al. 2017). Focusing on elevational gradients, Guo et al. (2018) recently reported an interaction effect between average temperature conditions and forest loss at the site level in relation to rates of elevational shift, although the change in climate over time itself was not a major predictor in their models. The influence on range dynamics of climate change, disturbances and their interaction has not been well investigated over a broad latitudinal gradient, especially in relation to the recruitment processes that ultimately drive range shifts.

In a previous study, we addressed a gap in the climate change/biodiversity literature by providing some of the first evidence of recent latitudinal range shifts of 11 tree species at northern latitudes across a broad geographical extent (Boisvert-Marsh et al. 2014). We interpreted our results as an early signal of the potential for some species to track (or not) changes in climate, but the direct effect of climate on range shifts was not evaluated at the time. Here, we investigate patterns and processes of latitudinal range shifts of four tree species in Québec, Canada across an area ~761 100 km^2. We use a repeat survey of 6309 forest plots between 1970 and 2014 and focus on common tree species that reach their northern range limit in the study area. The 15 warmest years on record have occurred consecutively since 2001 (National Center for Environmental Information, 2016) and so species could have benefited from extended growing seasons, especially at the northern edge of their distribution. We first define changes in latitudinal limits in relation to changes in tree saplings' occurrence patterns within forest plots resampled over two time periods (1970-1977 and 2003-2014). By examining changes in the frequency of occurrences in different portions of the study area along a latitudinal gradient, we can identify spatially explicit patterns of loss or gain (sapling recruitment) resulting in the shifts observed. As disturbances can provide opportunities for recruitment separately or in interaction with climate change (Leithead et al. 2010, Zhang et al. 2015), we then estimate the probability of observing a recruitment event in response to changes in climate, disturbance and their interaction, using a multimodel selection approach. We generally expected the probability of sapling recruitment to increase with warming, especially at these high latitudes, but that relationship can change in space (Cavanaugh et al. 2014, Fisichelli et al. 2014, Miller et al. 2017). We also expected the disturbance signal to be more important than the climate signal given the prevalence of disturbances in the study area.

4.3 - Methods

4.3.1 **-** *Study area*

The province of Québec (Canada) encompasses about 2% of all forested areas in the world and a significant proportion of all boreal forests (Saucier et al. 2003); *Ministry of Forests, Wildlife and Parks* (MFFP), <http://www.mffp.gouv.qc.ca/english/international/forests/index.jsp >). Our study area (Fig. 4.1) covers roughly 761 100 km² in Quebec, from 45°N to 53°N (the northern limit of current forestry activities), and from 80°W to 61°W (Saucier et al. 2003). Two major vegetation zones, each with two forest types, are part of the study area: the northern temperate zone and the boreal forest zone (Saucier et al. 2003). The former includes *Acer saccharum* dominated forests to the south and mixed *Abies balsamea* (L.) Mill.-*Betula alleghaniensis* Britt. forests to the north. The latter includes *A. balsamea*-*Betula papyrifera* Marsh. forests to the south and vast *P. mariana*-moss forests to the north (Saucier et al. 2003).

4.3.2 **-** *Data collection*

We used extensive forest inventories of permanent plots to monitor long-term forest dynamics throughout the study area, ensuring consistency in sampling (Ministère des Forêts, Faune et des Parcs 2015; Dataset available from https://www.donneesquebec.ca/recherche/fr/dataset/placettes-echantillons-permanentes-1970-a-aujourd-hui). Data collection started in 1970 and is ongoing. Four inventory campaigns have been completed across the permanent plot network. Previous work (Boisvert-Marsh et al. 2014) considered range shifts in tree species between 1970-1977 (hereafter called P_1) and 1992-2002 (P_2). This study uses P_1 and the most recent complete inventory available from the MFFP, 2003-2014 (hereafter called P_3 for continuity). Plots of 400 m^2 are usually paired for sampling at an average distance of 425 m. Plot density decreases northward, along with tree species diversity (1 pair of plots per 26 km^2 in the *A. saccharum* forest, 1 pair per 104 km^2 in the *Abies balsamea* forest and 1 pair per 259 km^2 in the *Picea mariana* forest).

We focused on four deciduous species typical of the temperate and mixed forest domains: *Fagus grandifolia* Ehrh., *Acer saccharum* Marsh.*,* *Betula alleghaniensis* Britt. and *Acer rubrum*

L. All species reach their northern limit in the study area, showed significant northward expansion in an earlier time period (Boisvert-Marsh et al. 2014), and had sufficient occurrences for statistical analysis. We used species data from the earliest (1970-1977; P_1) and most recent inventory (2003-2014; P_3); each inventory took between 7 and 11 years to complete. Within these inventories, the precise survey date at each plot was known and used to access climate information. Plots were sampled on average 33.8 ± 3.79 years apart. Of those plots where at least one of the study species was likely to be observed, 72% were inventoried within 3 years of the mean (minimum: 26 years, maximum: 44 years). So, we expect the temporal discrepancy across the study area to be minimal on overall forest dynamics. For inventory purposes, the MFFP defines a sapling has having a diameter at breast height (DBH) of 1.1-9.0cm DBH, grouped by 2cm DBH classes, and >=1.3m tall. Saplings of the smallest size class (1.1-3.0 cm DBH; hereafter called "saplings") are considered to be indicative of successful establishment and were retained for this study. Sapling sampling methods are consistent between inventories, but seedling data collection had only begun in P_2 and therefore seedlings were not considered. Species occurrence data, as indicated by presence/absence at a plot, were used to assess changes in spatial patterns over time. Saplings of a given species were either present or absent in P_1 and P_3. Climate has been shown to predict frequency of occurrence at different latitudes better than species importance value in a plot (Canham and Thomas 2010, Chambers et al. 2013), especially approaching species range limits (Pironon et al. 2017).

4.3.3 - *Disturbance data*

In each plot, presence/absence of each type of disturbance were noted during each inventory (for a list of variables, see Fig. 4.1 and Section 8.3.1). When the inventories began (P_1), 29.0% of plots had been affected by natural (windthrow, fire, insect outbreaks) and/or anthropogenic disturbances (i.e. logging: selective harvest, partially harvested or clearcut). The proportion of disturbed plots increased to 30.6% in P_3, mainly driven by anthropogenic disturbance (15.8% of plots in P_1, 19.0% in P_3), whereas natural disturbances were somewhat less prevalent in P_3 over P_1 (13.2% of plots in P_1, 11.6% in P_3). In this study, we differentiated only between 'natural disturbances' (all types) and 'logging' (all types), and their timing as observed in each inventory.

4.3.4 - *Climate data*

Climate data used in this study covers the period from 1965 to 2014. This includes a 5-year period prior to the first forest inventory in 1970 and ends with the most recent inventory. These climate data were modeled from Environment Canada weather station data using the BioSIM program (Regnière and Saint-Amant 2014), which interpolates temperature and precipitation around a sampling plot at a 1km resolution using a weighted average of the four closest weather stations, correcting for differences in elevation. Climate observations attributed to the forest plots reveal a study area characterized by strong latitudinal climatic gradients. When all plots are considered over the whole time period, mean annual temperature ranged from 6.9°C in the south to -4.4°C in the north. During that time, mean annual temperature increases ranged from +0.08°C to +1.91°C, with no plots showing a decrease. There were, however, monthly or seasonal variations, including cooling for some plots. The strongest warming occurred in the southwest and center-north of the study area and in the recent time period (P_3). Overall annual precipitation ranged from 743mm to 1543mm. Precipitation gradients exist, decreasing from south to north and from east to west. There was no overall significant change in annual precipitation between 1965 and 2014, but trends varied greatly among plots. Change in total annual precipitation ranged from -268mm to +269mm, averaging - 0.302 mm overall. For a list of all climate variables used in this study, see Section 8.3.1 in Supporting Information.

4.3.5 - *Assessing latitudinal shifts*

We used two methods to assess latitudinal shifts (Fig. 4.1). First, using species occurrence data, we quantified the magnitude and direction of latitudinal shifts as the change in limit location over time. We used the percentile approach to define limits because it reduces the potential bias of extreme latitudinal data points (Lenoir et al. 2009). Latitudinal shifts were assessed at both the median (50^{th}) percentile of distribution and at the 90^{th} percentile of distribution (northernmost) using relevant methods for each (described in Section 8.1 and Boisvert-Marsh et al. 2014). Note that, because of the northern location of our study area, the 50^{th} percentile of latitude does not reflect the median latitude of the entire north-south range of a species but the median within our study area. However, within our study area, the 90^{th} percentile does encompass the northernmost range limit for our four study species and captures sufficient presence points for statistical analysis in the next step. Latitudinal differences were calculated between inventories (P_3 - P_1), with positive values indicating northward latitudinal shift and negative values southward. The significance level was set to 0.05 using non-parametric methods appropriate for non-independent samples (bootstrap resampling at the 50th percentile, pooled confidence intervals at the 90th percentile).

Because latitudinal limits are determined based on occurrence patterns at different latitudes, northward shifts over time can occur when 1) the number of plots occupied south of the limit of interest (in this case, 50th or 90th percentile of latitude) decreases more than north of that limit; 2) when the number of plots occupied north of a limit increases more than south of that limit or 3) a combination of both 1 and 2. To understand changes in latitudinal limits across the northern range, we examined changes in plot occurrence between P_1 and P_3 in different portions of the study area as determined by latitudinal limits in P_1. Three portions of the study area were evaluated: 1) south of the species' P_1 distribution median (i.e., <50th), 2) north of the species' P_1 median (i.e., >50th) and 3) north of the species' P_1 northernmost limit (i.e., >90th). McNemar's test for paired samples was used to see if the frequency of presence/absence in an area was statistically different ($p <= 0.05$) between the two inventories.

4.3.6 **-** *The relationship between climate change, disturbances and sapling recruitment*

For this analysis, we focused on plots where a given species (saplings) was absent in P_1, but present in P_3. This was considered a recruitment event or occurrence gain (hereafter called Occ_{gain}). Sampled plots with Occ_{gain} were compared with plots where there was no recruitment (species absent in both time periods). Plots where there was no observed recruitment needed nevertheless to be suitable for the species. To determine suitable 'absences', we used a consensus species distribution modelling approach based on overall climate gradients related to temperature and precipitation, edaphic variables and topographic factors (Beauregard and de Blois 2014, Périé and de Blois 2016).

5.3.6.1 **-** *Climate vs. disturbance*

For each species, we evaluated the probability of observing an occurrence gain in relation to climate change, disturbance, and their interaction. Climate change was defined as the climate conditions observed in P_3 minus the climate conditions in P_1 (hereafter called Δclimate). Thirteen Δ climate variables were selected in preliminary analyses (Fig. 4.1) and grouped based on temporal variation (annual, seasonal, early or late season, monthly). Climate variables with a finer temporal resolution may have as much or more weight in models as annual ones, but could also point to specific life events (i.e., coincide with timing of flowering or establishment). Because we were measuring trends in climate associated with a given plot, each climate variable was averaged over a five-year period preceding the year of a recorded observation (e.g., 2000-2005 for a 2005 observation). Disturbance was characterized by whether a plot was disturbed or not, its type (logging vs. natural), and the timing of the disturbance event (Δclimate and disturbance variables listed in Fig. 4.1).

We used a multimodel selection approach (Alofs and Jackson 2015) to evaluate the probability of observing an Occ_{gain} in relation to our explanatory variables. Seven candidate models, relating different combinations of climate, climate change and disturbance to observed Occ_{gain} were tested in four different areas of the suitable distribution, based on the calculated latitudinal limit in P_1: a) entire suitable area, b) south of the 50th percentile (<50th), c) north of the 50th percentile (>50th) and d) north of the 90th percentile (>90th). Models 1 and 2 were the best Δclimate model and the best disturbance model respectively selected from pre-analyses on four non-nested submodels (Δclimate 1a-1d; Disturbance – 2a-2d). Best models were selected using the lowest AIC in each subgroup. The best Δclimate variable from Model 1 and the best disturbance variable from Model 2 were identified based on the highest absolute Wald z value, as obtained from the model outputs (Tables in Section 8.3.2) and were then used to construct Models 3 to 6. By using the model Wald z value, binary and continuous variables can be compared for their relative explanatory power in the various models (Agresti 2013). Models 3-6 evaluated combinations of best Δclimate and best disturbance variables, as main effects and in interaction, including their interactions with the climate gradient (Fig. 4.1, best variables listed in Table 4.1). Logistic regression with a logit link using a mixed-model approach was used to compare plots with Occ_{gain} to plots without gains. Longitudinal band (2° wide) was used as a random factor in the generalized linear mixed models to account for potential variation in the response variable induced by the broad east-west climatic gradient. All data analyses were done in R, version 3.3.2 (R Core Team, 2016).

4.4 - Results

4.4.1 - *Latitudinal shifts*

The latitudinal limits of saplings of all four species shifted northward between P_1 and P_3 for both the 50th and 90th percentiles of distribution (Fig. 4.2a). These shifts, however, were driven by different patterns of occurrence changes depending on the species and the portion of the study area examined (Fig. 4.2b). The greatest latitudinal shifts across the study area were seen for *A. rubrum* followed by *A. saccharum*. Their limits moved significantly northward for both the 50th and 90th percentiles (*A. rubrum:* +27.1km and +23.6km; *A. saccharum:* +18.2km and +17.4km; Tables 8.1.1 and 8.1.2). *Acer rubrum* underwent significant occurrence increases relative to the P_1 in all parts of the study area, but more so north of the 50th, including north of the 90th (Fig. 4.2b). *Acer saccharum*, on the other hand, underwent significant occurrence decreases south of the 50th, but saw significant occurrence increases north of the 50th and 90th percentiles. Smaller occurrence increases were observed compared to those of other species, but the combined effect of increase in the north and decrease in the south contributed to amplify latitudinal shifts for this species (Fig. 4.2b).

The latitudinal range of *B. alleghaniensis* shifted the least of all species, and its shifts were non-significant (+1.5km and +4.2km at 50th and 90th percentiles respectively: Fig. 4.2a, Tables 8.1.3.1 and 8.1.3.2). Nevertheless, *B. alleghaniensis* showed significant occurrence increases across the study area. The fact that these occurrence increases were relatively similar in all portions of the study area explains the limited overall shifts observed. *Fagus grandifolia* showed a non-significant northward shift at the 50th (+2.3km, Table 8.1.1), but a significant northward shift at the 90th (+13.2km, Table 8.1.2). Significant, relatively high occurrence increases were observed across the study area, but more so north of the 90th, explaining the significant shift observed at this latitude.

4.4.2 - *The relationship between climate change, disturbances and sapling recruitment*

Observed occurrence gains (Fig. 4.3) and their association with climate change and disturbance (Fig. 4.4) were spatially structured across the study area. When considering Model 1 alone (Δclimate), predictors measuring changes in early and late growing season variables were most often retained in pre-analyses: October Δgdd5 (6 times), April Δgdd5 (5), Annual Δgdd5 (3), and twice for monthly variables (Summer ΔTmax: 1 and July Δprecipitation: 1) (Table 4.1). When considering Model 2 only, which compared disturbance variables, those most often retained in pre-analyses were the models distinguishing between human or natural disturbance in the earliest time period (11 times - logging P_1: 7, natural $P_{1:}$ 4) or the latest (3 times - natural P_3: 2, logging $P_{3:}$ 1), followed by presence of disturbance (1) and newly disturbed in P_3 (1) (Table 4.1).

For forest plots, whereas annual Δgdd5 have increased almost everywhere, that increase has been more pronounced in the northwestern portion of the study area (Fig. 4.4d). Maximum summer temperatures have increased (Fig. 4.4c) and precipitation (Fig. 4.4e) have decreased to greater extents in the west. October Δgdd5 show positive (i.e., longer growing season in the fall) values mostly in the center of the study area and around the Gaspe peninsula in the east, but negative ones elsewhere (Fig. 4.4b). April Δgdd5 show the strongest increases in the southeastern corner (longer growing season in the spring) along the American border (Fig. 4.4a).

Overall, amongst all species, the best models (Table 4.2) were (in decreasing order): Model 3 (ΔC_{best} + $Dist_{best}$ - 7 times), Model 1 (Δclimate only - 2), Model 4 (ΔC_{best} x $Dist_{best}$ interaction - 2), Model 5 (Cgr x $Dist_{best}$ interaction: 2), Model 2 (Disturbance only - 1), Model 6 (Cgr x ΔC_{best} interaction - 1), and Model 7 (null model - 1). For individual species, however, relationships between the predictors and response varied depending on the portion of the study area. For *F. grandifolia*, larger increases in October Δgdd5 had a positive impact on recruitment when the entire suitable area was considered. This was also true north of the 50th percentile, even though half of the suitable plots saw decreases in October Δgdd5 (Fig. 4.4b). At the northern edge (>90th percentile) where this species had its strongest occurrence increases (Fig. 4.2b), the best model included Δclimate only, and larger increases in July Δprecipitation were associated with higher probability of gains in sapling occurrence (Occ_{gain}). Other seasonal climate variables at this latitude tended to have positive effects, except for an increase in March Δminimum temperature. South of the 90th percentile, larger increases in April Δgdd5 negatively affected Occ_{gain}. When retained in the model, logging in P_1 had a negative impact on Occ_{gain} in all portions of the study area, but was consistently outscored by ΔClimate variables in the best models. Logging in P_1 tended to interact positively with an extended growing season in the spring south of the 50th percentile, but the relationship was only marginally significant.

Acer saccharum's response was spatially structured across the entire study area, as evidenced by the inclusion of the latitudinal climate gradient term (gdd5 P_3 (CGr): Table 4.2). South of the 50th percentile, where occurrence decreases were observed (Fig. 4.2b), the best model was Δclimate only (Model 1) and larger increases in annual Δgdd5 reduced the probability of observing an occurrence gain. Approaching the northern range limit, models including ΔC_{best} and $Dist_{best}$ had the most support, with larger increases in April Δgdd5 increasing the probability of Occ_{gain}. In these models, disturbance variables for the most recent period (P_3) were retained.

Betula alleghaniensis had similar occurrence increases across the study area (Fig. 4.2b). Larger increases in maximum summer temperatures increased the probability of Occ_{gain} overall, while in the south larger increases in April Δgdd5 had a negative impact. North of the 50th percentile, a disturbance only model was retained, with natural disturbances in P_1 having a marginally negative impact. The null model was selected north of the 90th.

Finally, *A. rubrum* had significant gains everywhere, but not as great in the southern portion of the study area (Fig. 4.2b). This species seemed most impacted by disturbances relative to climate (Table 4.2), with past natural disturbances increasing the probability of Occ_{gain} south of the 50th percentile, while logging reduced gain probability north of the 50th. Extending the growing season in the fall reduced Occ_{gain} probability, most significantly at the northernmost edge.

4.5 - Discussion

The latitudinal shift patterns we observed for four northern temperate hardwood tree species were generally consistent with climate change predictions of northward shifts at the northern range limit (Périé and de Blois 2016) and with those of previous studies (Boisvert-Marsh et al. 2014, Sittaro et al. 2017). They also reveal shifts that result from spatially explicit responses, with different combinations of climate change and disturbance variables influencing the probability of sapling occurrence gains depending on location within the study area. Moreover, the best climate models retained mostly temperature rather than precipitation variables, and monthly or seasonal ones over annual ones. The former was expected as we focused on latitudinal gradients where strong temperature gradients prevail. The latter suggests the influence of local climate change at times critical for life events (reproduction, dispersal, establishment) leading to successful recruitment. Overall, our findings show responses to warming that vary depending on the geographical position and warming intensity.

We generally expected the disturbance signal to be greater than the climate signal given the prevalence of disturbances in the study area. On the contrary, support for climate change variables mostly outweighed (based on absolute Wald z value) disturbance ones. South of our study area into the United States, climate gradients and their changes were also shown to have impacts on tree range shifts (Bose et al. 2017b, Fei et al. 2017). Interestingly, despite our studying tree species at their northern range limit in eastern North America, greater extension of the growing season did not always lead to higher probability of sapling recruitment at a site. In fact, warming may be becoming stressful at southern locations. This was particularly evident for *F. grandifolia* and *A. saccharum,* the species with the most meridional northern limits in our dataset, and also to a lesser degree, for *B. alleghaniensis*. Conversely, the relationship between warming or extension of the growing season and sapling occurrence gains tended to be positive at northern locations for *A. saccharum* and *F. grandifolia*, coinciding with northward expansion. South of our study area, in the United States, *A. rubrum* and *B. alleghaniensis* showed northward shifts in abundance over a similar time period but, in contrast to our study, *A. saccharum* and *F. grandifolia* showed southward shifts (Fei et al. 2017). If the southward shift they observed for *A. saccharum* results from declining abundance in the northern part of their study area (Fei et al. 2017), this could be consistent with declining occurrence reported in the south of our study area and into New England (Bishop et al. 2015, Bose et al. 2017a). On the other hand, reports of increasing occurences in the south of our study area and through New England for *F. grandifolia* would contrast with southward shifts in abundance reported by Fei. et al (2017). Combining insights across the range could be useful to contextualise results in specific areas, although the time periods under consideration may not be similar. Divergence in the responses of early life stages across large latitudinal gradients has also been shown for two European congeneric species of *Acer* (*A. pseudoplatanus* L. and *A. platanoides* L.). Seedling germination and survival of these two species responded differently to experimental warming and precipitation treatments depending on their provenance along a climate gradient (Carón et al. 2015). Divergent latitudinal responses with climate warming have also been reported for growth of *Picea mariana,* suggesting that it could better withstand warming at northernmost locations than at southern locations (D’Orangeville et al. 2016). These enhanced growth effects at the northern range limit, however, could be transitory for this species as warming continues (D’Orangeville et al. 2018), especially for juvenile stages which are more sensitive to climate stress than adult stages (Munier et al. 2010, Kueppers et al. 2017).

Identifying responses to specific climate variables across broad latitudinal gradients can point to biological mechanisms and their role in facilitating or hampering species migration or adaptation (De Frenne et al. 2013). For instance, changing spring conditions put species at risk when late season frosts interrupt phenological processes (Körner and Basler 2010). Frost damage is an increasingly common occurrence under climate change (Augspurger 2013, Liu et al. 2018), and could explain in part why increasingly earlier springs can negatively impact recruitment at southern locations where earlier budburst and/or seedling germination would be vulnerable to spring frosts (Burns and Honkala 1990, Hufkens et al. 2012). At northern locations, fruit maturation and germination could benefit from a fall extension of the number of growing degree days (Morin et al. 2007). Over broad ranges, divergent responses for a given species may indicate intraspecific adaptation to local climatic conditions, resulting in differentiation of populations within the broad climatic tolerance of a species (Davis and Shaw 2001). These adaptations likely evolved in fairly stable climate conditions over the last few millennia, but the unprecedented, current rate of climate change could favor rapid migration over adaptation for long-lived species (Ordonez and Williams 2013). A close link between climate and phenology has implications for management, such as assisted migration efforts and seed transfers between climate zones (Pedlar et al. 2012).

When disturbance was retained in selected models, past logging had a negative effect on *F. grandifolia* and *A. rubrum*, the latter being the species most significantly affected by disturbance compared to climate. However, logging had a positive impact on *B. alleghaniensis*, possibly because of its commercial importance, resulting in it being selected during forest management activities. Management legacies have shown to leave lasting imprints on the European temperate forest (Perring et al. 2018), in the boreal forest of eastern Canada (Cyr et al. 2009), and in the eastern United States (Nowacki and Abrams 2015), but the trajectories are not always well understood. For instance, fire suppression has been proposed as a reason for *A. rubrum’s* expansion throughout its range (Abrams 1998), but this species has also increased at other locations, favoured mainly by smaller scale disturbances over larger ones (Leithead et al. 2010, Fisichelli et al. 2014).

Disturbances could act synergistically with climate warming, opening the canopy, reducing competition locally and facilitating species turnover at suitable sites (Thom et al. 2017). Disturbances could also have the opposite effect in areas where warming thresholds for recruitment are reached, exacerbating the negative impact of climate change. In our study area, although the model comprised of an interaction term between climate change and disturbance (Model 4) competed at times with the best selected model, this model was only selected twice with the interaction term being otherwise non or weakly significant. For *A. saccharum* north of the 90th percentile, spring warming and recent natural disturbances interacted negatively, possibly limiting range expansion, whereas for *F. grandifolia* in the south, spring warming interacted positively with logging. It is possible that for some species, changes in disturbance regime, including fire, may limit their ability to migrate and persist in the boreal forest (Boulanger et al. 2018). Using physiologically based simulations in the northeastern United States, Liang et al. (2018) reported that disturbances may expedite species' recruitment into new sites, but they had little effect on the velocity of simulated range boundary shifts. Following fires in California that occurred since 2004, Young et al. (2019) found little evidence of disturbance-mediated vegetation community reorganization on range shifts, from either low sensitivity of species to post-disturbance weather or widespread recruitment declines precipitated by unusually dry conditions. Interactions between climate change and disturbances warrant further investigation as management practices will need to be adapted to a changing climate, particularly to facilitate migration.

The influence of climate change, disturbances and their interactions can be much more complex than what we have captured in our models. Climate extremes are likely to be much more consequential for plants than changes in mean climate variables (Zimmermann et al. 2009). Vegetation responses could lag in time and disturbances can have long legacies, making it hard to assess the appropriate temporal scale for evaluating their relative impact on range dynamics (Kohyama and Shigesada 1995, Boucher et al. 2014, Renwick and Rocca 2015). Moreover, edaphic conditions play also an important role in limiting distribution (Beauregard and de Blois 2014), but we included them in selecting suitable habitats (Section 8.3). Land-use and landscape fragmentation also influence the ability of plant species to reach suitable sites (Miller and McGill 2018) and this influence may be more important where human activities are concentrated. Altered nutrient cycling could favour certain tree species to the detriment of others. For example, even if the trend has reversed since (Houle et al. 2015), increased nitrogen availability before the start of P_3, caused by atmospheric nitrate deposition (Fenn et al. 1998), could hasten turnover from coniferous to deciduous stands. It may have favoured the establishment of N-responsive species such as *A. saccharum* (Rothstein et al. 1996). Finally, the observed patterns of range shift do not imply that the species will keep up with the rapidly changing climate (Boisvert-Marsh et al. 2014, Sittaro et al. 2017, Aubin et al. 2018), although trees' recent latitudinal shifts match the direction predicted by species distribution models (Périé and de Blois 2016). In spite of these limitations and given the paucity of data on the relationship between ongoing climate change, disturbances and range dynamics, our models offer significant insights on forests' response.

In summary, tree recruitment response to climate change is spatially explicit, depending on the portion of the study area examined. Even at these northern latitudes, there is evidence of population differentiation and varying spatial patterns of climate change, with positive effects of warming on recruitment for a given species towards its northern range edge and negative ones in the southern portion of the study area. The importance of early- or late-season climate variables in explaining recruitment trends suggests that species are affected at critical stages of their life cycle for reproduction and/or dispersal. Given the prevalence of anthropogenic disturbances in the study area, climate change's influence on recruitment is stronger than expected, and responses to disturbances tend to be species-specific. There is limited support for interaction effects between climate change and disturbances in this dataset. Continued monitoring of forest species is crucial to understand fully the long-term implications of these spatially explicit responses to global changes and the factors that could influence the capacity of species to migrate or adapt, with the goal of adapting management and conservation practices accordingly.

4.6 - Acknowledgements

We acknowledge the Ministère des Forêts, de la Faune et des Parcs (MFFP, Quebec) for providing initial access to forest inventory data. We also highlight the work of the countless people over the last 45 years who worked on the inventories. We thank Marie-Claude Lambert for helping with dataset preparation and R scripts, Dr. Frieda Beauregard and four anonymous reviewers for helpful suggestions, and Kim Chapman for manuscript revision. The research was supported by grants from the MFFP and from the Natural Sciences and Engineering Research Council of Canada to SdB and from the Department of Plant Science to LBM. The authors declare no conflict of interest.

4.7 - Author contributions

LBM, CP, and SdB conceived the original study idea and designed the methodology; LBM along with SdB led the analysis of the data and the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

4.8 - Data Accessibility

Forest inventory data, including species data and edaphic and disturbance variables, are available from https://www.donneesquebec.ca/recherche/fr/dataset/placettes-echantillons-permanentes-1970-a-aujourd-hui. The BioSIM program used to interpolate climate data is available from https://cfs.nrcan.gc.ca/publications?id=34818.

Table 4.1: Best variable retained from the Δclimate model (Model 1) and the disturbance model (Model 2) between P_1 (1970-1977) and P_3 (2003-2014). The best variable was obtained from pre-analyses which tested models in four different areas of the distribution, based on the calculated latitudinal limit in P_1: entire suitable area, south of the 50th percentile of distribution, north of the 50th percentile, and north of the 90th percentile. The sign of the coefficient of the explanatory variable in each model indicates the relationship between the explanatory variable and occurrence gains (plots not occupied by saplings in P_1 but occupied in P_3, +: positive, -: negative). Variables in bold indicate the Δclimate or disturbance variable with the highest Wald z value. For complete model details (coefficient values, standard errors and p values), see Tables in Section 8.3.2. Species are ordered from left to right from the most meridional to most boreal northernmost limit (90th percentile) in P_1.

	Fagus grandifolia		***Acer saccharum***		***Betula alleghaniensis***		***Acer rubrum***	
	ΔClimate	Disturbance	ΔClimate	Disturbance	ΔClimate	Disturbance	ΔClimate	Disturbance
Entire suitable	**October Δgdd5 (+)***	Natural P_1 (-) *	Annual Δgdd5 (-)	**Natural P_3 (-)**	**Summer ΔTMax (+)***	Logging P_1 (+) *	October Δgdd5 (-)*	**Logging P_1 (-)*****
<50th	**April Δgdd5 (-)****	Logging P_1 (-)	**Annual Δgdd5 (-)****	New Disturbance P_3 (+)	**April Δgdd5 (-)***	Logging P_1 (+) .	October Δgdd5 (-) .	**Natural P_1 (+)***
>50th	October Δgdd5 (+) .	**Natural P_1 (-) ***	**April Δgdd5 (+)***	Logging P_3 (+)	**April Δgdd5 (+) .**	Natural P_1 (-) .	October Δgdd5 (-) .	**Logging P_1 (-)*****
>90th	**July Δprecip (+) *****	Disturbance (-)	April Δgdd5 (+)	**Natural P_3 (-)**	**Annual Δgdd5 (-)**	Logging P_1 (-)	October Δgdd5 (-) .	**Logging P_1 (-) .**

Significance levels: p<0.1: .; p<0.05: *; p<0.01: **, p<0.001: ***.

Table 4.2: Best models from multimodel selection assessing the relationship between occurrence gain compared to climate change and disturbance. For each species, candidate models were assessed for four different areas of the distribution, based on the calculated latitudinal limit in P_1 (1970-1977): entire suitable area, south of the 50th percentile of distribution (<50th), north of the 50th percentile (>50th), and north of the 90th percentile (>90th). The variable with the highest overall model Wald z value is in bold. The coefficient sign is indicated (+: positive relationship between occurrence gains and explanatory variables; -: negative relationship). The difference between the AICc score of the best model and null model (ΔAICc), Akaike weight (Wt) and R^2 of the best model are included for reference. For complete model outputs, see Tables in Section 8.3.2.

Fagus grandifolia

	Best model	AICc	ΔAICc w/ null (Wt)	R^2	Explanatory variables
Entire suitable	*Model 3* ~ $\Delta C_{best} + Dist_{best}$	700.16	-4.35 (0.30)	0.0732	**October Δgdd5** (+) * + Natural P_1 (-) .
<50th	*Model 4* ~ $\Delta C_{best} + Dist_{best} + \Delta C_{best} \times Dist_{best}$	287.36	-3.38 (0.39)	0.1204	**April Δgdd5** (-)** + Logging P_1 (-)* + April Δgdd5 x Logging P_1 (+) .
>50th	*Model 3* ~ $\Delta C_{best} + Dist_{best}$	405.85	-5.9 (0.55)	0.0847	**October Δgdd5** (+)* + Logging P_1 (-) .
>90th	*Model 1* ~ C (Monthly ΔC)	319.23	-4.46 (0.41)	0.1193	January ΔTMin (+) + March ΔTMax (-) . + July ΔTMax (+) . + **July ΔPrecip (+)*****

Acer saccharum

	Best model	AICc	ΔAICc w/ null (Wt)	R^2	Explanatory variables
Entire suitable	*Model 5* ~ $\Delta C_{best} + Dist_{best} + CGr + \Delta C_{best} \times CGr$	935.68	-6.06 (0.56)	0.0504	Annual Δgdd5 (+) + Natural P_3 (-) + **gdd5 P_3** (+)** + Annual Δgdd5 x gdd5 P_3 (-)*
<50th	*Model 1* ~ Δ C (Annual ΔC)	304.61	-7.69 (0.71)	0.1612	**Annual Δgdd5** (-)** + Δ Total Annual Precipitation (-)*
>50th	*Model 3* ~ $\Delta C_{best} + Dist_{best}$	625.37	-4.48 (0.49)	0.0403	**April Δgdd5** (+)* + Logging P_3 (+) .
>90th	*Model 4* ~ $\Delta C_{best} + Dist_{best} + \Delta C_{best} \times Dist_{best}$	247.19	-1.1 (0.36)	0.035	April Δgdd5 (+) + Natural P_3 (+) + **April Δgdd5 x Natural P_3 (-)**

Betula alleghaniensis

	Best model	AICc	ΔAICc w/ null (Wt)	R^2	Explanatory variables
Entire suitable	*Model 6* ~ ΔC_{best} + $Dist_{best}$ + CGr + $Dist_{best}$ x CGr	890.88	-7.56 (0.24)	0.0646	**Summer ΔTMax** (+)** + Logging P_1 (+) + gdd5 P_3 (-) . + Logging P_1 x gdd5 P_3 (+) .
<50th	*Model 3* ~ ΔC_{best} + $Dist_{best}$	410.03	-4.32 (0.55)	0.0859	**April Δgdd5** (-)* + Logging P_1 (+) .
>50th	*Model 2* ~ Dist (Disturbance type P_1)	485.98	-1.4 (0.37)	0.0415	Logging P_1 (+) + **Natural P_1 (-).**
>90th	*Model 7* Null	151.99	0 (0.48)	--	--

Acer rubrum

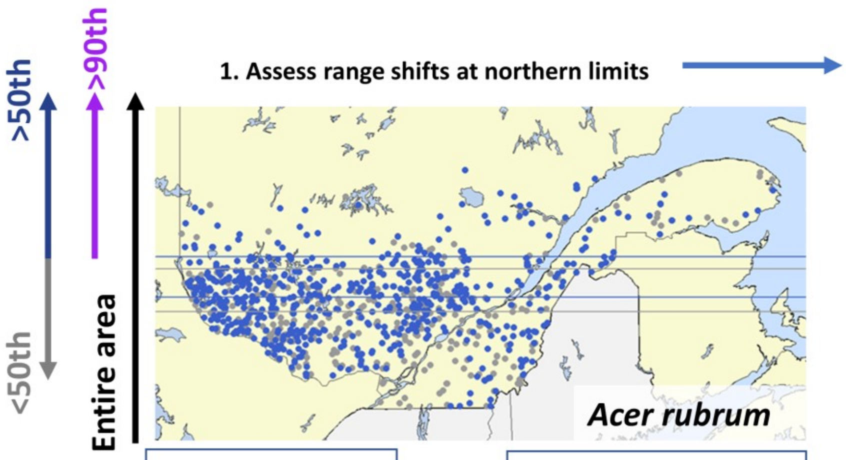
	Best model	AICc	ΔAICc w/ null (Wt)	R^2	Explanatory variables
Entire suitable	*Model 6* ~ ΔC_{best} + $Dist_{best}$ + CGr + $Dist_{best}$ x CGr	1410.24	-28.89 (0.93)	0.0738	October Δgdd5 (-)** + **Logging P_1** (-) *** + gdd5 P_3 (-)** + Logging P_1 x gdd5 P_3 (+)**
<50th	*Model 3* ~ ΔC_{best} + $Dist_{best}$	544.62	-3.76 (0.41)	0.0276	October Δgdd5 (-) . + **Natural P_1** (+)*
>50th	*Model 3* ~ ΔC_{best} + $Dist_{best}$	873.61	-18.72 (0.54)	0.0751	October Δgdd5 (-) + **Logging P_1** (-)***
>90th	*Model 3* ~ ΔC_{best} + $Dist_{best}$	281.05	-4.7 (0.53)	0.0729	**October Δgdd5** (-)* + Logging P_1 (-) .

P_1 – 1970-1977; P_3 – 2003-2014.

ΔC_{best} – Δclimate variable retained for a given species x area of range considered. $Dist_{best}$ – Disturbance variable retained. CGr – Climate gradient across study area, as denoted by gdd5 P_3.

Significance levels: $p<0.1$: .; $p<0.05$: *; $p<0.01$: **, $p<0.001$: P_1 – 1970-1977, P_3 – 2003-2014

1. Assess range shifts at northern limits



Latitudinal range shift
50th, 90th

AND

Changes in plot occurrence
Entire area, <50th, **>50th**, **>90th**

2. Evaluate candidate models explaining shifts across parts of northern range: Entire area, <50th, **>50th**, **>90th**

	Model type	**Variables included** *(Response ~ Explanatory)*
Model 1: Best Δ Climate (Δ C) model		
1a	Annual Δ C	Occ_{gain} ~ Annual Δgdd5 + Annual Δprecip + $1 \vert \mathit{LongGroup}$
1b	Seasonal Δ C	Occ_{gain} ~ Winter ΔTmin + Fall ΔTmean + Spring ΔTmin + Summer ΔTmax + Growing season Δprecip + $1 \vert \mathit{LongGroup}$
1c	Monthly Δ C	Occ_{gain} ~ March ΔTmax + July ΔTmax + January ΔTmin + July Δprecip + $1 \vert \mathit{LongGroup}$
1d	Early & late growing season Δ C	Occ_{gain} ~ April Δgdd5 + October Δgdd5 + $1 \vert \mathit{LongGroup}$
Model 2: Best Disturbance (Dist) model		
2a	Dist type P_1	Occ_{gain} ~ Logging P_1 + Natural P_1 + $1 \vert \mathit{LongGroup}$
2b	Dist type P_3	Occ_{gain} ~ Logging P_3 + Natural P_3 + $1 \vert \mathit{LongGroup}$
2c	Dist Presence	Occ_{gain} ~ Disturbance + New disturbance P_3 + $1 \vert \mathit{LongGroup}$
2d	Dist timing	Occ_{gain} ~ Disturbance P_1 + Disturbance P_3 + $1 \vert \mathit{LongGroup}$
Models 3-6: Combined models		
3	Best Δ climate + Best disturbance	Occ_{gain} ~ ΔC_{best} + $Dist_{best}$ + $1 \vert \mathit{LongGroup}$
4	Interaction - Best Δ climate + Best disturbance	Occ_{gain} ~ ΔC_{best} + $Dist_{best}$ + ΔC_{best} x $Dist_{best}$ + $1 \vert \mathit{LongGroup}$
5	Interaction - Climate gradient & Δ Climate (Entire area only)	Occ_{gain} ~ ΔC_{best} + $Dist_{best}$ + CGr + ΔC_{best} x CGr + $1 \vert \mathit{LongGroup}$
6	Interaction - Climate gradient & Disturbance (Entire area only)	Occ_{gain} ~ ΔC_{best} + $Dist_{best}$ + CGr + $Dist_{best}$ x CGr + $1 \vert \mathit{LongGroup}$
Model 7 - Null Model		
7	Null model	Occ_{gain} ~ $1 \vert \mathit{LongGroup}$

Figure 4.1: Workflow for assessing how latitudinal range shifts are related to climate change and/or disturbance in Quebec, Canada.

1) *Assess range shifts*, i.e. magnitude and direction of latitudinal shifts as the change in limit location over time (*Acer rubrum* shown), lower limits=50th; upper limits=90th; Grey: 1970-1977 (P_1). Blue: 2003-2014 (P_3), and change in plot occurrence (occurrence in P_1; occurrence in P_3). Points show plots occupied in their respective inventories (P_1 or P_3). Range shifts are quantified as the difference between the pairs of lines. Occurrence changes were assessed for four different areas of the distribution, based on the calculated latitudinal limit in P_1 (example shown on left): Entire suitable area, south of the 50th percentile of distribution (<50th), north of the 50th percentile (>50th), and north of the 90th percentile (>90th).

2*) Evaluate candidate models explaining shifts*: We evaluated the probability of observing an occurrence gain (Occ_{gain}) in relation to climate change (Δclimate), disturbance, and their interaction. Model 1 (Best ΔC) and Model 2 (Best Disturbance) were selected (by lowest AIC) each from four non-nested submodels including either climate change variables or disturbance variables. Models 3 combined the climate change variable with the highest model Wald z value from the ΔClimate model and the disturbance variable with the highest model Wald z value from the Disturbance model. Model 4 includes an interaction term between climate and disturbance and models 5 and 6 include a climate gradient variable (CGr: growing degree days, base 5°C in P_3). For more details, see Section 8.3.1.

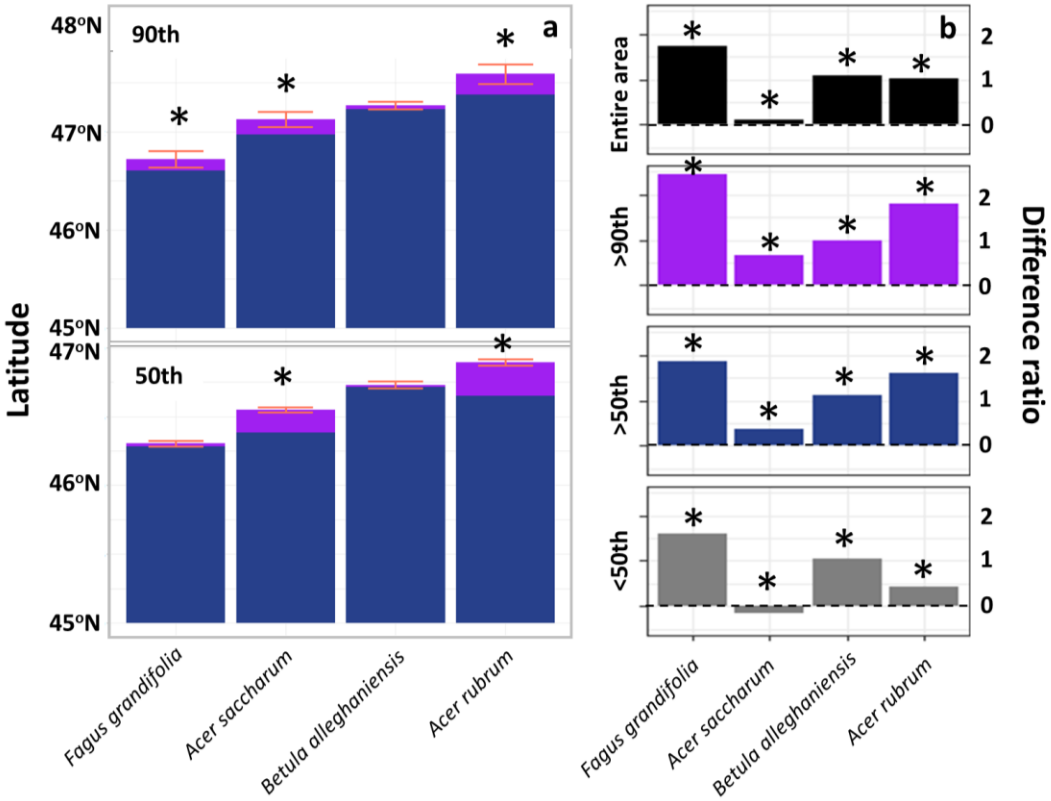


Figure 4.2: Summary of evidence for latitudinal shifts between P_1 (1970-1977) and P_3 (2003-2014) for saplings of four tree species in Quebec, Canada using latitudinal limit shifts (a) and occurrence changes (b). For latitudinal limit shifts, the latitudinal limit in P_1 is indicated by the height of the blue bar while the P_3 limit and its difference relative to the P_1 limit is indicated by the height of the purple bar. This was assessed at both the median (50th, bottom) and the northernmost (90th, top) limit. For changes in plots occupied, the difference in number of plots occupied between the two inventories relative to the number occupied in P_1 is represented for four areas (Entire suitable area, south of the 50th percentile of distribution (<50th), north of the 50th percentile (>50th), and north of the 90th percentile (>90th). * denotes significant latitudinal shifts or change in number of plots occupied ($p<0.05$).

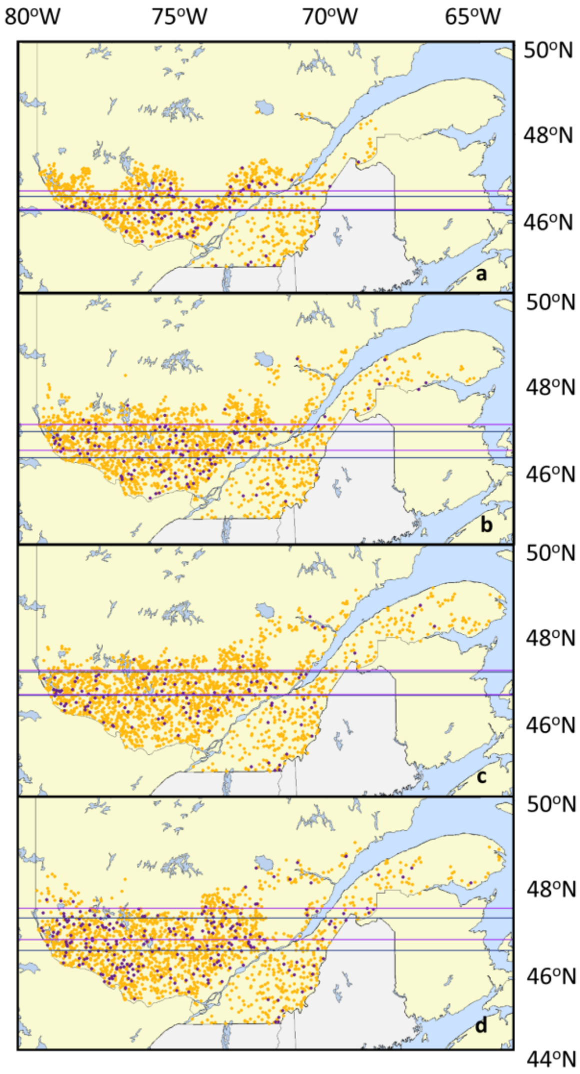


Figure 4.3: Maps of sapling occurrence gains for four tree species between P_1 (1970-1977) and P_3 (2003-2014) in Quebec, Canada. Species, ordered from most meridional to most boreal northernmost limit (90th percentile), are a) *Fagus grandifolia*, b) *Acer saccharum*, c) *Betula alleghaniensis* and d) *Acer rubrum.* The blue lines represent the 50th and 90th percentiles of latitude in P_1. The purple lines represent the 50th and 90th percentiles of latitude in P_3. Purple dots represent a sapling gain observed in P_3 while yellow dots represent plots suitable for a given species, based on species distribution models.

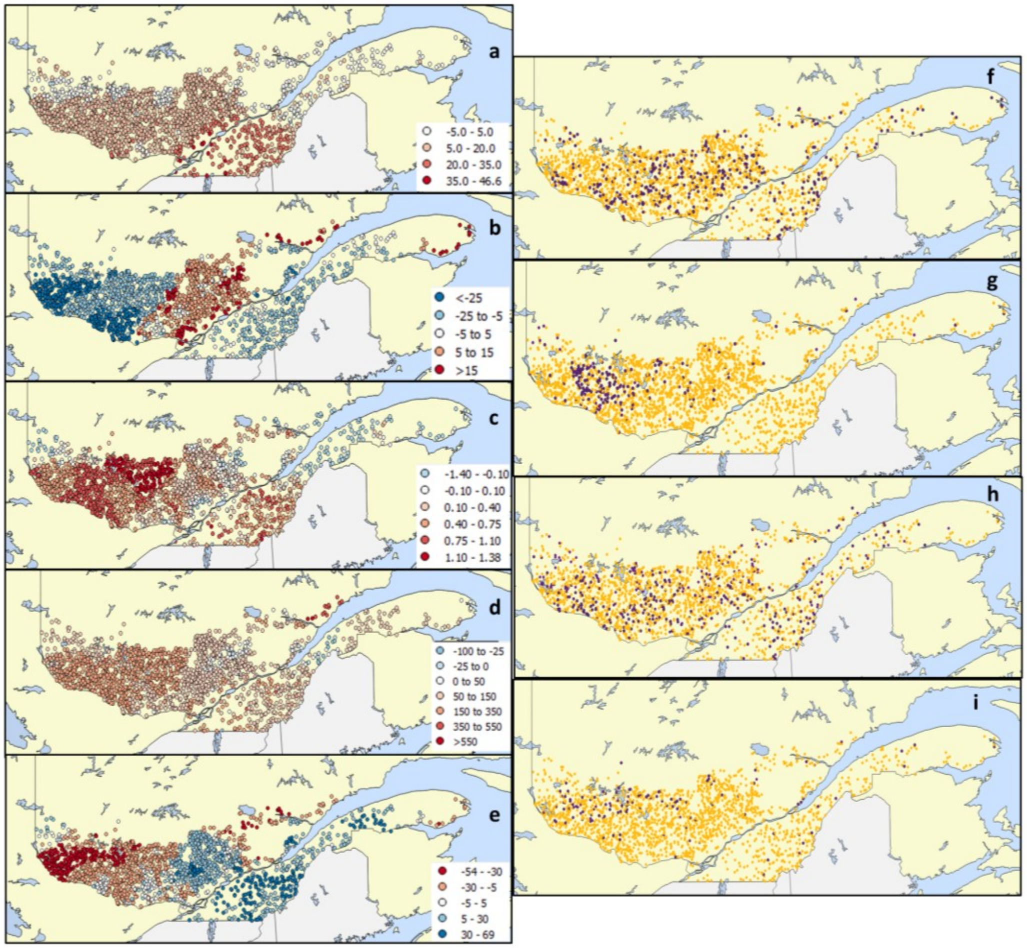


Figure 4.4: Maps of changes in selected climate change variables (Δclimate: a-e) and disturbance (f-i) between P_1 (1970-1977) and P_3 (2003-2014) in Quebec, Canada. The Δclimate variables depicted are the ones selected in Δclimate models (Model 1): from top to bottom, a) April Δgdd5 (change in growing degree days), b) October Δgdd5, c) Summer Maximum temperature (Summer ΔTMax), d) Annual Δgdd5, e) ΔJuly precipitation). Legends indicate the magnitude of change; blue denotes plots that experienced cooler temperature (^{0}C), fewer growing degree days or wetter conditions (mm) between the two periods and red denotes plots that experienced warmer temperature, more growing degree days or drier conditions. The disturbance variables depicted are those selected in Disturbance models (Model 2): from top to bottom, f) Logging P_1, g) Natural P_1, h) Logging P_3, i) Natural P_3. Purple dots represent plots where disturbance and its type were recorded in a given period while yellow dots represent plots where no disturbance was recorded.

4.9 - References

Abrams, M. D. 1998. The red maple paradox. BioScience **48**:355-364.

Agresti, A. 2013. Categorical Data Analysis (3rd edition). Wiley-Interscience. Hoboken, NJ, United States.

Alofs, K. M., and D. A. Jackson. 2015. The abiotic and biotic factors limiting establishment of predatory fishes at their expanding northern range boundaries in Ontario, Canada. Global Change Biology **21**:2227-2237.

Aubin, I., L. Boisvert-Marsh, H. Kebli, D. W. McKenney, J. H. Pedlar, K. Lawrence, E. H. Hogg, Y. Boulanger, S. Gauthier, and C. Ste-Marie. 2018. Tree vulnerability to climate change: improving exposure-based assessments using traits as indicators of sensitivity. Ecosphere **9**:e02108.

Augspurger, C. K. 2013. Reconstructing patterns of temperature, phenology, and frost damage over 124 years: Spring damage risk is increasing. Ecology **94**:41-50.

Beauregard, F., and S. de Blois. 2014. Beyond a Climate-Centric View of Plant Distribution: Edaphic Variables Add Value to Distribution Models. PloS one **9**:e92642.

Berteaux, D., M. Ricard, M.-H. St-Laurent, N. Casajus, C. Périé, F. Beauregard, and S. de Blois. 2018. Northern protected areas will become important refuges for biodiversity tracking suitable climates. Scientific Reports **8**:4623.

Bishop, D. A., C. M. Beier, N. Pederson, G. B. Lawrence, J. C. Stella, and T. J. Sullivan. 2015. Regional growth decline of sugar maple (*Acer saccharum*) and its potential causes. Ecosphere **6**:art179.

Boisvert-Marsh, L., C. Périé, and S. de Blois. 2014. Shifting with climate? Evidence for recent changes in tree species distribution at high latitudes. Ecosphere **5**:art83.

Bose, A. K., A. Weiskittel, and R. G. Wagner. 2017a. Occurrence, pattern of change, and factors associated with American beech-dominance in stands of the northeastern USA forest. Forest Ecology and Management **392**:202-212.

Bose, A. K., A. Weiskittel, R. G. Wagner, and A. Pauchard. 2017b. A three decade assessment of climate-associated changes in forest composition across the north-eastern USA. Journal of Applied Ecology **54**:1592-1604.

Boucher, Y., P. Grondin, and I. Auger. 2014. Land use history (1840–2005) and physiography as determinants of southern boreal forests. Landscape Ecology **29**:437-450.

Boulanger, Y., A. R. Taylor, D. T. Price, D. Cyr, and G. Sainte-Marie. 2018. Stand-level drivers most important in determining boreal forest response to climate change. Journal of Ecology **106**:977-990.

Burns, R. M., and B. H. Honkala. 1990. Silvics of North America. USDA Forest Service, Washington, DC.

Canham, C. D., and R. Q. Thomas. 2010. Frequency, not relative abundance, of temperate tree species varies along climate gradients in eastern North America. Ecology **91**:3433-3440.

Carón, M. M., P. De Frenne, J. Brunet, O. Chabrerie, S. A. O. Cousins, G. Decocq, M. Diekmann, B. J. Graae, T. Heinken, A. Kolb, J. Lenoir, T. Naaf, J. Plue, F. Selvi, M. Wulf, and K. Verheyen. 2015. Divergent regeneration responses of two closely related tree species to direct abiotic and indirect biotic effects of climate change. Forest Ecology and Management **342**:21-29.

Cavanaugh, K. C., J. R. Kellner, A. J. Forde, D. S. Gruner, J. D. Parker, W. Rodriguez, and I. C. Feller. 2014. Poleward expansion of mangroves is a threshold response to decreased frequency of extreme cold events. Proceedings of the National Academy of Sciences **111**:723-727.

Chambers, D., C. Périé, N. Casajus, and S. de Blois. 2013. Challenges in modelling the abundance of 105 tree species in eastern North America using climate, edaphic, and topographic variables. Forest Ecology and Management **291**:20-29.

Chen, I.-C., J. K. Hill, R. Ohlemüller, D. B. Roy, and C. D. Thomas. 2011. Rapid range shifts of species associated with high levels of climate warming. Science **333**:1024-1026.

Cyr, D., S. Gauthier, Y. Bergeron, and C. Carcaillet. 2009. Forest management is driving the eastern North American boreal forest outside its natural range of variability. Frontiers in Ecology and the Environment **7**:519-524.

D'Orangeville, L., L. Duchesne, D. Houle, D. Kneeshaw, B. Côté, and N. Pederson. 2016. Northeastern North America as a potential refugium for boreal forests in a warming climate. Science **352**:1452-1455.

D'Orangeville, L., D. Houle, L. Duchesne, R. P. Phillips, Y. Bergeron, and D. Kneeshaw. 2018. Beneficial effects of climate warming on boreal tree growth may be transitory. Nature Communications **9**:3213.

Dainese, M., S. Aikio, P. E. Hulme, A. Bertolli, F. Prosser, and L. Marini. 2017. Human disturbance and upward expansion of plants in a warming climate. Nature Climate Change **7**:577.

Dale, V. H., L. A. Joyce, S. McNulty, R. P. Neilson, M. P. Ayres, M. D. Flannigan, P. J. Hanson, L. C. Irland, A. E. Lugo, C. J. Peterson, D. Simberloff, F. J. Swanson, B. J. Stocks, and B. Michael Wotton. 2001. Climate Change and Forest Disturbances. BioScience **51**:723-734.

Davis, M. B., and R. G. Shaw. 2001. Range Shifts and Adaptive Responses to Quaternary Climate Change. Science **292**:673-679.

De Frenne, P., B. J. Graae, F. Rodríguez-Sánchez, A. Kolb, O. Chabrerie, G. Decocq, H. De Kort, A. De Schrijver, M. Diekmann, O. Eriksson, R. Gruwez, M. Hermy, J. Lenoir, J. Plue, D. A. Coomes, and K. Verheyen. 2013. Latitudinal gradients as natural laboratories to infer species' responses to temperature. Journal of Ecology **101**:784-795.

Evans, P., and C. D. Brown. 2017. The Boreal-Temperate Forest Ecotone Response to Climate Change. Environmental Reviews **25**:423-431.

Fei, S., J. M. Desprez, K. M. Potter, I. Jo, J. A. Knott, and C. M. Oswalt. 2017. Divergence of species responses to climate change. Science Advances **3**:e1603055.

Fenn, M. E., M. A. Poth, J. D. Aber, J. S. Baron, B. T. Bormann, D. W. Johnson, A. D. Lemly, S. G. McNulty, D. F. Ryan, and R. Stottlemyer. 1998. Nitrogen excuss in North American ecosystems: Predisposing factors, ecosystem responses, and management strategies. Ecological Applications **8**:706-733.

Fisichelli, N. A., L. E. Frelich, and P. B. Reich. 2014. Temperate tree expansion into adjacent boreal forest patches facilitated by warmer temperatures. Ecography **37**:152-161.

Girardin, M. P., O. Bouriaud, E. H. Hogg, W. Kurz, N. E. Zimmermann, J. M. Metsaranta, R. de Jong, D. C. Frank, J. Esper, U. Büntgen, X. J. Guo, and J. Bhatti. 2016. No growth stimulation of Canada’s boreal forest under half-century of combined warming and CO2 fertilization. Proceedings of the National Academy of Sciences **113**:E8406-E8414.

Guo, F., J. Lenoir, and T. C. Bonebrake. 2018. Land-use change interacts with climate to determine elevational species redistribution. Nature Communications **9**:1315.

Houle, D., C. Marty, and L. Duchesne. 2015. Response of canopy nitrogen uptake to a rapid decrease in bulk nitrate deposition in two eastern Canadian boreal forests. Oecologia **177**:29-37.

Hufkens, K., M. A. Friedl, T. F. Keenan, O. Sonnentag, A. Bailey, J. O'Keefe, and A. D.

Richardson. 2012. Ecological impacts of a widespread frost event following early spring leaf-out. Global Change Biology **18**:2365-2377.

Kohyama, T., and N. Shigesada. 1995. A size-distribution-based model of forest dynamics along a latitudinal environmental gradient. Pages 117-126 Global change and terrestrial ecosystems in monsoon Asia. Springer.

Körner, C., and D. Basler. 2010. Phenology Under Global Warming. Science **327**:1461-1462.

Kueppers, L. M., E. Conlisk, C. Castanha, A. B. Moyes, M. J. Germino, P. de Valpine, M. S. Torn, and J. B. Mitton. 2017. Warming and provenance limit tree recruitment across and beyond the elevation range of subalpine forest. Global Change Biology **23**:2383-2395.

Leithead, M. D., M. Anand, and L. C. R. Silva. 2010. Northward migrating trees establish in treefall gaps at the northern limit of the temperate-boreal ecotone, Ontario, Canada. Oecologia **164**:1095-1106.

Lembrechts, J. J., A. Pauchard, J. Lenoir, M. A. Nuñez, C. Geron, A. Ven, P. Bravo-Monasterio, E. Teneb, I. Nijs, and A. Milbau. 2016. Disturbance is the key to plant invasions in cold environments. Proceedings of the National Academy of Sciences **113**:14061-14066.

Lenoir, J., J.-C. Gégout, J.-C. Pierrat, J.-D. Bontemps, and J.-F. Dhôte. 2009. Differences between tree species seedling and adult altitudinal distribution in mountain forests during the recent warm period (1986-2006). Ecography **32**:765-777.

Lenoir, J., T. Hattab, and G. Pierre. 2017. Climatic microrefugia under anthropogenic climate change: implications for species redistribution. Ecography **40**:253-266.

Lenoir, J., and J. C. Svenning. 2015. Climate-related range shifts – a global multidimensional synthesis and new research directions. Ecography **38**:15-28.

Liang, Y., M. J. Duveneck, E. J. Gustafson, J. M. Serra-Diaz, and J. R. Thompson. 2018. How disturbance, competition, and dispersal interact to prevent tree range boundaries from keeping pace with climate change. Global Change Biology **24**:e335-e351.

Liu, Q., S. Piao, I. A. Janssens, Y. Fu, S. Peng, X. Lian, P. Ciais, R. B. Myneni, J. Peñuelas, and T. Wang. 2018. Extension of the growing season increases vegetation exposure to frost. Nature Communications **9**:426.

Miller, A. E., T. L. Wilson, R. L. Sherriff, and J. Walton. 2017. Warming drives a front of white spruce establishment near western treeline, Alaska. Global Change Biology **23**:5509-5522.

Miller, K. M., and B. J. McGill. 2018. Land use and life history limit migration capacity of eastern tree species. Global Ecology and Biogeography **27**:57-67.

Ministère des Forêts, Faune et des Parcs. 2015. Normes techniques, Placettes-Échantillons Permanentes, 4e inventaire écoforetier du Québec méridional. Ministère des Forêts, Faune et Parcs, Direction des Inventaires Forestiers, Québec, Québec.

Morin, X., C. Augspurger, and I. Chuine. 2007. Process-based modeling of species' distributions: What limits temperate tree species' range boundaries? Ecology **88**:2280-2291.

Munier, A., L. Hermanutz, J. D. Jacobs, and K. Lewis. 2010. The interacting effects of temperature, ground disturbance, and herbivory on seedling establishment: implications for treeline advance with climate warming. Plant Ecology **210**:19-30.

National Center for Environmental Information. 2016. State of the climate: Global analysis for annual 2015. Retrieved from http://www.ncdc.noaa.gov/sotc/global/201513

Nowacki, G. J., and M. D. Abrams. 2015. Is climate an important driver of post-European vegetation change in the Eastern United States? Global Change Biology **21**:314-334.

Ordonez, A., and J. W. Williams. 2013. Climatic and biotic velocities for woody taxa distributions over the last 16 000 years in eastern North America. Ecology Letters **16**:773-781.

Pedlar, J. H., D. W. McKenney, I. Aubin, T. Beardmore, J. Beaulieu, L. Iverson, G. A. O'Neill, R. S. Winder, and C. Ste-Marie. 2012. Placing Forestry in the Assisted Migration Debate. BioScience **62**:835-842.

Périé, C., and S. de Blois. 2016. Dominant forest tree species are potentially vulnerable to climate change over large portions of their range even at high latitudes. PeerJ **4**:e2218.

Perring, M. P., M. Bernhardt-Römermann, L. Baeten, G. Midolo, H. Blondeel, L. Depauw, D. Landuyt, S. L. Maes, E. De Lombaerde, M. M. Carón, M. Vellend, J. Brunet, M. Chudomelová, G. Decocq, M. Diekmann, T. Dirnböck, I. Dörfler, T. Durak, P. De Frenne, F. S. Gilliam, R. Hédl, T. Heinken, P. Hommel, B. Jaroszewicz, K. J. Kirby, M. Kopecký, J. Lenoir, D. Li, F. Máliš, F. J. G. Mitchell, T. Naaf, M. Newman, P. Petřík, K. Reczyńska, W. Schmidt, T. Standovár, K. Świerkosz, H. Van Calster, O. Vild, E. R. Wagner, M. Wulf, and K. Verheyen. 2018. Global environmental change effects on plant community composition trajectories depend upon management legacies. Global Change Biology **24**:1722-1740.

Pironon, S., G. Papuga, J. Villellas, A. L. Angert, M. B. García, and J. D. Thompson. 2017. Geographic variation in genetic and demographic performance: new insights from an old biogeographical paradigm. Biological Reviews **92**:1877-1909.

R Core Team. 2016. R v.3.3.2: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Regnière, J., and R. Saint-Amant. 2014. BioSIM 10 - User's Manual. Laurentian Forestry Centre, Canadian Forest Service, Natural Resources Canada, Sainte-Foy, Québec.

Renwick, K. M., and M. E. Rocca. 2015. Temporal context affects the observed rate of climate-driven range shifts in tree species. Global Ecology and Biogeography **24**:44-51.

Rothstein, D. E., D. R. Zak, and K. S. Pregitzer. 1996. Nitrate deposition in northern hardwood forests and the nitrogen metabolism of Acer saccharum marsh. Oecologia **108**:338-344.

Saucier, J.-P., P. Grondin, A. Robitaille, and J.-F. Bergeron. 2003. Zones de végétation et les domaines bioclimatiques du Québec. Direction des inventaires forestiers, Ministère des Ressources naturelles et de la Faune, Québec, Québec.

Schwörer, C., D. G. Gavin, I. R. Walker, and F. S. Hu. 2017. Holocene tree line changes in the Canadian Cordillera are controlled by climate and topography. Journal of Biogeography **44**:1148-1159.

Sittaro, F., A. Paquette, C. Messier, and C. A. Nock. 2017. Tree range expansion in eastern North America fails to keep pace with climate warming at northern range limits. Global Change Biology **23**:3292-3301.

Smithers, B. V., M. P. North, C. I. Millar, and A. M. Latimer. 2018. Leap frog in slow motion: Divergent responses of tree species and life stages to climatic warming in Great Basin subalpine forests. Global Change Biology **24**:e442-e457.

Thom, D., W. Rammer, and R. Seidl. 2017. Disturbances catalyze the adaptation of forest ecosystems to changing climate conditions. Global Change Biology **23**:269-282.

Xu, L., R. B. Myneni, F. S. Chapin, T. V. Callaghan, J. E. Pinzon, C. J. Tucker, Z. Zhu, J. Bi, P. Ciais, H. Tømmervik, E. S. Euskirchen, B. C. Forbes, S. L. Piao, B. T. Anderson, S. Ganguly, R. R. Nemani, S. J. Goetz, P. S. A. Beck, A. G. Bunn, C. Cao, and J. C. Stroeve. 2013. Temperature and vegetation seasonality diminishment over northern lands. Nature Climate Change **3**:581-586.

Yalcin, S., and S. J. Leroux. 2017. Diversity and suitability of existing methods and metrics for quantifying species range shifts. Global Ecology and Biogeography **26**:609-624.

Young, D. J. N., C. M. Werner, K. R. Welch, T. P. Young, H. D. Safford, and A. M. Latimer. 2019. Post-fire forest regeneration shows limited climate tracking and potential for drought-induced type conversion. Ecology **100**:e02571.

Zhang, Y., Y. Bergeron, X.-H. Zhao, and I. Drobyshev. 2015. Stand history is more important than climate in controlling red maple (*Acer rubrum* L.) growth at its northern distribution limit in western Quebec, Canada. Journal of Plant Ecology **8**:368-379.

Zhu, K., C. W. Woodall, and J. S. Clark. 2012. Failure to migrate: lack of tree range expansion in response to climate change. Global Change Biology **18**:1042-1052.

Zimmermann, N. E., N. G. Yoccoz, T. C. Edwards, E. S. Meier, W. Thuiller, A. Guisan, D. R. Schmatz, and P. B. Pearman. 2009. Climatic extremes improve predictions of spatial patterns of tree species. Proceedings of the National Academy of Sciences **106**:19723-19728.

CONNECTING TEXT

In Chapter 3, I calculated the latitudinal shift at the northern range edge for eight species, showing support for northward expansion. Direct observations from such studies of range shifts can be incorporated into modelling of species distributions in response to climate change to improve projections. In the following study, I integrated ecological knowledge, including species-specific dispersal ability and life history, on 10 Canadian tree species from a variety of sources, including results from Chapter 3, to simulate changes in range limits constrained by dispersal in relation to changes in the spatial distribution of suitable habitats based on climate change alone. In doing so, I propose a novel way to translate observations of migration velocity obtained from observed range shifts and species traits into dispersal kernels.

Chapter 5 - DISPERSAL-BASED SCENARIOS FOR CANADIAN TREES SHOW LIMITED RANGE TRACKING UNDER CLIMATE CHANGE

Authors : Laura Boisvert-Marsh[1,2], John H. Pedlar[2], Sylvie de Blois[1,3], Amael Le Squin[4], Daniel W. McKenney[2], Charlene Williams[5,6], Isabelle Aubin[2]

Affiliations

[1] Department of Plant Science, Macdonald Campus of McGill University, 21111 Lakeshore, Ste-Anne-de-Bellevue, Québec, H9X 3V9, Canada.

[2] Great Lakes Forestry Centre, Canadian Forest Service, Natural Resources Canada, Sault Ste Marie, ON, Canada

[3] McGill School of Environment, McGill University, 3534 University St., Montreal, Quebec, H3A 2A7

[4] Département de Biologie, Université de Sherbrooke, 2500 Boulevard de l'Université, Sherbrooke, QC, Canada

[5] Atlantic Forestry Centre, Canadian Forest Service, Natural Resources Canada, Fredericton, NB, Canada

[6] Vineland Research and Innovation Centre, 4890 Victoria Ave N, Lincoln, ON, Canada

This chapter is currently in revision for publication in Diversity and Distributions.

5.1 - Abstract

Species distribution models based on climatic variables have provided valuable information regarding the nature and magnitude of changes to which tree species are likely to be exposed under climate change. These models typically project that climate envelopes will shift by hundreds of kilometers by the end of this century, a rate which will almost undoubtedly exceed the natural migratory capacity of tree species. Yet, few models exist that integrate species-specific life traits with climate projections for tree species at large scales. We developed a novel, data-driven method that integrates data on observed range shifts with trait data on key components of species dispersal capacity and growth. This knowledge was used to simulate dispersal scenarios for 10 important Canadian forest species. These models were applied across eastern Canada over 90 years at a resolution that approximates seed dispersal (25m resolution across ~3.7 million km^2). Simulations show that all species demonstrate northward latitudinal shift at the leading edge through 2100, but the magnitude and rate vary by species and time period. Specifically, most shifts in the short term will occur from range filling, which is influenced by the degree of patchiness in species' current distributions. Following this initial burst, subsequent colonization is mediated by long distance dispersal and life history traits. Based on the distribution that remains climatically suitable through 2100, simulated distribution area increased for five of the species studied here. Changes in simulated distribution area were influenced by the extent of area colonized at the leading edge and the amount of suitable habitat lost at the rear edge. The climate envelope shift projected for 2100 far exceeded the leading edge of the migration-constrained range shift for all 10 species, particularly for temperate species. This study underlines the limited extent to which trees will be able to track climate change via natural migration. Integrating observed migration velocities, life history and seed dispersal traits into process-based models allow for more realistic evaluations of tree vulnerability to climate change.

5.2 - Introduction

At northern latitudes, species distribution models coupled with climate projections have revealed that climatically suitable habitat could shift by hundreds of kilometers by the end of this century. Even at high latitudes, not all areas are projected to remain suitable for a range of tree species (Thuiller et al. 2005, Iverson et al. 2008, McKenney et al. 2011b, Périé and de Blois 2016). Indeed, these models provide valuable information on the degree to which tree species are likely to be exposed to climatic changes (i.e. exposure), as well as the extent to which species may need to migrate given their current distribution to track their suitable climate (Aubin et al. 2018). They do not provide, however, an indication of the future distribution of species in a changing climate. To do so would require integrating the different processes by which migration effectively occurs for plants through a series of discrete events that involve reproduction, dispersal and successful establishment at suitable sites. Because these processes depend on species traits in interaction with environmental conditions, the ability to migrate will vary among tree species. Historical evidence has shown species' response to climate to vary considerably thereby influencing the rate at which species migrate poleward (Davis 1981, Williams and Jackson 2007). Moreover, the projected rate of climatic shifts for this century is expected to far exceed the natural migratory capacity of many species (Prasad et al. 2013, Sittaro et al. 2017) as well as rates of post glacial climatic changes (Marcott et al. 2013). Studies of recent changes in tree distributions have indeed reported latitudinal shifts in response to several decades of climate change that are unlikely to match rates of climate warming at northern latitudes (Boisvert-Marsh et al. 2014, Sittaro et al. 2017, Boisvert-Marsh and de Blois submitted).

A number of platforms have been developed to account for migration potential in projections of species' distribution in a warming climate through data on reproduction, dispersal and/or establishment in relation to habitat suitability (reviewed in Snell et al. 2014, Keyel et al. 2016). Such modelling platforms can be used with individual species or groupings of species (e.g. Dynamic global vegetation models, LPJ, Sitch et al. 2003). They have been applied across a range of spatial extents and resolutions (Snell et al. 2014), often compromising between the two because of heavy computational requirements and long model run times. Processes can be incorporated as part of discrete event simulators (e.g. SpaDES, Chubaty and McIntire 2017) or as extensions within a modelling platform (e.g. LANDIS-II, Scheller et al. 2007). While some models have successfully integrated species-specific life traits that compare individual species ability to migrate across broad scales (Scheller and Mladenoff 2008, Meier et al. 2012, Miller and McGill 2018, Bouchard et al. 2019), there are still important limitations. In particular, fully evaluating migration potential requires substantial data inputs on key population processes from a variety of sources, of which the data are rarely found in a readily workable format (Anderson 2013, Willis et al. 2015). When integrating species information, it is typically done using expert opinion or coarsely aggregated information (Aubin et al. 2016), which may reduce the predictive power of modelling efforts (Angert et al. 2011). Addressing such limitations should help improve our knowledge of key processes determining species' responses to climate warming and lead to more realistic projections of range shifts.

For any given species, the ability to disperse and their associated distances influence migration potential. Studies that incorporate migratory ability typically employ dispersal kernels, a probability density function that describes the probability that a seed or seedling disperses to a distance relative to a source (Iverson et al. 2004, Engler et al. 2009). Collecting field information on dispersal can be resource intensive. For wind-dispersed seeds, the kernels are often calibrated with seed trap data, which involves setting out containers that collect falling seed at set distances over one or more trapping seasons (Bullock et al. 2017). Most of the time, these traps are set in non-treed areas that do not necessarily approximate conditions in forested areas, which is where most dispersal, and hence migration, is expected to happen (Greene and Johnson 1995, Clark 1998). Assessing dispersal via animal vectors (e.g. endozoochrory, exozoochrory) is even more complicated since it involves tracking both the propagule and the disperser (Myers et al. 2004). Consequently, most plant and tree species do not have published literature values for dispersal kernels. When they are used, compromises on which species are modelled and which kernels are employed (species-specific vs. for instance single broad kernels for all species or by plant functional type) are usually required but can make it difficult to evaluate a broad range of species (Snell et al. 2014). One possible avenue to overcome these hurdles is to parameterize the mathematical functions underlying dispersal kernels originally developed for small areas using data from observed changes in distribution at broad scale. Measured latitudinal (or altitudinal) shifts, based on observed changes in species' occurrence patterns in space and time, could provide a solution to estimate dispersal distance at a (regional) scale relevant to most climate change studies. Combined with other relevant data sources, these quantitative assessments of range limit shifts made possible by the availability of data from repeated forest census (e.g. inventories of permanent and temporary forest plot networks in Canada, described in Boisvert-Marsh et al. 2014, and the United States, described in Woodall et al. 2009) could contribute to fill a gap in data availability to provide a reasonable approximation of dispersal distances indicative of migration potential.

Our objective in this study was to develop projections of the distribution of tree species in a warming climate incorporating available dispersal data as an original contribution to the development of process-based models of species' responses to climate change. We simulated potential migration over this century in eastern Canada (~3.7 million km^2) for 10 important forest species selected to represent a range of life histories, observed migration rates and dispersal abilities. We employed a data-driven approach to parameterize our models for each species, using data from observed range shifts with trait data on species dispersal capacity and growth within a flexible modelling framework (MigClim, Engler et al. 2012) that integrates species characteristics with projected climate conditions. In doing so, we proposed a method to translate observations of migration velocity from range shifts into dispersal kernels that quantify the probabilities of short- and long-distance dispersal events. We used the outputs of these models to quantify the potential shift in range limits projected through 2100 and compared the outcome to projected changes in climate suitability without dispersal constraints.

5.3 - Methods

5.3.1 - Modelling framework

All models were run in R version 3.4.3 (R Core Team 2017). The MigClim.migrate function within the MigClim package integrates dispersal ability and life history characteristics with current and projected environmental conditions to produce a cell-based model of species dispersal (Engler et al. 2012). MigClim requires the following inputs (described below) in a raster format to simulate dispersal under climate change: 1) a map defining a species' initial distribution and barriers to dispersal, 2) species' dispersal parameters, 3) life history traits influencing time to seed production, and 4) a series of maps indicating how the distribution of potentially suitable climate habitats changes through time. Ten common tree species, for which the study area captures the leading edge of their distribution, were selected for this study (Table 1). We simulated dispersal processes in eastern Canada over an area that includes the entirety or a major part of their current distribution (~3.7million km^2). These species are common and represent a range of life histories and observed migration potential. Model inputs are described below.

5.3.2 - *MigClim model inputs*

1) Initial species distribution and barriers to dispersal

Current tree species distributions and estimates of tree biomass were obtained from Canada-wide raster grids (at 250m resolution) of forest inventory attributes, which were interpolated using a k nearest neighbour (kNN) analysis of both forest inventory photo plot data and satellite data based on the 2001 inventory year (see Beaudoin et al. 2014 for details). A number of steps were undertaken to clean this data prior to generating the current tree species distributions. To avoid including stands that were not at full seed production at the first time step and to minimize data quality issues over species identification for these stands, only stands over 40 years of age were included in the current study. Coniferous and deciduous proportions which were not identified to species by Beaudoin et al. (2014) were added to individual species distributions on a region-by-region basis in southern Ontario, southern Quebec and the Maritimes based on species' relative importance in each ecoregion as provided in the Canadian National Vegetation Classification (Baldwin et al. 2019). To remove species attribution outside the known species range, the entire range for each species was validated on a case-by-case basis using Farrar (1995), the Canadian National Vegetation Classification (Baldwin et al. 2019), and expert opinion. Finally, species initial distributions were converted to presence/absence based on a minimum aboveground biomass cut off of 0.25 tonnes/ha. The cleaned species initial distribution raster files were downscaled from 250m to 25m to incorporate dispersal at a scale relevant for species. Barriers to dispersal were considered in the model and included large bodies of water (lakes, rivers, oceans). Land use and land cover were indirectly considered in the initial distributions because of the constraints placed on stands and species during file preparation. This removed areas without appreciable forest cover, such as urbanized and agricultural areas. However, land use and land cover type were not considered explicitly as barriers to dispersal, nor were they used to constrain where a species could colonize.

2) Species dispersal parameters

Calibrating migration kernel functions

Dispersal kernels represent the statistical distribution of dispersal distances in a population, a probability density function that describes the probability that a seed or seedling disperses to a distance relative to a source. Availability of published dispersal kernels was limited for our species, so we developed dispersal kernels for each of them using the 2Dt function (Clark et al. 1999), a commonly used kernel especially for wind dispersed species that performs moderately well in comparison to other distributions (Bullock et al. 2017). This function requires mean and median dispersal distances in order to be solved. The dispersal distances we used to calibrate the function were obtained from common seed fall distance, which characterises the influence of individual trees on dispersal patterns at local scales, and migration velocity, which describes the distance by which the distribution of a species has been reported to shift yearly at broad spatial scales (Boisvert-Marsh et al. 2014). Common seed fall distances here were obtained from Burns and Honkala (1990). Measures of distribution shifts were based on paleoecological and contemporary observations (Ordonez and Williams 2013, Williams and Beardmore, unpublished data, Chapter 8, see Table 5.1 and Table 8.4.1.1). To focus on migration during periods of warming, reported rates were taken for expanding fronts at the northern limit, where possible, and were averaged over available sources. Including measures of latitudinal distribution shifts integrates larger scale effects into the dispersal kernel and acts as a proxy for population-level processes (e.g. abundance or prevalence) and/or seed production. Population size can have an impact on simulated migration distances over multiple generations (Clark et al. 2001), underscoring its importance in broad scale assessments.

Given that seed fall patterns are typically right-hand skewed (i.e. most seeds fall relatively close to source while a smaller proportion fall further away, Nathan and Muller-Landau 2000) and all study species showed greater migration velocities than typical seed fall distances (Table 5.1), the common seed fall distance was used as the median and the distribution shift from observed migration velocity was used as the mean for parameterizing the 2Dt distribution as described below.

Estimating 2Dt

The distribution of 2Dt is as follows (formulation from Greene et al. 2004):

Equation 5.1: $$\frac{a}{\pi b[1 + \frac{x^2}{b}]^{a+1}}$$, where x is the distance from a given cell

The unknowns, *a* and *b*, are the 2Dt distribution parameters to be solved. Let $\mu > 0$ and $m > 0$ be the mean and median of the 2Dt (*a, b*) distribution, respectively (positive real numbers):

Equation 5.2: $$m = \sqrt{b(2^{1/a} - 1)}$$

Equation 5.3: $$\mu = \frac{\sqrt{\pi b}}{2\Gamma(a)}\Gamma(a - 0.5)$$

Eqs. 5.2 and 5.3 are intractable, hence the Newton-Raphson method is used to derive a numerical solution based on the mean and median. The numerical method used is from the rootSolve package (Soetaert 2009) and we expect the solution to be unique. The first Eq. 5.2 gives:

Equation 5.4: $$b = \frac{m^2}{2^{1/a} - 1}$$

By inserting Eq. 5.4 in Eq. 5.3, and reorganizing the terms ($m > 0$):

Equation 5.5: $$0 = \frac{m}{2\Gamma(a)}\sqrt{\frac{\pi}{2^{1/a} - 1}}\Gamma(a - 0.5) - \mu$$

To prove existence and uniqueness of a solution to *a*, we need to verify that the function

Equation 5.6:

$$f(a) = \frac{m\sqrt{\pi}}{2\sqrt{2^{1/a}-1}} \frac{\Gamma(a-0.5)}{\Gamma(a)}$$

is a continuous decreasing function on]0.5*,* ∞[and investigate the limits of *f* at its boundaries. A plot of f as a function of *a* confirms this hypothesis (see Fig. 8.4.1.1). Given:

$$\lim_{a \to 0.5} f = \infty$$
$$\lim_{a \to \infty} f \approx 1.065m$$

Eq. 5.5 should provide a unique5 solution if:

Equation 5.7:

$$\mu > 1.065m$$

All the species satisfied this condition. Estimated parameters for *a* and *b* are found in Table 5.1.

For each species, the probability that a seed will fall at least a certain distance away from the source cell was used in the MigClim model (probability of dispersal >0m from source, >25m, >50m, etc.). To calculate the probability, the cumulative distribution function was used based on the estimated parameters a and b and where x is the distance from the source cell (i.e. n-1 cells * 25m) (Eq. 5.8).

Equation 5.8:

$$\left(\frac{b}{b+x^2}\right)^a$$

Long distance dispersal

The probability of long distance dispersal (LDD) was also incorporated into the model. The dispeRsal function (Tamme et al. 2014) was used to model long distance dispersal based on widely available plant traits. The dispeRsal function provides confidence intervals of the maximum estimated distance; the lower and upper bounds of the confidence interval were used as the LDD_{min} and LDD_{max} arguments in the MigClim function (rounded to the nearest 25m). For the present study, two different models were tested, and the outputs were assessed against published literature values. The model for wind dispersed species includes dispersal syndrome and terminal velocity and the model for animal dispersed species includes dispersal syndrome, seed mass and relative height of seed release. The probability of an LDD event was estimated as the cumulative probability between the LDD_{min} and LDD_{max} estimates based on the area under the 2Dt function (see previous section).

3) Life history traits influencing time to seed production

Once dispersal and establishment has occurred, the age at which seed production starts (age of sexual maturity), the age at which optimum seed production is achieved and growth rate were used to characterise the potential for seed production and dispersal in a cell (parameters in Table 5.3). Slow life histories make it such that trees initiate seed production at a relatively advanced age, but do not immediately reach their full reproductive potential. In fact, the age at which seed production starts and the age at which full reproductive output is achieved can be quite different and may be an important constraint in range expansions (Travis et al. 2011). Once the minimum age is attained, probability of seed production increases according to a sigmoid distribution until the age at which maximum seed production is achieved. Between these years, the growth rate is used to modulate the inflection point of the curve. Once the optimum age is attained, the probability of seed production by a given cell reaches 1 and is held constant. Data on these seed production-related traits were obtained from an exhaustive review of the literature. These trait data will be made available through the TOPIC database (Aubin et al. 2020).

4) Maps of suitable climates through time

Climate suitability of each cell in our study area was determined for each time step using species distribution models. These models (see McKenney et al. 2011a for details) were generated using the ANUCLIM package (Xu and Hutchinson 2013) and tree occurrence data from an extensive database of North American plant occurrence locations (http://planthardiness.gc.ca/). Climate estimates were obtained at each species occurrence location by interrogating spatial models (described in McKenney et al. 2011b) for the following six climate variables: mean annual temperature, maximum temperature of the hottest month, minimum temperature of the coldest month, total annual precipitation, precipitation of the hottest three months, and precipitation of the coldest three months. These six variables provide a good summary of the moisture and temperature gradients that may impact tree growth and survival (McKenney et al. 2007). For the current work, we employed the 'core' climate profile for each species (i.e., the climate space delimited by the 5th and 95th percentiles of each climate variable), which has been shown to closely align with species' actual distributions (McKenney et al. 2007). Grids of future climate (see Price et al. 2011 for details) for the same six variables were obtained for three time periods (2011-2040, 2041-2070, and 2071- 2100) based on projections from the Canadian Earth System Model (CanESM2; Arora et al. 2011) under a high carbon emissions scenario (Representative Concentration Pathway, RCP 8.5; van Vuuren et al. 2011). Other pathways may be closer to eventual outcomes (Hausfather and Peters 2020); however, emissions in the first two decades of the 21st century were tracking somewhere between the scenarios postulated by RCP 6.0 and RCP 8.5 (Rogelj et al. 2018). Under RCP 8.5, winter temperatures are projected to increase by 7-9°C in the Canadian boreal forest and 5-7°C in the eastern temperate forest (Zhang et al. 2019). Projected temperature increases in the summer are more uniform, falling in the order of 5-7°C across much of Canada (Zhang et al. 2019).

5.3.3 **-** *Model runs*

Dispersal was simulated for 90 steps with each step corresponding to 1 year. Dispersal was assessed on a 25m by 25m resolution raster grid across eastern Canada, which corresponds to ~14 billion cells. The fine resolution of the grid was selected to represent a realistic scale for local dispersal processes and to adequately represent decreasing probability of successful dispersal with increasing distance. At each time step, each cell, including initially occupied cells and those colonized during the model runs, is tested to assess whether it is still suitable. If it is suitable, that cell is subjected to model parameters. If an adjacent cell is colonized during this step, the year is recorded, the colonized cell becomes potentially productive and subjected to seed production and dispersal parameters once the minimum age of sexual maturity is attained. If the cell is no longer suitable, the cell dispersal probability is reset to 0 and the cell is converted to indicate the climate period when it becomes unsuitable. A species climate suitability model persists for 30 steps, corresponding to the 30 year period each one covers. (i.e. time steps 1-30 = species climate suitability model #1, 2011-2040; Time steps 31-60 = species climate suitability model #2, 2041-2070; Time steps 61-90 = species climate suitability model #3, 2071-2100). Hence, the time steps correspond to the years between 2011 and 2100. It should be noted that this test of climatic suitability also occurs at time step #1.

Given the small grid resolution across a broad area (~14 billion cells), the computation requirements exceeded MigClim's capacity. To overcome this, it was necessary to cut the gridded distribution into smaller blocks to facilitate computation. Five model iterations were run on each block, then stitched back together once computation on all blocks were completed. Two grids were constructed, each fully overlapping the other to reduce the edge effect from each model run. Average year colonized was calculated for each cell across the 10 total model runs across the entire study area. It should be noted that this process required a significant amount of time to run for each species across all blocks, ranging from 4 days for species with low migration ability to 8+ weeks for those with higher migration potential.

5.3.4 - *Post modelling analyses*

Once modelling was complete, a number of post-hoc analyses were conducted to assess range movement at both small and broad scales, proportion of suitable and unsuitable habitat, and climate envelope shift. To assess localized dispersal effects, we computed the cumulative distance between the initial distribution and cells colonized by the end of the model runs (see Fig. 5.1 for example of how this was calculated). To do this, the initial distribution was randomly sampled at the leading edge and an area extracted based on a set window size. Then, the extracted area was assessed to see if that window captured one or more cells colonized at year 90. If this condition was met, a cumulative distance cost transition was calculated based on a d16 pattern between the initial distribution cell(s) and all cells colonized at year 90. These distance values were stored, and a distribution was created from these stored values resulting from all iterations of the algorithm. Two runs were completed, one to assess the minimum window size necessary to capture cells that satisfy both conditions and one with a fixed window size as determined in the previous step. This script was iterated 100 times for window sizes between 500m and 20000m and 500 times at a fixed window size (varies among species). Once all iterations were completed, the distribution of values was plotted and the minimum, 10th percentile, median, 90th percentile and maximum distance (in meters) from the initial distribution as well as the standard deviation was calculated. This algorithm was tested on all areas at the leading edge, whether or not they were contiguous as long as they satisfy the conditions stated above. This analysis provides an indication of how far a species can spread around a newly occupied area resulting from long distance dispersal.

Next, the proportion of initial distribution and subsequently colonized cells to suitable and unsuitable habitat was calculated in 10 year intervals. Then, to assess range-wide trends in shifting limits, the latitudinal range shift (LRS) was assessed as the difference between the initial distribution and simulated distribution at the end of a given climate envelope period (i.e. at year 30, year 60 and year 90). LRS were assessed in 50km wide bands running north-south across the entire distribution at the 90th, 95th and 99th percentiles of latitude. Calculating LRS at different percentiles provides an indication of the predominant patterns underlying shifts. For example, latitudinal shift at the 90th percentile provides an indication of range filling whereas latitudinal shift at the 99th percentile is an indicator of range extension. Average LRS were calculated as the mean of the difference in latitude for occupied bands weighted by the number of occupied cells in each. Positive LRS values indicate the range limit has shifted northward between the initial distribution and the time step of interest whereas negative values indicate a southward shift (see (Boisvert-Marsh et al. 2014 for discussion of causes). Range shift velocity was calculated by the range shift divided by the number of years elapsed in the simulation (30, 60 or 90 years). Calculated range shifts and velocity included cells that were part of the initial distribution and colonized but that become unsuitable at some point in the model runs. This was done because we assumed that the species may persist under unsuitable climate conditions, even if conditions for seed production and colonization are not met (Hampe and Jump 2011).

Finally, we quantified the latitudinal disparity between the upper limit of species' simulated distribution (i.e., dispersal-constrained) and the lower limit of its climate envelope. The latitudinal disparity was calculated in two ways to capture different dynamics. First, we calculated the difference between the 95th percentile of the species climatic envelope (upper latitudinal limit) and the 95th percentile of the simulated distribution in the corresponding time step (30, 60, 90 years). We then calculated the difference between the minimum latitude of a species' climate envelope (lower latitudinal limit) for each projection (2011-2040, 2041-2070 or

2071-2100), and the 99th percentile of latitude of the simulated distribution in the corresponding time step (30, 60 or 90 years). In both cases, positive values indicate that the climate envelope is at a higher latitude than the simulated distribution in a given time step. Conversely, negative values indicate that the simulated distribution is at a higher latitude than the climate envelope. Disparities were assessed in 50km wide bands across the entire east-west distribution.

5.4 - Results

Parameterizing the 2Dt kernel using seed fall distances and migration velocity resulted in species-specific dispersal probabilities that were then used in simulations (Fig. 5.1). Common seed fall distances used for the median ranged from 30m (*Quercus rubra*) to 200m (*Betula papyrifera and Populus tremuloides*) while migration velocity used for the mean ranged from 107.57 (*Quercus rubra*) to 451.6m (*Populus tremuloides*) (Table 5.1). Long distance dispersal values varied from a lower bound of 100m (*Quercus rubra*) to an upper bound of 5575m (*Populus tremuloides*), but most were limited to <1700m (Table 5.2). The 2Dt function resulted in relatively high probabilities of dispersal at both short and long distances. On average, the probability of long distance dispersal (LDD) was 0.123 but varied widely among species (*Populus tremuloides* - 0.0222 between LDD_{min} 1275m and LDD_{max} 5575m; *Betula papyrifera* – 0.2988 between 275 and 1000m, Table 5.2).

Based on both life history traits and dispersal probabilities, MigClim simulated distributions resulted in species-specific patterns of colonized cells (Fig. 5.2 a-j). Based on these simulations, newly colonized area through to the end of the third time period (2071-2100) somewhat compensated for the loss of suitable initial distribution (Table 5.4), but not for all species (Fig. 5.3). *Acer rubrum* and *Acer saccharum* retained 82.21 and 96.28% of their initial distribution respectively through to 2100 (Table 5.4). Six species lost more than 50% of their initial distribution (Table 5.4). *Thuja occidentalis* lost the most initial habitat, with only 7.19% of its initial distribution remaining suitable through to 2100. Similar trends were observed in the proportion of initial distribution (Table 5.4) and colonised area becoming unsuitable (Fig. 5.3), but overall proportions were lower for the latter. Most of the initial distribution and colonized area that became unsuitable in the third time period (2071-2100) occurred in the southern portion of the study area (In Fig. 5.2, blue-green = initial distribution that remains climatically suitable; orange = initial distribution that becomes unsuitable).

Based on the distribution that remains climatically suitable, simulated distribution area increased for almost all species in the first time period (2011-2040), but this trend started changing in the 2041-2070 and 2071-2100 time periods (Fig. 5.4a). *Thuja occidentalis* showed decreases in simulated suitable distribution area over all time periods while *Acer rubrum* and *Quercus rubra* showed consistent increases (Fig. 5.4a). After gains in the first time period, three species started to show declines in overall suitable area as of 2041-2070, followed by another two in 2071-2100 (Fig. 5.4a). Despite this loss, they still showed overall increases in suitable area (Fig. 5.4b). Those species that showed the greatest loss by 2100 included slower growing species such as *Betula alleghaniensis* and *Thuja occidentalis* as well as *Pinus strobus*. The other two species demonstrated among the highest losses in suitable area (Fig. 5.3, Fig. 5.4, Table 5.4).

Looking at localized dispersal patterns, the median of cumulative distance between an initial distribution and a cell colonized at year 90 ranged from 1.2km and 18.0km (Table 5.5, see Fig. 5.1 for example of resultant dispersal patterns). With the exception of *Populus tremuloides* and *Acer rubrum*, species showed a cumulative distance over 90 years of less than 6km between the initial distribution to the edge of colonized cells. On the other hand, assessments of latitudinal shift across the entire northern edge provide a different portrait of range-wide patterns for species. All species showed northward latitudinal shift through 2100, but the magnitude and rate varied by species and time period. Considering all species, simulated latitudinal range limits at the 90th percentile shifted between 26-292km, translating to a velocity of ~300m/year (*Acer saccharum*) to ~3.2km/year (*Betula papyrifera*) over the entire 90 years (Fig. 5.5). At the 99th percentile, LRS across all 90 years varied from 16km to 171km, translating into a shift of 181m/year (*Acer saccharum*) to 1.9km/year (*Betula papyrifera*). The greatest latitudinal shift and rate tended to occur within the first time period (years 1-30) and decreased thereafter, but this depended on the percentile of latitude considered (Fig. 5.5). Most species showed larger shifts at the 90th over the 99th limit, with the exceptions being *Acer rubrum* and *Betula alleghaniensis*. When examining trends in range shifts across the distribution, latitudinal shifts varied greatly along the west-east gradient. The largest shifts tended to occur where there is considerable filling around sparsely occupied areas of the initial distribution. For example, longitudinal bands where species like *Populus tremuloides*, *Betula papyrifera* and *Picea mariana* were present but not frequent showed high LRS values, up to 300-500km in some cases (Fig. 8.4.2.3). On the other hand, *Acer saccharum* and *Betula alleghaniensis* tended to show more modest latitudinal shifts at the core of their range, (~25 to 60km, Fig. 8.4.2.3).

The magnitude of envelope shift in each time period exceeded simulated species latitudinal shift (Fig. 5.6) but varied greatly with longitudinal position and initial species distribution. Southerly distributed species exhibited higher latitudinal disparities between climate envelope and simulated range limit. For these species, the climate envelope in parts of Quebec surpassed the simulated limit by 900 to 1500 km by the end of the third time period (2071-2100) (Fig. 5.6, approx. longitudinal bands 29-45). For northerly distributed species, the greatest disparities are situated where there is suitable climatic habitat in the islands of the territory of Nunavut. For three species (*Populus tremuloides*, *Picea mariana* and *Abies balsamea*), negative disparities were found (i.e. simulated distribution exceeded climate envelope) on the western edge in areas where the climate was not suitable in the first time period. Six species demonstrated at least one longitudinal band where the minimum latitude of the climate envelope surpassed the northern limit of the simulated distribution by 2100 (Fig. 8.4.2.4). Some of these bands were only sparsely occupied but others are within the core of the distribution, such as for *Thuja occidentalis* and *Abies balsamea* (parts of Ontario and Quebec, Fig. 5.1).

5.5 - Discussion

Climate envelope or species distribution models typically project considerable gains in suitable climatic habitat in this century for tree species along the northern edge of their distribution (e.g. Iverson et al. 2008, McKenney et al. 2011b, Périé and de Blois 2016). Integrating information on reproduction and dispersal in process-based models improves our ability to evaluate whether tree species can indeed migrate to colonize newly suitable habitats and where they risk being trapped in unsuitable conditions. The discrepancies we observed between the projected climate envelope and the simulated migration responses of species depend on these processes, but also on species' initial distribution and geographic barriers. We found that the most rapid range shifts occurred for species with scattered populations at their northern range edge at the start of model simulations (*Betula papyrifera, Populus tremuloides, Picea mariana*), which provided them with a head start for range expansion. Northern boreal species indeed showed smaller latitudinal discrepancies than mixed temperate forest species at their northern limit. However, because of their geographical locations, these boreal species in fact can quickly run out of room to migrate. Once colonisation has occurred, subsequent spread is further modulated by the age at which species start producing seeds and the time to reach full production, favouring species with rapid life histories such as *Acer rubrum*. Using dispersal kernels, Clark (1998) showed velocity to be indeed sensitive to life history. Depending on dispersal distances and life history characteristics of species, range filling will be a more important process than range expansion at least in the short term.

Some loss in climatically suitable area is projected for all species but this varied depending on where they are currently distributed. Two species projected to retain the highest proportion of their initial distribution as climatically suitable in Canada, *Acer rubrum* and *Acer saccharum*, are also distributed into the United States. Even though this area was not included in the model simulations, the southern climates are captured in the climate envelope projections. However, four of the six species that lost the most suitable initial area are distributed mainly in Canada and three are widely distributed boreal species (*Abies balsamea, Picea mariana and Betula papyrifera*). Other species that showed high overall loss in suitable initial area by 2100 included *Pinus strobus, Betula alleghaniensis and Thuja occidentalis*. The latter two are slow to moderate growing species that experienced high losses of suitable climate without much colonization at the leading edge to compensate.

To calibrate our kernels, we used evidence from different scales to account for other larger scale factors that are not typically considered in migration studies that consider dispersal. The median employed in the 2Dt kernel, common seed fall distance, is representative of individual-based processes of dispersal whereas the mean, based on migration velocity, was based on range-wide evidence that acts as a proxy for other considerations (e.g. population size, colonization potential). Additionally, we used a trait-based approach to characterise long distance dispersal (LDD_{min} and LDD_{max}), which were then used to define the probability of such an event. Compared to some studies where LDD_{max} is very large (Prasad et al. 2013, Miller and McGill 2018) or unbounded (Hickler et al. 2012), our LDD_{max} values were relatively small but also similar to other estimates (McLachlan et al. 2005, Bouchard et al. 2019). These distances placed constraint on cumulative distance away from currently occupied sites for species, even if the probabilities of LDD shown here were generally high.

Long distance dispersal events have long been thought to explain the rapid post glaciation spread of trees (Delcourt and Delcourt 1991, Clark et al. 1998, Giesecke et al. 2010) at the end of the Pleistocene, especially if seed fall distances have a long 'fat' tail (Clark 1998). In most cases, our method to define LDD resulted in lower limits that exceeded the mean of the dispersal kernel, a pattern we would expect to see. In the case of *Betula papyrifera*, however, migration velocity exceeded the lower limit of LDD we used ($\mathrm{LDD_{min}}$ - 282m vs. 2Dt kernel mean - 451.6m). While LDD values were not used to calibrate the kernels themselves, the probability of such an event in this case would not be as rare as one might expect (Clark 1998). For this species, the migration velocity from literature sources (Table 8.4.1.1) varied considerably and points to other factors underlying contemporary trends, such as frequency and intensity of disturbance (Brice et al. 2019, Boisvert-Marsh and de Blois In review). Despite a high probability for LDD, $\mathrm{LDD_{max}}$ for *Betula papyrifera* was restricted to 1km, limiting how far it could spread within a generation. For comparison purposes, we set our $\mathrm{LDD_{min}}$ to the 95th percentile of the distance from the dispeRsal model output (ranges from 528 to 5582m, see Table 5.2) and $\mathrm{LDD_{max}}$ to 10000m in test trials to examine the long tail of the kernel distribution beyond the LDD we used in our simulations. The probability of these distant dispersal events for all species were much lower than the ones we had obtained (Fig. 8.4.2.2, Table 8.4.2.1), implying that such very long-distance dispersal events would be rare.

We showed that the cumulative distance traversed over 90 years is limited, ranging from a median distance of 12.9 m/year for *Acer saccharum* to 200.0 meters/year for *Populus tremuloides,* with an average of median distance 48.4m/year across all species. Other published sources show estimates of range spread of the order of 51-133m/year (Ordonez and Williams 2013) and 1.7 to 1500m (Corlett and Westcott 2013) over a range of species. Models by Clark et al. (2001) that varied rates of reproduction across generations found that the cumulative distance travelled for *Acer rubrum* was roughly 45m/year on average, which is close to our findings (median=57.8m/year).

Latitudinal shift at the 90th percentile provides an indication of range filling whereas latitudinal shift at the 99th percentile is an indicator of range extension. Acknowledging that we used observed migration velocities from different sources to calibrate our models, we expected the estimated values for latitudinal shifts to match those reported for contemporary latitudinal shifts. Compared to this study, Boisvert-Marsh et al. (2019) over the short term (~30-40 years) showed magnitude of range shift for *Acer saccharum* (22.2 km simulated at the 90th in this study: Fig. 5.5; vs. 17km observed at the 90th in Boisvert-Marsh et al. 2019) and *Acer rubrum* (32km simulated vs. 24km observed) similar to those of the present study. Other species such as *Betula alleghaniensis* and *Thuja occidentalis* showed observed shifts of 4 and 7km respectively in the same time frame (Boisvert-Marsh et al. 2019, Boisvert-Marsh and de Blois In review). While lower than the simulated shifts presented for the first period here, the magnitude lines up with the longer term estimates after the initial pulse (*Betula alleghaniensis*: 5km between 60 and 90 years; *Thuja occidentalis*: ~ 12km in this study). In some cases, simulations of migration outcomes for species with scattered populations at their northern edge tended to overestimate latitudinal shifts compared to their observed values (*Betula papyrifera* – 292km here vs. 71km observed; *Populus tremuloides* 226.6km here vs. 19km observed). Indeed, at the 99th percentile, most species presented simulated rates between ~180m/year (*Acer saccharum*) and 900m/year (*Picea mariana*) over 90 years, which falls in line with other published values (Ordonez and Williams 2013). Process-based model projections are difficult to calibrate and validate without empirical data to support their findings. Hence, long-term assessments of observed range shifts are crucial to understanding whether the dispersal simulations we present here are supported by field observations.

Several of our study species have a portion of their distributions in the United States south of our study area; however, much of the U.S. distribution is projected to become climatically unsuitable for species like *Abies balsamea* and *Thuja occidentalis* during this century (Iverson et al. 2008, McKenney et al. 2011b, Périé and de Blois 2016). Thus, Canada may encompass much of the suitable climate habitat for these species in the future. Note, however, that large areas of southern Quebec and Ontario are also projected to become climatically unsuitable for all our study species by the end of the century, with pockets around the Great Lakes acting as climate refugia. For the purposes of the latitudinal shift calculation, however, we considered areas which are projected to become unsuitable by the end of the century to be stable, i.e. retain their initial distribution and colonized areas before becoming unsuitable. If observed, this persistence can delay precipitous changes but also prevent better suited genotypes or species from becoming established (Urban et al. 2012, Renwick et al. 2016). Trees in areas with unsuitable climate conditions and/or extreme climate variability within suitable periods could undergo mortality, which would affect the migration rates reported here. Extreme events can rapidly increase background mortality rates (Hanski 1998, Holt 2003) and have already been observed in some areas (Hogg et al. 2008, van Mantgem et al. 2009, Michaelian et al. 2011). On the other hand, mortality may benefit maladapted populations; for example, high mortality in early life stages at the range limit can act as a range shaping mechanism, selecting for adapted alleles that can tolerate novel climates (Bussotti et al. 2015). Additionally, mortality of maladapted populations/individuals could benefit northward migrating species by reducing competition (Kuparinen et al. 2010), providing openings for migrating species (Leithead et al. 2010). Indices of species-specific sensitivities could be used to inform their susceptibility to mortality and/or their ability to withstand environmental instability (Potter et al. 2017, Boisvert-Marsh et al. 2020, Royer-Tardif et al. In review)

We used correlative models of species' distributions based on an early technique that focuses on statistical summaries of climatic variables underlying known occurrences (ANUCLIM). The nature of inferred species-climate relationships, particularly the assumption that climatic niche limits approximate fitness limitations, lies at the heart of these models. Even in absence of changes to suitable climate area, however, agreement between range limits and climate limits may be the exception, not the rule. A broad assessment of tree species in the United States found that the geographic edge was only weakly correlated with climate limits (Oldfather et al. 2020). Non-climatic habitat factors and barriers to dispersal can define range limits before climatic limits are attained (Lafleur et al. 2010, Beauregard and de Blois 2014, Warren and Bradford 2014, Pagel et al. 2020), therefore determining whether or not species were in equilibrium with their climatic niche at the start of model runs. Land use and habitat connectivity (Parks et al. 2020) and disturbances (Liang et al. 2018), as well as biotic factors like competition (Louthan et al. 2015) or species complementarity/facilitation (Ettinger and HilleRisLambers 2013, Boisvert-Marsh and de Blois In review) can all influence establishment.

Given that the focus of the current work was to compare dispersal ability in relation to rapid climatic change, we opted for a relatively simple climate envelope model that uses a potential worst case scenario (RCP 8.5). Other studies have employed different consensus-based outputs of multiple statistical models or concentration pathways, additional variables (notably edaphic variables, Périé and de Blois 2016) and/or modelling techniques (e.g. integrative approaches, Talluto et al. 2016). These models tend to present more conservative projections for species distributions than our models based on climate alone. In addition, models based on long-term averages of annual variables employed across a broad suite of species do not adequately capture specific processes that may influence future projections. For example, growth and recruitment have been shown to vary along spatial and climatic gradients, possibly linked to critical life events (Morin et al. 2007, D'Orangeville et al. 2016, Boisvert-Marsh et al. 2019). Hence, other approaches or climate change projections could offer a different portrait of latitudinal disparity in our area.

Whether it be in areas that are suitable or unsuitable, species have the potential to respond in the context of relatively short-term climate change. Their ability to disperse via natural vectors at the leading edge and their ability to persist in areas projected to become climatically unsuitable resulted in species-specific patterns of range change. If they hold true, these shifts could fundamentally change forest community composition from what we currently observe. Our simulations could be improved by integrating edaphic and land use data, variable reproductive output and dispersal distances, including density dependent functions, establishment and juvenile survival and more sophisticated species distribution models. What has not been considered, however, is the influence of human-mediated dispersal, whether as an intended or unintended consequence of our choices. The species considered here are relatively common and could be considered candidates for forestry-based assisted migration (Pedlar et al. 2012) or could be planted beyond their natural range for aesthetic (Van der Veken et al. 2008) or non-forestry commercial purposes (Legault et al. 2019). Humans have the ability to transport propagules considerably farther and faster than natural vectors and can take active measures to ensure tree survival. Like climate refugia of the past (Davis 1983), assisted colonization could provide new nuclei for range expansion. While our study underlines the extent to which trees will be able to track climate change via natural migration, suggesting potential for migration failure for some species (*sensu* Aubin et al. 2018), human-mediated migration could offset dispersal limitations and migration lags, leading to more rapid range expansion than what our models suggest. Given the latitudinal discrepancy projected, our results suggest that mixed temperate forest species would benefit more from assistance than northern boreal species which may need refuges.

5.6 - Acknowledgements

The authors would like to thank Kellina Higgins for surveying the literature on species traits. We are grateful to André Beaudoin and Pierre Bernier for providing access to the datasets of species initial distribution and to Ken Baldwin and Bill Meades for their expertise on Canadian tree distributions. We also thank Tannis Beardmore for providing access to the database on paleoecological migration and biotic velocity. This work was supported by the Forest Change Initiative (Canadian Forest Service, Natural Resources Canada).

Table 5.1: List of the 10 tree species selected for this study as well as their median and mean dispersal distances used to estimate a and b parameters of 2Dt migration kernels. Median distances, considered as the distance that seeds most commonly travel from the source tree, were obtained from reported literature values. Mean distances were taken from broad scale studies of observed migration velocities.

Species	Species Code	Median (m)	Mean distance (m)	Estimated 2Dt a	Estimated 2Dt b
Abies balsamea	ABIBAL	40	122.49	0.6372	813.1
Acer rubrum	ACERUB	100	229.89	0.7170	6137.1
Acer saccharum	ACESAC	100	121.87	2.015	24355.4
Betula alleghaniensis	BETALL	100	151.93	1.052	10728.3
Betula papyrifera	BETPAP	200	451.6	0.7240	24923.7
Picea mariana	PICMAR	80	238.09	0.6431	3301.9
Pinus strobus	PINSTR	60	149.13	0.6899	2079.4
Populus tremuloides	POPTRE	200	312.09	1.010	40537.7
Quercus rubra	QUERUB	30	107.57	0.6096	425.1
Thuja occidentalis	THUOCC	50	114.2	0.7195	1542.6

Table 5.2: Input variables into estimating long distance dispersal (LDD) and its associated probability for the 10 selected tree species. LDD was estimated using the dispeRsal model (Tamme et al. 2014) that used dispersal syndrome and terminal velocity (wind dispersed seeds) or seed mass and release height (animal dispersed). The lower and upper bounds of the confidence intervals of the maximum estimated distance from the dispeRsal model were used as the LDD_{min} and LDD_{max} arguments in the MigClim function. The probability of LDD event between these values was computed as the area under the 2Dt function.

	Input values					Outputs		
	Dispersal syndrome					LDD (m)		
Species	Primary	Secondary	Seed mass (mg)	Terminal velocity (m/s)	Release height (m)	Min	Max	Probability
Abies balsamea	Wind, with specialized structures			0.86		295.0 (300)	1011.4 (1000)	0.045
Acer rubrum	Wind, with specialized structures			0.74		288.4 (300)	1002.2 (1000)	0.131
Acer saccharum	Wind, with specialized structures			1.10		153.2 (150)	528.0 (525)	0.2622
Betula alleghaniensis	Wind, with specialized structures			0.64		282.7 (275)	1007.1 (1000)	0.1034
Betula papyrifera	Wind, with specialized structures			0.64		282.7 (275)	1007.1 (1000)	0.2988
Picea mariana	Wind, with specialized structures			0.75		369.3 (375)	1281.4 (1275)	0.0781
Pinus strobus	Wind, with specialized structures			0.97		243.3 (250)	833.0 (850)	0.0899
Populus tremuloides	Wind, with specialized structures			0.35		1281.5 (1275)	5582.8 (5575)	0.0222
Quercus rubra	Gravity	Animal	3623.2		30	106.0 (100)	1668.1 (1675)	0.1375
Thuja occidentalis	Wind, with specialized structures			1.00		230.8 (225)	791.0 (800)	0.0663

Table 5.3: Parameters used to quantify seed production for the 10 selected tree species

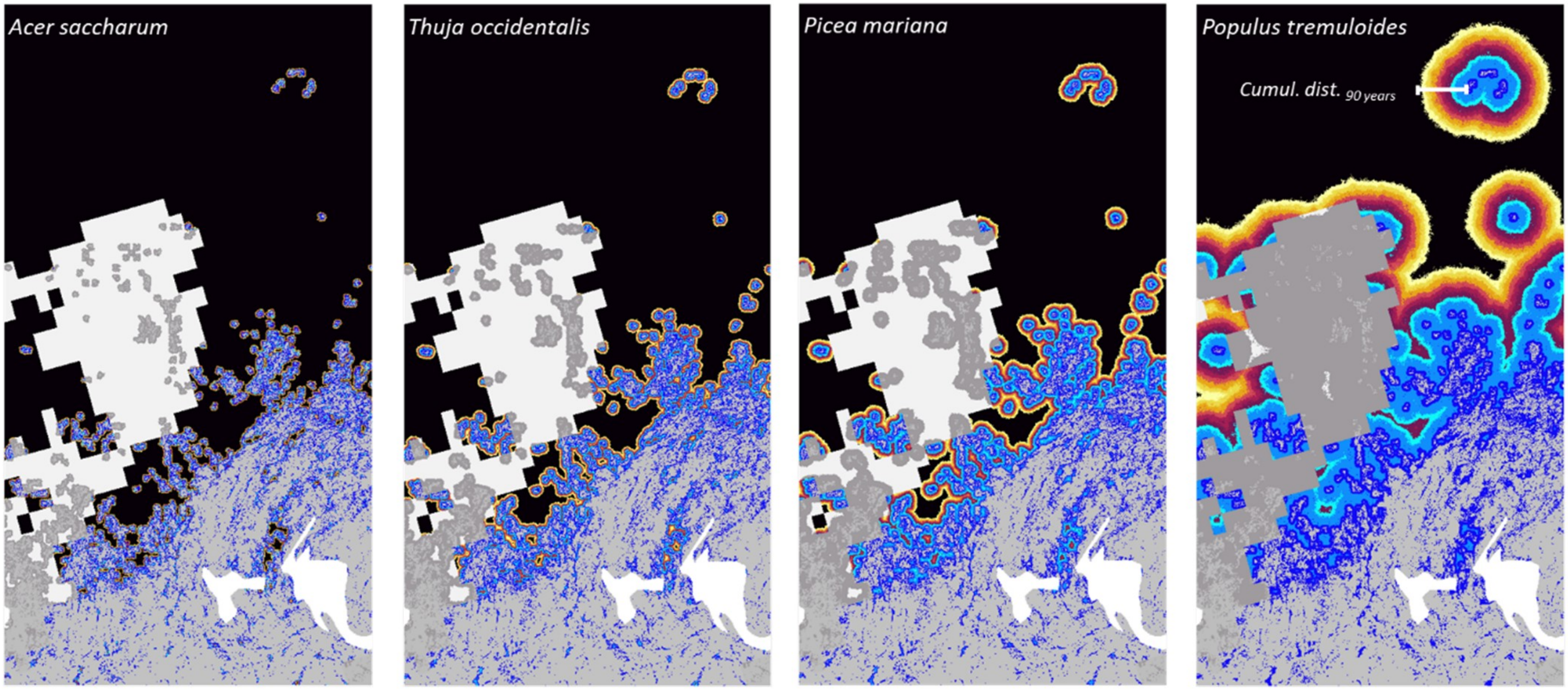
Species	Age sexual maturity	Age of optimum seed production	Growth rate
Abies balsamea	18	30	Slow
Acer rubrum	4	35	Medium-fast
Acer saccharum	22	40	Slow
Betula alleghaniensis	11	70	Medium-slow
Betula papyrifera	15	40	Fast
Picea mariana	10	30	Slow
Pinus strobus	13	20	Fast
Populus tremuloides	10	20	Fast
Quercus rubra	18	45	Moderate
Thuja occidentalis	6	30	Moderate

Table 5.4: Area and proportion of initial distribution of the 10 selected tree species that remains suitable through each climate envelope modelling step

Species	Initial	2011-2040		2041-2070		2071-2100	
	Area (in km^2)	Area (in km^2)	% of initial	Area (in km^2)	% of initial	Area (in km^2)	% of initial
Abies balsamea	1,622,185	1,595,532	98.357	1,198,472	73.880	399,400	24.621
Acer rubrum	449,445	449,445	100	449,247	99.956	432,744	96.284
Acer saccharum	330,609	330,609	100	330,332	99.916	271,787	82.208
Betula alleghaniensis	368,738	368,281	99.877	362,716	98.367	117,081	31.752
Betula papyrifera	1,433,949	1,432,786	99.919	1,388,947	96.862	571,070	39.825
Picea mariana	2,266,388	2,255,972	99.541	1,661,619	73.316	594,353	26.225
Pinus strobus	356,338	356,338	100	355,844	99.861	115,634	32.451
Populus tremuloides	1,680,609	1,679,744	99.949	1,669,182	99.320	1,133,974	67.474
Quercus rubra	130,083	129,799	99.781	123,234	94.735	87,156	67.000
Thuja occidentalis	511,517	511,517	100	452,001	88.365	36,767	7.188

Table 5.5: Cumulative distance (in meters) between initial distribution cell and cell colonized at year 90 and the rate (m/year), as an indication of localized dispersal effects in the model simulations. Values taken from a randomized sample (n= 500) across the distribution where the full spread was attained (i.e. where an initial distribution cell and cell colonized at 90 years were found).

Species	Minimum		Median		90th percentile		Maximum		Std. deviation
	Distance (m)	Rate (m/year)	Distance (m)	Rate (m/year)	Distance (m)	Rate (m/year)	Distance (m)	Rate (m/year)	Distance (m)
Abies balsamea	1981.6	22.0	2281.2	25.3	2441.6	27.1	3068.8	34.1	140.6
Acer rubrum	4825.7	53.6	5203.0	57.8	5447.4	60.5	6068.4	67.4	199.1
Acer saccharum	1056.4	11.7	1164.9	12.9	1298.6	14.4	1411.8	15.9	75.9
Betula alleghaniensis	1456.8	16.2	1782.1	19.8	1961.8	21.8	2345.8	26.1	133.3
Betula papyrifera	2943.2	32.7	3107.5	34.5	3237.1	36.0	3582.9	39.8	115.5
Picea mariana	3150.0	35.0	3605.9	40.1	4107.5	45.6	4608.2	51.2	294.5
Pinus strobus	2751.6	30.6	2931.2	32.6	3042.0	33.8	3208.8	35.7	85.8
Populus tremuloides	14880.9	165.3	17996.0	200.0	19016.6	211.3	20553.2	228.4	954.0
Quercus rubra	2045.8	22.7	2859.7	31.8	3223.1	35.8	5079.0	56.4	335.2
Thuja occidentalis	2336.4	26.0	2600.2	28.9	2775.1	30.8	3458.7	38.4	130.6



Migration velocity
Median = 100m; Mean = 121.87m
2Dt kernel a – 2.0149; b – 24355.37
Long distance dispersal
Distance – 150m, 525m
Probability – 0.2622
Post-colonization
ASM: 22 years; SDOPT: 40 years;
Growth rate = Slow

Cumul. distance $_{\mathbf{90\ years}}$ = 1411.8m

Migration velocity
Median = 50m; Mean = 114.2m
2Dt kernel a – 0.7194; b – 1542.63
Long distance dispersal
Distance – 225m, 800m
Probability – 0.0663
Post-colonization
ASM: 6 years; SDOPT: 30 years;
Growth rate = Moderate

Cumul. distance $_{\mathbf{90\ years}}$ = 3458.7m

Migration velocity
Median = 80m; Mean = 238.09m
2Dt kernel a – 0.6431; b – 3301.9
Long distance dispersal
Distance – 375m, 1275m
Probability – 0.0781
Post-colonization
ASM: 10 years; SDOPT: 30 years;
Growth rate = Slow

Cumul. distance $_{\mathbf{90\ years}}$ = 4608.2m

Migration velocity
Median = 200m; Mean = 312.09m
2Dt kernel a – 1.01; b – 40537.7
Long distance dispersal
Distance – 1275m, 5575m
Probability – 0.0222
Post-colonization
ASM: 10 years; SDOPT: 20 years;
Growth rate = Fast

Cumul. distance $_{\mathbf{90\ years}}$ = *20553.2m*

Figure 5.1: Map of fictive distribution that shows simulation outcomes based on the parameters included in the MigClim model including traits on migration velocity, long distance dispersal and growth. Initial distribution shown in light grey. Blues depict years 1-30 of simulations; Reds = 31-60 and yellows = 61-90. Shading within colours show breaks by decennial (from dark to light). Area in white depicts unsuitable habitat and dark grey depicts cells colonized before area becomes unsuitable. Cumulative distance (example of calculation depicted by the white line in *Populus tremuloides*) is the distance between cells of the initial distribution at cells colonized at year 90 of simulations.

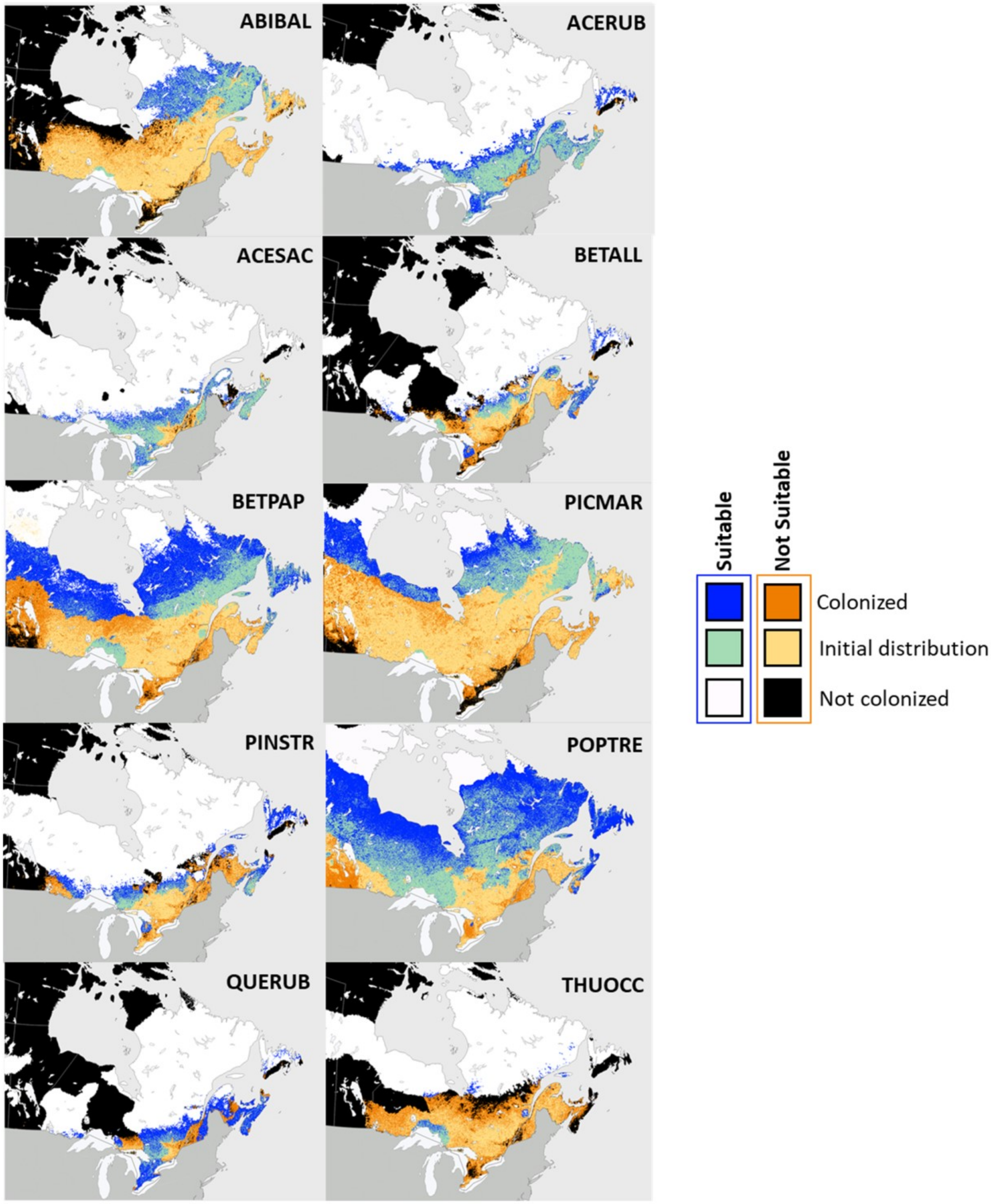

ABIBAL
ACERUB
ACESAC
BETALL
BETPAP
PICMAR
PINSTR
POPTRE
QUERUB
THUOCC
Suitable
Not Suitable
Colonized
Initial distribution
Not colonized

Figure 5.2: Maps of simulated species distributions through to 2100 in eastern Canada based on dispersal ability and life history traits. Final climate envelope suitability shown is based on the projection 2071-2100 but areas colonized are based on areas that were suitable at the start of each projection (2011-2040 and 2041-2070, not shown). Green-blue areas and dark blue areas respectively indicate initial distribution and colonized areas within the suitable climate envelope through to 2100. Yellow areas and orange areas indicate respectively areas of initial distribution that becomes unsuitable and colonized areas before climate becomes unsuitable. Areas that are not colonized in the model runs are indicated in either white (suitable) or black (not suitable).

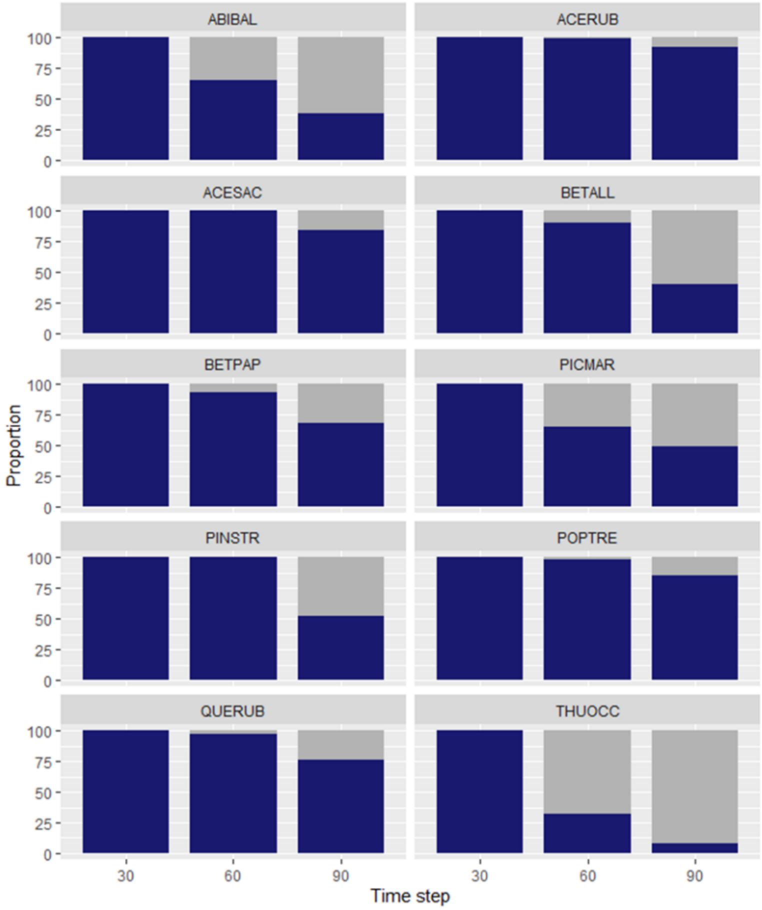


Figure 5.3: Proportion of colonized cells that remain suitable through model runs (blue) or become unsuitable (grey). The time step indicated at the bottom refers to the year of the model at the end of the climate envelope projection employed (Model after 30 years: 2011-2040, 60 years: 2041-2071, 90 years: 2071-2100 respectively).

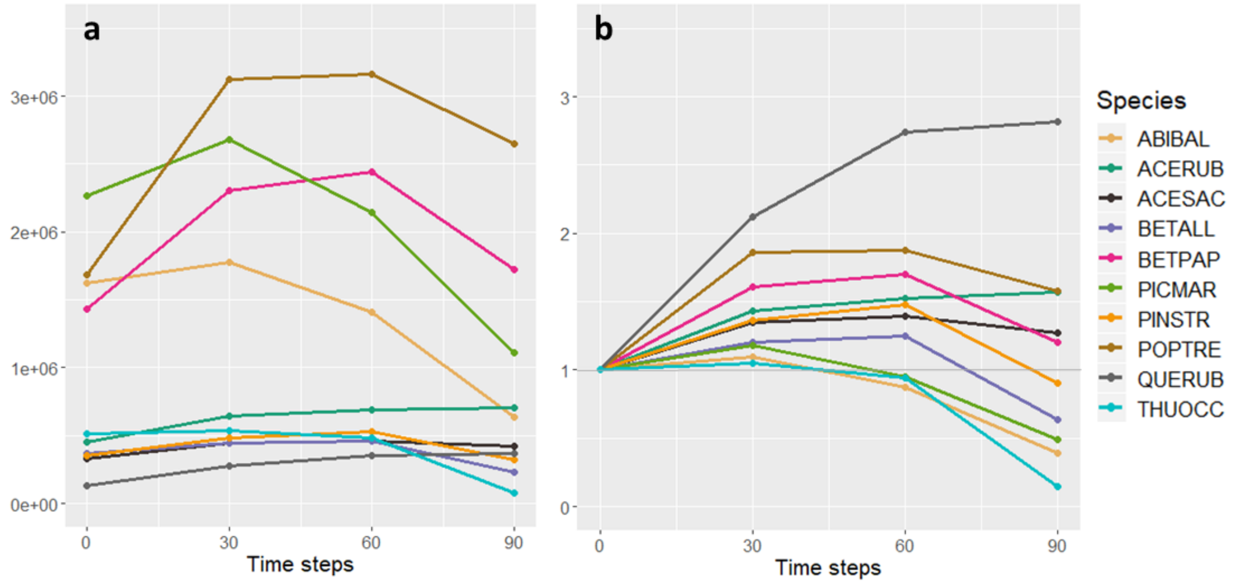


Figure 5.4: Simulated distribution area (in km^2) (a) and ratio of area occupied relative to initial distribution (b) at a given time step. Range area and ratio includes cells from the initial distribution that remain suitable and cells colonized that remain suitable through the model time step (indicated at the bottom). For b), ratios greater than 1 indicate that more cells are occupied relative to the number occupied in the initial distribution. Values less than 1 indicate that fewer occupied cells are suitable at a given time step relative to the number occupied in the initial distribution. The time step indicated at the bottom refers to the year of the model at the end of the climate envelope projection employed (Model after 30 [2011-2040], 60 [2041-2071], 90 years [2071-2100] respectively).

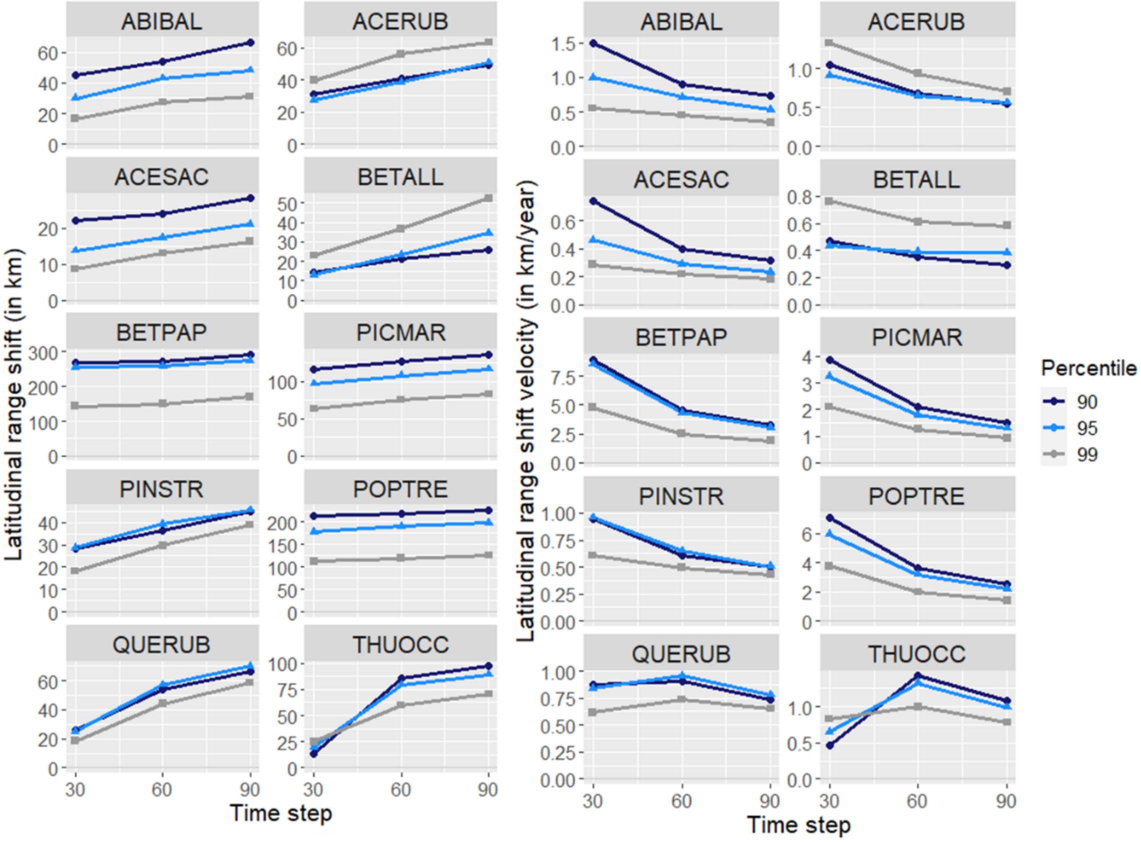


Figure 5.5: Range shift and range shift velocity by decade for the 10 selected tree species. Latitudinal limits are calculated as a percentile of latitude of occupied cells, whether they are suitable or not. Three range limits are calculated, 90th, 95th and 99th. The average latitudinal limits are calculated across latitudinal bands weighted by the number of cells in a given band relative to the total number of cells across the species distribution. Range shifts are based on the average latitudinal limit in the last year of a given climate suitability model (Model after 30 years [2011-2040], 60 years [2041-2071], 90 years [2071-2100] respectively) relative to the average latitudinal limit of the initial distribution. Range shift velocity is calculated as the range shift divided by the number of years elapsed of the model run. At a given percentile, positive values denote latitudinal limits that are at a higher latitude than the latitude of the initial distribution.

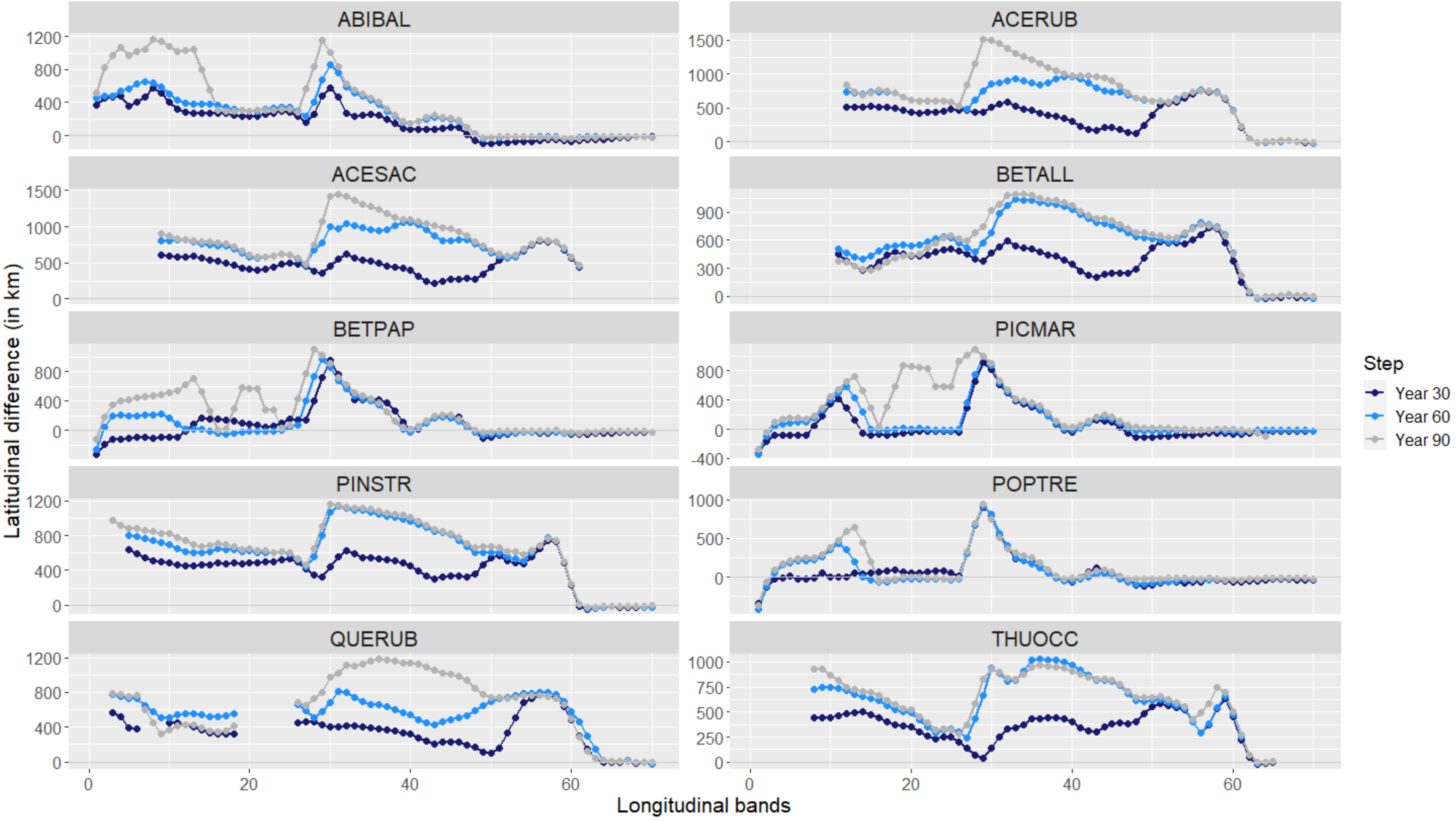


Figure 5.6: Latitudinal difference between the upper edge of the suitable climate envelope relative to the upper edge of a species' simulated distribution. The upper edge of the climate envelope here is defined as the 95th latitude of a species' suitable climate envelope within a given projection (2011-2040, 2041-2070, 2071-2100). The upper edge of a species' simulated distribution is defined as the 95th percentile of latitude at the end of the time period covered by the climate envelope (time step: 30 years, 60 years or 90 years). Positive values indicate that the climate envelope is at a higher latitude than the simulated species distribution in a given time step. Analyses were conducted on a rolling average of 3 longitudinal bands (1= western edge of study area, 70 = eastern edge).

5.7 - References

Anderson, R. P. 2013. A framework for using niche models to estimate impacts of climate change on species distributions. Annals of the New York Academy of Sciences **1297**:8-28.

Angert, A. L., L. G. Crozier, L. J. Rissler, S. E. Gilman, J. J. Tewksbury, and A. J. Chunco. 2011. Do species' traits predict recent shifts at expanding range edges? Ecology Letters **14**:677-689.

Arora, V. K., J. F. Scinocca, G. J. Boer, J. R. Christian, K. L. Denman, G. M. Flato, V. V. Kharin, W. G. Lee, and W. J. Merryfield. 2011. Carbon emission limits required to satisfy future representative concentration pathways of greenhouse gases. Geophysical Research Letters **38**.

Aubin, I., L. Boisvert-Marsh, H. Kebli, D. McKenney, J. Pedlar, K. Lawrence, E. H. Hogg, Y. Boulanger, S. Gauthier, and C. Ste-Marie. 2018. Tree vulnerability to climate change: improving exposure-based assessments using traits as indicators of sensitivity. Ecosphere **9**:e02108.

Aubin, I., F. Cardou, L. Boisvert-Marsh, E. Garnier, M. Strukelj, and A. D. Munson. 2020. Managing data locally to answer questions globally: the role of collaborative science in ecology. Journal of Vegetation Science **31**:509-517.

Aubin, I., A. D. Munson, F. Cardou, P. J. Burton, N. Isabel, J. H. Pedlar, A. Paquette, A. R. Taylor, S. Delagrange, H. Kebli, C. Messier, B. Shipley, F. Valladares, J. Kattge, L. Boisvert-Marsh, and D. McKenney. 2016. Traits to stay, traits to move: a review of functional traits to assess sensitivity and adaptive capacity of temperate and boreal trees to climate change. Environmental Reviews **24**:164-186.

Baldwin, K., K. Chapman, D. Meidiner, P. Uhlig, L. Allen, S. Basquill, D. Faber-Langendoen, N. Flynn, C. Kennedy, W. Mackenzie, M. Major, W. Meades, C. Morneau, and J.-P. Saucier. 2019. The Canadian National Vegetation Classification: Principles, Methods and Status. Natural Resources Canada, Canadian Forest Service, Sault Ste Marie, Ontario.

Beaudoin, A., P. Y. Bernier, L. Guindon, P. Villemaire, X. J. Guo, G. Stinson, T. Bergeron, S. Magnussen, and R. J. Hall. 2014. Mapping attributes of Canada's forests at moderate resolution through kNN and MODIS imagery. Canadian Journal of Forest Research **44**:521-532.

Beauregard, F., and S. de Blois. 2014. Beyond a Climate-Centric View of Plant Distribution: Edaphic Variables Add Value to Distribution Models. PloS one **9**:e92642.

Boisvert-Marsh, L., and S. de Blois. In review. Unravelling potential northward migration pathways for tree species under climate change. Journal of Biogeography.

Boisvert-Marsh, L., C. Périé, and S. de Blois. 2014. Shifting with climate? Evidence for recent changes in tree species distribution at high latitudes. Ecosphere **5**:art83.

Boisvert-Marsh, L., C. Périé, and S. de Blois. 2019. Divergent responses to climate change and disturbance drive recruitment patterns underlying latitudinal shifts of tree species. Journal of Ecology **107**:1956-1969.

Boisvert-Marsh, L., S. Royer-Tardif, F. Doyon, P. Nolet, and I. Aubin. 2020. Using a trait-based approach to compare tree species sensitivity to climate change stressors in Eastern Canada and inform adaptation practices. Forests **11**: 989.

Bouchard, M., N. Aquilué, C. Périé, and M.-C. Lambert. 2019. Tree species persistence under warming conditions: A key driver of forest response to climate change. Forest Ecology and Management **442**:96-104.

Brice, M.-H., K. Cazelles, P. Legendre, and M.-J. Fortin. 2019. Disturbances amplify tree community responses to climate change in the temperate–boreal ecotone. Global Ecology and Biogeography **28**:1668-1681.

Bullock, J. M., L. Mallada González, R. Tamme, L. Götzenberger, S. M. White, M. Pärtel, and D. A. P. Hooftman. 2017. A synthesis of empirical plant dispersal kernels. Journal of Ecology **105**:6-19.

Burns, R. M., and B. H. Honkala. 1990. Silvics of North America. Volume 1. Conifers.

Bussotti, F., M. Pollastrini, V. Holland, and W. Brüggemann. 2015. Functional traits and adaptive capacity of European forests to climate change. Environmental and Experimental Botany **111**:91-113.

Chubaty, A., and E. McIntire. 2017. SpaDES: Develop and run spatially explicit discrete event simulation models. R package version 2.0.

Clark, J. S. 1998. Why Trees Migrate So Fast: Confronting Theory with Dispersal Biology and the Paleorecord. The American Naturalist **152**:204-224.

Clark, J. S., C. Fastie, G. Hurtt, S. T. Jackson, C. Johnson, G. A. King, M. Lewis, J. Lynch, S. Pacala, C. Prentice, and E. W. Schupp. 1998. Reid's paradox of rapid plant migration. BioScience **48**:13-24.

Clark, J. S., M. Lewis, and L. Horvath. 2001. Invasion by Extremes: Population Spread with Variation in Dispersal and Reproduction. The American Naturalist **157**:537-554.

Clark, J. S., M. Silman, R. Kern, E. Macklin, and J. HilleRisLambers. 1999. Seed dispersal near and far: patterns across temperate and tropical forests. Ecology **80**:1475-1494.

Corlett, R. T., and D. A. Westcott. 2013. Will plant movements keep up with climate change? Trends in Ecology & Evolution **28**:482-488.

D'Orangeville, L., L. Duchesne, D. Houle, D. Kneeshaw, B. Côté, and N. Pederson. 2016. Northeastern North America as a potential refugium for boreal forests in a warming climate. Science **352**:1452-1455.

Davis, M. B. 1981. Quaternary History and the Stability of Forest Communities. Pages 132-153 *in* D. C. West, H. H. Shugart, and D. B. Botkin, editors. Forest Succession: Concepts and Application. Springer New York, New York, NY.

Davis, M. B. 1983. Holocene vegetational history of the eastern United States.*in* H. E. Wright, editor. Late Quaternary Environments of the United States. Vol. II. The Holocene. Univ. Minnesota Press, Minneapolis, Minnesota.

Delcourt, H. R., and P. Delcourt. 1991. Quaternary ecology: a paleoecological perspective. Springer Science & Business Media.

Engler, R., W. Hordijk, and A. Guisan. 2012. The MIGCLIM R package – seamless integration of dispersal constraints into projections of species distribution models. Ecography **35**:872-878.

Engler, R., C. F. Randin, P. Vittoz, T. Czáka, M. Beniston, N. E. Zimmermann, and A. Guisan. 2009. Predicting future distributions of mountain plants under climate change: does dispersal capacity matter? Ecography **32**:34-45.

Ettinger, A. K., and J. HilleRisLambers. 2013. Climate isn't everything: Competitive interactions and variation by life stage will also affect range shifts in a warming world. American Journal of Botany **100**:1344-1355.

Farrar, J. L. 1995. Trees in Canada. Canadian Forest Service and Fitzhenry & Whiteside Ltd., Ottawa, Ontario, Canada.

Giesecke, T., P. A. Miller, M. T. Sykes, A. E. K. Ojala, H. Seppä, and R. H. W. Bradshaw. 2010. The effect of past changes in inter-annual temperature variability on tree distribution limits. Journal of Biogeography **37**:1394-1405.

Greene, D. F., C. D. Canham, K. D. Coates, and P. T. Lepage. 2004. An evaluation of alternative dispersal functions for trees. Journal of Ecology **92**:758-766.

Greene, D. F., and E. A. Johnson. 1995. Long-distance wind dispersal of tree seeds. Canadian Journal of Botany **73**:1036-1045.

Hampe, A., and A. S. Jump. 2011. Climate Relicts: Past, Present, Future. Annual Review of Ecology, Evolution, and Systematics **42**:313-333.

Hanski, I. 1998. Metapopulation dynamics. Nature **396**:41-49.

Hausfather, Z., and G. P. Peters. 2020. Emissions–the 'business as usual'story is misleading. Nature Publishing Group.

Hickler, T., K. Vohland, J. Feehan, P. A. Miller, B. Smith, L. Costa, T. Giesecke, S. Fronzek, T. R. Carter, W. Cramer, I. Kühn, and M. T. Sykes. 2012. Projecting the future distribution of European potential natural vegetation zones with a generalized, tree species-based dynamic vegetation model. Global Ecology and Biogeography **21**:50-63.

Hogg, E. H., J. P. Brandt, and M. Michaelian. 2008. Impacts of a regional drought on the productivity, dieback, and biomass of western Canadian aspen forests. Canadian Journal of Forest Research **38**:1373-1384.

Holt, R. D. 2003. On the evolutionary ecology of species' ranges. Evolutionary Ecology Research **5**:159-178.

Iverson, L. R., A. M. Prasad, S. N. Matthews, and M. Peters. 2008. Estimating potential habitat for 134 eastern US tree species under six climate scenarios. Forest Ecology and Management **254**:390-406.

Iverson, L. R., M. W. Schwartz, and A. M. Prasad. 2004. How fast and far might tree species migrate in the eastern United States due to climate change? Global Ecology and Biogeography **13**:209-219.

Keyel, A. C., J. L. K. Gerstenlauer, and K. Wiegand. 2016. SpatialDemography: a spatially explicit, stage-structured, metacommunity model. Ecography **39**:1129-1137.

Kuparinen, A., O. Savolainen, and F. M. Schurr. 2010. Increased mortality can promote evolutionary adaptation of forest trees to climate change. Forest Ecology and Management **259**:1003-1008.

Lafleur, B., D. Paré, A. D. Munson, and Y. Bergeron. 2010. Response of northeastern North American forests to climate change: Will soil conditions constrain tree species migration? Environmental Reviews **18**:279-289.

Legault, S., D. Houle, A. Plouffe, A. Ameztegui, D. Kuehn, L. Chase, A. Blondlot, and T. D. Perkins. 2019. Perceptions of US and Canadian maple syrup producers toward climate change, its impacts, and potential adaptation measures. PloS ONE **14**.

Leithead, M. D., M. Anand, and L. C. R. Silva. 2010. Northward migrating trees establish in treefall gaps at the northern limit of the temperate-boreal ecotone, Ontario, Canada. Oecologia **164**:1095-1106.

Louthan, A. M., D. F. Doak, and A. L. Angert. 2015. Where and When do Species Interactions Set Range Limits? Trends in Ecology & Evolution **30**:780-792.

Marcott, S. A., J. D. Shakun, P. U. Clark, and A. C. Mix. 2013. A Reconstruction of Regional and Global Temperature for the Past 11,300 Years. Science **339**:1198-1201.

McKenney, D. W., M. F. Hutchinson, P. Papadopol, K. Lawrence, J. Pedlar, K. Campbell, E. Milewska, R. F. Hopkinson, D. Price, and T. Owen. 2011a. Customized Spatial Climate Models for North America. Bulletin of the American Meteorological Society **92**:1611-1622.

McKenney, D. W., J. H. Pedlar, K. Lawrence, K. Campbell, and M. F. Hutchinson. 2007. Potential Impacts of Climate Change on the Distribution of North American Trees. BioScience **57**:939-948.

McKenney, D. W., J. H. Pedlar, R. B. Rood, and D. Price. 2011b. Revisiting projected shifts in the climate envelopes of North American trees using updated general circulation models. Global Change Biology **17**:2720-2730.

McLachlan, J. S., J. S. Clark, and P. S. Manos. 2005. Molecular indicators of tree migration capacity under rapid climate change. Ecology **86**:2088-2098.

Meier, E. S., H. Lischke, D. R. Schmatz, and N. E. Zimmermann. 2012. Climate, competition and connectivity affect future migration and ranges of European trees. Global Ecology and Biogeography **21**:164-178.

Michaelian, M., E. H. Hogg, R. J. Hall, and E. Arsenault. 2011. Massive mortality of aspen following severe drought along the southern edge of the Canadian boreal forest. Global Change Biology **17**:2084-2094.

Miller, K. M., and B. J. McGill. 2018. Land use and life history limit migration capacity of eastern tree species. Global Ecology and Biogeography **27**:57-67.

Morin, X., C. Augspurger, and I. Chuine. 2007. Process-based modeling of species' distributions: what limits temperate tree species' range boundaries? Ecology **88**:2280-2291.

Myers, J. A., M. Vellend, S. Gardescu, and P. L. Marks. 2004. Seed dispersal by white-tailed deer: implications for long-distance dispersal, invasion, and migration of plants in eastern North America. Oecologia **139**:35-44.

Nathan, R., and H. C. Muller-Landau. 2000. Spatial patterns of seed dispersal, their determinants and consequences for recruitment. Trends in Ecology & Evolution **15**:278-285.

Oldfather, M. F., M. M. Kling, S. N. Sheth, N. C. Emery, and D. D. Ackerly. 2020. Range edges in heterogeneous landscapes: Integrating geographic scale and climate complexity into range dynamics. Global Change Biology **26**:1055-1067.

Ordonez, A., and J. W. Williams. 2013. Climatic and biotic velocities for woody taxa distributions over the last 16 000 years in eastern North America. Ecology Letters **16**:773-781.

Pagel, J., M. Treurnicht, W. J. Bond, T. Kraaij, H. Nottebrock, A. Schutte-Vlok, J. Tonnabel, K. J. Esler, and F. M. Schurr. 2020. Mismatches between demographic niches and geographic distributions are strongest in poorly dispersed and highly persistent plant species. Proceedings of the National Academy of Sciences **117**:3663.

Parks, S. A., C. Carroll, S. Z. Dobrowski, and B. W. Allred. 2020. Human land uses reduce climate connectivity across North America. Global Change Biology **26**: 2944-2955.

Pedlar, J. H., D. W. McKenney, I. Aubin, T. Beardmore, J. Beaulieu, L. Iverson, G. A. O'Neill, R. S. Winder, and C. Ste-Marie. 2012. Placing Forestry in the Assisted Migration Debate. BioScience **62**:835-842.

Périé, C., and S. de Blois. 2016. Dominant forest tree species are potentially vulnerable to climate change over large portions of their range even at high latitudes. PeerJ **4**:e2218.

Potter, K. M., B. S. Crane, and W. W. Hargrove. 2017. A United States national prioritization framework for tree species vulnerability to climate change. New Forests **48**:275-300.

Prasad, A. M., J. D. Gardiner, L. R. Iverson, S. N. Matthews, and M. Peters. 2013. Exploring tree species colonization potentials using a spatially explicit simulation model: implications for four oaks under climate change. Global Change Biology **19**:2196-2208.

Price, D. T., D. McKenney, L. Joyce, R. Siltanen, P. Papadopol, and K. Lawrence. 2011. High-resolution interpolation of climate scenarios for Canada derived from general circulation model simulations. Information Report NOR-X-421. Edmonton, AB.: Natural Resources Canada, Canadian Forest Service, Northern Forestry Centre. 104 p.

R Core Team. 2017. R v3.4.3 - R: A language and environment for statistical computing. R Core Team, Vienna, Austria.

Renwick, K. M., M. E. Rocca, and T. J. Stohlgren. 2016. Biotic disturbance facilitates range shift at the trailing but not the leading edge of lodgepole pine's altitudinal distribution. Journal of Vegetation Science **27**:780-788.

Rogelj, J., A. Popp, K. V. Calvin, G. Luderer, J. Emmerling, D. Gernaat, S. Fujimori, J. Strefler, T. Hasegawa, G. Marangoni, V. Krey, E. Kriegler, K. Riahi, D. P. van Vuuren, J. Doelman, L. Drouet, J. Edmonds, O. Fricko, M. Harmsen, P. Havlík, F. Humpenöder, E. Stehfest, and M. Tavoni. 2018. Scenarios towards limiting global mean temperature increase below 1.5 °C. Nature Climate Change **8**:325-332.

Royer-Tardif, S., L. Boisvert-Marsh, J. Godbout, N. Isabel, and I. Aubin. In review. Finding common ground: Toward comparable indicators of adaptive capacity of tree species to a changing climate. Ecology and Evolution

Scheller, R. M., J. B. Domingo, B. R. Sturtevant, J. S. Williams, A. Rudy, E. J. Gustafson, and D. J. Mladenoff. 2007. Design, development, and application of LANDIS-II, a spatial landscape simulation model with flexible temporal and spatial resolution. Ecological Modelling **201**:409-419.

Scheller, R. M., and D. J. Mladenoff. 2008. Simulated effects of climate change, fragmentation, and inter-specific competition on tree species migration in northern Wisconsin, USA. Climate Research **36**:191-202.

Sitch, S., B. Smith, I. C. Prentice, A. Arneth, A. Bondeau, W. Cramer, J. O. Kaplan, S. Levis, W. Lucht, M. T. Sykes, K. Thonicke, and S. Venevsky. 2003. Evaluation of ecosystem dynamics, plant geography and terrestrial carbon cycling in the LPJ dynamic global vegetation model. Global Change Biology **9**:161-185.

Sittaro, F., A. Paquette, C. Messier, and C. A. Nock. 2017. Tree range expansion in eastern North America fails to keep pace with climate warming at northern range limits. Global Change Biology **23**:3292-3301.

Snell, R. S., A. Huth, J. E. M. S. Nabel, G. Bocedi, J. M. J. Travis, D. Gravel, H. Bugmann, A. G. Gutiérrez, T. Hickler, S. I. Higgins, B. Reineking, M. Scherstjanoi, N. Zurbriggen, and H. Lischke. 2014. Using dynamic vegetation models to simulate plant range shifts. Ecography **37**:1184-1197.

Soetaert, K. 2009. rootSolve: Nonlinear root finding, equilibrium and steady-state analysis of ordinary differential equations. R package version **1.0**.

Talluto, M. V., I. Boulangeat, A. Ameztegui, I. Aubin, D. Berteaux, A. Butler, F. Doyon, C. R. Drever, M.-J. Fortin, T. Franceschini, J. Liénard, D. McKenney, K. A. Solarik, N. Strigul, W. Thuiller, and D. Gravel. 2016. Cross-scale integration of knowledge for predicting species ranges: a metamodelling framework. Global Ecology and Biogeography **25**:238-249.

Tamme, R., L. Götzenberger, M. Zobel, J. M. Bullock, D. A. P. Hooftman, A. Kaasik, and M. Pärtel. 2014. Predicting species' maximum dispersal distances from simple plant traits. Ecology **95**:505-513.

Thuiller, W., S. Lavorel, M. B. Araujo, M. T. Sykes, and I. C. Prentice. 2005. Climate change threats to plant diversity in Europe. Proceedings of the National Academy of Sciences **102**:8245-8250.

Travis, J. M. J., C. M. Harris, K. J. Park, and J. M. Bullock. 2011. Improving prediction and management of range expansions by combining analytical and individual-based modelling approaches. Methods in Ecology and Evolution **2**:477-488.

Urban, M. C., J. J. Tewksbury, and K. S. Sheldon. 2012. On a collision course: competition and dispersal differences create no-analogue communities and cause extinctions during climate change. Proceedings of the Royal Society B: Biological Sciences **279**:2072-2080.

Van der Veken, S., M. Hermy, M. Vellend, A. Knapen, and K. Verheyen. 2008. Garden plants get a head start on climate change. Frontiers in Ecology and the Environment **6**:212-216.

van Mantgem, P. J., N. L. Stephenson, J. C. Byrne, L. D. Daniels, J. F. Franklin, P. Z. Fulé, M. E. Harmon, A. J. Larson, J. M. Smith, A. H. Taylor, and T. T. Veblen. 2009. Widespread Increase of Tree Mortality Rates in the Western United States. Science **323**:521.

van Vuuren, D. P., J. Edmonds, M. Kainuma, K. Riahi, A. Thomson, K. Hibbard, G. C. Hurtt, T. Kram, V. Krey, J.-F. Lamarque, T. Masui, M. Meinshausen, N. Nakicenovic, S. J. Smith, and S. K. Rose. 2011. The representative concentration pathways: an overview. Climatic Change **109**:5.

Warren, R. J., and M. A. Bradford. 2014. Mutualism fails when climate response differs between interacting species. Global Change Biology **20**:466-474.

Williams, C. and Beardmore, T. AFR Migration database. Canadian Forest Service, Atlantic Forestry Centre, Fredericton, New Brunswick. Unpublished Dataset

Williams, J. W., and S. T. Jackson. 2007. Novel climates, no-analog communities, and ecological surprises. Frontiers in Ecology and the Environment **5**:475-482.

Willis, S. G., W. Foden, D. J. Baker, E. Belle, N. D. Burgess, J. A. Carr, N. Doswald, R. A. Garcia, A. Hartley, C. Hof, T. Newbold, C. Rahbek, R. J. Smith, P. Visconti, B. E. Young, and S. H. M. Butchart. 2015. Integrating climate change vulnerability assessments from species distribution models and trait-based approaches. Biological Conservation **190**:167-178.

Woodall, C. W., C. M. Oswalt, J. A. Westfall, C. H. Perry, M. D. Nelson, and A. O. Finley. 2009. An indicator of tree migration in forests of the eastern United States. Forest Ecology and Management **257**:1434-1444.

Xu, T., and M. F. Hutchinson. 2013. New developments and applications in the ANUCLIM spatial climatic and bioclimatic modelling package. Environmental Modelling & Software **40**:267-279.

Zhang, X., G. Flato, M. Kirchmeier-Young, L. Vincent, H. Wan, X. Wang, R. Rong, J. Fyfe, G. Li, and V. Kharin. 2019. Changes in temperature and precipitation across Canada.

Chapter 6 – GENERAL DISCUSSION AND CONCLUSIONS

6.1 - Summary

In Chapter 3, I assessed whether shifts in the latitudinal distribution of tree species in Quebec, Canada are consistent with northward migration. I did this by quantifying latitudinal shifts of eight deciduous species of the temperate and boreal forest focusing on changes in the distribution of saplings over time. Then, based on the species found to show recruitment patterns consistent with northward migration, I evaluated occupancy patterns with particular attention on putative migration sites, sites that were not occupied in the reference period, and identified pairwise co-occurrence patterns at migration sites. All eight target species showed northward shifts driven mostly by increased recruitment and occupancy gains with latitude. This pattern was matched by increasing association with northerly species at migration sites. Climatic conditions at migration sites were initially colder than occupied sites in P_1. However, these migration sites warmed through the contemporary period, corresponding to the period where species establishment took place, suggesting recent climatic suitability. Undisturbed forests can resist species turnover for a time but disturbance-linked decreases in conifer basal area likely weakened priority effects that could have constrained deciduous species establishment. I also provided evidence of migration for species like *Betula papyrifera* and *Acer rubrum* that are better adapted to boreal edaphic conditions and disturbances, and which could lead the way northward for other, more meridional species. This research offers among the first evidence of sustained latitudinal shifts over multiple sampling periods, allowing us to assess whether short-term dynamics truly capture directional changes. Additionally, this is one of the few studies to examine interspecific influence on species migration at broad scales.

In Chapter 4, I evaluated whether climate change explains observed patterns of species range shifts in forests. Using a multimodel selection approach, I estimated the probability of observing a recruitment event in response to sets of variables related to changes in climate and disturbance as well as their interaction. I found that tree recruitment response to climate change is spatially explicit and depended on the portion of the study area examined. Notably, climate change variables were more often selected than disturbance variables in the models. Even at northern latitudes, I found positive effects of warming on recruitment for a given species towards its northern range edge and negative ones in the southern portion of the study area, mainly linked to early- or late-season climate variables. Given that trends are already detectable in the southern portion of the study area, continued monitoring is necessary to track whether these effects are transitory in order to rapidly adapt management and conservation practices accordingly. This study is among the first evidence of the influence of recent climate change on observed recruitment patterns at broad latitudinal scales.

In Chapter 5, I assessed whether tree species have the potential to migrate fast enough to keep up with projected rate of climate change. I used observed rates of range shift and species-specific traits that influence dispersal and growth in combination with biophysical projections of species climate envelopes up to the end of the 21st century. Based on the distribution that remains climatically suitable, simulated distribution area increased for five of the study species through 2100. Changes in simulated distribution area were influenced by the extent of area colonized at the leading edge and the amount of suitable habitat lost at the rear edge. Climate envelope shift projected for 2100 far exceeded the leading edge of the migration-constrained range shift for all 10 species, even more so for temperate species. Integrating observed range shifts and species traits into process-based models allowed for more realistic evaluations of tree ability for unassisted migration with climate change, filling a critical research gap. This work overcomes the lack of empirical data on dispersal for species and proposes a novel way to translate observed range shifts into dispersal kernels that can be incorporated into process-based modelling studies. Given the inputs used, this method could be applied beyond tree species to other taxa for which information is available.

6.2 - General discussion

Integrating patterns using multiple lines of evidence from across the chapters gives a synthetic view of how species range change has occurred and provides insight into potential future range dynamics. In total, 13 species were evaluated over the three studies (see Table of Species Studied at the beginning of the thesis, page xi) and patterns emerged for several species. Overall, *Acer rubrum* seems to be the clear “winner” in the migration studies. As shown in Chapters 3 and 4, it shows evidence of recent observed migration at rates that approach those simulated in Chapter 5. This species also showed the highest number of occupancy gains in the northern half of its range of any of the species considered in Chapter 3. Additionally, the proportion of these sites that were considered unsuitable in the reference period (P_1) by the species distribution models (SDM) increased from south to north. While the results from Chapter 3 suggest that warming may have influenced occupancy gains for this species, the results from Chapter 4 show that its shift is better explained by disturbance than by climate across its range in Quebec. The latter results, though, do not completely rule out the influence of warming on the recent expansion of this species – the two top variables in the SDM were growing degree days and January minimum temperature – and most migration sites recently colonized by *Acer rubrum* were found to be not suitable in P_1. This suggests that disturbances played a role in reducing priority effects from competing conifer species, facilitating its expansion – possibly linked with warming - into the southern boreal forest. Not only do disturbances facilitate its expansion, *Acer rubrum* appears to be fairly tolerant of edaphic conditions in the boreal forest. Sites with recent occupancy gains of this species tended to be characterised by thicker layers of mor humus than at sites occupied in the reference period, both characteristics typical of boreal sites. Given the broad ecological amplitude of this species (Abrams 1998), *Acer rubrum* is a good example of what Lindenmayer et al. (2010) and HilleRisLambers et al. (2013) termed an “ecological surprise” linked to climate change – i.e., where a species behaves unexpectedly in the face of environmental change, and species interactions modulate such a response – and *Acer rubrum* should be expected to continue gaining ground in the boreal forest.

Another species that has shown rapid northward expansion since the 1970s is *Betula papyrifera*. While this species was not studied in Chapter 4, the dispersal simulations from Chapter 5 show that much larger range shifts are possible for *Betula papyrifera.* Based on Chapter 3, the rate of migration will be mediated by how much infilling occurs and expansion will most likely be in conjunction with some combination of disturbance and drying of waterlogged soils, similar to what was hypothesized by Lafleur et al. (2010). In support of this, three quarters of migration sites where this species was detected were disturbed either in P_1 and/or P_3. Since natural disturbances like fire and insect outbreaks are expected to increase with climate change (Gauthier et al. 2015, Seidl et al. 2020), *Acer rubrum* and *Betula papyrifera* have the potential to continue to extend their range northward appreciably.

Two species show evidence of divergent responses to climate depending on latitudinal position. The results from Chapter 4 show that *Acer saccharum* and *Fagus grandifolia* tend to respond positively to climate warming toward their northern limit. Disturbance also contributed to the recent expansion of *Acer saccharum,* with between 75 and 80% of migration sites north of the 50th for this species having been disturbed in either P_1 or P_3. Moreover, *Acer saccharum* was the only species in Chapter 4 for which the climate x disturbance interaction model was significant. Despite the evidence of reduced priority effects, most of these disturbed migration sites tended to be deemed suitable by the SDM. Considering that migration sites characterised by mor humus were largely considered unsuitable, it could be that disturbance facilitated recruitment of *Acer saccharum* into sites at the northern edge of the temperate forest, but not into the boreal forest. This lends support to the hypothesis from Chapter 3 that potential migration pathways for this species through species like *Acer rubrum* could be needed. This was less the case for *Fagus grandifolia*, for which about 55% of migration sites north of the 50th were disturbed, mainly because of harvesting in the contemporary period. While the climate + disturbance model was retained north of the 50th for this species in Chapter 4, the monthly climate differences was the model retained north of the 90th, suggesting that climate played a more important role in its recent expansion.

In the southern portion of the study area, warming is already showing evidence of negative impacts for these species despite the study area being at high latitudes. South of the 50th percentile of latitude, I found that recruitment of *Acer saccharum* and *Fagus grandifolia* were negatively associated with greater increases in growing degree days between inventories. In another study from Quebec (D'Orangeville et al. 2016), *Picea mariana* showed evidence of negative responses in ring width south of 49°N latitude associated with lower soil moisture and higher temperature. For both *Acer saccharum* and *Picea mariana*, these negative responses coincide with the areas that are projected to become climatically unsuitable by 2071-2100.

Two species, *Betula alleghaniensis* and *Thuja occidentalis*, seem to be the most at risk of exposure to climate change. In Chapter 3, these two species showed small northward latitudinal shifts with positive, but non-significant occupancy ratio changes. Additionally, they showed very few sites with occupancy gains towards their northern limit. When they did show gains, *Thuja* shifted towards sites typical of temperate forest sites while *Betula alleghaniensis* had the highest proportion of migration sites north of the 50th and 90th that were considered suitable. In addition, the results from Chapter 4 show that neither the climate nor the disturbance model were retained for *Betula alleghaniensis*, suggesting that other factors are affecting its recruitment. In Chapter 5, simulated range shifts were also relatively small while climate exposure in southern Quebec and southern Ontario by 2071-2100 is considerable. These species are most at risk of climate-related recruitment failure and could need active measures to favour their persistence.

To quantify the range limit changes in Chapter 3, I focused on juvenile life stages alone since they should be the most responsive to climate change. The relative position of juvenile range limits as compared to range limits of mature trees have revealed apparently contradictory evidence as to the potential of tree species to shift with climate (Woodall et al. 2009, Zhu et al. 2012, Boisvert-Marsh et al. 2014). In particular, Zhu et al. (2012) found that the range limit (in this case 95th percentile of latitude in the United States) of trees was situated north of the range limits of seedlings, a pattern interpreted as indicative of range contraction. When comparing trends between the results found in our previous study (Boisvert-Marsh et al. 2014) and the results presented in Chapter 3, I do not find support for range contraction in our species; instead, I show evidence of continued sapling range expansion for most species, but at rates and occupancy patterns that vary between inventories (see Section 8.1 for comparisons). Seedling and sapling stages are particularly sensitive to climate (Munier et al. 2010, Kueppers et al. 2017). When climate is limiting, regeneration by seed may not occur or recruitment success might be limited (Tremblay et al. 2002, Renwick and Rocca 2015). Indeed, several recent studies that employed species distribution models have shown that the regeneration niche of juveniles does not fully encompass that of adults (Bell et al. 2014, Copenhaver-Parry et al. 2020). Our previous study (Boisvert-Marsh et al. 2014) found that tree range shifts were more difficult to detect compared to shifts in juveniles and, despite a remeasurement across all plots, the 45-year time frame is still too short to encompass the complete life cycle of the tree species considered here. While I recognize that not all saplings will become mature trees, their use instead of seedlings should have mitigated some of the effects of high mortality at early life stages and increase the likelihood that these individuals will be maintained through time (i.e., establishment). Hence, focusing on the range limit signal of juveniles through time should provide a clearer portrait of range shifts in relation to climate. Another possible avenue that could be used to further explore the strength of biotic interactions between migrating species is Joint Species Distribution

Modelling (Pollock et al. 2014). Such an approach would be useful to understand the extent to which current range limits are affected by competition (or facilitation) and the degree to which overlapping niches relate to shared environmental tolerances (including climate) and whether species could indeed respond to recent warming (Blois et al. 2013, Clark et al. 2014, Copenhaver-Parry and Bell 2018). The exceptional inventories from the MFFP are ongoing (fifth inventory expected to be completed by 2025) and will continue to provide unique insight into species range shifts.

The findings in Chapters 3 to 5 highlight how each step of the migration process for trees can be slow with the potential for considerable lag with climate change (Davis 1981, Travis et al. 2011, Corlett and Westcott 2013, Chuang and Peterson 2016). What is often overlooked in the discussion around rare dispersal events and post-glacial migration rates in range expansion is the impact of long generation times, propagule pressure and post-colonization population growth rate that moderate subsequent diffusion around newly colonized and occupied areas (Greene and Johnson 1995, Feurdean et al. 2013, Chuang and Peterson 2016). Our findings suggest that consistent and repeated range extending events across several generations are necessary before an appreciable change is detectable (Renwick and Rocca 2015). Admittedly, the patterns shown in Chapter 5 are based on the choices that were made for each of the modelling parameters. Different outcomes could be expected if the median and mean for the dispersal kernel were defined differently, influencing the probability of dispersal with increasing distance from the source. If the median and mean are relatively close, then the tail of the kernel becomes shorter, lowering the probability of long distance dispersal (LDD).

Probably the most immediate effect on outcomes from the range shift simulations was how LDD was defined. LDD events are rare, a probability that Clark et al. (2001) suggested should fall around 10%. LDD probabilities exceeded that value for half the species in Chapter 5, none more than for *Betula papyrifera*. LDD cut offs that are too low result in such high probabilities and could underestimate realized range shifts. While I did evaluate the rates modelled in Chapter 5 based partly on those observed in Chapter 3, there were cases where the simulated and observed rates were similar (e.g. *Acer rubrum* and *Acer saccharum*), while others were not. Even with the low LDD cut off and high LDD probability, the simulated rates for *Betula papyrifera* were the highest among the species considered in Chapter 5. This rate had more to do with the scattered initial distribution at its northern limit than with LDD cut off. This was not the only species that exhibited this pattern; this was the case for the most northerly species I examined here (*Abies balsamea* and *Picea mariana*). The extent to which filling will occur around these scattered populations in the boreal forest will be controlled by abiotic factors other than climate alone, such as edaphic conditions, substrate, nutrient status and waterlogging, as well as disturbance (Lloyd et al. 2003, Lafleur et al. 2010, Lembrechts et al. 2016, Bouchard et al. 2019, also see Chapter 4 and 5).

Migration is but one possible response to climate change, with the balance between dispersal, persistence, adaptation, and extirpation ultimately determining species' changes within their geographic range (Aitken et al. 2008). At the rear edge, the extent of range loss that occurs over the coming decades will depend on the interplay between persistence and mortality, adaptation and maladaptation. I showed in Chapter 3 what some of these resultant range shift patterns could look like. If extensive mortality occurs where unsuitable conditions are projected, as is the case for *Abies balsamea* and *Picea mariana*, then I would expect to see *northward range shift by southern range thinning* (i.e., southern range contraction) for these species, possibly accelerating the range shift rates that were shown here.

As mentioned previously, recipient systems resist change (e.g., Leak 1996), even when conditions are no longer suitable for a given species' persistence. Disturbances - such as those from logging, insect outbreaks, fire and windthrow - break the inertia that inhibit new, possibly better suited, species from moving in (Urban et al. 2012, Renwick et al. 2016). While Chapter 3 demonstrated that disturbances and the reductions in basal area that this entails contributed to species establishing at new sites, Chapter 4 showed that the relative influence of disturbance was outweighed by climate for most species x area combinations. Other studies in Quebec have concluded differently but these studies also approached this question differently (Danneyrolles et al. 2019, Terrail et al. 2019, Elzein et al. 2020). Two of these studies (Terrail et al. 2019, Elzein et al. 2020) focused principally on disturbance to explain composition changes within the overall community. Danneyrolles et al. (2019) directly compared the influence of climate change and disturbance on the forest community. One major difference with my study is the time scale considered. Terrail et al. (2019; 1821-1900), Danneyroles et al. (2019: as early as 1790) and

Elzein et al. (2020; models based on 1930 inventory year) all considered a much longer time frame than the one considered in Chapters 3 and 4 (1970-2015). While warming associated with climate change has been occurring since the Industrial Revolution (Hansen et al. 2006), warming has accelerated even within the time frame of the forest inventories (Chapter 4; Zhang et al. 2019, NOAA National Centers for Environmental Information, 2020). My studies in Chapters 3 and 4 capture the period of most intense warming, possibly explaining the detectable climate signal. Another difference with respect to my study is the spatial extent considered. Historical data is notoriously hard to collect to ensure comparable methodologies, so compromises between resolution (inventories aggregated to 25km^2 – Danneyroles et al. 2019) and/or area covered (Terrail et al. 2019 and Elzein et al. 2020 – within the *Abies balsamea – Betula alleghaniensis* domain of the Lower St. Lawrence region) are required. Instead, my study showed changes in site-level dynamics of plot occupancy in relation to climate change then scaled across the entire commercial forest in Quebec.

Brice et al. (2019) found that moderate to major disturbances are amplifying species turnover at the ecotone between the mixed temperate forest and the boreal forest. Using the same dataset as the one employed in Chapters 3 and 4, they found that the relative importance of disturbance outweighed the influence of climate, a pattern opposite to ours for at least some species. Several differences should be noted between how we addressed the question. First, they considered community-level responses to climate and disturbance, not its influence on individual species (same community metrics used as well in Danneyroles et al. 2019: change in Community Temperature Index and Community Shade Index). I show in Chapter 4 that species responses to climate and disturbance vary greatly and depend on the part of the study area under consideration. Additionally, Brice et al. (2019) employed differences in annual climate metrics. I found that species responses to climate were not always linked to differences in annual variables, but most often linked to monthly or seasonal ones; this may have affected their ability to detect changes. Also, they considered abundance of mature trees only (diameter at breast height greater than 9.1cm, same threshold used in Danneyroles et al. 2019) whereas I considered recruitment and occupancy gains based on saplings only. As pointed out in Chapter 4, climate has been shown to predict frequency of occurrence across latitudes better than species abundance in a plot (Canham and Thomas 2010, Chambers et al. 2013), especially approaching species range limits (Pironon et al. 2017), a pattern which is further supported here. When assessed over time, the recruitment and occupancy gains shown here are indicative of recent colonization events whereas species abundance could instead reflect changes in forest dynamics and reflect ecological succession.

There are some commonalities in the results of our two studies. Brice et al. (2019) also found that most species turnover could be attributed to losses of *Abies balsamea*, *Picea glauca* and *Picea mariana* (pairwise associates evaluated in Chapter 3) in the area where they become common. Indeed, the patterns in Chapter 3 are consistent with their findings, showing that migration sites were often characterised by decreasing basal area, particularly of conifers and that most migration sites had been subjected to disturbance in one or both inventories. Additionally, while not reported in the research chapters, I conducted analyses on tree occupancy changes for these species and also found losses in occupancy around the 50th percentile (results in Section 8.1.3). They also found that thermophilization of plots at the ecotone (from the *Acer saccharum-Betula alleghaniensis* domain to the *Abies balsamea-Betula papyrifera* domain) was attributable to gains in *Acer rubrum* and *Acer saccharum* and gains in *Betula papyrifera* resulted in thermophilization in the *Picea mariana*-feathermoss domain. I also found similar trends in Chapter 3 and showed additional evidence of how this dynamic could benefit northward migration of *Acer rubrum* and *Betula papyrifera* further into the boreal forest. My results suggest that all species show potential to associate with *Abies balsamea*, but less so with *Picea mariana*. Indeed, in Chapter 4, *Acer rubrum* was found to be associated with harvesting across its entire range, but with increasing support for the influence of climate at its northern limit. Additionally, Chapter 3 showed that temperate species benefited from the decrease in basal area in *Abies balsamea*, while the two pioneer boreal species – *Betula papyrifera* and *Populus tremuloides* – benefited from lower basal area of *Picea mariana*, likely because of their more northerly distribution. Moreover, for *Acer saccharum*, it was the only species in Chapter 4 for which the climate x disturbance interaction model was significant. Additionally, between 75 and 80% of migration sites north of the 50th for this species had been disturbed in either P_1 or P_3. In Brice et al. (2019), disturbance from harvesting and natural disturbances showed the highest proportion of explained variance in the multiple regression models. Loss of conifers from disturbances could have provided opportunities for migration that may not have otherwise been available. Brice et al. also found that natural disturbances explained a significant proportion of the variance in their model. We found a similar pattern as well, reporting that natural disturbances in P_3 was most associated with migration sites for six target species considered in Chapter 3 (exceptions *Acer saccharum* and *Betula alleghaniensis*). Disturbance from fire and insect outbreaks are projected to increase through the 21st century as well as continued harvesting in the area. Overall, disturbance in this area should facilitate continued northward migration of both *Acer rubrum* and *Betula papyrifera*, possibly to the benefit of other species following these leaders.

One dynamic not explicitly quantified but that warrants consideration is the condition of the understory and its constituent species. Both of these characteristics can act as a filter for determining which species can establish. The amount of woody debris, relative cover of species that grow on the soil (i.e. moss and lichen) and exposure of ground and mineral soil will influence the ability of seeds to germinate. Likewise, closed canopies and dense understory conditions can greatly influence the amount of light that reaches the soil and determine which species survive during the seedling and sapling stages. Understory conditions can also determine whether the species that do establish are the ones that were intended. Once disturbance has occurred, formation of a recalcitrant layer (Aubin et al. 2014), site paludification (Fenton et al. 2005) and improper site restoration practices (Azeria et al. 2020), among others, can drive succession to favour non-target species and delay return to desirable ecological communities. Such competition between species should exert considerable influence on juvenile life stages through constraints on regeneration. For migrating species, understory conditions could have influenced which species colonized across the inventories and ultimately the rates of latitudinal range shift shown in Chapter 3 (Ettinger and HilleRisLambers 2013, Anderegg and HilleRisLambers 2019). An interesting way to integrate understory conditions would be to use a co-occurrence framework to assess whether certain understory species are associated with tree species recruitment.

6.3 - Adapting forest management practices in a climate change context

This thesis studies a number of tree species that are of commercial interest in Quebec and Canada, revealing the extent to which species particularly benefit from ameliorated conditions at the leading edge, and which ones will need assistance. Consequently, forestry practices will need to adapt in order to mitigate potential impacts (Gauthier et al. 2014). Shifting suitable climatic conditions are having considerable impacts on tree regeneration and productivity as well as ecological succession, but their incorporation into planting guidelines and management plans is not commonplace.

Anticipating climate change in forest management plans requires careful consideration of which options work best in a given area and developing adaptation strategies that align with priorities across a range of scenarios and spatial scales. Because of their long life cycle and their ability to remain on the landscape even when the climate is no longer suitable, trees are at risk of maladaptation from warming if nothing is done to identify potential sensitivities with measures taken accordingly. Reconciling differences in species sensitivity can be challenging for practitioners working in different geographic areas and management contexts. Reforestation after harvesting will need to consider what species are likely to do well in the near (next 20-30 years, during juvenile phase) and mid-range (adult phase, but within rotation) future. Differences in sensitivity to climate between juveniles and mature trees add another layer of complexity in making decisions based on future projections about which species or genotype/phenotypes should be planted.

Instead of ignoring the potential impacts, new practices and approaches need to be developed explicitly with climate in mind, and will require the right tools and knowledge to inform such decisions (Morin et al. 2015). Yet, how to implement new policies and practices is less certain (Aubin et al. 2011, Morin et al. 2015, Ameztegui et al. 2018). Improving our understanding of which mechanisms underlie species sensitivity to climate stressors is important to inform adaptation measures in forest management planning and practices (Nagel et al. 2017, Messier et al. 2019, Boisvert-Marsh et al. 2020). Climate-smart forest management planning has particular relevance at species range limits. Species like *Betula papyrifera*, *Acer rubrum* and *Populus tremuloides* are susceptible to mortality of mature stems from drought and forest fire but may not need much assistance post-disturbance to re-establish populations relatively quickly (Boisvert-Marsh et al. 2020). The results of Chapter 3 support this finding, since these species show among the highest range shifts. On the other hand, the results from Chapter 4 for *Acer saccharum* show that disturbance can override the positive climate response at the range edge for recruitment of *Acer saccharum*. Similarly, *Betula alleghaniensis* is not strongly associated with either disturbance or climate warming at its northern range edge, a finding that suggests caution in managing this species. Species for which tree range limits are situated north of saplings (e.g. *Betula alleghaniensis*, Section 8.1.3) suggests potential for fitness-related range limits and could benefit from additional management considerations to promote recruitment at their northern edge.

6.4 – Range shifts and the Assisted Migration debate

This thesis has shown that forest management practices have influenced species migration patterns in Quebec, deliberately or not. The inability to migrate at a pace that keeps up with suitable conditions places forest management at the forefront of climate change ecology, namely in its ability to speed up species turnover, either naturally or via assisted migration (Pedlar et al. 2012). How forest practitioners deal with novel species as they move northward will require paradigm shifts in how silviculture is practiced. Current operating procedures do not consider the impacts of harvesting on naturally migrating species because non-target species found in managed stands are usually controlled for and/or eliminated. I show evidence here that *Acer rubrum*, a non-target species in silviculture, could pave the way for other species, a finding that should be further investigated. If confirmed, it will challenge forest practitioners to reconsider management practices of this species, particularly in northern areas where it is not typically found.

Realistically, the most rapid source of species turnover is going to be assisted migration, or the deliberate movement of species for conservation or management purposes. In forestry, most species movements for this purpose are currently done within their range limits (Pedlar et al. 2012). This type of species movement is called *assisted population migration*, i.e., using seed or planting stock from source areas where conditions are currently like those projected for the target area. These kinds of movements are often considered for species that face considerable exposure to climate change and limited ability to migrate, such as was shown for *Thuja occidentalis* and *Betula alleghaniensis* in Chapter 4. Within-range population movements seem to have generally high acceptance and potential for implementation (Peterson St-Laurent et al. 2018) and, in reality, there is already a considerable framework that supports these kinds of movements. Tools exist to inform how seed transfer should occur (Pedlar et al. 2011). Provenance trials can inform how populations respond to various temperate and precipitation variables and which ones are well suited for relocation purposes (Pedlar and McKenney 2017, Li et al. 2020). Guidelines have been developed to assist forest management practitioners and land owners in assessing species potential exposure at a local scale and whether assisted migration is an option to consider (Janowiak et al. 2014). On the other hand, there are legitimate reasons against moving species outside of their range. Invasion ecology has shown numerous examples of the impacts of moving species around, deliberately or not (Ricciardi and Simberloff 2009). Species commonly used in plantations and that have been introduced to an area can escape and become invasive when they possess the characteristics common to other known invaders (Essl et al. 2010, Van Kleunen et al. 2010). To avoid some of these pitfalls, frameworks for species risk assessments are being developed that evaluate suites of plant traits characteristic of invasive species in order to avoid selecting them for assisted migration (Park et al. 2018). Additionally, many of the species studied here are already used elsewhere, so inferences about how these species might respond in novel climates can be evaluated. Risk assessment frameworks originally developed for invasive species need to be adjusted to the context of unassisted range expansions of native species into newly available habitat (Essl et al. 2019, Urban 2020). Traits related to dispersal alone do not necessarily predict migration success (Angert et al. 2011) and establishment factors should also be explicitly considered in such assessments (Estrada et al. 2016, Aubin et al. 2018).

I show in Chapter 5 that suitable climatic habitat exceeds species ability to migrate, so *range extending assisted migration* will likely need to be considered for certain species, particularly if they are expected to show decline within the same jurisdiction (e.g. *Acer saccharum* in southern Quebec). While caution should be exercised as informed by risk frameworks, these types of translocations are being tested (e.g. Muller et al. 2019) and should be at least considered, albeit with caution. Again, tools exist to inform this type of decision making (see for e.g., McKenney et al. 1999, Boulet and Huot 2013, Périé et al. 2014, Swanston et al. 2016, Aubin et al. 2018) and some of the results in this thesis can provide insight. Species distribution models that adequately incorporate edaphic factors can identify suitable habitats separated by dispersal barriers (or unsuitable habitat) for short to medium distance range expansions (e.g., less than 50km northward). Minimum distances for such assisted migration can be inferred from the $\mathrm{LDD}_{\mathrm{min}}$ cut offs employed in Chapter 5. Given the lifespan and generation time of trees, such experiments will take time before they show transferable results. Starting such experiments at smaller scales based on thoughtful and deliberate actions could likely mitigate negative effects. Ecosystem-based management approaches offer promise over practices that focus mainly on timber production by instead determining how to enhance resiliency in forest ecosystems (Messier et al. 2019). Since climate change has the potential to dramatically redraw distribution maps in the not so distant future, its potential impacts must be considered in management frameworks.

6.5 - Conclusion

Unlike for mobile taxa, plant migration is a synthetic response of discrete events that accumulate into broader range movement. Range dynamics result from the short- and/or long-distance dispersal of propagules that land in habitats suitable for germination and grow into individuals capable in turn of producing seeds. The net sum of these individual events will shift the frequency of species occurrence in space and time and, ultimately, range boundaries. Range expansion implies successful colonization and establishment at sites previously unoccupied. As climate warms, it is assumed that conditions at cold range edges should be alleviated such that colonization for fitness-limited species should become increasingly successful in marginal populations. This thesis explored whether observed patterns of recent range dynamics are consistent with expectations with respect to climate change.

Overall, this thesis improved our knowledge about tree species responses to climate change across time and space, showing how local factors translate into responses at broader scales and which processes underlie the patterns observed. Overall, the information from this thesis helps inform conservation and forest management practices by showing which species will likely expand their ranges without assistance, such as *Acer rubrum* and *Betula papyrifera*, and which ones will likely need at least some intervention, such as *Betula alleghaniensis* and *Thuja occidentalis* as well as *Acer saccharum* to an extent. Developing management strategies that consider climate-tracking species and those that could be left behind is an important step, and this thesis can help incorporate ecological knowledge into the planning process.

6.6 - Future work

Building on this work, several other questions could be subsequently addressed:

1. Directly assess consistency of range shift patterns between P_1 and P_2 (1970-1977 to 1992-2002) vs. P_2 and P_3 (1992-2002 up to 2003-2015) for both trees and saplings. Assess whether saplings that were detected in historical inventory become trees. This information would help to better understand temporal context in species range shifts and whether range shifts of saplings result into lasting shifts in range limits
2. Use species distribution modelling to assess the juvenile bioclimatic niche relative to the adult bioclimatic niche. Understand how probabilities of the life stages co-vary through space and evaluate whether spatial differences in niche relate to differences in climate sensitivity. This information would help to better understand whether current range limits coincide with climate-related fitness limitations.
3. Follow up on the analyses in Chapter 3, by further investigating the effects of site-level on species migration of *Acer saccharum*, *Acer rubrum* and *Betula papyrifera;* compare localized changes in species composition by focusing on pairs of plots where one has been disturbed and one has not. This would help to better understand post-disturbance successional pathways in migration patterns.
4. Conduct analyses similar to those in Chapter 4 but with boreal conifer species. Specifically, evaluate whether certain climate variables are linked with loss in relation to regeneration and recruitment. This information would help to better understand if climate change is already inducing recruitment failure for conifer species and the importance of disturbance in this dynamic.
5. Develop a suite of trait-based indicators linking temperature to differential species sensitivity to assess whether plants are indeed responding to warming. This information would help to assess whether species are showing responses to climate before range shifts are detectable.

Chapter 7 – REFERENCES

Abrams, M. D. 1998. The red maple paradox. BioScience **48**:355-364.

Adam, J. C., A. F. Hamlet, and D. P. Lettenmaier. 2009. Implications of global climate change for snowmelt hydrology in the twenty-first century. Hydrological Processes **23**:962-972.

Aitken, S. N., S. Yeaman, J. A. Holliday, T. Wang, and S. Curtis-McLane. 2008. Adaptation, migration or extirpation: climate change outcomes for tree populations. Evolutionary Applications **1**:95-111.

Alberto, F. J., S. N. Aitken, R. Alía, S. C. González-Martínez, H. Hänninen, A. Kremer, F. Lefèvre, T. Lenormand, S. Yeaman, R. Whetten, and O. Savolainen. 2013. Potential for evolutionary responses to climate change – evidence from tree populations. Global Change Biology **19**:1645-1661.

Alofs, K. M., D. A. Jackson, and N. P. Lester. 2014. Ontario freshwater fishes demonstrate differing range-boundary shifts in a warming climate. Diversity and Distributions **20**:123-136.

Ameztegui, A., K. A. Solarik, J. R. Parkins, D. Houle, C. Messier, and D. Gravel. 2018. Perceptions of climate change across the Canadian forest sector: The key factors of institutional and geographical environment. PloS one **13**:e0197689.

Anderegg, L. D. L., and J. HilleRisLambers. 2019. Local range boundaries vs. large-scale trade-offs: climatic and competitive constraints on tree growth. Ecology Letters **22**:787-796.

Anderson, J. T., and S. M. Wadgymar. 2020. Climate change disrupts local adaptation and favours upslope migration. Ecology Letters **23**:181-192.

Angert, A. L., M. Bayly, S. N. Sheth, and J. R. Paul. 2018. Testing Range-Limit Hypotheses Using Range-Wide Habitat Suitability and Occupancy for the Scarlet Monkeyflower (*Erythranthe cardinalis*). The American Naturalist **191**:E76-E89.

Angert, A. L., L. G. Crozier, L. J. Rissler, S. E. Gilman, J. J. Tewksbury, and A. J. Chunco. 2011. Do species' traits predict recent shifts at expanding range edges? Ecology Letters **14**:677-689.

Araújo, M. B., and A. T. Peterson. 2012. Uses and misuses of bioclimatic envelope modeling. Ecology **93**:1527-1539.

Asselin, H., and S. Payette. 2006. Origin and long-term dynamics of a subarctic tree line. Écoscience **13**:135-142.

Aubin, I., L. Boisvert-Marsh, H. Kebli, D. McKenney, J. Pedlar, K. Lawrence, E. H. Hogg, Y. Boulanger, S. Gauthier, and C. Ste-Marie. 2018. Tree vulnerability to climate change: improving exposure-based assessments using traits as indicators of sensitivity. Ecosphere **9**:e02108.

Aubin, I., O. Deshaies, F. Cardou, and L. Sirois. 2014. Management legacy in the understory of North American mixed boreal regenerating stands. Forest Ecology and Management **320**:129-137.

Aubin, I., C. M. Garbe, S. Colombo, C. R. Drever, D. W. McKenney, C. Messier, J. Pedlar, M. A. Saner, L. Venier, A. M. Wellstead, R. Winder, E. Witten, and C. Ste-Marie. 2011. Why we disagree about assisted migration: Ethical implications of a key debate regarding the future of Canada's forests. The Forestry Chronicle **87**:755-765.

Aubin, I., A. Munson, F. Cardou, P. J. Burton, N. Isabel, J. H. Pedlar, A. Paquette, A. R. Taylor, S. Delagrange, H. Kebli, C. Messier, B. Shipley, F. Valladares, J. Kattge, L. Boisvert-Marsh, and D. McKenney. 2016. Traits to stay, traits to move: a review of functional traits to assess sensitivity and adaptive capacity of temperate and boreal trees to climate change. Environmental Reviews **24**: 164-186.

Azeria, E. T., K. Santala, A. A. C. S. McIntosh, and I. Aubin. 2020. Plant traits as indicators of recovery of reclaimed wellsites in forested areas: Slow but directional succession trajectory. Forest Ecology and Management **468**: 118180.

Baldwin, K., L. Allen, S. Basquill, K. Chapman, D. Downing, N. Flynn, W. MacKenzie, M. Major, W. Meades, D. Meidinger, C. Morneau, J.-P. Saucier, J. Thorpe, and P. Uhlig. 2018. Vegetation Zones of Canada: a Biogeoclimatic Perspective. [Map]. Scale 1:5000000. Natural Resources Canada. Canadian Forest Service, Sault Ste. Marie, ON. .

Baldwin, K., J.-P. Saucier, B. Meades, and K. Chapman. 2016. Eastern North American Forest/ Forêts boréales de l'Est de l'Amérique du Nord. Great Lakes Forestry Centre, Sault Ste Marie, ON.

Baldwin, K., J.-P. Saucier, and P. Uhlig. 2019a. Eastern North American Temperate Hardwood – Conifer Forest. Forêts mixtes de la zone tempérée de l'Est de l'Amérique du Nord. Great Lakes Forestry Centre, Sault Ste. Marie, ON.

Baldwin, K., P. Uhlig, and M. Wester. 2019b. Eastern Canadian Temperate Deciduous Forest. Forêts décidues de la zone tempérée du Canada. Great Lakes Forestry Centre, Sault Ste. Marie, ON.

Barras, N., and M. Kellman. 1998. The supply of regeneration micro-sites and segregation of tree species in a hardwood/boreal forest transition zone. Journal of Biogeography **25**:871-881.

Bauhus, J., D. Paré, and L. Côté. 1998. Effects of tree species, stand age and soil type on soil microbial biomass and its activity in a southern boreal forest. Soil Biology and Biochemistry **30**:1077-1089.

Beaudet, M., J. Brisson, C. Messier, and D. Gravel. 2007. Effect of a major ice storm on understory light conditions in an old-growth *Acer–Fagus* forest: Pattern of recovery over seven years. Forest Ecology and Management **242**:553-557.

Beaudet, M., C. Messier, D. Paré, J. Brisson, and Y. Bergeron. 1999. Possible mechanisms of sugar maple regeneration failure and replacement by beech in the Boisé-des-Muir old-growth forest, Québec. Écoscience **6**:264-271.

Beauregard, F. 2016. Potential for northern range expansion of the understory flora of temperate Québec : edaphic, climatic and biotic factors. McGill University Libraries, [Montreal].

Beauregard, F., and S. de Blois. 2014. Beyond a Climate-Centric View of Plant Distribution: Edaphic Variables Add Value to Distribution Models. PloS ONE **9**:e92642.

Beauregard, F., and S. de Blois. 2016. Rapid latitudinal range expansion at cold limits unlikely for temperate understory forest plants. Ecosphere **7**:e01549.

Beckage, B., B. Osborne, D. G. Gavin, C. Pucko, T. Siccama, and T. Perkins. 2008. A rapid upward shift of a forest ecotone during 40 years of warming in the Green Mountains of Vermont. Proceedings of the National Academy of Sciences of the United States of America **105**:4197-4202.

Bell, D. M., J. B. Bradford, and W. K. Lauenroth. 2014. Early indicators of change: divergent climate envelopes between tree life stages imply range shifts in the western United States. Global Ecology and Biogeography **23**:168-180.

Berteaux, D., N. Casajus, and S. De Blois. 2014. Changements climatiques et biodiversité du Québec. Presses de l'Université du Québec, Québec.

Bertin, R. I. 2008. Plant phenology and distribution in relation to recent climate change. Journal of the Torrey Botanical Society **135**:126-146.

Bishop, D. A., C. M. Beier, N. Pederson, G. B. Lawrence, J. C. Stella, and T. J. Sullivan. 2015. Regional growth decline of sugar maple (*Acer saccharum*) and its potential causes. Ecosphere **6**:art179.

Blois, J. L., P. L. Zarnetske, M. C. Fitzpatrick, and S. Finnegan. 2013. Climate Change and the Past, Present, and Future of Biotic Interactions. Science **341**:499.

Bohner, T., and J. Diez. 2020. Extensive mismatches between species distributions and performance and their relationship to functional traits. Ecology Letters **23**:33-44.

Boisvert-Marsh, L., C. Périé, and S. de Blois. 2014. Shifting with climate? Evidence for recent changes in tree species distribution at high latitudes. Ecosphere **5**:art83.

Boisvert-Marsh, L., C. Périé, and S. de Blois. 2019. Divergent responses to climate change and disturbance drive recruitment patterns underlying latitudinal shifts of tree species. Journal of Ecology **107**:1956-1969.

Boisvert-Marsh, L., S. Royer-Tardif, F. Doyon, P. Nolet, and I. Aubin. 2020. Using a trait-based approach to compare tree species sensitivity to climate change stressors in Eastern Canada and inform adaptation practices. Forests **11**: 989.

Bose, A. K., A. Weiskittel, and R. G. Wagner. 2017. Occurrence, pattern of change, and factors associated with American beech-dominance in stands of the northeastern USA forest. Forest Ecology and Management **392**:202-212.

Bouchard, M., N. Aquilué, C. Périé, and M.-C. Lambert. 2019. Tree species persistence under warming conditions: A key driver of forest response to climate change. Forest Ecology and Management **442**:96-104.

Boudreault, P.-A. 2016. Limite nordique de la forêt commerciale: Un appel à la prudence [online]. Agence Science Presse, Montréal.

Boulanger, Y., A. R. Taylor, D. T. Price, D. Cyr, E. McGarrigle, W. Rammer, G. Sainte-Marie, A. Beaudoin, L. Guindon, and N. Mansuy. 2017. Climate change impacts on forest landscapes along the Canadian southern boreal forest transition zone. Landscape Ecology **32**:1415-1431.

Boulanger, Y., A. R. Taylor, D. T. Price, D. Cyr, and G. Sainte-Marie. 2018. Stand-level drivers most important in determining boreal forest response to climate change. Journal of Ecology **106**:977-990.

Boulet, B., and M. Huot. 2013. Le Guide sylvicole du Québec : Les fondements biologiques de la sylviculture. Publications du Québec, Québec, Québec.

Brady, S. P., D. I. Bolnick, R. D. H. Barrett, L. Chapman, E. Crispo, A. M. Derry, C. G. Eckert, D. J. Fraser, G. F. Fussmann, A. Gonzalez, F. Guichard, T. Lamy, J. Lane, A. G. McAdam, A. E. M. Newman, A. Paccard, B. Robertson, G. Rolshausen, P. M. Schulte, A. M. Simons, M. Vellend, and A. Hendry. 2019. Understanding Maladaptation by Uniting Ecological and Evolutionary Perspectives. The American Naturalist **194**:495-515.

Breshears, D. D., T. E. Huxman, H. D. Adams, C. B. Zou, and J. E. Davison. 2008. Vegetation synchronously leans upslope as climate warms. Proceedings of the National Academy of Sciences **105**:11591-11592.

Brice, M.-H., K. Cazelles, P. Legendre, and M.-J. Fortin. 2019. Disturbances amplify tree community responses to climate change in the temperate–boreal ecotone. Global Ecology and Biogeography **28**:1668-1681.

Brisson, J., and A. Bouchard. 2003. In the past two centuries, human activities have caused major changes in the tree species composition of southern Québec, Canada. Écoscience **10**:236-246.

Brown, C. D., and M. Vellend. 2014. Non-climatic constraints on upper elevational plant range expansion under climate change. Proceedings of the Royal Society B: Biological Sciences **281**. doi: 10.1098/rspb.2014.1779

Brown, J. H. 1984. On the Relationship between Abundance and Distribution of Species. The American Naturalist **124**:255-279.

Brown, J. H., G. C. Stevens, and D. M. Kaufman. 1996. The geographic range: Size, shape, boundaries, and internal structure. Annual Review of Ecology and Systematics **27**:597-623.

Brown, P. M., and R. Wu. 2005. Climate and disturbance forcing of episodic tree recruitment in a southwestern Ponderosa pine landscape. Ecology **86**:3030-3038.

Buermann, W., P. R. Bikash, M. Jung, D. H. Burn, and M. Reichstein. 2013. Earlier springs decrease peak summer productivity in North American boreal forests. Environmental Research Letters **8**:024027.

Burnham, K., and D. Anderson. 2002. Model Selection and Multivariate Inference: A Practical Information–Theoretical Approach. Springer, New York.

Burns, R. M., and B. H. Honkala. 1990. Silvics of North America. USDA Forest Service, Washington, DC.

Bussotti, F., M. Pollastrini, V. Holland, and W. Brüggemann. 2015. Functional traits and adaptive capacity of European forests to climate change. Environmental and Experimental Botany **111**:91-113.

Butt, S., P. Ramprasad, and A. Fenech. 2005. Changes in the landscape of southern Ontario Canada since 1750: impacts of European colonization. Integrated Mapping Assessment:83-92.

Caccianiga, M., and S. Payette. 2006. Recent advance of white spruce (*Picea glauca*) in the coastal tundra of the eastern shore of Hudson Bay (Québec, Canada). Journal of Biogeography **33**:2120-2135.

Cahill, A. E., M. E. Aiello-Lammens, M. Caitlin Fisher-Reid, X. Hua, C. J. Karanewsky, H. Y. Ryu, G. C. Sbeglia, F. Spagnolo, J. B. Waldron, and J. J. Wiens. 2014. Causes of warm-edge range limits: systematic review, proximate factors and implications for climate change. Journal of Biogeography **41**:429-442.

Cale, J. A., S. A. McNulty, S. A. Teale, and J. D. Castello. 2013. The impact of beech thickets on biodiversity. Biological Invasions **15**:699-706.

Canham, C. D. 1988. Growth and Canopy Architecture of Shade-Tolerant Trees: Response to Canopy Gaps. Ecology **69**:786-795.

Canham, C. D., and L. Murphy. 2016. The demography of tree species response to climate: seedling recruitment and survival. Ecosphere **7**:e01424.

Canham, C. D., and R. Q. Thomas. 2010. Frequency, not relative abundance, of temperate tree species varies along climate gradients in eastern North America. Ecology **91**:3433-3440.

Caplat, P., P. Edelaar, R. Y. Dudaniec, A. J. Green, B. Okamura, J. Cote, J. Ekroos, P. R. Jonsson, J. Löndahl, S. V. M. Tesson, and E. J. Petit. 2016. Looking beyond the mountain: dispersal barriers in a changing world. Frontiers in Ecology and the Environment **14**:261-268.

Carón, M. M., P. De Frenne, J. Brunet, O. Chabrerie, S. A. O. Cousins, L. De Backer, M. Diekmann, B. J. Graae, T. Heinken, A. Kolb, T. Naaf, J. Plue, F. Selvi, G. R. Strimbeck,

M. Wulf, and K. Verheyen. 2014. Latitudinal variation in seeds characteristics of *Acer platanoides* and *A. pseudoplatanus*. Plant Ecology **215**:911-925.

Case, T. J., R. D. Holt, M. A. McPeek, and T. H. Keitt. 2005. The community context of species' borders: ecological and evolutionary perspectives. Oikos **108**:28-46.

Castorani, M. C., D. C. Reed, P. T. Raimondi, F. Alberto, T. W. Bell, K. C. Cavanaugh, D. A. Siegel, and R. D. Simons. 2017. Fluctuations in population fecundity drive variation in demographic connectivity and metapopulation dynamics. Proceedings of the Royal Society B: Biological Sciences **284**:20162086.

Cavanaugh, K. C., J. R. Kellner, A. J. Forde, D. S. Gruner, J. D. Parker, W. Rodriguez, and I. C. Feller. 2014. Poleward expansion of mangroves is a threshold response to decreased frequency of extreme cold events. Proceedings of the National Academy of Sciences **111**:723-727.

Cavanaugh, K. C., J. D. Parker, S. C. Cook-Patton, I. C. Feller, A. P. Williams, and J. R. Kellner. 2015. Integrating physiological threshold experiments with climate modeling to project mangrove species' range expansion. Global Change Biology **21**:1928-1938.

Chambers, D., C. Périé, N. Casajus, and S. de Blois. 2013. Challenges in modelling the abundance of 105 tree species in eastern North America using climate, edaphic, and topographic variables. Forest Ecology and Management **291**:20-29.

Chardon, N. I., W. K. Cornwell, L. E. Flint, A. L. Flint, and D. D. Ackerly. 2015. Topographic, latitudinal and climatic distribution of *Pinus coulteri*: geographic range limits are not at the edge of the climate envelope. Ecography **38**:590-601.

Chardon, N. I., S. Pironon, M. L. Peterson, and D. F. Doak. 2020. Incorporating intraspecific variation into species distribution models improves distribution predictions, but cannot predict species traits for a wide-spread plant species. Ecography **43**:60-74.

Chen, I.-C., J. K. Hill, R. Ohlemüller, D. B. Roy, and C. D. Thomas. 2011. Rapid range shifts of species associated with high levels of climate warming. Science **333**:1024-1026.

Cheng, R., and P. Lee. 2008. Urban sprawl and other major land use conversions in Ontario's greenbelt from 1993 to 2007: A change analysis project using satellite imagery. Report to the David Suzuki Foundation and the Greenbelt Foundation. Edmonton: Global Forest Watch Canada. Cover Image:4.

Chuang, A., and C. R. Peterson. 2016. Expanding population edges: theories, traits, and trade-offs. Global Change Biology **22**:494-512.

Clark, J. S., A. E. Gelfand, C. W. Woodall, and K. Zhu. 2014. More than the sum of the parts: forest climate response from joint species distribution models. Ecological Applications **24**:990-999.

Clark, J. S., M. Lewis, and L. Horvath. 2001. Invasion by Extremes: Population Spread with Variation in Dispersal and Reproduction. The American Naturalist **157**:537-554.

Clark, J. S., E. Macklin, and L. Wood. 1998. Stages and Spatial Scales of Recruitment Limitation in Southern Appalachian Forests. Ecological Monographs **68**:213-235.

Cleland, E. E., J. M. Allen, T. M. Crimmins, J. A. Dunne, S. Pau, S. E. Travers, E. S. Zavaleta, and E. M. Wolkovich. 2012. Phenological tracking enables positive species responses to climate change. Ecology **93**:1765-1771.

Collin, A., C. Messier, and N. Bélanger. 2017. Conifer Presence May Negatively Affect Sugar Maple's Ability to Migrate into the Boreal Forest Through Reduced Foliar Nutritional Status. Ecosystems **20**:701-716.

Comte, L., and G. Grenouillet. 2013. Do stream fish track climate change? Assessing distribution shifts in recent decades. Ecography **36**:1236-1246.

Cook, B. I., E. M. Wolkovich, and C. Parmesan. 2012. Divergent responses to spring and winter warming drive community level flowering trends. Proceedings of the National Academy of Sciences **109**:9000-9005.

Copenhaver-Parry, P. E., and D. M. Bell. 2018. Species interactions weakly modify climate-induced tree co-occurrence patterns. Journal of Vegetation Science **29**:52-61.

Copenhaver-Parry, P. E., C. J. W. Carroll, P. H. Martin, and M. V. Talluto. 2020. Multi-scale integration of tree recruitment and range dynamics in a changing climate. Global Ecology and Biogeography **29**:102-116.

Corlett, R. T., and D. A. Westcott. 2013. Will plant movements keep up with climate change? Trends in Ecology & Evolution **28**:482-488.

Crête, M., and L. Marzell. 2006. Évolution des forêts québécoises au regard des habitats fauniques: analyse des grandes tendances sur trois décennies. Forestry Chronicle **82**:368-382.

Cyr, D., S. Gauthier, Y. Bergeron, and C. Carcaillet. 2009. Forest management is driving the eastern North American boreal forest outside its natural range of variability. Frontiers in Ecology and the Environment **7**:519-524.

D'Arrigo, R. D., R. K. Kaufmann, N. Davi, G. C. Jacoby, C. Laskowski, R. B. Myneni, and P. Cherubini. 2004. Thresholds for warming-induced growth decline at elevational tree line in the Yukon Territory, Canada. Global Biogeochemical Cycles **18**. https://doi.org/10.1029/2004GB002249

D'Orangeville, L., L. Duchesne, D. Houle, D. Kneeshaw, B. Côté, and N. Pederson. 2016. Northeastern North America as a potential refugium for boreal forests in a warming climate. Science **352**:1452-1455.

Dale, V. H., L. A. Joyce, S. McNulty, R. P. Neilson, M. P. Ayres, M. D. Flannigan, P. J. Hanson, L. C. Irland, A. E. Lugo, C. J. Peterson, D. Simberloff, F. J. Swanson, B. J. Stocks, and B. M. Wotton. 2001. Climate Change and Forest Disturbances. BioScience **51**:723-734.

Danneyrolles, V., S. Dupuis, G. Fortin, M. Leroyer, A. de Römer, R. Terrail, M. Vellend, Y. Boucher, J. Laflamme, Y. Bergeron, and D. Arseneault. 2019. Stronger influence of anthropogenic disturbance than climate change on century-scale compositional changes in northern forests. Nature Communications **10**:1265. https://doi.org/10.1038/s41467-019-09265-z

Davis, M. B. 1981. Quaternary History and the Stability of Forest Communities. Pages 132-153 *in* D. C. West, H. H. Shugart, and D. B. Botkin, editors. Forest Succession: Concepts and Application. Springer New York, New York, NY.

Davis, M. B., and R. G. Shaw. 2001. Range Shifts and Adaptive Responses to Quaternary Climate Change. Science **292**:673-679.

Davis, M. B., K. D. Woods, S. L. Webb, and R. P. Futyma. 1986. Dispersal versus climate - Expansion of *Fagus* and *Tsuga* into the upper Great-Lakes Region. Vegetatio **67**:93-103.

de Blois, S., L. Boisvert-Marsh, C.-A. Lovat, C. Byun, P. Gomez-Garcia, R. Otfinowski, E. Groenveld, and C. Lavoie. 2013. Outils pour évaluer les risques d'invasion biologique dans un contexte de changements climatiques. McGill University, Montréal, Québec.

De Frenne, P., B. J. Graae, F. Rodríguez-Sánchez, A. Kolb, O. Chabrerie, G. Decocq, H. De Kort, A. De Schrijver, M. Diekmann, O. Eriksson, R. Gruwez, M. Hermy, J. Lenoir, J.

Plue, D. A. Coomes, and K. Verheyen. 2013. Latitudinal gradients as natural laboratories to infer species' responses to temperature. Journal of Ecology **101**:784-795.

Devictor, V., R. Julliard, D. Couvet, and F. Jiguet. 2008. Birds are tracking climate warming, but not fast enough. Proceedings of the Royal Society B-Biological Sciences **275**:2743-2748.

Dobrowski, S. Z., A. K. Swanson, J. T. Abatzoglou, Z. A. Holden, H. D. Safford, M. K. Schwartz, and D. G. Gavin. 2015. Forest structure and species traits mediate projected recruitment declines in western US tree species. Global Ecology and Biogeography **24**:917-927.

Domon, G., and A. Bouchard. 2007. The landscape history of Godmanchester (Quebec, Canada): two centuries of shifting relationships between anthropic and biophysical factors. Landscape Ecology **22**:1201-1214.

Duchesne, L., and R. Ouimet. 2008. Population dynamics of tree species in southern Quebec, Canada: 1970–2005. Forest Ecology and Management **255**:3001-3012.

Duchesne, L., R. Ouimet, and D. Houle. 2002. Basal Area Growth of Sugar Maple in Relation to Acid Deposition, Stand Health, and Soil Nutrients. Journal of Environmental Quality **31**:1676-1683.

Elith, J., S. J. Phillips, T. Hastie, M. Dudík, Y. E. Chee, and C. J. Yates. 2011. A statistical explanation of MaxEnt for ecologists. Diversity and Distributions **17**:43-57.

Elliott, G. P. 2012. Extrinsic regime shifts drive abrupt changes in regeneration dynamics at upper treeline in the Rocky Mountains, USA. Ecology **93**:1614-1625.

Elliott, K. A. 1998. The forests of southern Ontario. The Forestry Chronicle **74**:850-854.

Elzein, T., G. R. Larocque, L. Sirois, and D. Arseneault. 2020. Comparing the predictions of gap model with vegetation and disturbance data in south-eastern Canadian mixed forests. Forest Ecology and Management **455**:117649.

Engler, R., W. Hordijk, and A. Guisan. 2012. The MIGCLIM R package – seamless integration of dispersal constraints into projections of species distribution models. Ecography **35**:872-878.

Eriksson, O., and J. Ehrlén. 2008. Seedling recruitment and population ecology. Pages 239-254 *in* M. A. Leck, V. T. Parker, and R. L. Simpson, editors. Seedling ecology and evolution. . Cambridge University Press, Cambridge, UK.

Essl, F., S. Dullinger, P. Genovesi, P. E. Hulme, J. M. Jeschke, S. Katsanevakis, I. Kühn, B. Lenzner, A. Pauchard, P. Pyšek, W. Rabitsch, D. M. Richardson, H. Seebens, M. van Kleunen, W. H. van der Putten, M. Vilà, and S. Bacher. 2019. A Conceptual Framework for Range-Expanding Species that Track Human-Induced Environmental Change. BioScience **69**:908-919.

Essl, F., D. Moser, S. Dullinger, T. Mang, and P. E. Hulme. 2010. Selection for commercial forestry determines global patterns of alien conifer invasions. Diversity and Distributions **16**:911-921.

Estrada, A., I. Morales-Castilla, P. Caplat, and R. Early. 2016. Usefulness of Species Traits in Predicting Range Shifts. Trends in Ecology & Evolution **31**:190-203.

Etterson, J. R., H. E. Schneider, N. L. S. Gorden, and J. J. Weber. 2016. Evolutionary insights from studies of geographic variation: Contemporary variation and looking to the future. American Journal of Botany **103**:5-9.

Ettinger, A. K., and J. HilleRisLambers. 2013. Climate isn't everything: Competitive interactions and variation by life stage will also affect range shifts in a warming world. American Journal of Botany **100**:1344-1355.

Evans, P., and C. D. Brown. 2017. The Boreal-Temperate Forest Ecotone Response to Climate Change. Environmental Reviews **25**:423-431.

Fei, S., J. M. Desprez, K. M. Potter, I. Jo, J. A. Knott, and C. M. Oswalt. 2017. Divergence of species responses to climate change. Science Advances **3**:e1603055.

Fenton, N., N. Lecomte, S. Légaré, and Y. Bergeron. 2005. Paludification in black spruce (*Picea mariana*) forests of eastern Canada: Potential factors and management implications. Forest Ecology and Management **213**:151-159.

Feurdean, A., S. A. Bhagwat, K. J. Willis, H. J. B. Birks, H. Lischke, and T. Hickler. 2013. Tree migration-rates: narrowing the gap between inferred post-glacial rates and projected rates. PloS one **8**:e71797-e71797.

Fisichelli, N. A., L. E. Frelich, and P. B. Reich. 2014. Temperate tree expansion into adjacent boreal forest patches facilitated by warmer temperatures. Ecography **37**:152-161.

Gallien, L., W. Thuiller, N. Fort, M. Boleda, F. J. Alberto, D. Rioux, J. Lainé, and S. Lavergne. 2016. Is There Any Evidence for Rapid, Genetically-Based, Climatic Niche Expansion in the Invasive Common Ragweed? PloS one **11**:e0152867-e0152867.

Gallinat, A. S., R. B. Primack, and D. L. Wagner. 2015. Autumn, the neglected season in climate change research. Trends in Ecology & Evolution **30**:169-176.

Gamache, I., and S. Payette. 2005. Latitudinal response of subarctic tree lines to recent climate change in eastern Canada. Journal of Biogeography **32**:849-862.

Gaston, K. 2009. Geographic range limits: achieving synthesis. Proceedings of the Royal Society B-Biological Sciences **276**:1395-1406.

Gauthier, S., P. Bernier, P. J. Burton, J. Edwards, K. Isaac, N. Isabel, K. Jayen, H. Le Goff, and E. A. Nelson. 2014. Climate change vulnerability and adaptation in the managed Canadian boreal forest. Environmental Reviews **22**:256-285.

Gauthier, S., P. Bernier, T. Kuuluvainen, A. Z. Shvidenko, and D. G. Schepaschenko. 2015. Boreal forest health and global change. Science **349**:819.

Giencke, L. M., M. Dovčiak, G. Mountrakis, J. A. Cale, and M. J. Mitchell. 2014. Beech bark disease: spatial patterns of thicket formation and disease spread in an aftermath forest in the northeastern United States. Canadian Journal of Forest Research **44**:1042-1050.

Giles, B. E., and J. Goudet. 1997. Genetic differentiation in *Silene dioica* metapopulations: Estimation of spatiotemporal effects in a successional plant species. American Naturalist **149**:507-526.

Gill, A. L., A. S. Gallinat, R. Sanders-DeMott, A. J. Rigden, D. J. Short Gianotti, J. A. Mantooth, and P. H. Templer. 2015. Changes in autumn senescence in northern hemisphere deciduous trees: a meta-analysis of autumn phenology studies. Annals of Botany **116**:875-888.

Girardin, M. P., O. Bouriaud, E. H. Hogg, W. Kurz, N. E. Zimmermann, J. M. Metsaranta, R. de Jong, D. C. Frank, J. Esper, U. Büntgen, X. J. Guo, and J. Bhatti. 2016. No growth stimulation of Canada's boreal forest under half-century of combined warming and CO2 fertilization. Proceedings of the National Academy of Sciences **113**:E8406-E8414.

Gomes, V. H. F., S. D. Ijff, N. Raes, I. L. Amaral, R. P. Salomão, L. de Souza Coelho, F. D. de Almeida Matos, … and H. ter Steege. 2018. Species Distribution Modelling: Contrasting presence-only models with plot abundance data. Scientific Reports **8**:1003. https://doi.org/10.1038/s41598-017-18927-1

Gravel, D., M. Beaudet, and C. Messier. 2011. Sapling age structure and growth series reveal a shift in recruitment dynamics of sugar maple and American beech over the last 40 years. Canadian Journal of Forest Research **41**:873-880.

Greene, D. F., and E. A. Johnson. 1995. Long-distance wind dispersal of tree seeds. Canadian Journal of Botany **73**:1036-1045.

Griffith, T. M., and M. A. Watson. 2005. Stress avoidance in a common annual: reproductive timing is important for local adaptation and geographic distribution. Journal of Evolutionary Biology **18**:1601-1612.

Griffith, Timothy M., and Maxine A. Watson. 2006. Is Evolution Necessary for Range Expansion? Manipulating Reproductive Timing of a Weedy Annual Transplanted beyond Its Range. The American Naturalist **167**:153-164.

Groeneveld, E., F. Belzile, and C. Lavoie. 2014. Sexual reproduction of Japanese knotweed (*Fallopia japonica* s.l.) at its northern distribution limit: New evidence of the effect of climate warming on an invasive species. American Journal of Botany **101**:459-466.

Grubb, P. J. 1977. The maintenance of species-richness in plant communities: The importance of the regeneration niche. Biological Reviews **52**:107-145.

Guisan, A., T. C. Edwards, and T. Hastie. 2002. Generalized linear and generalized additive models in studies of species distributions: setting the scene. Ecological Modelling **157**:89-100.

Guisan, A., and N. E. Zimmermann. 2000. Predictive habitat distribution models in ecology. Ecological Modelling **135**:147-186.

Hampe, A., and A. S. Jump. 2011. Climate Relicts: Past, Present, Future. Annual Review of Ecology, Evolution, and Systematics **42**:313-333.

Hampe, A., and R. J. Petit. 2005. Conserving biodiversity under climate change: the rear edge matters. Ecology Letters **8**:461-467.

Hansen, J., M. Sato, R. Ruedy, K. Lo, D. W. Lea, and M. Medina-Elizade. 2006. Global temperature change. Proceedings of the National Academy of Sciences of the United States of America **103**:14288-14293.

Hanski, I. 1998. Metapopulation dynamics. Nature **396**:41-49.

Hargreaves, A. L., and C. G. Eckert. 2019. Local adaptation primes cold-edge populations for range expansion but not warming-induced range shifts. Ecology Letters **22**:78-88.

Hargreaves, A. L., K. E. Samis, and C. G. Eckert. 2014. Are Species' Range Limits Simply Niche Limits Writ Large? A Review of Transplant Experiments beyond the Range. The American Naturalist **183**:157-173.

Harper, J. L. 1977. Population biology of plants. Academic Press, London ;.

Harrell, F. E., K. L. Lee, R. M. Califf, D. B. Pryor, and R. A. Rosati. 1984. Regression modelling strategies for improved prognostic prediction. Statistics in Medicine **3**:143-152.

Harrell Jr, F. E. 2013. Hmisc: Harrell miscellaneous. R package version 3.12-2. [Computer software]. Available from http://cran.r-project.org/web/packages/Hmisc.

Harsch, M. A., and J. HilleRisLambers. 2016. Climate Warming and Seasonal Precipitation Change Interact to Limit Species Distribution Shifts across Western North America. PloS one **11**:e0159184.

Harsch, M. A., P. E. Hulme, M. S. McGlone, and R. P. Duncan. 2009. Are treelines advancing? A global meta-analysis of treeline response to climate warming. Ecology Letters **12**:1040-1049.

Henry, H. A. L. 2008. Climate change and soil freezing dynamics: historical trends and projected changes. Climatic Change **87**:421-434.

Hickling, R., D. B. Roy, J. K. Hill, R. Fox, and C. D. Thomas. 2006. The distributions of a wide range of taxonomic groups are expanding polewards. Global Change Biology **12**:450-455.

HilleRisLambers, J., M. A. Harsch, A. K. Ettinger, K. R. Ford, and E. J. Theobald. 2013. How will biotic interactions influence climate change–induced range shifts? Annals of the New York Academy of Sciences **1297**:112-125.

Hoch, G., and C. Körner. 2012. Global patterns of mobile carbon stores in trees at the high-elevation tree line. Global Ecology and Biogeography **21**:861-871.

Holt, R. D. 2003. On the evolutionary ecology of species' ranges. Evolutionary Ecology Research **5**:159-178.

Hopkin, A., T. Williams, R. Sajan, J. Pedlar, and C. Nielsen. 2003. Ice storm damage to eastern Ontario forests: 1998-2001. The Forestry Chronicle **79**:47-53.

Houle, G., and L. Filion. 1993. Interannual Variations in the Seed Production of *Pinus banksiana* at the Limit of the Species Distribution in Northern Quebec, Canada. American Journal of Botany **80**:1242-1250.

Iverson, L. R., A. M. Prasad, S. N. Matthews, and M. Peters. 2008. Estimating potential habitat for 134 eastern US tree species under six climate scenarios. Forest Ecology and Management **254**:390-406.

Iverson, L. R., A. M. Prasad, and M. W. Schwartz. 2005. Predicting potential changes in suitable habitat and distribution by 2100 for tree species of the eastern United States. Journal of Agricultural Meteorology **61**:29-37.

Janowiak, M. K., C. W. Swanston, L. M. Nagel, L. A. Brandt, P. R. Butler, S. D. Handler, P. D. Shannon, L. R. Iverson, S. N. Matthews, A. Prasad, and M. P. Peters. 2014. A Practical Approach for Translating Climate Change Adaptation Principles into Forest Management Actions. Journal of Forestry **112**:424-433.

Jobidon, R., Y. Bergeron, A. Robitaille, F. Raulier, S. Gauthier, L. Imbeau, J.-P. Saucier, and C. Boudreault. 2015. A biophysical approach to delineate a northern limit to commercial forestry: the case of Quebec's boreal forest. Canadian Journal of Forest Research **45**:515-528.

Jobin, B., C. Latendresse, A. Baril, C. Maisonneuve, C. Boutin, and D. Côté. 2014. A half-century analysis of landscape dynamics in southern Québec, Canada. Environmental Monitoring and Assessment **186**:2215-2229.

Jobin, B., C. Latendresse, M. Grenier, C. Maisonneuve, and A. Sebbane. 2010. Recent landscape change at the ecoregion scale in Southern Québec (Canada), 1993–2001. Environmental Monitoring and Assessment **164**:631-647.

Jones, N. T., and B. Gilbert. 2016. Biotic forcing: the push & pull of plant ranges. Plant Ecology **217**:1331-1344.

Kellman, M. 2004. Sugar maple (*Acer saccharum* Marsh.) establishment in boreal forest: results of a transplantation experiment. Journal of Biogeography **31**:1515-1522.

Kelly, A. E., and M. L. Goulden. 2008. Rapid shifts in plant distribution with recent climate change. Proceedings of the National Academy of Sciences of the United States of America **105**:11823-11826.

Kennedy, J. P., L. Garavelli, N. K. Truelove, D. J. Devlin, S. J. Box, L. M. Chérubin, and I. C. Feller. 2017. Contrasting genetic effects of red mangrove (*Rhizophora mangle* L.) range expansion along West and East Florida. Journal of Biogeography **44**:335-347.

Kirkpatrick, M., and N. H. Barton. 1997. Evolution of a Species' Range. The American Naturalist **150**:1-23.

Körner, C., D. Basler, G. Hoch, C. Kollas, A. Lenz, C. F. Randin, Y. Vitasse, and N. E. Zimmermann. 2016. Where, why and how? Explaining the low-temperature range limits of temperate tree species. Journal of Ecology **104**:1076-1088.

Kueppers, L. M., E. Conlisk, C. Castanha, A. B. Moyes, M. J. Germino, P. de Valpine, M. S. Torn, and J. B. Mitton. 2017. Warming and provenance limit tree recruitment across and beyond the elevation range of subalpine forest. Global Change Biology **23**:2383-2395.

Kwit, M. C., L. S. Rigg, and D. Goldblum. 2010. Sugar maple seedling carbon assimilation at the northern limit of its range: the importance of seasonal light. Canadian Journal of Forest Research **40**:385-393.

Lafleur, B., D. Paré, A. D. Munson, and Y. Bergeron. 2010. Response of northeastern North American forests to climate change: Will soil conditions constrain tree species migration? Environmental Reviews **18**:279-289.

Laganière, J., D. Paré, and R. L. Bradley. 2010. How does a tree species influence litter decomposition? Separating the relative contribution of litter quality, litter mixing, and forest floor conditions. Canadian Journal of Forest Research **40**:465-475.

Landhäusser, S. M., D. Deshaies, and V. J. Lieffers. 2010. Disturbance facilitates rapid range expansion of aspen into higher elevations of the Rocky Mountains under a warming climate. Journal of Biogeography **37**:68-76.

Leak, W. B. 1996. Long-Term Structural Change in Uneven-Aged Northern Hardwoods. Forest Science **42**:160-165.

Lee-Yaw, J. A., H. M. Kharouba, M. Bontrager, C. Mahony, A. M. Csergő, A. M. E. Noreen, Q. Li, R. Schuster, and A. L. Angert. 2016. A synthesis of transplant experiments and ecological niche models suggests that range limits are often niche limits. Ecology Letters **19**:710-722.

Leithead, M., L. R. Silva, and M. Anand. 2012. Recruitment patterns and northward tree migration through gap dynamics in an old-growth white pine forest in northern Ontario. Plant Ecology **213**:1699-1714.

Leithead, M. D., M. Anand, and L. C. R. Silva. 2010. Northward migrating trees establish in treefall gaps at the northern limit of the temperate-boreal ecotone, Ontario, Canada. Oecologia **164**:1095-1106.

Lembrechts, J. J., A. Pauchard, J. Lenoir, M. A. Nuñez, C. Geron, A. Ven, P. Bravo-Monasterio, E. Teneb, I. Nijs, and A. Milbau. 2016. Disturbance is the key to plant invasions in cold environments. Proceedings of the National Academy of Sciences **113**:14061-14066.

Lenoir, J., J.-C. Gégout, J.-C. Pierrat, J.-D. Bontemps, and J.-F. Dhôte. 2009. Differences between tree species seedling and adult altitudinal distribution in mountain forests during the recent warm period (1986-2006). Ecography **32**:765-777.

Lenoir, J., J. C. Gegout, P. A. Marquet, P. de Ruffray, and H. Brisse. 2008. A Significant Upward Shift in Plant Species Optimum Elevation During the 20th Century. Science **320**:1768-1771.

Lenoir, J., T. Hattab, and G. Pierre. 2017. Climatic microrefugia under anthropogenic climate change: implications for species redistribution. Ecography **40**:253-266.

Lenoir, J., and J. C. Svenning. 2015. Climate-related range shifts – a global multidimensional synthesis and new research directions. Ecography **38**:15-28.

Lenz, A., Y. Vitasse, G. Hoch, and C. Körner. 2014. Growth and carbon relations of temperate deciduous tree species at their upper elevation range limit. Journal of Ecology **102**:1537-1548.

Li, W., J. A. Kershaw, K. K. L. Costanza, and A. R. Taylor. 2020. Evaluating the potential of red spruce (*Picea rubens* Sarg.) to persist under climate change using historic provenance trials in eastern Canada. Forest Ecology and Management **466**:118139.

Liang, Y., M. J. Duveneck, E. J. Gustafson, J. M. Serra-Diaz, and J. R. Thompson. 2018. How disturbance, competition, and dispersal interact to prevent tree range boundaries from keeping pace with climate change. Global Change Biology **24**:e335-e351.

Lindenmayer, D. B., G. E. Likens, C. J. Krebs, and R. J. Hobbs. 2010. Improved probability of detection of ecological "surprises". Proceedings of the National Academy of Sciences **107**:21957.

Lloyd, A. H., K. Yoshikawa, C. L. Fastie, L. Hinzman, and M. Fraver. 2003. Effects of permafrost degradation on woody vegetation at arctic treeline on the Seward Peninsula, Alaska. Permafrost and Periglacial Processes **14**:93-101.

Loarie, S. R., P. B. Duffy, H. Hamilton, G. P. Asner, C. B. Field, and D. D. Ackerly. 2009. The velocity of climate change. Nature **462**:1052-1055.

Louthan, A. M., D. F. Doak, and A. L. Angert. 2015. Where and When do Species Interactions Set Range Limits? Trends in Ecology & Evolution **30**:780-792.

Lovat, C.-A. 2013. Clinal variation and phenology in two conspecifics of *Phragmites australis* (Cav.) Trin. Ex Steud in Northeastern North America : implications for current management and future climate change. McGill University Libraries, [Montréal].

Maggini, R., A. Lehmann, M. Kéry, H. Schmid, M. Beniston, L. Jenni, and N. Zbinden. 2011. Are Swiss birds tracking climate change?: Detecting elevational shifts using response curve shapes. Ecological Modelling **222**:21-32.

Máliš, F., M. Kopecký, P. Petřík, J. Vladovič, J. Merganič, and T. Vida. 2016. Life stage, not climate change, explains observed tree range shifts. Global Change Biology **22**:1904-1914.

Marris, E. 2007. The escalator effect. Nature Reports Climate Change:94-96.

Matías, L., and A. S. Jump. 2015. Asymmetric changes of growth and reproductive investment herald altitudinal and latitudinal range shifts of two woody species. Global Change Biology **21**:882-896.

McKenney, D. W., B. G. Mackey, and D. Joyce. 1999. Seedwhere: a computer tool to support seed transfer and ecological restoration decisions. Environmental Modelling & Software **14**:589-595.

McKenney, D. W., J. H. Pedlar, R. B. Rood, and D. Price. 2011. Revisiting projected shifts in the climate envelopes of North American trees using updated general circulation models. Global Change Biology **17**:2720-2730.

McLachlan, J. S., J. S. Clark, and P. S. Manos. 2005. Molecular indicators of tree migration capacity under rapid climate change. Ecology **86**:2088-2098.

Messaoud, Y., Y. Bergeron, and A. Leduc. 2007. Ecological factors explaining the location of the boundary between the mixedwood and coniferous bioclimatic zones in the boreal biome of eastern North America. Global Ecology & Biogeography **16**:90-102.

Messier, C., J. Bauhus, F. Doyon, F. Maure, R. Sousa-Silva, P. Nolet, M. Mina, N. Aquilué, M.-J. Fortin, and K. Puettmann. 2019. The functional complex network approach to foster forest resilience to global changes. Forest Ecosystems **6**:21.

Miller, A. E., T. L. Wilson, R. L. Sherriff, and J. Walton. 2017. Warming drives a front of white spruce establishment near western treeline, Alaska. Global Change Biology **23**:5509-5522.

Miller, K. M., and B. J. McGill. 2018. Land use and life history limit migration capacity of eastern tree species. Global Ecology and Biogeography **27**:57-67.

Ministère des Forêts, Faune et des Parcs. 2015. Normes techniques, Placettes-Échantillons Permanentes, 4e inventaire écoforetier du Québec méridional. Ministère des Forêts, Faune et Parcs, Direction des Inventaires Forestiers, Québec, Québec.

Moore, J.-D., and R. Ouimet. 2006. Ten-year effect of dolomitic lime on the nutrition, crown vigor, and growth of sugar maple. Canadian Journal of Forest Research **36**:1834-1841.

Morin, A., and S. Payette. 1984. Expansion récente du melèze a la limite des forêts (Québec nordique). Canadian Journal of Botany **62**:1404-1408.

Morin, M. B., D. Kneeshaw, F. Doyon, H. Le Goff, P. Bernier, V. Yelle, A. Blondlot, and D. Houle. 2015. Climate change and the forest sector: Perception of principal impacts and of potential options for adaptation. The Forestry Chronicle **91**:395-406.

Morin, X., C. Augspurger, and I. Chuine. 2007. Process-based modeling of species' distributions: what limits temperate tree species' range boundaries? Ecology **88**:2280-2291.

Morin, X., and W. Thuiller. 2009. Comparing niche- and process-based models to reduce prediction uncertainty in species range shifts under climate change. Ecology **90**:1301-1313.

Muller, J. J., L. M. Nagel, and B. J. Palik. 2019. Forest adaptation strategies aimed at climate change: Assessing the performance of future climate-adapted tree species in a northern Minnesota pine ecosystem. Forest Ecology and Management **451**:117539.

Munier, A., L. Hermanutz, J. D. Jacobs, and K. Lewis. 2010. The interacting effects of temperature, ground disturbance, and herbivory on seedling establishment: implications for treeline advance with climate warming. Plant Ecology **210**:19-30.

Murphy, H. T., J. VanDerWal, and J. Lovett-Doust. 2006. Distribution of abundance across the range in eastern North American trees. Global Ecology & Biogeography **15**:63-71.

Murphy, H. T., J. VanDerWal, and J. Lovett-Doust. 2010. Signatures of range expansion and erosion in eastern North American trees. Ecology Letters **13**:1233-1244.

Nadeau, C. P., A. K. Fuller, and D. L. Rosenblatt. 2015. Climate-smart management of biodiversity. Ecosphere **6**:1-17.

Nagati, M., M. Roy, S. Manzi, F. Richard, A. Desrochers, M. Gardes, and Y. Bergeron. 2018. Impact of local forest composition on soil fungal communities in a mixed boreal forest. Plant and Soil **432**:345-357.

Nagel, L. M., B. J. Palik, M. A. Battaglia, A. W. D'Amato, J. M. Guldin, C. W. Swanston, M. K. Janowiak, M. P. Powers, L. A. Joyce, C. I. Millar, D. L. Peterson, L. M. Ganio, C. Kirschbaum, and M. R. Roske. 2017. Adaptive Silviculture for Climate Change: A National Experiment in Manager-Scientist Partnerships to Apply an Adaptation Framework. Journal of Forestry **115**:167-178.

Nicotra, A. B., O. K. Atkin, S. P. Bonser, A. M. Davidson, E. J. Finnegan, U. Mathesius, P. Poot, M. D. Purugganan, C. L. Richards, F. Valladares, and M. van Kleunen. 2010. Plant phenotypic plasticity in a changing climate. Trends in Plant Science **15**:684-692.

NOAA National Centers for Environmental Information. 2020. State of the Climate: Global Climate Report for Annual 2019. Retrieved from https://www.ncdc.noaa.gov/sotc/global/201913

Nolet, P., S. Delagrange, K. Bannon, C. Messier, and D. Kneeshaw. 2015. Liming has a limited effect on sugar maple – American beech dynamics compared with beech sapling elimination and canopy opening. Canadian Journal of Forest Research **45**:1376-1386.

Nolet, P., S. Delagrange, D. Bouffard, F. Doyon, and E. Forget. 2008. The successional status of sugar maple (*Acer saccharum*), revisited. Ann. For. Sci. **65**:208.

Nowacki, G. J., and M. D. Abrams. 2015. Is climate an important driver of post-European vegetation change in the Eastern United States? Global Change Biology **21**:314-334.

Oldfather, M. F., M. M. Kling, S. N. Sheth, N. C. Emery, and D. D. Ackerly. 2020. Range edges in heterogeneous landscapes: Integrating geographic scale and climate complexity into range dynamics. Global Change Biology **26**:1055-1067.

Olivieri, I., D. Couvet, and P. H. Gouyon. 1990. The genetic of transient populations - Research at the metapopulation level. Trends in Ecology & Evolution **5**:207-210.

Ontario Government. 2007. Ecological land classification primer: Central and southern Ontario.

Ordonez, A., and J. W. Williams. 2013. Climatic and biotic velocities for woody taxa distributions over the last 16 000 years in eastern North America. Ecology Letters **16**:773-781.

Ouranos. 2015. Synthèse des connaissances sur les changements climatiques au Québec. Édition 2015. Montréal, Québec.

Panchen, Z. A., R. B. Primack, A. S. Gallinat, B. Nordt, A.-D. Stevens, Y. Du, and R. Fahey. 2015. Substantial variation in leaf senescence times among 1360 temperate woody plant species: implications for phenology and ecosystem processes. Annals of Botany **116**:865-873.

Park, A., C. Talbot, and R. Smith. 2018. Trees for tomorrow: an evaluation framework to assess potential candidates for assisted migration to Manitoba's forests. Climatic Change **148**:591-606.

Parmesan, C. 2006. Ecological and Evolutionary Responses to Recent Climate Change. Annual Review of Ecology, Evolution, and Systematics **37**:637-669.

Parmesan, C., and G. Yohe. 2003. A globally coherent fingerprint of climate change impacts across natural systems. Nature **421**:37-42.

Pauli, H., M. Gottfried, K. Reier, C. Klettner, and G. Grabherr. 2007. Signals of range expansions and contractions of vascular plants in the high Alps: observations (1994-2004) at the GLORIA*master site Schrankogel, Tyrol, Austria. Global Change Biology **13**:147-156.

Pedlar, J., D. McKenney, J. Beaulieu, S. Colombo, J. McLachlan, and G. O'Neill. 2011. The implementation of assisted migrationin Canadian forests. The Forestry Chronicle **87**:766-777.

Pedlar, J. H., and D. W. McKenney. 2017. Assessing the anticipated growth response of northern conifer populations to a warming climate. Scientific Reports **7**:43881.

Pedlar, J. H., D. W. McKenney, I. Aubin, T. Beardmore, J. Beaulieu, L. Iverson, G. A. O'Neill, R. S. Winder, and C. Ste-Marie. 2012. Placing Forestry in the Assisted Migration Debate. BioScience **62**:835-842.

Périé, C., and S. de Blois. 2016. Dominant forest tree species are potentially vulnerable to climate change over large portions of their range even at high latitudes. PeerJ **4**:e2218.

Périé, C., S. de Blois, M.-C. Lambert, and N. Casajus. 2014. Effets anticipés des changements climatiques sur l'habitat des espèces arborescentes au Québec. Direction de la recherche forestière, Ministère des Ressources naturelles, editor. Gouvernement du Québec, Québec. 46p.

Perring, M. P., M. Bernhardt-Römermann, L. Baeten, G. Midolo, H. Blondeel, L. Depauw, D. Landuyt, S. L. Maes, E. De Lombaerde, M. M. Carón, M. Vellend, J. Brunet, M. Chudomelová, G. Decocq, M. Diekmann, T. Dirnböck, I. Dörfler, T. Durak, P. De Frenne, F. S. Gilliam, R. Hédl, T. Heinken, P. Hommel, B. Jaroszewicz, K. J. Kirby, M. Kopecký, J. Lenoir, D. Li, F. Máliš, F. J. G. Mitchell, T. Naaf, M. Newman, P. Petřík, K. Reczyńska, W. Schmidt, T. Standovár, K. Świerkosz, H. Van Calster, O. Vild, E. R. Wagner, M. Wulf, and K. Verheyen. 2018. Global environmental change effects on plant community composition trajectories depend upon management legacies. Global Change Biology **24**:1722-1740.

Peterson, M. L., D. F. Doak, and W. F. Morris. 2019. Incorporating local adaptation into forecasts of species' distribution and abundance under climate change. Global Change Biology **25**:775-793.

Peterson St-Laurent, G., S. Hagerman, and R. Kozak. 2018. What risks matter? Public views about assisted migration and other climate-adaptive reforestation strategies. Climatic Change **151**:573-587.

Pironon, S., G. Papuga, J. Villellas, A. L. Angert, M. B. García, and J. D. Thompson. 2017. Geographic variation in genetic and demographic performance: new insights from an old biogeographical paradigm. Biological Reviews **92**:1877-1909.

Pisaric, M. F. J., D. J. King, A. J. M. MacIntosh, and R. Bemrose. 2008. Impact of The 1998 Ice Storm on The Health and Growth of Sugar Maple (*Acer saccharum* Marsh.) Dominated Forests in Gatineau Park, Quebec. The Journal of the Torrey Botanical Society **135**:530-539, 510.

Pollock, L. J., R. Tingley, W. K. Morris, N. Golding, R. B. O'Hara, K. M. Parris, P. A. Vesk, and M. A. McCarthy. 2014. Understanding co-occurrence by modelling species simultaneously with a Joint Species Distribution Model (JSDM). Methods in Ecology and Evolution **5**:397-406.

Pulliam, H. R. 2000. On the relationship between niche and distribution. Ecology Letters **3**:349-361.

Purves, D. W. 2009. The demography of range boundaries versus range cores in eastern US tree species. Proceedings of the Royal Society B-Biological Sciences **276**:1477-1484.

Rathcke, B., and E. P. Lacey. 1985. Phenological Patterns of Terrestrial Plants. Annual Review of Ecology and Systematics **16**:179-214.

Reed, T. E., D. E. Schindler, and R. S. Waples. 2011. Interacting Effects of Phenotypic Plasticity and Evolution on Population Persistence in a Changing Climate. Conservation Biology **25**:56-63.

Regnière, J., and R. Saint-Amant. 2014. BioSIM 10 - User's Manual. Laurentian Forestry Centre, Canadian Forest Service, Natural Resources Canada, Sainte-Foy, Québec.

Reich, P. B., K. M. Sendall, K. Rice, R. L. Rich, A. Stefanski, S. E. Hobbie, and R. A. Montgomery. 2015. Geographic range predicts photosynthetic and growth response to warming in co-occurring tree species. Nature Climate Change **5**:148-152.

Renwick, K. M., and M. E. Rocca. 2015. Temporal context affects the observed rate of climate-driven range shifts in tree species. Global Ecology and Biogeography **24**:44-51.

Renwick, K. M., M. E. Rocca, and T. J. Stohlgren. 2016. Biotic disturbance facilitates range shift at the trailing but not the leading edge of lodgepole pine's altitudinal distribution. Journal of Vegetation Science **27**:780-788.

Reyer, C. P. O., S. Leuzinger, A. Rammig, A. Wolf, R. P. Bartholomeus, A. Bonfante, F. de Lorenzi, M. Dury, P. Gloning, R. Abou Jaoudé, T. Klein, T. M. Kuster, M. Martins, G. Niedrist, M. Riccardi, G. Wohlfahrt, P. de Angelis, G. de Dato, L. François, A. Menzel, and M. Pereira. 2013. A plant's perspective of extremes: terrestrial plant responses to changing climatic variability. Global Change Biology **19**:75-89.

Ricciardi, A., and D. Simberloff. 2009. Assisted colonization is not a viable conservation strategy. Trends in Ecology & Evolution **24**:248-253.

Root, T. L., J. T. Price, K. R. Hall, S. H. Schneider, C. Rosenzweig, and J. A. Pounds. 2003. Fingerprints of global warming on wild animals and plants. Nature **421**:57-60.

Royer-Tardif, S., L. Boisvert-Marsh, J. Godbout, N. Isabel, and I. Aubin. In review. Finding common ground: Toward comparable indicators of adaptive capacity of tree species to a changing climate. Ecology and Evolution

Sagarin, R. D., and S. D. Gaines. 2002. The 'abundant centre' distribution: to what extent is it a biogeographical rule? Ecology Letters **5**:137-147.

Santala, K., I. Aubin, M. Hoepting, M. Bachand, and D. Pitt. 2019. Managing conservation values and tree performance: Lessons learned from 10 year experiments in regenerating eastern white pine (*Pinus strobus* L.). Forest Ecology and Management **432**:748-760.

Saucier, J.-P., P. Grondin, A. Robitaille, and J.-F. Bergeron. 2003. Zones de végétation et les domaines bioclimatiques du Québec. Direction des inventaires forestiers, Ministère des Ressources naturelles et de la Faune, Québec, Québec.

Schenker, G., A. Lenz, C. Körner, and G. Hoch. 2014. Physiological minimum temperatures for root growth in seven common European broad-leaved tree species. Tree Physiology **34**:302-313.

Schwörer, C., D. G. Gavin, I. R. Walker, and F. S. Hu. 2017. Holocene tree line changes in the Canadian Cordillera are controlled by climate and topography. Journal of Biogeography **44**:1148-1159.

Seidl, R., J. Honkaniemi, T. Aakala, A. Aleinikov, P. Angelstam, M. Bouchard, Y. Boulanger, P. J. Burton, L. De Grandpré, S. Gauthier, W. D. Hansen, J. U. Jepsen, K. Jõgiste, D. D. Kneeshaw, T. Kuuluvainen, O. Lisitsyna, K. Makoto, A. S. Mori, D. S. Pureswaran, E. Shorohova, E. Shubnitsina, A. R. Taylor, N. Vladimirova, F. Vodde, and C. Senf. 2020. Globally consistent climate sensitivity of natural disturbances across boreal and temperate forest ecosystems. Ecography **43**:967-978.

Sexton, J. P., S. B. Hangartner, and A. A. Hoffmann. 2014. Genetic isolation by environment or distance: which pattern of gene flow is most common? Evolution **68**:1-15.

Sexton, J. P., P. J. McIntyre, A. L. Angert, and K. J. Rice. 2009. Evolution and Ecology of Species Range Limits. Annual Review of Ecology, Evolution, and Systematics **40**:415-436.

Sheth, S. N., and A. L. Angert. 2018. Demographic compensation does not rescue populations at a trailing range edge. Proceedings of the National Academy of Sciences **115**:2413.

Shoo, L. P., S. E. Williams, and J. M. Hero. 2006. Detecting climate change induced range shifts: Where and how should we be looking? Austral Ecology **31**:22-29.

Sittaro, F., A. Paquette, C. Messier, and C. A. Nock. 2017. Tree range expansion in eastern North America fails to keep pace with climate warming at northern range limits. Global Change Biology **23**:3292-3301.

Slaton, M. R. 2015. The roles of disturbance, topography and climate in determining the leading and rear edges of population range limits. Journal of Biogeography **42**:255-266.

Solarik, K. A., C. Messier, R. Ouimet, Y. Bergeron, and D. Gravel. 2018. Local adaptation of trees at the range margins impacts range shifts in the face of climate change. Global Ecology and Biogeography **27**:1507-1519.

St.Clair, S. B., W. E. Sharpe, and J. P. Lynch. 2008. Key interactions between nutrient limitation and climatic factors in temperate forests: a synthesis of the sugar maple literature. Canadian Journal of Forest Research **38**:401-414.

Stahl, U., B. Reu, and C. Wirth. 2014. Predicting species' range limits from functional traits for the tree flora of North America. Proceedings of the National Academy of Sciences **111**:13739.

Svenning, J.-C., and F. Skov. 2004. Limited filling of the potential range in European tree species. Ecology Letters **7**:565-573.

Swanston, C. W., M. K. Janowiak, L. A. Brandt, P. R. Butler, S. D. Handler, P. D. Shannon, A. D. Lewis, K. Hall, R. T. Fahey, and L. Scott. 2016. Forest adaptation resources: climate change tools and approaches for land managers. US Department of Agriculture, Forest Service, Northern Research Station. Newtown Square, PA.

Talluto, M. V., I. Boulangeat, A. Ameztegui, I. Aubin, D. Berteaux, A. Butler, F. Doyon, C. R. Drever, M.-J. Fortin, T. Franceschini, J. Liénard, D. McKenney, K. A. Solarik, N. Strigul, W. Thuiller, and D. Gravel. 2016. Cross-scale integration of knowledge for predicting species ranges: a metamodelling framework. Global Ecology and Biogeography **25**:238-249.

Terrail, R., S. Dupuis, V. Danneyrolles, M.-J. Fortin, Y. Boucher, and D. Arseneault. 2019. Reorganization of tree assemblages over the last century in the northern hardwoods of eastern Canada. Applied Vegetation Science **22**:474-483.

Thom, D., W. Rammer, and R. Seidl. 2017. Disturbances catalyze the adaptation of forest ecosystems to changing climate conditions. Global Change Biology **23**:269-282.

Thomas, C. D. 1994. Extinction, Colonization, and Metapopulations: Environmental Tracking by Rare Species. Conservation Biology **8**:373-378.

Thuiller, W., B. Lafourcade, R. Engler, and M. B. Araújo. 2009. BIOMOD – a platform for ensemble forecasting of species distributions. Ecography **32**:369-373.

Thuiller, W., S. Lavorel, M. B. Araujo, M. T. Sykes, and I. C. Prentice. 2005. Climate change threats to plant diversity in Europe. Proceedings of the National Academy of Sciences **102**:8245-8250.

Tingley, M. W., and S. R. Beissinger. 2009. Detecting range shifts from historical species occurrences: new perspectives on old data. Trends in Ecology & Evolution **24**:625-633.

Travis, J. M. J., C. M. Harris, K. J. Park, and J. M. Bullock. 2011. Improving prediction and management of range expansions by combining analytical and individual-based modelling approaches. Methods in Ecology and Evolution **2**:477-488.

Tremblay, M. F., Y. Bergeron, D. Lalonde, and Y. Mauffette. 2002. The potential effects of sexual reproduction and seedling recruitment on the maintenance of red maple (*Acer rubrum* L.) populations at the northern limit of the species range. Journal of Biogeography **29**:365-373.

Urban, M. C. 2020. Climate-tracking species are not invasive. Nature Climate Change.

Urban, M. C., J. J. Tewksbury, and K. S. Sheldon. 2012. On a collision course: competition and dispersal differences create no-analogue communities and cause extinctions during climate change. Proceedings of the Royal Society B: Biological Sciences **279**:2072-2080.

Van Couwenberghe, R., C. Collet, J.-C. Pierrat, K. Verheyen, and J.-C. Gégout. 2013. Can species distribution models be used to describe plant abundance patterns? Ecography **36**:665-674.

Van Kleunen, M., E. Weber, and M. Fischer. 2010. A meta-analysis of trait differences between invasive and non-invasive plant species. Ecology Letters **13**:235-245.

van Mantgem, P. J., N. L. Stephenson, J. C. Byrne, L. D. Daniels, J. F. Franklin, P. Z. Fule, M. E. Harmon, A. J. Larson, J. M. Smith, A. H. Taylor, and T. T. Veblen. 2009. Widespread increase of tree mortality rates in the Western United States. Science **323**:521-524.

Venier, L. A., I. D. Thompson, R. Fleming, J. Malcolm, I. Aubin, J. A. Trofymow, D. Langor, R. Sturrock, C. Patry, R. O. Outerbridge, S. B. Holmes, S. Haeussler, L. De Grandpré, H. Y. H. Chen, E. Bayne, A. Arsenault, and J. P. Brandt. 2014. Effects of natural resource development on the terrestrial biodiversity of Canadian boreal forests. Environmental Reviews **22**:457-490.

Villellas, J., D. F. Doak, M. B. García, and W. F. Morris. 2015. Demographic compensation among populations: what is it, how does it arise and what are its implications? Ecology Letters **18**:1139-1152.

Vitasse, Y., G. Hoch, C. F. Randin, A. Lenz, C. Kollas, J. F. Scheepens, and C. Körner. 2013. Elevational adaptation and plasticity in seedling phenology of temperate deciduous tree species. Oecologia **171**:663-678.

Warren, R. J., and M. A. Bradford. 2014. Mutualism fails when climate response differs between interacting species. Global Change Biology **20**:466-474.

Wilson, R. J., D. Gutierrez, J. Gutierrez, D. Martinez, R. Agudo, and V. J. Monserrat. 2005. Changes to the elevational limits and extent of species ranges associated with climate change. Ecology Letters **8**:1138-1146.

Woodall, C. W., C. M. Oswalt, J. A. Westfall, C. H. Perry, and M. D. Nelson. 2008. Tree migration detection through comparisons of historic and current forest inventories. Page 1 CD *in* W. McWilliams, G. Moisen, and R. Czaplewski, editors. 2008 Forest Inventory and Analysis (FIA) Symposium. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Park City, UT.

Woodall, C. W., C. M. Oswalt, J. A. Westfall, C. H. Perry, M. D. Nelson, and A. O. Finley. 2009. An indicator of tree migration in forests of the eastern United States. Forest Ecology and Management **257**:1434-1444.

Woodall, C. W., K. Zhu, J. A. Westfall, C. M. Oswalt, A. W. D'Amato, B. F. Walters, and H. E. Lintz. 2013. Assessing the stability of tree ranges and influence of disturbance in eastern US forests. Forest Ecology and Management **291**:172-180.

Xu, L., R. B. Myneni, F. S. Chapin, T. V. Callaghan, J. E. Pinzon, C. J. Tucker, Z. Zhu, J. Bi, P. Ciais, H. Tømmervik, E. S. Euskirchen, B. C. Forbes, S. L. Piao, B. T. Anderson, S. Ganguly, R. R. Nemani, S. J. Goetz, P. S. A. Beck, A. G. Bunn, C. Cao, and J. C. Stroeve. 2013. Temperature and vegetation seasonality diminishment over northern lands. Nature Climate Change **3**:581-586.

Young, D. J. N., C. M. Werner, K. R. Welch, T. P. Young, H. D. Safford, and A. M. Latimer. 2019. Post-fire forest regeneration shows limited climate tracking and potential for drought-induced type conversion. Ecology **100**:e02571.

Zadworny, M., M. L. McCormack, J. Mucha, P. B. Reich, and J. Oleksyn. 2016. Scots pine fine roots adjust along a 2000-km latitudinal climatic gradient. New Phytologist **212**:389-399.

Zhang, X., G. Flato, M. Kirchmeier-Young, L. Vincent, H. Wan, X. Wang, R. Rong, J. Fyfe, G. Li, and V. Kharin. 2019. Changes in temperature and precipitation across Canada; Chapter 4. Pages 112-193 *in* E. Bush and D. S. Lemmen, editors. Canada's Changing Climate Report. Governemnt of Canada, Ottawa, Ontario.

Zhu, K., C. W. Woodall, and J. S. Clark. 2012. Failure to migrate: lack of tree range expansion in response to climate change. Global Change Biology **18**:1042-1052.

Zhu, K., C. W. Woodall, S. Ghosh, A. E. Gelfand, and J. S. Clark. 2014. Dual impacts of climate change: forest migration and turnover through life history. Global Change Biology **20**:251-264.

Zohner, C. M., L. Mo, S. S. Renner, J.-C. Svenning, Y. Vitasse, B. M. Benito, A. Ordonez, F. Baumgarten, J.-F. Bastin, V. Sebald, P. B. Reich, J. Liang, G.-J. Nabuurs, S. de-Miguel, G. Alberti, C. Antón-Fernández, R. Balazy, U.-B. Brändli, H. Y. H. Chen, C. Chisholm, E. Cienciala, S. Dayanandan, T. M. Fayle, L. Frizzera, D. Gianelle, A. M. Jagodzinski, B. Jaroszewicz, T. Jucker, S. Kepfer-Rojas, M. L. Khan, H. S. Kim, H. Korjus, V. K. Johannsen, D. Laarmann, M. Lang, T. Zawila-Niedzwiecki, P. A. Niklaus, A. Paquette, H. Pretzsch, P. Saikia, P. Schall, V. Šebeň, M. Svoboda, E. Tikhonova, H. Viana, C. Zhang, X. Zhao, and T. W. Crowther. 2020. Late-spring frost risk between 1959 and 2017 decreased in North America but increased in Europe and Asia. Proceedings of the National Academy of Sciences **117**:12192-12200.

Zurell, D., W. Thuiller, J. Pagel, J. S. Cabral, T. Münkemüller, D. Gravel, S. Dullinger, S. Normand, K. H. Schiffers, K. A. Moore, and N. E. Zimmermann. 2016. Benchmarking novel approaches for modelling species range dynamics. Global Change Biology **22**:2651-2664.

Chapter 8 – APPENDICES TO CHAPTERS

8.1 - Appendix for Assessing range shifts

8.1.1 – Introduction

This thesis builds upon previous work that assessed range limit shifts for trees and saplings of 11 species between comprehensive forest inventories conducted between 1970-1977 (hereafter called P_1) and 1992-2002 (hereafter called P_2) (results shown in Boisvert-Marsh et al. 2014). After the most recent inventory was completed in 2015 (P_3: 2003-2015), we undertook analyses to assess whether the patterns we found for tree and saplings in the original study were consistent between inventories. The results shown here are a permanent record of this work and serve as the basis for further analyses in each of the three chapters. Specifically, the results shown later in this section are meant to replace some of the supplemental methods and results reported for Chapters 3 and 4. Chapter 3 considered eight species: *Ostrya virginiana*, *Fagus grandifolia*, *Acer saccharum*, *Betula alleghaniensis*, *Thuja occidentalis*, *Acer rubrum*, *Populus tremuloides, Betula papyrifera*. Chapter 4 considered four species: *Fagus grandifolia*, *Acer saccharum*, *Betula alleghaniensis*, *Thuja occidentalis*, *Acer rubrum.*

8.1.2 – Methods

8.1.2.1 – Study area

The province of Québec (Canada) encompasses about 2% of all forested areas in the world and a significant proportion of all boreal forests (Saucier *et al.*, 2003); Ministère des Forêts, de la Faune et des Parcs (MFFP), public communication, <http://www.mffp.gouv.qc.ca/english/international/forests/index.jsp >). The study area covers roughly 761 100 km² in Quebec, from 45°N up to around 53°N (the commercial treeline at the time), and from 80°W to 61°W (Saucier *et al.*, 2003). Two major vegetation zones, each with two forest types, are part of the study area: the northern temperate zone and the boreal forest zone. The former includes *Acer saccharum* dominated forests to the south and mixed *Abies balsamea-Betula alleghaniensis* forests to the north. The latter includes *A. balsamea-B. papyrifera* forests to the south and vast *Picea*-feathermoss forests to the north (Saucier *et al.*, 2003). The northern limit of the study area roughly coincides with the ecotone between the end of continuous boreal forest and the beginning of the taiga.

The study area is characterized by strong latitudinal climatic gradients. Average annual temperature from 1965 to 2014 ranged from 6.9°C in the south to -4.4°C in the north. Annual precipitation ranged from 743 to 1543mm, decreasing in the study area from south to north and from east to west. Drier than average conditions are found in the center of the province and the Lower North Shore (south of Labrador), whereas wetter than average conditions are concentrated in the center-north.

8.1.2.2 – Data collection

We used exhaustive forest inventories of permanent plots to monitor long-term forest dynamics throughout the study area (MFFP, 2015; Dataset available from https://www.donneesquebec.ca/recherche/fr/dataset/placettes-echantillons-permanentes-1970-a-aujourd-hui). Data collection started in 1970 and is ongoing. Plots of 400 m^2 are usually paired (main and satellite) for sampling at an average distance of 425 m. Plot density decreases northward with tree species diversity (1 pair of plots per 26 km^2 in the *A. saccharum* forest, 1 pair per 104 km^2 in the *A. balsamea* forest and 1 pair per 259 km^2 in the *P. mariana* forest).

According to MFFP, a merchantable tree has a diameter at breast height (DBH) of at least 9.1cm, whereas saplings range from 1.1- 9.0cm DBH, grouped by 2cm DBH classes, and are at least 1.3m tall. The smallest class of saplings available (1.1-3.0 cm DBH; hereafter called “saplings”) was considered the juvenile life stage in this study. The merchantable tree life stage (DBH ≥ 9.1 cm; hereafter called “trees”) was also analyzed. Saplings of the smallest size class are considered to be indicative of successful establishment.

For species data, we sampled saplings and trees in each of three time periods, with each inventory taking between 7 to 12 years to complete: 1970-1977 (P_1), 1992-2002 (P_2), and 2003-2015 (P_3). Within these time periods, the precise date of a record was known. Only occurrence data were used. Evidence has shown that climate predicts frequency of occurrence at different latitudes better than it predicts importance value in a plot (Canham & Thomas, 2010, Chambers *et al.*, 2013).

8.1.2.3 – Assessing range shifts

Methods

The sapling and mature tree distribution of 11 species were investigated for evidence of latitudinal shifts: *Ostrya virginiana* – American hophornbeam, *Fagus grandifolia* – American beech, *Acer saccharum* – Sugar maple, *Betula alleghaniensis* – Yellow birch, *Thuja occidentalis* – Eastern white cedar, *Acer rubrum* – Red maple, *Populus tremuloides* – Trembling aspen, *Betula papyrifera* – White birch, *Picea glauca* – White spruce, *Abies balsamea* – Balsam fir, *Picea mariana* – Black spruce. These species reach or approach their northernmost latitudinal limit in the study area (under 53°N) (Farrar, 1995, Little, 1971, Soper & Heimburger, 1990) and show a minimum of 50 occurrences in each of the time periods considered—P_1 (1970-1977), P_2 (1992-2002) and P_3 (2003-2015). Main and satellite plots were considered separately to account for small- and large-scale dispersal processes, resulting in a total of 6309 resampled plots.

To assess latitudinal limits for saplings and mature trees for a given species, we employed a two-pronged approach based on the methodology described in Boisvert-Marsh et al. (2014). In the first part of our assessment, we calculated two latitudinal limits of species distribution based on presences of a given species in P_1, P_2 and P_3: the median (50th percentile of latitude) and northernmost (90th percentile of latitude) range limit within the study area. The limits in the reference period (P_1 or P_2) defined latitudinal zones in the southern (below the 50th), northern (above the 50th) and northernmost (above the 90th) portions of the range. Taking into account location-specific variation in distribution is important since range shift is likely to result in distributional changes across different portions of the range, and not only at extreme range boundaries (Boisvert-Marsh et al., 2014, Woodall et al., 2009, Zhu et al., 2012). The percentile approach was chosen to define limits because it reduces the potential bias of extreme latitudinal data points (Lenoir et al., 2009). The 90th percentile was used because it captured sufficient presence points for statistical analysis for the selected species. Note that, because of the northern location of our study area with respect to the overall range, the 50th percentile of latitude does not reflect the median latitude of the entire north-south range of a species but the median within the study area, whereas the 90th percentile represents the extreme northern edge within the study area, which encompasses at least part of these species' northern limits in eastern North America.

The location of each limit was calculated differently at the median and northernmost limits. At the median, all plots occupied by a given species in the study area were used to calculate the 50th percentile of latitude for P_1, P_2, and P_3. At the northernmost limit, tree species tended to show distinct longitudinal patterns often resulting in distributional limits at greatly differing latitudes. To take these spatial patterns into account, a window of two 0.5° longitude-wide bands (1°) spanning the latitudinal breadth of the study area (45-53°N) was used to calculate the 90th percentile of latitude in 0.5° steps, to smooth out sharp differences from one band to the next (38 bands in total). A weighted average of the 90th percentile of latitude (i.e. weighted by the number of occupied plots in each band with >=1 occurrence) was calculated for P_1, P_2, and P_3.

Once limits were calculated, we determined the magnitude and direction of latitudinal shifts between P_1 and P_3 (P_3-P_1), metrics analysed and presented in Chapter 3 and 4 then utilised in Chapter 5 to calibrate dispersal kernels. We also present here latitudinal shifts between P_1 and P_2 (P_2-P_1) as well as between P_2 and P_3 (P_3-P_2) as a permanent record of this work. Positive values indicate northward latitudinal shift and negative values indicate southward shifts. For latitudinal shifts, significance level was assessed depending on how latitudinal limits were calculated. To assess significance at the 50th percentile, standard error in latitudinal range shifts was estimated using bootstrap resampling with replacement (Efron, 1979). To do this, one sample from each inventory (P_1 and P_3) was removed at each permutation and a new latitudinal range shift was calculated. Standard error was estimated from a distribution of LRS values (n=500 000 iterations). In this case, significance level was assessed at $p <= 0.05$ based on a t distribution. To account for unequal sample sizes resulting from unoccupied bands and the lack of independence between the two samples at the 90th percentile, pooled variance was calculated on the computed latitudes from occupied bands. A latitudinal shift was significant if the upper and lower bounds of the confidence interval ($p <= 0.05$, t distribution) did not include zero.

The second part of our assessment involved examining how the dynamic of occupancy patterns within the zones defined by latitudinal limits in P_1 drove the latitudinal shifts observed. Northward latitudinal shifts, as measured in the first part, can occur when a) occurrence losses south of the limit of interest (i.e. 50th or 90th) outnumber gains north of it (hereafter referred to as “thinning”), or b) when occurrence gains north of a limit are greater than south of it. Based on occurrence patterns and latitudinal limits calculated in P_1, we quantified the occurrence gains or losses in P_3 north and south of the P_1 limit for saplings. McNemar's test for paired samples was used to see if the frequency of presence/absence was statistically different ($p <= 0.05$) between the two inventories.

Combined range shift pattern for a given species is based on combined evidence from latitudinal shift patterns and occupancy dynamics as described above (see Fig. 8.1.1 for examples). *Northward range expansion* results from northward latitudinal shifts as well as relatively higher occupancy ratios north of a limit of interest (50th or 90th) relative to changes in occupancy ratios below (increase or decrease). *Northward shift by southern range thinning* can occur when northward latitudinal shifts occur as a result of a decrease in occupancy change ratios south of the limit of interest. *Southward shift by southern range filling* occurs when southward latitudinal shifts are found in combination with higher occupancy change ratios south of the percentile of interest. *Southward shift by northern range thinning* takes place when southward latitudinal shifts combine with decreased occupancy change ratios take place north of the percentile of interest. shift. Bold font indicates that both tests for latitudinal shift patterns and occupancy dynamics are significant.

Literature cited

Boisvert-Marsh, L., et al. (2014). "Shifting with climate? Evidence for recent changes in tree species distribution at high latitudes." Ecosphere **5**(7): art83.

Efron, B. (1979). "Bootstrap Methods: Another Look at the Jackknife." The Annals of Statistics **7**(1): 1-26.

Farrar, J. L. (1995). Trees in Canada. Ottawa, Fitzhenry and Whiteside Ltd.

Lenoir, J., et al. (2009). "Differences between tree species seedling and adult altitudinal distribution in mountain forests during the recent warm period (1986-2006)." Ecography **32**(5): 765-777.

Little, E. L. (1971). Atlas of United States trees, volume 1, conifers and important hardwoods, U.S. Department of Agriculture Miscellaneous Publication 1146**:** 9 p. .

Soper, J. H. and M. L. Heimburger (1990). Shrubs of Ontario. Toronto, Ontario, Royal Ontario Museum.

Woodall, C. W., et al. (2009). "An indicator of tree migration in forests of the eastern United States." Forest Ecology and Management **257**(5): 1434-1444.

Zhu, K., et al. (2012). "Failure to migrate: lack of tree range expansion in response to climate change." Global Change Biology **18**(3): 1042-1052.

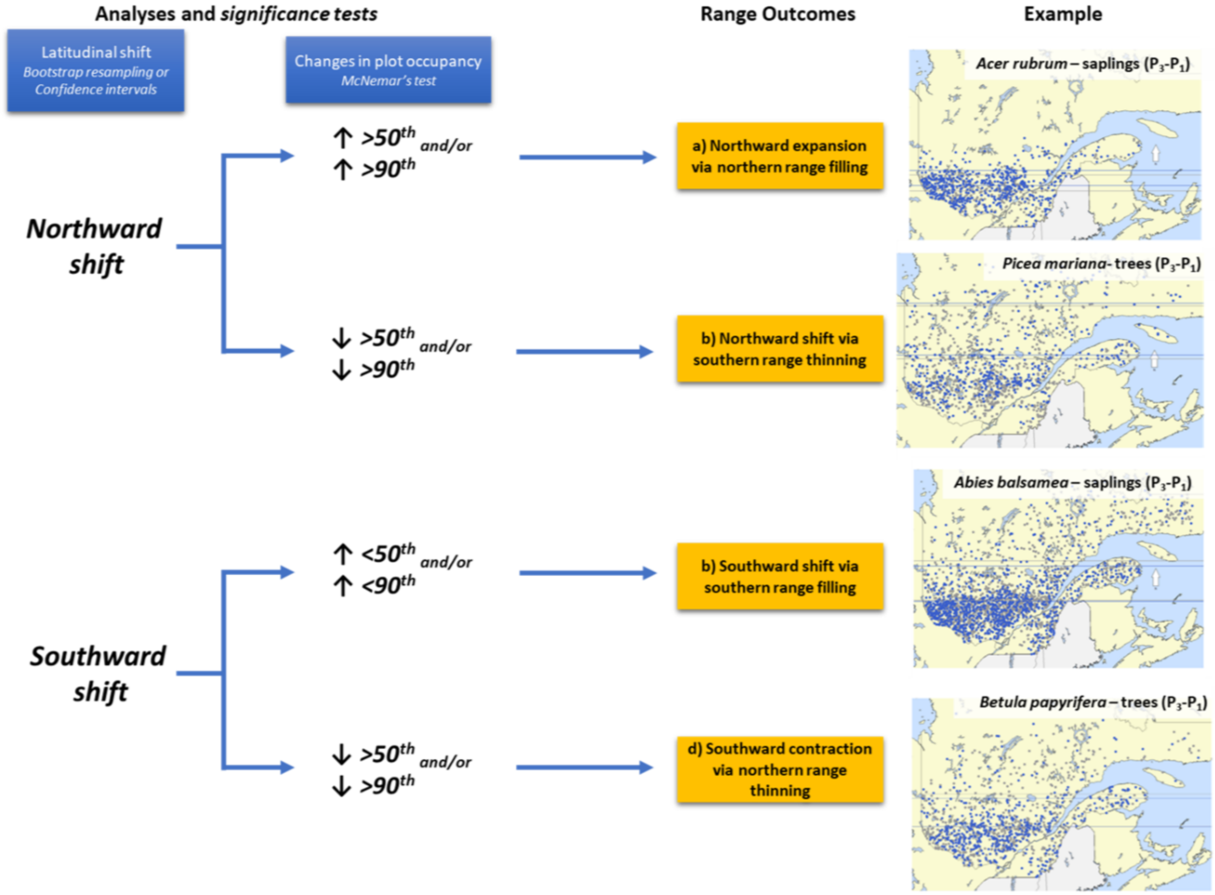


Figure 8.1.1 Workflow for assessing range shifts (analyses, significance tests, possible outcomes) and species examples. Tests used were latitudinal range shifts (lower limits=50th; upper limits=90th; Grey: 1970-1977 (P_1). Blue: 2003-2015 (P_3), change in plot occupancy (occupancy in P_1; occupancy in P_3). Example of a) significant northward expansion (saplings of *Acer rubrum*), b) significant southward shift from southern filling (=increased plot occupancy in southern areas; saplings of *Abies balsamea*), c) significant northward shift by southern thinning (=decreased plot occupancy in southern areas; trees of *Picea mariana*) and d) significant southward contraction by northern thinning (=decreased plot occupancy in northern areas; trees of *Betula papyrifera*). Points show plots occupied in a given time period (P_1 or P_3).

8.1.3 – Results

Table 8.1.1: Latitudinal range shifts (in km) at the median (50th percentile of latitude within study area) for each life stage (sapling and trees) between P_3-P_1 (1970-1977 vs. 2003-2015). Significance at the 50th percentile is assessed to ($p<0.05$) using Bootstrap resampling (n=500 000).

	Saplings					**Trees**				
	P_2-P_1	P_3-P_1	error	t value	p	P_2-P_1	P_3-P_1	error	t value	p
Abies balsamea	-5.7387	-5.7387	3.0335	-1.8919	*0.0585*	5.1597	5.4622	2.9597	1.0496	0.2939
Acer rubrum	18.4637	27.0485	5.0958	5.3077	**<0.001**	-1.8447	3.6275	3.4019	1.0665	0.2862
Acer saccharum	9.0787	18.1851	4.1875	4.3432	**<0.001**	2.1202	2.9287	3.5127	0.8337	0.4045
Betula alleghaniensis	0	1.5640	5.7786	0.2707	0.7867	2.1332	1.4624	2.8069	0.5208	0.6025
Betula papyrifera	1.4796	6.9142	5.9902	1.1542	0.2484	-2.2589	-2.3937	2.6243	-0.9118	0.3619
Fagus grandifolia	1.9958	2.3010	4.9221	0.4675	0.6401	-1.5831	-1.4913	3.6574	-0.4076	0.6836
Ostrya virginiana	-0.0877	7.5092	8.8201	0.8514	0.3946	-0.1447	-0.0978	6.1060	-0.0160	0.9872
Picea glauca	-20.1132	-13.1479	8.0455	-1.6343	0.1022	7.2020	9.1305	3.2881	2.7767	**0.0055**
Picea mariana	-45.4756	-37.0307	17.4516	-2.1219	**0.0338**	12.3218	18.5506	8.0136	2.3148	**0.0206**
Populus tremuloides	-29.5704	-11.1322	16.2617	-0.6846	0.4936	0.4692	5.7896	5.5490	1.0434	0.2968
Thuja occidentalis	8.2773	9.7414	9.2873	1.0489	0.2942	2.9567	3.1064	4.3522	1.7877	*0.0738*

Table 8.1.2: Latitudinal range shifts (in km) at the northernmost limit (90th percentile of latitude within study area) for each life stage between P_3-P_1 (1970-1977 vs. 2003-2015). Significance is assessed using pooled standard deviation across all longitudinal bands, weighted by the number of observations in each band. Significant shifts are those where the confidence interval does not intersect 0 ($p<0.05$). The shift between P_1 and P_2 is also given as an indication (Boisvert-Marsh et al. 2014).

	Saplings					**Trees**				
	P_2-P_1	P_3-P_1	Pooled std. dev	Lower C.I.	Upper C.I.	P_2-P_1	P_3-P_1	Pooled std. dev	Lower C.I.	Upper C.I.
Abies balsamea	-19.6159	-24.6320	147.4900	-57.7909	8.5276	10.5151	6.6540	148.0566	-26.6326	39.9405
Acer rubrum	18.8656	23.8839	45.2292	12.5334	35.2345	3.8820	12.8169	43.0232	2.1074	23.5257
Acer saccharum	9.5227	17.0518	33.0642	8.7542	25.3493	4.8902	6.6939	34.2892	-1.8409	15.2294
Betula alleghaniensis	8.1319	4.1814	38.2988	-6.1290	14.4929	4.9271	7.2200	40.1023	-2.7624	17.2018
Betula papyrifera	35.0682	70.9812	67.8175	55.5299	86.4333	-17.5983	-25.2385	100.3570	-47.8012	-2.6760
Fagus grandifolia	12.8205	13.1901	30.2624	4.0367	22.3417	-3.4867	-3.1334	26.3731	-11.0164	4.7490
Ostrya virginiana	8.2906	14.3601	15.7743	8.9778	19.7424	-2.5364	-1.6400	21.6687	-8.5290	5.2499
Picea glauca	-10.0932	5.9740	94.5414	-15.7137	27.6612	8.2931	9.8313	94.5687	-11.5714	31.2336
Picea mariana	-9.7680	-5.0927	77.7506	-22.5723	12.3877	8.8411	12.6702	88.4545	-7.2167	32.5566
Populus tremuloides	23.8761	19.3984	68.2819	2.1222	36.6769	-6.3386	-4.7405	69.5277	-21.1455	11.6649
Thuja occidentalis	6.8332	7.0196	57.1055	-7.805	21.8446	0.8604	5.5939	52.7421	-7.7517	18.9390

Table 8.1.3: Number of plots occupied by saplings of a given species and difference in each time period (P_1 = 1970-1977; P_3 = 2003-2015) in different parts of the study area (Entire study area: All, <50th, >50th and >90th), as set by their calculated limits in P_1. McNemar's test for paired samples was used to test if frequency of presence/absence was statistically different ($p< 0.05$).

	Entire study area				**<50th**			
	P_1	P_3	Ratio	p value	P_1	P_3	Ratio	p value
Abies balsamea	2248	2720	0.210	**<0.0001**	1124	1443	0.284	**<0.0001**
Acer rubrum	425	860	1.024	**<0.0001**	213	307	0.441	**<0.0001**
Acer saccharum	592	658	0.111	**0.0075**	296	256	-0.135	**0.0185**
Betula alleghaniensis	147	306	1.082	**<0.0001**	74	149	1.014	**<0.0001**
Betula papyrifera	704	944	0.341	**<0.0001**	352	446	0.267	**0.00013**
Fagus grandifolia	117	319	1.726	**<0.0001**	59	150	1.542	**<0.0001**
Ostrya virginiana	54	111	1.056	**<0.0001**	27	48	0.778	**0.0043**
Picea glauca	236	255	0.081	0.383	118	142	0.203	0.131
Picea mariana	1581	1827	0.156	**<0.0001**	791	989	0.250	**<0.0001**
Populus tremuloides	169	263	0.556	**<0.0001**	85	139	0.635	**0.0002**
Thuja occidentalis	130	154	0.185	*0.0742*	65	60	-0.077	0.661

	>50th				**>90th**			
	P_1	P_3	Ratio	p value	P_1	P_3	Ratio	p value
Abies balsamea	1124	1277	0.136	**<0.0001**	389	390	0.002	1
Acer rubrum	213	554	1.601	**<0.0001**	61	170	1.787	**<0.0001**
Acer saccharum	296	402	0.358	**<0.0001**	77	129	0.675	**<0.0001**
Betula alleghaniensis	74	157	1.122	**<0.0001**	22	44	1	**0.0043**
Betula papyrifera	352	498	0.415	**<0.0001**	96	201	1.094	**<0.0001**
Fagus grandifolia	59	169	1.864	**<0.0001**	23	79	2.435	**<0.0001**
Ostrya virginiana	27	63	1.333	**<0.0001**	12	30	1.5	**0.0046**
Picea glauca	118	113	-0.042	0.773	64	58	-0.094	0.621
Picea mariana	791	839	0.061	**0.0148**	311	309	-0.006	0.931
Populus tremuloides	85	125	0.471	**0.0049**	39	49	0.256	0.308
Thuja occidentalis	65	94	0.446	**0.0021**	25	30	0.2	0.424

Table 8.1.4: Number of plots occupied by trees of a given species and difference in each time period (P_1 = 1970-1977; P_3 = 2003-2015) in different parts of the study area (Entire study area: All, <50th, >50th and >90th), as set by their calculated limits in P_1. McNemar's test for paired samples was used to test if frequency of presence/absence was statistically different ($p< 0.05$).

	Entire study area				**<50th**			
	P_1	P_3	Ratio	p value	P_1	P_3	Ratio	p value
Abies balsamea	4018	3841	-0.044	**<0.0001**	2985	2809	-0.059	**<0.0001**
Acer rubrum	1440	1671	0.160	**<0.0001**	720	809	0.124	**<0.0001**
Acer saccharum	1243	1237	-0.005	0.769	622	597	-0.040	**0.037**
Betula alleghaniensis	1492	1500	0.005	0.764	746	735	-0.015	0.59
Betula papyrifera	2872	2724	-0.052	**<0.0001**	1436	1397	-0.027	0.154
Fagus grandifolia	422	467	0.107	**0.0015**	211	238	0.128	**0.012**
Ostrya virginiana	182	174	-0.044	0.526	92	89	-0.033	0.795
Picea glauca	1877	1827	-0.027	0.17	938	825	-0.120	**<0.0001**
Picea mariana	3064	2664	-0.131	**<0.0001**	1533	1225	-0.201	**<0.0001**
Populus tremuloides	1096	1019	-0.070	**0.0063**	548	483	-0.119	0.0018
Thuja occidentalis	646	606	-0.062	**0.0014**	535	492	-0.080	0.0034

	>50th				**>90th**			
	P_1	P_3	Ratio	p value	P_1	P_3	Ratio	p value
Abies balsamea	1033	1032	-0.001	1	650	631	-0.029	0.174
Acer rubrum	720	862	0.197	**<0.0001**	189	248	0.312	**<0.0001**
Acer saccharum	621	640	0.031	0.151	165	188	0.139	**0.0056**
Betula alleghaniensis	746	765	0.025	0.202	183	203	0.109	**0.029**
Betula papyrifera	1436	1327	-0.076	**<0.0001**	330	246	-0.255	**<0.0001**
Fagus grandifolia	211	229	0.085	*0.064*	79	76	-0.038	0.689
Ostrya virginiana	90	85	-0.056	0.614	28	27	-0.036	1
Picea glauca	939	1002	0.067	**0.0146**	367	403	0.098	**0.029**
Picea mariana	1531	1439	-0.060	**<0.0001**	532	526	-0.011	0.627
Populus tremuloides	548	536	-0.022	0.558	127	121	-0.047	0.634
Thuja occidentalis	111	114	0.027	0.775	111	114	0.027	0.775

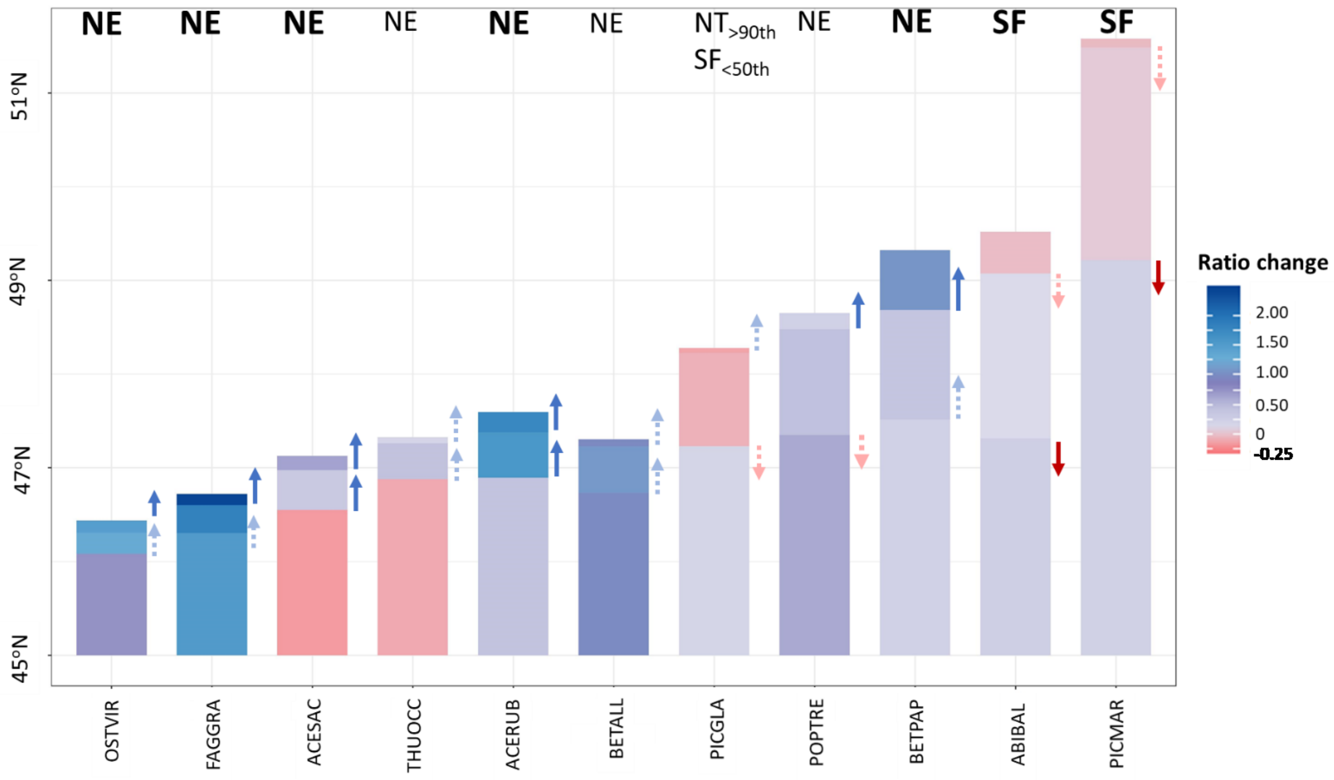


Figure 8.1.2 Summary of evidence for sapling range shifts between first period and third period (1970-1977 vs. 2003-2015; P_3-P_1). Overall response was assessed by combining a) latitudinal range shifts (LRS; as indicated by arrows; upward blue – northward, downward red – southward, significance to 0.05 indicated by solid arrow), b) occupancy changes in specific parts of the range; gradient colour (legend on right) indicates increase in the ratio of plots occupied relative to P_1. Ratios indicative of an increase in the overall number of plots occupied are in purple/blue tones whereas ratios indicative of a decrease in the overall number of plots are in red tones. Combined range shift pattern for a given species based on latitudinal shift patterns and occupancy dynamics is indicated at the top (NE – northward range expansion, NT – northward shift by southern range thinning, SF – southward shift by southern range filling, ST – southward shift by northern range thinning). Bold font indicates that both tests for latitudinal shift patterns and occupancy dynamics are significant. Species are ordered from left to right according to their 90th percentile latitudinal limit.

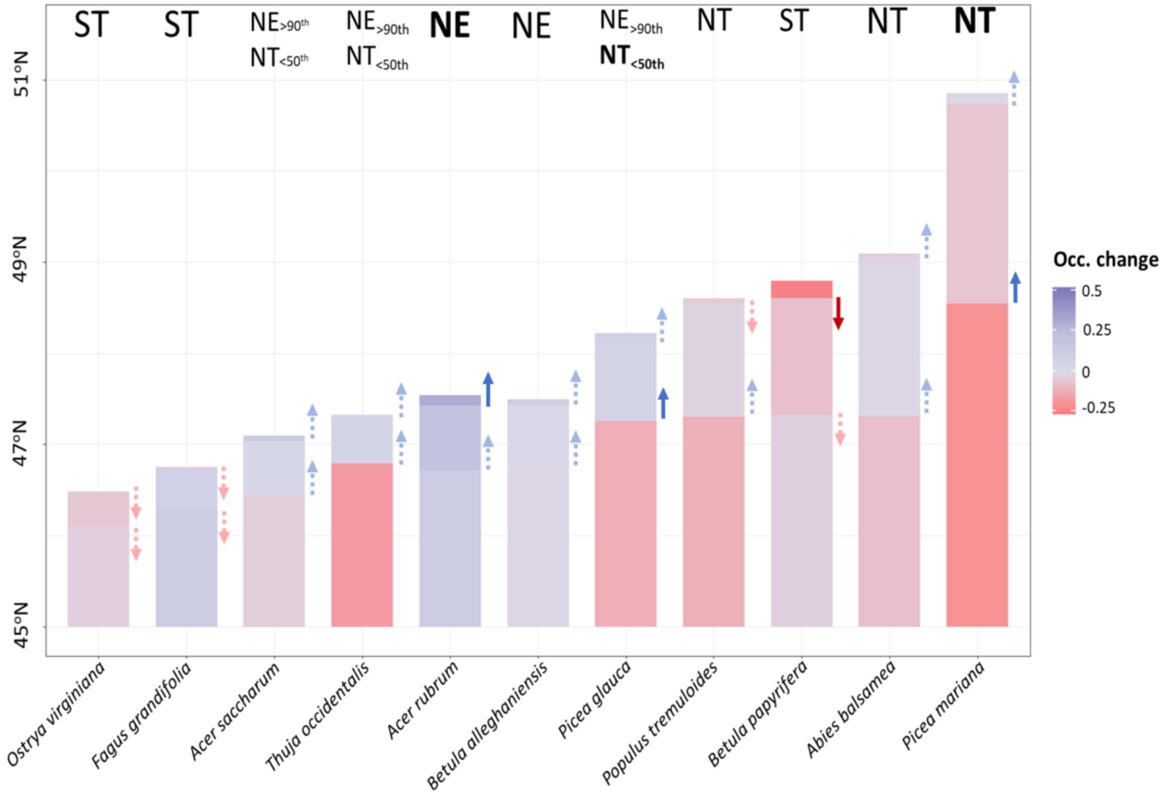


Figure 8.1.3 Summary of evidence for tree range shifts in trees between first period and third period (1970-1977 vs. 2003-2015; P_3-P_1). Overall response was assessed by combining a) latitudinal range shifts (LRS; as indicated by arrows; upward blue – northward, downward red – southward, significance to 0.05 indicated by solid arrow), b) occupancy changes in specific parts of the range; gradient colour (legend on right) indicates increase in the ratio of plots occupied relative to P_1. Ratios indicative of an increase in the overall number of plots occupied are in purple/blue tones whereas ratios indicative of a decrease in the overall number of plots are in red tones. Combined range shift pattern for a given species based on latitudinal shift patterns and occupancy dynamics is indicated at the top (NE – northward range expansion, NT – northward shift by southern range thinning, SF – southward shift by southern range filling, ST – southward shift by northern range thinning). Bold font indicates that both tests for latitudinal shift patterns and occupancy dynamics are significant. Species are ordered from left to right according to their 90th percentile latitudinal limit.

8.2 – Appendices to Chapter 3

8.2.1 - Appendix 1: Additional methods and results for Assessing range shifts

Table 8.2.1.1: Summary table of species occurrences for each time period, P1 and P3 per latitudinal zones. ‘Plots occupied’ refer to the total number of plots showing the presence of a species in any size class (i.e. all stems >=1.1cm DBH). ‘Plots with recruitment’ refer to the total number of plots showing saplings of the species. ‘Occupancy gains’ refer to the number of plots with saplings of the species in P_3 but where the species was not recorded in P_1 (no stems >1.1cm DBH).

		P_1			**P_3**				
		Plots occupied	**Plots with recruitment**		**Plots occupied**	**Plots with recruitment**		**Occupancy gains**	
Species	**Lat. zone**	**N**	**N**	**%**	**N**	**N**	**%**	**N**	**%**
Ostrya virginiana	Entire	212	54	0.2547	259	111	0.4286	34	0.3063
	<50th	92	27	0.2935	106	48	0.4528	10	0.2083
	>50th	119	27	0.2269	152	63	0.4145	24	0.381
	>90th	64	12	0.1875	79	30	0.3797	13	0.4333
Fagus grandifolia	Entire	442	117	0.2647	556	319	0.5737	65	0.2038
	<50th	219	59	0.2694	281	150	0.5338	34	0.2267
	>50th	223	59	0.2646	275	169	0.6145	31	0.1834
	>90th	109	23	0.2110	123	79	0.6423	16	0.2025
Acer saccharum	Entire	1297	592	0.4564	1337	658	0.4921	91	0.1383
	<50th	631	296	0.4691	616	255	0.414	29	0.1137
	>50th	666	296	0.4444	721	403	0.5589	62	0.1538
	>90th	209	77	0.3684	244	129	0.5287	30	0.2326
Betula alleghaniensis	Entire	1536	147	0.0957	1588	306	0.1927	58	0.1895
	<50th	724	74	0.1022	743	149	0.25	40	0.2685
	>50th	812	74	0.0911	845	157	0.1858	18	0.1146
	>90th	314	22	0.0701	337	44	0.1306	7	0.1591
Thuja occidentalis	Entire	661	130	0.1967	635	154	0.2425	25	0.1623
	<50th	364	65	0.1786	317	60	0.1893	9	0.15
	>50th	297	65	0.2189	318	94	0.2956	16	0.1702
	>90th	115	25	0.2174	122	30	0.2459	7	0.2333
Acer rubrum	Entire	1559	425	0.2726	1996	860	0.4309	301	0.35
	<50th	749	213	0.2844	887	307	0.3461	101	0.329
	>50th	810	213	0.2630	1109	553	0.4986	200	0.3617
	>90th	230	61	0.2652	339	170	0.5015	75	0.4412
Populus tremuloides	Entire	1162	169	0.1454	1203	263	0.2186	78	0.2966
	<50th	656	85	0.1296	668	138	0.2066	36	0.2609
	>50th	505	85	0.1683	534	125	0.2341	42	0.336
	>90th	212	39	0.1840	226	49	0.2168	23	0.4694

Betula papyrifera	Entire	3085	704	0.2282	3144	944	0.33	214	0.2267
	<50th	1727	352	0.2038	1779	446	0.2507	94	0.2108
	>50th	1358	352	0.2592	1365	498	0.3648	120	0.241
	>90th	464	96	0.2069	455	201	0.4418	68	0.3383

8.2.2 - Appendix 2: Additional details on methodology and results for species distribution modelling and characterizing migration sites

8.2.2.1 - Species distribution models

We ran species distribution models for all target species (*Acer rubrum, Acer saccharum, Betula alleghaniensis, Betula papyrifera, Fagus grandifolia, Ostrya virginiana, Populus tremuloides and Thuja occidentalis*) and 3 additional co-occurring species (*Abies balsamea, Picea glauca*, and *Picea mariana*) considered in our analysis. Outputs from the SDMs were needed to calculate an expected C-score index constrained to sites suitable for pairs of species (see below) and helped us characterize conditions at sites with occupancy gains (migration sites). We used a consensus modelling approach (Guisan and Zimmermann 2000) similar to the one used in previous studies in this area (Chambers et al. 2013, Beauregard and de Blois 2014, Périé and de Blois 2016). Species presence/absence (as recorded as a presence for any stem >1.1cm DBH) in P_1 (1970-1977), our reference period, was associated with growing degree days (base 5°C, 1965-1980), average annual total precipitation (1965-1980), average minimum January temperature (1965-1980), humus type, surface deposit, drainage, and soil texture of B horizon. Collection of soil and topographic data in permanent plots started in P_2 (as early as 1992). For the purpose of this study, soil factors were considered constant through time and were mainly taken from P_3 or, if necessary, from P_2. The climate data was obtained from Environment Canada weather station data interpolated to a 1km resolution using BioSIM (Regnière and Saint-Amant 2014). Edaphic and topographic variables were obtained directly from the field inventories from the *Ministère des Forêts, de la Faune et des Parcs* of Québec (MFFP) (Ministère des Forêts 2015). Topographic variables were not shown to add additional insight to the models and were not retained in the SDM modelling step (not shown).

***Climate data* -** Climate data used in this study covers the period from 1965 to 1980. This includes a 5-year period prior to the first forest inventory in 1970 and ends 3 years after completion of this inventory period. These climate data were modeled from Environment Canada weather station data using the BioSIM program (Regnière & Saint-Amant, 2014), which interpolates temperature and precipitation around a sampling plot at a 1km resolution using a weighted average of the four closest weather stations, correcting for differences in elevation.

Variable selection - In the modelling step, a clustering algorithm (Harrell et al. 1984) was used to select the most parsimonious climate variables from a set of 12 climatic variables, as per (Beauregard and de Blois 2014): Average annual temperature (°C), Annual temperature range (coldest month, warmest month), (C°) Growing degree days (5°C base temperature), Growing degree days accumulated within the frost free period, Julian date of the last spring freeze, Julian date of the first fall freeze, Length of frost free period (days), Julian date when the sum of growing degree days reaches 100, Total annual precipitation (mm), Total precipitation from April to September (mm), Total precipitation of the wettest month (mm), Total precipitation of the driest month (mm). The varclus algorithm in the Hmisc package (version 3.16-0; Harrell, 2013) uses the Spearman correlation coefficient to perform a hierarchical clustering analysis. Variables were selected based on high R^2 within a cluster and low R^2 between clusters. Three climatic variables were retained for the species distribution model step: 1) Growing degree days (base 5ºC), 2) January minimum temperature and 3) total annual precipitation. Climate observations attributed to the forest plots reveal a study area characterized by strong latitudinal climatic gradients. When all plots are considered over the whole time period, annual growing degree days ranged from 2134 GDD in the south to 671 GDD in the north and minimum January temperatures varied from -14.21ºC to -32.21ºC. Overall annual precipitation ranged from 688mm to 1485mm. Precipitation gradients exist, decreasing from south to north and from east to west. Selected climatic variables were further checked for multicollinearity. Minimum temperature was moderately correlated with growing degree days (0.75) but was retained for its biological importance and East-West spatial structuring.

Modelling approach - Modelling was done using the biomod2 package (Thuiller et al. 2016), with Generalized Linear Models (GLM), Generalized additive models (GAM), Classification tree analysis (CTA), Random Forest (RF), Flexible discriminant analysis (FDA). For GLMs, polynomial terms were employed for all species, except in the case of *Abies balsamea* where simple terms fitted the model best. The retained GLM model was selected using a backward stepwise procedure based on the model at which subsequent (i.e., simpler) models did not further decrease AIC. For GAMs, k=3 splines were used as the smoothing function. For FDAs, the regression method used was multivariate adaptive regression splines with 1 dimension. For RFs and CTAs, 1000 and 50 decision trees were employed respectively. Because separate training data were not available, ten-fold cross validation was conducted on each model run to determine model accuracy using a 70/30 data split, for a total of 50 models across all model types and runs for each species. The Area under the Receiver Operator Curve (ROC) was used to evaluate the model quality of each run, with model runs achieving a ROC value greater than 0.7 retained to build an ensemble. The ensemble model used the mean probability of presence in a plot calculated across all retained model runs. The probabilities were then used to obtain cut offs of site suitability/non-suitability defined as the probability at which model sensitivity (i.e., ability to correctly identify presences) and specificity (i.e., ability to correctly identify absences) is maximized. To assess the importance of predictor variables in the ensemble model for a given species, the relative importance of each predictor variable was calculated by taking its score and dividing by the sum of all predictors (Bucklin et al. 2015). The top three most important variables are shown in Table 8.2.2.1.1

Table 8.2.2.1.1: a) Model performance from the species distribution models for eleven species and b) most important variables. Presence of a species was considered over all plots where the species was observed (stems > 1.1cm DBH) in the reference period P_1 (1970-1977). Variables included growing degree days (base 5°C: GDD), Annual precipitation, Minimum January temperature, humus type, surface deposit, drainage, and soil texture of B horizon. Species which were used only as companion species for the pairwise association analysis are highlighted in grey.

a)		**Model performance**				
	AUC	**Sensitivity**	**Specificity**	**Cut off**	**TSS**	**Kappa**
Ostrya virginiana	0.984	99.528	94.356	0.615	0.934	0.604
Fagus grandifolia	0.966	99.546	87.675	0.0745	0.871	0.578
Acer saccharum	0.957	95.679	82.698	0.1065	0.783	0.696
Betula alleghaniensis	0.903	93.155	74.817	0.1795	0.677	0.575
Thuja occidentalis	0.943	95.461	83.741	0.1265	0.789	0.556
Acer rubrum	0.901	88.118	76.000	0.2365	0.641	0.542
Populus tremuloides	0.932	87.177	85.617	0.2375	0.727	0.633
Picea glauca	0.897	86.616	76.485	0.3325	0.63	0.598
Betula papyrifera	0.848	86.349	66.677	0.4035	0.529	0.527
Abies balsamea	0.888	71.069	87.935	0.7295	0.586	0.565
Picea mariana	0.896	83.656	77.181	0.4585	0.607	0.607

b)	**Most important**		**2nd**		**3rd**	
	Variable	**Rel. import.**	**Variable**	**Rel. import.**	**Variable**	**Rel. import.**
Ostrya virginiana	GDD (base 5°C)	0.4403	Humus type	0.2113	January min. temperature	0.1193
Fagus grandifolia	GDD (base 5°C)	0.2890	Humus type	0.2094	January min. temperature	0.1917
Acer saccharum	Humus type	0.3408	GDD (base 5°C)	0.2765	January min. temperature	0.1512
Betula alleghaniensis	Humus type	0.3509	GDD (base 5°C)	0.1877	Surface deposit	0.1609
Thuja occidentalis	GDD (base 5°C)	0.3266	Humus type	0.2087	January min. temperature	0.1637
Acer rubrum	GDD (base 5°C)	0.4438	January min. temperature	0.1640	Surface deposit	0.1488
Populus tremuloides	GDD (base 5°C)	0.2975	Humus type	0.2142	Surface deposit	0.2001
Picea glauca	January min. temperature	0.2971	GDD (base 5°C)	0.2064	Surface deposit	0.1917
Betula papyrifera	GDD (base 5°C)	0.2871	Humus type	0.2356	January min. temperature	0.2281
Abies balsamea	January min. temperature	0.3851	Surface deposit	0.2043	Humus type	0.1657
Picea mariana	Humus type	0.2671	GDD (base 5°C)	0.2211	January min. temperature	0.1908

8.2.2.2 - Characterizing migration sites

Along with information on pairwise species associations for all species considered in the reference period (P_1 – C-score analysis) and in migration plots (adapted metric of co-occurrence analysis), we recorded additional data on abiotic conditions and disturbances. That information was compiled as the proportion of plots falling under a given category of variables for all occupied plots in P_1 as a reference as well as for migration plots to elucidate migration trends. Here, “occupied sites” refers to sites where a given species was detected in the reference period P_1 (any stem greater than 1.1cm diameter at breast height). “Migration sites” refers to sites where a given species was not detected in P_1 but where saplings were detected in P_3 (stems with DBH between 1.1 and 3.0cm). Within each category of a variable, the information was further subdivided between suitable and unsuitable plots as determined by species distribution models. We provide here how each category was defined as well as the results for that variable.

8.2.2.2.1 - Humus type and depth

In each plot, humus type was noted in the field during each inventory (MFFP et al. 2016). Humus comprises the LFH layer and occasionally the Ah layer if well defined (see description of mull). Humus type was grouped into 4 categories (as arranged from prevalence from south to north).

Table 8.2.2.2.1: Humus type considered

Type	**Description**
Mull	Intense mixing of OM (organic matter) and mineral soil. Usually under deciduous cover. Decomposition usually by soil fauna
Moder	Intermediate between mull and mor
Mor	Accumulating OM. Usually under conifers, abrupt transition between organic and mineral layers and low Ph. Decomposition mainly by fungus
Organic	Includes all categories where the humus layer is mainly defined by organic material. Includes Peaty mor, Peat, Organic soils and Anmoor. Found in poorly drained sites

For each target species, the number of migration sites where a given humus type was present relative to the total number of migration sites was calculated (expressed as %). In addition, within each category, the proportion of these migration sites classified as either suitable or unsuitable was also calculated (between 0 and 1). As a reference, we also provide the percentage of occupied sites in the reference period P1 in each category. Depth of the humus layer was also measured as the height between the top of the LFH to the mineral layer or bedrock (including Ah if horizon clearly defined). For each target species, the mean depth was also calculated in occupied sites, at all migration sites and for migration sites classified as suitable or non-suitable.

Table 8.2.2.2.2: Proportions of occupied sites and migration sites by humus type

>50th	Mull				Moder				Mor				Organic			
	Occupied P_1	Migration sites			Occupied P_1	Migration sites			Occupied P_1	Migration sites			Occupied P_1	Migration sites		
spp	%	%	Non suitable	Suit	%	%	Non suitable	Suit	%	%	Non suitable	Suit	%	%	Non suitable	Suit
Ostrya virginiana	5.00	8.33	0.00	1.00	82.50	54.17	0.62	0.38	12.50	37.50	1.00	0.00	0	0	--	--
Fagus grandifolia	4.04	3.23	0.00	1.00	73.54	64.52	0.15	0.85	22.42	32.26	1.00	0.00	0	0	--	--
Acer saccharum	3.60	3.23	0.00	1.00	71.02	54.84	0.03	0.97	24.32	40.32	0.68	0.32	1.05	1.61	1	0
Betula alleghaniensis	1.60	0.00	0.00	0.00	52.03	55.56	0.00	1.00	43.40	44.44	0.50	0.50	2.97	0	--	--
Thuja occidentalis	0.67	0.00	0.00	0.00	25.59	31.25	0.80	0.20	61.95	50.00	0.75	0.25	11.78	18.75	0	1
Acer rubrum	0.87	1.00	0.50	0.50	36.34	28.50	0.51	0.49	60.82	67.00	0.57	0.43	1.97	3.5	1	0
Populus tremuloides	2.37	2.38	1.00	0.00	13.44	11.90	0.80	0.20	82.02	80.95	0.76	0.24	2.17	4.76	1	0
Betula papyrifera	0.96	0.83	1.00	0.00	12.08	10.83	0.31	0.69	79.68	69.17	0.33	0.67	7.28	19.17	0.83	0.17

>90th	%	%	Non suitable	Suit	%	%	Non-suit	Suit	%	%	Non suitable	Suit	%	%	Non suitable	Suit
Ostrya virginiana	0.00	7.69	0	1	84.62	53.85	0.86	0.14	15.38	38.46	1	0	0	0	--	--
Fagus grandifolia	8.26	6.25	0	1	70.64	50.00	0.25	0.75	21.10	43.75	1	0	0	0	--	--
Acer saccharum	5.74	3.33	0	1	64.11	60.00	0.06	0.94	29.67	36.67	1	0	0.48	0	--	--
Betula alleghaniensis	2.55	0.00	0	0	38.85	42.86	0	1	55.73	57.14	0.50	0.50	2.88	0	--	--
Thuja occidentalis	1.74	0.00	--	--	17.39	42.86	1	0	63.48	57.14	1.00	0.00	17.39	0	--	--
Acer rubrum	2.17	1.33	1	0	24.78	18.67	0.86	0.14	71.74	78.67	0.73	0.27	1.3	1.33	1	0
Populus tremuloides	1.41	4.35	1	0	8.45	8.70	0.50	0.50	87.32	78.26	0.72	0.28	2.82	8.7	1	0
Betula papyrifera	0.22	0.00	--	--	2.80	5.88	0.75	0.25	87.93	77.94	0.49	0.51	9.05	16.17	0.91	0.09

Table 8.2.2.2.3: Mean depth of the humus layer at migration sites and in occupied sites in P_1.

	Occupied P_1		Migration sites					
>50th			Overall		Non-suitable		Suitable	
Species Name	Mean	St. dev	Mean	St. dev	Mean	St. dev	Mean	St. dev
Ostrya virginiana	6.59	2.65	6.17	2.3	5.76	2.46	7.14	1.57
Fagus grandifolia	7.32	3.79	7.32	3.43	6.54	2.6	7.89	3.89
Acer saccharum	6.89	4.02	7.74	8.98	11.05	15.63	6.28	2.27
Betula alleghaniensis	7.77	7.64	7.11	2.93	6.25	3.1	7.36	2.95
Thuja occidentalis	12.59	17.98	24.88	33.73	10.8	7.25	48.33	47.56
Acer rubrum	7.36	6.04	9.47	14.74	11.73	19.21	6.53	2.58
Populus tremuloides	8.46	6.67	8.52	5.58	8.42	5.83	8.89	4.83
Betula papyrifera	11.76	13.05	16.62	19.77	26	26.55	9.68	7.13

	Occupied P_1		Migration sites					
>90th			Overall		Non-suitable		Suitable	
Species Name	Mean	St. dev	Mean	St. dev	Mean	St. dev	Mean	St. dev
Ostrya virginiana	6.2	2.39	5.69	2.02	5.55	2.16	6.5	0.71
Fagus grandifolia	7.6	3.72	5.88	2.09	6.11	2.26	5.57	1.99
Acer saccharum	6.49	2.81	6.57	2.58	7.83	2.41	5.72	2.4
Betula alleghaniensis	7.5	7.79	7	3.06	5	4.24	7.8	2.59
Thuja occidentalis	16.3	22.43	13	7.7	13	7.7	--	--
Acer rubrum	6.72	4.68	8.2	10.94	8.84	12.42	6.17	2.71
Populus tremuloides	10.01	9.29	8.57	5.85	8.24	6.28	9.5	4.81
Betula papyrifera	14.57	13.5	16.4	11.81	19.26	12.91	12.55	9

8.2.2.2.2 - Soil texture

Samples of soil texture of the B horizon was also obtained from field inventories. Where available, soil texture based on laboratory analysis was used. Otherwise, soil texture obtained from field assessment was used. Six categories were defined based on the dominant texture class from the sample taken.

Table 8.2.2.2.4: Soil texture classes of the B horizon

Category	**Description**
Sandy loam	Includes modifiers
Loam	Includes modifiers
Silt loam	Includes modifiers
Clay	All categories with greater than 50% clay
Sand	Includes fine to coarse sand
Absent soil horizon	Soil horizon not present

For each target species, the number of migration sites where a given soil texture type was present relative to the total number of migration sites was calculated (expressed as %). In addition, within each category, the proportion of these migration sites classified as either suitable or unsuitable was also calculated (between 0 and 1). As a reference, we also provide the percentage of occupied sites in the reference period P_1 in each category.

Table 8.2.2.2.5: Proportions of occupied sites in P1 and migration sites by soil texture class of the B horizon

>50th	Sandy loam				Loam				Silt loam			
	Occupied P_1	Migration sites			Occupied P_1	Migration sites			Occupied P_1	Migration sites		
Species Name	%	%	Non suitable	Suitable	%	%	Non suitable	Suitable	%	%	Non suitable	Suitable
Ostrya virginiana	66.67	62.50	0.67	0.33	10.83	12.50	0.67	0.33	2.50	0.00	--	--
Fagus grandifolia	65.47	41.94	0.38	0.62	9.42	16.13	0.20	0.80	6.73	6.45	1.00	0.00
Acer saccharum	60.81	54.84	0.18	0.82	11.86	14.52	0.56	0.44	6.91	9.68	0.33	0.67
Betula alleghaniensis	58.20	44.44	0.25	0.75	11.22	27.78	0.20	0.80	5.55	0.00	--	--
Thuja occidentalis	45.45	25.00	0.50	0.50	9.09	12.50	1.00	0.00	8.75	6.25	1.00	0.00
Acer rubrum	58.59	55.00	0.59	0.41	9.77	9.00	0.56	0.44	8.65	11.00	0.18	0.82
Populus tremuloides	47.83	50.00	0.90	0.10	7.11	9.52	1.00	0.00	4.94	11.90	0.60	0.40
Betula papyrifera	53.39	46.67	0.34	0.66	7.07	9.17	0.09	0.91	4.34	1.67	0.00	1.00

	Clay				Sand				Absent soil profile			
	Occupied P_1	Migration sites			Occupied P_1	Migration sites			Occupied P_1	Migration sites		
Species Name	%	%	Non suitable	Suitable	%	%	Non suitable	Suitable	%	%	Non suitable	Suitable
Ostrya virginiana	0.00	0.00	--	--	16.67	16.67	0.75	0.25	3.33	8.33	1.00	0.00
Fagus grandifolia	0.90	0.00	--	--	13.90	32.26	0.40	0.60	3.59	3.23	1.00	0.00
Acer saccharum	3.45	1.61	0.00	1.00	12.91	19.35	0.50	0.50	4.05	0.00	--	--
Betula alleghaniensis	3.33	11.11	0.50	0.50	17.88	11.11	0.00	1.00	3.45	5.56	0.00	1.00
Thuja occidentalis	5.72	0.00	--	--	20.20	25.00	0.75	0.25	6.06	12.50	1.00	0.00
Acer rubrum	2.84	1.00	1.00	0.00	15.57	15.50	0.77	0.23	4.08	7.50	0.40	0.60
Populus tremuloides	12.06	7.14	0.33	0.67	23.32	19.05	0.63	0.38	4.55	2.38	1.00	0.00
Betula papyrifera	7.14	9.17	0.36	0.64	21.06	16.67	0.60	0.40	5.60	14.17	0.71	0.29

>90th	Sandy loam				Loam				Silt loam			
	Occupied P_1	Migration sites			Occupied P_1	Migration sites			Occupied P_1	Migration sites		
Factor	%	%	Non suitable	Suitable	%	%	Non suitable	Suitable	%	%	Non suitable	Suitable
Ostrya virginiana	68.75	69.23	0.78	0.22	7.81	7.69	1	0	1.56	0.00	--	--
Fagus grandifolia	62.39	50.00	0.63	0.37	12.84	18.75	0	1	10.09	6.25	1	0
Acer saccharum	57.42	50.00	0.2	0.8	14.35	16.67	0.6	0.4	9.09	6.67	1	0
Betula alleghaniensis	55.91	42.86	0.33	0.67	11.50	14.29	0	1	3.83	0.00	--	--
Thuja occidentalis	38.94	28.57	1	0	12.39	28.57	1	0	4.42	14.29	1	0
Acer rubrum	56.77	60.00	0.76	0.24	12.66	1.33	1	0	7.42	8.00	0.17	0.83
Populus tremuloides	42.58	56.52	0.92	0.08	6.70	4.35	1	0	2.39	8.70	0.5	0.5
Betula papyrifera	54.23	50.00	0.53	0.47	7.16	2.94	0	1	3.25	0.00	--	--

	Clay				Sand				Absent soil profile			
	Occupied P_1	Migration sites			Occupied P_1	Migration sites			Occupied P_1	Migration sites		
	%	%	Non suitable	Suitable	%	%	Non suitable	Suitable	%	%	Non suitable	Suitable
Ostrya virginiana	0.00	0.00	--	--	17.19	7.69	1	0	4.69	15.38	1	0
Fagus grandifolia	0.92	0.00	--	--	12.84	18.75	0.67	0.33	0.92	6.25	1	0
Acer saccharum	9.09	3.33	0	1	8.61	23.33	0.57	0.43	1.44	0.00	--	--
Betula alleghaniensis	7.03	28.57	0.5	0.5	18.85	14.29	0	1	2.24	0.00	--	--
Thuja occidentalis	13.27	0.00	--	--	16.81	0.00	--	--	5.31	28.57	1	0
Acer rubrum	6.11	13.33	1	0	13.97	21.33	0.94	0.06	3.06	4.00	0.67	0.33
Populus tremuloides	20.10	13.04	0.33	0.67	21.53	13.04	0.33	0.67	6.70	4.35	1	0
Betula papyrifera	7.38	13.24	0.33	0.67	20.17	17.65	0.83	0.17	5.21	13.24	0.67	0.33

8.2.2.2.3 - Surficial deposits

Surficial deposits at each plot were observed and relevant geomorphological processes (erosion, accumulation, alteration or aggradation) noted (MFFP et al. 2016). Six categories were considered.

Table 8.2.2.2.6: Surficial deposit categories considered

Category	**Description**
Subsidence	Deposits of rocky material often resulting from subsidence (e.g., rock slides or landslides)
Glacial	Deposits left by retreating glaciers (~10000 ybp in eastern Canada). *Most common category in study area.*
Glacial with rocks	Deposits left by retreating glaciers with large areas of exposed bedrock
Fluvial	Deposits of fluvial origins. Includes fluvial deposits of glacial origin
Still water	Deposits left by still water sources. Includes marine, lacustrine and along coastlines
Organic	Deposits of organic origin and nature

For each target species, the number of migration sites where a given surface deposit was present relative to the total number of migration sites was calculated (expressed as %). In addition, within each category, the proportion of these migration sites classified as either suitable or unsuitable was also calculated (between 0 and 1). As a reference, we also provide the percentage of occupied sites in the reference period P1 in each category.

Table 8.2.2.2.7: Proportion of occupied sites in P_1 and migration sites by surficial deposit

>50th	Deposits from subsidence				Glacial deposits				Glacial deposits with rock			
	Occupied P_1	Migration sites			Occupied P_1	Migration sites			Occupied P_1	Migration sites		
spp	%	%	Non suitable	Suitable	%	%	Non suitable	Suitable	%	%	Non suitable	Suitable
Ostrya virginiana	3.33	0.00	--	--	81.67	79.17	0.68	0.32	12.50	12.50	0.67	0.33
Fagus grandifolia	0.90	0.00	--	--	90.13	83.87	0.38	0.62	7.62	9.68	0.33	0.67
Acer saccharum	2.85	0.00	--	--	90.69	90.32	0.29	0.71	3.90	4.84	0.33	0.67
Betula alleghaniensis	3.95	11.11	0.50	0.50	88.90	83.33	0.20	0.80	2.47	5.56	0.00	1.00
Thuja occidentalis	3.70	12.50	1.00	0.00	76.09	50.00	0.75	0.25	3.70	12.50	0.50	0.50
Acer rubrum	3.71	1.50	0.67	0.33	86.53	80.00	0.52	0.48	4.82	5.00	0.60	0.40
Populus tremuloides	3.75	7.14	1.00	0.00	66.80	71.43	0.87	0.13	4.94	7.14	1.00	0.00
Betula papyrifera	7.44	15.00	0.17	0.83	74.67	60.00	0.39	0.61	4.86	8.33	0.20	0.80

	Fluvial deposits				Deposits originated from still water				Organic deposits			
	Occupied P_1	Migration sites			Occupied P_1	Migration sites			Occupied P_1	Migration sites		
	%	%	Non suitable	Suit	%	%	Non suitable	Suit	%	%	Non suitable	Suit
Ostrya virginiana	0.00	8.33	1.00	0.00	2.50	0.00	--	--	0.00	0.00	--	--
Fagus grandifolia	0.00	0.00	--	--	1.35	6.45	1.00	0.00	0.00	0.00	--	--
Acer saccharum	1.05	1.61	1.00	0.00	1.35	1.61	0.00	1.00	0.00	1.61	1.00	0.00
Betula alleghaniensis	2.34	0.00	--	--	1.23	0.00	--	--	0.99	0.00	--	--
Thuja occidentalis	5.05	6.25	1.00	0.00	4.71	0.00	--	--	6.40	18.75	0.00	1.00
Acer rubrum	2.72	6.50	0.77	0.23	1.48	4.00	0.75	0.25	0.49	3.00	1.00	0.00
Populus tremuloides	9.09	9.52	0.25	0.75	13.64	4.76	0.00	1.00	0.59	0.00	--	--
Betula papyrifera	3.53	3.33	0.75	0.25	5.67	5.00	1.00	0.00	3.39	7.50	1.00	0.00

>90th	Deposits from subsidence				Glacial deposits				Glacial deposits with rock			
	Occupied P_1	Migration sites			Occupied P_1	Migration sites			Occupied P_1	Migration sites		
	%	%	Non suitable	Suitable	%	%	Non suitable	Suitable	%	%	Non suitable	Suitable
Ostrya virginiana	0.00	0.00	--	--	87.50	84.62	0.82	0.18	10.94	7.69	1.00	0.00
Fagus grandifolia	1.83	0.00	--	--	90.83	93.75	0.53	0.47	5.50	0.00	--	--
Acer saccharum	8.13	0.00	--	--	89.00	93.33	0.36	0.64	0.96	3.33	1.00	0.00
Betula alleghaniensis	10.22	28.57	0.50	0.50	84.35	57.14	0.25	0.75	1.92	14.29	0.00	1.00
Thuja occidentalis	9.73	28.57	1.00	0.00	67.26	57.14	1.00	0.00	4.42	14.29	1.00	0.00
Acer rubrum	11.35	4.00	0.67	0.33	82.10	78.67	0.71	0.29	2.62	4.00	1.00	0.00
Populus tremuloides	7.18	8.70	1.00	0.00	57.42	65.22	0.87	0.13	4.78	4.35	1.00	0.00
Betula papyrifera	8.68	10.29	0.00	1.00	73.10	70.59	0.58	0.42	7.38	5.88	0.50	0.50

	Fluvial deposits				Deposits originated from still water				Organic deposits			
	Occupied P_1	Migration sites			Occupied P_1	Migration sites			Occupied P_1	Migration sites		
	%	%	Non suitable	Suitable	%	%	Non suitable	Suitable	%	%	Non suitable	Suitable
Ostrya virginiana	0.00	7.69	1.00	0.00	1.56	0	--	--	0.00	0	--	--
Fagus grandifolia	0.00	0.00	--	--	1.83	6.25	1.00	0.00	0.00	0	--	--
Acer saccharum	0.48	3.33	1.00	0.00	1.44	0	--	--	0.00	0	--	--
Betula alleghaniensis	1.28	0.00	--	--	1.28	0	--	--	0.96	0	--	--
Thuja occidentalis	3.54	0.00	--	--	4.42	0	--	--	10.62	0	--	--
Acer rubrum	3.06	5.33	1.00	0.00	0.44	6.67	1.00	0.00	0.44	1.33	1.00	0.00
Populus tremuloides	7.66	13.04	0.33	0.67	21.53	8.7	0.00	1.00	1.44	0	--	--
Betula papyrifera	1.52	1.47	1.00	0.00	4.56	7.35	1.00	0.00	4.77	4.41	1.00	0.00

8.2.2.2.4 - Drainage

Drainage was classified based on evidence of standing water, soil texture, presence of mottling on soil profile and slope (MFFP et al. 2016). Four categories were considered.

Table 8.2.2.2.8: Drainage categories considered

Category
Fast to excessive
Good to moderate
Imperfect
Slow to very slow

For each target species, the number of migration sites where a given drainage class was present relative to the total number of migration sites was calculated (expressed as %). In addition, within each category, the proportion of these migration sites classified as either suitable or unsuitable was also calculated (between 0 and 1). As a reference, we also provide the percentage of occupied sites in the reference period P1 in each category.

Table 8.2.2.2.9: Proportions of occupied sites in P_1 and migration sites by drainage class.

	Fast to excessive				Good to moderate			
	Occupied P_1	Migration sites			Occupied P_1	Migration sites		
>50th	%	%	Non-suitable	Suitable	%	%	Non-suitable	Suitable
Ostrya virginiana	1.67	4.17	0.00	1.00	97.50	87.50	0.71	0.29
Fagus grandifolia	0.90	0.00	--	--	97.76	100.00	0.42	0.58
Acer saccharum	0.30	0.00	--	--	95.80	91.94	0.28	0.72
Betula alleghaniensis	1.11	0.00	--	--	89.77	100.00	0.22	0.78
Thuja occidentalis	2.36	0.00	--	--	75.42	75.00	0.75	0.25
Acer rubrum	1.24	1.50	0.67	0.33	90.11	87.00	0.54	0.46
Populus tremuloides	2.37	2.38	1.00	0.00	83.79	88.10	0.78	0.22
Betula papyrifera	2.21	2.50	0.33	0.67	82.77	74.17	0.33	0.67
	Imperfect				Slow to very slow			
Ostrya virginiana	0.83	8.33	1.00	0.00	0.00	0.00	--	--
Fagus grandifolia	1.35	0.00	--	--	0.00	0.00	--	--
Acer saccharum	3.60	6.45	0.50	0.50	0.30	1.61	1.00	0.00
Betula alleghaniensis	7.27	0.00	--	--	1.85	0.00	--	--
Thuja occidentalis	12.12	6.25	1.00	0.00	10.10	18.75	0.00	1.00
Acer rubrum	7.54	8.00	0.63	0.38	1.11	3.50	1.00	0.00
Populus tremuloides	12.85	7.14	0.67	0.33	0.99	2.38	1.00	0.00

Betula papyrifera	10.75	10.00	0.42	0.58	4.27	13.33	1.00	0.00
>90th	Fast to excessive				Good to moderate			
	Occupied P_1	Migration sites			Occupied P_1	Migration sites		
Factor	%	%	Non-suitable	Suitable	%	%	Non-suitable	Suitable
Ostrya virginiana	0.00	0.00	--	--	98.44	84.62	0.82	0.18
Fagus grandifolia	0.92	0.00	--	--	98.17	100.00	0.56	0.44
Acer saccharum	0.00	0.00	--	--	99.04	96.67	0.38	0.62
Betula alleghaniensis	0.96	0.00	--	--	91.05	100.00	0.29	0.71
Thuja occidentalis	4.42	0.00	--	--	69.91	85.71	1.00	0.00
Acer rubrum	1.31	4.00	0.67	0.33	94.76	86.67	0.77	0.23
Populus tremuloides	1.91	0.00	--	--	79.90	86.96	0.75	0.25
Betula papyrifera	2.60	4.41	0.33	0.67	82.21	70.59	0.52	0.48
	Imperfect				Slow to very slow			
Ostrya virginiana	1.56	15.38	1.00	0.00	0.00	0.00	--	--
Fagus grandifolia	0.92	0.00	--	--	0.00	0.00	--	--
Acer saccharum	0.96	3.33	1.00	0.00	0.00	0.00	--	--
Betula alleghaniensis	6.07	0.00	--	--	1.92	0.00	--	--
Thuja occidentalis	11.50	14.29	1.00	0.00	14.16	0.00	--	--
Acer rubrum	3.06	8.00	0.67	0.33	0.87	1.33	1.00	0.00
Populus tremuloides	15.79	8.70	0.50	0.50	2.39	4.35	1.00	0.00
Betula papyrifera	10.85	11.76	0.50	0.50	4.34	13.24	1.00	0.00

8.2.2.2.5 - Soil pH

Soil pH was taken as the pH of the B horizon based on samples originating from field inventories. For each target species, we calculated mean pH for all sites occupied in P1 and for all migration sites. We also calculated mean pH for migration sites categorised as suitable or unsuitable. It should be noted that soil pH was not available for all sites (missing from sites in the Gaspésie région, in the Bas St-Laurent region and in the Lanaudière region).

Table 8.2.2.2.10: Mean soil pH of the B horizon at occupied sites in P_1 and at migration sites

>50th	Occupied P_1		Migration sites					
			All		Non-suitable only		Suitable only	
Species	Mean	St. dev	Mean	St. dev	Mean	St.dev	Mean	St.dev
Ostrya virginiana	5.78	0.60	5.74	0.74	5.55	0.74	6.13	0.60
Fagus grandifolia	5.72	0.53	5.87	0.54	6.05	0.52	5.71	0.52
Acer saccharum	5.74	0.55	5.69	0.57	5.77	0.57	5.66	0.58
Betula alleghaniensis	5.77	0.60	5.63	0.78	5.77	0.67	5.59	0.85
Thuja occidentalis	5.84	0.67	5.55	0.73	5.48	0.81	5.67	0.72
Acer rubrum	5.80	0.60	5.90	0.61	5.95	0.60	5.82	0.62
Populus tremuloides	5.79	0.65	5.57	0.48	5.51	0.48	5.78	0.45
Betula papyrifera	5.71	0.62	5.67	0.55	5.73	0.53	5.63	0.56

>90th	Occupied P_1		Migration sites					
			All		Non-suitable		Suitable	
Species	Mean	St. dev	Mean	St. dev	Mean	St.dev	Mean	St.dev
Ostrya virginiana	5.68	0.58	5.92	0.70	5.79	0.72	6.45	0.21
Fagus grandifolia	5.73	0.57	5.81	0.55	6.10	0.49	5.34	0.22
Acer saccharum	5.80	0.57	5.71	0.59	5.73	0.61	5.69	0.60
Betula alleghaniensis	5.84	0.58	5.27	0.76	5.60	--	5.10	0.99
Thuja occidentalis	5.76	0.74	5.25	0.07	5.25	0.07	--	--
Acer rubrum	5.76	0.57	5.90	0.64	5.96	0.63	5.70	0.65
Populus tremuloides	5.76	0.65	5.58	0.39	5.55	0.37	5.67	0.47
Betula papyrifera	5.63	0.60	5.71	0.58	5.73	0.54	5.67	0.66

8.2.2.2.6 – Climate

Climate data used in this study covers 1965 to 1980 which encompasses the entire reference period P_1. Mean growing degree days, January minimum temperature and annual precipitation were calculated for migration sites as well as for migration sites classified as either suitable or unsuitable. Means for sites occupied by a target species in P_1 were also calculated as a reference. We also used climate data for the P_3 period (1998-2015) to calculate the difference with P_1 as an indication of changes in climate between the inventories (ΔP_3-P_1).

Table 8.2.2.2.11: Mean of annual growing degree days in P1 (1965-1980) in occupied sites in P1 and at migration sites. At migration sites, the difference in climate means between P1 and P3 was also calculated (ΔP_3-P_1)

	Occupied sites in P_1		Migration sites											
			All				Non-suitable only				Suitable only			
			P_1		ΔGDD P_3-P_1		P_1		ΔGDD P_3-P_1		P_1		ΔGDD P_3-P_1	
	Mean	St. dev	Mean	St. dev	Mean	St. dev	Mean	St. dev	Mean	St. dev	Mean	St. dev	Mean	St. dev
	>50th													
Ostrya virginiana	1554.66	94.721	1540.79	102.597	171.81	38.250	1512.45	101.837	179.27	25.740	1609.61	69.946	153.69	57.451
Fagus grandifolia	1463.26	95.074	1481.42	111.312	156.57	49.941	1429.15	130.661	137.09	49.627	1519.18	78.838	170.65	46.507
Acer saccharum	1418.71	108.346	1391.66	112.677	152.25	45.334	1347.31	75.228	141.69	49.055	1411.27	121.371	156.92	43.369
Betula alleghaniensis	1353.61	116.076	1367.46	122.104	149.59	37.405	1351.36	164.618	139.03	46.205	1372.06	114.633	152.60	35.956
Thuja occidentalis	1408.38	96.407	1408.26	109.897	114.95	65.443	1342.35	60.503	111.13	65.618	1518.10	80.472	121.32	70.853
Acer rubrum	1386.51	109.319	1372.69	102.682	149.00	45.752	1316.29	85.322	153.50	37.570	1445.95	72.852	143.17	54.262
Populus tremuloides	1265.30	122.370	1212.91	125.697	102.06	65.595	1186.38	126.187	104.15	63.740	1310.19	61.076	94.40	75.603
Betula papyrifera	1193.20	161.822	1136.62	186.416	118.64	54.286	1044.56	220.558	128.46	37.372	1204.67	118.282	111.39	63.282
	>90th													
Ostrya virginiana	1522.76	76.123	1505.33	110.806	190.48	23.249	1497.42	117.208	184.56	19.915	1548.82	74.084	223.05	3.752
Fagus grandifolia	1464.66	103.138	1441.31	75.952	140.10	59.654	1419.67	75.016	125.58	54.967	1469.14	72.888	158.77	64.382
Acer saccharum	1362.74	89.309	1346.09	74.422	145.80	54.212	1317.02	59.339	130.81	54.033	1365.47	78.587	155.79	53.478
Betula alleghaniensis	1307.03	93.398	1275.60	99.302	131.90	45.449	1229.44	129.332	122.72	72.147	1294.07	95.488	135.58	41.690
Thuja occidentalis	1359.72	94.141	1331.79	55.431	80.14	49.410	1331.79	55.431	80.14	49.410	--	--	--	--
Acer rubrum	1314.66	87.752	1325.06	88.367	138.55	53.945	1302.54	85.235	153.67	39.806	1396.39	54.502	90.65	65.202
Populus tremuloides	1202.18	132.775	1206.51	138.072	73.94	67.359	1168.86	136.617	73.33	63.090	1313.18	75.378	75.67	84.982
Betula papyrifera	1064.31	156.914	1041.66	166.922	103.42	54.505	966.92	174.476	124.66	34.868	1142.16	84.354	74.86	63.129

Table 8.2.2.2.12: Mean of minimum January temperature in P1 (1965-1980) in occupied sites in P1 and at migration sites. At migration sites, the difference in climate means between P1 and P3 was also calculated (ΔP_3-P_1)

	Occupied sites in P_1		Migration sites											
			All				Non-suitable only				Suitable only			
			P_1		ΔTmin P_3-P_1		P_1		ΔTmin P_3-P_1		P_1		ΔTmin P_3-P_1	
	Mean	St. dev	Mean	St. dev	Mean	St. dev	Mean	St. dev	Mean	St. dev	Mean	St. dev	Mean	St. dev
	>50th													
Ostrya virginiana	-19.80	1.164	-19.96	1.332	1.63	0.668	-20.27	1.371	1.78	0.512	-19.22	0.943	1.27	0.896
Fagus grandifolia	-20.54	1.282	-20.28	1.403	1.46	0.543	-20.73	1.652	1.32	0.499	-19.95	1.130	1.57	0.562
Acer saccharum	-20.83	1.423	-21.34	1.439	1.39	0.502	-22.06	1.127	1.30	0.573	-21.01	1.455	1.43	0.469
Betula alleghaniensis	-21.43	1.516	-20.96	1.637	1.56	0.559	-21.24	1.893	1.64	0.520	-20.88	1.627	1.53	0.586
Thuja occidentalis	-21.05	1.759	-19.90	1.937	1.51	0.812	-20.05	2.326	1.46	0.549	-19.63	1.179	1.60	1.191
Acer rubrum	-21.17	1.719	-21.81	1.295	1.51	0.687	-22.33	1.150	1.33	0.619	-21.12	1.146	1.73	0.708
Populus tremuloides	-22.62	2.241	-23.29	2.031	1.02	0.696	-23.23	2.202	1.00	0.730	-23.53	1.295	1.11	0.582
Betula papyrifera	-22.76	2.531	-22.85	2.854	1.10	0.661	-24.20	2.758	1.12	0.576	-21.86	2.507	1.09	0.722
	>90th													
Ostrya virginiana	-20.25	1.004	-20.55	1.331	1.93	0.444	-20.58	1.413	1.87	0.450	-20.37	1.099	2.25	0.292
Fagus grandifolia	-20.31	1.496	-20.78	1.430	1.28	0.461	-20.91	1.780	1.16	0.377	-20.61	0.906	1.42	0.546
Acer saccharum	-21.05	1.719	-21.71	1.616	1.30	0.500	-22.40	1.286	1.09	0.528	-21.24	1.678	1.44	0.441
Betula alleghaniensis	-21.57	1.846	-20.82	2.328	1.53	0.736	-20.99	3.121	1.35	0.403	-20.76	2.383	1.61	0.864
Thuja occidentalis	-20.65	2.425	-19.20	2.281	1.40	0.657	-19.20	2.281	1.40	0.657	NA	NA	NA	NA
Acer rubrum	-20.98	2.207	-22.12	1.681	1.31	0.742	-22.44	1.531	1.29	0.741	-21.12	1.786	1.36	0.763
Populus tremuloides	-23.52	2.458	-24.11	2.083	1.14	0.636	-24.11	2.351	1.05	0.671	-24.11	1.185	1.41	0.471
Betula papyrifera	-23.92	3.143	-23.82	2.995	1.04	0.549	-25.15	2.016	1.10	0.458	-22.03	3.189	0.96	0.652

Table 8.2.2.2.13: Mean of total annual precipitation in P1 (1965-1980) in occupied sites in P1 and at migration sites. At migration sites, the difference in climate means between P1 and P3 was also calculated (ΔP_3-P_1)

	Occupied sites in P_1		Migration sites											
			All				Non-suitable only				Suitable only			
			P_1		ΔPrecip P_3-P_1		P_1		ΔPrecip P_3-P_1		P_1		ΔPrecip P_3-P_1	
	Mean	St. dev	Mean	St. dev	Mean	St. dev	Mean	St. dev	Mean	St. dev	Mean	St. dev	Mean	St. dev
	>50th													
Ostrya virginiana	985.80	77.713	986.99	75.310	41.77	36.295	982.07	80.519	38.47	27.915	998.95	64.938	49.78	53.535
Fagus grandifolia	1046.48	100.789	1025.47	60.395	42.70	45.287	1040.12	58.499	49.78	37.498	1014.90	61.145	37.59	50.603
Acer saccharum	1039.47	82.800	1044.32	85.185	27.44	38.405	1029.83	95.751	8.07	35.300	1050.72	80.455	36.00	36.926
Betula alleghaniensis	1059.63	101.590	1068.39	110.561	17.73	45.781	995.66	85.383	-1.40	8.548	1089.17	110.500	23.20	50.784
Thuja occidentalis	1004.02	51.119	1006.85	64.048	30.04	43.842	1027.43	71.533	36.45	36.845	972.56	28.950	19.35	55.710
Acer rubrum	1026.87	73.342	1006.26	72.055	6.73	46.739	1013.35	81.208	3.28	45.150	997.06	57.216	11.21	48.623
Populus tremuloides	995.92	78.492	996.67	68.469	3.23	62.494	1008.85	59.317	0.85	68.908	951.99	84.230	11.95	30.228
Betula papyrifera	1021.97	92.767	1014.14	93.023	-30.20	78.678	988.61	80.901	-53.35	92.662	1033.01	97.368	-13.08	61.806
	>90th													
Ostrya virginiana	986.21	54.641	995.20	60.140	37.92	29.006	992.20	64.931	34.87	25.716	1011.72	24.422	54.69	53.087
Fagus grandifolia	1105.08	88.394	1041.08	43.240	43.13	41.458	1049.43	44.626	52.26	43.255	1030.34	42.186	31.38	38.938
Acer saccharum	1055.83	85.087	1053.66	104.635	12.00	33.725	1050.77	111.079	-3.66	32.300	1055.58	103.360	22.44	31.253
Betula alleghaniensis	1056.77	82.040	1098.04	120.612	2.81	57.313	1052.40	94.836	0.19	6.331	1116.29	134.590	3.85	70.089
Thuja occidentalis	1005.07	56.732	1032.95	80.111	46.78	39.917	1032.95	80.111	46.78	39.917	NA	NA	NA	NA
Acer rubrum	1037.22	69.569	1008.74	69.891	-1.93	56.064	1008.06	75.564	-4.27	55.107	1010.90	49.470	5.51	60.016
Populus tremuloides	965.14	74.715	974.29	65.871	4.50	62.939	995.12	56.029	-3.26	70.850	915.27	58.239	26.48	24.130
Betula papyrifera	994.59	64.280	999.61	74.802	-50.82	91.128	976.74	59.804	-71.48	96.216	1030.37	82.623	-23.04	76.898

8.2.2.2.7 – Disturbance

In each plot, presence/absence of disturbance were noted in the field during inventories. When the inventories began (P_1), 29.0% of plots had evidence of natural (windthrow, fire, insect outbreaks) and/or anthropogenic disturbances (logging: selective harvest, partially harvested or clearcut). The proportion of disturbed plots increased to 30.6% in P_3, mainly driven by anthropogenic disturbance (15.8% of plots in P_1, 19.0% in P_3), whereas natural disturbances were somewhat less prevalent in P_3 over P_1 (13.2% of plots in P_1, 11.6% in P_3). Five types of disturbances were recorded, 4 in both time periods: logging, fire, windthrow, insect outbreaks and forest dieback (MFFP et al. 2016). They were further combined into 2 classes, anthropogenic (logging) and natural (fire, windthrow, insect outbreaks), because of the low prevalence of each of the natural disturbances on the landscape. Severity of disturbance was also recorded, undisturbed (<25% of plot affected), light (25-75% of plot affected) and severe (>75% of plot affected), but was not found to provide additional information (Boisvert-Marsh et al. 2019). Disturbance variables were grouped into 6 variables, based on their type and timing. For each target species, the number of migration sites where a given disturbance type was observed relative to the total number of migration sites was calculated (expressed as %). In addition, within each category, the proportion of these migration sites classified as either suitable or unsuitable was also calculated (between 0 and 1).

Table 8.2.2.2.14: Disturbance variables considered

Category	**Description**
Undisturbed	Sites not affected by disturbance as recorded in P_1 and P_3
Harvest P_1	>25% plot affected by harvesting as recorded in P_1. No disturbance recorded in P_3
Natural P_1	>25% plot affected by fire, windthrow or insect outbreaks in P_1. No disturbance recorded in P_3
Harvest P_3	>25% plot affected by harvesting as recorded in P_3. No disturbance recorded in P_1
Natural P_3	>25% plot affected by fire, windthrow, insect outbreaks or crown dieback as recorded in P_3. No disturbance recorded in P_1
Disturbed P_1 and P_3	>25% plot affected by fire, windthrow, insect outbreaks, crown dieback and/or harvest as recorded in P_1 and P_3.

Table 8.2.2.2.15: Proportion of migration sites affected by each disturbance type considered.

>50th	Undisturbed			Harvest P_1			Natural P_1		
	%	Non-suitable	Suitable	%	Non-suitable	Suitable	%	Non-suitable	Suitable
Ostrya virginiana	54.17	0.62	0.38	16.67	0.50	0.50	0	--	--
Fagus grandifolia	45.16	0.43	0.57	19.35	0.33	0.67	3.23	0.00	1.00
Acer saccharum	25.81	0.31	0.69	22.58	0.29	0.71	11.29	0.43	0.57
Betula alleghaniensis	33.33	0.00	1.00	22.22	0.00	1.00	11.11	0.50	0.50
Thuja occidentalis	50.00	0.50	0.50	18.75	0.67	0.33	0	--	--
Acer rubrum	38.50	0.56	0.44	9.00	0.72	0.28	10.50	0.67	0.33
Populus tremuloides	11.90	1.00	0.00	4.76	0.00	1.00	14.29	1.00	0.00
Betula papyrifera	25.00	0.53	0.47	11.67	0.14	0.86	15.83	0.37	0.63

	Disturbed P_1 and P_3			Harvest P_3			Natural P_3		
	%	Non-suitable	Suitable	%	Non-suitable	Suitable	%	Non-suitable	Suitable
Ostrya virginiana	8.33	1	0	20.83	1.00	0.00	0	--	--
Fagus grandifolia	0	--	--	32.26	0.50	0.50	0	--	--
Acer saccharum	8.06	0.2	0.8	19.35	0.25	0.75	9.68	0.50	0.50
Betula alleghaniensis	11.11	0.5	0.5	16.67	0.33	0.67	5.56	1.00	0.00
Thuja occidentalis	12.5	1	0	18.75	0.67	0.33	0	--	--
Acer rubrum	8	0.31	0.69	22.00	0.57	0.43	11.00	0.55	0.45
Populus tremuloides	14.29	0.83	0.17	23.81	0.80	0.20	19.05	0.75	0.25
Betula papyrifera	6.67	0.38	0.63	14.17	0.35	0.65	19.17	0.70	0.30

>90th

	Undisturbed			Harvest P_1			Natural P_1		
	%	Non-suitable	Suitable	%	Non-suitable	Suitable	%	Non-suitable	Suitable
Ostrya virginiana	46.15	0.83	0.17	15.38	0.50	0.50	0	--	--
Fagus grandifolia	43.75	0.57	0.43	25.00	0.50	0.50	0	--	--
Acer saccharum	20.00	0.50	0.50	26.67	0.25	0.75	10.00	0.33	0.67
Betula alleghaniensis	42.86	0.00	1.00	0.00	--	--	0	--	--
Thuja occidentalis	42.86	1.00	0	14.29	1.00	0.00	0	--	--
Acer rubrum	42.67	0.75	0.25	8.00	0.83	0.17	9.33	0.86	0.14
Populus tremuloides	13.04	1.00	0	4.35	0	1.00	13.04	1.00	0.00
Betula papyrifera	25.00	0.71	0.29	8.82	0	1.00	13.24	0.67	0.33

	Disturbed P_1 and P_3			Harvest P_3			Natural P_3		
	%	Non-suitable	Suitable	%	Non-suitable	Suitable	%	Non-suitable	Suitable
Ostrya virginiana	15.38	1	0	23.08	1	0	0.00	--	--
Fagus grandifolia	0.00	--	--	0.00	--	--	0.00	--	--
Acer saccharum	10.00	0.33	0.67	13.33	0.50	0.50	20.00	0.50	0.50
Betula alleghaniensis	28.57	0.50	0.50	14.29	0	1	14.29	1.00	0.00
Thuja occidentalis	28.57	1	0	14.29	1	0	0.00	--	--
Acer rubrum	2.67	0	1	22.67	0.76	0.24	13.33	0.80	0.20
Populus tremuloides	13.04	0.67	0.33	26.09	0.83	0.17	17.39	0.50	0.50
Betula papyrifera	7.35	0.20	0.80	13.24	0.56	0.44	27.94	0.74	0.26

8.2.2.2.8 - Basal area

According to the MFFP classification, a merchantable tree has a diameter at breast height (DBH) of at least 9.1 cm; all merchantable trees had their diameter measured and condition assessed in each inventory. We calculated basal area (in m^2/ha) for each live stem (including other tree species not assessed in this study) with a DBH greater than 9.1 cm. In each plot, total basal area in P_1 and P_3 and difference between P_1 and P_3 was calculated for all species present, conifer species only (including other conifer species not studied here), as well as for the two conifer species characteristic of the boreal forest separately (*Picea mariana* and *Abies balsamea*).

For each target species, mean basal area in P_1 and difference in basal between P_1 and P_3 for each of these categories were calculated for migration sites and for sites occupied in P_1. In addition, mean basal area in P_1 and the difference in basal area between P_1 and P_3 (ΔP_3-P_1) for sites classified as either suitable or unsuitable was also calculated.

Table 8.2.2.2.16: Mean basal area at occupied sites in P_1 and at migration sites and changes in basal area between P_1 and P_3 at migration sites

>50th	Occupied sites P_1		Migration sites							
	BA P_1		BA P_1		ΔBA P_3-P_1					
					All sites		Non-suitable only		Suitable only	
	Mean	St. dev	Mean	St. dev	Mean	St. dev	Mean	St. dev	Mean	St. dev
Species Name	Total basal area									
Ostrya virginiana	22.67	7.505	19.44	10.464	2.11	10.710	-0.25	11.225	7.87	7.013
Fagus grandifolia	23.07	6.51	23.15	7.032	-1.05	8.579	-2.99	9.249	0.35	8.035
Acer saccharum	21.36	7.653	19.62	10.966	-0.31	13.096	0.09	13.552	-0.49	13.048
Betula alleghaniensis	20.67	8.409	18.70	6.721	-1.80	9.224	-9.38	3.577	0.36	9.254
Thuja occidentalis	24.22	9.808	12.08	7.965	1.53	9.424	0.71	11.184	2.88	6.146
Acer rubrum	20.50	8.235	19.12	10.282	-3.68	12.636	-3.04	13.013	-4.52	12.153
Populus tremuloides	18.00	10.204	21.37	12.791	-17.14	15.389	-18.62	15.52	-11.73	14.43
Betula papyrifera	18.98	10.754	16.54	13.448	-5.96	16.737	-8.62	13.316	-4.00	18.725
	All conifer species									
Ostrya virginiana	2.73	4.514	1.85	3.523	0.36	2.452	-0.44	1.822	2.30	2.833
Fagus grandifolia	2.89	4.407	7.31	8.176	-3.77	6.740	-5.06	8.407	-2.83	5.298
Acer saccharum	4.59	5.877	8.20	8.473	-0.61	9.073	0.51	8.308	-1.11	9.442
Betula alleghaniensis	8.32	7.972	8.57	8.644	-4.81	8.361	-9.87	5.056	-3.36	8.682
Thuja occidentalis	16.22	9.821	7.03	4.978	-0.22	7.688	-1.88	8.543	2.55	5.591
Acer rubrum	8.72	7.939	9.85	9.439	-3.08	9.464	-2.72	10.192	-3.55	8.461
Populus tremuloides	8.67	8.879	16.98	12.356	-14.30	14.365	-16.00	14.502	-8.09	12.686
Betula papyrifera	12.62	10.771	15.44	13.415	-6.44	15.687	-8.49	12.614	-4.92	17.554
	Abies balsamea									
Ostrya virginiana	1.12	2.15	0.97	2.259	-0.19	2.192	-0.72	2.11	1.10	1.949
Fagus grandifolia	1.38	2.4	3.77	4.667	-2.01	3.903	-2.20	4.731	-1.86	3.321
Acer saccharum	2.54	3.674	4.47	4.725	-1.17	5.818	-0.72	8.249	-1.37	4.457
Betula alleghaniensis	4.95	5.57	5.28	7.574	-2.97	8.508	-8.59	9.041	-1.37	7.957
Thuja occidentalis	6.46	5.617	3.60	4.698	-1.90	5.850	-3.02	7.226	-0.05	1.448
Acer rubrum	4.69	5.533	4.44	5.846	-1.78	6.374	-1.64	6.896	-1.96	5.658
Populus tremuloides	2.14	4.047	6.79	9.05	-5.97	9.427	-7.02	9.984	-2.12	5.961
Betula papyrifera	6.37	8.08	7.45	11.074	-3.52	11.365	-2.96	6.934	-3.94	13.794
	Picea mariana									
Ostrya virginiana	0.01	0.069	--	--	--	--	--	--	--	--
Fagus grandifolia	0.16	0.972	0.08	0.39	-0.08	0.390	-0.02	0.078	-0.12	0.51
Acer saccharum	0.17	0.917	0.41	1.705	-0.29	1.856	-0.04	0.348	-0.40	2.216
Betula alleghaniensis	0.41	1.575	1.20	2.882	-0.89	2.717	-2.40	4.35	-0.46	2.095
Thuja occidentalis	1.25	3.284	1.56	1.977	0.31	2.226	0.00	1.372	0.82	3.312
Acer rubrum	1.03	2.824	1.46	3.272	-0.28	3.429	-0.17	4.195	-0.42	2.06
Populus tremuloides	3.86	6.791	7.47	10.411	-6.86	10.608	-7.71	11.628	-3.77	4.711
Betula papyrifera	4.41	7.425	6.17	8.557	-2.83	8.843	-4.81	9.721	-1.37	7.89

>90th	Occupied sites P_1		Migration sites							
	BA P_1		BA P_1		ΔBA P_3-P_1					
					All		Non-suitable only		Suitable only	
	Mean	St. dev	Mean	St. dev	Mean	St. dev	Mean	St. dev	Mean	St. dev
Species Name	Total basal area									
Ostrya virginiana	22.44	6.214	20.52	9.033	-0.58	11.900	-2.62	11.663	10.65	6.431
Fagus grandifolia	23.00	6.537	18.64	8.83	-1.68	7.783	-4.26	11.782	3.64	12.43
Acer saccharum	20.20	7.839	23.79	8.392	0.48	12.599	-2.46	8.034	-0.68	7.955
Betula alleghaniensis	18.90	8.336	18.92	9.228	-4.41	12.591	-8.75	4.913	-2.67	14.784
Thuja occidentalis	23.23	11.344	10.98	8.447	2.41	10.126	2.41	10.126	--	--
Acer rubrum	19.14	8.461	17.38	10.011	-2.41	12.097	-2.63	13.088	-1.72	8.483
Populus tremuloides	17.85	11.637	21.34	11.643	-17.03	14.818	-18.62	15.883	-12.49	11.206
Betula papyrifera	21.14	11.118	18.17	11.95	-8.45	15.037	-9.95	12.72	-6.43	17.722
	All conifer species									
Ostrya virginiana	2.88	3.779	2.74	4.567	-0.65	2.041	-0.86	2.148	0.53	0.749
Fagus grandifolia	2.70	4.304	5.77	5.662	-3.39	6.041	-1.52	4.609	1.97	9.159
Acer saccharum	4.77	5.471	6.69	8.32	0.58	7.763	-4.21	7.17	-2.33	4.514
Betula alleghaniensis	8.23	7.732	13.70	9.939	-9.43	11.900	-12.56	6.361	-8.18	13.98
Thuja occidentalis	16.96	11.377	6.74	5.63	-0.68	8.658	-0.68	8.658	--	--
Acer rubrum	8.57	8.211	9.29	8.964	-1.94	9.733	-2.57	10.53	0.05	6.449
Populus tremuloides	9.04	9.623	17.30	11.579	-14.41	13.935	-16.59	14.862	-8.24	9.261
Betula papyrifera	16.23	11.103	17.78	11.789	-8.82	14.707	-10.08	11.895	-7.12	17.898
	Abies balsamea									
Ostrya virginiana	1.60	2.628	1.66	2.927	-1.11	2.141	-1.41	2.193	0.53	0.749
Fagus grandifolia	1.17	2.114	4.13	4.521	-2.09	4.443	-3.44	5.564	-0.28	4.502
Acer saccharum	3.08	4.097	4.61	5.84	-1.54	5.110	-2.17	5.241	-1.99	3.566
Betula alleghaniensis	5.68	6.16	9.95	10.522	-6.94	12.723	-14.68	9.587	-3.85	13.34
Thuja occidentalis	7.64	6.385	3.77	5.369	-2.34	6.694	-2.34	6.694	--	--
Acer rubrum	5.33	6.424	4.01	5.94	-1.12	6.949	-1.65	7.517	0.53	4.499
Populus tremuloides	1.48	3.582	6.06	8.574	-5.22	9.017	-6.11	9.566	-2.69	7.385
Betula papyrifera	6.99	8.254	8.34	10.678	-3.62	11.195	-3.57	7.059	-3.69	15.24
	Picea mariana									
Ostrya virginiana	0.02	0.091	--	--	--	--	--	--	--	--
Fagus grandifolia	0.14	0.604	0.05	0.278	-0.15	0.541	0.05	0.17	-0.08	0.358
Acer saccharum	0.17	0.932	0.15	0.541	-0.03	0.301	-0.03	0.094	-0.31	0.818
Betula alleghaniensis	0.54	1.883	1.46	2.749	-1.36	2.648	-0.35	0.493	-1.76	3.122
Thuja occidentalis	1.10	2.638	1.49	2.488	0.05	1.674	0.05	1.674	--	--
Acer rubrum	0.92	2.583	1.91	3.961	-0.23	4.332	-0.13	4.731	-0.53	2.799
Populus tremuloides	5.33	7.865	9.56	11.219	-8.98	11.458	-10.79	12.598	-3.84	5.19
Betula papyrifera	8.11	9.306	8.45	9.836	-4.85	9.876	-5.87	10.202	-3.48	9.421

8.2.2.3 - Additional results for co-occurrence analyses

Table 8.2.2.3.1: Co-occurrence index values for plots with occupancy gains in P_3. The target species are in the first column and the co-occurring species in the first row (ABIBAL = *Abies balsamea*, ACERUB = *Acer rubrum*, ACESAC = *Acer saccharum*, BETALL = *Betula alleghaniensis*, BETPAP = *Betula papyrifera*, PICGLA = *Picea glauca*, PICMAR = *Picea mariana*). For a given target species, we show the proportion of shared presences of a co-occurring species in P_1 (1970-1977, any stem >1.1cm DBH of co-occurring species) relative to the total number of plots with occupancy gains in P_3 (see Eq. 3.1 in main text) for the entire area and for each of the three latitudinal zones. Species that are at once target and co-occurring species are greyed out.

Species	**Area**	**ACESAC**	**BETALL**	**ACERUB**	**PICGLA**	**BETPAP**	**ABIBAL**	**PICMAR**
Ostrya virginiana	Entire	0.8824	0.2647	0.5	0.1471	0.5	0.3824	0
	<50th	1	0.2	0.4	0.1	0.6	0.3	0
	>50th	0.8333	0.2917	0.5417	0.1667	0.4583	0.4167	0
	>90th	0.8462	0.3846	0.5385	0.1538	0.4615	0.4615	0
Fagus grandifolia	Entire	0.8308	0.4769	0.7077	0.3077	0.3846	0.6615	0.0923
	<50th	0.8824	0.3529	0.7353	0.1765	0.4412	0.5	0.1176
	>50th	0.7742	0.6129	0.6774	0.4516	0.3226	0.8387	0.0645
	>90th	0.75	0.625	0.625	0.375	0.4375	0.75	0.125
Acer saccharum	Entire		0.5495	0.5385	0.5055	0.5275	0.7912	0.1868
	<50th		0.3793	0.5862	0.4828	0.4138	0.7241	0.1379
	>50th		0.629	0.5161	0.5161	0.5806	0.8226	0.2097
	>90th		0.7	0.4	0.5333	0.6333	0.8	0.0333
Betula alleghaniensis	Entire	0.7241		0.4138	0.2759	0.3276	0.6207	0.1207
	<50th	0.8		0.5	0.25	0.275	0.55	0.05
	>50th	0.5556		0.2222	0.3333	0.4444	0.7778	0.2778
	>90th	0.4286		0	0.5714	0.7143	1	0.4286
Thuja occidentalis	Entire	0.24	0.28	0.44	0.52	0.56	0.88	0.56
	<50th	0.4444	0.3333	0.7778	0.4444	0.4444	1	0.4444
	>50th	0.125	0.25	0.25	0.5625	0.625	0.8125	0.625
	>90th	0	0	0.2857	0.5714	0.5714	0.7143	0.5714
Acer rubrum	Entire	0.2525	0.3322		0.485	0.6678	0.711	0.3588
	<50th	0.5446	0.4257		0.4653	0.4356	0.6436	0.198
	>50th	0.105	0.285		0.495	0.785	0.745	0.44
	>90th	0.0141	0.1867		0.4933	0.7867	0.72	0.4933
Populus tremuloides	Entire	0.1026	0.1667	0.2179	0.4103	0.6282	0.7308	0.5256
	<50th	0.2222	0.3611	0.4167	0.5	0.5556	0.8333	0.3611
	>50th	0	0	0.0476	0.3333	0.6905	0.6429	0.6667
	>90th	0	0	0.087	0.3478	0.6087	0.6957	0.7391
Betula papyrifera	Entire	0.1355	0.1589	0.1822	0.2804		0.6822	0.5187
	<50th	0.2766	0.3191	0.3617	0.3085		0.734	0.3723
	>50th	0.0508	0.0333	0.0417	0.2583		0.6417	0.6333
	>90th	0	0.0769	0.0714	0.1912		0.6912	0.75

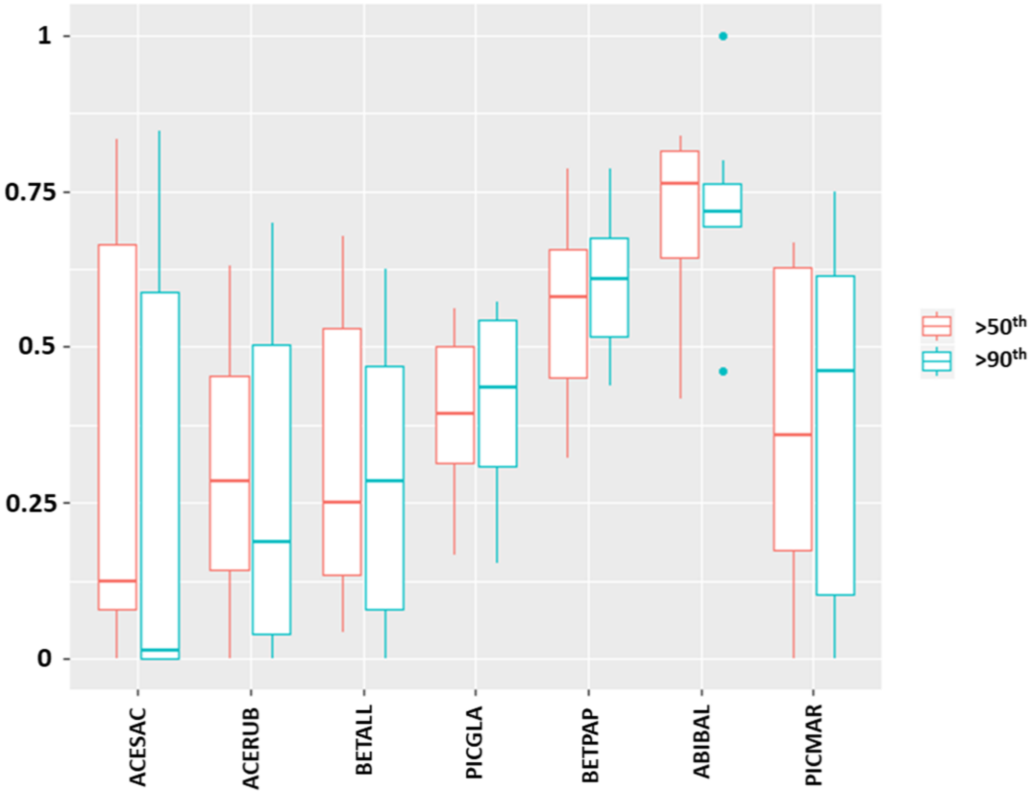


Figure 8.2.2.3.1: Boxplots of pairwise index values between target species and companion species, as grouped by associated species (7 in total) and latitudinal zone of the target species under consideration (north of the 50th, north of the 90th). ABIBAL = Abies balsamea, ACERUB = Acer rubrum, ACESAC = *Acer saccharum*, BETALL = *Betula alleghaniensis*, BETPAP = *Betula papyrifera*, PICGLA = *Picea glauca*, PICMAR = *Picea mariana*

Table 8.2.2.3.2: Results of Dunn's post-hoc multiple comparisons to test for differences in pairwise co-occurrence index values between a target species (species 1) above the 50th and the above the 90th and each of the co-occurring species (species 2) in that latitudinal zone. Bold indicates significant values to $p <= 0.05$ while italicized font indicates values where $p < 0.1$.

				>50th		**>90th**	
Species1	**Species2**	**n1**	**n2**	**statistic**	**$p_{adjusted}$**	**statistic**	**$p_{adjusted}$**
Acer saccharum	*Betula alleghaniensis*	7	7	-0.4674	1	-0.159	1
Acer saccharum	*Betula papyrifera*	7	7	1.367	1	1.8724	0.8562
Acer saccharum	*Picea glauca*	7	8	0.1127	1	0.4458	1
Acer saccharum	*Picea mariana*	7	8	0.0171	1	0.6374	1
Acer saccharum	*Acer rubrum*	7	7	-0.2646	1	-0.1766	1
Acer saccharum	*Abies balsamea*	7	8	2.6711	0.1361	*2.8642*	*0.0794*
Acer rubrum	*Betula alleghaniensis*	7	7	-0.2028	1	0.0177	1
Acer rubrum	*Betula papyrifera*	7	7	1.6316	1	2.049	0.6474
Acer rubrum	*Picea glauca*	7	8	0.386	1	0.6282	1
Acer rubrum	*Picea mariana*	7	8	0.2903	1	0.8198	1
Acer rubrum	*Abies balsamea*	*7*	*8*	*2.9443*	*0.0647*	**3.0466**	**0.0486**
Betula alleghaniensis	*Betula papyrifera*	7	7	1.8344	1	2.0313	0.6474
Betula alleghaniensis	*Picea glauca*	7	8	0.5955	1	0.61	1
Betula alleghaniensis	*Picea mariana*	7	8	0.4998	1	0.8016	1
Betula alleghaniensis	***Abies balsamea***	**7**	**8**	**3.1538**	**0.0338**	**3.0283**	**0.0492**
Picea glauca	*Betula papyrifera*	8	7	1.2991	1	1.488	1
Picea glauca	*Picea mariana*	8	8	-0.099	1	0.1983	1
Picea glauca	*Abies balsamea*	8	8	2.6481	0.1376	2.5032	0.2215
Betula papyrifera	*Picea mariana*	7	8	-1.3947	1	-1.2964	1
Betula papyrifera	*Abies balsamea*	7	8	1.2592	1	0.9304	1
Abies balsamea	*Picea mariana*	8	8	-2.747	0.1142	-2.305	0.3599

8.2.2.4 - Calculating C-scores in species pairwise co-occurrence analyses

As a reference to provide context for interpreting potentially novel species associations observed at migration sites, we needed to consider pairwise associations in P_1. The strength of pairwise associations between 8 target species and each of 7 co-occurring species at a site was calculated using a constrained C-score index (Gotelli, 2000) which is a measure of shared occurrences between a species pair relative to the total number of observations for each. The index was calculated across the entire study area and in 1° latitudinal bands for each combination of target species and associated species. Using latitudinal bands allowed for a more detailed analysis of association patterns across the study area (Bar-Massada and Belmaker, 2017). A minimum of 5 occurrences per latitudinal band was required for the simulated null model (see below).

Based on the method proposed by Stone and Roberts (1990) and as described by Gotelli and McCabe (2002), the C-score for each species pair *ij* is calculated as follows:

$$\text{Eq 8.2.1 - } C_{ij\ \mathrm{observed}} = (R_i - S)(R_j - S)$$

where R_i is the total number of occurrences for species i and Rj is the total number of occurrences for species j, and S is the number of sites that contain both i and j. Thus, for any particular species pair, the C-score is a numerical index that ranges from 0 to R_iR_j . The observed C-score was then compared to the expected C-score, which is based on a simulated null model (randomized n=10000) constrained by environmental conditions suitable for both species (Peres-Neto, Olden, & Jackson, 2001). Environmental constraints were obtained on a species-by-species basis using a consensus species distribution modelling approach (described in previous section). The difference between the observed and expected C-score was transformed into a standardized effect size (SES) value to allow comparison between species and latitudinal bands. SES is calculated as follows:

$$\text{Eq 8.2.2 -} SES = (C_{ij\ \mathrm{observed}} - C_{ij\ \mathrm{simulated}})/\sigma_{\mathrm{simulated}}$$

where $C_{ij\ \mathrm{observed}}$ is the C score as calculated in the previous step, $C_{ij\ \mathrm{simulated}}$ and $\sigma_{\mathrm{simulated}}$ is the mean and standard deviation respectively of the simulated null model values. For the purpose of this study, the sign of the SES values was inversed to facilitate interpretation. Significance was based on p-values from one-tailed permutation tests; SES values greater than 1.7 indicate positive association between a species pair (probability that observed SES is greater than expected SES to p<=0.05) and SES values smaller than -1.7 suggest spatial segregation (probability that observed SES is greater than expected SES to p<=0.05), i.e., the species do not tend to co-occur. Association analyses were conducted using the 'ecospat' package (Di Cola et al., 2017).

Table 8.2.2.4.1: Associations between target and co-occurring species pairs based on standardized effect size (SES) calculated across the study area. The standardized effect size (SES) was calculated from modelled C-score values for each target species as a measure of strength of the association between species pairs, based on plot occupancy in P_1 (1970-1977). Analyses were conducted across the study area (marked as overall) and for 1° wide latitudinal bands across the study area (45°N to 53°N, centered on the midpoint of the band) using all observations of stems greater than 1.1cm diameter at breast height. These analyses were constrained to suitable habitats, as determined by the species distribution models based on climatic and edaphic variables (see SDM section for further details). SES values highlighted in blue indicate significant association between pairs (SES >= 1.7, significant to $p<0.05$ according to one-tailed test) and values highlighted in red indicate significant non association (SES <= -1.7, usually significant to $p<0.05$ according to one-tailed test).

			SES by latitudinal band						
Target species	**Co-occurring species**	**Overall**	**45-46**	**46-47**	**47-48**	**48-49**	**49-50**	**50-51**	**51-52**
OSTVIR	ACESAC	5.4929	3.9944	3.9089	NA	NA	NA	NA	NA
OSTVIR	BETALL	-6.0575	-2.1305	-4.8033	NA	NA	NA	NA	NA
OSTVIR	ACERUB	-7.7647	-1.6508	-5.1599	NA	NA	NA	NA	NA
OSTVIR	PICGLA	-1.3579	-1.0862	-2.1763	NA	NA	NA	NA	NA
OSTVIR	BETPAP	-1.8411	0.8832	-2.5811	NA	NA	NA	NA	NA
OSTVIR	ABIBAL	-3.8269	-1.6045	-3.8829	NA	NA	NA	NA	NA
OSTVIR	PICMAR	3.7725	1.0209	3.0357	NA	NA	NA	NA	NA
FAGGRA	ACESAC	6.1115	3.8782	4.5346	2.0112	NA	NA	NA	NA
FAGGRA	BETALL	-4.4576	0.2155	-4.3420	-0.7514	NA	NA	NA	NA
FAGGRA	ACERUB	-7.7061	-1.7613	-4.4310	-0.6002	NA	NA	NA	NA
FAGGRA	PICGLA	-3.6736	-1.3250	-3.1472	-2.8172	NA	NA	NA	NA
FAGGRA	BETPAP	-7.2063	-0.4849	-5.8310	-3.5541	NA	NA	NA	NA
FAGGRA	ABIBAL	-8.581	-5.1380	-8.4173	-2.0791	NA	NA	NA	NA
FAGGRA	PICMAR	9.9033	3.7449	6.7376	7.9439	NA	NA	NA	NA
ACESAC	ACESAC	NA	NA	NA	NA	NA	NA	NA	NA
ACESAC	BETALL	-5.2765	-2.4378	-3.2025	-0.6963	0.8663	NA	NA	NA
ACESAC	ACERUB	-8.4457	-2.6911	-5.4877	1.1242	-0.0023	NA	NA	NA
ACESAC	PICGLA	-4.4953	-4.3990	-2.8118	-0.3918	0.6838	NA	NA	NA
ACESAC	BETPAP	-13.6136	-2.5871	-11.1333	-6.0539	-1.0227	NA	NA	NA
ACESAC	ABIBAL	-9.5312	-7.3405	-12.2320	-0.9374	3.2550	NA	NA	NA
ACESAC	PICMAR	7.7504	3.9918	5.1823	6.6661	-0.5795	NA	NA	NA
BETALL	ACESAC	-5.2765	-2.4378	-3.2025	-0.6963	0.8663	NA	NA	NA
BETALL	BETALL	NA	NA	NA	NA	NA	NA	NA	NA
BETALL	ACERUB	-0.8738	3.7530	-0.3376	-0.4066	0.9328	NA	NA	NA

BETALL	PICGLA	3.5711	1.4711	3.9550	2.9914	-1.2750	NA	NA	NA
BETALL	BETPAP	-5.9799	-1.4705	-5.1647	-3.6160	1.0501	NA	NA	NA
BETALL	ABIBAL	7.4283	3.9556	2.4894	4.9670	3.9789	NA	NA	NA
BETALL	PICMAR	2.7694	6.2282	5.2230	-0.9696	-2.3856	NA	NA	NA
THUOCC	ACESAC	-2.5077	-0.1519	-0.3450	-0.1780	-0.6311	NA	NA	NA
THUOCC	BETALL	11.0129	3.5004	10.3801	6.8607	-0.4984	NA	NA	NA
THUOCC	ACERUB	-6.808	1.1206	-1.5967	-6.5062	-2.6995	NA	NA	NA
THUOCC	PICGLA	5.3371	3.7708	2.7831	2.8859	1.7822	-0.2013	NA	NA
THUOCC	BETPAP	3.8325	1.1022	1.9624	3.1527	1.6184	-0.7271	NA	NA
THUOCC	ABIBAL	10.998	4.1505	7.3952	5.7751	2.3420	1.2878	NA	NA
THUOCC	PICMAR	-2.807	-3.7867	-1.7410	-2.3551	-2.1586	0.1544	NA	NA
ACERUB	ACESAC	-8.4457	-2.6911	-5.4877	1.1242	-0.0023	NA	NA	NA
ACERUB	BETALL	-0.8738	3.7530	-0.3376	-0.4066	0.9328	NA	NA	NA
ACERUB	ACERUB	NA	NA	NA	NA	NA	NA	NA	NA
ACERUB	PICGLA	1.1762	-0.0405	1.9798	-0.9625	0.0413	NA	NA	NA
ACERUB	BETPAP	7.4368	2.9587	5.0629	4.2162	3.3093	NA	NA	NA
ACERUB	ABIBAL	7.868	4.2894	5.8433	1.7566	2.8218	NA	NA	NA
ACERUB	PICMAR	4.7988	0.5215	6.0873	0.1818	-1.5824	NA	NA	NA
POPTRE	ACESAC	-3.8012	-2.6677	-1.6677	0.7651	-1.5984	NA	NA	NA
POPTRE	BETALL	-6.7796	-1.4766	-2.5903	-4.1995	-2.8598	NA	NA	NA
POPTRE	ACERUB	1.8197	3.4575	2.0363	1.0004	0.0445	NA	NA	NA
POPTRE	PICGLA	-2.3642	-0.4556	-0.6603	-2.4430	2.4067	1.3516	5.4312	NA
POPTRE	BETPAP	8.7049	2.9124	6.7928	4.3798	3.3580	2.8156	3.1198	NA
POPTRE	ABIBAL	-4.0586	2.5824	1.7134	-6.2820	-2.1608	-1.9076	-1.8678	NA
POPTRE	PICMAR	-1.9786	-0.4651	-2.6479	0.2507	-0.4194	-1.4822	-0.3344	NA
BETPAP	ACESAC	-13.6136	-2.5871	-11.1333	-6.0539	-1.0227	NA	NA	NA
BETPAP	BETALL	-5.9799	-1.4705	-5.1647	-3.6160	1.0501	NA	NA	NA
BETPAP	ACERUB	7.4368	2.9587	5.0629	4.2162	3.3093	NA	NA	NA
BETPAP	PICGLA	5.4706	-0.3336	3.3395	5.5639	3.0990	1.8234	0.8669	0.4292
BETPAP	BETPAP	NA	NA	NA	NA	NA	NA	NA	NA
BETPAP	ABIBAL	14.9617	1.0731	8.1455	9.9501	6.8746	3.8158	0.2075	3.7417
BETPAP	PICMAR	-2.3292	1.0878	3.2787	-2.5691	-2.2858	-3.3763	-1.5965	0.6676

Literature cited

Beauregard, F. and S. de Blois (2014). "Beyond a Climate-Centric View of Plant Distribution: Edaphic Variables Add Value to Distribution Models." PLoS ONE **9**(3): e92642.

Bar-Massada, A., and Belmaker, J. (2017). Non-stationarity in the co-occurrence patterns of species across environmental gradients. *Journal of Ecology, 105*(2), 391-399. doi:10.1111/1365-2745.12713

Boisvert-Marsh, L., et al. (2019). "Divergent responses to climate change and disturbance drive recruitment patterns underlying latitudinal shifts of tree species." Journal of Ecology **107**(4): 1956-1969.

Chambers, D., et al. (2013). "Challenges in modelling the abundance of 105 tree species in eastern North America using climate, edaphic, and topographic variables." Forest Ecology and Management **291**: 20-29.

Guisan, A. and N. E. Zimmermann (2000). "Predictive habitat distribution models in ecology." Ecological Modelling **135**(2–3): 147-186.

Harrell, F. E., et al. (1984). "Regression modelling strategies for improved prognostic prediction." Statistics in Medicine **3**(2): 143-152.

Harrell Jr, F. E. (2013). "Hmisc: Harrell miscellaneous. R package version 3.12-2." [Computer software]. Available from http://cran.r-project.org/web/packages/Hmisc.

Ministère des Forêts, Faune et des Parcs (2015). Normes techniques, Placettes-Échantillons Permanentes, 4e inventaire écoforetier du Québec méridional. Québec, Québec, Ministère des Forêts, Faune et Parcs, Direction des Inventaires Forestiers**:** 256.

Périé, C. and S. de Blois (2016). "Dominant forest tree species are potentially vulnerable to climate change over large portions of their range even at high latitudes." PeerJ **4**: e2218.

Regnière, J. and R. Saint-Amant (2014). BioSIM 10 - User's Manual. Sainte-Foy, Québec, Laurentian Forestry Centre, Canadian Forest Service, Natural Resources Canada**:** 74.

Thuiller, W., et al. (2016). biomod2: Ensemble platform for species distribution modeling. R package version 3.3-7, R Foundation for Statistical Computing Vienna, Austria.

8.2.3 - Appendix 3: Maps of tree species distributions within Quebec, Canada.

Study area

Our study area covers roughly 761100 km² in Quebec, Canada from 45°N to 53°N and from 80°W to 61°W. Two major vegetation zones, each with two forest types, are part of the study area: the northern temperate zone and the boreal forest zone (Saucier et al. 2003).

The former includes Acer saccharum dominated forests to the south (background colours in brown and ochre tones in the following maps) and mixed *Abies balsamea-Betula alleghaniensis* forests to the north (background colour in grey). The latter includes *Abies balsamea-Betula papyrifera* forests to the south (background colour in light blue) and *Picea mariana*-feathermoss forests to the north (background colour in blue). The northern limit of the study area roughly coincides with the ecotone between the continuous boreal forest and the taiga.

Data collection

We used extensive forest inventories of permanent plots to monitor long-term forest dynamics throughout the study area, ensuring consistency in sampling (Ministère des Forêts 2015). Data collection started in 1970 and is ongoing. Four inventory campaigns have been completed across the permanent plot network.

Species data

Tree species data are available from three forest inventories, P_1 (1970-1977) and P_3 (2003-2015). A total of 6309 plots were resampled across the three inventories. We used data from P_1 and P_3 for this study. Analyses focused on eight tree species reaching or approaching their northern limit in the study area: *Ostrya virginiana*, *Fagus grandifolia*, *Acer saccharum*, *Betula alleghaniensis*, *Thuja occidentalis*, *Acer rubrum*, *Populus tremuloides*, *Betula papyrifera*. Saplings of these species showed evidence of northward latitudinal shifts in previous studies (Boisvert-Marsh et al. 2014) and in this one.

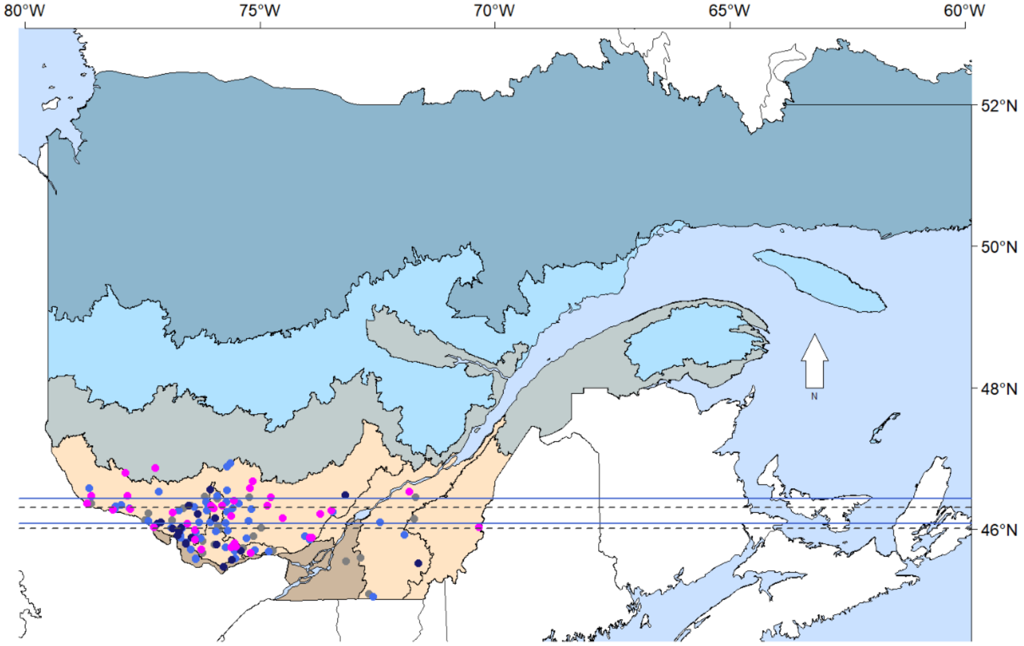
References

Boisvert-Marsh, L., et al. (2014). "Shifting with climate? Evidence for recent changes in tree species distribution at high latitudes." Ecosphere 5(7): art83.

Ministère des Forêts, Faune et des Parcs (2015). Normes techniques, Placettes-Échantillons Permanentes, 4e inventaire écoforetier du Québec méridional. Québec, Québec, Ministère des Forêts, Faune et Parcs, Direction des Inventaires Forestiers. 256 p.

Saucier, J.-P., et al. (2003). Zones de végétation et les domaines bioclimatiques du Québec. Québec, Québec, Direction des inventaires forestiers, Ministère des Ressources naturelles et de la Faune. Maps retrieved from https://mffp.gouv.qc.ca/forets/inventaire/inventaire-zones-carte.jsp.

Figure 8.2.3.1: (Top) Map of plots occupied by saplings of Ostrya virginiana in P_1 (1970-1977) and P_3 (2003-2015). Dark blue points are plots occupied by saplings in P_1 and P_3. Grey points are plots occupied by saplings in P_1 but where saplings are absent in P_3. Magenta points are plots occupied by saplings in P_3 where the species was not observed in P_1 (all stems >1.1cm diameter at breast height). Light blue points are plots occupied by saplings in P_3 where the species was observed in P_1. Lower horizontal lines = 50th percentile of latitude; Upper horizontal lines = 90th. Dashed grey = P_1 (1970-1977); Blue = P_3 (2003-2015). (Bottom) Map of plots occupied by species in P_1 (1970-1977, all stems > 1.1 cm diameter at breast height).



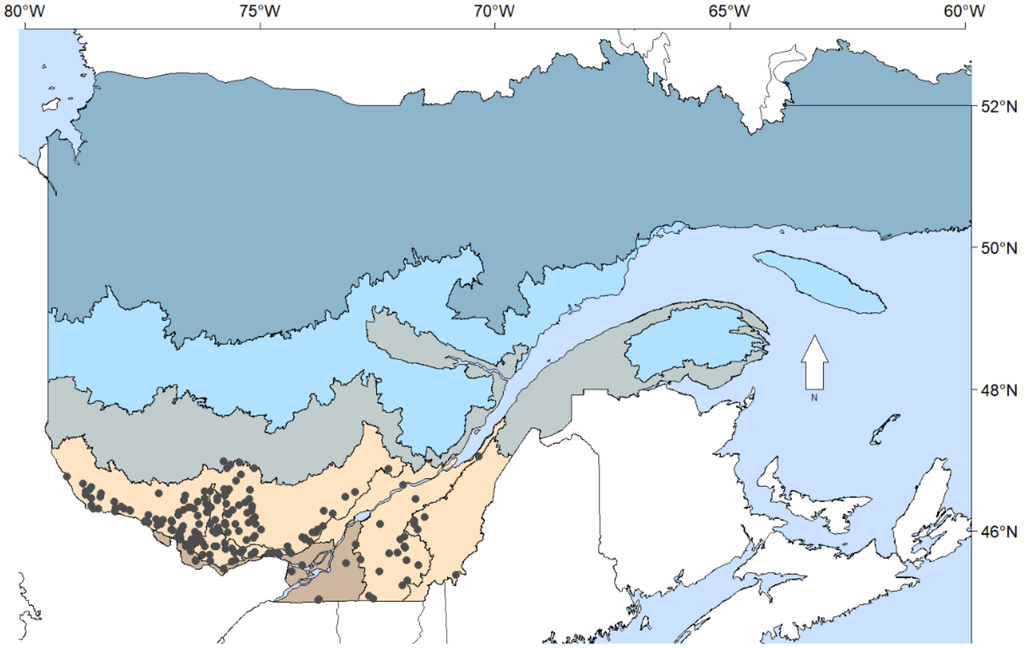


Figure 8.2.3.2: Map of plots occupied by saplings of Fagus grandifolia in P_1 (1970-1977) and P_3 (2003-2015). Dark blue points are plots occupied by saplings in P_1 and P_3. Grey points are plots occupied by saplings in P_1 but where saplings are absent in P_3. Magenta points are plots occupied by saplings in P_3 where the species was not observed in P_1 (all stems >1.1cm diameter at breast height). Light blue points are plots occupied by saplings in P_3 where the species was observed in P_1. Lower horizontal lines = 50th percentile of latitude; Upper horizontal lines = 90th. Dashed grey = P_1 (1970-1977); Blue = P_3 (2003-2015). (Bottom) Map of plots occupied by species in P_1 (1970-1977, all stems > 1.1 cm diameter at breast height).

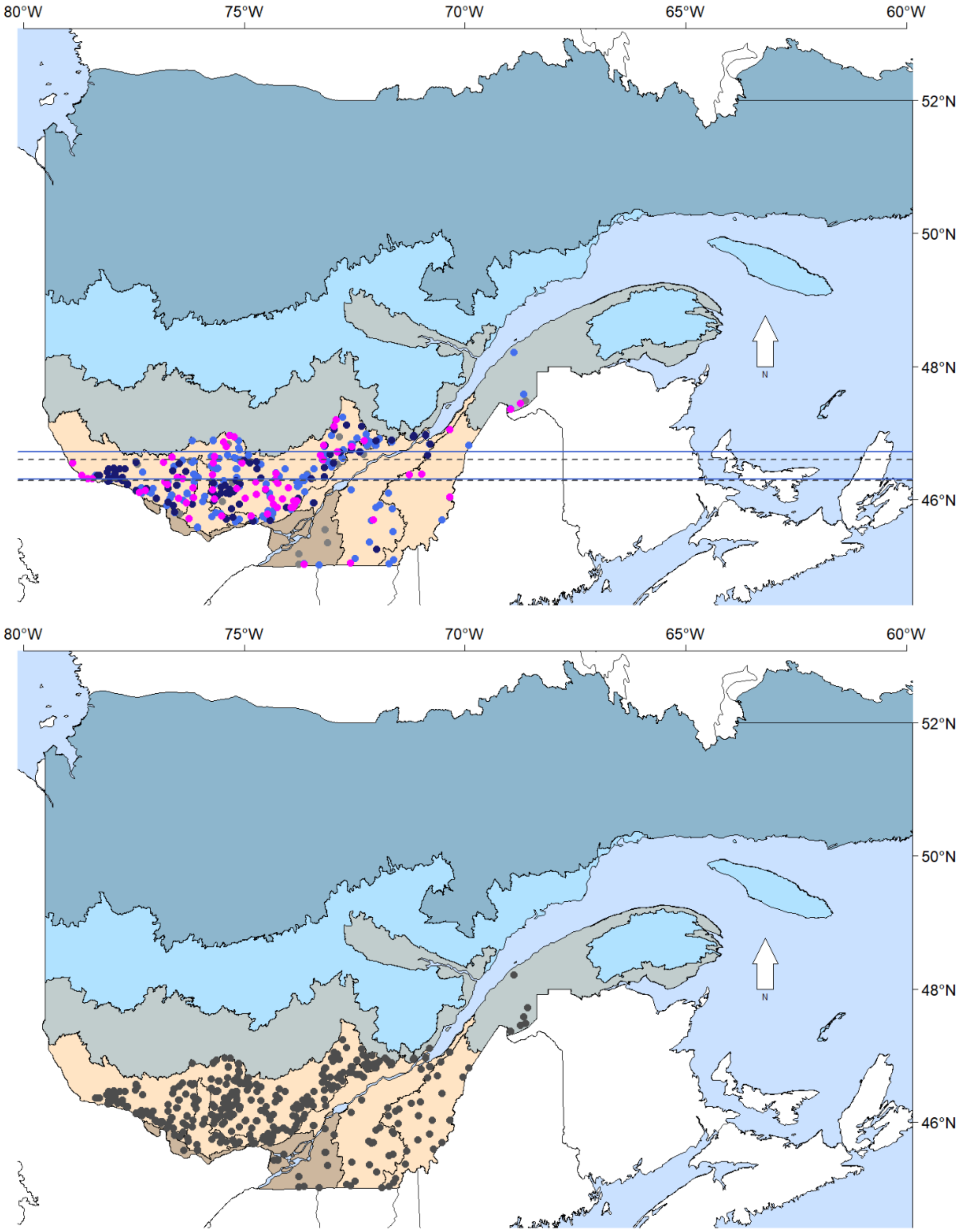
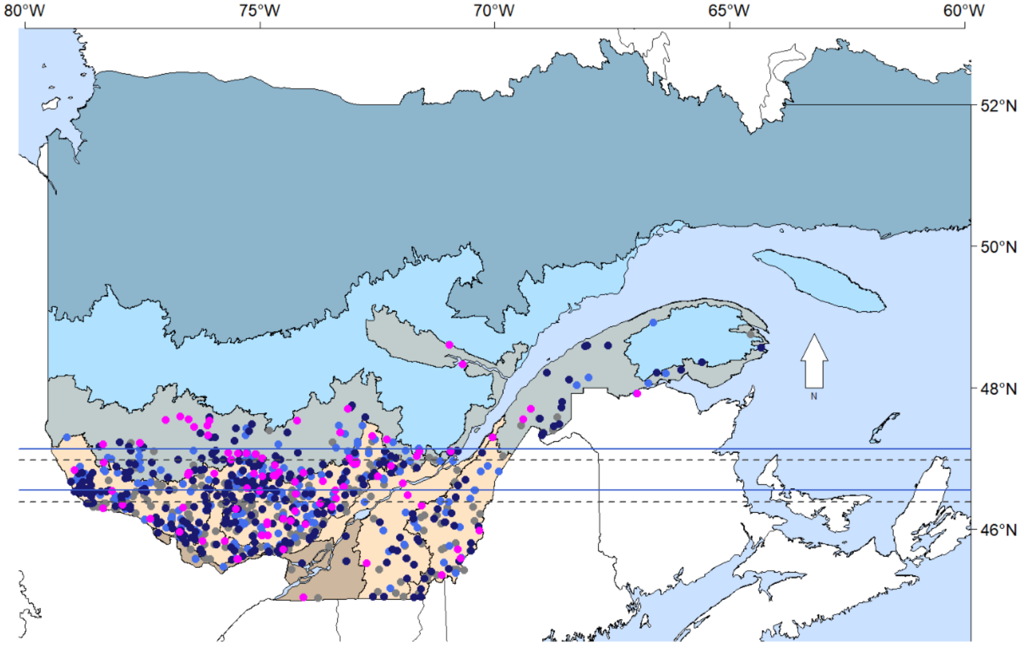


Figure 8.2.3.3: Map of plots occupied by saplings of Acer saccharum in P_1 (1970-1977) and P_3 (2003-2015). Dark blue points are plots occupied by saplings in P_1 and P_3. Grey points are plots occupied by saplings in P_1 but where saplings are absent in P_3. Magenta points are plots occupied by saplings in P_3 where the species was not observed in P_1 (all stems >1.1cm diameter at breast height). Light blue points are plots occupied by saplings in P_3 where the species was observed in P_1. Lower horizontal lines = 50th percentile of latitude; Upper horizontal lines = 90th. Dashed grey = P_1 (1970-1977); Blue = P_3 (2003-2015). (Bottom) Map of plots occupied by species in P_1 (1970-1977, all stems > 1.1 cm diameter at breast height).



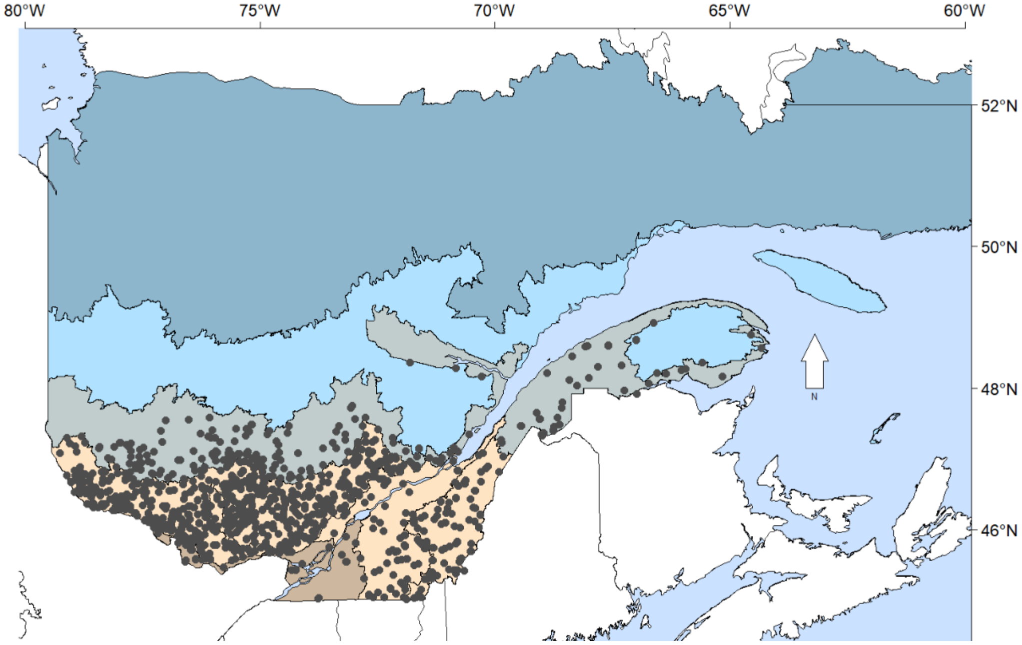


Figure 8.2.3.4: Map of plots occupied by saplings of Betula alleghaniensis in P_1 (1970-1977) and P_3 (2003-2015). Dark blue points are plots occupied by saplings in P_1 and P_3. Grey points are plots occupied by saplings in P_1 but where saplings are absent in P_3. Magenta points are plots occupied by saplings in P_3 where the species was not observed in P_1 (all stems >1.1cm diameter at breast height). Light blue points are plots occupied by saplings in P_3 where the species was observed in P_1. Lower horizontal lines = 50th percentile of latitude; Upper horizontal lines = 90th. Dashed grey = P_1 (1970-1977); Blue = P_3 (2003-2015). (Bottom) Map of plots occupied by species in P_1 (1970-1977, all stems > 1.1 cm diameter at breast height).

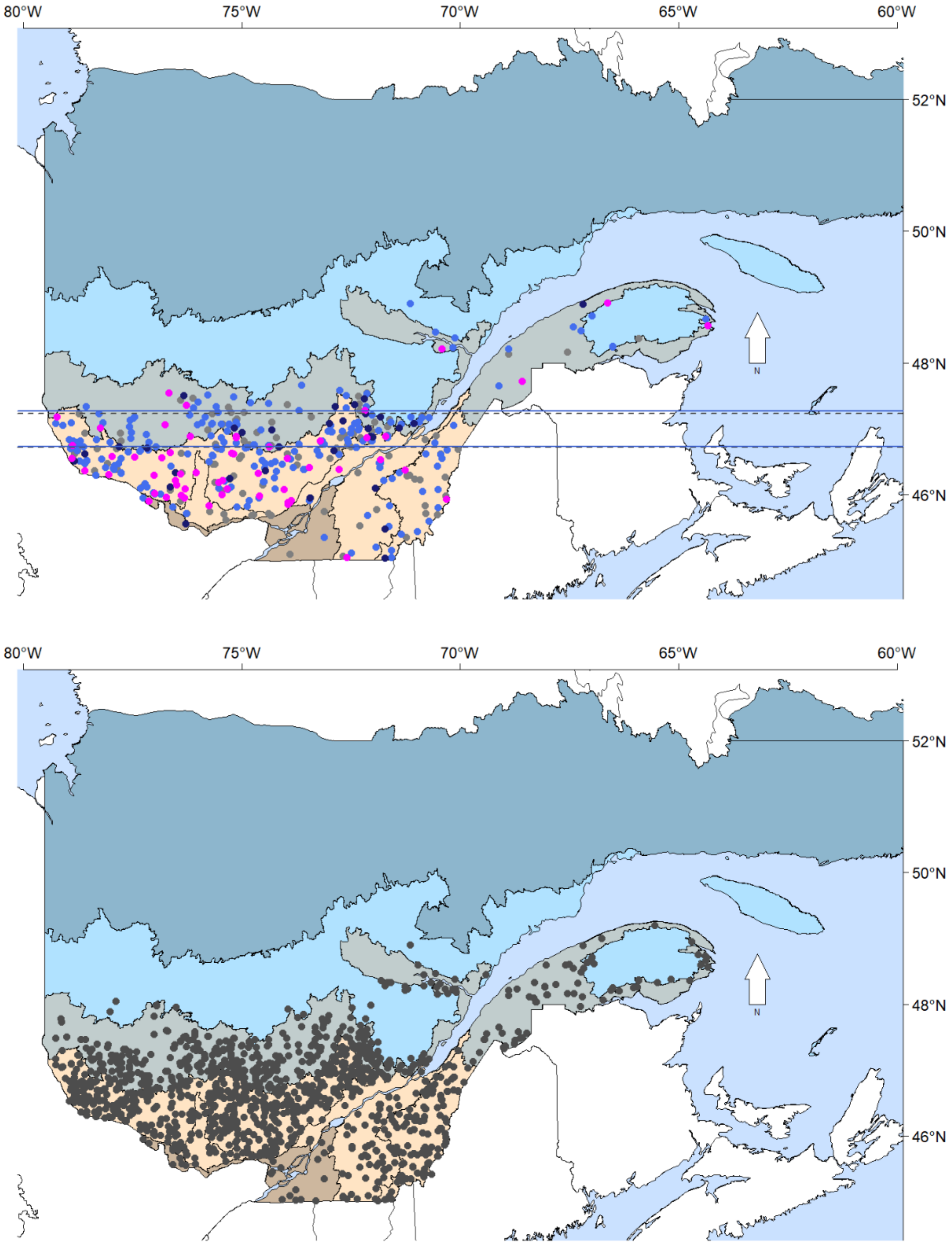
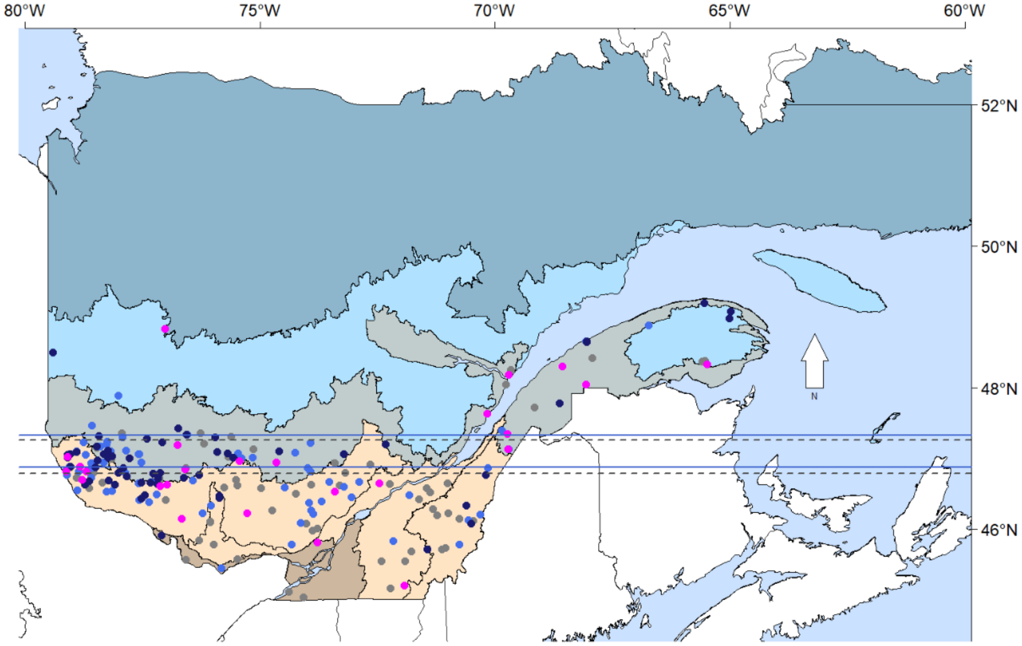


Figure 8.2.3.5: Map of plots occupied by saplings of Thuja occidentalis in P_1 (1970-1977) and P_3 (2003-2015). Dark blue points are plots occupied by saplings in P_1 and P_3. Grey points are plots occupied by saplings in P_1 but where saplings are absent in P_3. Magenta points are plots occupied by saplings in P_3 where the species was not observed in P_1 (all stems >1.1cm diameter at breast height). Light blue points are plots occupied by saplings in P_3 where the species was observed in P_1. Lower horizontal lines = 50th percentile of latitude; Upper horizontal lines = 90th. Dashed grey = P_1 (1970-1977); Blue = P_3 (2003-2015). (Bottom) Map of plots occupied by species in P_1 (1970-1977, all stems > 1.1 cm diameter at breast height).



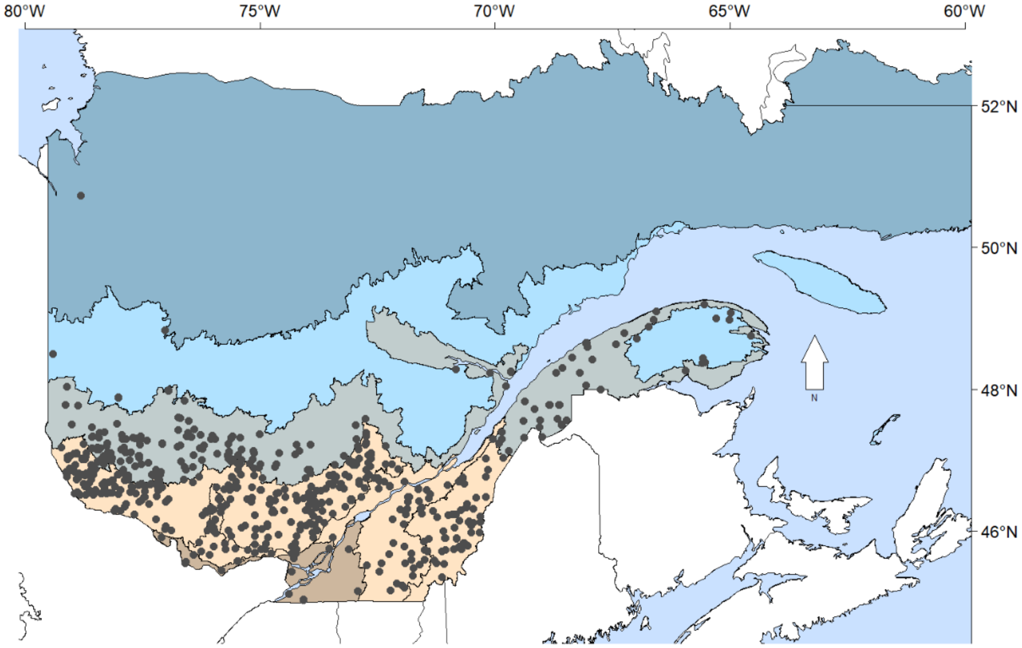
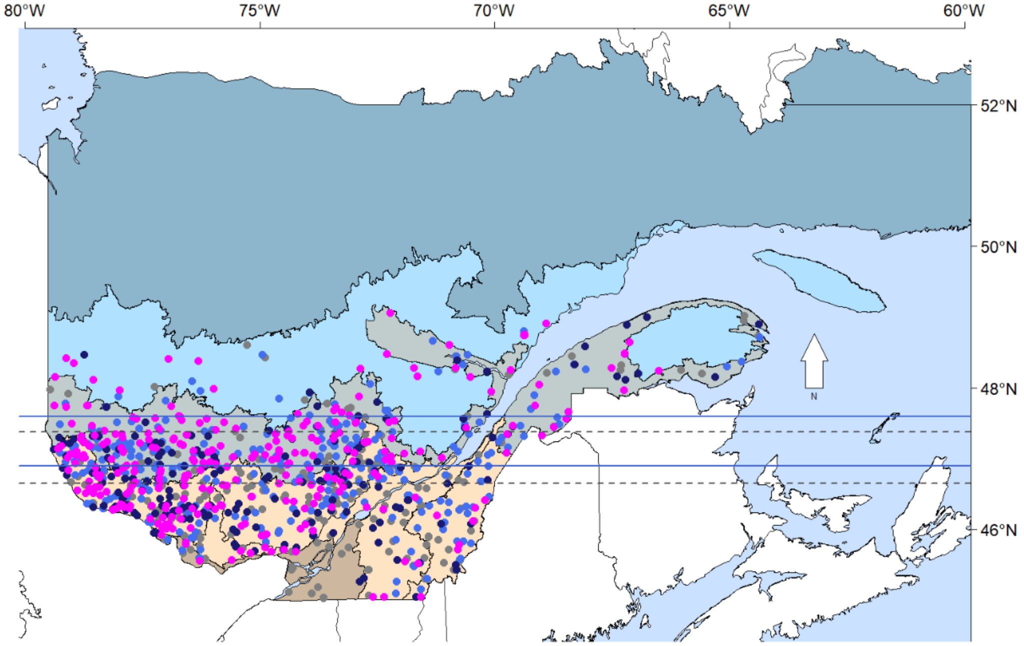


Figure 8.2.3.6: Map of plots occupied by saplings of Acer rubrum in P_1 (1970-1977) and P_3 (2003-2015). Dark blue points are plots occupied by saplings in P_1 and P_3. Grey points are plots occupied by saplings in P_1 but where saplings are absent in P_3. Magenta points are plots occupied by saplings in P_3 where the species was not observed in P_1 (all stems >1.1cm diameter at breast height). Light blue points are plots occupied by saplings in P_3 where the species was observed in P_1. Lower horizontal lines = 50th percentile of latitude; Upper horizontal lines = 90th. Dashed grey = P_1 (1970-1977); Blue = P_3 (2003-2015). (Bottom) Map of plots occupied by species in P_1 (1970-1977, all stems > 1.1 cm diameter at breast height).



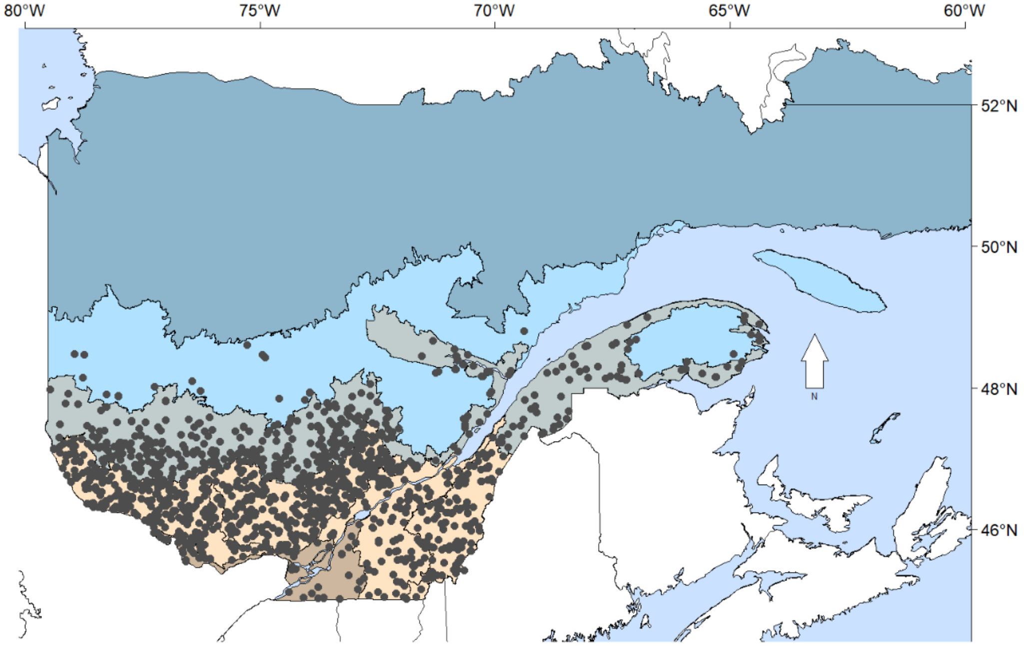


Figure 8.2.3.7: Map of plots occupied by saplings of Populus tremuloides in P_1 (1970-1977) and P_3 (2003-2015). Dark blue points are plots occupied by saplings in P_1 and P_3. Grey points are plots occupied by saplings in P_1 but where saplings are absent in P_3. Magenta points are plots occupied by saplings in P_3 where the species was not observed in P_1 (all stems >1.1cm diameter at breast height). Light blue points are plots occupied by saplings in P_3 where the species was observed in P_1. Lower horizontal lines = 50th percentile of latitude; Upper horizontal lines = 90th. Dashed grey = P_1 (1970-1977); Blue = P_3 (2003-2015). (Bottom) Map of plots occupied by species in P_1 (1970-1977, all stems > 1.1 cm diameter at breast height).

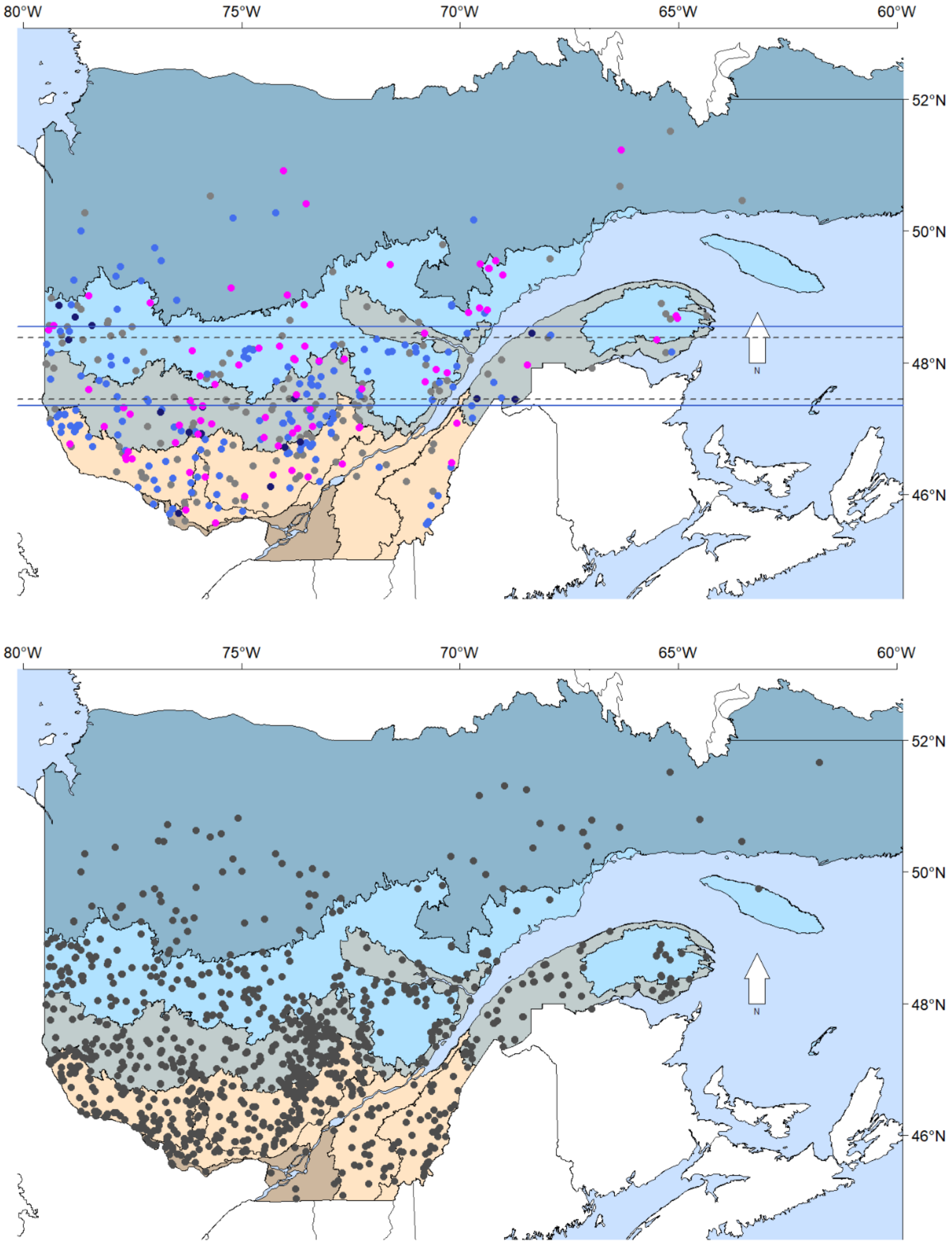
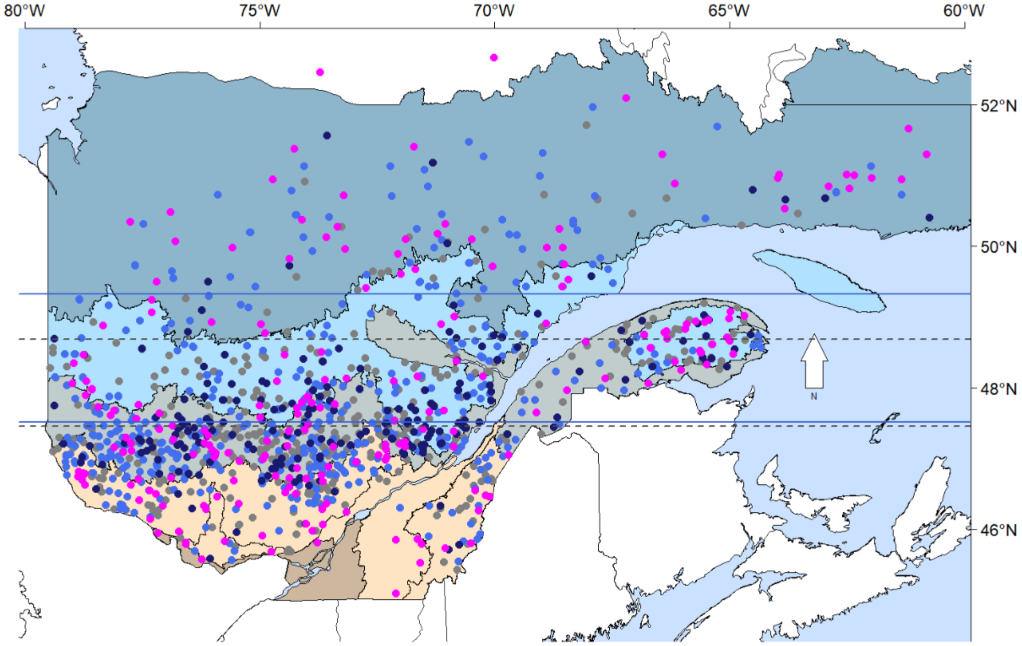
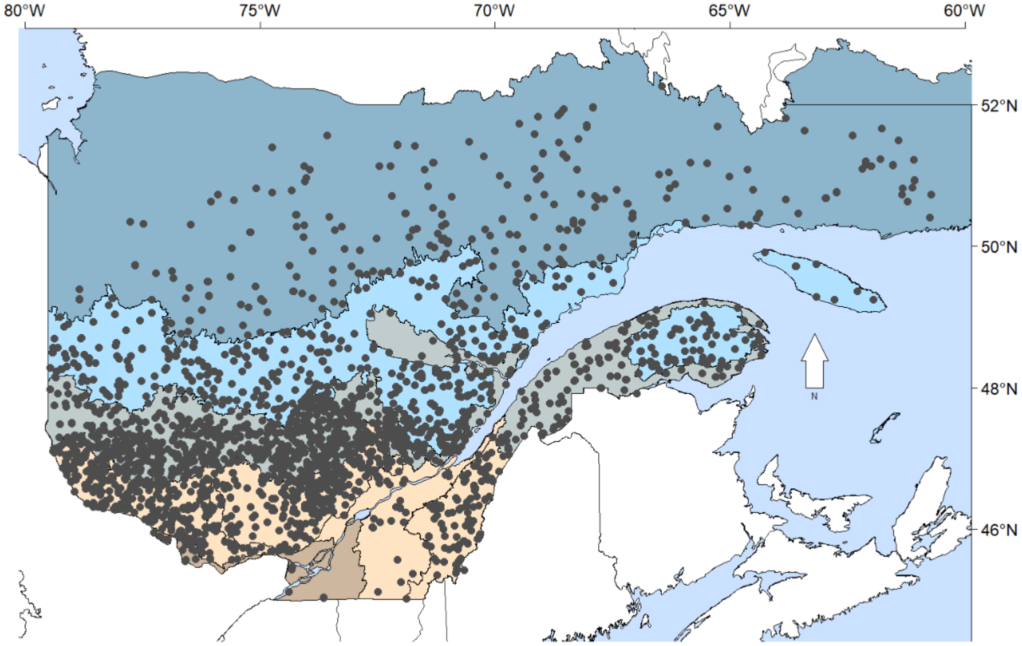


Figure 8.2.3.8: Map of plots occupied by saplings of Betula papyrifera in P_1 (1970-1977) and P_3 (2003-2015). Dark blue points are plots occupied by saplings in P_1 and P_3. Grey points are plots occupied by saplings in P_1 but where saplings are absent in P_3. Magenta points are plots occupied by saplings in P_3 where the species was not observed in P_1 (all stems >1.1cm diameter at breast height). Light blue points are plots occupied by saplings in P_3 where the species was observed in P_1. Lower horizontal lines = 50th percentile of latitude; Upper horizontal lines = 90th. Dashed grey = P_1 (1970-1977); Blue = P_3 (2003-2015). (Bottom) Map of plots occupied by species in P_1 (1970-1977, all stems > 1.1 cm diameter at breast height).





8.3 – Appendices to Chapter 4

8.3.1 – Appendix 1: Supplemental methods and results for The relationship between climate change, disturbances, and sapling recruitment

Methods- Defining suitable absences

To define the area where species could realistically colonize and establish, we selected suitable 'absences' using a consensus modelling approach (Guisan and Zimmermann 2000) similar to previous studies in this area (Chambers et al. 2013, Beauregard and de Blois 2014, Périé and de Blois 2016). Species presence/absence, as defined by the suitable climatic area for both saplings and trees together, was associated with growing degree days (base 5ºC, 1965-2014), average annual total precipitation (1965-2014), average minimum January temperature (1965-2014), humus type, surface deposit, drainage, cardinal direction, and soil texture of B horizon, recorded during the inventory. The climate data was obtained from Environment Canada weather station data interpolated to a 1km resolution using BioSIM (Regnière and Saint-Amant 2014). Edaphic and topographic variables were obtained directly from the field inventories from the *Ministère des Forêts, de la Faune et des Parcs* of Québec (MFFP) (Ministère des Forêts 2015).

In the inventories, plots were paired (main and satellite) on the landscape, separated by ~425m as they represented about one day's work for a field crew. Paired plots were merged into a single occurrence of presence/absence to account for potential spatial autocorrelation in climate variables. Plots were not averaged to avoid merging edaphic conditions, which can vary considerably even over distances of 425m. Instead, species presence/absence and its associated climatic and edaphic information were retained from the main plot *a priori* (either species present or absent from both main and satellite or only present in the main). If absent in the main but present in the satellite, then the satellite plot was used.

In the species distribution modelling step, a clustering algorithm (Harrell et al. 1984) was used to select the most parsimonious climate variables from a set of 13 climatic variables, as per (Beauregard and de Blois 2014) : Average annual temperature (°C), Annual temperature range (coldest month, warmest month), (C°) Growing degree days (5°C base temperature), Growing degree days accumulated within the frost free period, Julian date of the last spring freeze, Julian date of the first fall freeze, Length of frost free period (days), Julian date when the sum of growing degree days reaches 100, Total annual precipitation (mm), Total precipitation from April to September (mm), Total precipitation of the wettest month (mm), Total precipitation of the driest month (mm). The varclus algorithm in the Hmisc package (version 3.16-0; Harrell, 2013) uses the Spearman correlation coefficient to perform a hierarchical clustering analysis. Variables were selected based on high R^2 within a cluster and low R^2 between clusters. Three climatic variables were retained for the species distribution model step: 1) Growing degree days (base 5°C), 2) minimum temperature for the winter months (December to February) and 3) total annual precipitation. Selected climatic variables were further checked for multicollinearity. Minimum temperature was moderately correlated with growing degree days (0.63) but was retained for its biological importance and East-West spatial structuring. A species distribution modelling under consensus approach was done using the BIOMOD2 package (Thuiller et al., 2016), with Generalized Linear Models, Generalized additive models, Classification tree analysis, Random Forest, Flexible discriminant analysis. An ensemble model was built as the consensus of the five aforementioned models. A probability cut-off that determines whether a plot is suitable or not was calculated by maximizing both model sensitivity (ability to accurately predict presence) while balancing for model specificity (ability to accurately predict absence). Because we were concerned with accurate plot presence over absences, the model sensitivity was set at 95%, or the ability to accurately predict 95% of presences, with no cut-off set for absences. The cutoff was used to convert model probabilities into a binary presence/absence response. These bioclimatic conditions were used to restrict absences in the next step to the zone where a species can realistically establish.

Table 8.3.1.1: Model performance from the species distribution models to define the suitable area for four species. Presence of a species was considered over all plots where the species was observed, either in P1 and/or P3 (from 1970-1977 or 2003-2014). Variables included growing degree days (base 5oC), Annual precipitation, Minimum January temperature, humus type, surface deposit, drainage, cardinal direction, and soil texture of B horizon.

	Model performance	**Most important variables**		
	Area under ROC	1st	2nd	3rd
Acer rubrum	0.924	gdd5	Min. January temperature	Surface deposit
Acer saccharum	0.957	gdd5	Humus type	Min. January temperature
Betula alleghaniensis	0.911	gdd5	Min. January temperature	Annual precipitation
Fagus grandifolia	0.961	gdd5	Min. January temperature	Annual precipitation

Methods - Multimodel selection approach

In this step, a generalized linear mixed model approach with a logistic response (1 = sapling gain, i.e. species not observed in P_1, but observed in P_3; 0 = absence, i.e., no recruitment at a site that was suitable for a species, see above for details) was used to evaluate the relationship between explanatory variables and the probability of observing a gain. Candidate models were constructed under a multimodel selection approach (Burnham and Anderson 2002) based on a pre-determined set of hypotheses about the types of climate or disturbances that could influence dynamics of species occurrence. Pre-analyses evaluated the best model from each type: a) climate differences only (called Δ climate – Model 1) and b) disturbance only (Model 2). The best model from Δ climate and disturbance was assessed on the lowest AICc value and highest Akaike weight.

Δ *Climate models*

Climate change variables (hereafter referred to as Δ Climate) were selected for the different trends they can represent and their biological importance (Table S5, Model 1). Average annual variables (both precipitation and temperature) are commonly used to assess relationship with climate (e.g. Fei et al. 2017). However, climatic variables related to timing of key biological events (phenology, extension of growing season) could elicit a stronger response (Cavanaugh et al. 2014). Δ *Climate v*ariables were calculated as the difference between average values for the five years preceding the recorded observation in the inventory (mean climate value in P_3 minus mean climate value in P_1, e.g. P_1 observation in 1975, average value over 1970-1975). Tmin (minimum temperature of month (12)/season (4)/year), Tmax (maximum temperature of month (12)/season (4)/year), Tmean (mean temperature of month (12)/season (4)/year) and total precipitation (annual/ seasonal (4), growing season precipitation (1)/monthly (12)) were calculated as well as monthly (12) and annual growing degree days (base 5ºC). This large set of potential Δ Climate variables was evaluated using variable clustering using the Hmisc package in R 3.2.2 (Harrell Jr 2013) to avoid multicollinearity. Therefore, 13 Δ climate variables were selected and grouped into 4 models (see below). All variables had a correlation of less than 0.6 between individual and groups of variables.

Disturbance

Four types of disturbances were recorded in both time periods: logging, fire, windthrow and insect outbreaks. They were further combined into 2 classes, anthropogenic (logging) and natural (fire, windthrow, insect outbreaks), because of the low prevalence of each of the natural disturbances on the landscape. Severity of disturbance was also recorded: none (<25% of plot affected), light (25-75% of plot affected) and severe (>75% of plot affected) but was not found to provide additional information (not shown). Disturbance variables were grouped into 4 models, based on their type and timing (Table 8.5.1, Model 2).

Table 8.3.1.2: Models used to test relationship of climate change (Δ C), disturbance, and their interaction in explaining recruitment events, i.e. where a given species (saplings) was absent in P_1, but present in P_3 (denoted as Occ_{gain}).

	Model type	**Variables included** *(Response ~ Explanatory)*
Model 1: Best Δ Climate (Δ C) model		
1a	Annual Δ C	Occ_{gain} ~ Annual Δgdd5 + Annual Δprecip + *1|LongGroup*
1b	Seasonal Δ C	Occ_{gain} ~ Winter ΔTmin + Fall ΔTmean + Spring ΔTmin + Summer ΔTmax + Growing season Δprecip + *1|LongGroup*
1c	Monthly Δ C	Occ_{gain} ~ March ΔTmax + July ΔTmax + January ΔTmin + July Δprecip + *1|LongGroup*
1d	Early & late growing season Δ C	Occ_{gain} ~ April Δgdd5 + October Δgdd5 + *1|LongGroup*
Model 2: Best Disturbance (Dist) model		
2a	Dist type P_1	Occ_{gain} ~ Logging P_1 + Natural P_1 + *1|LongGroup*
2b	Dist type P_3	Occ_{gain} ~ Logging P_3 + Natural P_3 + *1|LongGroup*
2c	Dist Presence	Occ_{gain} ~ Disturbance + New disturbance P_3 + *1|LongGroup*
2d	Dist timing	Occ_{gain} ~ Disturbance P_1 + Disturbance P_3 + *1|LongGroup*
Models 3-6: Combined models		
3	Best Δ climate + Best disturbance	Occ_{gain} ~ $ΔC_{best}$ + $Dist_{best}$ + *1|LongGroup*
4	Interaction - Best Δ climate + Best disturbance	Occ_{gain} ~ $ΔC_{best}$ + $Dist_{best}$ + $ΔC_{best}$ x $Dist_{best}$ + *1|LongGroup*
5	Interaction - Climate gradient & Δ Climate (Entire area only)	Occ_{gain} ~ $ΔC_{best}$ + $Dist_{best}$ + CGr + $ΔC_{best}$ x CGr + *1|LongGroup*
6	Interaction - Climate gradient & Disturbance (Entire area only)	Occ_{gain} ~ $ΔC_{best}$ + $Dist_{best}$ + CGr + $Dist_{best}$ x CGr + *1|LongGroup*
Model 7 - Null Model		
7	Null model	Occ_{gain} ~ *1|LongGroup*

The best Δclimate variable from Model 1 and best disturbance variable from Model 2 were selected based on the highest absolute Wald z value, as obtained from the model outputs and were used to construct Models 3 through 6. Models 3-6 tested all possible interactions between the best Δ climate variable, the best disturbance variable, as well as the average length of the growing season for 1998-2014 (P_3). When considering the entire suitable area, growing season length in P_3 was included to assess its importance for occurrence gains, specifically whether position along the average climatic gradient influenced the importance of Δ climate or disturbance in the model**.** All climate variables were scaled along the z distribution to minimize scale conflicts which can adversely affect interpretability of GLMM outputs. They were not however centered to preserve the direction of climatic change. The Wald z score from the models was used to compare standardized variable support across each combination of predictor variable category and species distribution area.

References

Saucier J.-P., P. Grondin, A. Robitaille and J.-F. Bergeron. 2003. Vegetation zones and bioclimatic domains in Quebec. Direction des Inventaires Forestiers, Ministère des Forêts, Faune et Parcs. Available from http://www.mrn.gouv.qc.ca/forets/connaissances/connaissances-inventaire-zones-carte.jsp#erabBouleau. Last accessed 6 December 2017.

Thuiller, W., Georges, D., Engler, R., Breiner, F., Georges, M. D., & Thuiller, C. W. (2016). Package 'biomod2'. R package 3.3.7. [Computer software]. Available from https://cran.r-project.org/web/packages/biomod2/index.html

8.3.2 – Appendix 2: Supplemental results from Disentangling the relationship between climate change, disturbances, and sapling recruitment.

Table 8.3.2.1: AICc scores for all partial (climate or disturbance) and full models (includes interactions between climate and disturbance, average climate and disturbance and average climate and climate). Scores are presented by species (4: Acer rubrum, Acer saccharum, Betula alleghaniensis, Fagus grandifolia) and area considered (Entire suitable, <50th, >50th, >90th). Model with lowest AICc value per grouping is highlighted in bold.

All

		K	AICc	Δ AICc		AICcWt		LL
Δ Climate				Group	Best	Group	Best	
	Average annual differences	4	706.91	3.36		0.141		-352.59
	Seasonal changes in temps and precip	6	709.89	6.34		0.032		-343.56
	Changes in selected monthly variables	6	708.22	4.67		0.073		-340.16
	Changes in early and late growing season variables	4	703.55	0	3.39	0.755	0.054	-343.81
Disturbance								
	Human vs. natural disturbance (P1: 1970-1977)	4	701.03	0	0.87	0.496	0.191	-346.5
	Timing of disturbance	4	702.45	1.42		0.244		-347.21
	Human vs. natural disturbance (P3: 2003-2014)	4	707.44	6.41		0.02		-349.7
	Presence of disturbance	4	702.48	1.45		0.24		-347.22
Best models								
	Δ Climate+Disturbance	4	700.16		0		0.295	-346.06
	Δ Climate+Disturbance+Δ Climate*Disturbance	5	700.65		0.49		0.231	-345.3
	Δ Climate+Disturbance+Length of growing season	5	702.18		2.02		0.108	-346.06
	Δ Climate+Disturbance*Length of growing season	6	704.07		3.91		0.042	-346
8.5	Δ Climate*Length of growing season+Disturbance	6	703.92		3.75		0.045	-345.92
	Null	2	704.51		4.35		0.034	-350.25

<50th

	K	AICc	Δ AICc		AICcWt		LL
Δ Climate			Group	Best	Group	Best	
Average annual differences	4	293.66	5.1		0.068		-142.78
Seasonal changes in temps and precip	6	298.44	9.88		0.006		-143.12
Changes in selected monthly variables	6	293.92	5.36		0.059		-140.86
Changes in early and late growing season variables	4	288.56	0	1.2	0.867	0.212	-140.23
Disturbance							
Human vs. natural disturbance (P1: 1970-1977)	4	293.81	0	6.46	0.327	0.015	-142.86
Timing of disturbance	4	294.31	0.5		0.254		-143.11
Human vs. natural disturbance (P3: 2003-2014)	4	295.97	2.15		0.111		-143.94
Presence of disturbance	4	293.93	0.12		0.308		-142.92
Best models							
Δ Climate+Disturbance	4	287.78		0.42		0.314	-139.84
Δ Climate+Disturbance+Δ Climate*Disturbance	5	287.36		0		0.387	-138.61
Null	2	291.94		3.38		0.071	-143.96

>50th

	K	AICc	Δ AICc		AICcWt		LL
Δ Climate			Group	Best	Group	Best	
Average annual differences	4	414.73	5.66		0.028		-203.34
Seasonal changes in temps and precip	6	415.35	6.28		0.021		-201.62
Changes in selected monthly variables	6	409.12	0.05		0.469		-198.51
Changes in early and late growing season variables	4	409.08	0	3.23	0.481	0.109	-200.51
Disturbance							
Human vs. natural disturbance (P1: 1970-1977)	4	409.34	0	3.49	0.662	0.096	-200.65
Timing of disturbance	4	412.57	3.23		0.132		-202.26
Human vs. natural disturbance (P3: 2003-2014)	4	414.04	4.7		0.063		-202.99
Presence of disturbance	4	412.41	3.07		0.143		-202.18
Best models							
Δ Climate+Disturbance	4	405.85		0		0.549	-198.9
Δ Climate+Disturbance+Δ Climate*Disturbance	5	407.7		1.85		0.218	-198.81
Null	2	411.75		5.9		0.029	-203.87

>90th

	K	AICc	Δ AICc	AICcWt	LL

Δ Climate			Group	Best	Group	Best	
Average annual differences	4	324.97	4.53		0.075		-158.46
Seasonal changes in temps and precip	6	327.82	7.37		0.018		-157.84
Changes in selected monthly variables	6	319.23	0	0	0.724	0.406	-154.16
Changes in early and late growing season variables	4	323.2	2.75		0.183		-157.57
Disturbance							
Human vs. natural disturbance (P1: 1970-1977)	4	325.25	0.21		0.319		-158.6
Timing of disturbance	4	326.13	1.09		0.206		-159.04
Human vs. natural disturbance (P3: 2003-2014)	4	327.21	2.17		0.12		-159.58
Presence of disturbance	4	325.04	0	5.81	0.355	0.022	-158.49
Best models							
Δ Climate+Disturbance	4	319.37		0.14		0.379	-155.66
Δ Climate+Disturbance+Δ Climate*Disturbance	5	321.19		1.96		0.152	-155.55
Null	2	323.84		4.61		0.041	-159.91

Table 8.3.2.2: Model coefficients for those considered in second selection, including best partial model (climate and disturbance) and full models (includes interactions between climate and disturbance, average climate and disturbance and average climate and climate). Coefficients and significance are presented by species (4: *Acer rubrum*, *Acer saccharum*, *Betula alleghaniensis*, *Fagus grandifolia*) and area considered (Entire suitable, <50th, >50th, >90th). Model with lowest AICc value per grouping is highlighted in green. In each model, the best single variable (by absolute z score) is indicated by the red text. Significance levels: p<0.1: .; p<0.05: *; p<0.01: **, p<0.001: ***

		Fagus grandifolia								
		Model1			Model2			Model3		
	Variable	Coef	SE	z score	Coef	SE	z score	Coef	SE	z score
All	October gdd5	0.311	0.128	2.436*				0.269	0.131	2.051*
All	Natural P1				-1.093	0.527	-2.074 *	-0.921	0.528	-1.744 .
All	gdd5_9814									
All	October gdd5 * Natural P1									
All	gdd5_9814 * Natural P1									
All	gdd5_9814*October gdd5									
<50th	April gdd5	-0.666	0.223	-2.986**				-0.641	0.259	-2.477*
<50th	Logging P1				-0.638	0.457	-1.397	-0.707	0.459	-1.540
<50th	April gdd5 * Logging P1									
>50th	October gdd5	0.273	0.151	1.807 .				0.278	0.139	2.004*
>50th	Natural P1				-1.518	0.732	-2.073 *	-1.275	0.735	-1.734 .
>50th	October gdd5 * Natural P1									
>90th	July precip	0.636	0.188	3.379***				0.518	0.196	2.638**
>90th	Disturbed in either period				-0.530	0.367	-1.446	-0.553	0.319	-1.734 .
>90th	July precip * disturbed									

		Model4			Model5			Model6		
	Variable	Coef	SE	z score	Coef	SE	z score	Coef	SE	z score
All	October gdd5	0.283	0.132	2.148*	0.269	0.133	2.022 *	0.152	0.261	0.583
All	Natural P1	-2.571	1.848	-1.391	-1.194	1.007	-1.186	-0.958	0.536	-1.786 .
All	gdd5_9814				-0.015	0.171	-0.086	-0.002	0.170	-0.011
All	October gdd5 * Natural P1	-1.250	1.200	-1.042						
All	gdd5_9814 * Natural P1				0.391	1.171	0.334			
All	gdd5_9814*October gdd5							0.104	0.197	0.528
<50th	April gdd5	-0.769	0.276	-2.789 **						
<50th	Logging P1	-2.273	1.126	-2.018 *						
<50th	April gdd5 * Logging P1	1.099	0.656	1.674.						
>50th	October gdd5	0.286	0.140	2.039 *						
>50th	Natural P1	-1.842	1.717	-1.073						
>50th	October gdd5 * Natural P1	-0.479	1.213	-0.395						
>90th	July precip	0.588	0.247	2.375 *						
>90th	Disturbed in either period	-0.550	0.320	-1.716 .						
>90th	July precip * disturbed	-0.164	0.351	-0.468						

		Acer saccharum								
		Model1			Model2			Model3		
	Variable	Coef	SE	z score	Coef	SE	z score	Coef	SE	z score
All	gdd5_diff	-0.236	0.341	-0.691				-0.245	0.326	-0.752
All	Natural P3				-0.838	0.521	-1.610	-0.885	0.517	-1.711 .
All	gdd5_9814									

All	gdd5 * Natural P3									
All	gdd5_9814 * Natural P3									
All	gdd5_9814 * gdd5_diff									
<50th	gdd5_diff	-2.532	0.802	-3.158**				-2.324	0.802	-2.897**
<50th	New disturbance P3				0.434	0.472	0.920	0.271	0.371	0.731
<50th	gdd5_diff* New disturbance P3									
>50th	April gdd5	0.496	0.233	2.125*				0.500	0.219	2.281*
>50th	Logging P3				0.388	0.243	1.597	0.467	0.241	1.935 .
>50th	April gdd5 * Logging P3									
>90th	April gdd5	0.350	0.545	0.644				0.208	0.506	0.411
>90th	Natural P3				-1.374	1.033	-1.330	-1.465	1.026	-1.428
>90th	April gdd5 * Natural P3									

		Model4			Model5			Model6		
Variable		Coef	SE	z score	Coef	SE	z score	Coef	SE	z score
	gdd5_diff	-0.230	0.327	-0.703	-0.427	0.359	-1.189	0.040	0.350	0.113
All	Natural P3	-0.302	1.612	-0.188	-0.678	0.651	-1.041	-0.831	0.520	-1.599
All	gdd5_9814				0.272	0.142	1.918 .	0.969	0.313	3.094***
All	gdd5 * Natural P3	-0.814	2.189	-0.372						
All	gdd5_9814 * Natural P3				-0.298	1.030	-0.289			
All	gdd5_9814 * gdd5_diff							-1.099	0.449	-2.45*
All										
<50th	gdd5_diff	-2.515	0.908	-2.771**						
<50th	New disturbance P3	-0.240	1.189	-0.202						
<50th	gdd5_diff* New disturbance P3	0.825	1.806	0.457						
>50th	April gdd5	0.560	0.257	2.179*						

>50th	Logging P3	0.649	0.478	1.357
>50th	April gdd5 * Logging P3	-0.201	0.462	-0.436
>90th	April gdd5	0.320	0.506	0.634
>90th	Natural P3	0.802	1.166	0.688
>90th	April gdd5 * Natural P3	-10.838	8.314	-1.304

	Betula alleghaniensis									
		Model1			Model2			Model3		
	Variable	Coef	SE	z score	Coef	SE	z score	Coef	SE	z score
All	Summer Tmax	0.458	0.227	2.023*				0.456	0.194	2.356*
All	Logging P1				0.417	0.213	1.961*	0.514	0.211	2.436*
All	gdd5_9814									
All	Summer Tmax * Logging P1									
All	gdd5_9814 * Logging P1									
All	gdd5_9814 *Summer Tmax									
<50th	April gdd5	-0.584	0.256	-2.283*				-0.547	0.257	-2.13*
<50th	Logging P1				0.530	0.300	1.767 .	0.510	0.298	1.713 .
<50th	April gdd5 * Logging P1									
>50th	April gdd5	0.604	0.324	1.864 .				0.406	0.295	1.377
>50th	Natural P1				-1.046	0.604	-1.732 .	0.352	0.301	1.170
>50th	April gdd5* Natural P1									
>90th	Annual gdd5	-0.519	0.632	-0.822				-0.252	0.586	-0.430
>90th	Logging P1				-0.082	0.647	-0.126	-0.102	0.648	-0.157
>90th	Annual gdd5 * Logging P1									

		Model4			Model5			Model6		
	Variable	Coef	SE	z score	Coef	SE	z score	Coef	SE	z score
All	Summer Tmax	0.335	0.214	1.562	0.516	0.199	2.594**	0.549	0.219	2.511 *
All	Logging P1	0.158	0.368	0.430	0.203	0.287	0.708	0.512	0.211	2.427 *
All	gdd5_9814				-0.334	0.179	-1.871 .	-0.106	0.223	-0.472
All	Summer Tmax * Logging P1	0.477	0.390	1.222						
All	gdd5_9814 * Logging P1				0.550	0.318	1.727 .			
All	gdd5_9814 *Summer Tmax							-0.130	0.297	-0.436
<50th	April gdd5	-0.528	0.298	-1.772 .						
<50th	Logging P1	0.588	0.699	0.841						
<50th	April gdd5 * Logging P1	-0.062	0.498	-0.124						
>50th	April gdd5	0.489	0.345	1.415						
>50th	Natural P1	0.571	0.565	1.010						
>50th	April gdd5* Natural P1	-0.298	0.662	-0.450						
>90th	Annual gdd5	-0.215	0.623	-0.345						
>90th	Logging P1	0.033	1.059	0.031						
>90th	Annual gdd5 * Logging P1	-0.282	1.796	-0.157						

Acer rubrum

		Model1			Model2			Model3		
	Variable	Coef	SE	z score	Coef	SE	z score	Coef	SE	z score
All	October gdd5	-0.142	0.069	-2.046*				-0.158	0.069	-2.299*
All	Logging P1				-0.831	0.219	-3.801***	-0.859	0.216	-3.972***
All	gdd5_9814									
All	October gdd5 * Logging P1									
All	gdd5_9814*Logging P1									
All	gdd5_9814*October gdd5									

<50th	October gdd5	-0.198	0.120	-1.652 .				-0.199	0.120	-1.658 .
<50th	Natural P1				0.769	0.374	2.057*	0.727	0.345	2.106*
<50th	October gdd5 * Natural P1									
>50th	October gdd5	-0.153	0.092	-1.668 .				-0.103	0.085	-1.209
>50th	Logging P1				-1.276	0.325	-3.923***	-1.244	0.324	-3.839***
>50th	October gdd5 * Logging P1									
>90th	October gdd5	-0.337	0.199	-1.694 .				-0.397	0.182	-2.182*
>90th	Logging P1				-1.003	0.543	-1.847 .	-0.929	0.543	-1.711 .
>90th	October gdd5 * Logging P1									
		Model4			Model5			Model6		
	Variable	Coef	SE	z score	Coef	SE	z score	Coef	SE	z score
All	October gdd5	-0.119	0.072	-1.638	-0.201	0.073	-2.757**	-0.274	0.101	-2.714**
All	Logging P1	-1.101	0.282	-3.898***	-1.501	0.342	-4.39***	-0.860	0.217	-3.965***
All	gdd5_9814				-0.372	0.125	-2.976**	-0.208	0.122	-1.709 .
All	October gdd5 * Logging P1	-0.358	0.228	-1.575						
All	gdd5_9814*Logging P1				0.937	0.324	2.887**			
All	gdd5_9814*October gdd5							0.107	0.108	0.992
<50th	October gdd5	-0.178	0.123	-1.448						
<50th	Natural P1	0.037	1.002	0.037						
<50th	October gdd5 * Natural P1	-0.516	0.676	-0.763						
>50th	October gdd5	-0.108	0.089	-1.222						
>50th	Logging P1	-1.227	0.333	-3.685***						
>50th	October gdd5 * Logging P1	0.071	0.340	0.209						
>90th	October gdd5	-0.365	0.189	-1.93 .						

>90th	Logging P1	-1.081	0.636	-1.7 .
>90th	October gdd5 * Logging P1	-0.439	0.734	-0.598

Table 8.3.2.3: Model coefficients for the partial climate model of *Fagus grandifolia* (American beech). Coefficients and significance are presented by area considered (Entire suitable, <50th, >50th, >90th). Model with lowest AICc value per grouping is highlighted in green. In each model, the best single variable (by absolute z score) is indicated by the red text.

	Entire suitable distribution				**<50th**			
Model 1: Average annual differences								
Variables	**Est.**	**SE**	**Wald z**	**Pr(>|z|)**	**Est.**	**SE**	**Wald z**	**Pr(>|z|)**
(Intercept)	-2.103	0.391	-5.375	0.000	-1.188	0.714	-1.665	0.096
Δ Annual gdd5	-0.625	0.494	-1.264	0.206	-1.046	0.793	-1.318	0.188
Δ Total Annual Precipitation	0.013	0.174	0.072	0.943	-0.509	0.359	-1.418	0.156

Random effects:								
Groups	**Variance**	**Std.Dev.**			**Variance**	**Std.Dev.**		
LongGroup2	0.203	0.450			0.025	0.158		
Model 2: Seasonal changes in temps and precip								
Variables	**Est.**	**SE**	**Wald z**	**Pr(>|z|)**	**Est.**	**SE**	**Wald z**	**Pr(>|z|)**
(Intercept)	-2.517	0.524	-4.800	0.000	-2.312	1.092	-2.118	0.034
ΔWinter Minimum Temperature	-0.362	0.412	-0.881	0.379	-0.679	0.707	-0.960	0.337
ΔFall Mean Temperature	0.514	0.389	1.321	0.187	0.488	0.562	0.869	0.385
ΔSummer Maximum Temperature	-0.050	0.270	-0.186	0.853	-0.200	0.473	-0.424	0.672
ΔTotal Growing Season Precipitation	0.048	0.191	0.252	0.801	0.098	0.597	0.164	0.870
Random effects:								
Groups	**Variance**	**Std.Dev.**			**Variance**	**Std.Dev.**		
LongGroup2	0.113	0.336			0.726	0.852		
	Model 3: Changes in selected monthly variables							
	Est.	**SE**	**Wald z**	**Pr(>|z|)**	**Est.**	**SE**	**Wald z**	**Pr(>|z|)**
(Intercept)	-2.570	0.294	-8.730	<2e-16	-1.519	0.546	-2.785	0.005
ΔJanuary Minimum Temperature	0.710	0.445	1.596	0.111	0.307	0.694	0.443	0.658
ΔMarch Maximum Temperature	-0.537	0.327	-1.643	0.100	-0.945	0.500	-1.891	0.059
ΔJuly Maximum Temperature	0.180	0.223	0.807	0.419	0.228	0.401	0.568	0.570
ΔJuly Total Precipitation	0.163	0.131	1.244	0.214	-0.511	0.303	-1.690	0.091

Random effects:								

Groups	**Variance**	**Std.Dev.**			**Variance**	**Std.Dev.**		
LongGroup2	0.042	0.206			0.061	0.246		
Model 4: Changes in early and late growing season variables								
Variables	**Est.**	**SE**	**Wald z**	**Pr(>|z|)**	**Est.**	**SE**	**Wald z**	**Pr(>|z|)**
(Intercept)	-2.133	0.275	-7.744	0.000	-0.919	0.348	-2.640	0.008
ΔApril gdd5	-0.108	0.160	-0.671	0.502	-0.666	0.223	-2.986	0.003
ΔOctober gdd5	0.311	0.130	2.397	0.017	0.277	0.150	1.851	0.064

Random effects:								
Groups	**Variance**	**Std.Dev.**			**Variance**	**Std.Dev.**		
LongGroup2	0.066	0.258			0.000	0.000		

	>50th				**>90th**			
Model 1: Average annual differences								
Variables	**Est.**	**SE**	**Wald z**	**Pr(>|z|)**	**Est.**	**SE**	**Wald z**	**Pr(>|z|)**
(Intercept)	-2.621	0.532	-4.927	0.000	-3.009	0.649	-4.634	0.000
Δ Annual gdd5	0.006	0.675	0.009	0.993	0.151	0.800	0.189	0.850
Δ Total Annual Precipitation	0.232	0.225	1.031	0.303	0.473	0.282	1.679	0.093

Random effects:								
Groups	**Variance**	**Std.Dev.**			**Variance**	**Std.Dev.**		
LongGroup2	0.051	0.226			0.378	0.615		
Model 2: Seasonal changes in temps and precip								
Variables	**Est.**	**SE**	**Wald z**	**Pr(>|z|)**	**Est.**	**SE**	**Wald z**	**Pr(>|z|)**
(Intercept)	-3.280	0.709	-4.626	0.000	-2.628	0.704	-3.731	0.000
ΔWinter Minimum Temperature	-0.041	0.563	-0.073	0.942	-1.117	0.602	-1.855	0.064
ΔFall Mean Temperature	0.703	0.440	1.599	0.110	1.046	0.503	2.079	0.038
ΔSummer Maximum Temperature	0.161	0.308	0.521	0.602	0.141	0.330	0.427	0.670
ΔTotal Growing Season Precipitation	0.277	0.251	1.103	0.270	0.365	0.290	1.256	0.209
Random effects:								
Groups	**Variance**	**Std.Dev.**			**Variance**	**Std.Dev.**		
LongGroup2	0.000	0.000			0.000	0.000		
Model 3: Changes in selected monthly variables								
	Est.	**SE**	**Wald z**	**Pr(>|z|)**	**Est.**	**SE**	**Wald z**	**Pr(>|z|)**
(Intercept)	-2.959	0.395	-7.491	0.000	-2.549	0.379	-6.724	0.000

ΔJanuary Minimum Temperature	0.899	0.508	1.769	0.077	0.463	0.519	0.893	0.372
ΔMarch Maximum Temperature	-0.488	0.338	-1.445	0.149	-0.673	0.373	-1.805	0.071
ΔJuly Maximum Temperature	0.287	0.211	1.357	0.175	0.390	0.220	1.773	0.076
ΔJuly Total Precipitation	0.336	0.153	2.188	0.029	0.636	0.188	3.379	0.001

Random effects:								
Groups	**Variance**	**Std.Dev.**			**Variance**	**Std.Dev.**		
LongGroup2	0.000	0.000			0.000	0.000		
Model 4: Changes in early and late growing season variables								
Variables	**Est.**	**SE**	**Wald z**	**Pr(>|z|)**	**Est.**	**SE**	**Wald z**	**Pr(>|z|)**
(Intercept)	-2.687	0.352	-7.627	0.000	-2.865	0.390	-7.347	0.000
ΔApril gdd5	0.275	0.258	1.063	0.288	0.364	0.295	1.232	0.218
ΔOctober gdd5	0.273	0.151	1.807	0.071	0.381	0.175	2.173	0.030

Random effects:								
Groups	**Variance**	**Std.Dev.**			**Variance**	**Std.Dev.**		
LongGroup2	0.000	0.000			0.000	0.000		

Table 8.3.2.4: Model coefficients for the partial disturbance model of *Fagus grandifolia* (American beech). Coefficients and significance are presented by area considered (Entire suitable, <50th, >50th, >90th). Model with lowest AICc value per grouping is highlighted in green. In each model, the best single variable (by absolute z score) is indicated by the red text.

	Entire suitable distribution				**<50th**			
	Model 1: Disturbance type in P1 (1970-1977)							
Variables	**Est.**	**SE**	**Wald z**	**Pr(>|z|)**	**Est.**	**SE**	**Wald z**	**Pr(>|z|)**
(Intercept)	-2.353	0.235	-10.022	<2e-16	-2.308	0.436	-5.297	0.000
Logging P1	-0.443	0.271	-1.635	0.102	-0.638	0.457	-1.397	0.162
Natural P1	-1.093	0.527	-2.074	0.038	0.035	0.795	0.045	0.964

Random effects:								
Groups	**Variance**	**Std.Dev.**			**Variance**	**Std.Dev.**		
LongGroup2	0.183	0.428			0.480	0.693		
	Model 2: Disturbance type in P3 (2003-2014)							
Variables	**Est.**	**SE**	**Wald z**	**Pr(>|z|)**	**Est.**	**SE**	**Wald z**	**Pr(>|z|)**
(Intercept)	-2.499	0.237	-10.546	<2e-16	-2.439	0.452	-5.392	0.000
Logging P3	0.056	0.233	0.239	0.811	0.048	0.361	0.133	0.894
Natural P3	-0.662	0.734	-0.902	0.367	0.191	1.094	0.174	0.862
Random effects:								
Groups	**Variance**	**Std.Dev.**			**Variance**	**Std.Dev.**		
LongGroup2	0.177	0.421			0.501	0.708		
	Model 3: Disturbance timing							
Variables	**Est.**	**SE**	**Wald z**	**Pr(>|z|)**	**Est.**	**SE**	**Wald z**	**Pr(>|z|)**
(Intercept)	-2.340	0.247	-9.485	<2e-16	-2.330	0.456	-5.105	0.000
Disturbance (any type) P1	-0.595	0.251	-2.373	0.018	-0.510	0.408	-1.251	0.211
Disturbance (any type) P3	-0.041	0.228	-0.179	0.858	0.059	0.351	0.168	0.866

Random effects:								
Groups	**Variance**	**Std.Dev.**			**Variance**	**Std.Dev.**		
LongGroup2	0.185	0.430			0.498	0.706		
	Model 4: Presence of disturbance vs. new disturbance							
Variables	**Est.**	**SE**	**Wald z**	**Pr(>|z|)**	**Est.**	**SE**	**Wald z**	**Pr(>|z|)**
(Intercept)	-2.350	0.250	-9.411	<2e-16	-2.391	0.463	-5.168	0.000
Presence of disturbance (P1 and/or P3)	-0.596	0.262	-2.270	0.023	-0.440	0.424	-1.037	0.300

New disturbance P3	0.586	0.306	1.917	0.055	0.686	0.485	1.413	0.158

Random effects:								
Groups	**Variance**	**Std.Dev.**			**Variance**	**Std.Dev.**		
LongGroup2	0.186	0.432			0.510	0.714		

	>50th				**>90th**			
	Model 1: Disturbance type in P1 (1970-1977)							
Variables	**Est.**	**SE**	**Wald z**	**Pr(>|z|)**	**Est.**	**SE**	**Wald z**	**Pr(>|z|)**
(Intercept)	-2.379	0.169	######	<2e-16	-2.666	0.313	-8.513	<2e-16
Logging P1	-0.243	0.340	-0.715	0.474	-0.174	0.375	-0.465	0.642
Natural P1	-1.508	0.738	-2.044	0.041	-1.067	0.747	-1.429	0.153

Random effects:								
Groups	**Variance**	**Std.Dev.**			**Variance**	**Std.Dev.**		
LongGroup2	0.007	0.081			0.292	0.540		
	Model 2: Disturbance type in P3 (2003-2014)							
Variables	**Est.**	**SE**	**Wald z**	**Pr(>|z|)**	**Est.**	**SE**	**Wald z**	**Pr(>|z|)**
(Intercept)	-2.542	0.189	######	<2e-16	-2.725	0.319	-8.538	<2e-16
Logging P3	0.074	0.309	0.240	0.810	-0.189	0.372	-0.509	0.611
Natural P3	-1.099	1.029	-1.067	0.286	-0.658	1.030	-0.638	0.523
Random effects:								
Groups	**Variance**	**Std.Dev.**			**Variance**	**Std.Dev.**		
LongGroup2	0.032	0.178			0.315	0.562		
	Model 3: Disturbance timing							
Variables	**Est.**	**SE**	**Wald z**	**Pr(>|z|)**	**Est.**	**SE**	**Wald z**	**Pr(>|z|)**
(Intercept)	-2.360	0.209	######	<2e-16	-2.596	0.337	-7.711	0.000
Disturbance (any type) P1	-0.553	0.320	-1.728	0.084	-0.396	0.353	-1.123	0.262
Disturbance (any type) P3	-0.096	0.304	-0.314	0.753	-0.269	0.360	-0.748	0.455

Random effects:								
Groups	**Variance**	**Std.Dev.**			**Variance**	**Std.Dev.**		
LongGroup2	0.027	0.164			0.315	0.562		
	Model 4: Presence of disturbance vs. new disturbance							
Variables	**Est.**	**SE**	**Wald z**	**Pr(>|z|)**	**Est.**	**SE**	**Wald z**	**Pr(>|z|)**
(Intercept)	-2.334	0.213	######	<2e-16	-2.525	0.337	-7.502	0.000

Presence of disturbance (P1 and/or P3)	-0.603	0.337	-1.787	0.074	-0.530	0.367	-1.446	0.148
New disturbance P3	0.426	0.399	1.069	0.285	-0.020	0.488	-0.040	0.968

Random effects:								
Groups	**Variance**	**Std.Dev.**			**Variance**	**Std.Dev.**		
LongGroup2	0.026	0.161			0.314	0.560		

Table 8.3.2.5: Model coefficients for the partial climate model of *Acer saccharum* (Sugar maple). Coefficients and significance are presented by area considered (Entire suitable, <50th, >50th, >90th). Model with lowest AICc value per grouping is highlighted in green. In each model, the best single variable (by absolute z score) is indicated by the red text.

	Entire suitable distribution				**<50th**			
Model 1: Average annual differences								
Variables	**Est.**	**SE**	**Wald z**	**Pr(>|z|)**	**Est.**	**SE**	**Wald z**	**Pr(>|z|)**
(Intercept)	-2.611	0.156	-16.716	<2e-16	-0.553	0.604	-0.916	0.360
Δ Annual gdd5	-0.236	0.341	-0.691	0.490	-2.532	0.802	-3.158	0.002
Δ Total Annual Precipitation	-0.071	0.148	-0.481	0.631	-0.577	0.290	-1.988	0.047

Random effects:								
Groups	**Variance**	**Std.Dev.**			**Variance**	**Std.Dev.**		
LongGroup2	0.069	0.262			0.083	0.288		
Model 2: Seasonal changes in temps and precip								
Variables	**Est.**	**SE**	**Wald z**	**Pr(>|z|)**	**Est.**	**SE**	**Wald z**	**Pr(>|z|)**
(Intercept)	-3.054	0.446	-6.846	0.000	-0.917	0.785	-1.168	0.243
ΔWinter Minimum Temperature	0.080	0.348	0.230	0.818	-1.114	0.556	-2.003	0.045
ΔFall Mean Temperature	0.391	0.355	1.102	0.270	0.585	0.413	1.417	0.157
ΔSummer Maximum Temperature	0.179	0.199	0.896	0.370	-0.651	0.458	-1.421	0.155
ΔTotal Growing Season Precipitation	0.014	0.154	0.089	0.929	-0.789	0.314	-2.515	0.012
Random effects:								
Groups	**Variance**	**Std.Dev.**			**Variance**	**Std.Dev.**		
LongGroup2	0.031	0.176			0.000	0.000		
Model 3: Changes in selected monthly variables								
Variables	**Est.**	**SE**	**Wald z**	**Pr(>|z|)**	**Est.**	**SE**	**Wald z**	**Pr(>|z|)**
(Intercept)	-2.866	0.266	-10.776	<2e-16	-2.026	0.562	-3.603	0.000
ΔMarch Maximum Temperature	0.130	0.250	0.519	0.604	0.117	0.457	0.256	0.798
ΔJuly Maximum Temperature	-0.034	0.159	-0.212	0.832	-0.372	0.374	-0.995	0.320
ΔJanuary Minimum Temperature	0.213	0.323	0.659	0.510	-0.796	0.641	-1.242	0.214
ΔJuly Total Precipitation	-0.048	0.123	-0.393	0.694	-0.094	0.312	-0.302	0.763

Random effects:								

Groups	Variance	Std.Dev.			Variance	Std.Dev.		
LongGroup2	0.070	0.265			0.452	0.673		
Model 4: Changes in early and late growing season variables								
Variables	**Est.**	**SE**	**Wald z**	**Pr(>|z|)**	**Est.**	**SE**	**Wald z**	**Pr(>|z|)**
(Intercept)	-2.576	0.152	-16.946	<2e-16	-1.695	0.629	-2.693	0.007
ΔApril gdd5	0.022	0.093	0.238	0.812	-0.646	0.280	-2.308	0.021
ΔOctober gdd5	0.048	0.116	0.416	0.677	-0.080	0.320	-0.250	0.803

Random effects:								
Groups	**Variance**	**Std.Dev.**			**Variance**	**Std.Dev.**		
LongGroup2	0.057	0.238			0.290	0.539		

	>50th				**>90th**			
Variables	**Est.**	**SE**	**Wald z**	**Pr(>|z|)**	**Est.**	**SE**	**Wald z**	**Pr(>|z|)**
(Intercept)	-2.734	0.284	-9.621	<2e-16	-2.837	0.402	-7.058	0.000
Δ Annual gdd5	0.139	0.358	0.388	0.698	-0.329	0.552	-0.597	0.550
Δ Total Annual Precipitation	0.070	0.205	0.342	0.733	0.058	0.345	0.168	0.866

Random effects:								
Groups	**Variance**	**Std.Dev.**			**Variance**	**Std.Dev.**		
LongGroup2	0.047	0.217			0.000	0.000		
Variables	**Est.**	**SE**	**Wald z**	**Pr(>|z|)**	**Est.**	**SE**	**Wald z**	**Pr(>|z|)**
(Intercept)	-4.059	0.635	-6.393	0.000	-2.164	0.745	-2.905	0.004
ΔWinter Minimum Temperature	0.833	0.534	1.560	0.119	-0.921	0.741	-1.242	0.214
ΔFall Mean Temperature	0.343	0.433	0.793	0.428	-0.128	0.598	-0.213	0.831
ΔSummer Maximum Temperature	0.446	0.304	1.466	0.143	0.076	0.286	0.265	0.791
ΔTotal Growing Season Precipitation	0.196	0.210	0.931	0.352	-0.078	0.354	-0.220	0.826
Random effects:								
Groups	**Variance**	**Std.Dev.**			**Variance**	**Std.Dev.**		
LongGroup2	0.085	0.291			0.000	0.000		
Variables	**Est.**	**SE**	**Wald z**	**Pr(>|z|)**	**Est.**	**SE**	**Wald z**	**Pr(>|z|)**
(Intercept)	-3.134	0.320	-9.793	<2e-16	-2.518	0.421	-5.984	0.000

ΔMarch Maximum Temperature	0.024	0.282	0.086	0.932	-0.264	0.402	-0.656	0.512
ΔJuly Maximum Temperature	0.099	0.161	0.617	0.537	-0.067	0.220	-0.303	0.762
ΔJanuary Minimum Temperature	0.556	0.400	1.388	0.165	-0.461	0.588	-0.785	0.433
ΔJuly Total Precipitation	0.030	0.135	0.220	0.826	0.085	0.248	0.343	0.732

Random effects:								
Groups	**Variance**	**Std.Dev.**			**Variance**	**Std.Dev.**		
LongGroup2	0.021	0.146			0.000	0.000		
Variables	**Est.**	**SE**	**Wald z**	**Pr(>|z|)**	**Est.**	**SE**	**Wald z**	**Pr(>|z|)**
(Intercept)	-3.046	0.279	-10.903	<2e-16	-3.274	0.415	-7.882	0.000
ΔApril gdd5	0.496	0.233	2.125	0.034	0.350	0.545	0.644	0.520
ΔOctober gdd5	0.006	0.138	0.040	0.968	-0.045	0.190	-0.238	0.812

Random effects:								
Groups	**Variance**	**Std.Dev.**			**Variance**	**Std.Dev.**		
LongGroup2	0.044	0.209			0.000	0.000		

Table 8.3.2.6: Model coefficients for the partial disturbance model of *Acer saccharum* (Sugar maple). Coefficients and significance are presented by area considered (Entire suitable, <50th, >50th, >90th). Model with lowest AICc value per grouping is highlighted in green. In each model, the best single variable (by absolute z score) is indicated by the red text.

	Entire suitable distribution				**<50th**			
Model 1: Disturbance type in P1 (1970-1977)								
Variables	**Est.**	**SE**	**Wald z**	**Pr(>|z|)**	**Est.**	**SE**	**Wald z**	**Pr(>|z|)**
(Intercept)	-2.555	0.158	#####	<2e-16	-2.567	0.339	-7.564	0.000
Logging P1	0.029	0.225	0.128	0.898	-0.355	0.429	-0.829	0.407
Natural P1	-0.389	0.346	-1.124	0.261	-0.022	0.772	-0.028	0.977

Random effects:								
Groups	**Variance**	**Std.Dev.**			**Variance**	**Std.Dev.**		
LongGroup2	0.067	0.258			0.296	0.544		
Model 2: Disturbance type in P3 (2003-2014)								
Variables	**Est.**	**SE**	**Wald z**	**Pr(>|z|)**	**Est.**	**SE**	**Wald z**	**Pr(>|z|)**
(Intercept)	-2.600	0.163	#####	<2e-16	-2.595	0.347	-7.471	0.000
Logging P3	0.207	0.203	1.018	0.309	-0.113	0.380	-0.299	0.765
Natural P3	-0.838	0.521	-1.610	0.107	0.009	1.063	0.009	0.993
Random effects:								
Groups	**Variance**	**Std.Dev.**			**Variance**	**Std.Dev.**		
LongGroup2	0.071	0.266			0.286	0.535		
Model 3: Disturbance timing								
Variables	**Est.**	**SE**	**Wald z**	**Pr(>|z|)**	**Est.**	**SE**	**Wald z**	**Pr(>|z|)**
(Intercept)	-2.569	0.174	#####	<2e-16	-2.529	0.356	-7.106	0.000
Disturbance (any type) P1	-0.094	0.201	-0.467	0.641	-0.296	0.390	-0.759	0.448
Disturbance (any type) P3	0.040	0.196	0.206	0.837	-0.112	0.367	-0.306	0.760

Random effects:								
Groups	**Variance**	**Std.Dev.**			**Variance**	**Std.Dev.**		
LongGroup2	0.068	0.260			0.287	0.536		
Model 4: Presence of disturbance vs. new disturbance								
Variables	**Est.**	**SE**	**Wald z**	**Pr(>|z|)**	**Est.**	**SE**	**Wald z**	**Pr(>|z|)**
(Intercept)	-2.574	0.178	#####	<2e-16	-2.633	0.369	-7.139	0.000
Presence of disturbance (P1 and/or P3)	-0.078	0.215	-0.364	0.716	-0.234	0.407	-0.575	0.565
New disturbance P3	0.132	0.250	0.529	0.597	0.434	0.472	0.920	0.358

Random effects:								
Groups	**Variance**	**Std.Dev.**			**Variance**	**Std.Dev.**		
LongGroup2	0.068	0.260			0.310	0.557		

	>50th				**>90th**			
Model 1: Disturbance type in P1 (1970-1977)								
Variables	**Est.**	**SE**	**Wald z**	**Pr(>|z|)**	**Est.**	**SE**	**Wald z**	**Pr(>|z|)**
(Intercept)	-2.629	0.164	######	<2e-16	-3.208	0.240	######	<2e-16
Logging P1	0.199	0.267	0.745	0.456	0.714	0.422	1.691	0.091
Natural P1	-0.384	0.392	-0.980	0.327	-0.050	0.636	-0.079	0.937

Random effects:								
Groups	**Variance**	**Std.Dev.**			**Variance**	**Std.Dev.**		
LongGroup2	0.034	0.184			0.000	0.000		
Model 2: Disturbance type in P3 (2003-2014)								
Variables	**Est.**	**SE**	**Wald z**	**Pr(>|z|)**	**Est.**	**SE**	**Wald z**	**Pr(>|z|)**
(Intercept)	-2.684	0.166	######	<2e-16	-3.057	0.235	######	<2e-16
Logging P3	0.388	0.243	1.597	0.110	0.390	0.403	0.968	0.333
Natural P3	-0.911	0.602	-1.513	0.130	-1.374	1.033	-1.330	0.184
Random effects:								
Groups	**Variance**	**Std.Dev.**			**Variance**	**Std.Dev.**		
LongGroup2	0.036	0.190			0.000	0.000		
Model 3: Disturbance timing								
Variables	**Est.**	**SE**	**Wald z**	**Pr(>|z|)**	**Est.**	**SE**	**Wald z**	**Pr(>|z|)**
(Intercept)	-2.696	0.193	######	<2e-16	-3.248	0.293	######	<2e-16
Disturbance (any type) P1	0.023	0.239	0.095	0.924	0.476	0.388	1.229	0.219
Disturbance (any type) P3	0.163	0.235	0.695	0.487	0.096	0.393	0.245	0.807

Random effects:								
Groups	**Variance**	**Std.Dev.**			**Variance**	**Std.Dev.**		
LongGroup2	0.043	0.207			0.000	0.000		
Model 4: Presence of disturbance vs. new disturbance								
Variables	**Est.**	**SE**	**Wald z**	**Pr(>|z|)**	**Est.**	**SE**	**Wald z**	**Pr(>|z|)**
(Intercept)	-2.651	0.200	######	<2e-16	-3.277	0.322	######	<2e-16
Presence of disturbance (P1 and/or P3)	0.024	0.261	0.091	0.928	0.531	0.439	1.210	0.226
New disturbance P3	0.023	0.298	0.078	0.938	-0.367	0.468	-0.784	0.433

Random effects:								
Groups	**Variance**	**Std.Dev.**			**Variance**	**Std.Dev.**		
LongGroup2	0.042	0.206			0.000	0.000		

Table 8.3.2.7: Model coefficients for the partial climate model of *Betula alleghaniensis* (Yellow birch). Coefficients and significance are presented by area considered (Entire suitable, <50th, >50th, >90th). Model with lowest AICc value per grouping is highlighted in green. In each model, the best single variable (by absolute z score) is indicated by the red text.

	Entire suitable distribution				**<50th**			
Model 1: Average annual differences								
Variables	**Est.**	**SE**	**Wald z**	**Pr(>|z|)**	**Est.**	**SE**	**Wald z**	**Pr(>|z|)**
(Intercept)	-2.809	0.233	-12.075	<2e-16	-2.498	0.520	-4.808	0.000
Δ Annual gdd5	0.159	0.299	0.531	0.596	-0.004	0.620	-0.006	0.995
Δ Total Annual Precipitation	0.120	0.140	0.861	0.389	-0.063	0.236	-0.264	0.791

Random effects:								
Groups	**Variance**	**Std.Dev.**			**Variance**	**Std.Dev.**		
LongGroup2	0.038	0.194			0.076	0.276		
Model 2: Seasonal changes in temps and precip								
Variables	**Est.**	**SE**	**Wald z**	**Pr(>|z|)**	**Est.**	**SE**	**Wald z**	**Pr(>|z|)**
(Intercept)	-3.547	0.463	-7.665	0.000	-3.553	0.813	-4.369	0.000
ΔWinter Minimum Temperature	0.434	0.377	1.152	0.249	0.013	0.497	0.027	0.979
ΔFall Mean Temperature	0.111	0.341	0.326	0.745	0.449	0.469	0.957	0.339
ΔSummer Maximum Temperature	0.458	0.227	2.023	0.043	0.797	0.422	1.889	0.059
ΔTotal Growing Season Precipitation	0.193	0.154	1.251	0.211	0.039	0.291	0.132	0.895
Random effects:								
Groups	**Variance**	**Std.Dev.**			**Variance**	**Std.Dev.**		
LongGroup2	0.047	0.217			0.059	0.242		
Model 3: Changes in selected monthly variables								
Variables	**Est.**	**SE**	**Wald z**	**Pr(>|z|)**	**Est.**	**SE**	**Wald z**	**Pr(>|z|)**
(Intercept)	-2.885	0.253	-11.423	<2e-16	-2.791	0.430	-6.494	0.000
ΔMarch Maximum Temperature	0.200	0.245	0.817	0.414	0.487	0.393	1.239	0.215
ΔJuly Maximum Temperature	0.198	0.157	1.259	0.208	0.366	0.341	1.071	0.284
ΔJanuary Minimum Temperature	-0.062	0.313	-0.197	0.844	-0.579	0.436	-1.327	0.185
ΔJuly Total Precipitation	0.005	0.112	0.046	0.963	-0.129	0.178	-0.724	0.469

Random effects:								
Groups	**Variance**	**Std.Dev.**			**Variance**	**Std.Dev.**		
LongGroup2	0.026	0.162			0.032	0.179		
Model 4: Changes in early and late growing season variables								
Variables	**Est.**	**SE**	**Wald z**	**Pr(>|z|)**	**Est.**	**SE**	**Wald z**	**Pr(>|z|)**
(Intercept)	-2.732	0.203	-13.451	<2e-16	-1.686	0.430	-3.923	0.000
ΔApril gdd5	0.005	0.147	0.031	0.975	-0.584	0.256	-2.283	0.022
ΔOctober gdd5	-0.094	0.108	-0.876	0.381	0.045	0.184	0.243	0.808

Random effects:								
Groups	**Variance**	**Std.Dev.**			**Variance**	**Std.Dev.**		
LongGroup2	0.031	0.175			0.121	0.348		

	>50th				**>90th**			
Model 1: Average annual differences								
Variables	**Est.**	**SE**	**Wald z**	**Pr(>|z|)**	**Est.**	**SE**	**Wald z**	**Pr(>|z|)**
(Intercept)	-2.816	0.274	-10.293	<2e-16	-2.979	0.457	-6.523	0.000
Δ Annual gdd5	0.122	0.363	0.336	0.737	-0.519	0.632	-0.822	0.411
Δ Total Annual Precipitation	0.158	0.230	0.688	0.491	0.331	0.426	0.776	0.438

Random effects:								
Groups	**Variance**	**Std.Dev.**			**Variance**	**Std.Dev.**		
LongGroup2	0.000	0.000			0.000	0.000		
Model 2: Seasonal changes in temps and precip								
Variables	**Est.**	**SE**	**Wald z**	**Pr(>|z|)**	**Est.**	**SE**	**Wald z**	**Pr(>|z|)**
(Intercept)	-3.594	0.641	-5.607	0.000	-2.912	0.874	-3.334	0.001
ΔWinter Minimum Temperature	0.866	0.534	1.621	0.105	-0.750	1.043	-0.719	0.472
ΔFall Mean Temperature	-0.208	0.414	-0.503	0.615	0.239	0.844	0.283	0.777
ΔSummer Maximum Temperature	0.217	0.218	0.998	0.318	0.128	0.351	0.364	0.716
ΔTotal Growing Season Precipitation	0.226	0.236	0.955	0.340	0.180	0.376	0.477	0.633
Random effects:								
Groups	**Variance**	**Std.Dev.**			**Variance**	**Std.Dev.**		
LongGroup2	0.000	0.000			0.000	0.000		
Model 3: Changes in selected monthly variables								
Variables	**Est.**	**SE**	**Wald z**	**Pr(>|z|)**	**Est.**	**SE**	**Wald z**	**Pr(>|z|)**
(Intercept)	-3.065	0.343	-8.949	<2e-16	-2.895	0.510	-5.678	0.000

ΔMarch Maximum Temperature	-0.021	0.297	-0.069	0.945	-0.398	0.575	-0.692	0.489
ΔJuly Maximum Temperature	0.137	0.164	0.837	0.403	0.304	0.291	1.044	0.297
ΔJanuary Minimum Temperature	0.369	0.452	0.816	0.415	-0.158	0.722	-0.219	0.827
ΔJuly Total Precipitation	-0.034	0.150	-0.229	0.819	0.551	0.357	1.546	0.122

Random effects:								
Groups	**Variance**	**Std.Dev.**			**Variance**	**Std.Dev.**		
LongGroup2	0.000	0.000			0.000	0.000		
Model 4: Changes in early and late growing season variables								
Variables	**Est.**	**SE**	**Wald z**	**Pr(>|z|)**	**Est.**	**SE**	**Wald z**	**Pr(>|z|)**
(Intercept)	-3.276	0.302	-10.849	<2e-16	-3.339	0.442	-7.547	0.000
ΔApril gdd5	0.604	0.324	1.864	0.062	-0.010	0.719	-0.013	0.989
ΔOctober gdd5	-0.224	0.134	-1.671	0.095	-0.041	0.264	-0.156	0.876

Random effects:								
Groups	**Variance**	**Std.Dev.**			**Variance**	**Std.Dev.**		
LongGroup2	0.000	0.000			0.000	0.000		

Table 8.3.2.8: Model coefficients for the partial disturbance model of *Betula alleghaniensis* (Yellow birch). Coefficients and significance are presented by area considered (Entire suitable, <50th, >50th, >90th). Model with lowest AICc value per grouping is highlighted in green. In each model, the best single variable (by absolute z score) is indicated by the red text.

	Entire suitable distribution				**<50th**			
Model 1: Disturbance type in P1 (1970-1977)								
Variables	**Est.**	**SE**	**Wald z**	**Pr(>|z|)**	**Est.**	**SE**	**Wald z**	**Pr(>|z|)**
(Intercept)	-2.725	0.155	-17.567	<2e-16	-2.662	0.216	-12.320	<2e-16
Logging P1	0.417	0.213	1.961	0.050	0.530	0.300	1.767	0.077
Natural P1	-0.790	0.434	-1.822	0.069	-0.331	0.625	-0.530	0.596

Random effects:								
Groups	**Variance**	**Std.Dev.**				**Variance**		**Std.Dev.**
LongGroup2	0.055	0.234			0.074	0.272		
Model 2: Disturbance type in P3 (2003-2014)								
Variables	**Est.**	**SE**	**Wald z**	**Pr(>|z|)**	**Est.**	**SE**	**Wald z**	**Pr(>|z|)**
(Intercept)	-2.704	0.142	-19.027	<2e-16	-2.644	0.205	-12.878	<2e-16
Logging P3	0.144	0.220	0.655	0.513	0.318	0.303	1.050	0.294
Natural P3	-0.087	0.365	-0.238	0.812	0.358	0.771	0.464	0.643
Random effects:								
Groups	**Variance**	**Std.Dev.**				**Variance**		**Std.Dev.**
LongGroup2	0.037	0.191			0.054	0.231		
Model 3: Disturbance timing								
Variables	**Est.**	**SE**	**Wald z**	**Pr(>|z|)**	**Est.**	**SE**	**Wald z**	**Pr(>|z|)**
(Intercept)	-2.749	0.159	-17.266	<2e-16	-2.778	0.238	-11.695	<2e-16
Disturbance (any type) P1	0.130	0.200	0.652	0.514	0.378	0.287	1.316	0.188
Disturbance (any type) P3	0.092	0.202	0.456	0.649	0.333	0.294	1.135	0.256

Random effects:								
Groups	**Variance**	**Std.Dev.**				**Variance**		**Std.Dev.**
LongGroup2	0.037	0.194			0.063	0.251		
Model 4: Presence of disturbance vs. new disturbance								
Variables	**Est.**	**SE**	**Wald z**	**Pr(>|z|)**	**Est.**	**SE**	**Wald z**	**Pr(>|z|)**
(Intercept)	-2.703	0.165	-16.356	<2e-16	-2.737	0.251	-10.923	<2e-16
Presence of disturbance (P1 and/or P3)	0.112	0.215	0.521	0.602	0.440	0.313	1.405	0.160
New disturbance P3	-0.162	0.263	-0.615	0.539	-0.214	0.378	-0.568	0.570

Random effects:								
Groups	**Variance**	**Std.Dev.**				**Variance**		**Std.Dev.**
LongGroup2	0.040	0.200			0.072	0.268		

	>50th				**>90th**			
Model 1: Disturbance type in P1 (1970-1977)								
Variables	**Est.**	**SE**	**Wald z**	**Pr(>|z|)**	**Est.**	**SE**	**Wald z**	**Pr(>|z|)**
(Intercept)	-2.715	0.154	-17.642	<2e-16	-3.199	0.273	-11.731	<2e-16
Logging P1	0.257	0.303	0.849	0.396	-0.203	0.647	-0.313	0.754
Natural P1	-1.046	0.604	-1.732	0.083	######	######	0.000	1.000

Random effects:								
Groups	**Variance**	**Std.Dev.**				**Variance**		**Std.Dev.**
LongGroup2	0.000	0.000			0.000	0.000		
Model 2: Disturbance type in P3 (2003-2014)								
Variables	**Est.**	**SE**	**Wald z**	**Pr(>|z|)**	**Est.**	**SE**	**Wald z**	**Pr(>|z|)**
(Intercept)	-2.717	0.156	-17.456	<2e-16	-3.283	0.294	-11.167	<2e-16
Logging P3	-0.051	0.326	-0.156	0.876	-0.577	0.773	-0.747	0.455
Natural P3	-0.149	0.419	-0.356	0.722	0.255	0.660	0.386	0.699
Random effects:								
Groups	**Variance**	**Std.Dev.**				**Variance**		**Std.Dev.**
LongGroup2	0.000	0.000			0.000	0.000		
Model 3: Disturbance timing								
Variables	**Est.**	**SE**	**Wald z**	**Pr(>|z|)**	**Est.**	**SE**	**Wald z**	**Pr(>|z|)**
(Intercept)	-2.686	0.178	-15.066	<2e-16	-3.136	0.319	-9.829	<2e-16
Disturbance (any type) P1	-0.099	0.282	-0.350	0.726	-0.612	0.645	-0.948	0.343
Disturbance (any type) P3	-0.089	0.278	-0.322	0.748	-0.192	0.542	-0.355	0.723

Random effects:								
Groups	**Variance**	**Std.Dev.**				**Variance**		**Std.Dev.**
LongGroup2	0.000	0.000			0.000	0.000		
Model 4: Presence of disturbance vs. new disturbance								
Variables	**Est.**	**SE**	**Wald z**	**Pr(>|z|)**	**Est.**	**SE**	**Wald z**	**Pr(>|z|)**
(Intercept)	-2.635	0.183	-14.396	<2e-16	-3.219	0.340	-9.469	<2e-16
Presence of disturbance (P1 and/or P3)	-0.177	0.299	-0.591	0.554	-0.580	0.676	-0.859	0.390
New disturbance P3	-0.079	0.370	-0.214	0.831	0.638	0.741	0.861	0.389

Random effects:								

Groups	Variance	Std.Dev.				Variance		Std.Dev.	
LongGroup2	0.000	0.000			0.000	0.000			

Table 8.3.2.9: Model coefficients for the partial climate model of Acer rubrum (Red maple). Coefficients and significance are presented by area considered (Entire suitable, <50th, >50th, >90th). Model with lowest AICc value per grouping is highlighted in green. In each model, the best single variable (by absolute z score) is indicated by the red text.

	Entire suitable distribution				**<50th**			
Model 1: Average annual differences								
Variables	**Est.**	**SE**	**Wald z**	**Pr(>|z|)**	**Est.**	**SE**	**Wald z**	**Pr(>|z|)**
(Intercept)	-1.868	0.182	-10.245	<2e-16	-2.111	0.410	-5.150	0.000
Δ Annual gdd5	0.049	0.258	0.191	0.848	0.300	0.520	0.576	0.564
Δ Total Annual Precipitation	-0.275	0.118	-2.326	0.020	-0.307	0.169	-1.821	0.069

Random effects:								
Groups	**Variance**	**Std.Dev.**			**Variance**	**Std.Dev.**		
LongGroup2	0.007	0.082			0.000	0.000		
Model 2: Seasonal changes in temps and precip								
Variables	**Est.**	**SE**	**Wald z**	**Pr(>|z|)**	**Est.**	**SE**	**Wald z**	**Pr(>|z|)**
(Intercept)	-2.007	0.297	-6.751	0.000	-1.956	0.589	-3.320	0.001
ΔWinter TMin	0.517	0.255	2.030	0.042	0.231	0.418	0.551	0.581
ΔFall TMean	-0.295	0.206	-1.436	0.151	-0.246	0.344	-0.715	0.475
ΔSummer TMax	-0.036	0.135	-0.266	0.790	0.159	0.354	0.449	0.653
ΔTotal Growing Season Precipitation	-0.257	0.122	-2.105	0.035	-0.301	0.223	-1.350	0.177
Random effects:								
Groups	**Variance**	**Std.Dev.**			**Variance**	**Std.Dev.**		
LongGroup2	0.000	0.000			0.000	0.000		
Model 3: Changes in selected monthly variables								
Variables	**Est.**	**SE**	**Wald z**	**Pr(>|z|)**	**Est.**	**SE**	**Wald z**	**Pr(>|z|)**
(Intercept)	-2.250	0.184	-12.216	<2e-16	-2.334	0.350	-6.670	0.000
ΔMarch Maximum Temperature	0.428	0.175	2.437	0.015	0.598	0.315	1.894	0.058
ΔJuly Maximum Temperature	-0.127	0.109	-1.165	0.244	-0.055	0.295	-0.187	0.852
ΔJanuary Minimum Temperature	-0.018	0.215	-0.082	0.935	-0.286	0.386	-0.743	0.458
ΔJuly Total Precipitation	-0.184	0.076	-2.427	0.015	-0.347	0.144	-2.415	0.016

Random effects:								
Groups	**Variance**	**Std.Dev.**			**Variance**	**Std.Dev.**		

LongGroup2	0.000	0.000			0.000	0.000		
Model 4: Changes in early and late growing season variables								
Variables	**Est.**	**SE**	**Wald z**	**Pr(>|z|)**	**Est.**	**SE**	**Wald z**	**Pr(>|z|)**
(Intercept)	-1.734	0.144	-12.059	<2e-16	-1.781	0.323	-5.515	0.000
ΔApril gdd5	-0.227	0.114	-1.994	0.046	-0.269	0.189	-1.421	0.155
ΔOctober gdd5	-0.142	0.069	-2.046	0.041	-0.198	0.120	-1.652	0.099

Random effects:								
Groups	**Variance**	**Std.Dev.**			**Variance**	**Std.Dev.**		
LongGroup2	0.000	0.000			0.000	0.000		

	>50th				**>90th**			
Model 1: Average annual differences								
Variables	**Est.**	**SE**	**Wald z**	**Pr(>|z|)**	**Est.**	**SE**	**Wald z**	**Pr(>|z|)**
(Intercept)	-1.792	0.192	-9.319	<2e-16	-2.042	0.338	-6.043	0.000
Δ Annual gdd5	0.002	0.275	0.008	0.993	0.147	0.457	0.320	0.749
Δ Total Annual Precipitation	-0.172	0.176	-0.977	0.328	-0.180	0.297	-0.604	0.546

Random effects:								
Groups	**Variance**	**Std.Dev.**			**Variance**	**Std.Dev.**		
LongGroup2	0.000	0.000			0.000	0.000		
Model 2: Seasonal changes in temps and precip								
Variables	**Est.**	**SE**	**Wald z**	**Pr(>|z|)**	**Est.**	**SE**	**Wald z**	**Pr(>|z|)**
(Intercept)	-2.159	0.394	-5.484	0.000	-1.974	0.579	-3.408	0.001
ΔWinter TMin	0.674	0.340	1.982	0.048	1.215	0.672	1.808	0.071
ΔFall TMean	-0.261	0.269	-0.971	0.332	-1.198	0.517	-2.317	0.021
ΔSummer TMax	-0.054	0.148	-0.368	0.713	-0.017	0.231	-0.072	0.943
ΔTotal Growing Season Precipitation	-0.194	0.180	-1.079	0.281	-0.325	0.302	-1.075	0.282
Random effects:								
Groups	**Variance**	**Std.Dev.**			**Variance**	**Std.Dev.**		
LongGroup2	0.000	0.000			0.000	0.000		
Model 3: Changes in selected monthly variables								
Variables	**Est.**	**SE**	**Wald z**	**Pr(>|z|)**	**Est.**	**SE**	**Wald z**	**Pr(>|z|)**
(Intercept)	-2.154	0.226	-9.534	<2e-16	-2.312	0.414	-5.582	0.000
ΔMarch Maximum Temperature	0.393	0.211	1.858	0.063	0.649	0.444	1.462	0.144
ΔJuly Maximum Temperature	-0.066	0.121	-0.549	0.583	-0.332	0.230	-1.442	0.149

ΔJanuary Minimum Temperature	0.008	0.271	0.030	0.976	-0.249	0.419	-0.595	0.552
ΔJuly Total Precipitation	-0.066	0.102	-0.653	0.514	-0.441	0.237	-1.862	0.063

Random effects:								
Groups	**Variance**	**Std.Dev.**			**Variance**	**Std.Dev.**		
LongGroup2	0.000	0.000			0.000	0.000		
Model 4: Changes in early and late growing season variables								
Variables	**Est.**	**SE**	**Wald z**	**Pr(>|z|)**	**Est.**	**SE**	**Wald z**	**Pr(>|z|)**
(Intercept)	-1.888	0.206	-9.148	<2e-16	-1.792	0.304	-5.888	0.000
ΔApril gdd5	0.039	0.227	0.170	0.865	-0.391	0.490	-0.798	0.425
ΔOctober gdd5	-0.153	0.092	-1.668	0.095	-0.337	0.199	-1.694	0.090

Random effects:								
Groups	**Variance**	**Std.Dev.**			**Variance**	**Std.Dev.**		
LongGroup2	######	######			0	0		

Table 8.3.2.10: Model coefficients for the partial disturbance model of Acer rubrum (Red maple). Coefficients and significance are presented by area considered (Entire suitable, <50th, >50th, >90th). Model with lowest AICc value per grouping is highlighted in green. In each model, the best single variable (by absolute z score) is indicated by the red text.

	Entire suitable distribution				**<50th**			
Model 1: Disturbance type in P1 (1970-1977)								
Variables	**Est.**	**SE**	**Wald z**	**Pr(>|z|)**	**Est.**	**SE**	**Wald z**	**Pr(>|z|)**
(Intercept)	-1.783	0.090	-19.738	< 2e-16	-2.057	0.142	-14.482	<2e-16
Logging P1	-0.831	0.219	-3.801	0.000	-0.304	0.305	-0.996	0.319
Natural P1	0.260	0.209	1.245	0.213	0.769	0.374	2.057	0.040

Random effects:								
Groups	**Variance**	**Std.Dev.**			**Variance**	**Std.Dev.**		
LongGroup2	0.009	0.094			0.006	0.075		
Model 2: Disturbance type in P3 (2003-2014)								
Variables	**Est.**	**SE**	**Wald z**	**Pr(>|z|)**	**Est.**	**SE**	**Wald z**	**Pr(>|z|)**
(Intercept)	-1.991	0.102	-19.534	<2e-16	-2.192	0.170	-12.910	<2e-16
Logging P3	0.311	0.160	1.938	0.053	0.332	0.254	1.304	0.192
Natural P3	0.383	0.251	1.528	0.127	1.155	0.542	2.132	0.033
Random effects:								
Groups	**Variance**	**Std.Dev.**			**Variance**	**Std.Dev.**		
LongGroup2	0.016	0.127			0.034	0.186		
Model 3: Disturbance timing								
Variables	**Est.**	**SE**	**Wald z**	**Pr(>|z|)**	**Est.**	**SE**	**Wald z**	**Pr(>|z|)**
(Intercept)	-1.890	0.115	-16.456	<2e-16	-2.200	0.183	-12.036	<2e-16
Disturbance (any type) P1	-0.345	0.158	-2.181	0.029	0.034	0.251	0.137	0.891
Disturbance (any type) P3	0.319	0.146	2.177	0.029	0.428	0.241	1.776	0.076

Random effects:								
Groups	**Variance**	**Std.Dev.**			**Variance**	**Std.Dev.**		
LongGroup2	0.021	0.146			0.031	0.175		
Model 4: Presence of disturbance vs. new disturbance								
Variables	**Est.**	**SE**	**Wald z**	**Pr(>|z|)**	**Est.**	**SE**	**Wald z**	**Pr(>|z|)**
(Intercept)	-1.835	0.120	-15.299	<2e-16	-2.152	0.188	-11.423	<2e-16
Presence of disturbance (P1 and/or P3)	-0.308	0.168	-1.829	0.067	0.112	0.269	0.418	0.676

New disturbance P3	0.466	0.194	2.399	0.017	0.180	0.319	0.565	0.572

Random effects:								
Groups	**Variance**	**Std.Dev.**			**Variance**	**Std.Dev.**		
LongGroup2	0.025	0.158			0.031	0.177		

	>50th				**>90th**			
Model 1: Disturbance type in P1 (1970-1977)								
Variables	**Est.**	**SE**	**Wald z**	**Pr(>|z|)**	**Est.**	**SE**	**Wald z**	**Pr(>|z|)**
(Intercept)	-1.619	0.100	-16.274	< 2e-16	-1.754	0.171	-10.239	<2e-16
Logging P1	-1.276	0.325	-3.923	0.000	-1.003	0.543	-1.847	0.065
Natural P1	0.010	0.249	0.040	0.968	-0.515	0.630	-0.817	0.414

Random effects:								
Groups	**Variance**	**Std.Dev.**			**Variance**	**Std.Dev.**		
LongGroup2	0.000	0.000			0.000	0.000		
Model 2: Disturbance type in P3 (2003-2014)								
Variables	**Est.**	**SE**	**Wald z**	**Pr(>|z|)**	**Est.**	**SE**	**Wald z**	**Pr(>|z|)**
(Intercept)	-1.882	0.112	-16.771	<2e-16	-1.947	0.186	-10.492	<2e-16
Logging P3	0.330	0.207	1.596	0.111	0.281	0.365	0.769	0.442
Natural P3	0.176	0.285	0.616	0.538	-0.702	0.753	-0.932	0.351
Random effects:								
Groups	**Variance**	**Std.Dev.**			**Variance**	**Std.Dev.**		
LongGroup2	0.004	0.065			0.000	0.000		
Model 3: Disturbance timing								
Variables	**Est.**	**SE**	**Wald z**	**Pr(>|z|)**	**Est.**	**SE**	**Wald z**	**Pr(>|z|)**
(Intercept)	-1.712	0.123	-13.953	< 2e-16	-1.761	0.202	-8.726	<2e-16
Disturbance (any type) P1	-0.591	0.207	-2.861	0.004	-0.820	0.429	-1.913	0.056
Disturbance (any type) P3	0.264	0.184	1.436	0.151	0.023	0.345	0.067	0.947

Random effects:								
Groups	**Variance**	**Std.Dev.**			**Variance**	**Std.Dev.**		
LongGroup2	0.003	0.054			0.000	0.000		
Model 4: Presence of disturbance vs. new disturbance								
Variables	**Est.**	**SE**	**Wald z**	**Pr(>|z|)**	**Est.**	**SE**	**Wald z**	**Pr(>|z|)**
(Intercept)	-1.652	0.127	-13.016	< 2e-16	-1.743	0.205	-8.508	<2e-16

Presence of disturbance (P1 and/or P3)	-0.575	0.218	-2.635	0.008	-0.833	0.442	-1.883	0.060
New disturbance P3	0.662	0.250	2.652	0.008	0.798	0.501	1.593	0.111

Random effects:								
Groups	**Variance**	**Std.Dev.**			**Variance**	**Std.Dev.**		
LongGroup2	0.005	0.072			0.000	0.000		

8.4 - Appendices to Chapter 5

8.4.1 - From Appendix 1: Supplementary details on how migration velocity was obtained

Three data sources were consulted to calculate migration velocity employed as the mean in the 2Dt kernels.

First, we used contemporary range limit shifts based on changes in plot occupancy patterns within Quebec, Canada (Boisvert-Marsh, in prep). The data comes from extensive forest resource inventories that have been conducted across 761 000km^2 in this area since 1970 (see Boisvert-Marsh et al. 2014 for description). We employed data from the most historical inventory (conducted between 1970-1977) and the most contemporary one (2003-2015). To calculate shifts, a percentile approach was used to define latitudinal zones based on the recorded presence of saplings of a given species in a plot and its associated latitude. The zones' limits were set at the median (50th) percentile of latitudinal distribution and at the 90th percentile of distribution (northernmost) using relevant methods for each (see Boisvert-Marsh et al. 2014 for a detailed explanation). The changes in the location of the 50th and the 90th latitudinal limits between P_3 and P_1 were computed. Positive values indicate northward latitudinal shift and negative values southward. Range limit shifts (LRS) were calculated for two life stages: trees (diameter at breast height greater than 9.1cm) and saplings (stems between 1.1 and 3.0cm diameter at breast height). For our purposes, we considered range limit shifts of trees at both the 50th and 90th percentiles of distribution where a poleward shift has already been detected (i.e. positive shifts only). When this was not possible, we also considered latitudinal shifts for saplings. Average LRS between shifts at the 50th and shifts at the 90th, were employed for a given species. This average shift was transformed into migration velocity (meters/year) then divided by the mean number of years between the two inventories (33.8 ± 3.79 years on average).

In addition, we used evidence from paleoecological observations to supplement contemporary observations. First, we employed the AFR database (Williams and Beardmore date unknown), which contains migration velocities between various potential glacial refugia situated throughout eastern North America and fossilized pollen records in Atlantic Canada. Potential refugia included southern refugium (south of the ice sheet at the last glacial maximum), the Torngat mountains, Chic Choc Mountains, Long Range mountains, Main-a-Dieu, Grand Banks of Newfoundland, Sable Island, and Georges Bank (several refugia mapped in Shaw 2005).

Velocity was calculated as the distance between each of these refugia and the earliest fossilized pollen collected with the study area divided by the number of years between the date of the last glacial maximum (21500 years before present [ybp]) and the collection dates of each pollen sample found. For our purposes, we eliminated refugia that were not likely to be sources for a given species (i.e. north of current leading edge). Based on the remaining potential refugia, an average velocity was calculated across all potential sources.

Finally, we employed a continental wide database of biotic velocity as complied by Ordonez and Williams (2013). Species distributions were reconstructed based on genus-level observations of pollen records from the NEOTOMA database. These distributions were based on interpolated surfaces that incorporated both occurrence and relative abundance. Latitudinal shifts were based on changes in occurrence at the 95th percentile of the core distribution. We used their observations shifts at the northern limit from three time periods that correspond to periods with the most rapid climatic change: 16 to14k ybp, 14-12k ybp and 12-10k ybp. An average shift was calculated across the three periods, which were then converted from kilometers per decade to meters per year.

Table 8.4.1.1: Migration velocity (in meters per year), as calculated from various data sources. The mean shown here is the average of the data sources for which values were available. This value (in bold) was employed in the 2Dt dispersal kernel as the kernel mean parameter.

Species Name	**Mean**	AFR migration database[1]	Boisvert-Marsh, In prep[2]	Ordonez and Williams 2013[3]
Abies balsamea	**122.49**	95.65	157.5	114.33
Acer rubrum	**229.89**	315.51	240.5	133.67
Acer saccharum	**121.87**	90.95	141	133.67
Betula alleghaniensis	**151.93**	273.28	128.5	54.00
Betula papyrifera	**451.6**	187.29	1113.5	54.00
Picea mariana	**238.09**	136.60	468	109.67
Pinus strobus	**149.13**	191.60		106.67
Populus tremuloides	**312.09**	88.68	535.5	
Quercus rubra	**107.57**	160.15		55
Thuja occidentalis	**114.2**	54.60	195	93

[1] Williams, C. and Beardmore, T. AFR Migration database. Canadian Forest Service, Atlantic Forestry Centre, Fredericton, New Brunswick. Unpublished Dataset

[2] Boisvert-Marsh, L. In prep. *Patterns and processes affecting northward migration of tree species in a changing climate.* (Doctoral Dissertation, McGill University, Montreal, Canada).

[3] Ordonez, Alejandro, and John W. Williams. Climatic and biotic velocities for woody taxa distributions over the last 16 000 years in eastern North America. Ecology Letters 16.6 (2013): 773-781.

Other references

Boisvert-Marsh, L., C. Périé, and S. de Blois. 2014. Shifting with climate? Evidence for recent changes in tree species distribution at high latitudes. Ecosphere **5**:art83.

Shaw, J. (2005). Palaeogeography of Atlantic Canadian continental shelves from the last glacial maximum to the present, with an emphasis on Flemish cap. Journal of Northwest Atlantic Fishery Science 37:119-126.

8.4.2 - From Appendix 2: Supplemental results

Table 8.4.2.1: Long distance dispersal probabilities for the 10 tree species in this study, as calculated by the 2Dt dispersal kernels shown above. The probabilities were calculated for two distances: 1) between $\mathrm{LDD}_{\mathrm{min}}$ and $\mathrm{LDD}_{\mathrm{max}}$, which corresponds to the values used in the model simulations of the main manuscript and 2) from $\mathrm{LDD}_{\mathrm{max}}$ to 10000m, to provide insight into the probability of dispersing beyond the thresholds employed in the manuscript.

	Distance		**Probability**	
	$\mathrm{LDD}_{\mathrm{min}}$	$\mathrm{LDD}_{\mathrm{max}}$	$\mathrm{LDD}_{\mathrm{min}}$ to $\mathrm{LDD}_{\mathrm{max}}$	Prob $\mathrm{LDD}_{\mathrm{max}}$ to 10000m
Abies balsamea	295.0 (300)	1011.4 (1000)	0.0450	0.0098
Acer rubrum	288.4 (300)	1002.2 (1000)	0.1310	0.0240
Acer saccharum	153.2 (150)	528.0 (525)	0.2622	0.0053
Betula alleghaniensis	282.7 (275)	1007.1 (1000)	0.1034	0.0079
Betula papyrifera	282.7 (275)	1007.1 (1000)	0.2988	0.0630
Picea mariana	369.3 (375)	1281.4 (1275)	0.0781	0.0168
Pinus strobus	243.3 (250)	833.0 (850)	0.0899	0.0170
Populus tremuloides	1281.5 (1275)	5582.8 (5575)	0.0222	0.0008
Quercus rubra	106.0 (100)	1668.1 (1675)	0.1375	0.0042
Thuja occidentalis	230.8 (225)	791.0 (800)	0.0663	0.0127

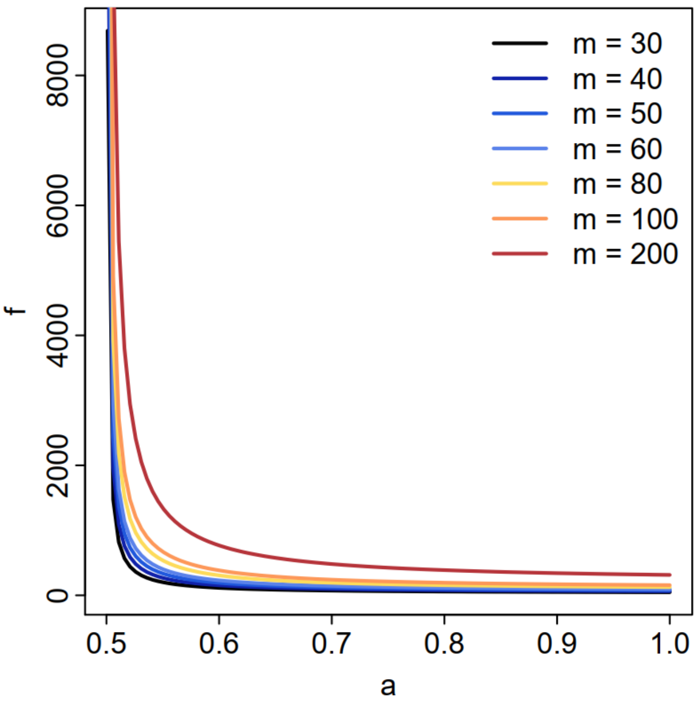
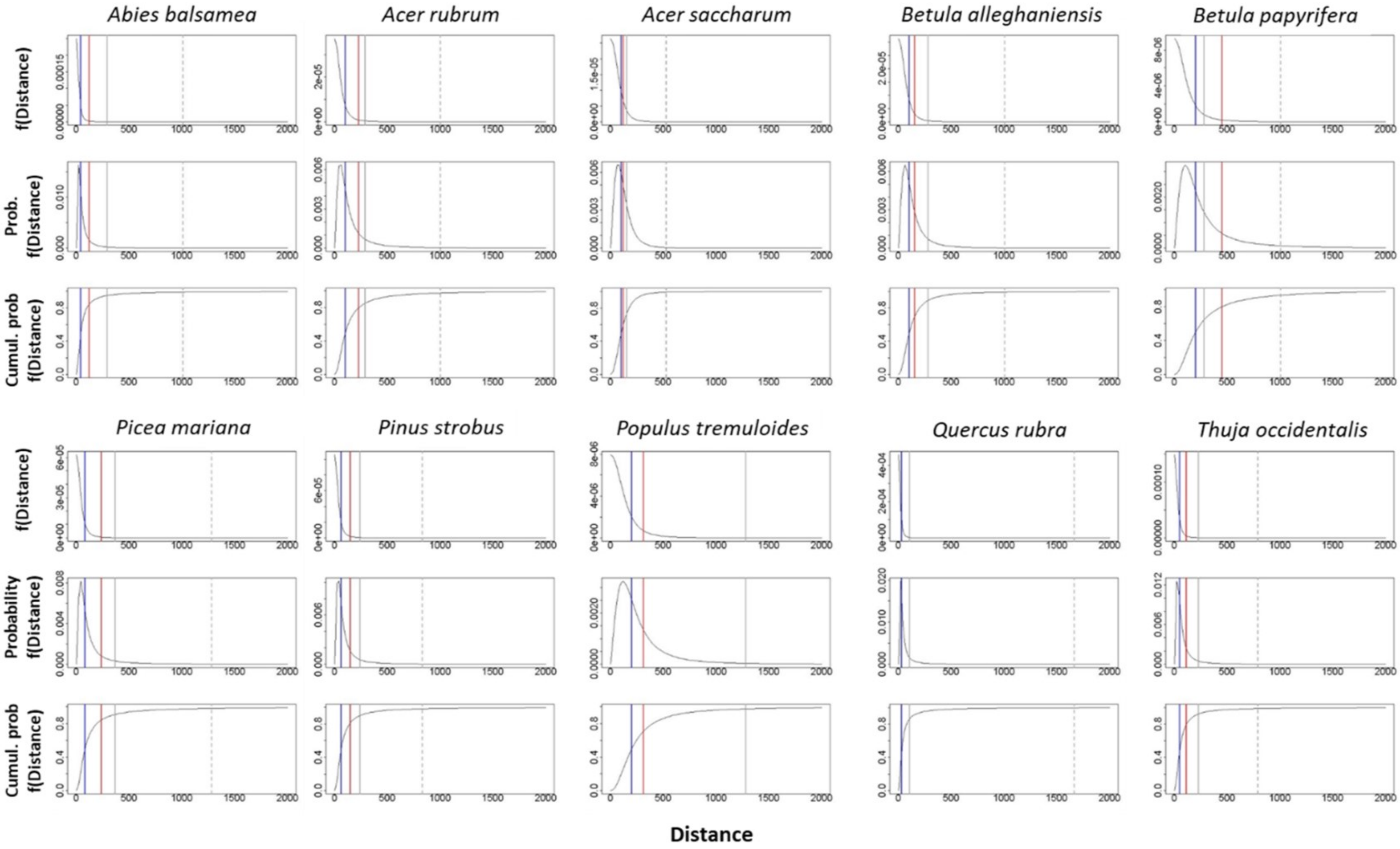


Figure 8.4.2.1: Proof of solution to a as provided in Eq. 5.6 of the main text. Plot here shows that the function f is continually decreasing with a from]0.5, ∞[(truncated here from]0.5,1] for visibility). a is used in the 2Dt function to define dispersal probabilities with distance.

Figure 8.4.2.2: Probability functions of the 2Dt dispersal kernels employed in the MigClim simulations. The x axis shows the distance from the source. The kernels were calibrated using the median (blue vertical line) and mean (red vertical line), as defined by the common seed fall distance and migration velocity respectively. The solid grey vertical line denotes the minimum distance of long distance dispersal (LDD_{min} in the main text) while the broken grey vertical line denote the maximum distance (LDD_{max}). These values were obtained through a regression model of long distance dispersal (dispeRsal: Tamme et al. 2014) and represent the confidence interval of model results.


Abies balsamea
Acer rubrum
Acer saccharum
Betula alleghaniensis
Betula papyrifera
f(Distance)
Prob. f(Distance)
Cumul. prob f(Distance)
Picea mariana
Pinus strobus
Populus tremuloides
Quercus rubra
Thuja occidentalis
f(Distance)
Probability f(Distance)
Cumul. prob f(Distance)
0
500
1000
1500
2000
Distance

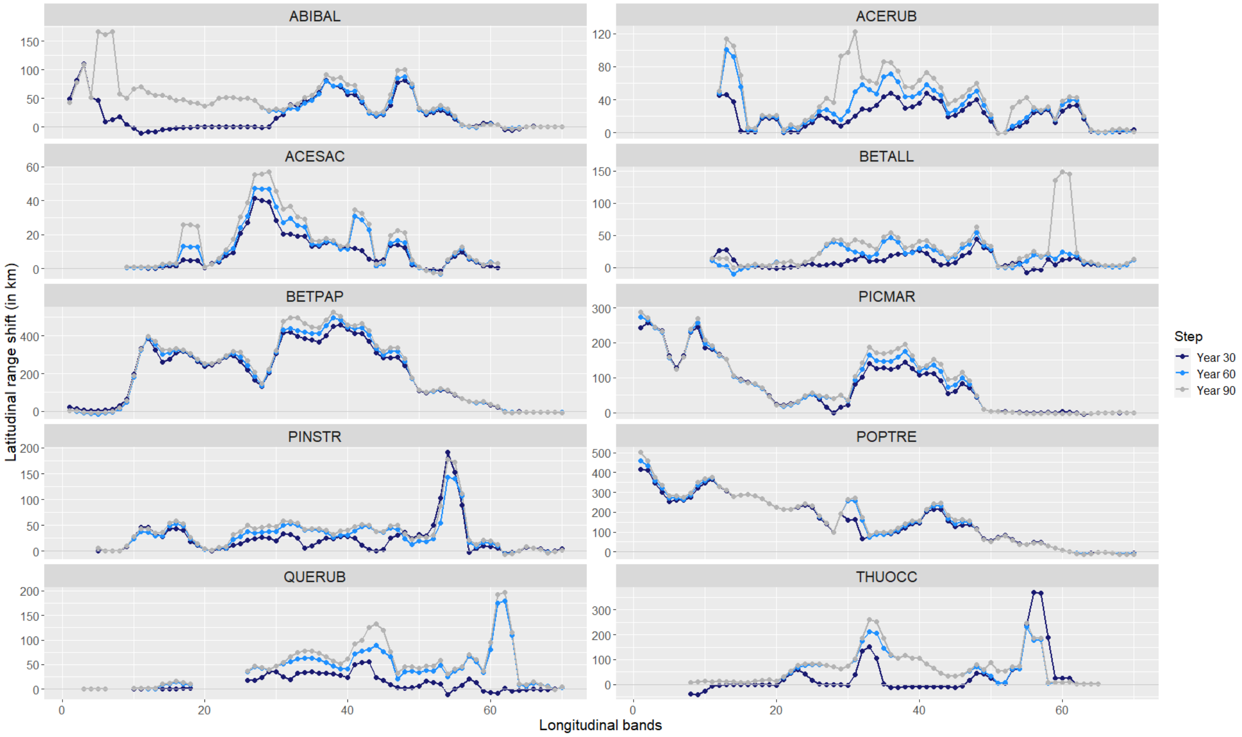


Figure 8.4.2.3: Range shift per longitudinal band for the 10 tree species in this study. Latitudinal limits shown are calculated as the 95th percentile of latitude of occupied cells, whether they are suitable or not. Range shifts in a longitudinal band are based on the latitudinal limit in the last year of a given climate suitability model (Model after 30 [2011-2040], 60 [2041-2071], 90 years [2071-2100] respectively) relative to the latitudinal limit of the initial distribution. Only bands where cells were occupied in the initial distribution and model runs at 30, 60 and 90 years are shown. Positive values denote latitudinal limits at in a given time step at the 95th percentile that are at a higher latitude than the 95th percentile of latitude of the initial distribution. Analyses were conducted on a rolling average of 3 longitudinal bands (1= western edge of study area, 72 = eastern edge)

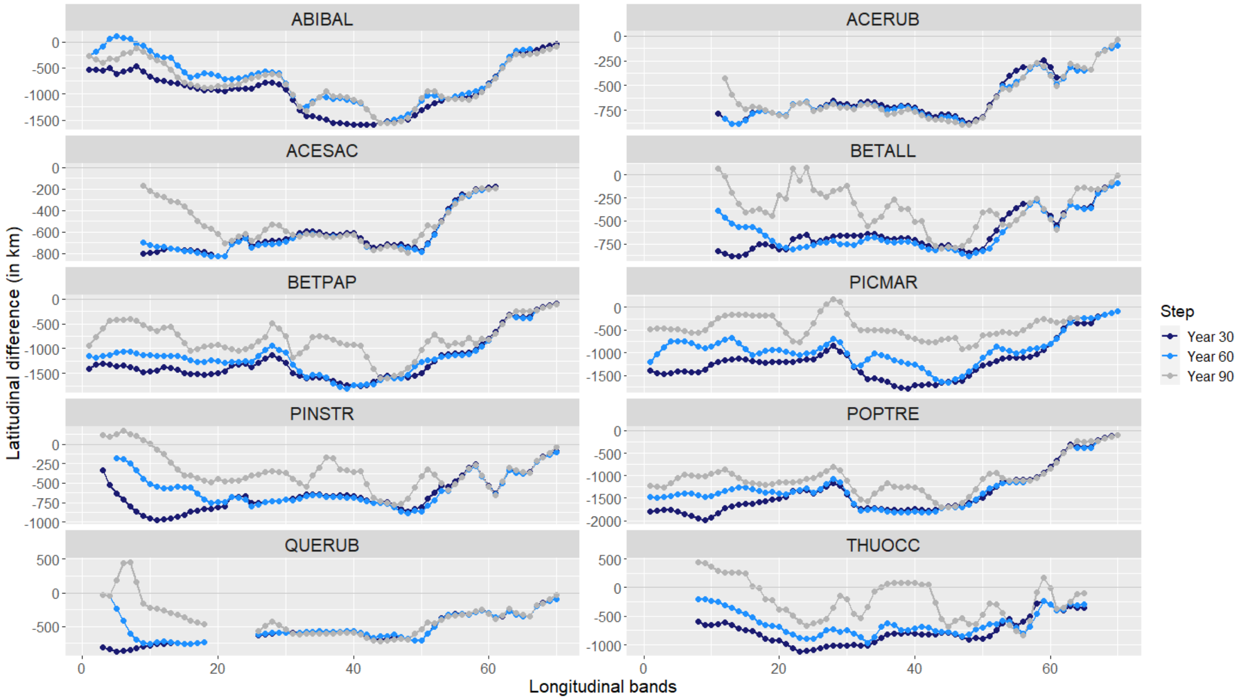


Figure 8.4.2.4: Latitudinal difference between the lower edge of the suitable climate envelope relative to the upper edge of a species' simulated distribution for the 10 tree species in this study. The lower edge of the climate envelope here is defined as the minimum latitude of a species' suitable climate envelope within a given projection (2011-2040, 2041-2070, 2071-2100). The upper edge of a species' simulated distribution is defined as the 99th percentile of latitude at the end of the time period covered by the climate envelope (time step: 30 years, 60 years or 90 years). Positive values indicate that the climate envelope is at a higher latitude than the simulated species distribution in a given time step. Analyses were conducted on a rolling average of 3 longitudinal bands (1= western edge of study area, 70 = eastern edge).