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LIMITED MIGRATION:
WILL SUGAR MAPLE TAP OUT TO CLIMATE CHANGE?

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MIGRATION LIMITÉE:
L'INFLUENCE DU CHANGEMENT CLIMATIQUE SUR LE RECRUTEMENT DE L'ÉRABLE À SUCRE

THÈSE
PRÉSENTÉE
COMME EXIGENCE PARTIELLE
DU DOCTORAT EN BIOLOGIE

PAR
KEVIN SOLARIK

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A man can be as great as he wants to be. If you believe in yourself and have the courage, the determination, the dedication, the competitive drive, and if you are willing to sacrifice the little things in life and pay the price for the things that are worthwhile, it can be done.

Vince Lombardi

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DEDICATION

I would like to dedicate this thesis to my family. First, to my parents Andrew and Rosie for supporting me from the beginning through this entire ride over the years and instilling in me a solid work ethic, thank you from the bottom of my heart. To my brother Thomas and sister Cristina, you have both set the bar high for a younger brother, and as a result has forced me to go to the limits of the academic world to match your standard, thank you. To Zeus, who if it wasn't for your hopeless stares for the afternoon walks for fresh air, I would be still writing this thesis in confusion. Finally, I would like to thank my wife, Amanda, for the unwavering support and reminding me that those long nights of writing and analyzing data would eventually pay off. You are my rock, and I wouldn't be able to have done it without you. I love you, to the moon and back.

FOREWARD

A change in federal government spending in 2010 led to significant reductions in scientific and environmental funding, and almost ensured that my position at Natural Resources Canada – Canadian Forest Service in Edmonton would not be renewed when my term-contract would expire. Before this would happen, I began looking for a new direction. Following potential job interests and interviews, led to a number of email exchanges with potential supervisor Christian Messier surrounding the possibility of beginning doctoral studies. Confusion surrounding my future was abound, however, Christian assured me that the project; focused on potential impacts of climate change on the eastern temperate forest, would provide an ample opportunity to work with some world class researchers and allow me to further develop my research abilities. After a few more discussions with Christian and eventual co-supervisor Dominique Gravel, together we agreed that the fit matched. A project focused on gaining a better understanding of tree species range dynamics excited me, so I decided to take the cross-country trip back home to begin the research. After bringing me up to speed on their expectations; which was to be part of a larger strategic research grant, I quickly found myself happy with my decision. In the first year, I was fortunate enough to be awarded an FCM-FONCER modelling scholarship that afforded me to develop my computer simulation and modelling skills. The remaining funding throughout this adventure was through the support of the

NSERC's prestigious Alexandre Graham Bell Doctoral Fellowship over the next three years and allowed me to complete the project.

This thesis is composed of a general introduction, three chapters that represent the core of my original work conducted over the past four plus years, a general conclusion; which outlines the major findings and advancements through this research, and finally, an annex for supplemental information. The three individual chapters are presented in the typical scientific article format, and have either been published in an academic peer-reviewed journal, have been submitted to an academic journal, or are currently in an internal review process with collaborators at time of submission of this thesis. For each of the three projects, I was responsible for the development, data collection, analysis, and composition of the projects with the help of my supervisory committee and aid from a select number of collogues, whom are co-authored on the individual works.

Each chapter includes an introduction outlying the current status of scientific literature surrounding the research topic, a hypothesis, and objectives/predictions proposed to be tackled. The chapters also contain all the field, lab, and model methodology conducted when applicable, data analysis, results, and finally a discussion section outlying how the resulting findings fit into the bigger scientific picture.

The first chapter entitled *"Assessing tree germination resilience to global warming: A manipulative experiment using sugar maple (Acer saccharum)"* has been published in Seed Science Research. 26, 153-164 in March of 2016. The co-authors are Dominique Gravel, Aitor Ameztegui, Yves Bergeron, and Christian Messier. Each of the co-authors contributed to the objectives, general structures and revision of the manuscript.

The second chapter entitled *"Local adaptation of trees at the range margins slows range shifts in the face of climate change"* is expected to be submitted to an academic journal shortly after the deposition of this thesis. The co-authors of this manuscript include my project supervisors Christian Messier, Dominique Gravel, with the addition of Yves Bergeron, and Rock Ouimet from the Provincial Ministry who provided the site locations to perform the seed transplants in the study. Each co-author contributed to the general structure and revision of the manuscript.

The third chapter entitled *"Priority effects are preventing range shifts of temperate tree species into the boreal forest"* is expected to be submitted shortly after the thesis submission. The co-authors include my supervisors Christian Messier, Dominique Gravel, and Yves Bergeron. An additional co-author, Kévin Cazelles, was also included for his profound help in the modelling and coding aspects involved in the analysis portion of this project. All co-authors also contributed to general focus, and direction of the manuscript and its revisions.

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LIST OF ABBREVIATIONS AND ACRONYMS

a.s.l	Above sea level
DBH	Diameter at breast height
UQAM	Université du Québec à Montréal
UQAT	Université du Québec à Abitibi-Témiscamingue
ANOVA	Analysis of Variance
RESEF	Réseau d`étude et de surveillance des écosystèmes forestiers Québécois
pH	potential of Hydrogen
HSD	Honest Significant Difference
MRT	Multivariate Regression Tree Analysis
SDM	Species Distribution Models
SE	Standard Error
YBP	Years before Present

LIST OF SYMBOLS AND UNITS OF MEASURMENT

ha^{-1}	Hectare
km	Kilometer
m	meter
°	Degrees
°C	Degrees Celsius
%	Percent
C$	Canadian Dollars
Π	Pi
α	Sigma
χ	Chi
p	Probability value
~	Approximately
$\geq$	Greater than or equal to
$\leq$	Less than or equal to
ml	milliliter
g	grams
n	number

RÉSUMÉ

Le rythme accéléré des changements climatiques influence à différents degrés tous les domaines de la biosphère. En effet, le réchauffement global confronte de nombreuses espèces animales et végétales à s'adapter localement aux changements ou à migrer vers de plus favorables conditions afin de diminuer les effets négatifs causés par ces nouvelles conditions abiotiques. Il devient cependant de plus en plus évident que certaines espèces n'ont pas la capacité de s'adapter ou de migrer rapidement, et donc ces espèces pourraient faire face à une diminution significative de leur succès reproductif à la grandeur de leur aire de distribution. Les arbres sont des organismes particulièrement vulnérables aux changements climatiques rapides de par leur caractère sessile qui demande généralement une longue période de régénération combinée avec une dispersion très précise de leurs propagules, ce qui pourrait fortement diminuer leur succès reproductif et leur adaptabilité. Ces limitations pourraient donc imposer un retard de migration significatif aux espèces arborescentes. L'objectif principal de la thèse de doctorat ci-présente sera donc d'identifier les principaux facteurs qui contrôlent les aires de distribution ainsi que les dynamiques spatiales des espèces arborescentes afin d'améliorer notre capacité de prédire les futures aires de distribution de ces espèces. Afin d'atteindre cet objectif, ma thèse s'est principalement intéressée à l'érable à sucre (*Acer saccharum*), une espèce arborescente tempérée de grande importance qui devrait migrer selon les projections de changement global. Cette espèce a cependant démontré une sensibilité aux changements climatiques, principalement lors des premières étapes de croissance.

En premier lieu, j'ai travaillé à la caractérisation des impacts potentiels de l'adaptation locale, de la température, ainsi que des changements de température sur les semences d'érable à sucre et leur capacité à germer. Dans cet environnement

contrôlé, j'ai identifié que l'aire de distribution spécifique avait une grande capacité d'adaptation à la température. En effet, les semences de provenance nordique étaient capables de germer en conditions plus froides constantes et en traitement de température froide variable, alors que les semences en provenance du sud étaient mieux adaptées aux traitements de variation de température chaude. Somme tout, ce premier chapitre a permis d'identifier l'érable à sucre comme une espèce aux exigences très spécifiques en matière de température lors de la fin de la dormance et de la germination des graines, peu importe l'origine des semences. Ces résultats nous ont permis par la suite de prédire la germination de l'espèce sous trois scénarios potentiels de changement climatique, ainsi que d'identifier qu'une réduction significative de la germination de l'érable à sucre est fort probable.

Au sein du deuxième chapitre, mon objectif était de caractériser l'influence relative de l'adaptation locale (de par l'utilisation de semences de différentes provenances) sur la capacité de l'érable à sucre à germer, à s'établir et à survivre à travers une grande variété de sites situés à l'intérieur de l'aire de distribution de l'espèce. Afin d'atteindre cet objectif, j'ai établi une expérience de transplantation de semences à grande échelle. Au cours de cette expérience, j'ai planté des semences provenant d'une multitude de sites (de prélèvement) représentant l'ensemble de l'aire de distribution de l'espèce à plusieurs sites (de transplantation) qui se trouvent à l'intérieur de, à la limite, et passé la limite de l'aire de distribution de l'érable à sucre. Mes résultats démontrent que les semences provenant du Nord possèdent la meilleure capacité pour l'espèce de germer et d'établir un semi, puisque ces semences se retrouvent dans les conditions les plus semblables aux conditions originales. Malgré que la germination des semences était plus grande à l'intérieur de l'aire de distribution spécifique, nos résultats suggèrent qu'une semence qui germine et s'établit après la deuxième année a un taux de survie comparable peu importe sa location à l'intérieur ou à l'extérieur de l'aire de distribution. Ces résultats suggèrent donc que les variables liées au climat sont les principaux facteurs d'influence contrôlant la germination des semences et l'établissement précoce des semis à l'intérieur de l'aire de distribution de l'espèce. L'influence du microsite/substrat a cependant un effet significatif sur le recrutement à l'extérieur de l'aire de distribution. En résumé, ces résultats démontrent que l'expansion de l'aire de distribution de l'érable à sucre pourrait être limitée lors des premières étapes de croissance par l'adaptation locale aux microsites ainsi que par le climat à l'intérieur de l'aire de distribution.

Pour le troisième chapitre, j'ai tenté d'identifier les principaux facteurs démographiques influençant le recrutement des espèces arborescentes à l'intérieur de la zone (écotone) de transition tempérée-boréale, une zone où la migration induite par le climat devrait se produire en premier. L'objectif de ce chapitre était donc de tester si des effets de priorité imposés par les espèces arborescentes boréales résidentes

ralentissent le recrutement des espèces tempérées. Afin d'atteindre cet objectif, j'ai employé des techniques de modélisation inverse et de données spatialement explicites pour investiguer l'influence relative de la dispersion des semis, de la fécondité, de la compatibilité de substrat, et finalement de l'identité biotique du voisinage local sur le recrutement de semis. Nos résultats démontrent que les canopées boréales influencent effectivement la distribution de certains substrats. Ainsi, les substrats boréaux, caractérisés par un couvert d'aiguilles et de bois en décomposition, sont hautement défavorables aux grandes densités de semis d'espèces tempérées et diminuent leur recrutement. De plus, la dispersion des semis était hautement localisée, étant généralement situés à proximité des arbres parents. Ces résultats soulignent que le recrutement des espèces arborescentes tempérées à l'intérieur de l'écotone est restreint par des effets de priorité importants imposés par les espèces arborescentes boréales. En conclusion, ces effets imposés par les arbres de la forêt boréale causeront d'importants retards dans l'expansion de l'aire de distribution des espèces tempérées.

Au final, les résultats de la thèse de doctorat ci-présente apportent un savoir précieux contribuant à la compréhension des facteurs influençant le recrutement dans le contexte de dynamiques d'aire de distribution. En s'appuyant sur les résultats d'une expérience en laboratoire, combinés avec une expérience de transplantation à grande échelle ainsi qu'avec une évaluation du système naturel à l'intérieur de l'écotone tempéré-boréal, la thèse de doctorat ci-présente fournit une quantité notable d'informations clés qui pourront être utilisées pour améliorer notre capacité de prédire les effets des changements globaux au sein des écosystèmes forestiers.

Mots-clés: changement climatique, réchauffement global, aire de distribution spécifique, érable à sucre, température, adaptation locale, effets de priorité, écotone, recrutement de semis, germination de semences, démographie.

ABSTRACT

Climate change is occurring at such a rapid rate that is altering all realms of the biosphere in some fashion or another. More specifically, it is encouraging many animal and plant species to either adapt locally to the changes occurring or to migrate to areas which maintain a more favourable climate. Although, it is becoming increasingly evident that certain species lack the ability to adapt or migrate under rapid climate change, may face significant mismatches in their fitness. Trees are especially vulnerable to these rapid changes associated with climate change, as they are sessile organisms that generally require long regeneration periods, combined with highly localized propagule dispersal that could lead to significant declines in fitness, adaptability, and lags in species migration. It is thus the primary objective of this thesis to identify the driving factors which are currently controlling tree species ranges and their dynamics as a means of better estimating future tree species distributions. To do so, I focused much of my attention on sugar maple (*Acer saccharum)*; a dominant temperate tree species that has been projected to migrate in the future under climate change, however, has also been shown to be sensitive to changes in climate, particularly at the earliest life stages.

First, I focused on assessing the potential impact of local adaptation, temperature, and temperature shifting on sugar maple seed and its ability to germinate. In this controlled environment, I was able to identify a strong species range adaptation to temperature, where northern seed provenances germinated much better under colder constant incubation temperatures and cold shifting treatments, while southern seed provenances were better adapted to warm shifting treatments. Collectively, I was able to find that sugar maple has a very narrow species specific temperature requirement to break seed dormancy and ensure seed germination, regardless of seed origin. Using these results, I then forecasted the influence of three future climate warming scenarios

on seed germination, and found that sugar maple will face a significant collapse in seed germination rates under the projected changes with climate.

In the second chapter, I was interested in finding out the relative influence local adaptation (through the use of various seed provenances) may play on the ability of sugar maple to germinate, establish, and survive within a range of sites pertaining to its species range limit. To do so, I established a large scale seed transplant experiment, where seed from multiple provenances representing the entire sugar maple species range were transplanted to sites within, at, and beyond the current species range limit. I found that seed from the northern seed provenances currently provides the best opportunity for a species to germinate and establish seedlings. Surprisingly, I found that although seed germination and seedling establishment was much higher at sites within the species range following the first year, seedling survival was comparable within, at, or beyond the current range limit after the second year. Further, I found that climatic related variables were primarily responsible for controlling seed germination and early establishment within the range, however, the influence of microsite/substrate drove recruitment beyond its current range. Together, I found strong evidence suggesting that sugar maple's range expansion would be constrained due to the species being locally adapted at its early stages of recruitment to climate and microsites occurring within its current range.

In the third chapter, I wanted to identify the primary demographic factors driving tree species recruitment within the temperate-boreal transition zone (ecotone), where climate induced temperate species migration is expected to occur first. My objective of this study was to test whether priority effects imposed by resident boreal trees were slowing the recruitment of temperate trees. To do so, I investigated the relative influence of seedling dispersion, fecundity, substrate favourability, and the influence of local biotic neighborhood on seedling recruitment. I found that boreal canopies were indeed influencing the distribution of certain substrates. As a result, the boreal influenced substrates; needle cover and decayed wood were found to be highly unfavourable for seedling densities of temperate tree species, and were ultimately inhibiting their recruitment. In addition, seedling dispersion was found to be highly localized, where seedlings were generally dispersed within close proximities to their parent trees. Together, these main findings highlight that temperate tree species recruitment within the ecotone are being constrained by magnified priority effects imposed by boreal tree species. Ultimately, these effects imposed by boreal trees will lead to significant lags in temperate tree species range expansion.

The results presented in this doctoral research thesis improve our understanding of the driving factors controlling recruitment within the context of range dynamics. By

using results collected from the laboratory, a manipulated seed transplant experiment, and an assessment of the natural system occurring within the temperate-boreal ecotone, I provide invaluable information that can be used to further assist in predicting the effects of future climate change within the forested ecosystems.

Keywords: climate change, global warming, species range, sugar maple, temperature, local adaptation, priority effects, ecotone, seedling recruitment, seed germination, demography.

INTRODUCTION

The increasing concentrations of greenhouse gases (GHG) (i.e. CO_2, CH_4, and H_20_{vapour}) being emitted into the atmosphere; where CO_2 alone has increased approximately 70% (ppm concentrations between 1970 and 2004) are the primary cause of climate change (Schaub 2009). As a result of these increases in GHG, it is forecasted that by the end of this century the mean global temperature is expected to rise between 2-4°C (IPCC 2014). Although there exists considerable variability in these projections, they remain conservative. For example, temperature projections that have been corrected to incorporate simply the post-industrial CO_2 ppm concentrations have mean global temperature rising by as much as 3.5°C to 6.2°C by the end of this century (Peters *et al.,* 2013). While temperature projections for the next century have the most leveled headed scientists nearly pressing the panic button, a greater emphasis is no longer being made on whether climate change is actually occurring, but rather on the rate and magnitude of such changes.

Unfortunately, climate change and its fallout is not occurring uniformly across the globe, as variability in space and time become important aspects to interpret potential effects and impacts. For example, the warming that is occurring in the far north (≥60°N) has already been considerable; as much as +1.36°C $century^{-1}$ (1875-2008), with an accelerated warming rate in the most recent decade (+1.35°C $decade^{-1}$)

(Bekryaev *et al,* 2010). Here in the mid-latitudes (40-60°N) of northeastern North America projections have been estimated to be along the lines of the global average (2-4°C), however, the most pessimistic warnings have mean temperatures reaching as high as 7°C by the end of the current century (Feng *et al.,* 2014). Mean temperature increases don't only make things warmer, they also cause significant cascading effect(s) down on many other processes and cycles. For example, the hydrological cycle has already been altered by increased warming over the past few decades, resulting in shifts in the tropical belt (Lu *et al.,* 2009). These changes can then influence the formation of Hadley cells, and ultimately impact trade winds and precipitation globally (Seidel *et al.,* 2008). Indirectly, these changes will also increase the uncertainty surrounding inter-annual variability of precipitation globally and locally, and is also expected to increase the frequency and magnitude of extreme weather events (i.e., drought, flooding) (Coumou and Rahmstorf 2012).

Climate change is also having a significant effect on the biosphere, where considerable changes have already been documented in forested ecosystems across the globe. For example, the growing season in Canada's boreal forest has already extended a number of weeks since the 1960s (Price *et al.,* 2013), which directly influences the plant photosynthetic activity and growth (Bertini *et al.,* 2011). A number of other changes are also occurring; latitudinal shifts of the tree line (Harsch *et al.,* 2009), site productivity (Albert and Schmidt 2010), and changes in species composition(s), all have a profound impact on community assemblages, processes, and interactions (Iverson and Prasad 2010). Although, not all reports of these changes are unidirectional; some studies are reporting net benefits in tree growth associated with a prolonged growing season with rising temperatures and CO_2 rates (Pretzsch *et al.,* 2014; Wu *et al.,* 2014), while others are reporting significant increases in tree mortality (See Global Review by Allen *et al.,* 2010). It thus becomes critical to identify the most susceptible areas and species where such prominent changes in climate will undoubtedly impact the health of the forested ecosystem and its proponents. By successfully doing so, we will be able to not only better identify the direct/indirect impacts of climate change, but also be able to better project future conditions to allow for better mitigation.

Trees can be especially vulnerable to the expected rapid changes associated with climate change, where a combination of their lack of mobility, time to reach reproductive maturity, and typically limited propagule dispersal, result in very slow demographical changes (Petit and Hampe 2006; Lenoir and Svenning 2013; Aitken *et al., 2016*). During the last significant warming period (Holocene – 11,500YBP), trees were able to attain "reasonable" migration rates (10-20 km annually) (King and Herstrom 1997), that may have reached as high as 70 km annually (Davis 1981; Tirpak 1990). However, unlike trees during the Holocene; which went relatively undisturbed over long periods and migrated through primary succession (i.e., glacial retreat), trees today are forced to migrate to areas where trees are already established (ex. temperate trees attempting to migrate into the boreal forest) and are exposed to priority effects; early colonizing species monopolize resources (i.e. space, light, nutrients) and make it difficult for invading species to compete, and ultimately colonize (Urban and De Meester 2009). Also, unlike the slower more progressive warming which occurred during the Holocene, trees today are being subjected to a more pronounced and rapid warming over a shorter time frame. Furthermore, to make matters even more unfavorable, trees are also being exposed to a variety of anthropogenic (i.e. habitat fragmentation - deforestation, urbanization, pollution) and natural disturbances (i.e. insect outbreaks and fire), both projected to increase in magnitude and frequency under climate change (Volney and Hirsch 2005; Bergeron *et al.,* 2010; Price *et al.,* 2013). Ultimately, present day tree migration rates should be expected to be considerably slower than those of the past.

Current estimates have most North American tree species being capable of migrating at rates of 100-1000m year^{-1} (~50 km century^{-1}) (Overpeck *et al.,* 1991), however, this remains a far cry from the "required rate" (300-490 km century^{-1}) generally believed trees would be required to reach in order to maintain one's climate niche (Thomas 2004; McLachlan *et al.*, 2005; Ibanez et al.2009; Périe *et al.,* 2014). Under current warming, trees have already begun to show their ability to migrate along both elevational (Lenoir *et al.,* 2008; Beckage *et al.,* 2008; Kharuk *et al.,* 2010; Brown and Vellend 2014) and latitudinal gradients (Graignac *et al.,* 2014; Foster and D'Amato 2015; Putnam and Reich 2016). However, it is becoming increasingly clear that not all species will be able to maintain such rapid rates of migration, and thus mismatches in their reproductive fitness should be expected to occur (Renwick and Rocca 2015; Aitken and Bemmels 2016). A recent meta-analysis conducted by Zhu *et al.,* (2012) highlighted that more than half of the 92 tree species located in the eastern United States would experience some form of species range contraction or lag due to climate change, where only a fifth of the tree species would be forecasted to keep pace with changes in climate. Ultimately, if species aren't able to keep up with the "required rate" to maintain pace with climate change, the focus needs to turn to what are the cause(s) of such lag or delay.

A species range limit or periphery is likely to be the area of first observational change(s) for expansion or contraction due to climate change (Sexton et al. 2009; Svenning *et al.,* 2014). Species range limits are generally highly mobile, where they are typically expanding and contracting frequently through time (Kirkpatrick and Barton 1997; Sexton *et al.,* 2009). Beyond a species range limit, individuals are typically not present due to a combination of unfavorable abiotic and biotic factors, which stress the species beyond some physiological limit associated with their reproductive fitness (Hu and He 2006; Blanquart *et al.,* 2013; Renwick *et al.,* 2015). A number of inhibitors have been proposed as reasons for range limits and/or the cause of the inability of a species to migrate; climate (Williams *et al.*, 2010; Fishchelli *et al.*, 2015), dispersal limitations (Hargreaves and Eckert 2014), edaphic effects (Lavergne *et al.*, 2010; Brown and Vellend 2014), and biotic interactions (HilleRisLambers *et al.*, 2013; Moran and Ormond 2015; Urli *et al.*, 2016) remain the most prominent. The increased stress caused individually and/or in combination of these factors creates high environmental variability at the species range limit or ecotone; where one biome transitions into another causing species overlap (Sexton *et al.*, 2009; Boulangeat *et al.*, 2012; Hargraves *et al.*, 2014). These zones contain the last complete life cycle (seed dispersed by parent tree which then becomes an adult tree) of a population (Renwick *et al.*, 2015) and are likely to interact in novel ways first under climate change as they respond to novel species and environmental interactions (Williams and Jackson 2007; Svenning *et al.*, 2014).

Currently, species distribution models (SDMs) are the standard approach for predicting the dynamics of range shifts in response to environmental changes (Parmeasan 2006; Chen *et al.*, 2011). Although considerable advances have been made using SDMs to predict changes under climate change (Thuiller *et al.*, 2008; Chevin *et al.*, 2010; Boulangeat *et al.*, 2012), concerns still remain with their accuracy (Shaw and Etterson 2012). For instance, temperate tree species have been projected to be present by the end of this century at locations where there are currently no trees (i.e. tundra) (McKenney *et al.*, 2007). These models have been criticized for being too simplistic, and typically ignore several other factors important to range dynamics; dispersal abilities and barriers, demography, habitat fragmentation, genetic variability, biotic interactions, and often natural disturbances (Sexton et al. 2009; Lavergne *et al.*, 2010; Alberto *et al.*, 2013). In addition, SDMs lack the ability to consider how plants can evolve to environmental conditions (Reed *et al.*, 2011; Moran and Ormond 2015). Recent efforts however have made great strides to include phenotypic plasticity and evolutionary response to ecosystem changes (Atkins and Travis 2010; Lu *et al.,* 2014), which when population differentiation is accounted for, species range shifts are even more constrained than when models consider spatial homogeneity (Valladares *et al.,* 2014). These findings suggest that in order for species to maintain their climatic niche under climate change, they will either need to have a high genetic mutation rate or high local diversity at the range periphery to deal with novel changes expected to occur.

Local adaptation (i.e. individuals of the same species that are better suited to their local environment than others of the same species) is measured through the connectivity between the adaptive variability genetically (e.g., selection, drift, migration) and how the environmental conditions play upon it (Kawecki and Ebert 2004). The ability to adapt to local conditions plays a fundamental role in the generation and maintenance of biodiversity (Blanquart *et al.,* 2013), and will greatly impact the expansion or contraction of a species' geographical range as they interact with the local climate and other species (Kaltz and Shykoff 1998; Sexton *et al.,* 2009). Although the concept of local adaptation has been known for nearly a century (Turesson 1922), there still remains considerable gaps in our knowledge of how influential adaptation is and could be with regards to a climate induced species range shifts. Tree species that maintain or expand their current distribution under climate change should either be resilient in place or migrate to more favorable environments, where their success will hinge on the species' ability to express certain favorable genetic and non-genetic traits (adaptive evolution, gene flow, phenotypic plasticity). Successfully doing so, will either enhance its fitness or at a minimum buffer the potential mismatches that may cause significant setbacks under future changes (Nicotra *et al.,* 2010; Gonzalez *et al.,* 2013; Anderson 2016). The species ability to adapt is especially important if certain life events are temporal and/or climatically sensitive (e.g., leaf out period, flowering, seed dormancy) (Morin and Chuine 2014).

Trees in the past have shown the ability to naturally adapt and evolve in response to the complex interaction(s) between abiotic and biotic factors and their processes occurring within their local environment (Sexton et al. 2009). Trees have been shown to have adapted to temperature and precipitation (Kim and Donohue 2013), as well as their influence to herbivory, pollinators, and even edaphic characteristics (Johnson *et al.,* 2010; Garrido et al., 2012; Brown and Vellend 2014). As trees can maintain a large geographical range, it can lead to higher levels of within-population genetic variation, which in turn benefits a species to adapt and acclimate more rapidly to changes in the future (Hamrick 2004). Species whom maintain higher diversity and/or adaptability are at an advantage, where the expression of preferential alleles to deal with a novel suite of environmental variability under climate change could help buffer populations – first at the local scale and then at the species level (Savolainene and Oney 2013). However, if a natural population lacks sufficient genetic variability or population size, especially at their range periphery - the potential for adapting could be severely constrained, at least until it adapts (Franks et al., 2014). Measuring the ability of a species to adapt to climate change remains pertinent, especially since the individuals at the range limit are not always the most adaptive (Duputié et al., 2015) and changes can be species and boundary limit dependent (Blanquart et al., 2013). Our understanding of species adaptation at their range periphery remains limited, especially as the number of potential inhibitors and their degree of contribution can be complex (Kim and Donohue 2013; Aitken and Whitlock 2013; Brown and Vellend 2014; Urli *et al.,* 2016).

Sugar maple makes an ideal candidate to investigate the contributing factors which determine the causes of its current range limit and associated dynamics under climate change. Sugar maple is a tree species which is wide spread, long lived, and dominant within much of its 12.5 million ha^{-1} distribution within the forests of northeastern North America (Godman 1990). Since migrating northward from its southern refugia during the last glacial event, sugar maple's distribution has remained considerably stable over the past 6,000 years (Miller and Parker 2009). As a result of this stability, sugar maple has been able to adapt to a wide range of abiotic and biotic conditions across a range of forest communities; ranging from the temperate-boreal forest ecotone of its northern limit to its southern range limit with the mixed-wood forests of the southeastern plain (Godman 1990). Likely due to such variation in living conditions, sugar maple has been able to express considerable genetic diversity from its southern to northern range (Gunter *et al.,* 2000), which includes a number of regional genetic ecotypes (Kriebel and Gabriel 1969). Sugar maple may currently possess the necessary adaptability to be evolutionary rescued (Gonzalez *et al.,* 2013) and overcome potential deleterious impacts of climate change, however it remains to be investigated.

Like several other North American temperate tree species, sugar maple has been forecasted to migrate northward under climate change (Boisvert-Marsh *et al.,* 2014). However, sugar maple has evolved to possess a specific sensitivity to climate associated with key fitness processes that could leave it prone to mismatches under climate change. For example, sugar maples' ability to develop flowers in early spring has been adapted to more stable past climate conditions, where increased variability in earlier spring conditions in the future may negatively impact flower development (Chuine and Beaubien 2001; Morin and Chuine 2014). Next, if flower development does ensue, the development of viable seed must occur, and then subsequent germination. Sugar maple possess a morphologically mature, but dormant embryo that requires an extended period (30-90 days) of cool and moist (stratification) conditions (Janerette 1979; McCarragher *et al.,* 2011). Matching the duration and temperature specific requirements for seed germination could be in peril under future climate change. Sugar maple could be touted as the "*Goldilocks*" of tree species, where like Goldilocks; who held a similar preference to the temperature of her porridge, sugar maple seeds are particular to the temperature of their environment, and unfavourable changes (temperature and duration) could lead to a collapse in successful seed germination and impact natural recruitment success of the species. Concerns surrounding sugar maple's fitness thus should be raised, especially at the northern range periphery, where adult trees currently grow much slower (Reich *et al.,* 2015), and their offspring (if produced) should be subjected to much higher environment variability (Walters and Reich 1996; Clark *et al.,* 2003; Kellman 2004; Brown and Vellend 2014). Although sugar maple's abundance has increased since post-settlement (circa.1850) (Houle *et al.,* 2012), recent declines associated with changes in environmental conditions (Duchesne *et al.,* 2005; St.Clair *et al.,* 2008) highlight a potentially higher sensitivity to changes than previously believed, and could impact reproductive fitness even more in a rapidly changing future (Goldblum *et al.,* 2010; McCarragher *et al.,* 2011).

As many plant species will lack the ability to disperse and colonize areas to maintain rates comparable to those currently projected under climate change (Loarie *et al.,* 2009), it becomes imperative that research be undertaken to identify the potential severity of important bottlenecks (i.e. points of resistance where significant reductions in fitness or abundance occur) associated with species distribution range lag (Parmesan 2006; Sexton *et al.,* 2009; Svenning *et al.,* 2014). Bottlenecks can be caused by a number of processes, where a species could be maladapted to its environment, which then leads to declines in species fitness or ability to regenerate (Kawecki and Ebert, 2004; Kingsolver *et al.,* 2013; Franks *et al.,* 2014; Savage and Vellend 2015). Currently our understanding of the key processes controlling species ranges and their dynamics although improving (Svenning *et al.,* 2014; Urli *et al.,* 2016) remains limited.

To date, our best means of assessing a species' ability to migrate empirically in the future remains reciprocal transplant studies; attempt to identify the fitness response of a single or multiple population(s) of a species by gathering information as to how it responds to the local environment. While these types of studies have a long history of use (Hall 1932), many still knowingly ignore key life stages (i.e. seed germination and initial seedling establishment) through the use of greenhouse grown seedlings (but see Brown and Vellend 2014). By transplanting seedlings rather than seed, studies ignore significant bottlenecks in recruitment, which can falsely inflate interpretations of the likelihood of a tree species ability to migrate. Furthermore, greenhouse grown seedlings are typically grown in "favourable conditions" (inside or outside), which generally ensures that healthy seedlings are being transplanted. Ultimately, the lack of empirical studies transplanting seeds leaves a significant gap in our knowledge to be able to accurately estimate possible rate(s) of colonization a species can attain. By doing so, we will be able to further our understanding by including more factors and processes that influence the demographics of range limits (Sexton *et al.,* 2009; Walck *et al.,* 2011; Svenning *et al.,* 2014).

To date, most research conducted with an interest in assessing the ability of a species to migrate has generally been done within an altitudinal context exclusively (ex. Lenoir *et al.,* 2008; Beckage *et al.,* 2008; Brown and Vellend 2014). Although this approach allows for more rapid field assessments (less travel time between field sites), it limits the inter-site variability gained through assessing multiple ecotone sites (Graignic *et al.,* 2014; Putnam and Reich 2016). To help mitigate the demand for latitudinal studies, a heavy dependence on SDMs has been used (Parmeasan 2006; Chen *et al.,* 2011). However, as mentioned earlier, these models ignore many important variables and processes known to influence species migration and are often limited by the data used (Lavergne *et al.,* 2010; Alberto *et al.,* 2013; Thuiller *et al.,* 2013). Further, it is often that studies are restricted into making accurate projections into species migration or lag as they often only have data representing a portion of a species latitudinal distribution (Woodall *et al.,* 2010; Zhu *et al.,* 2012). In the context of northward tree species migration under climate change, it will become increasingly important for the collection of more empirical data, particularly at the earliest life stages in order to accurately assess the present and plausible future changes occurring in the forested ecosystem. This becomes especially important to include sites and populations across the entire species range and compare results with sites at their range margins, where these populations still remain under sampled (Brown and Vellend 2014; Graignic *et al.,* 2014; Foster *et al.,* 2016).

As it becomes more pertinent to accurately predict the impacts of climate change on the forested ecosystem, my central objective for this thesis was to identify the key contributing and/or inhibiting factors that influence the demographics of trees in the context of species range shifts under climate change. In the first chapter of the thesis, I begin by taking an in depth approach at investigating the effect of local adaptation, temperature, and temperature shifting – a proxy for early or late spring conditions on seed germination of sugar maple *(Acer saccharum).* I performed this assessment in a controlled laboratory setting as a means of isolating the effect of temperature and its influence on seed germination. I hypothesized that seed origin affects the range of temperature for optimal germination due to local adaptation. The primary objective(s) of within this study was to first identify the optimal incubation temperature across the species range, and for each seed provenance used within the study, while also identifying if an upper temperature threshold existed that inhibited germination. Second, I identify the influence of warmer and cooler temperature shifts on seed germination as a means of simulating an earlier or late spring. Finally, I identify the potential changes in future seed germination across the range of sugar maple under a series of future climate warming scenarios (+2°C, +5°C, and +7°C); which are in line with the projected warming expected to occur over the next century.

In the second chapter of the thesis, I assessed the effect of provenance and local adaptation of sugar maple seed collected from across the entire species range to conditions within, at, and beyond its current species range. I hypothesized that the demography at the species' range limit would be constrained due to the species being adapted to conditions within the species range. To investigate this, I established a 12 site seed transplant study that included sites within the current species range, at the range limit (ecotone), and beyond the current species range limit to assess the ability of sugar maple seed to germinate, establish seedlings, and survive in association with the local environmental conditions. I made the following predictions: (i) southern seed provenances will be the most maladapted to the environmental conditions occurring at and beyond the current northern range limit, as they are the furthest in proximity of their origins (provenance effect), (ii) early seedling establishment will be best within sites which meet the species specific climatic requirements needed to ensure seed germination (climate effect), and (iii) upon seedling establishment, local microsite conditions more closely resembling those within the range limit will favour higher survival rates (microsite effect).

While in the first chapter I manipulated temperature and temperature timing on seed germination in a controlled environment, and in the second chapter I modified the site and as a result the local environmental (abiotic and biotic factors) contributors, in the third chapter, I was interested in investigating the natural system. In particular, I was curious to know how the resident environment at the ecotone influenced seedling recruitment. I hypothesized that priority effects (imposed by resident boreal tree species) slow recruitment of temperate tree species, and thus contribute to the lag in temperate tree range expansion. To do so, I investigated the relative importance of a series of contributing factors highlighted as influential to species migration; seedling dispersion, fecundity and substrate favourability, and the influence of the local biotic environment – as a proxy of the potential effect of resident trees. I made the following predictions: (i) boreal trees will influence the spatial distribution of substrates within a stand, with which these substrates will (ii) influence the seedling density of temperate tree species, and (iii) limited seedling dispersal will magnify priority effects from boreal tree species.

The thesis then ends with a global conclusion that summarizes the key findings and advancements made within each of the three main chapters and how they fit in the scientific literature. I also offer some general emerging ideas/advances in practices and theories, followed by some limitations of the research. I then conclude by offering some potential future research directions that would further enrich our understanding of range dynamics under climate change that were not taken in this thesis.

CHAPTER I

ASSESSING TREE GERMINATION RESILIENCE TO GLOBAL WARMING: A MANIPULATIVE EXPERIMENT USING SUGAR MAPLE (ACER SACCHARUM)

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1.1 Abstract

A climate warming of 2-5°C by the end of the century will impact the likelihood of seed germination of sugar maple (*Acer saccharum*), a dominant tree species which possesses a restricted temperature range to ensure successful reproduction. We hypothesize that seed origin affects germination due to the species' local adaptation to temperature. We tested this by experimentally investigating the effect of incubation temperature and temperature shifting on sugar maple seed germination from 7 different seed sources representing the current species range. Survival analysis showed that seeds from the northern range had the highest germination percentage, while the southern range had the lowest. Mean germination percentage under constant temperatures was best when temperatures were ≤5°C, whereas germination percentages plummet at temperatures ≥11°C (5.8%). Cool shifting increased germination by 19.1% over constant temperature treatments and 29.3% over warm shifting treatments. Both shifting treatments caused earlier germination relative to the constant temperature treatments. A climate warming of up to +5°C is shown to severely reduce germination of seeds from the southern range. However, under a more pronounced warming of 7°C, seed germination at the northern range become more affected and are comparable to seed from the southern range. This study states that the high seed germination percentage found in sugar maple at the northern range makes it fairly resilient to the warmest projected temperature increase for the next century. These findings provide forest managers the necessary information to make accurate projections when considering strategies for future regeneration while also considering climate warming.

Keywords: *Acer saccharum*, climate change, climate warming, seed germination, stratification, sugar maple, temperature.

1.2 Introduction

Recent climate change projections have global mean temperature increasing 2-5°C for the mid-latitudes of North America (between 40°N and 60°N) by the end of the 21st century (Feng *et al.*, 2014). Coupled with increasing uncertainty surrounding inter-annual variability of precipitation in the future (Kharin *et al.*, 2007), changes in plant population and community dynamics become an area of concern (Walck *et al.*, 2011; McCarragher *et al.*, 2011). Noticeable shifts in species distributions have already been documented (Lenoir *et al.*, 2008; Beckage *et al.*, 2008), and are predicted to continue in the future (Zhu *et al.*, 2012) as species attempt to maintain their bioclimatic niches (Goldblum and Rigg, 2005; Iverson and Prasad, 2010).

Tree migration will hinge on the successful germination, maturation and eventual reproduction at higher altitudes and latitudes (Loarie *et al.*, 2009; Chen *et al.*, 2011). A species which fails to migrate at fast enough rates will be subjected to increasing stress and be forced to adapt to the new climatic regimes or it will decline. As a result, this could likely cause pockets of variable fitness and reproductive success within the current species range (Dangleish *et al.*, 2010; Walck *et al.*, 2011). Under the predicted changes, significant reductions in reproductive success among trees should be expected, especially when species specific climate and temperature limitations exist (Chuine and Beaubien, 2001). A possible mismatch between genotype and the environment can bring into question the long term persistence of the species, particularly in terms of successful reproduction (Hoeksema and Fored, 2008; Blanquart *et al.*, 2013). Regional variability in reproductive success could become concerning as species at the trailing and/or leading edge would be exposed to the highest pressures within forest transitions zones (Hu and He, 2006; Sexton *et al.*, 2009).

Sugar maple (*Acer saccharum* Marshall.) is a long lived, deciduous and shade-tolerant tree species found present on 12.5 million ha^{-1} of northeastern part of North America (Godman *et al.,* 1990). A major ecological and economically important tree species (it supports a C$200 million annual syrup industry (FPAQ, 2016), sugar maple could face significant declines in reproductive success due to its seed requiring very specific abiotic conditions to ensure germination (Bradford, 1995; Caspersen and Saprunoff, 2005). It possesses a morphologically mature, yet dormant seed embryo that requires an extended period of stratification (i.e. cool and moist conditions) at near freezing temperatures to break dormancy and ensure germination (Zasada and Strong, 2003). A dormant seed is one that is unable to germinate in a specified period of time due to any combination(s) of the following reasons: (i) immature embryos, (ii) seed coats impermeable to water and/or gases, (iii) inhibitors, (iv) light requirement, and (v) mechanical restrictions by the seed coat, which are otherwise favorable for its germination (Maguire 1984; Baskin and Baskin, 2004). Typically, sugar maple seeds will develop and ripen by late summer (September – October), disperse by late fall (October-December), and remain dormant for the winter months before germinating in spring. Future climatic conditions could impact the specific time and temperature requirements needed for germination, ultimately impacting the long-term persistence of this tree species. It is predicted that climate change will lead to sharper seasonal changes, particularly in early spring, where temperature shifts are most abrupt. It also is the time of year where many of the earliest life stage processes (i.e., germination and seedling establishment) take place. Climate warming will lead to earlier springs, which in return will cause faster snow melt and reduced snow cover in northern altitudes and latitudes (Mankin and Diffenbaugh, 2015). These abrupt changes could lead to a much smaller window of stratification and in turn, reduce the likelihood of seed germination for sugar maple. Another concern with earlier snow melt is the potential for increased freeze-thaw events; which can expose seeds and seedlings to abrupt changes in colder temperatures that will increase early germinant mortality (Decker *et al.,* 2003).

Freeze-thaw events as a result of earlier springs have already been documented to severely impact other important processes, such as bud break, flower development, and seed ripening, which all could further reduce reproductive success (Chuine and Beaubien, 2001; Morin *et al.,* 2008; Drescher *et al.*, 2014).

Currently, little is known about the variability associated with climatic requirements for germination and the potential influence it may have across a species range (Hedhly *et al.,* 2009). Sugar maple provides an ideal candidate to investigate these concerns, as it maintains a large range and is sensitive to climate (Goldblum *et al.,* 2010). While some studies have assessed germination percentage (directly or indirectly) within the sugar maple range, most have been limited to either a single seed origin or only provided minimal insight into the influence of temperature on germination (ex. Webb and Dumboff, 1969; Simmonds and Dumboff, 1974; McCarragher *et al.,* 2011). To our knowledge, only limited research in Acer has been conducted at the northern range margin (Tremblay *et al.,* 1996; Graginac *et al.,* 2014), while largely ignoring the mid- and southern species range. While it has long been known that seed germination is likely to be linked to seed origin (Mayer and Poljakoff-Mayber, 1975), it has yet to be thoroughly assessed with the influence of temperature and temperature shifts.

The general objective of this study is to perform an assessment of the impact of local adaptation, temperature, and temperature shifting on seed germination. Such information is necessary to make more accurate predictions of future tree reproduction. We hypothesize that seed origin affects the range of temperature for optimal germination due to local adaptation. More specifically, our primary objectives in this study were to (1) identify the optimal incubation temperature across the species range, and for each seed origin; (2) identify the influence of warmer and cooler temperature shifts to simulate an early or late spring and its associated effects, and (3) identify the potential changes in future seed germination across the range of sugar maple under a series of warming climate scenarios. We did this by implementing a fully factorial experimental design to investigate the influence of nine constant incubation temperature treatments, sixteen warm shift treatments, and sixteen cool shift treatments on seeds from seven different origins.

1.3 Methods

1.3.1 Seed, Source(s), and Storage

In this study 28,700 sugar maple seeds from 7 origins across the current species range were used (Figure. 1.1). All seeds were collected in the fall of 2013 and were air dried at room temperature (20°C) until seed moisture content ranged between 9.5% and 15%. Once dried, the samaras were mechanically tumbled until the wing portion of the seeds was removed. Seeds were then passed through an air/gravity feed sorter, where filled seeds were separated from unfilled seeds, which ensured seed viability (filled seeds) above 95% for each seed origin. To further reinforce that seeds were filled, we used either x-rays on a subset of seeds from each origin or pressed the seeds between fingers during counting, prior to the commencement of the germination trials (Graignic *et al.,* 2014). Seeds were stored at -3°C for two months before initiating the experiment (Yawney and Carl, 1974).

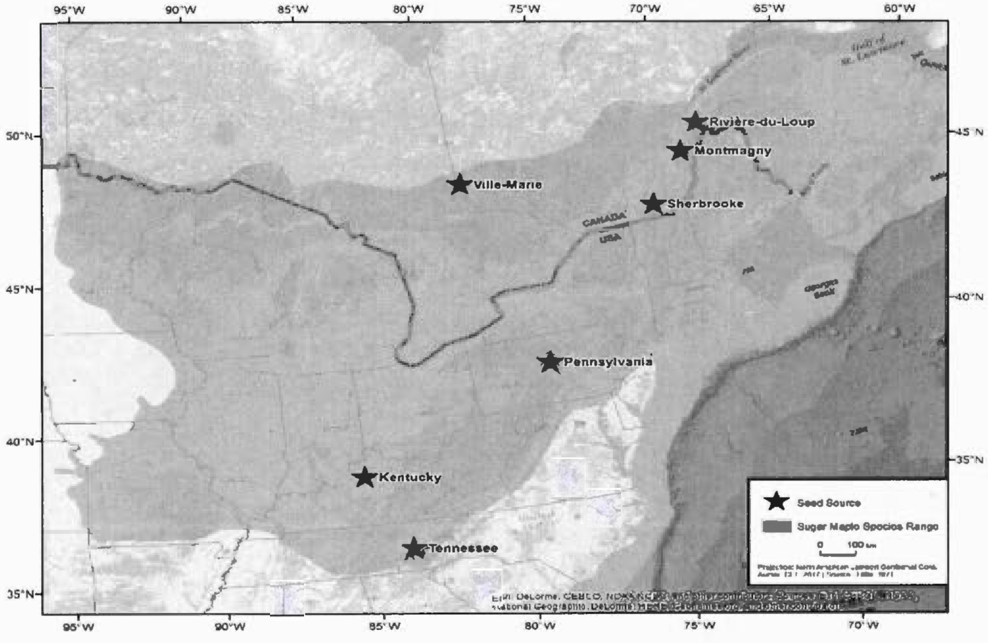

Figure 1.1. Approximate seed origins used in the study: (1) Ville-Marie, Québec, (2) Rivière du Loup, Québec, (3) Montmagny, Québec, (4) Sherbrooke, Québec, (5) Pennsylvania, U.S.A, (6) Kentucky, U.S.A, and (7) Tennessee, U.S.A. Seed origins are overlaid on sugar maple's native species range which is adopted from Little (1971).

1.3.2 Treatments - Constant Incubation Temperature

All seeds were soaked in tap water and kept at 3°C for 14 days (Janerette, 1979); a common treatment done to soften the hard seed coat, and provide a period of water uptake, which increases overall germination success (Webb and Dumbroff, 1969). This process mimics the natural stratification that occurs during the cool, wet conditions of overwintering and early spring. Forty-one seed lots (100 seeds/lot) from each of the seven seed origins were prepared and individually wrapped in mesh screening and enclosed within moist Kimpak-cellulose wadding, and then wrapped in aluminium foil (Janerette, 1978b) to be used for all combination of treatments. Seed lots from each seed origin were placed within a series of growth chambers (CONVIRON, ATC26, Winnipeg, Canada), each maintained at the following 6 constant temperatures: 3°C, 5°C, 7°C, 9°C, 11°C, 13°C for 90 days. Since growth chambers present limitations to work at low temperatures (≤3°C), Sanyo MIR-154-PA incubators (SANYO Electric Biomedical Co., Osaka, Japan) were used for the 3 colder constant temperature treatments: -1°C, 0°C, 1°C. Nine out of the 41 seed lots/origin were selected at random from each of the 7 origins (7 seed origins x 9 constant stratification temperatures). A HOBO Pendent temperature data logger (Onset, Bourne, Massachusetts, USA) was placed in each of the chambers and incubators to ensure that the assigned temperatures remained consistent throughout the entire measurement period. Temperature was recorded hourly over the entire 90 days. Seed germination was monitored weekly, where germinated seeds were counted and discarded, yielding a temporal sequence of germination. Protrusion of the radicle through the seed coat was the criterion for which germination was deemed successful.

1.3.3 Temperature Shifts

In addition to the nine constant incubation temperature treatments, we investigated the potential influence of temperature shifting on seed germination. By suddenly changing the incubation temperature during the experiment provides insight into abrupt changes in temperature that may occur in an early or late spring once snow has melted (when present). We chose to change incubation temperature after 2 weeks (half the time period industrial nurseries use for germination trials), as a means of mimicking the influence of rapid temperature change, commonly seen in early spring.

To conduct the shifting treatments, we placed seed lots in either a cool (-1°C, 0°C, 1°C, 3°C) or warm (7°C, 9°C, 11°C, 13°C) initial incubation temperature for 2 weeks. Seed lots were then shifted to one of the opposite treatments (i.e., seed lots initially placed in a cool incubation temperature were then shifted to one of the warm incubation temperatures, and vice versa) for the remainder of the study (11 weeks). For example, 4 individual seed lots from Kentucky that were initially placed at -1°C for 2 weeks, would be transferred to each of warmer treatments (7°C, 9°C, 11°C, and 13°C) and would be identified as a warm shift treatment. This would be repeated for each seed origin and each treatment combination for both the warm and cool shifts using the remaining 32 seed lots/origin for a total of 224 seed lots (22,400 seeds).

1.3.4 Statistical Analysis

Data were analyzed following the recommendations of McNair *et al.*, (2012), where survival analysis is deemed the most appropriate method to quantify seed germination (Pérez and Kettner, 2013). This statistical approach also allows for the analysis of individual seeds rather than cumulative germination percentages, while providing the flexibility to interpret multiple contributing factors simultaneously over repeated measures (McNair *et al.*, 2012; Pérez and Kettner, 2013). In our study, seeds that germinated (the event of interest) within the study period (90 days) were coded as 1. Seeds that did not germinate by the end of the study were considered to be "right-censored" observations and coded as 0. Germination was estimated using the Kaplan-Meier non-parametric maximum likelihood estimator to estimate the survival function for each seed origin and temperature treatment. The survival function ($S(t) = \Pr(T>t)$ determines the event time (i.e., the time required for a seed to germinate) for a random variable T that exceeds a given time t. S is the probability between 0 and 1, while T must be a positive number. Essentially, survivor curves will begin with $S(t)=$

1 when T is 0, and decrease in a step function as t increases. The Kaplan-Meier estimator of the survivor function $\dot{S}(t)$, is a nonparametric method that will allow inferences into censored data and make no assumptions about the distribution of time to germinate. If k distinct event times are denoted as $t_1 < t_2 < \ldots < t_k$, the Kaplan-Meier estimator $\dot{S}(t)$ for $t_l \leq t \leq t_k$ would be given by:

$$\dot{S}(t) = \Pi\, (1 - d_i / n_i)$$

$$i{:}\ t_i \leq t$$

where t_i represents a distinct event time (week of stratification); n_i are the number of individuals (seeds) at risk of the event (germination) at each t_i; and di represents the number of individuals censored at time t_i. Our study follows other standard germination experiments, where the observation scheme is commonly known as 'periodic simultaneous observation - seeds were examined weekly rather than continuously (interval censored data). Although the Kaplan-Meier estimator calculates the survivor function when event times are assumed to be exact, it is safe and appropriate to apply this analysis to interval censored data when no seeds are lost during the weekly counts (McNair *et al.,* 2012). Weekly germination in this study refers to the number of seeds germinated in a given week, whereas cumulative germination refers to the germination at the end of the study. The null hypothesis is that survival functions are the same for all seed origins and all temperature treatments. We assessed the influence of temperature by comparing (1) constant incubation temperatures, (2) a warm temperature shift, and (3) a cool temperature shift for each seed origin. Additionally, we conducted pairwise comparisons to identify statistical differences between origins and treatments using the Fleming-Harrington test (McNair *et al.,* 2012). Supplemental one-way ANOVAs were conducted to compare cumulative germination percentages between sites and temperature treatments within sites. When data did not meet the assumptions of normality and homogeneity of variance, an inverse transformation (1/(1+X)) was used. All post hoc analysis for the cumulative germination data were performed using the Tukey- Kramer's test (TukeyHSD). All analyses were performed using the statistical software R v 3.0.3 (R Development Core Team, 2015) with the 'survival' package (Therneau, 2015).

1.3.5 Climate Warming Scenarios

We used the North American Spatial Climate Model (McKenney *et al.,* 2011) to help predict the potential influence of climate warming on sugar maple seed germination. Using each of the seven seed origin's approximate location (Table 1.1), we placed a circular buffer (50 km radius) around the central point to calculate the local annual and monthly mean temperature for the years 1901 to 2010.

Table 1.1. Approximate geographical location (decimal degrees) of sugar maple seed sources used in the study.

Seed Source	Latitude	Longitude
Tennessee, USA	35.78°	-83.67°
Kentucky, USA	38.26°	-84.95°
Pennsylvania, USA	41.13°	-77.62°
Sherbrooke , Canada	45.49°	-72.17°
Montmagny, Canada	46.95°	-70.46°
Ville-Marie, Canada	47.33°	-79.39°
Rivière-du-Loup, Canada	47.73°	-69.48°

We then calculated the local stratification temperature; determined by choosing the likely stratification window: approximately a period of 90 days of cool, moist conditions required for sugar maple seed to germinate (Janerette, 1979). This was done by taking the mean of three months, beginning with the first month closest to the freezing point, followed by the subsequent 2 following months in late winter/early spring. To assess the influence of projected climate warming on seed germination success, we investigated three scenarios: (i) +2°C warming, (ii) +5°C warming, and (iii) +7°C warming. These warming scenarios were then added to the initial stratification temperature determined at each site for the 1901-2010. The resulting cumulative germination and percent change (in relation to 1901-2010) was based on the findings of the constant incubation temperature treatments in the present study by seed origin.

1.4 Results

1.4.1 Effects of Seed Origin and Constant Incubation Temperatures

Cumulative germination percentage was on average (across all origins and all constant incubation temperatures) 51.4%, with weekly germination percentage peaking at week 7 (12.2% of total) (Figure 1.2). The effect of seed origin on germination was found to have a stronger effect than constant incubation temperature ($\chi2=7552.60$, $p < 0.0001$; Table 1.2). We found a clear dichotomy between the survival curves (Figure 1.3A) and cumulative germination percentages (Figure 1.4) for the northern (Sherbrooke, Montmagny, Ville-Marie and Rivière-du-Loup) and southern (Tennessee, Kentucky, and Pennsylvania) seed origins (final cumulative mean germination: 70.2% and 32.1%, respectively). Northern seed origins also tended

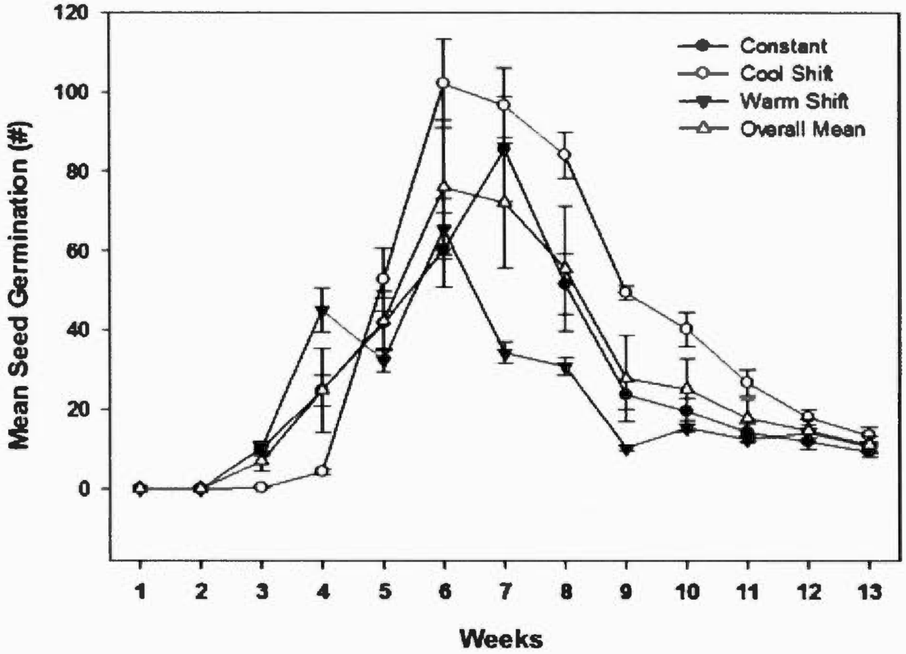

Figure 1.2. Mean cumulative number of seeds germinated per week and standard error bars by temperature treatment.

to peak in germination much faster (week 6) than those in the southern range, where germination peaked roughly two weeks later (Figure 1.5). We found that all seed origins showed statistically different survival curves, except for the following three pairs: Pennsylvania with (1) Tennessee, (2) Kentucky, and (3) Sherbrooke with Montmagny (Table 1.3, Figure 1.3A). The best overall cumulative germination percentage by seed origin was from the most northern seed source: Rivière-du-Loup (75.1%), while the worst came from Kentucky (28.4%) (Figure 1.3A).

Table 1.2. Seed origin and temperature treatment effects on weekly germination rate. Significant values determined in bold using a Fleming-Harrington test ($\alpha \leq 0.05$).

Seed Origin	**Treatment**	**Chi-Square**	**DF**	**P**
Overall	Seed Origin	7552.60	6	**<0.0001**
	Constant	1782.74	8	**<0.0001**
	Cool Shift	408.22	15	**<0.0001**
	Warm Shift	1308.72	15	**<0.0001**
Tennessee	Constant	192.36	8	**<0.0001**
	Cool Shift	138.10	15	**<0.0001**
	Warm Shift	92.56	15	**<0.0001**
Kentucky	Constant	158.71	8	**<0.0001**
	Cool Shift	39.54	15	**0.0005**
	Warm Shift	122.20	15	**<0.0001**
Pennsylvania	Constant	498.88	8	**<0.0001**
	Cool Shift	265.21	15	**<0.0001**
	Warm Shift	373.28	15	**<0.0001**
Sherbrooke	Constant	407.83	8	**<0.0001**
	Cool Shift	248.91	15	**<0.0001**
	Warm Shift	209.19	15	**<0.0001**
Montmagny	Constant	699.18	8	**<0.0001**
	Cool Shift	360.47	15	**<0.0001**
	Warm Shift	502.05	15	**<0.0001**
Ville-Marie	Constant	792.20	8	**<0.0001**
	Cool Shift	433.56	15	**<0.0001**
	Warm Shift	548.82	15	**<0.0001**
Rivière-du-Loup	Constant	763.45	8	**<0.0001**
	Cool Shift	659.93	15	**<0.0001**
	Warm Shift	782.30	15	**<0.0001**

The effect of constant incubation temperature on the germination was highly significant (χ^2=1782.74, $p < 0.0001$, Table 1.2, Figure 1.3B). When temperatures were maintained ≤5 °C, cumulative germination was generally high (~74%) (Figure 1.6).The poorest cumulative germination occurred at the highest incubation temperatures: 11°C (8.4%) and 13°C (4.1%) (Figures 1.3B and 5). All constant incubation temperatures >5°C were found to be significantly different from cooler temperatures ($p < 0.0001$, Table 1.4) (See Annex A - Tables A1.1-A1.1.7 for pairwise comparisons of constant incubation temperature differences by seed origin). Cooler constant incubation temperatures (≤7°C) also impacted the timing of peak germination, where they tended to germinate earlier than those at higher temperatures (Figure 1.7A).

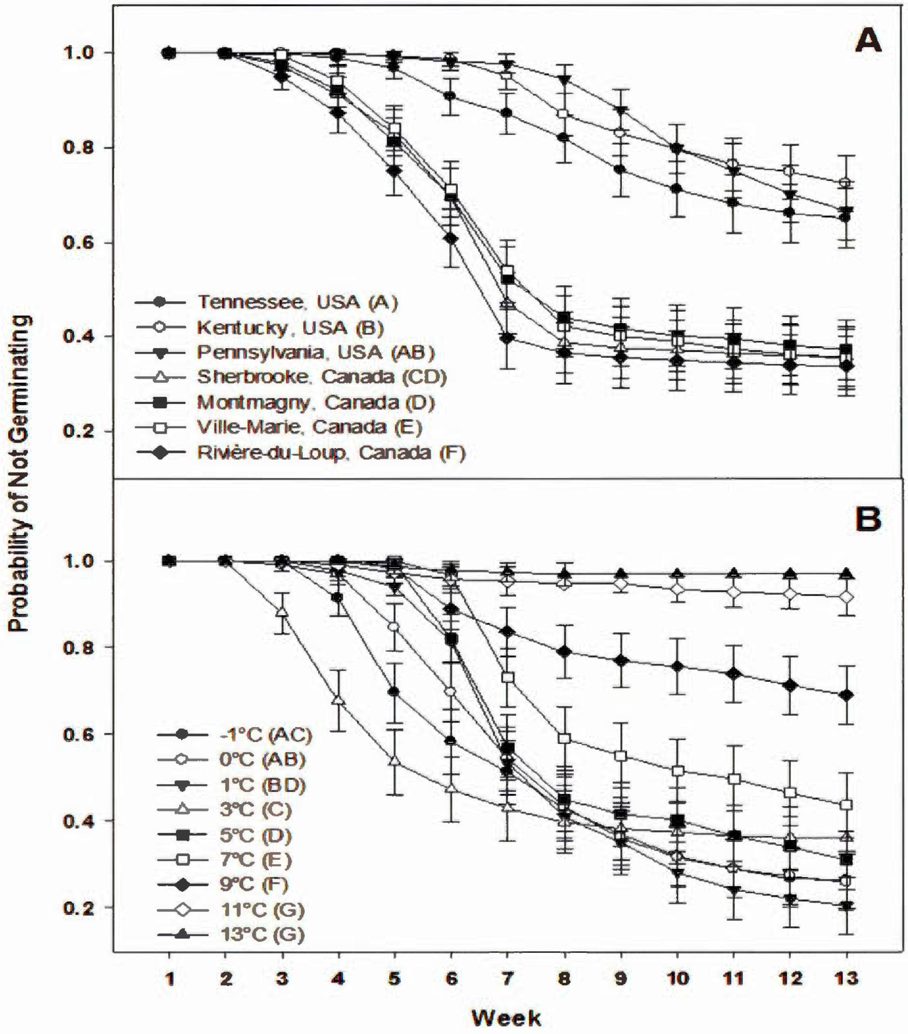

Figure 1.3. Kaplan-Meier mean estimates and 95% confidence limits of survival functions for the probability of not germinating within constant incubation temperatures versus weeks stratified for (A) seed origin, and (B) temperature. Seed origin and temperature treatments with the same letters were not significantly different (Fleming-Harrington test, $\alpha \leq 0.05$).

1.4.2 Effects of Temperature Shifting

Cool shifting significantly improved cumulative germination percentage by 19.5% and caused earlier peak germination by one week when compared with the constant incubation treatments (χ^2=408.22, p<0.001, Table 1.2, Figure 1.2). Cool shifting was increasingly beneficial to cumulative germination percentages as seed origin shifted northward (Figure 1.4). Seeds originating in Tennessee experienced a slight decline (-0.2%) compared with constant incubation temperatures, but differences from constant incubation temperatures were statistically significant only for the two northernmost locations: Ville-Marie (+26.6%) and Rivière-du-Loup (+28.0%; Figure 1.4). Cool shifting also tended to minimize the differences in cumulative germination between treatments within sites, where 6.3% was found to be the largest difference in germination between -10°C and -11°C (See Annex A – Tables A1.8-A1.23. for pairwise comparisons of warm and cool shifting differences by seed origin).

Table 1.3. Pairwise comparisons for seed origin effect on seed germination. Significant differences in bold (Fleming-Harrington test, $\alpha \leq 0.05$).

	Kentucky	Pennsylvania	Sherbooke	Montmagy	Ville-Marie	Rivière -du-Loup
Tennessee	**0.0002**	0.1724	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**
Kentucky		0.4474	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**
Pennsylvania			**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**
Sherbrooke				0.0804	**<0.0001**	**<0.0001**
Montmagny					**<0.0001**	**0.0105**
Ville-Marie						**<0.0001**

Alternatively, warm shifting significantly reduced cumulative germination percentage by 11.2% when compared to the constant incubation temperature treatments, and by 29.3% when compared to the cool shifting treatments (χ^2=1308.72, $p<0.001$, Table 1.2, Figure 1.4). Warm shifting also caused earlier peak germination by one week when compared to the constant incubation temperature treatments (Figure 1.2). Reducing the magnitude of warm shifting to ≤7°C on average resulted in reasonably high germination percentage (59%), while germination drastically declined at warmer (>7°C) shifts (34.5%) (Table 1.5). Reductions in germination percentage due to warmer shifts (when compared with constant incubation temperatures) were minimized the most for Tennessee and Kentucky, the southernmost seed origins (-8%). Concurrently, the most severe reductions in germination due to warmer shifts occurred within some of the northernmost latitudinal seed origins: Montmagny (-12.4%) and Ville-Marie (-19.9%) (Figure 1.4).

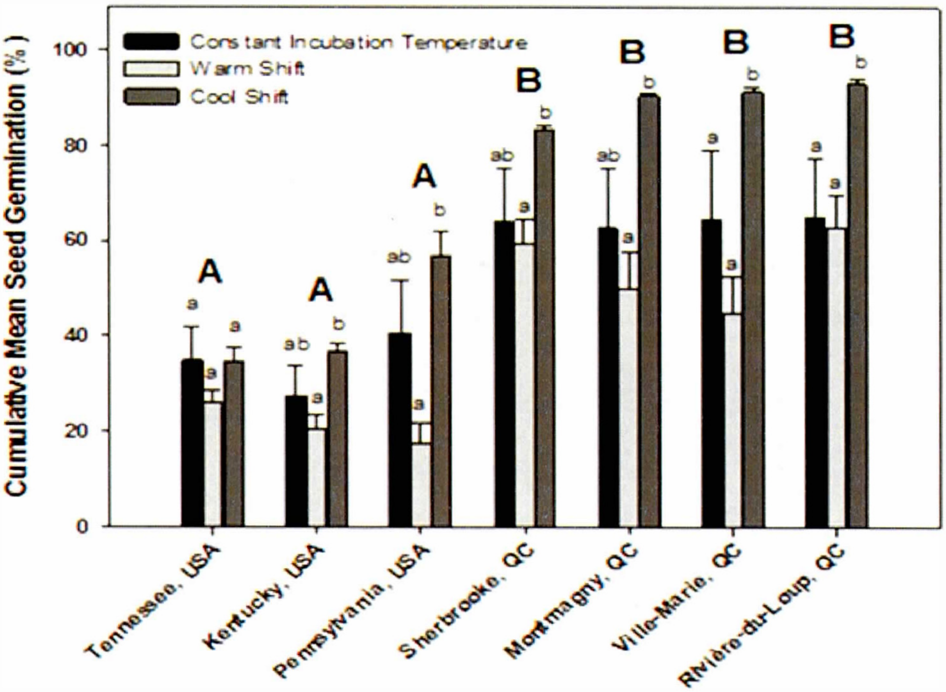

Figure 1.4. Cumulative mean seed germination (%) by seed origin for constant incubation temperatures, warm, and cool shift treatments. Capital letters refer to site comparisons, where lower case refer to treatment differences within site only. Different characters are statistically significant (Fleming-Harrington test, $\alpha \leq 0.05$)

1.4.3 Estimating Possible Future Germination under Climate Warming

The stratification temperature for each seed origin also decreased with a northward latitudinal shift. In a warming scenario of +2°C, we found decreases in germination by as much as 27% and 32% in Kentucky and Pennsylvania seed origins respectively. Minimal reductions (<3%) in germination percentage occurred in origins northward of Pennsylvania under the same warming scenario. Under the second climate warming scenario, +5°C, significant declines in germination occurred across the entire species range (Table 1.4). Again however, the most northern seed origins (Ville-Marie and Rivière-du-Loup) experienced only slight declines (<4%), where all other origins experienced declines of ≥14%. In the most dire of climate scenarios (+7°C), cumulative germination was greatly reduced regardless of origin. Sharp declines (-20%) were seen across the range and by as much as 75% (Sherbrooke). Interestingly, under this scenario the least impacted cumulative germination occurred in the species southern range (Tennessee, -23%) (Table 1.6).

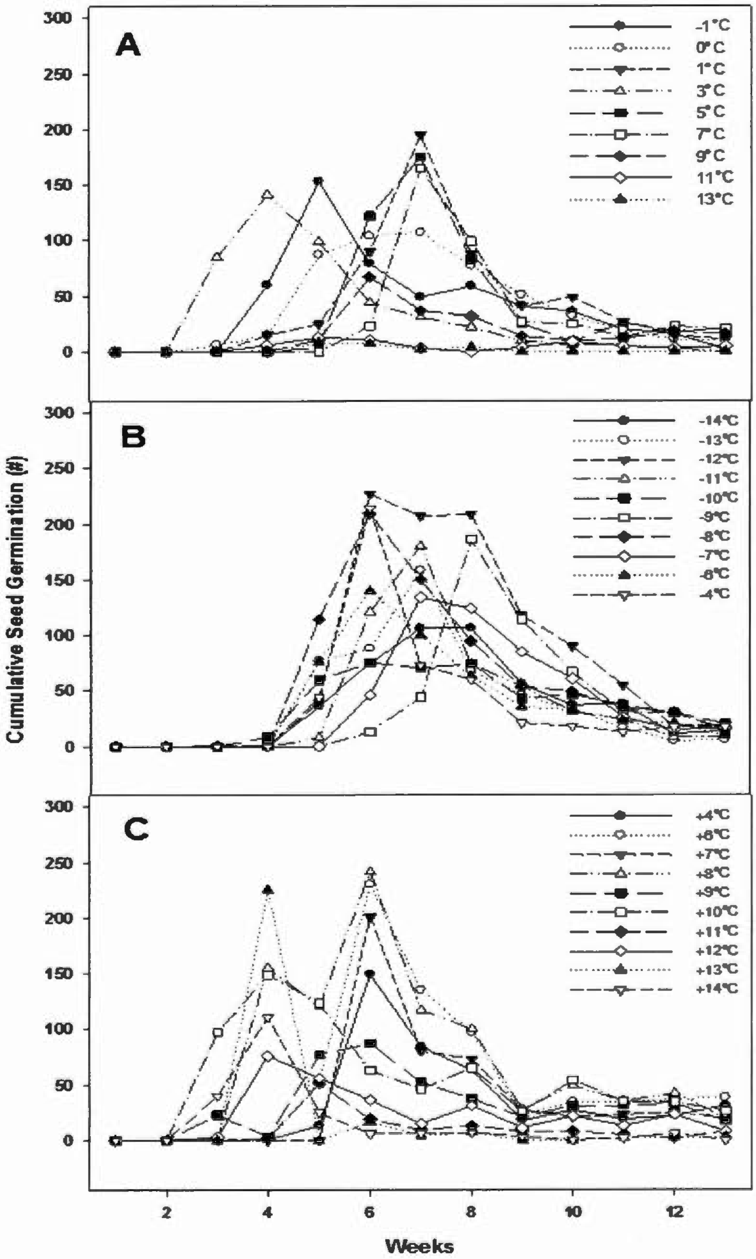

Figure 1.5. Cumulative seed germination by (a) constant incubation temperature, (B) cool shifting, and (C) warm shifting by weeks stratified.

1.5 Discussion

This paper shows a novel experimental procedure to test for the effect of seed origin, constant incubation temperature and temperature shifting on seed germination. We were able to assess the potential deleterious impacts of future climate warming on sugar maple, which is known to have a very narrow temperature requirement to ensure successful germination (Zasada and Strong, 2003; McCarragher *et al.*, 2011). We found strong evidence of local adaptation of seed germination to temperature and temperature shifting. We were also able to identify precisely the ideal stratification temperature, timing, and temperature thresholds associated with germination for sugar maple throughout its range. When comparing to constant incubation temperatures, seeds originating in the southern range were much better adapted to warm shifting, while cool shifting was more beneficial to the seeds from northern latitudes (Figure 1.4).

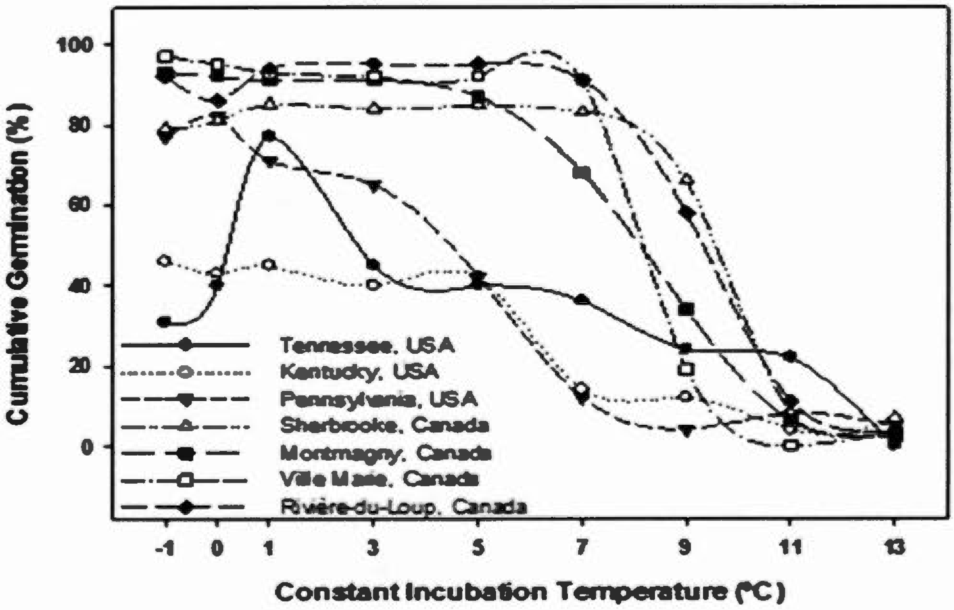

Figure 1.6. Seed germination (%) by seed origin at varying constant incubation temperature.

1.5.1 Effects of Constant Incubation Temperature

The best cumulative germination percentage was observed at constant incubation temperatures below <1°C, coupled with subtle differences up until 5°C, considerable declines occur beyond 5°C regardless of seed origin (Table 1.4, Figures 1.3B and 1.6). These findings reinforce the fact that sugar maple does hold the capacity to germinate under snow cover (Tubbs 1965), where temperatures are stable around the freezing point. We also found that sugar maple is capable of germinating below the freezing point, where cumulative germination reached 73% in the -1°C treatment (Figures 1.3B and 1.6), and potentially could germinate at colder temperatures. In this study, by using a large range of temperatures and by sampling seeds from a wide range of origins we now can accurately report the influence of temperature and temperature shifting throughout the natural distribution of sugar maple. While McCarragher *et al.,* (2011) argued that 7°C provides the optimum incubation temperature, we consistently found that regardless of seed origin this temperature is systematically the beginning of germination decline (Figure 1.6). Beyond an incubation temperature of 7°C, germination percentage decline further, and nearly cease beyond 13°C (4.1%) (Figure 1.6). These findings coincide with other previous studies (Shih *et al.*, 1985; Hance and Bevington, 1992; McCarragher *et al.,* 2011), whom found little (<3%) or no seeds germinating beyond this temperature. At these warmer temperatures, the level of inhibitors remains high (Webb *et al.,* 1973) and restricts the morphological and anatomical changes required for embryonic axis growth, thus reducing the likelihood of germination (Simmonds and Dumbrof, 1974; Hance and Bevington, 1992). Increased seed respiration rates also occur, which have been shown to be responsible for loss of seed viability at higher temperatures (Simmonds and Dumbrof, 1974). We also incurred much higher frequency of the presence and development of fungal communities, which were not present at cooler temperatures (<9°C). Fungal communities have been reported to colonize maple seeds at high temperatures and ultimately could contribute to increased contamination leading to seed death (Shih *et al.,* 1985).

Table 1.4. Pairwise comparisons for overall constant incubation temperature effect on seed germination. Significant differences in bold (Fleming-Harrington test, $\alpha \leq 0.05$).

	0°C	1°C	3°C	5°C	7°C	9°C	11°C	13°C
-1°C	0.5329	**<0.0001**	0.8879	**0.0023**	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**
0°C		0.0859	**0.0134**	**0.0177**	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**
1°C			**<0.0001**	0.9999	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**
3°C				**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**
5°C					**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**
7°C						**<0.0001**	**<0.0001**	**<0.0001**
9°C							**<0.0001**	**<0.0001**
11°C								0.8811

1.5.2 Shifting Temperatures

Shifting the temperature in our treatments significantly influenced the cumulative germination percent. We found that warm shifting significantly reduced germination for all seed origins, while only the magnitude differed (Figure 1.4). The warm shifting treatments in our study were used to mimic what could essentially happen naturally in a warmer and earlier spring, where increased snow melt and reduced snow pack are predicted to occur with climate change (Mankin and Diffenbaugh, 2015). Rapid spring warming essentially would impact seeds negatively in number of ways: (1) shorter period of overwintering stratification, (2) seeds and seedlings which are able to germinate would no longer be insulated by the snow cover and be subjected to potentially multiple freeze-thaw events, (3) lose the competitive advantage of early establishment over species unable to germinate/establish under snow, (4) change in water supply: from slow, progressive to rapid snow melt, and finally (5) expose germinates much earlier to herbivory, bacterial and fungal infection.

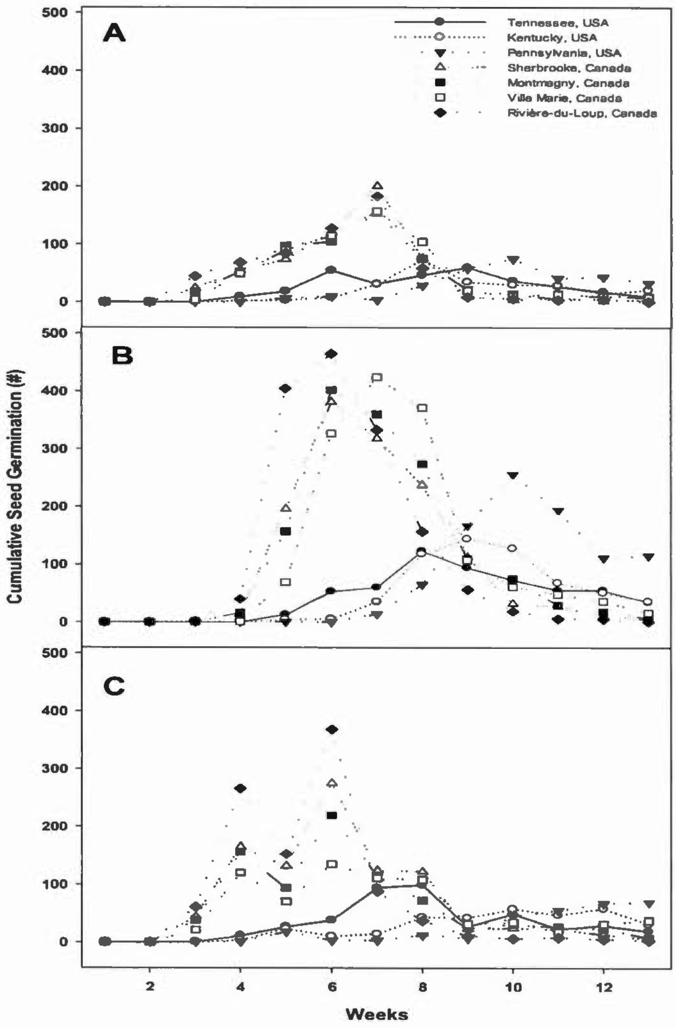

Figure 1.7. Cumulative germination by seed origin under (a) constant incubation temperature, (B) cool shifting, and (C) warm shifting by weeks stratified.

In contrast, for seeds exposed to cool shifting treatments we found that germination was generally greatly improved (Figure 1.4). A longer, cooler spring essentially can prolong the stratification window (allowing seed development to break dormancy), delay snow melt, reduce the onset of competitors, and reduce bacterial and fungal infection. Surprisingly, the only seed source to not experience a net benefit of a cool shifting, Tennessee, came at the southern range of sugar maple. We suggest that this lack of improvement in germination was likely due to the seeds adapting more readily to warm shifting and a warmer climate it has adapted to, which are much more likely to occur at these southern latitudes (Figure 1.8).

1.5.3 Germination Timing

It is extremely difficult to predict exactly when a seed will germinate with so many factors that must be considered (abiotic and genetic), but this study reinforces the link between seed origin and peak germination. Slight variations in genetics could be playing a significant role in seeds breaking dormancy and germinating over the natural species' range (Sexton *et al.,* 2009). Variations in phenology were apparent within our study as differences occurred between seed origin and incubation temperature, where a number of subtle differences in time to germination. Seeds from all origins germinated after 4 weeks, which is consistent with most germination studies (Janerette, 1978a; Shih *et al.,* 1985). As a whole, germination followed the expected distribution: few seeds germinated early (before week 5), most in mid-weeks (6-9), and few beyond (Figure 1.3). Unlike McCarragher *et al.*, (2011), who found seeds from Illinois (central origin) tended to germinate earliest (within 25 days), we found that seeds from the northern range not only started to germinate earlier, but also peaked 2-3 weeks sooner (week 6) than those from the central range (week 10) or southern range (week 8-9) (Figure 1.5). We suggest that sugar maple has adapted locally to temperature, where in cooler climates seeds will germinate earlier under snow to benefit from colonizing when competition is low. On the contrary, in warmer climates, the competitive advantage to germinating early under the snow or shortly after is minimized or lost, thus delaying germination proves to be advantageous; allowing competition to provide sugar maple a protective cover from warmer temperatures and increased water stress (Berkowitz et al., 1995).

While in this study we did perform pre-incubation treatments as a means of getting seeds to germinate uniformly (at least in terms of a starting point) (Janerette, 1978a), our study reinforces the fact that slight variations/abnormalities within the seed and seed structures of the same species may exist. As pointed out by Simmonds and Dumbrof (1974), lower incubation temperatures help facilitate the production of gibberellins, cytokinins and the removal of inhibitors (abscisic and phenolic acids) in sugar maple seeds (Enu-Kwesi and Dumbroff, 1980). Attaining a full energy charge necessary for normal cellular function also occurs at lower temperatures, and could become limited if temperatures are too high. While considerable research has been conducted on the inner workings of sugar maple seed (ex. Shih *et al.,* 1985; Walker *et al.,* 1985), we speculate that differences within these processes are linked to seed origin and influenced by the species local adaptation to temperature. Ultimately, if temperatures remain or become high during a portion of the stratification period, seeds may experience dormancy induction (secondary dormancy). This occurs when seeds are supplied with water but are exposed to unfavorable conditions (i.e. high temperature, low oxygen) after breaking primary dormancy (Ellis *et al.,* 1985). This may have occurred within our study where seeds which were exposed to the warmest shifts germinated rapidly (Figure 1.5C), followed by a rapid decline, presumably becoming dormant again because of the high temperature.

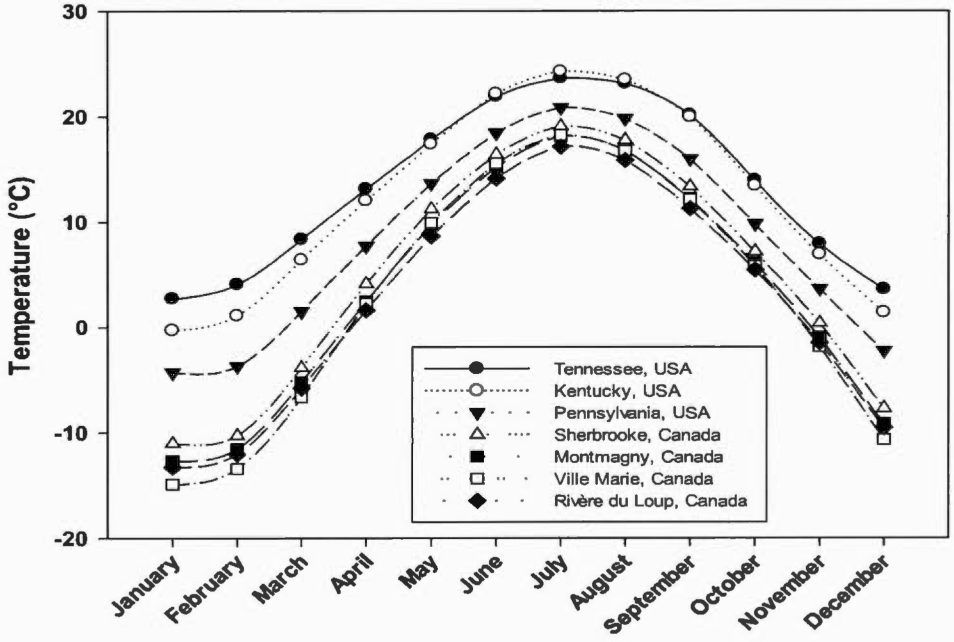

Figure 1.8. Monthly mean temperature for each sugar maple seed source used in the study for the time period 1901-2010. Monthly mean temperature was extrapolated from McKenney et al. (2011) climate model.

1.5.4 Global Warming and Future Implications on Germination

As temperature is predicted to increase as much as +7°C in the mid latitudes (40-60°N) of North America by the end of the 21st century, drastic changes undoubtedly will occur in many key biological processes, in particular, phenology, growth and productivity, and species interactions (Morin *et al.*, 2008). Being able to accurately predict how each these processes will change (alone and together) becomes extremely critical for future forest management strategies. This task will prove extremely difficult, as the time frame for the expected warming is to take place within one or two tree life cycles. This means that trees that are currently of reproductive age and their offspring will face these predicted rapid warming events. It thus becomes imperative to assess now the resilience and ability of different key species to successfully germinate, establish, grow, and reproduce under the rapid warming expected by the end of this century (Kremer *et al.,* 2012). Providing forest managers this necessary information helps identify differences in germination within a species and allows for better prediction and strategies when identifying the ideal planting stock or adjusting expectations for natural seeding. Changes in initial life stages (seed germination and seedling establishment) could eventually become important at larger scales if they are not initially constrained maternally (flower, fruit and seed development). A lack of successful germination will slow future tree migration rates, as a particular issue when considering the potential deleterious impacts of climate change (Zhu *et al.,* 2012).

Table 1.5. Mean cumulative germination % by cool and warm shifting treatment differences. *Note:* To assist in brevity, here we present the difference in shifting treatments (example: a treatment initially placed at -1°C and shifted to 7°C would have a difference of +8 and reported below as so).

Cool Shift Treatment (°C)	Mean Cumulative Germination (%)	Warm Shift Treatment (°C)	Mean Cumulative Germination (%)
-14	68.43	+14	29.43
-13	71.29	+13	37.00
-12	70.21	+12	21.00
-11	72.71	+11	17.86
-10	66.38	+10	34.19
-9	71.43	+9	58.86
-8	66.71	+8	43.29
-7	72.57	+7	67.14
-6	71.62	+6	48.57
-4	68.14	+4	61.00

According to our results, under the current temperature projections (+2°C-7°C), substantial decreases in successful germination of sugar maple seeds are expected to occur (Table 1.4). Under the most conservative warming predictions (+2°C), cumulative germination percentage could decrease by up to 32% in the midrange of the species distribution (species range average: -9.7%). Under moderate warming (+5°C), and even upper threshold warming (7°C), substantial declines (up to 75%) are expected (Table 1.6). While we understand that these predictions are strictly due to temperature, and could be moderated to some degree by the amount of precipitation, geographic location, and annual variability, we expect germination to decline at even higher rates. Morin *et al.,* (2008) predict a significant reduction in southern populations of sugar maple due to decreases in fitness associated fruiting maturation caused by later flowering as a result of a delay in dormancy break. Warmer temperatures should also be expected to increase drought stress on the ripening process and eventual seed maturation, which in turn will affect seed dormancy and the conditions required to break dormancy and further impeded the induction germination. As an implied mean global warming of 3.2°C, Morin *et al.,* (2008) predict a -25% reduction in species range, which is approximately our findings in terms of reduction of germination success at moderate warming scenarios (Table 1.6).

Table 1.6. (A) Local historic mean annual temperature (1901-2010) by seed origin with the associated stratification temperature* and resulting cumulative seed germination percent. (B) Cumulative seed germination and percent change under three climate change scenarios: (i) +2°C, (ii) +5°C, and (iii) +7°C (Seed germination % extrapolated from Figure 1.6).

Seed Origin	(A)			(B)								
	Historical Local Temperature (1901-2010)			Climate Change Scenarios								
				+2°C			+5°C			+7°C		
	Mean Annual Temperature (°C)	Stratification Temperature (°C)*	Germination (%)	Stratification Temperature+ (°C)	Germination (%)	Change (%)	Stratification Temperature+ (°C)	Germination (%)	Change (%)	Stratification Temperature+ (°C)	Germination (%)	Change (%)
Tennessee, USA	13.4	5.1	39	7.1	34	-5	10.1	23	-16	12.1	9	-30
Kentucky, USA	12.3	4.8	43	6.8	16	-27	9.8	10	-33	11.8	3	-40
Pennsylvania, USA	8.4	4.8	47	6.8	15	-32	9.8	4	-43	11.8	8	-39
Sherbrooke, Canada	4.7	3.9	83	5.9	83	0	8.9	69	-14	10.9	8	-75
Montmagny, Canada	3.4	2.3	91	4.3	90	-1	7.3	64	-27	9.3	28	-63
Ville-Marie, Canada	2.7	1.8	93	3.9	90	-3	6.9	89	-4	8.9	33	-60
Rivière-du-Loup, Canada	2.6	1.5	95	3.5	95	0	6.5	92	-3	8.5	66	-29

*Stratification temperature was determined from calculating a likely "stratification window" (period for which sugar maple should generally germinate in - approximately 90 days or average over 3 months), which was done by taking the first monthly temperature closest to the freezing point or below followed by subsequent 2 months). + Stratification temperatures within the climate change scenarios were calculated by adding the associated increase due to projected climate change (+2°C, +5°C, +7°C) to the historical stratification temperature.

While warming is already occurring and is expected to continue, northern populations are believed to be particularly at risk since warming is occurring fastest and at a time (in the spring) where many key processes (flowering, fruit ripening, stratification) are occurring (Bekryaev *et al.,* 2010; Feng *et al.,* 2014). Ironically, even though seeds from the southern range had a lower cumulative germination percent, they appear to be better adapted to deal with warm shifts. However, as pointed out by Morin *et al.*, (2008), the southern populations could quickly become in dire straits if the number of cool stratification days are even further limited. Currently, the best germination occurs in the upper latitudes even under the worst of circumstances (+7°C) (Table 1.6). Although these severe declines in germination percentage are expected at the northern range, perhaps the current sugar maple regeneration dynamics at the southern range could provide insight into future management and germination expectations at the northern range.

Our study points to the sensitivity sugar maple possesses to temperature and temperature shifting across its species range in regards to seed germination. We find that sugar maple seeds need cooler temperatures (≤5°C) with minimal temperature shifting (≤7°C) to ensure successful germination in early spring, regardless of seed origin. Using different climate warming scenarios we show that significant declines in cumulative germination across the sugar maple species range would occur. Although, in a natural setting, the potential negative effect(s) climate warming could have on the reproductive success of sugar maple will be compounded at each of the key stages of reproduction required to ensure the successful development of a viable seed in a given year.

CHAPTER II

LOCAL ADAPTATION OF TREES AT THE RANGE MARGINS SLOWS RANGE SHIFTS IN THE FACE OF CLIMATE CHANGE

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2.1 Abstract

The ability of tree species to track their climatic niche at rates comparable to climate change is concerning, particularly if those species are constrained by local adaptation. Local adaptation can be beneficial for range expansion when populations located at the leading margin are the fittest. In long-lived, sessile organisms such as trees, local adaptation can however slow down range expansion when climate change happens much faster than its ability to migrate, leading to the maladaptation of these populations. Here, we investigate experimentally a series of factors thought to constrain the seedling phase at the leading edge of the distribution of a dominant tree species, sugar maple (*Acer saccharum* Marshall.). First, we find that seed provenance from the northern portion of the range provides the best opportunity for establishment beyond the current range, where current climatic conditions are more similar than those of the central or southern portions of the species range. Second, while we find seedling establishment was highest within the species range, survival rates were comparable to those at the range margin and beyond, regardless of seed provenance. Third, we find that the local climate is the most influential factor for establishment and survival within and at the range margin; however, a lack of suitable microsites were also found to constrain seedling recruitment beyond its margin. Our study highlights the complex interaction between climate and microsite conditions required to ensure successful seedling establishment. Ultimately, sugar maple risks severe maladaptation causing migration lag under a rapidly warming climate if: (i) the climate warms beyond its specific threshold requirements associated with seed germination, and (ii) an absence of favourable microsite conditions ensuring seedling establishment and survival.

Keywords: biotic interactions, climate change, demography, local adaptation, migration rate, range shift, temperate-boreal forest transition.

2.2 Introduction

Rapid shifts of species geographical ranges are expected to occur along latitudinal and altitudinal gradients as species track their climatic niche under global warming (Chen *et al.*, 2011; Zhu *et al.*, 2012; Duputié *et al.*, 2015). The challenge is no longer to establish whether changes will occur, but rather the rate and magnitude of the shifts occurring (Svenning *et al.*, 2014). Concerns however arise for species that may lack the ability to migrate at rates comparable to those projected by the end of this century (Parmesan 2003; IPCC, 2013). If a species is locally adapted; better suited to the local environment than other populations of the same species (Kawecki and Ebert 2004) at its range margin, it could prove beneficial as it ensures that the genotypes colonizing new areas are the fittest because environmental conditions are most similar to the ones at the margin (Alberto *et al.*, 2013; Atkins *et al.*, 2016). Migration lags can however result in maladaptation of populations at the range margin if the environment is changing too fast, which can further slow migration rates (Kawecki and Ebert, 2004; Chuine 2010; Franks *et al.*, 2014; Svenning *et al.*, 2014). Reports of species range shifts lagging behind the rate of climate change are common (Loarie *et al.*, 2009; Chen *et al.*, 2011; Zhu *et al.* 2012) and caused by factors such as dispersal limitations (Hargreaves *et al.*, 2014), unfavourable climate (Williams *et al.*, 2010; Cahill *et al.*, 2014), biotic interactions (HilleRisLambers *et al.*, 2013; Moran and Ormond 2015), and unfavourable microsites (Lavergne *et al.*, 2010; Brown and Vellend 2014). Currently, our understanding of how these factors interact and play on species migration is lacking, particularly at the earliest life stages of plants (Sexton *et al.*, 2009; Brown and Vellend 2014; Svenning *et al.*, 2014).

Species distribution models (SDMs) are used to predict the shift of climatic suitability areas in response to climate change the standard approach for predicting the dynamics of range shifts in response to environmental changes (Parmesan 2006; Elith and

Leathwick, 2009; Chen *et al.*, 2011). Concerns about their usage still remain (Shaw and Etterson 2012) despite considerable technical advances (Thuiller *et al.*, 2008; Chevin *et al.*, 2010; Boulangeat *et al.*, 2012). For instance, temperate tree species have been projected to be present by the end of this century at locations in the tundra where there are currently no trees and the soil is permanently frozen (McKenney *et al.*, 2007). These models have been criticized for being too simplistic, and typically ignore several factors critical to range dynamics such as dispersal abilities and barriers, demography, habitat fragmentation, genetic variability, biotic interactions, and natural disturbances (Sexton *et al.* 2009; Lavergne *et al.* 2010; Alberto *et al.* 2013). In addition, SDMs lack the ability to consider how plants can evolve to novel environmental conditions (Reed *et al.*, 2011; Moran and Ormond 2015). Recent efforts however, have made great strides to include species-specific phenotypic plasticity and evolutionary response to novel ecosystems (Atkins and Travis 2010; Lu *et al.*, 2014). These revealed that species range shifts are significantly constrained by local adaptation (Valladares *et al.*, 2014). As SDMs are predicting shifts of climatically suitable areas well beyond the dispersal and establishment ability of many species, mismatches are likely to result in severe maladaptation (Anderson 2016).

Trees are particularly vulnerable to rapid climate change, where a combination of immobility, time to reach reproductive maturity, and limited dispersal collectively result in slow demographical changes (Petit and Hampe 2006; Lenoir and Svenning 2013; Aitken *et al.*, 2016). Trees are in their present location because they were able to adapt to the past and current local climate and environmental conditions; however, under climate change they must be able to express enough favourable phenotypic plasticity (rapidly) (e.g., leaf out period, flowering, onset of dormancy, growth) to ensure persistence in the future (Nicotra *et al.*, 2010; Alberto *et al.*, 2013). Even though trees typically possess wide geographic ranges, and can generally have high genetic diversity and gene flow (highly fecund), these attributes do not necessarily translate to fast demographics nor adaptive capacity (Petit and Hampe 2006; Alberto *et al.,* 2013). A locally adapted population at the range margin may possess the valuable genetic variation allowing for increased fitness improving migration success into nearby environments. However, it could also prove detrimental if the climate changes much faster than its migration rates of the species and results in species lag (Duputié *et al.,* 2015; Aitken and Bemmels 2016).

Typically, species fitness declines towards its range limit due to a combination of increased unfavourable abiotic and biotic stressors that are beyond its physiological limits (Sexton *et al.,* 2009; Blanquart *et al.,* 2013; Godsoe *et al.,* 2017). An increase in unfavourable environments occurs as a species gets further from its distribution centre (centre-periphery hypothesis) (Gimenz-Benavides 2007). However, if a population can become locally adapted, it could minimize any potential mismatches in fitness and increase the likelihood of adaptation, and thus lead to successful range shift (Savolainene *et al.,* 2007; Kim and Donohue 2013; Anderson 2016). Studies with a primary focus on determining the driving factors responsible for range lag at the seedling stage within the range limits currently remain few (Sagarin and Gaines 2002; Brown and Vellend 2014; Nagamistu *et al.,* 2015; Putnam and Reich 2016).

We hypothesize that the demography at range limits will be constrained due to local adaptation within the distribution. Here, we investigate the local adaptation of sugar maple (*Acer saccharum* Marshall.) at, and beyond its current northern species range limit. Sugar maple provides an ideal candidate to investigate local adaptation in the establishment phase, as it maintains a wide geographic range throughout much of northeastern North America (Godman 1990) and has been shown to express quite high genetic diversity (Gunter *et al.,* 2000). Although, sugar maple has been projected to migrate under climate change (Zhu *et al.,* 2012; Boisvert-Marsh *et al.,* 2014), certain species-specific climatic constraints exist within its germination and establishment stages, such as seeds requiring a specific stratification period to break dormancy (Solarik *et al.,* 2016). Further, the current northern range limit may also impose an increase in unfavourable conditions on a number of influential phenological processes associated with fecundity (i.e. fruit development, maturation, and quality) and slow growth in these cooler conditions (Morin and Chuine 2014; Reich *et al.,* 2015).

We established a seed transplant experiment to investigate the potential influence local adaptation may play on early seedling establishment and survival of sugar maple from seed. We make the following predictions: (i) southern seed provenances will be the most maladapted to the environmental conditions occurring at and beyond the current northern range limit, as they are the furthest in proximity of their origins (provenance effect), (ii) early seedling establishment will be best within sites which meet the species specific climatic requirements needed to ensure seed germination (climate effect), and (iii) upon seedling establishment, local microsite conditions more closely resembling those within the range limit will favour higher survival rates (microsite effect). Currently, we have very little empirical evidence on potential local adaptation of seed germination and establishment in regards to the abiotic and biotic environment, so we used a fully randomized factorial design, where we crossed climatic conditions, biotic environment, and seed provenance. We did this by collecting seed from 6 provenances representing the entire species range and seeded them to 4 sites located within the species limit, 4 sites at the northern range limit, and 4 sites beyond the current species northern range limit. This design allowed us to examine if any potential local adaptation in seedling establishment and survival currently exists within the species range, while also making inferences into potential barriers for seedling establishment in new environments. To date, few studies have assessed local adaptation at the seed germination and establishment stages, which remains the lynch pin to long-term species migration success under climate change (Donohue *et al.,* 2010).

2.3 Methods

2.3.1 Study Area & Experimental Design

The study was carried out along the northern species range limit of sugar maple in Québec, Canada (Figure 2.1, Table 2.1). We selected sites based on three bioclimatic regions associated with the sugar maple species range limit: (i) temperate zone - (within range limit), (ii) mixedwood/transition (at northern range limit), and (iii) boreal zone (beyond the northern range limit). The temperate zone included sites that lay within the hardwood forest subzone consisting of the sugar maple-bitternut hickory (*A.saccharum and Carya cordiformis* (Wangenh.) K.Koch), sugar maple – basswood (*A.saccharum and Tilia Americana* L.), and sugar maple-yellow birch (*A.saccharum- Betula alleghaniensis* Britton) bioclimatic domains. The mixedwood zone consisted of sites within the balsam fir-yellow birch (*Abies balsamea* (L.) Miller and *B. alleghaniensis*) bioclimatic domain, while sites within the boreal zone were part of the balsam fir-white birch domain (*A. balsamea- Betula. Papyifera* Marshall) (Saucier *et al.,* 2003). Four sites within each of the above mentioned zones were selected from the permanent plot network *RESEF (Le Réseau d`Étude et de Surveillance des Écosystèmes Forestiers Québécois* or *The Québec forest ecosystems research and monitoring network*), which allowed us to choose sites based on comparable (between sites) upper mineral soil (0-15cm) exchangeable calcium concentrations; a well-known limiting factor to sugar maple regeneration and survival (Moore *et al.,* 2008; Bal *et al.,* 2015). All sites were undisturbed, uneven-aged stands, ranging in elevation from 200 m to 800 m a.s.l. (See Périé and Ouimet (2003) for full RESEF site and climatic descriptions).

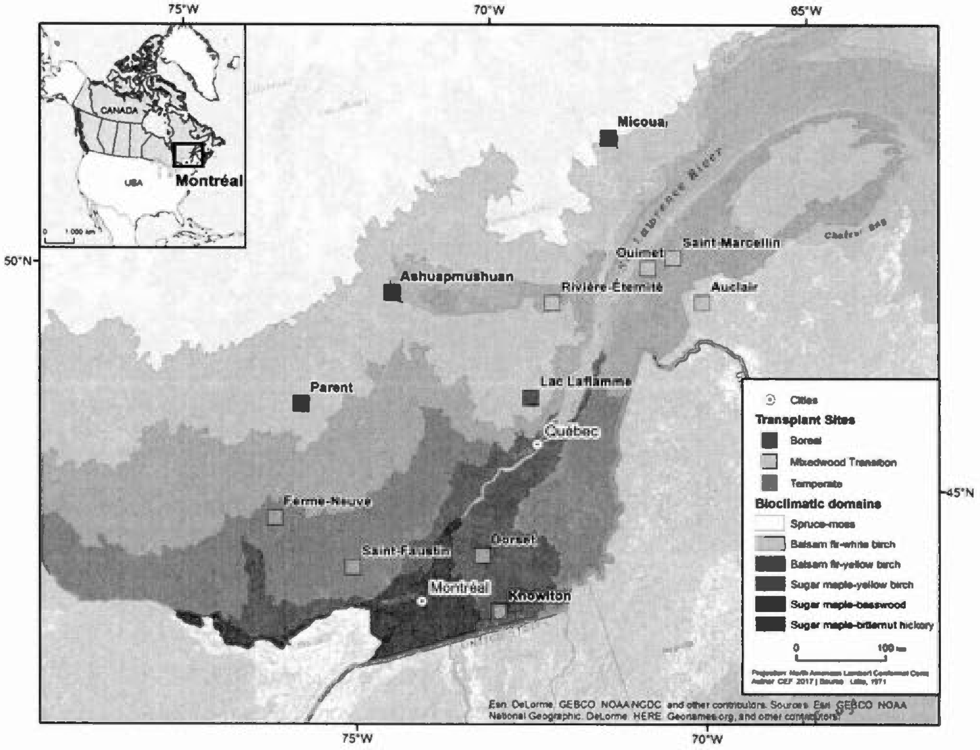

Figure 2.1. Approximate location of seed transplant sites used in the study, overlaid by the bioclimatic domains.

Seeds were collected in the late fall of 2013 from six provenances throughout the sugar maple range (~2,160km), following a latitudinal gradient from south to north (Figure 2.2, Table 2.1). Following collection, seeds were air dried until the samaras (fruiting body) became brittle, and then were placed in a mechanical tumbler to remove the wing portion from the seed. Seeds were then passed through a feed sorter, where filled seeds are separated from unfilled seeds. To further ensure that we were transplanting viable seeds, we tested a sub-sample of seeds from each provenance using x-rays to ensure viability was above 95% prior to transplanting the seeds at each field site. Seed lots (150 seeds/plot) were then weighted using an analytical balance in the laboratory to identify any potential differences in maternal effect caused by seed provenance.

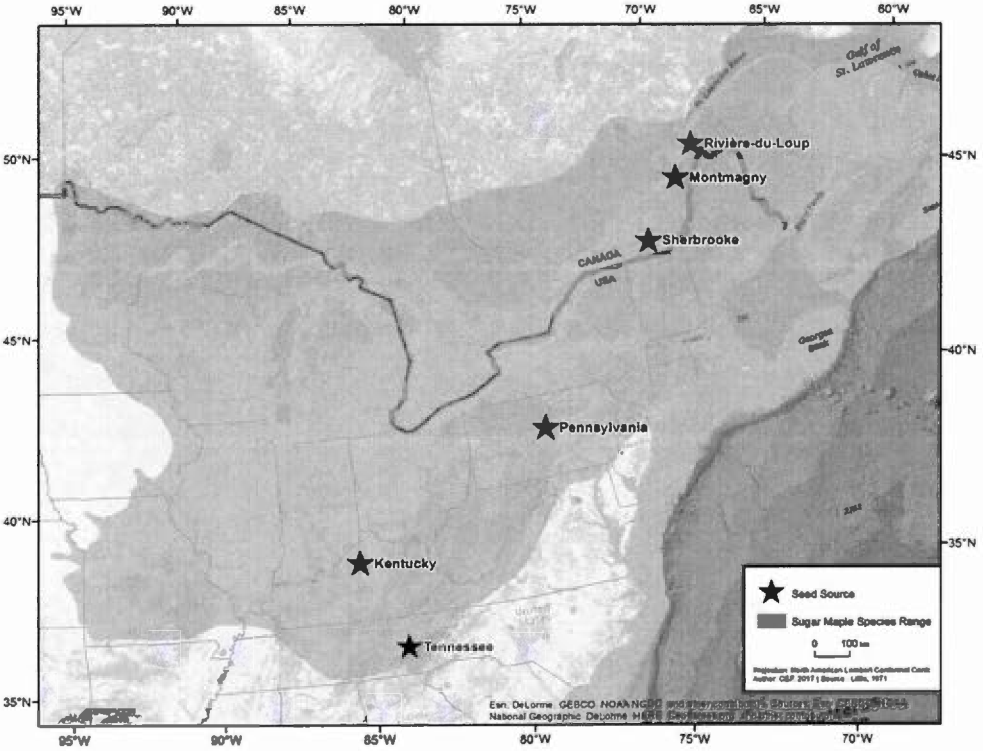

Figure 2.2. Approximate location of seed provenances used in the study, overlaid by the sugar maple species distribution map (Little 1971).

At each site, eighteen 1 m^2 plots (6 seed provenances x 3 replicates) were randomly established in the late fall of 2013 (Table 2.2). Seeding began in the late fall (approximately 1 month following natural seed dispersal) which provided two key benefits: (i) ensured no possibility of natural seeding from the overstorey canopy falling after the plot was established (seed already in plots prior to plot installation were removed through light scarification), and (ii) seeds are exposed to the local overwintering and early spring stratification conditions (i.e. cool, moist conditions) unique to each site. All transplant plots were positioned at a distance of at least ≥ 2 m from any overstorey trees to minimize the influence of the bole and shading. Seeds lots were then hand broadcasted evenly across each 1 m^2 plot. When snow was already present at the time of seeding, it was removed, the plot was seeded, and then the snow was redistributed over the seeds. We installed 1 m^2 metal cages (15 cm in height) over the plots to eliminate the presence and impact of seed predation by granivores (i.e., squirrels, voles, and mice) or browsing by deer. (See Photo in Annex B) We also installed in-situ HOBO Pendent ® data loggers to monitor ground level temperature and light conditions (December through to June); providing an accurate interpretation of the below canopy environment (De Frenne *et al.,* 2013). In total, 32 400 seeds were distributed over 216 transplant plots at twelve transplant sites.

Table 2.1. Approximate geographical location (decimal degrees) and elevation (meters) of each seed provenance and transplant sites used in the study.

Source/Zone	Location	Latitude	Longitude	Elevation(m)
Seed Source	Tennessee, USA	35.78°	-83.67°	365
	Kentucky, USA	38.26°	-84.95°	262
	Pennsylvania, USA	41.13°	-77.62°	426
	Sherbrooke , Canada	45.49°	-72.17°	301
	Montmagny, Canada	46.95°	-70.46°	327
	Rivière-du-Loup, Canada	47.73°	-69.48°	147
Boreal	Lac LaFlamme	47.32°	-71.11°	790
	Parent	47.90°	-74.63°	404
	Micoua	49.75°	-68.69°	212
	Ashuapmushuan	48.81°	-72.77°	277
Mixedwood/ Transition	Saint Marcellin	48.30°	-68.29°	319
	Rivière-Éternité	48.23°	-70.35°	391
	Ouimet	48.28°	-68.73°	335
	Auclair	47.75°	-68.08°	253
Temperate	Dorset	45.82°	-72.51°	536
	Knowlton	45.19°	-72.50°	330
	Ferme Neuve	46.77°	-75.46°	316
	Saint-Faustin	46.05°	-74.47°	432

2.3.2 Data Collection

We counted the number of 1st year seedlings within each of the plots in late spring-early summer of 2014 (Table 2.2). A plot level assessment was also conducted, where substrate coverage (%) of each of the following variables were taken: (i) moss cover, (ii) leaf litter, (iii) conifer needles, (iv) rock, (v) decayed logs (Decay classes: 4-7, Mills and Macdonald 2004); (vi) solid wood (Decay classes: 1-3, Mills and Macdonald 2004) and (vii) exposed mineral soil. In addition, an organic soil sample from the center of each of the plots was collected to measure forest floor pH (2.00 g of soil: 20 ml of distilled water (1:10); Carter and Gregorich 2007). The following year, we again re-measured the presence of transplanted seedlings (2nd year seedlings) in July 2015 (Table 2.2).

Table 2.2. Seeding and field measurement dates by transplant site.

Zone	Site	Seeded	1st Year Measurement	2nd Year Measurement
Boreal	Lac LaFlamme	27-28/11/13	23/06/2014	11/07/2015
	Parent	09/12/2013	16/06/2014	05/07/2015
	Micoua	01/12/2013	24/06/2014	13/07/2015
	Ashuapmushuan	30/11/2013	24/06/2014	12/07/2015
Mixed	Saint Marcellin	19/12/2013	13/06/2014	13/07/2015
	Rivière-Éternité	29/11/2013	25/06/2014	11/07/2015
	Ouimet	17/12/2013	13/06/2014	13/07/2015
	Auclair	18/12/2013	13/06/2014	14/07/2015
Temperate	Dorset	05/12/2013	10/06/2014	03/07/2015
	Knowlton	06/12/2013	10/06/2014	03/07/2015
	Ferme Neuve	08/12/2013	16/06/2014	06/07/2015
	Saint-Faustin	07/12/2013	17/06/2014	05/07/2015

2.3.3 *Data Analysis*

An analysis of the macroscale effects of each bioclimatic zone (temperate, mixedwood, and boreal) provided insight into the large scale influences occurring on recruitment. To do so, we used a mixed model approach to investigate the influence of each zone and seed provenance on 1st and 2nd year seedlings, and seedling survival (% difference between 1st and 2nd year). The zone (n=3) and seed provenance (n=6) were treated as fixed factors, while site (n=12) was treated as a random factor replicate within canopy composition. All data were averaged to these main effects prior to analysis. A square root transform was performed when residuals did not meet the assumptions of normality and homogeneity of variance. We also conducted a one-way ANOVA on seed lot weights to infer any potential differences in seed provenance. The Tukey-Kramer's HSD test (α =0.05) was used for all post-hoc comparisons of means. All data were analyzed using the mixed procedure (proc mixed) in SAS version 9.2 (SAS Institute Inc. 2016).

Additionally, we also conducted a microscale analysis to evaluate the potential influence of microsite on recruitment at the plot level within each of the specific zones. To do so, we used Multiple Regression Tree (MRT) analysis, which is a well-known procedure to make inferences on the contributing factors in natural regeneration surveys when multiple contributing factors are being considered simultaneously at different scales (De'ath *et al.,* 2002; Solarik *et al.,* 2010). In short, MRT analysis produces dichotomies in a categorised manner, where the independent variables that are more similar are clustered together, while those that are different are split apart. Here, we performed three MRT analyses, one for each zone; temperate, mixedwood, and boreal. The multiple dependent variables considered in these analyses were 1st year seedlings, 2nd year seedlings, and seedling survival, while the explanatory variables included were plot level substrate coverage (%): moss, leaf, needle, rock, decayed wood, solid wood, exposed soil, and soil pH. Additionally, we included the following site level climate variables: (i) mean temperature (ii) number of stratification days: days in early spring (March to May) with a mean daily temperature between -1°C and 7°C; determined to be the critical temperature range required to break seed dormancy in sugar maple (Solarik *et al.,* 2016), (iii) number of warm days: days with a mean temperature of >7°C (between March 1st and May 31st), (iv) shift ratio: ratio of stratification days to warm days, and finally, (v) light days: the number of days of recorded light. A Euclidian distance measure was used to determine dissimilarities within each MRT. The final tree selection was made using the interactive "pick" option by selecting the 1-SE (standard error) rule (Solarik et al. 2010). To further ensure we selected the correct regression tree, 5000 cross validation runs were performed. All data were analyzed using R version 3.2 (R Development Core Team 2016) and the "mvpart" library version 1.6-0 (Therneau and Atkinson 2013).

2.4 Results

A total of 2557 (7.8%) seedlings established the 1st year, of which 631 survived through to the second year (1.95%), resulting in a seedling survival rate of 24.7%. Transplant zone was found to only influence 1st year seedlings (p=0.0305) (Table 2.3, Figure 2.3). Although, sites within the temperate zone on average had nearly 3x more 1st year seedlings (14.0%) when compared with other zones (mixedwood: 4.7% and boreal: 5.0%), it had comparable survival rates (Figure 2.3). No significant differences were detected among 2nd year seedlings (p=0.3517) and survival (p-value=0.3982) among all three zones; however, survival did follow a noticeable declining trend (temperate→mixedwood→boreal) (Figure 2.3). Seed provenance significantly influenced both 1st (p=0.0065) and 2nd year seedlings (p=0.0396); however, again no relationship was found with survival (p=0.2939) (Table 2.3, Figure 2.4A). Interestingly, we did find that there was a trend for increased 1st and 2nd year seedling presence as seed originating further northward had generally increased establishment rates, but again we found no influence statistically on survival (Figure 2.4A).

Table 2.3. Analysis of variance of 1st year, 2nd year establishment, and survival rate for sugar maple seedlings. Significant values in bold using a Tukey-Kramer`s test ($\alpha < 0.05$).

Sources of Variation	dF	1st Year*	F Value	2nd Year*	F Value	Survival*	F Value
Zone (Boreal/Mixedwood/Temperate)	2	**0.0305**	4.28	0.3517	1.18	0.3982	1.02
Seed Origin	5	**0.0065**	3.74	**0.0396**	2.58	0.2939	1.27
Canopy x Origin	10	0.1208	1.66	0.5181	0.93	0.1717	1.50
Error	144						
Total	215						

*Represents data that were square root transformed

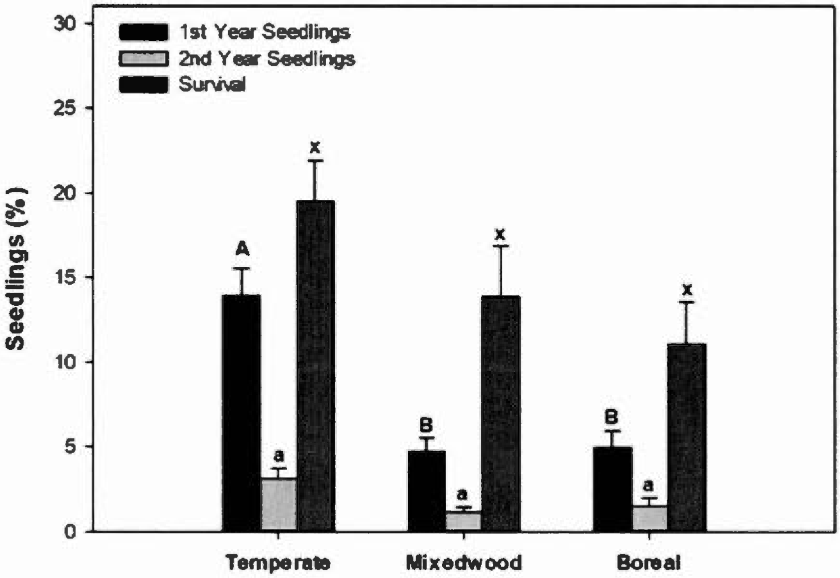

Figure 2.3. Sugar maple seedling presence and survival by bioclimatic zone. Bars with the same letter were not significantly different. Bars with the same letter were not statistically different (Tukey's HSD Test, α = 0.05).

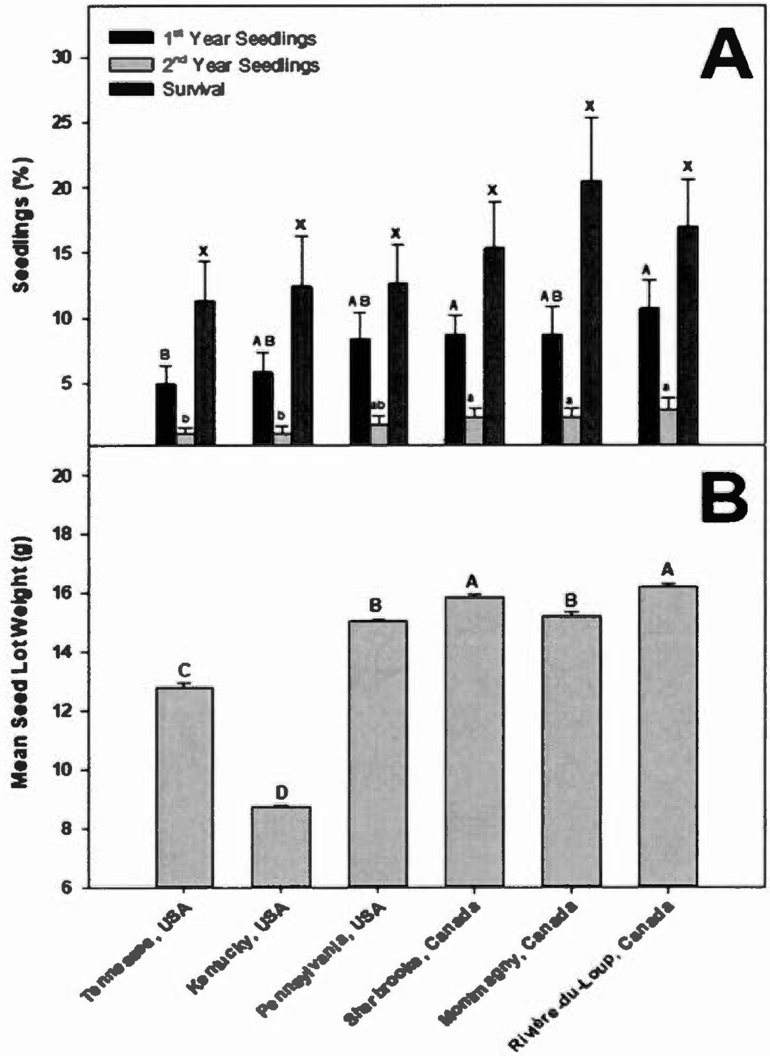

Figure 2.4. (A) Percent of seedlings per plot for 1st and 2nd year seedling presence (%), and survival (%) by seed provenance. Bars with the same letter were not significantly different (Tukey's HSD test, α=0.05). (B) Seed weight (150 seeds/g per plot) by seed origin. Bars with the same letter were not statistically different (Tukey's HSD Test, α = 0.05).

2.4.1 MRT

The boreal zone (beyond range) MRT produced a 6-leaf tree (leaf refers to terminal points within the analysis) that explained 58.7% of the total variance within the analysis (Figure 2.5). Forest floor pH explained the most variance (21.1% of total tree variance) of the five explanative factors within the boreal zone. Plots with a soil pH ≥ 4.61 (n=13) resulted in more than twice the rate of 1st year seedlings and nearly six fold increase in survival after 2 years when compared with more acidic plots (pH<4.61, n=59) (Figure 2.5). The second most influential factor was the number of days of recorded light days (12.7% variance explained), where more basic plots (pH≥4.61) receiving more days of light (≥52, n=5) improved both 1st year: +6.9% and 2nd year seedlings: +6.8%, and survival (+25.4%) when compared with plots receiving fewer days of light (<52, n=8). Needle coverage explained 9.7% of the total variance, where lower needle cover (<2.5%, n=11) within the acidic plots improved the presence of 1st and 2nd year seedlings (six and twelve times respectively), while the survival rate quadrupled when compared with plots maintaining higher needle coverage (≥2.5%, n=48).

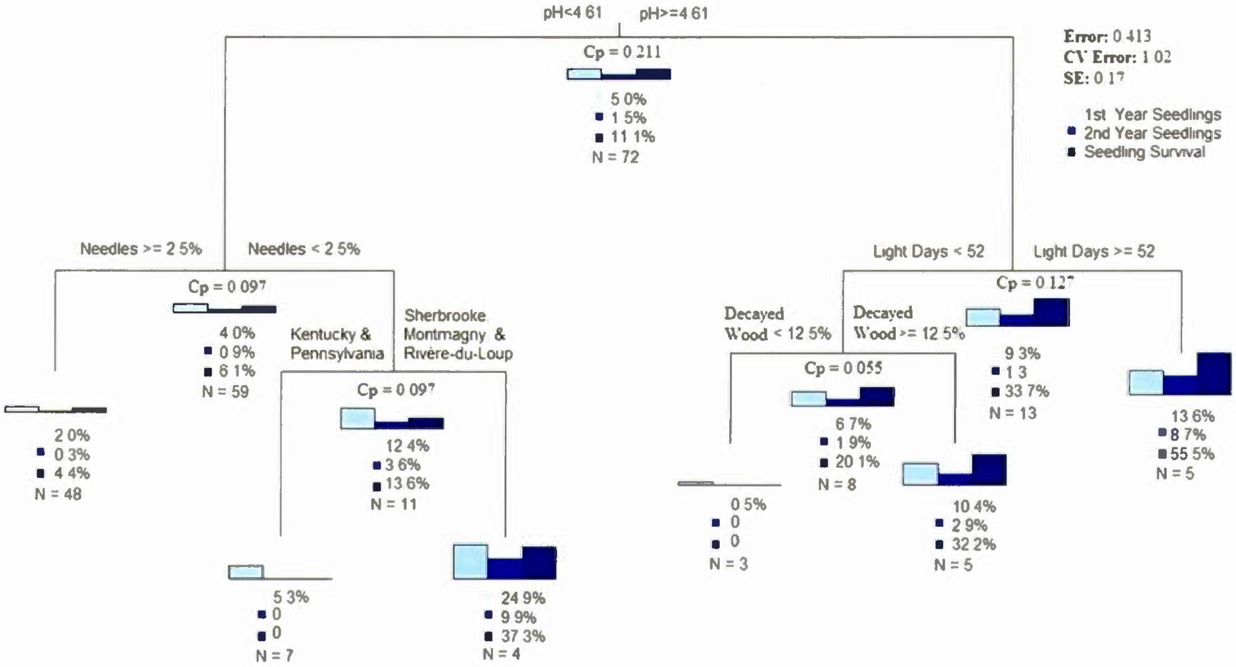

Figure 2.5. Multivariate Regression Tree analysis of boreal sites (beyond range limit) for 1st, 2nd second year seedling presence (%), and survival (%) per 1m^2 plot. This tree explained 58.7% of the total variance, and the vertical depth of each split is proportional to the variation explained, where the complexity parameter (Cp) refers to the amount of variance explained by the individual split.

Seed provenance (9.7% of total variance) provided the next split, where plots seeded with southern provenances (Kentucky and Pennsylvania, n=7) experienced reduced the presence of seedlings (1st year: -19.6% and 2nd year: -9.9%) and no survival after 2 years. On the other hand, northern seed provenances (Sherbrooke, Montmagny, and Rivière-du-Loup, n=4) had a survival rate of 37.3%. Decayed wood cover explained the least amount of variance within the boreal zone (5.5%), however, plots with more decayed wood (≥12.5%, n=5) did improve 1st year establishment by 10.4% and seedling survival by 32.2% compared to plots with less (<12.5%, n=5) (Figure 2.5).

At the northern range limit (mixedwood zone) the number of stratification days (recall: number of days with an average daily temperature between -1°C and 7°C) explained most of the variance within (16.5% of the total 57.7%) the 7 leaf MRT (Figure 2.6). Seeds exposed to fewer than 88.5 stratification days (n=18) had an improved presence of seedlings (1st year: %16.4% and 2nd year: +4.2%) and survival (20.5%) when compared with sites that had a more prolonged, cooler spring (Table 2.4). Seed provenance was the second most influential factor (14.8%), where seed from Rivière-du-Loup (northern most provenance) had improved seedling presence (1st year: +3.6% and 2nd year: 2.8%) and seedling survival (38.9%) compared to more southern provenances (Figure 2.6). Establishment and survival of Rivière-du-Loup seeds were surprisingly improved with more needle coverage (≥20.0%), where this split explained 11.4% of total variance. The final two factors influencing seedling presence and survival were soil pH and the amount of leaf litter, where all three of the remaining splits each variables explained 5.0% of total variance; seedling presence and survival improved with increases in both leaf cover and soil pH (Figure 2.6).

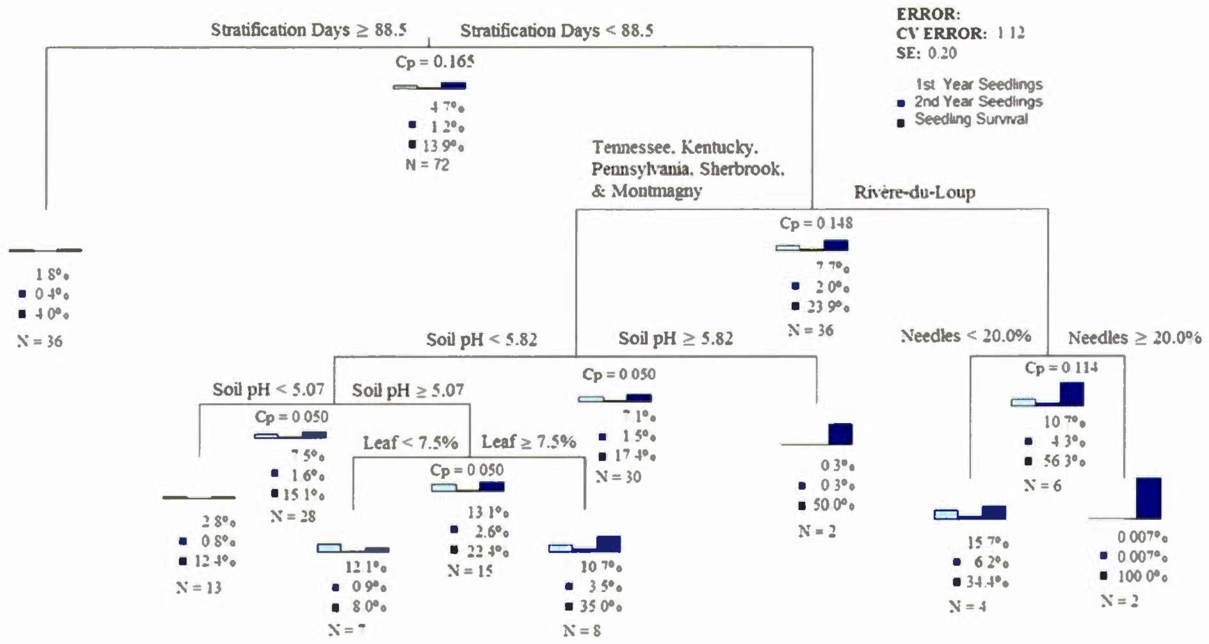

Figure 2.6. Multivariate Regression Tree analysis of <u>mixedwood sites</u> (at range limit) for 1st, 2nd second year seedling presence (%), and survival (%) per 1m^2 plot. This tree explained 57.7% of the total variance, and the vertical depth of each split is proportional to the variation explained, where the complexity parameter (Cp) refers to the amount of variance explained by the individual split.

Seedling presence and survival within the temperate zone (within range) was described best by a 6 leaf MRT that explained 36.6% of the total variance within these plots (Figure 2.7). Shift ratio; the ratio of stratification days to warm days, was determined to be the most influential factor (explained 12.7% of total variance). A larger ratio nearly doubled the rate of first year seedlings, while survival was improved seven-fold (24.7% vs 3.9%). Decayed wood was the second most influential factor (6.9%), where an increase in coverage within the recruitment plot (≥7.5%) improved seedling presence (1st: +9.1% and 2nd: 5.2%) and survival (+16.8%). Northern seed provenances (Sherbrooke northward) once again resulted in better survival over those from more southern provenances within plots, where more than 3x the survival occurred (52.6% vs 15.3%, Figure 2.7). The soil pH split explained 6.2 % of total variance within the biome, where more acidic plots (pH<4.03) had 5x fewer seedlings (8.0% vs 41.2%), and ¼ the survival rate of more plots possessing more basic soils. The final explanatory variable; average seed weight, explained the least amount of variance (3.9%), where plots seeded with lighter seeds (<0.103g) produced a third of the seedlings than those seeded with heavier seeds (≥0.103g) (Figure 2.7).

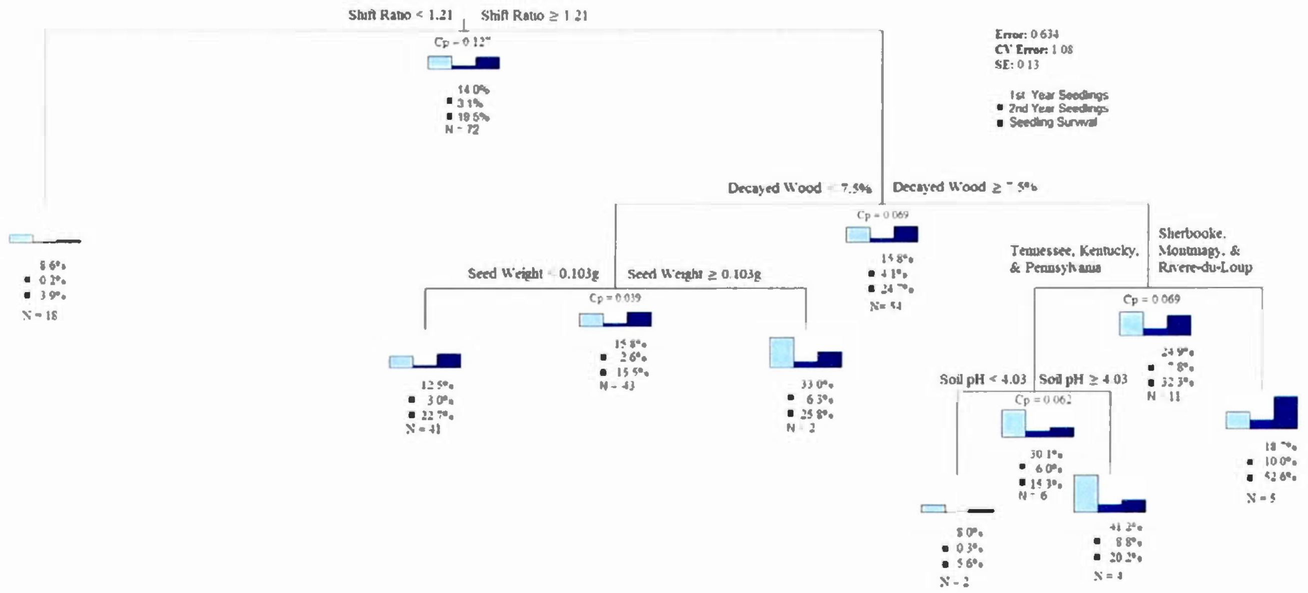

Figure 2.7. Multivariate Regression Tree analysis of <u>temperate sites</u> (within range limit) for 1st, 2nd second year seedling presence (%), and survival (%) per 1m^2 plot. This tree explained 39.3% of the total variance, and the vertical depth of each split is proportional to the variation explained, where the complexity parameter (Cp) refers to the amount of variance explained by the individual split.

2.5 Discussion

Our study shows evidence that successful seed germination, seedling establishment and early survival is constrained due to local adaptation. We found that seeds originating closer to the range margins were currently better able to produce seedlings at higher rates overall than those from either the central and southern portions of the species range; likely due to their closer original proximity to conditions they were transplanted to (Putnam and Reich 2016; Anderson 2016). In addition, we show that the strength and interplay of climatic and microsite play a significant role in sugar maple recruitment; however, their relative contribution are site and region specific (Figures 2.5-2.7).

2.5.1 Seed Provenance

Results from our study highlight the importance and direct link between seed provenance and the likelihood of successful seedlings establishment and survival. Here we found that seed originating from the most northern portions of the species range currently led to the best recruitment. These findings highlight local adaptation at these key early stages (Figure 2.4) and agree with our first prediction. Our results do not fully support the centre-periphery hypothesis: genetic variation and demographic performance of a species decrease from the center to the periphery of its range, as we find evidence that seeds from the norther portions of the range outperformed the central provenances. Parent trees living in these harsher fringe conditions at the range periphery would lead to a reduced and/or poorer quality seed crop (i.e., lower viability), which would subsequently lead to poorer recruitment rates (Johnstone *et* *al.,* 2009; Walck *et al.,* 2011; Castanha 2012). Surprisingly this was not the case in our study. Populations at the range margins are exposed to higher environmental variability (i.e., increased competition, colder climate) compared to their central range, which would lead to seeds that are better adapted to a wide range of conditions, including those northern conditions found beyond their current range (Cleavitt *et al.,* 2011; Anderson 2016). While we could not differentiate the genetic and phenotypic effect of seed provenance, we were able to differentiate a few clear effects. First, northern provenances had on average heavier seeds (Figure 2.4B) that improved the presence of seedlings. A heavier or larger seed size will provide greater energy reserves to a new germinate and improve its survival through: (i) a longer radical that can penetrate the forest floor more successfully, (ii) establish a larger seedling, (iii) provide greater initial resources for leaf formation, and (iv) delay the onset of carbon starvation in poorly lit understories (Walters and Reich 2000). A lighter seed at the southern portion of the range (which we report) has been previously reported in other sugar maple studies (Clark *et al.,* 2014), and has been associated with the delay in fruit maturation caused by late flowering in these warmer environments (Morin and Chuine 2014). Poorer recruitment rates for southern provenances could also highlight the inability of these warmer conditioned seeds to germinate in cooler climates (Solarik *et al.,* 2016).

If the climate warms faster than the species ability to adapt, seed from the northern range will become maladapted and lead to significant migration lag (Solarik *et al.,* 2016). As a result, southern seed provenances would then provide the best opportunity for improved recruitment at the future warmer northern range as they are currently better adapted to these conditions where we show some evidence of this within our range sites (Ngamitsu *et al.,* 2015; Aitken *et al.,* 2016; Solarik *et al.,* 2016).

Table 2.4. Seed transplant site specific climatic and light variables.

Zone	Site	Total Days Measured	Overall Mean Temperature (°C)	Stratification Days (-1°C to 7°C)	Shift Ratio	Negative Temperature Days	Light Measurements	
							Number of Days	Day of First Light
Boreal	Lac LaFlamme	204	-0.02	50	3.46	111	29	08/05/2013
	Parent	211	0.88	46	2.20	100	56	21/04/2013
	Micoua	219	1.20	40	2.87	108	46	09/05/2013
	Ashuapmushuan	219	1.77	45	2.05	107	58	29/04/2013
Mixedwood/ Transition	Saint Marcellin	211	2.56	95	3.38	96	42	29/04/2013
	Rivière-Éternité	219	1.90	82	4.71	107	39	10/05/2013
	Ouimet	211	2.08	101	4.41	106	39	8/05/2013
	Auclair	211	2.55	68	1.96	105	58	11/04/2013
Temperate	Dorset	204	3.15	101	2.07	63	51	20/04/2013
	Knowlton	204	3.45	79	1.21	75	63	09/04/2013
	Ferme Neuve	211	2.77	51	1.30	97	72	07/04/2013
	Saint-Faustin	211	3.09	51	1.20	101	70	09/04/2013

2.5.2 Climate

We found that climate, more specifically the timing of cool and warm temperatures, had a strong influence on sugar maple recruitment. The climatic influence was particularly apparent within the temperate and mixedwood zones (Figures 2.6 and 2.7). Our results support our second prediction; where sites matching sugar maple's stratification requirements led to the improved presence and survival of seedlings. Although our boreal sites did have lower overall mean temperatures (Table 2.4), mean temperature was found to be a poor predictor of seedling recruitment success. Local climate has been historically found to have a significant impact on all facets of plant species phenology, life history traits, and subsequent range (Turesson 1925; Morin and Chuine 2014), and our findings support this at the establishment phase. The number of stratification days within the mixedwood zone highlights sugar maple's adaptation to the timing of temperature, where sites not meeting these requirements will cause significant declines in seed germination (Solarik *et al.*, 2016).

The opposite could also be true however, where a surplus of warmer days coupled with a lack of precipitation has been shown to reduce recruitment at sugar maple's southern range (Clark *et al.,* 2014). We stress that the timing of certain temperatures, particularly in early spring when seeds are exposed to rapid fluctuations in temperature are more important than the average; highlighted by the effect of shift ratio (stratification days: warm days) in our temperate transplant sites (Figures 2.7 and 2.8).

Sites maintaining lower shift ratios had the highest presence of seedlings and survival. By first satisfying the stratification requirements to break seed dormancy, and then shift to warmer conditions that lead to snow melt and the commencement of seedling establishment (photosynthesis and growth) (Table 2.4, Figure 2.8). On the contrary, higher shift ratios tended to occur in cooler sites, where snow remained on sites longer, leading to a prolonged stratification period (Table 2.4). Snow pact when present (which occurred at all of our sites) provides an ideal stratification environment (approximately -1°C), and can also shelter seed and seedlings from potentially harmful early spring frost damage (Walck *et al.,* 2011; De Frenne *et al.,* 2013; Morin and Chuine 2014) and herbivory/predation (Gardescu 2003). If snow melt is delayed, it could inhibit new germinates from establishing. Overall, we found an inter-site difference of 34 days for the first day of recorded light (i.e. snow melt, Table 2.4) highlights a wide variation in site conditions within this study, which could be minimized under warmer, earlier springs as predicted in the future (Drescher and Thomas 2013; Price *et al.,* 2013). A warmer spring would cause earlier snow melt and accelerate water runoff, exposing seeds to a much narrower stratification window and reduce the likelihood of successful germination. Rapid warming, particularly in the spring at the range limit; where variability in the environment is highest (Sexton *et al.,* 2009) can further contribute to species maladaptation and increase the likelihood of migration lag. A meta-analysis (74 studies) performed by Hereford

(2009) looked at local adaptation and fitness trade-offs, suggests that while populations are often locally adapted, stochastic processes (genetic drift) can limit efficacy of divergent selections of certain favourable traits. These findings suggest the ability of a species to become locally adapted to future conditions could become reduced as the variability surrounding temperature and precipitation events in the future increases (Aitken *et al.*, 2013; IPCC 2013). Aubin *et al.*, (2016) reinforces this concern, where mean annual temperatures increase will only have a minimal impact on trees, chilling requirements, heat sum thresholds) should have a more profound impact on the ability of a species to adapt to future environmental conditions.

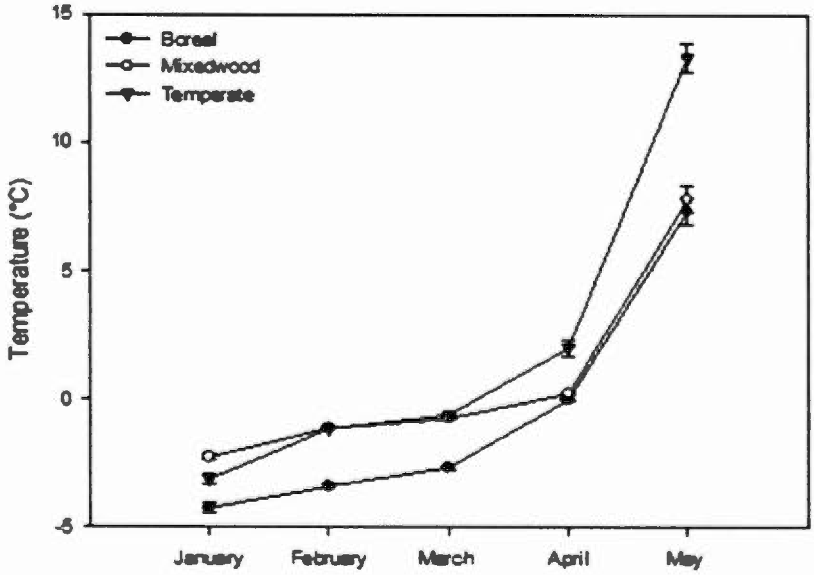

Figure 2.8. Mean monthly temperature (°C) by forest biome for winter and early spring.

2.5.3 Substrate

Our results confirm that sugar maple exhibits a considerable preference for certain substrates over others, reinforcing our prediction of a microsite effect on seedling presence. Beyond the current northern temperate range limit (boreal), soil pH was the most influential factor, and to a lesser extent within other zones. Regardless of site, seedlings were consistently found in higher numbers on soil within a higher pH (Figures 2.5-2.7). Typically, acidic soils lead to high concentrations of soluble aluminum, iron, and manganese, which are all well known to inhibit plant growth, and particularly detrimental for seedlings (Bal *et al.,* 2015; Collin 2017). Even though sugar maple seedlings were capable of establishing on acidic soils (pH<4.0); 76% of our recruitment plots had soil pH <5.0, it establishes and grows best on more basic soils (pH= 5.5-7.3, Godman *et al.,* 1990). Albeit acidic soils can reduce sugar maple's likelihood of establishing, it does not completely inhibit it. We speculate that this is likely due to the presence of other more beneficial nutrients present (i.e., magnesium) within the soil and/or the influence of other substrate factors helping reduce the influence of pH (Coughlan *et al.,* 2000; St.Clair *et al.,* 2008).

Sugar maple seedling presence improved when decayed wood was present (Figures 2.5 and 2.7). Decayed wood is generally considered as a safe site for seedling establishment (Harmon *et al.,* 1986) as it typically possess less seed pathogens over forest floor soil (O'Hanlon-Manners and Kotanen, 2004), absence of localized competition, elevated position, improved moisture retention, temperature, and can even combat soil erosion (DeLong *et al.,* 1997; Cornett *et al.,* 2000; McGee *et al.,* 2001). The presence of decayed wood also improves nutrient uptake (Simard *et al.,* 2003) and potential presence of beneficial mycorrhizas, which could improve marginal conditions in the boreal understorey. Although we did not identify decayed wood by species, which improves conspecific recruitment (Marx and Walters 2008; Lambert *et al.,* 2015), seedling establishment was improved regardless in its presence.

We generally found that an increase in needle cover within the plots inhibited the establishment and survival of sugar maple. The presence of an abundant needle layer on the forest floor has been shown to influence the immobilization of nutrients (Zak et al. 1999), which has been shown to greatly influence the health and growth of sugar maple seedlings (St. Clair *et al.,* 2008; Collin *et al.,* 2017). Leaf litter, although a weak predictor (5.0% of variance explained) and only significant within the mixedwood zone. Leaf litter has been suggested to be a generally favourable substrate for sugar maple to establish, as it maintains a radicle strong enough to pierce through dense leaf coverage if necessary and could provide a competitive advantage over smaller seeded tree species hoping to establish (McGee 2001; Caspersen and Sprunoff 2005).

Increasing empirical evidence suggests that edaphic factors may even outweigh the importance of climatic factors as the primary inhibitor of temperate tree migration (Brown and Vellend 2014). It is evident that soil conditions play a critical component in ensuring seedling establishment and survival, however, the relative influence becomes increasingly important as the likelihood of encountering more nutrient poor soils increases northward into the boreal regions (Graignic *et al.,* 2014; Brown and Velland 2014; Collin 2017). Significant migration lag could occur if temperate tree species are maladapted to establish upon boreal microsites – even if the climate becomes more favourable under climate change. Certain plant populations have been shown to adapt to specific soil types (Wright *et al.,* 2006) or local mycorrhizal community (Kranabetter *et al.,* 2012), however, in the absence of these conditions further lag will occur. Unlike climate, the turnover rate of soil conditions should be expected to occur over much longer time scales (Aitken *et al.,* 2013).

2.5.4 Light

The number of days of recorded light was an important predictor of sugar maple recruitment within the boreal biome. Plots receiving at least 46 days of recorded light had an improved seedling presence by 6.6%. Receiving adequate light in the understorey has long been understood as an important hurdle to be overcome for seedlings (Walters and Reich 1996; Schreeg *et al.,* 2005). Although we did not measure photosynthetic active radiation (PAR), and are unable to translate the quality of light received by seedlings, we were able to state when seedlings were first exposed to light across sites. Sites with delayed snow melt (i.e., fewer recorded days of light) delay the onset of photosynthesis, while seedlings at warmer sites are forced to compete earlier for light and resources. Albeit sugar maple is a highly shade tolerant tree species, understorey canopy light conditions must reach a certain threshold (typically +10 % of full sunlight) to ensure seedling survival (Canham 1988; Leithead *et al.,* 2010). In the absence of a forest canopy disturbance or gap, light thresholds within evergreen understories will likely need to be higher considering the lack of a photosynthetic window in the early spring and further contribute to the migration lag of temperate species.

2.5.5 Other Potential Constraining Factors

Often ignored in the context of species migrating northward in latitude is photoperiod (Way and Montgomery 2014). Many plant and animal species have adapted to photoperiod, where even the rate of carbon assimilation has been shown to change within the same species (Goldblum *et al.,* 2012). While photoperiod is stable, and declines with increasing latitude, under climate warming, species migrating northward could face novel combinations of light, temperature, and moisture due to a northward shifts and further contribute to migration lag. Issues may arise as responses to photoperiod are misinterpreted as thermal responses (Soolanayakanahally *et al.,* 2013), where seasonal triggers respond to the length of day: growth cessation, dormancy, and flowering time, which ultimately could influence the recruitment of invading species (Laube *et al.,* 2014).

Dispersal also remains another significant factor contributing to species migration and has long been hypothesized as being the primary inhibitor to species invasion; highly localized and generally falls within relatively short distances (<20.0m) of the parent tree (Greene *et al.,* 2004). A lack of long distance seed dispersal events (Clark *et al.,* 1998) combined with high inter-annual variability in seed crop; sugar maple masts every 3-7 years (Godman 1990), could cause severe migration lag strictly from a seed production and dispersal perspective at its northern range limit (Capsersen and Sprunoff 2005; Polechova *et al.,* 2009; Graignic *et al.,* 2014).

Predation may also play a significant role in slowing range shifts. Although we controlled seed predation within this study through the use of cages (See Photo Annex B), we outline the important role that biotic agents; predation, herbivory, disease, can have on the spatial distribution and recruitment dynamics of seedlings (e.g. Hsia and Francl 2009; Speed *et al.,* 2010; Walters *et al.,* 2016). While we did outline the importance of seed size (Walters and Reich 2000), larger seeds will likely be exposed to increased risk of predation outside its range, as temperate tree seeds are much more readily distinguishable than their often smaller boreal counterparts (Hewitt 1998), even though they will likely be much more limited in abundance (Kellman 2004; Brown and Vellend 2014). Naturally, predation is highly variable between microsites (Whelan *et al.,* 1991), but the threat of further reductions in seed abundance could prove costly, especially when considering the inter-annual variability of seed production (Gaston 2009; Walck *et al.,* 2011) and poor early establishment rates (Figures 2.3 and 2.4).

2.5.6 Future Species Ranges

While the results outlined in this study only refer to a single species, the findings provide considerable insight into plausible bottlenecks when considering the local adaptation of early seedlings in the context of species migration. We highlight that individually and collectively the contribution of maternal, climatic, and microsite greatly influence early seedling recruitment, however, their relative importance is site dependent.

Range shifts of hundreds of kilometers are required for temperate trees if they are to match their optimal climatic conditions of the future (McKenney *et al.,* 2011). For example, Boisvert-Marsh *et al.,* (2014) point to a rate of approximately 4.9 km/year for sugar maple under current and projected climate scenarios for 2050 in order to maintain its climatic niche. However, for this to occur in the most optimistic of scenarios, a number of recruitment bottlenecks must first be overcome. First, climate must be favourable enough for parent trees at the current range limit to be able to produce a sizeable seed crop, which then need to be dispersed in large quantities at long distances (Clark *et al.,* 1998). Second, the new local climate where the seed falls must favour any species-specific climatic requirements needed to ensure subsequent seed germination. Assuming the first two steps are satisfied, seedlings must then establish on a favourable substrate, while simultaneously overcoming any biotic pressures already present in the environment. Finally, the newly established seedling must then display enough phenotypic plasticity to withstand the novel conditions associated with resource uptake (i.e. water, light, nutrients) until it reaches reproductive maturity. Essentially, these five bottlenecks must all be recurrently overcome at considerable rates over extended periods of time to ensure a species ability to migrate at the range limit to maintain its future climatic niche.

Invading species will likely need to either outcompete the current species already established or delay migration until they senesce prior to detecting changes occurring at the adult/canopy stage (Hart *et al.,* 2014). Like others (Woodall *et al.,* 2009; Zhu *et al.,* 2012; Sittaro *et al.,* 2017), analyzing the seedling and sapling size classes particularly within the range margins can provide valuable insight into the current range expansion/contraction (Sexton *et al.,* 2009). Tree migration rates could also be artificially sped up with implementation of various forest management schemes, where the removal of native northern boreal trees in favour of planting/seeding temperate tree species beyond their current limit (Leithhead *et al.,* 2010). Further, natural disturbances could also facilitate temperate species migration as fire and insect outbreaks could open up canopy large gaps in established forests that would favour recruitment of invading species looking to move beyond their current range (Landhausser *et al.,* 2010; Zhang *et al.,* 2014; Willis *et al.,* 2015; Walters *et al,* 2016). However, our results suggest that transplanting seed or seedlings to colder climates may inhibit long term survival, where mismatches in climate could cause deleterious impacts to key life stages (seed germination, budburst, flowering, pollen development, and leaf unfolding) (Morin and Chiune 2014; Laube *et al.,* 2014). Ultimately, our study reinforces that sugar maple migration will be constrained due to its local adaptation at its recruitment stage to conditions within its current species range.

CHAPTER III

PRIORITY EFFECTS ARE PREVENTING RANGE SHIFTS OF TEMPERATE TREE SPECIES INTO THE BOREAL FOREST

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3.1 Abstract

Temperate tree species are expected to expand their distribution into the boreal forest in response to climate change. However, it is becoming increasingly clear that many species will experience significant setbacks in their migration due to a series of unfavourable conditions impacting their recruitment success, and thus their ability to colonize new locations. We quantify the relative influence of a series of factors important for tree seedling recruitment at range margins: dispersal, substrate favourability, and the influence of the local canopy neighborhood. We hypothesized that boreal trees are responsible for priority effects that influence the establishment of temperate tree species seedlings. To do so, we analyzed two recruitment stages (first year seedlings and older seedlings) for seven tree species; Abies balsamea (ABBA), Acer rubrum (ACRU), Acer saccharum (ACSA), Betula papyrifera (BEPA), Betula alleghaniensis (BEAL), Populus tremuloides (POTR), and Fagus grandifolia (FAGR) commonly found within the temperate-boreal ecotone forests of northeastern North America. Overall, we found that boreal canopy trees influence the distribution of substrates, more specifically the occurrence of needle cover and decayed wood in recruitment plots. This association between canopy and substrate led to highly unfavourable substrates that affected the seedling densities of all temperate tree species. In addition, we found that seedling dispersion was highly localized, where mean dispersal distance of all trees occurred in close proximity of parent trees. Ultimately, we found evidence that priority effects imposed by resident boreal trees are magnified as a result of unfavourable substrates and limited MDD (mean dispersal distance) of trees within these ecosystems, which together promise to cause significant lags in temperate tree species migration into the boreal forest in the future.

Key words: climate change, species range, migration, priority effects, transition zone, temperate forest, boreal forest, seedling recruitment.

3.2 Introduction

Climate change has already begun to force many plant species to shift their geographic distribution (Beckage *et al.*, 2008; Jump *et al.*, 2012; Boisvert-Marsh *et al.*, 2014; Kroiss and HilleRisLambers 2015). As a result, novel community and species interactions should be expected with species colonization and extinction (Williams *et al.*, 2004; Woodall *et al.*, 2013). The rate and magnitude of the projected changes will exceed the adaptive capacity of certain species (Kawecki and Ebert 2004; Iverson *et al.*, 2008; Sexton *et al.*, 2009; Duputié *et al.*, 2015; Aubin *et al.*, 2016). Species lacking the ability to disperse fast enough and/or the plasticity to maintain their fitness under climate change will lag behind their optimal distribution, which could lead to significant declines in their abundance and promote extinctions (Aitken *et al.*, 2008; Woodall *et al.*, 2013; Renwick and Rocca 2015; Solarik *et al.*, 2016; Anderson 2016).

Vulnerability to rapid changes in environmental conditions are particularly worrisome for trees because they are sessile organisms, long lived, slow to reach reproductive maturity, and typically have limited seed dispersal (Petit and Hampe 2006; Lenoir and Svenning 2013; but see Clark *et al.*, 1998). Theory predicts that range expansion rates should scale with the mean dispersal distance (MDD) and the population growth rate in novel environments (Svenning *et al.*, 2014). While we know much about dispersal kernels of forest trees (Greene *et al.*, 2004; Nathan *et al.*, 2012), much less is known about population dynamics at range margins. Rapid changes in climate can significantly impact tree development, survival, and phenology (Aitken *et al.*, 2008; Walck *et al.*, 2011; Vitasse *et al.*, 2013; Erickson *et al.*, 2015). Forest dynamics depend greatly on the regeneration stage, which is strongly influenced by the abiotic and biotic conditions occurring within the understory (De Frenne *et al.*, 2013). It is a key life stage that involves several important and environmentally sensitive phases:

flowering, pollination, seed maturation, propagule dispersal, seed germination, seedling establishment, and subsequent survival (Sexton et al., 2009; Fisichelli *et al.*, 2013; Kroiss and HilleRisLambers 2015; Tingstad *et al.*, 2015; Solarik *et al.*, 2016).

Species response to climate change will likely be detectable first within the transition zone (ecotone) where species ranges overlap (Harper *et al.*, 2005). Ecotones tend to have the highest environmental heterogeneity (Boulangeat *et al.*, 2012), are highly variable, and under constant contraction and expansion (Gaston *et al.*, 2003; Sexton *et al.*, 2009; Eppinga *et al.*, 2013). A species range limit is typically caused by a combination of some limitation in the species physiology to deal with environmental changes (i.e. northern ranges are too cold and southern ranges too hot) and its interaction with the local biotic community (Gosdose *et al.*, 2017); where even minor changes can cause significant reduction in fitness and impact the species ability to acquire resources (i.e., light, water, space; Beckage *et al.*, 2008; Fisichelli *et al.*, 2013). Migrating tree species will likely face negative biotic interactions at the range limit, as they migrate towards novel habitats, where competitors are already established (HillRisLambers *et al.*, 2013). Resident populations can further inhibit range shifts of invading species through priority effects (i.e., legacy effects). Such effects will occur when the resident species lowers the availability of resources (e.g. light, space, nutrients) or changes the environment (e.g. soil pH) in a way that gives it an advantage over invading species (Shulmann *et al.*, 1983; Urban and De Meester 2009). Priority effects can be long lasting (Davis *et al.*, 1998), as they can persist long after a resident species has become maladapted to the local environment, further delaying invading species from colonizing – even if they are better adapted to the local conditions (Atkins and Travis 2010). These effects have been shown to occur within many ecosystems (Case *et al.*, 2005; Sexton *et al.*, 2009; Fenton and Bergeron 2013) and can alter the association between the environment and species distribution (Urban and De Meester 2009; Leopold *et al.*, 2014).

Several factors have been proposed as key inhibitors of tree species range expansion: seed supply (fecundity) and dispersal are amongst the best studied (e.g. Clark *et al.*, 2003; Iverson *et al.*, 2008) and typically seen as the primary cause for migration lags (Case *et al.*, 2005; Sexton *et al.*, 2009; Hargreaves *et al.*, 2014). The limited availability of seed within periphery populations is undoubtedly constrained by the abundance, proximity, and fecundity of the parent trees in these populations (Aitken *et al.*, 2008; Sexton *et al.*, 2009; Martin and Canham 2010). However, even when a seed source is present and able to disperse propagules at greater distances (≥100m; Clark *et al.*, 1998) other factors can further impede successful recruitment. Unfavourable substrates could severely impact recruitment (Caspersen and Saprunoff 2005; Marx and Walters 2008), especially propagules travelling a greater distance from their parent (Kroiss and HilleRisLambers, 2015). The lack of suitable substrates for seedlings to first germinate and establish upon can have multiplicative effects, particularly at the range limit. A combination of novel edaphic effects could arise, where the absence or lack of key symbiotic microbial, fungal communities, and nutrients (e.g., calcium and magnesium) could impact seedling emergence, growth, and survival (LaFleur *et al.*, 2010; Urli *et al.*, 2016; Collin 2017). Further, as microclimate within the understorey is largely controlled by the overstorey canopy and its composition (i.e. light, temperature, competition, soil fertility), the conditions occurring within the ecotone (i.e., species range overlap) could cause a mosaic unfavourable recruitment sites altering the recruitment niche and demography (Grubb 1977; Kobe and Coates 1997; Benavides *et al.*, 2015; Ibanez *et al.*, 2015; Reich *et al.*, 2015).

Our understanding of the factors controlling recruitment within the temperate-boreal ecotone remains limited, where few empirical studies have assessed the influence of non-climatic factors on regeneration dynamics at range margins (Stanton-Geddes *et al.*, 2012; HilleRisLambers *et al.*, 2013, Brown and Vellend 2014). Although we have methods to evaluate recruitment limitations caused by seed dispersal and microsite favourability (Clark *et al.*, 1998), including response to forest management (LePage *et al.*, 2000; Caspersen and Sprunoff 2005), rarely are they done at range limits within undisturbed canopies (but see Drobyshev *et al.*, 2014 and Benavides *et al.*, 2015). Our objective in this study is test the hypothesis that priority effects are limiting recruitment of temperate tree species into the boreal forest. We do so by investigating the relative importance of a series of contributing factors known to influence tree seedling recruitment: seedling dispersion, fecundity and substrate favourability. We also consider the influence of local biotic neighborhood, as a proxy of the potential effect of resident trees on unmeasured environmental variables. We predict that (i) boreal trees will influence the spatial distribution of substrates within a stand, with which these substrates will (ii) influence the seedling density of temperate tree species, and (iii) limited seedling dispersal will magnify priority effects from boreal tree species.

3.3 Methods

3.3.1 *Study Sites*

The study was conducted at three permanent sample sites established as part of the QUICCFOR network (QUantifying and mapping the Impact of Climate Change on FORest productivity of Eastern North America); (i) Abitibi-Temiscaminque (hereafter referred to as Abitibi) (48° 9'45.14"N, 79°24'4.39"W), (ii) Le Bic (48°20'1.03"N, 68°49'3.79"W), and (iii) Sutton (45° 6'46.09"N, 72°32'28.67"W). All three sites are located within or at the limit of the northern temperate forest zone; where Abitibi is located within the balsam fir-yellow birch (Abies balsamea –Betula papyfrifera) domain, Le Bic within the balsam fir-yellow birch (Betula.

alleghaniensis) domain, while the Sutton site lies within the hardwood forest subzone, made up of the sugar maple (Acer saccharum) - basswood (Tilia Americana) domain (Saucier et 2003). Elevation at the three sites ranged from 350 m-400 m in Abitibi, 200 m to 320 m at Le Bic, and 500 m to 850 m at Sutton. The later drives a transition from primarily temperate dominated canopy species at the lower elevation (<650 m) to a balsam fir-yellow birch cover at higher elevation. Mean annual temperature ranges among sites from -15.4C in January to 19.7C in July, while annual precipitation ranged from 868-1314 mm (Environment Canada, 2016)

3.3.2 *Field Sampling*

A grid of 20 m x 20 m quadrats was established at each site to map overstorey canopy trees. Each site varied in plot size, where total area of mapped grids ranged from 200-320 m in width and 200-1000 m in plot length. All trees within the study grid had their coordinates mapped using Leica Flexline© TS06 and TCR805 Total Stations. Each tree with a diameter at breast height (DBH) ≥10.0 cm was mapped, identified by species, health status (living, dead, declining, fallen) and its DBH (1.3m) was measured. In the late spring of 2015, four recruitment plots (1 m^2) were established within each of the 20 m x 20 m grids at a 5 m x 5 m spacing (3424 total recruitment plots across all 3 sites). Recruitment was measured over two years (2015 and 2016) for two recruitment stages: (i) first year seedlings (referred to as stage 1); identified by the presences of cotyledons, absence of terminal bud scars, suppleness of the stem, and number of leaves, (ii) older seedlings (referred to as stage 2); which were not first year and were <30.0 cm in height. We visually estimated the percent coverage (to the nearest 5%, total summing to 100%) of the recruitment plots by the following substrates: grass, leaf, needles, moss, decayed logs (decay classes: 4-7, Mills and Macdonald 2004), solid logs (decay classes: 1-3, Mills and Macdonald 2004), and bole cover from overstorey/sapling trees. In addition to the substrates, we also assessed the cover of deciduous plant cover (non-canopy tree species and herbaceous cover) within the recruitment plot.

3.3.3 *Data Analysis*

3.3.3.1 *Ordination*

We performed a redundancy analysis (RDA) to investigate the association between substrate conditions and canopy composition. Essentially, an RDA is a canonical extension of a multiple regression that models multivariate response data, (Y matrix: substrate type) in relation to an explanatory variable (X matrix: canopy tree basal area) (Borcard *et al.,* 2011). Prior to analysis all response variables were standardized using the Hellinger Transformation, which reduces any extremely skewed values (Legendre and Gallagher 2001). Statistical significance was assessed by comparison of the initial F-statistic to the distribution of F-values obtained after 1000 permutations of the response matrix (Borcard *et al.* 2011) and the goodness-of-fit evaluated with the adjusted R^2 (Peres-Neto *et al.,* 2006). All RDAs were done using the "Vegan" package in R (Oksanen *et al.,* 2015).

3.3.3.2 *Seedling Distribution Model*

Seedling distribution data were analyzed using a modified version of the recruitment model first proposed by Ribbens *et al.,* (1994) and further developed by LePage *et al.,* (2000), who added substrate favourability, and again by Caspersen and Sprunoff

(2005) who added light availability. Below, we describe the model and processes included, and then the modifications we implemented to construct the final model. We then describe our methodology for parameter estimation.

We considered that the seedling produced by an individual parent tree *k*, follows a power function of the stem diameter of that tree (DBH_k);

[1] - Fecundity

$$R_i = STR\left(\frac{DBH_k}{30}\right)^2$$

where (R_i) is the number of recruits within a specific recruitment plot *i*. The total number of recruits (STR – standardized total recruits) is scaled to a parent tree with a DBH of 30.0cm (Ribbens *et al.*, 1994; LePage *et al.*, 2000; Uriarte *et al.*, 2005; Canham *et al.*, 2014). Typically the power exponent is not estimated as it has been shown to co-vary with STR, and we set it to 2 as in previous studies (Caspersen and Sprunoff 2005).

We tested two alternative forms of commonly used isotropic dispersal kernels (Nathan *et al.*, 2012). The first one being the power exponential dispersal kernel, with seed density declining monotonically with distance from the parent tree (Ribbens *et al.*, 1994; LePage *et al.*, 2000):

[2a] – Dispersal (exponential function)

$$g(d_k) = \frac{1}{K}e^{-Bd^{\beta}}$$

where *d* is the distance, *B* and β are estimated parameters, and K is a normalizer constant that ensures the probability will integrate to 1. Many previous studies have fixed β, however, some (Canham and Uriarte 2006; Canham *et al.*, 2014) allowed the parameter to vary, thus allowing the data to determine the appropriate shape, which we do here. The second dispersal kernel we tested was the lognormal, which has been shown to be more appropriate for both wind and animal-dispersed seeds (Greene *et al.*, 2004):

[2b] – Dispersal (lognormal)

$$g(d_k) = \frac{1}{K} e^{-1/2\left(\frac{ln\left(\frac{d}{X_O}\right)}{X_b}\right)^2}$$

where X_O is the median distance travelled, X_b determines the breadth or spread of the seed dispersal kernel, d is the distance from the center of the recruitment plot to a parent tree, and K is again a normalizer constant.

Ribbens *et al.*, (1994) combined equations [1] and [2a] to calculate the expected number of recruits in a quadrat *i* by the summation of the contribution of all conspecific parent trees:

[3] - Fecundity and Dispersal

$$R_i = g(d_k)\, STR \sum_{k=1}^{T} \left(\frac{DBH_k}{30}\right)^2$$

where R_i is the expected number of recruits in each recruitment plot *i* and *T* is the total number of parent trees in the mapped stand. LePage *et al.*, (2000) first introduced substrate favourability into equation [3] by weighting recruitment by the favourability of a particular substrate and its percent cover within a recruitment plot:

[4] - Substrate Favourability

$$R_i = \sum_{j=1}^{S} (c_{ij} f_{ij})\, g(d_k)\, STR \sum_{k=1}^{T} \left(\frac{DBH_k}{30}\right)^2$$

where S is the total number of substrates, c_{ij} is the percent cover of substrate j in recruitment plot i, and f_{ij} is a parameter that quantifies the favourability of the given substrate. f_j is constrained between 0 and 1; a value of 1 indicates that the density of seedlings in a given recruitment plot is limited by the size and proximity of parent trees and not the favourability of a certain substrate. On the contrary, a value of 0 indicates an unsuitable substrate and ultimately lowers seedling density.

As our focus in this study was to evaluate seedling recruitment in the context of species migration, where biotic interaction(s) from surrounding canopy trees may become increasingly important and influence micro-site conditions in a way that we cannot measure (e.g. if the presence of coniferous trees affect snow accumulation and melting), we introduce the local neighborhood effect from hetero-specific canopy trees. The effect of local neighborhood is accounted for by:

[5] – Neighborhood effect

$$R_i = \sum_{j=1}^{S} (c_{ij} f_{ij})\, g(d_k) e^{-P_b \sum_{l=1}^{B} a_l}\, STR \sum_{k=1}^{T} \left(\frac{DBH_k}{30}\right)^2$$

where B is the total number of hetero-specific canopy tree species within the local neighborhood (≤20.0m of recruitment plot center), a_l is the total basal area of hetero-specific overstorey canopy trees within the neighborhood, and P_b is a parameter that quantifying the importance of the neighborhood canopy – where a higher value of P_b indicates an unfavourable neighborhood for recruitment, and thus lowers seedling density.

3.3.3.3 *Parameter Estimation*

We performed maximum likelihood estimation (MLE) of parameters *STR*, P_z, *SCAL* (*X_o and B*) *SHAP* (*X_b and* β) f_j, and P_b for each of the most common tree species, recruitment stages, sites, and year of assessment. As recommended by Canham et al. (2014), we assumed that the expected number of recruits follows a zero-inflated Poisson distribution, where P_z accounts for the larger than expected number of zero recruits presented in the recruitment plots. The likelihood of observation Y_i given parameters theta is therefore:

[6]

$$\text{Prob}\ (Y_i \mid \Theta) = \begin{cases} P_z + (1 - P_z)Poisson(0|\Theta) if Y_i = 0, \\ (1 - P_z)Poisson(Y_i|\Theta) if Y_i > 0 \end{cases}$$

A large number of recruitment plots with zero seedlings can typically occur (ex. Benavides *et al.*, 2015) and consequently using a zero-inflated parameter avoids underestimating the total number of zeros found in the recruitment plots, as well as the over estimation of large count occurrences. We also tried with P_z set to zero to ensure all possible model combinations were tested (Table 3.1). Our analysis was performed on the most common boreal; *Abies balsamea* - ABBA and *Betula* papyrifera – BEPA, and temperate; *Acer* rubrum - ACRU, *Acer saccharum* –ACSA, *Betula alleghaniensis* -BEAL, *Populus tremuloides* POTR, and *Fagus grandifolia* - FAGR canopy tree species present at each site, which together accounted for 69.9% (Abitibi), 84.4% (Le Bic), and 94.5% (Sutton) of the total overstorey canopy basal area. (Note: Only ABBA, ACSA, and BEPA were present at all three sites)

We estimated seedling density strictly for plots that were at least 20.0m from the boundary of the mapped areas to avoid potential edge effects (Bin et al. 2011). We performed two separate dispersal analyses to evaluate the influence of long-distance dispersal: (i) a clipped analysis, where only parent trees within 20m of the recruitment plot centre were used, and (ii) a non-clipped analysis, where all parent trees within the mapped permanent plot were included for dispersal kernel estimations. Finally, we set the substrate favourability of grass, solid logs, rock, and canopy bole cover to 0 as they either had minimal coverage (<1%) within the recruitment plots overall or are inhibiting recruitment for obvious reason, and thus were not estimated in any of the analysis performed.

Maximum likelihood estimates were obtained with simulated annealing implemented in the GenSA package (Xiang *et al.*, 2013) of the statistical platform of R (R Development Core Team 2016).

Table 3.1. Summary of models tested by the inclusion of contributing factors (zero-inflation, fecundity, dispersal, substrate favourability, and neighborhood). The total number of models evaluated also includes the clipped and non-clipped versions of each of the models below, as well as the lognormal and exponential dispersal kernels.

Model ID	Distribution (Pz)	Fecundity (STR)	Dispersal	Substrate Favourability (f)	Neighborhood (P_b)
$A_{(NULL)}$	NO	YES	NO	NO	NO
B	YES	YES	NO	NO	NO
C	YES	YES	YES	NO	NO
D	YES	YES	NO	YES	NO
E	YES	YES	YES	YES	NO
F	YES	YES	NO	NO	YES
G	YES	YES	YES	NO	YES
H	YES	YES	NO	YES	YES
I	YES	YES	YES	YES	YES
J	NO	YES	NO	NO	NO
K	NO	YES	YES	NO	NO
L	NO	YES	NO	YES	NO
M	NO	YES	YES	YES	NO
N	NO	YES	NO	NO	YES
O	NO	YES	YES	NO	YES
P	NO	YES	NO	YES	YES
Q	NO	YES	YES	YES	YES

3.3.3.4 *Final Model selection and Confidence Intervals*

We first ran the null model [model A; Table 3.1), which was then tested against all possible model combinations [models B through Q; Table 3.1) for a given species, recruitment stage, site, clipped, and non-clipped dispersal. The Akaike's Information Criterion (AIC) was computed and models with the lowest AIC were assumed to be the best approximating. The McFadden adjusted Pseudo R^2 (Seghiri *et al.*, 2012) was also calculated against the null model to ensure the best final model selection. Confidence intervals were computed for each parameter by outputting the set of all estimates used in the annealing process, where on average it resulted in at least 100,000 set of parameters for each model. We then excluded the sets of values which the log-likelihood exceeded the critical value of the X^2 distribution ($\alpha = 0.05$ df = 1), where the minimum and maximum parameter values from the remaining sets (i.e., 95% confidence limits; see Caspersen and Sprunoff 2005). Below we report the best models fit for each species, recruitment stage, and site combination regardless if it was a clipped or non-clipped model for both the 2015 and 2016 seedling density data.

3.4 Results

3.4.1 *Substrate Distribution*

Our RDA analysis supported our first prediction as we found an association between the distribution of boreal canopy trees and the distribution of certain substrates at all our sites (Figures 3.1-3.3). The RDAs were all significant ($p \leq 0.001$), although they only explained between 3.2% (Le Bic) and 14.6% (Sutton) of the total variation in substrate distribution. First, we found a positive association between temperate canopy trees (ACRU, ACSA, and FAGR) and leaf coverage, and another between boreal trees (ABBA and BEPA) with needle and decayed wood coverage (Figures 1-3). These relationships were particularly apparent at the Sutton site, where an elevational gradient caused a more distinct separation in substrate cover and overstorey canopy composition (Figure 3.3).

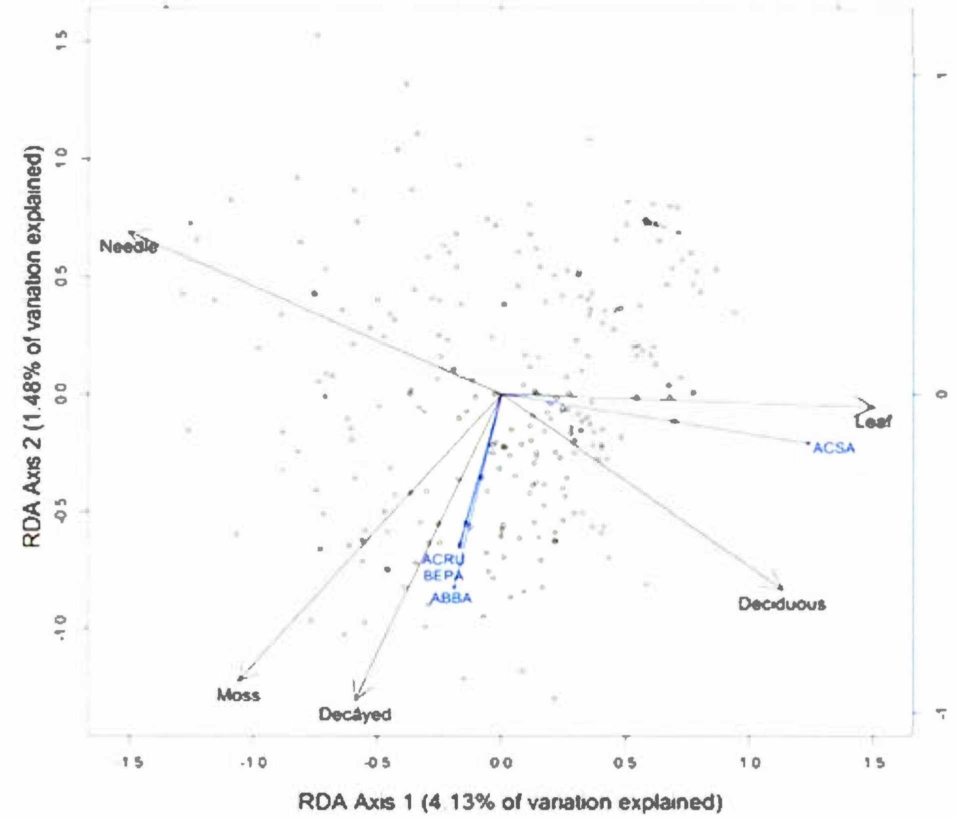


Figure 3.1. Redundancy Analysis (RDA) presenting symmetric scores (scaling =3) for overstorey canopy basal area and substrate coverage Abitibi (Adjusted $R^2 = 0.049$, $F= 4.27$, p-value = 0.001). Circles indicate recruitment plots, where the angles between the substrate variable and the explanatory variables reflect their correlations.

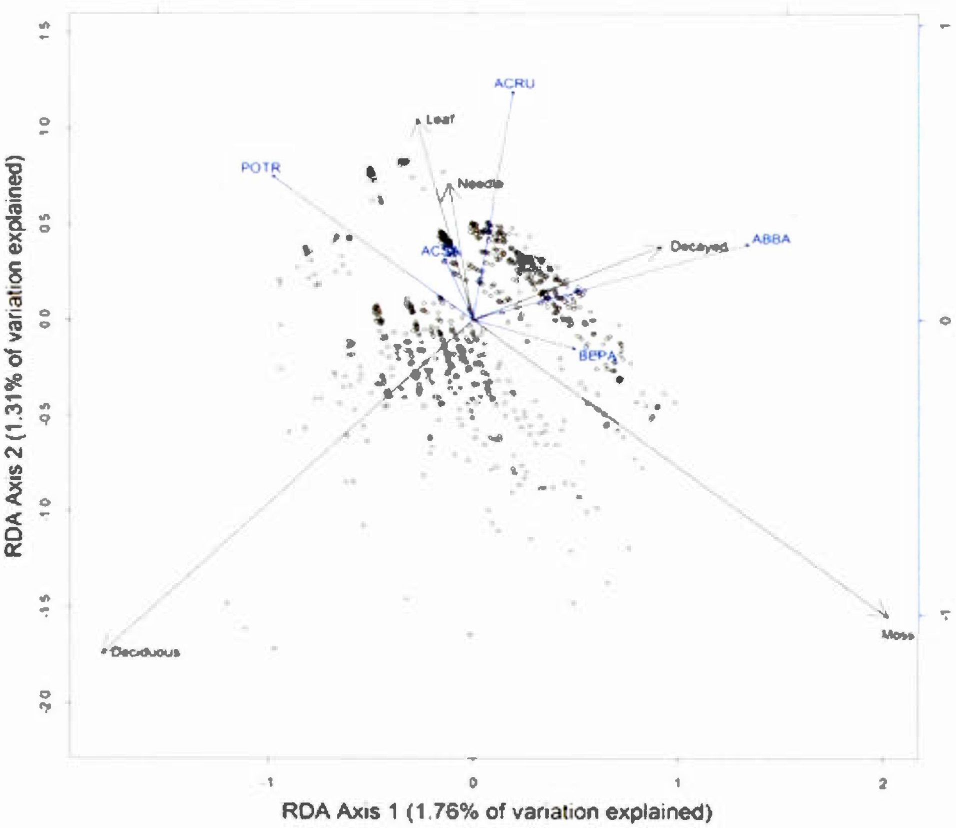


Figure 3.2. Redundancy Analysis (RDA) presenting symmetric scores (scaling =3) for overstorey canopy basal area and substrate coverage at Le Bic (Adjusted R^2 = 0.032, F= 6.16, p-value = 0.001). Circles indicate recruitment plots, where the angles between the substrate variable and the explanatory variables reflect their correlations.

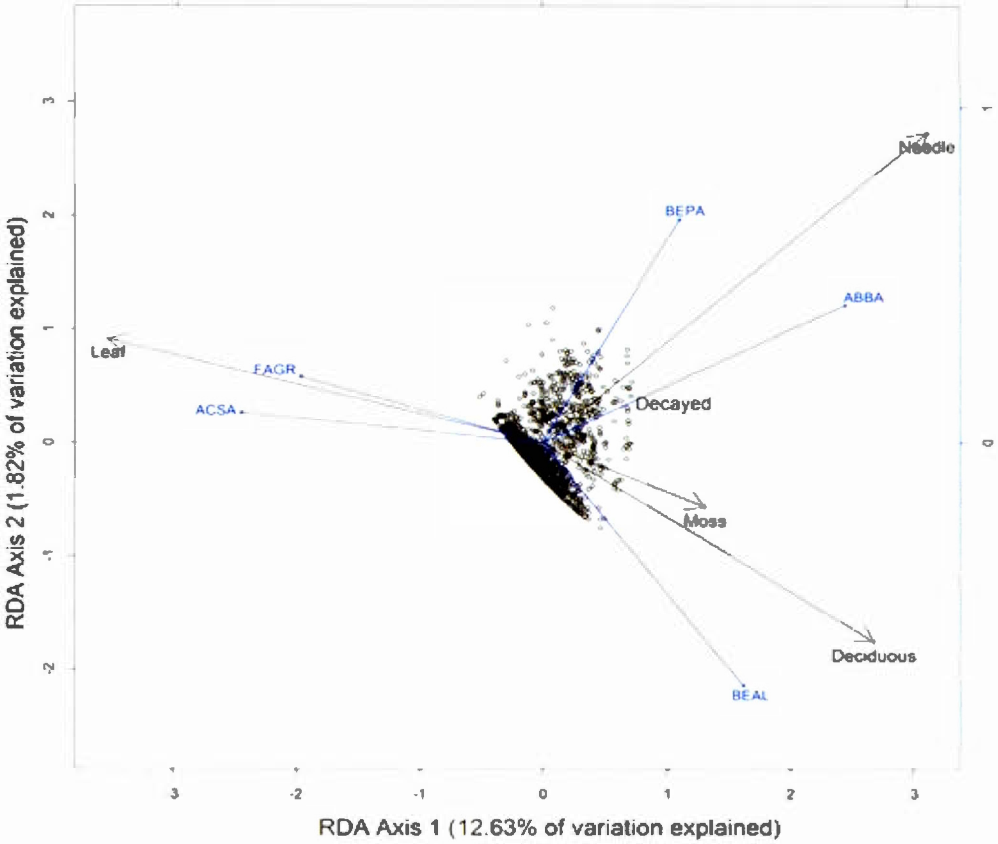


Figure 3.3. Redundancy Analysis (RDA) presenting symmetric scores (scaling =3) for overstorey canopy basal area and substrate coverage at Sutton (Adjusted R^2 = 0.1458, F= 53.39, p-value = 0.001). Circles indicate recruitment plots, where the angles between the substrate variable and the explanatory variables reflect their correlations.

3.4.2 *Model Fit*

Model fit differed across tree species, recruitment stages, site, and year, where the McFadden pseudo R^2 ranged from 0.0319 to 0.7331 (Table 3.2). Overall, model fit was slightly higher at Le Bic (0.3225) than the Abitibi (0.2645) and Sutton (0.2498) sites. Little change occurred in model fits between 2015 and 2016 at Abitibi (2015: 0.2521 and 2016: 0.2844) and Le Bic (2015: 0.3359 and 2016: 0.3091), however, models were nearly a third the accuracy in 2016 (0.1208) than in 2015 (0.3788) at Sutton. These differences were found to be especially apparent when considering recruitment stage, where model fit was better for the 2015 assessment year (stage 1: 0.4511 and stage 2: 0.3209) than those which occurred in the 2016 assessment (stage 1: 0.1557 and stage 2: 0.0930) overall - outlined by much higher presence of seedlings (Table AC1). Species specific recruitment models performed best overall for ACSA ($R^2 = 0.3521$) and worst for ABBA ($R^2 = 0.2111$) amongst the tree species which were present across all three sites. For species present within only one or two sites, POTR at Le Bic ($R^2 = 0.4115$) had the best fit overall across recruitment stage and years, while BEPA at Abitibi had the poorest ($R^2 = 0.0988$) (Table 3.2).

Table 3.2. Maximum likelihood estimates of the most parsimonious recruitment models by species, recruitment stage (Stage 1: 1st year seedlings, Stage 2: Older seedlings), year, and site. Model ID includes specific dispersal kernel in subscript; lognormal ($_L$), exponential ($_E$), and lognormal-clipped ($_{LC}$), exponential-clipped ($_{EC}$). NC: model did not converge, NS: non-significant.

Abitibi					
Stage		1		2	
Year		2015	2016	2015	2016
ABBA	Model ID	I_{LC}	K_L	E_{LC}	G_E
	McFadden R^2	0.2660	0.3136	0.3362	0.2038
	AIC	395.83	24.43	861.57	523.22
	Zero-Inflated	0.7285	0.8016	0.6438	0.6581
	STR	4600.1	1.7	2535.3	614.0
	MDD	9.72	13.7	10.5	23.8
	SHAP/SCAL	9.7/0.08	13.4/0.00	10.5/0.06	20.0/1.41
	Neighborhood	0.4644	NS	NS	0.3433
ACRU	Model	C_L	NC	D	B
	McFadden R^2	0.2723		0.2117	0.2648
	AIC	419.14		728.41	656.77
	Zero-Inflated	0.7351		0.5273	0.6619
	STR	435.3		12.0	2.8
	MDD	22.7		NS	NS
	SHAP/SCAL	20.0/0.50		NS	NS
	Neighborhood	NS		NS	NS
ACSA	Model	C_L	C_{LC}	E_L	C_L
	McFadden R^2	0.3481	0.2959	0.3849	0.2959
	AIC	290.18	44.11	961.36	704.46
	Zero-Inflated	0.7600	0.8742	0.4268	0.4241
	STR	190.6	33.7	2288.7	318.57
	MDD	18.3	14.1	22.5	21.6
	SHAP/SCAL	16.2/0.49	14.1/0.01	20.0/0.48	20.0/0.40
	Neighborhood	NS	NS	NS	NS
BEPA	Model	C_{LC}	NC	B	NC
	McFadden R^2	0.0865		0.1112	
	AIC	31.85		121.05	
	Zero-Inflated	0.5480		0.9106	
	STR	1.2		0.7	
	MDD	8.8		NS	
	SHAP/SCAL	8.7/0.04		NS	
	Neighborhood	NS		NS	

Table 3.2 (continued)

Le Bic					
Stage		1		2	
Year		2015	2016	2015	2016
ABBA	Model ID	C_{LC}	B	E_{LC}	E_L
	McFadden R^2	0.2971	0.0511	0.2859	0.1521
	AIC	172.01	245.97	364.95	424.29
	Zero-Inflated	0.8868	0.7309	0.6695	0.5463
	STR	64.5	0.6	1666.5	1014.8
	MDD	18.2	NS	12.9	15.9
	SHAP/SCAL	18.1/0.00	NS	12.9/0.01	14.9/0.37
	Neighborhood	NS	NS	NS	NS
ACRU	Model	H	E_E	D	C_L
	McFadden R^2	0.3747	0.3706	0.4274	0.3047
	AIC	563.97	4446.16	273.44	255.76
	Zero-Inflated	0.7344	0.3787	0.8202	0.8570
	STR	83.7	22318.5	46.2	259.8
	MDD	NS	17.0	NS	8.2
	SHAP/SCAL	NS	15.2/1.51	NS	7.6/0.39
	Neighborhood	0.2053	NS	NS	NS
ACSA	Model	D	E_L	D	D
	McFadden R^2	0.5317	0.3759	0.1396	0.2268
	AIC	271.50	998.21	234.61	236.21
	Zero-Inflated	0.8965	0.5210	0.7257	0.8393
	STR	24.4	7592.3	17.0	13.8
	MDD	NS	32.2	NS	NS
	SHAP/SCAL	NS	19.9/0.98	NS	NS
	Neighborhood	NS	NS	NS	NS
BEPA	Model	NC	C_L	G_L	K_L
	McFadden R^2		0.3513	0.2745	0.4080
	AIC		112.08	96.80	27.25
	Zero-Inflated		0.9411	0.7731	NS
	STR		521.9	1911.4	14.8
	MDD		19.7	15.0	43.1
	SHAP/SCAL		19.7/0.02	15.0/0.05	0.01/4.09
	Neighborhood		NS	1.0504	NS
POTR	Model	K_{LC}	NC	C_{LC}	K_{LC}
	McFadden R^2	0.5260		0.1668	0.5417
	AIC	17.49		108.37	8.00
	Zero-Inflated	NS		0.8533	NS
	STR	3.03		72.9	0.2
	MDD	7.0		10.8	6.9
	SHAP/SCAL	7.0/0.0		10.5/0.26	6.9/0.0
	Neighborhood	NS		NS	NS

Table 3.2 (continued)

Sutton					
Stage		1		2	
Year		2015	2016	2015	2016
ABBA	Model ID	NC	NC	C_L	K_L
	McFadden R^2			0.1188	0.0871
	AIC			46.72	31.83
	Zero-Inflated			0.8896	NS
	STR			586.9	37.5
	MDD			12.5	20.0
	SHAP/SCAL			11.6/0.40	20/0.04
	Neighborhood			NS	NS
ACSA	Model	H	E_L	E_L	E_L
	McFadden R^2	0.4371	0.3906	0.4744	0.2758
	AIC	1044.17	375.03	532.21	375.03
	Zero-Inflated	0.5768	0.7914	0.7779	0.5858
	STR	298.1	1104.2	1847.2	779.1
	MDD	NS	104.9	20.1	18.9
	SHAP/SCAL	NS	19.9/1.82	19.9/0.10	14.0/0.78
	Neighborhood	0.5373	NS	NS	NS
BEPA	Model	B	A	K_{LC}	A
	McFadden R^2	0.7331	0.0000	0.5417	0.0000
	AIC	20.74	34.68	8.00	258.41
	Zero-Inflated	0.9961	0.6843	NS	NS
	STR	6.0	0.0	2.3	0.0
	MDD	NS	NS	19.1	NS
	SHAP/SCAL	NS	NS	19.1/0.0	NS
	Neighborhood	NS	NS	NS	NS
BEAL	Model	Z·F	Z·F	Z·N	Z
	McFadden R^2	0.4203	0.0942	0.1554	0.0319
	AIC	142.65	247.94	89.68	99.02
	Zero-Inflated	0.9286	0.7239	0.9276	0.8754
	STR	42.1	1.1	9.1	0.4
	MDD	NS	NS	NS	NS
	SHAP/SCAL	NS	NS	NS	NS
	Neighborhood	NS	NS	1.1479	NS
FAGR	Model	C_L	C_{LC}	D	E_L
	McFadden R^2	0.2140	0.1381	0.3146	0.0700
	AIC	380.12	115.55	429.02	364.68
	Zero-Inflated	0.6812	0.7776	0.7417	0.4180
	STR	107.7	28.6	40.0	177.1
	MDD	7.7	6.7	NS	36.3
	SHAP/SCAL	6.9/0.46	6.7/0.13	NS	14.8/1.34
	Neighborhood	NS	NS	NS	NS

3.4.3 *Substrate Favourability*

We found that the favourability of certain substrates directly influence the distribution of seedling densities, and thus supported our second prediction. Overall, 21 of the final 56 recruitment models included substrate favourability (Table 3.2), where the relative influence differed amongst sites, recruitment stages, species, and years (Table 3.3). However, we found only a few consistent results concerning the favourability of substrates. First, temperate tree seedling densities were significantly and negatively impacted by the presence of boreal associated substrates: needle cover (ACRU: *f* = 0.1077, ACSA: *f* = 0.013, BEAL: *f* = 0.0378, and FAGR: *f* = 0.0431) and decayed wood (ACRU: *f* = 0.1454, ACSA: *f* = 0.1302, and FAGR: *f* = <0.001). Interestingly, ABBA, was favoured by these two conspecific substrates (needle *f* =0.3104 and decayed wood *f*=0.6573), at least at the Abitibi site. Second, we found that temperate canopy associated substrate: leaf cover, to be extremely unfavourable for boreal species (*f = 0.1838)* and certain temperate species (ACRU: *f* = 0.2120 and ACSA: *f* = 0.1673), but not others (BEAL: *f* = 0.4861 and FAGR: *f* = 0.3583) (Table 3.3). Finally, regardless of species, we found that the single best predictor of tree seedling densities was the presence of deciduous plant cover within the recruitment plots (global average across species, *f* = 0.5890). Deciduous plant cover overall was much more favourable across species at both Abitibi (site avg. *f* = 0.8849) and Le Bic (site avg. *f* = 0.7808), but was unfavourable at Sutton (site avg. *f* =0.2253). Deciduous plant cover was also found to be more favourable across all species for stage 2 recruitment than stage 1, particularly at Le Bic (1: *f* = 0.6964 and 2: *f* = 0.8483) and Sutton (1: *f* = 0.0812 and 2: *f* = 0.3694) (Table 3.3).

Table 3.3. Summary of substrate favourability for the most parsimonious models by species, seedling stage, year, and site. BEPA and POTR are absent as substrate favourability was not included within the final model selections for these species. 95% confidence limits of parameter estimates are (in parenthesis). NC: model did not converge, NS: non-significant.

Substrate Favorability		Abitibi				Le Bic				Sutton			
		Stage 1		Stage 2		Stage 1		Stage 2		Stage 1		Stage 2	
		2015	2016	2015	2016	2015	2016	2015	2016	2015	2016	2015	2016
ABBA	moss	0.361 (0.009-1.0)	NS	<0.001 (0.0-0.267)	NS	NS	NS	<0.001 (0.0-0.042)	0.230 (0.083-0.477)	NC	NC	NS	NS
	needles	0.406 (0.025-0.994)		0.215 (0.025-0.548)				0.013 (0.002-0.021)	<0.001 (0.0-0.050)				
	leaves	0.148 (0.037-0.623)		0.507 (0.080-0.919)				0.047 (0.043-0.092)	0.033 (0.014-0.079)				
	deciduous	0.976 (0.799-0.999)		0.566 (0.060-0.999)				0.993 (0.935-1.0)	0.999 (0.646-1.0)				
	decayed	0.464 (0.095-0.999)		0.850 (0.125-1.0)				0.0393 (0.002-0.144)	<0.001 (0.0-0.240)				
ACRU	moss	NS	NC	<0.001 (0.0-0.441)	NS	0.026 (0.0-0.201)	0.238 (0.077-0.380)	<0.001 (0.0-0.026)	NS	Species Absent			
	needles			0.242 (0.006-0.677)		0.077 (0.013-0.156)	0.112 (0.033-0.188)	<0.001 (0.0-0.015)					
	leaves			0.563 (0.150-0.991)		0.016 (0.0-0.079)	0.235 (0.083-0.352)	0.034 (0.014-0.069)					
	deciduous			0.998 (0.189-0.999)		0.809 (0.141-1.0)	0.976 (0.354-1.0)	0.999 (0.479-1.0)					
	decayed			0.348 (0.003-0.992)		0.232 (0.024-0.722)	<0.001 (0.014-0.243)	<0.001 (0.0-0.030)					
ACSA	moss	NS	NS	<0.001 (0.0-0.122)	NS	0.352 (0.012-1.0)	<0.001 (0.0-0.055)	0.0015 (0.0-0.132)	<0.001 (0.0-0.543)	0.067 (0.0-0.030)	<0.001 (0.0-0.280)	0.999 (0.151-1.0)	0.999 (0.344-1.0)
	needles			<0.001 (0.0-0.043)		<0.001 (0.0-0.183)	0.104 (0.005-0.234)	<0.001 (0.0-0.041)	<0.001 (0.0-0.274)	0.096 (0.0-0.256)	<0.001 (0.0-1.0)	<0.001 (0.0-0.622)	0.002 (0.0-0.877)
	leaves			0.277 (0.021-0.481)		0.151 (0.093-1.0)	0.180 (0.022-0.330)	0.008 (0.003-0.081)	0.113 (0.015-0.999)	0.067 (0.063-0.174)	0.190 (0.015-0.400)	0.235 (0.084-0.434)	0.286 (0.08-0.877)
	deciduous			0.999 (0.100-1.0)		<0.001 (0.0-0.999)	0.999 (0.132-1.0)	0.252 (0.160-1.0)	0.998 (0.154-1.0)	0.981 (0.212-1.0)	0.972 (0.0-0.596)	0.981 (0.183-1.0)	<0.001 (0.0-0.245)
	decayed			<0.001 (0.0-0.2575)		0.045 (0.0-1.0)	<0.001 (0.0-0.136)	0.015 (0.0-0.307)	<0.001 (0.0-1.0)	0.109 (0.096-0.293)	0.998 (0.060-1.0)	<0.001 (0.0-0.247)	<0.001 (0.0-0.245)
BEAL	moss	Species Absent				Species Absent				0.601 (0.138-0.999)	<0.001 (0.0-0.999)	NS	NS
	needles									0.076 (0.0-0.770)	<0.001 (0.0-0.995)		
	leaves									<0.001 (0.0-0.043)	0.972 (0.003-1.0)		
	deciduous									0.141 (0.046-0.316)	<0.001 (0.0-0.999)		
	decayed									0.999 (0.248-1.0)	<0.001 (0.0-0.999)		
FAGR	moss	Species Absent				Species Absent				NS	NS	<0.001 (0.0-0.124)	0.272 (0.0-0.999)
	needles											0.043 (0.196-1.0)	<0.001 (0.0-0.999)
	leaves											0.069 (0.014-0.087)	0.649 (0.269-1.0)
	deciduous											<0.001 (0.0-0.029)	0.497 (0.054-0.999)
	decayed											<0.001 (0.0-0.044)	<0.001 (0.0-0.999)

Substrate favourability was consistent across years for most species and recruitment stages. However, certain exceptions did exist. For example, deciduous plant cover was unfavourable for both recruitment stages of ACSA at Le Bic in 2015 (f<0.2500), but then became favourable in 2016 (f= 0.9999). The opposite can also occur, with deciduous plant cover favourable in (2015: f= 0.981) for stage 2 ACSA but not in 2016 (f<0.001) (Table 3.3).

3.4.4 *Seedling dispersal*

Dispersal was found to be a key driver of tree seedling recruitment as it was included within 31 of the final 56 models (Table 3.2). We found that mean distance dispersal (MDD) for the most parsimonious models, regardless of the clipped or non-clipped dispersal analyses, was within 20m when averaged across all factor combinations (Figure 3.4, Table 3.2). Overall, ACSA had the longest MDD by species on average (31.6m), POTR the shortest (8.2 m), while all other species generally were around 15.0m (Table 2). We found that the lognormal dispersal kernel provided a much better fit (29 out of 31) than the exponential kernel (Table 3.2). The non-clipped analysis was favoured in 20 of the final 31 models, particularly by *Acer* species (10 non-clipped versus 1 clipped). Seedling dispersal of ABBA (4:5), BEPA (2:3), and FAGR (1:2) showed no preference for clipped or non-clipped dispersal (MDD was well within 20m for these species). POTR favoured the more localized recruiting clipped analysis (0:3) (Table 3.2).

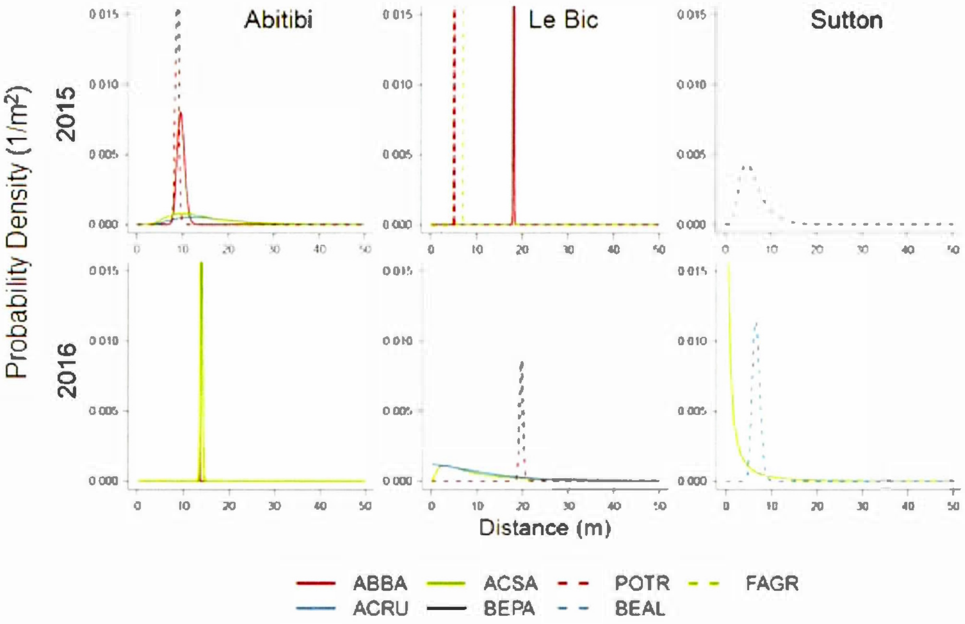


Figure 3.4. The estimated dispersal kernel for the most parsimonious model around parent trees for each of the seven tree species analyzed by site and year for first year seedlings.

3.4.5 *Neighborhood*

We found very little support for the influence of hetero-specific neighborhood (<20.0 m of recruitment plot centre). The effect of neighborhood was significant in only 6 of the 56 total models (Table 3.2), where the influence of neighborhood composition (as indicated by high *Pb* estimate) on recruitment was weak (*Pb* < 1.11, Tables 3.2 and AC1). We found no clear relationship with site, species, nor recruitment class or year of assessment.

3.5 Discussion

Our study linked fecundity, seedling dispersal, substrate favourability, and local neighborhood as a means of explaining the recruitment of seven tree species at the temperate-boreal ecotone of northeastern North America. We provide novel evidence that priority effects are inhibiting the recruitment of temperate tree species into the boreal forest. Our findings suggest that the relative strength of the priority effects imposed on temperature tree species is however dependent on the site, species, recruitment stage, and year. The variability amongst our models reveals the difficulty of modelling seedling recruitment (Caspersen and Sprunoff 2005; Bin *et al.,* 2011; Benavides *et al.,* 2015). Nonetheless, our extensive dataset and models allowed us to outperform (~28.0% of total variation explained) those who ran similar recruitment studies (Bin *et al.,* 2011).

3.5.1 *Substrate Favourability*

We found an association between the distribution of certain microsites and canopy tree composition. Substrate and its subsequent favourability were associated with a higher frequency of needle and decayed wood under boreal tree canopies, particularly in the presence of ABBA and BEPA (Figures 3.1-3.3). Our results confirm our hypothesis that priority effects from boreal species create substrates that ultimately impede the recruitment of temperate tree species. The first boreal type of substrate, needle cover, was particularly efficient at inhibiting recruitment of temperate tree species, in particular for maples ($f = 0.1150$). Typically, boreal forest substrates are characterized as being thick, acidic, and drier when compared within other forest floors (Collin 2017). Further, they can also have lower availability of nutrients (i.e., Ca, N, and Mg; Zak *et al.,* 1999; Collin 2017). ACSA has been shown to be particularly sensitive to nutrient availability, leading to declines in health and growth at the seedling stages (St.Clair *et al.,* 2008; Collin *et al.,* 2017). Albeit that needle cover causes significant changes to the recruitment environment for temperate tree seedlings, it was found to be more favourable ($f = 0.4064$) for first year seedlings of ABBA. Improved boreal recruitment on heavy needle cover highlights a preference for conspecific replacement (Rooney *et al.,* 2000), and could further impede temperate tree species migration by limiting microsite availability.

Unlike previous studies (ex. LePage *et al.,* 2000; Caspersen and Sprunoff 2005), we found that decayed wood was generally an unfavourable substrate for all temperate species, with the exception of one instance ($\text{ACSA}_{\text{stage2}}$, Sutton - 2016). We were surprised by this finding as decayed wood has long been cited as an extremely favourable, safe site for seedling recruitment within both temperate and boreal sites (Harmon *et al.,* 1986; Marx and Walters 2008). Interestingly, decayed wood was a favourable substrate for the smaller seeded tree species (ABBA and BEAL) within our study, which is consistent with other studies (ex. Caspersen and Sprunoff 2005; Marx and Walters 2008; Lambert *et al.,* 2016) (Table 3.3). Decayed wood can provide a beneficial substrate for these species as it is easier for their smaller radical to penetrate the softer medium. Decayed wood has also been shown to contain beneficial fungi (Fukasawa 2012), improved moisture and nutrient content, and even improve substrate temperature resulting in improved growth (Tedersoo *et al.,* 2008). Despite this affinity for decayed wood by ABBA and BEAL (Simard *et al.,* 2003), we highlight the difficulty in making global favourability conclusions as we found variation across years. For example, decayed wood was found to be a strong inhibitor ($f = 0.1091$) for $\text{ACSA}_{\text{stage1}}$ at Sutton in 2015, however, it became a highly favourable substrate ($f = 0.9979$) the following year, which was opposite of what we found for BEAL (Table 3.3). The low favourability of decayed wood for maples (ACRU and ACSA) may be due to a few reasons: (i) while decayed wood may be a preferred substrate for germination, it could become less favourable for subsequent growth and survival due to potentially poorer nutrient availability over time for large seeded species, (ii) the species of decayed wood is unfavourable; Marx and Walters (2008) showed that seedling growth and density can be directly influenced by the species of decayed wood it establishes upon, where nitrogen concentrations and mineralization rates can vary considerably between species of decayed wood. Similarly, Lambert *et al.,* (2016) showed that although conifer and birch decayed wood was found to be highly favourable for BEAL, maple decayed wood was not.

The best single predictor of tree seedling density across species and sites within the temperate-boreal ecotone was the presence of deciduous plant cover within our recruitment plots (Table 3.3). All species (exception of BEAL) were found to be positively associated to the presence of deciduous vegetation. These finding have been reported in other recruitment studies (Ibanez *et al.,* 2015; Benavides *et al.,* 2015), where the vegetative cover have been shown to improve tree seedling emergence and survival by offering shade and reducing transpiration demands (Muhamed *et al.,* 2013; Walters *et al.,* 2016). Further, it has also been suggested as providing protection from early spring frosting events (Morin and Chuine 2014), and refuge from herbivory (Cebriàn and Duarte 1994; Solarik *et al.,* 2010; Walters *et al.,* 2016). These benefits could play an extremely important role, particularly in the context of populations at the range margin as seedlings within the ecotone are already exposed to higher environmental variability (Boulangeat *et al.,* 2012), and these added benefits could improve survival within these marginal conditions (Castro *et al.,* 2004). On the contrary, an increased presence of deciduous cover could also impede early seedling recruitment through the direct competition for nutrients, light, and water (George and Bazzaz 1999; Davis *et al.,* 1999), which would ultimately reduce growth and survival of seedlings and saplings (Fei and Steiner 2008; Walters *et al.,* 2016). We have some evidence for this with $ACSA_{stage1}$ ($f = 0.2959$), however favourability of deciduous cover improved greatly for older ACSA seedlings ($f = 0.6460$). Although we did not directly measure light, we assume that the increased presence of deciduous plant cover within our recruitment plots was due to higher light availability caused by gaps in the canopy (Schumann *et al.,* 2003). Although Caspersen and Sprunoff (2005) failed to find a consistent argument for light limitation within their recruitment study, they were able to conclude that seedling densities of ABBA and ACSA declined with decreasing light availability. Similarly, Gasser *et al.,* (2010) found declining density of ACSA and BEAL seedlings with decreasing light availability. The distribution of vegetation could indicate the variability in light availability, and therefore influence the transition of first year seedlings to older seedlings (Messier *et al.,* 1998; Benavides *et al.,* 2015; Walters *et al.,* 2016).

3.5.2 *Seedling Dispersal*

Increased dispersal is generally expected to evolve through natural selection at expanding range margins (Hargreaves and Eckert 2014), especially if the ranges are dynamic and not static (Sexton *et al.,* 2009). Although there is evidence of long distance dispersal events occurring in the past (Clark *et al.,* 1998), like others (Ribbens *et al.,* 1994; LePage *et al.,* 2000; Caspersen and Sprunoff 2005; Fiscihelli *et al.,* 2013), we found that seedlings are establishing at distances within close proximity of their parents (Table 3.2, Figure 3.4). As a result, temperate tree species are at risk of significant migration lag. A shortened dispersal has been shown to promote the coexistence of tree species through the reduction of competitive exclusion (Hubbell *et al.,* 1999). However, if a species remains unable to disperse at greater distances, it will risk becoming maladapted to future climatic conditions (Kawecki and Ebert, 2004; Franks *et al.,* 2014). Species unable to disperse at rates comparable to the changing climate; suggested to being as much as 4.9km year^{-1} for ACSA (Boisvert-Marsh *et al.,* 2014), are at risk of being exposed to environmental conditions that could cause significant drop offs in fitness (Morin and Chuine 2014; Solarik *et al.,* 2016). On the contrary, although increasing dispersal distances provides an opportunity for greater range expansion, it also steepens the environmental gradient. For species with high MDD, expansion is limited by the adaptive plasticity of the species to these novel conditions (Gilbert *et al.,* 2017). As highlighted here, temperate tree species expanding further into the boreal forest will face higher occurrences of unfavourable substrates, which in turn can magnify the priority effects imposed by resident populations (Mohd *et al.,* 2016).

3.5.3 *Neighborhood*

We found little to no evidence that hetero-specific canopy trees within the local environment impact seedling density (Table 3.2). We suspect that this is due to the influence local neighborhood being captured within the favourability of substrates and the amount of light rather than the cumulative basal area of hetero-specific trees. However, the minimal influence of hetero-specific trees could suggest that they help minimize host specific enemies (i.e., seed predators, herbivory, pathogens), which have been shown to negatively affect conspecific recruitment (Moorcroft *et al.,* 2006; Pigot and Leather 2008; Ibáñez *et al.,* 2015). Perhaps the variability in canopy composition currently occurring in the ecotone offers a "middle of the road" compromise between boreal and temperate tree species, where the species better adapted to future climate conditions will eventually become dominant within these environments.

3.6 Conclusion

A combination of priority effects caused by a feedback of canopy trees on substrate distribution, and limited seedling dispersal, together highlight a conundrum for rapid migration of temperate tree species into the boreal forest. First, we found the presence of boreal trees in the canopy influenced the distribution of needle cover and decayed wood substrates. Then, together, these substrates inhibited the recruitment of temperate tree species, while favouring conspecific replacement. Second, we found that seedling dispersal was limited to areas in close proximity of parent trees. These results raise concerns about the species ability to maintain itself under new climatic conditions by tracking their climate optimums since the climate is changing more rapidly than they can move. In a recent modelling study by Vissault (2016), it was concluded that the temperate-boreal ecotone would eventually transition to exclusively temperate forest, with however, very little colonization of boreal forest by temperate tree species, even after considerable time (+10,000 years). Together, the modelling results and our empirical study would suggest that without major disturbances to alternative stable states might occur, at least for a long period of time, with the distribution of temperate and boreal forest frozen in time despite considerable climate change (Davis *et al.,* 1998). The evidence of priority effects imposed by boreal trees provides an explanation for the lack of rapid migration of tree species reported by Sittaro *et al.,* (2017). Ultimately, it should be expected that in the absence of forest management or a natural disturbance (i.e., fire or insect outbreak) that favour canopy gaps (Leithead *et al.,* 2010, 2012; Willis *et al.,* 2015), the rate of colonization/spread of temperate species into the boreal forest should be expected to lag considerably behind the rate of climate change (Aubin *et al.,* 2016). Finally, our results also highlight the difficulties in generalising the contributing factors that could limit tree recruitment within the transition zone since these systems show considerable variability amongst sites, recruitment stages, species, and years. Clearly, other factors not considered in this study could be involved or the processes involved are so strongly non-linear that deterministic chaos might be involved (Beninca *et al.,* 2015).

CONCLUSION

«Life is a pattern with complexity»
Alan Watts

Difficulties arise when trying to estimate the potential impacts climate change might have on the biosphere in the future, where considerable variability exists across scale and time. Further, the complexity associated with making future predictions based on these estimates can often cloud our understanding, analysis, and interpretation of the driving factors we believe to be controlling species response(s). Essentially, we can compare our efforts to trying to drive a car by always looking in the rear-view mirror, a difficult task needless to say, particularly when we know there is unforeseen turn or cliff ahead (i.e., climate change). One way to mitigate this problem (other than turning your head around) is to design research projects that are designed to use methods or approaches that incorporate conditions likely to occur in the future.

This thesis becomes timely in gathering some of the necessary information surrounding the influence of key abiotic and biotic factors associated with tree seedling recruitment in the context of species adaptation and migration under climate change. I thus, made a conscious effort into assessing a range of methods to address potential caveats or bottlenecks commonly overlooked, but critical to accurate assessment of a species ability to adapt to future environmental. Here, in the conclusion I summarize some of the new knowledge and key results discovered in this thesis, outline some limitations to conducting this research, then offer suggestions of potential alternatives that may be available to help speed up the natural rate of tree species migration under climate change. Finally, I will conclude with some perceived opportunities for future research in the context of species response, range dynamics, and the influencing factors driving these relationships.

In the first thesis chapter, the primary objectives included: (i) identifying the optimal sugar maple species-specific incubation temperature required to break seed dormancy and allow germination, (ii) identifying the impact a warmer or cooler temperature shift may have on seed germination during the incubation period (a means of mimicking potential earlier or later spring conditions in the future), and (iii) forecasting/projecting any potential changes in overall seed germination potential across the species range under three future climate warming scenarios projected for the end of this century. I was able to bring significant light to the potential deleterious impacts temperature could have on changing the likelihood of successful seed germination across a species range in a warmer future. While the effect of temperature has been done in a number of other studies for sugar maple (e.g. Webb and Dumboff, 1969; Simmonds and Dumboff, 1974; McCarragher *et al.,* 2011) to help identify the strict species specific requirements to break dormancy, it has typically been done under limited number of temperature and/or provenance treatments. Ultimately, by doing so, we minimize our ability to make species wide claims, thus I set out to test 287 independent temperature and temperature shifting treatments, and found that sugar maple indeed maintains a very narrow species-specific temperature breath (-1°C to 7°C) regardless of the seed's origins.

Collectively, the species has improved rates of germination when temperatures are near or below the freezing point (-1°C to +1°C), which is the lowest amongst all known forest tree species (Godman and Mattson 1981). Cumulative seed germination rates however, remained comparable until temperatures rise to, but not beyond 5.0°C. Beyond 5.0°C, any warmer temperature (regardless of provenance) causes significant declines in seed germination success (Figure 1.6), which was previously believed to occur at much higher temperatures (~10°C; Godman *et al.,* 1990; McCarragher *et al.,* 2011). Sugar maple's local adaptation associated with seed germination to temperature also showed a strong latitudinal trend, where northern provenances provided overall the best rates of cumulative germination, which collectively declined with the latitude of seed origin. On a positive note, although sugar maple's southern range had the lowest cumulative germination rates, these seeds were able to maintain comparable rates o germination under the warm shifting treatments; suggesting these seeds have likely adapted to much warmer and earlier spring conditions within the southern species ranges. In the context of climate warming, conditions at the northern ranges are likely to experience faster snow melt and reduced snow cover, which in turn could expose seeds and seedlings to higher temperature variability earlier in the season and may lead to severe maladaptation to warmer shifts in these populations (Price *et al.,* 2013; Mankin and Diffenbaugh, 2015). Collectively, having such variability amongst species response to germinate could benefit sugar maple under warmer conditions by providing evolutionary rescue (Gonzalez *et al.,* 2013) from its southern ranges. Finally, through the use of historical (1901-2010) average temperatures for the stratification months (March to May); I was able to forecast future seed germination under three future climate warming scenarios: +2°C, +5°C, and +7°C. By using these three scenarios, projections for significant declines across the species range are to be expected, where total losses of cumulative seed germination may be as high as 75% under the warmest scenarios (Table 1.6). Although these scenarios just consider temperature, and the drastic impact can be alleviated to some extent by other factors (i.e., precipitation), the conclusion remains clear: sugar maple possess seed which is locally adapted to temperature, and if increases in temperature, and fluctuations in temperature occur in early spring future, significant declines in overall recruitment should be expected (Walck *et al.,* 2011; Morin and Chuine 2014).

If the local environment is however, able to match the species specific requirements to ensure seed germination; often ignored when assessing a species' ability to establish (i.e., greenhouse grown seedlings are typically used) (Putnam and Reich 2016), the next bottleneck lies within the favourability of the local micro-environment (abiotic and biotic), which will help determine if the species is able to establish and persist over time (Walck *et al.,* 2011). To do so, I investigated the influence of site – which allowed for the simultaneous assessment of local climate and microsite by establishing a large-scale seed transplant experiment. Using the same seed provenances representing the entire sugar maple species range used in the first chapter, seeds were transplanted to 12 sites; representing three biomes: the current northern sugar maple species limit (temperate forest), at the species limit (temperate-boreal ecotone), and beyond (boreal forest) the current species limit. More specifically, the following predictions were made: (i) that southern seed provenances will be the most maladapted to the environmental conditions occurring at and beyond the current range limit (resulting in lower recruitment success), as they are the furthest in terms of proximity of their origins (provenance effect), (ii) early seedling establishment will be best within sites which meet the species specific climatic requirements needed to ensure seed germination (climate effect), and (iii) upon seedling establishment, local microsite conditions more closely resembling those within the range limit will favour higher survival rates (microsite effect).

Overall, I found that seed originating from the most northern portions of the species range provided the best opportunity for successful recruitment at and beyond their current range, which agrees with the first prediction (also coincides with the results of the first chapter). At least currently, sugar maple's best option to establishing from seed beyond its current range lies within the northern range populations, where the highest proportion of seeds germinated, established, and survived. The northern seed also had the largest seed mass; providing the best opportunity to establish a seedling regardless of the transplant site (Hewitt 1998). The increasing recruitment success of these seed origins, is likely due to the seed being preconditioned (i.e. locally adapted) to sites that are more climatically similar to those sites at and beyond their current range limit. Second, I found that sugar maple's recruitment was linked to climate, but more specifically the timing of specific temperatures, where the presence of first year seedlings was improved in sites which satisfied the species-specific stratification requirements to break seed dormancy (Table 2.4). Sites that did not match these species specific conditions had noticeable reductions in seedling establishment rates and these findings were particularly apparent within the temperate and mixedwood transplant sites. Shift ratio (stratification days to warm days) parameter; emphasizes the importance of meeting an equilibrium between the number of days required to break dormancy to those that are warming (daily mean of ≥7°C) (Figure 2.7). By shifting to warmer conditions following seed germination, seedlings are then able to establish on warmer soils (ideally moist as well due to snow melt), can begin photosynthesizing and gaining biomass (Walck *et al.,* 2011; Way and Montgomery 2014; Reich *et al.,* 2015). The influence of microsite pertained to our final prediction, which was that sugar maple would recruit better on sites more closely resembling those found within its species range. The influence of microsite on successful recruitment of tree seedlings has long been established (Jones 1945), and reinforced more recently (Caspersen and Sprunoff 2005; Bolton and D'Amato 2011). Ultimately, the relative importance of contributing microsite/substrate factors became gradually more important to the recruitment of sugar maple as we shift towards away from the temperate biome to the boreal - outlined by the number of microsite specific variables included in each of biome specific MRT analysis: temperate: 2x, mixedwood: 4x, boreal: 4x; which was also a highlight of my findings in the third chapter (Table 3.3). Together these findings suggest that when a species begins to get further in proximity from its origins that the likelihood of encountering more unfavourable substrates becomes more frequent and can further impede recruitment (i.e. priority effects). However, as I point out in the third chapter, it can be difficult to make global conclusions on substrate between years, sites, and species. Although there exists variability in favourability for certain factors/conditions for recruitment, I did find a number of consistencies within the second chapter. I found that sugar maple recruitment was highest when sites had less needle cover, higher soil pH, and generally when decomposed wood (coarse woody debris) was present. Overall, first year recruitment (includes germination and seedling establishment) was low (7.8%), especially considering that seed was ensured to having high variability (+95%) prior to transplanting. These much lower recruitment numbers emphasize the much stronger influence of the natural microclimate within the understorey (non-temperature variables) can be just as or more influential in determining the likelihood of seedling survival in the first few years (De Frenne *et al.,* 2013; Fisichelli *et al.,* 2014).

In the final chapter of the thesis, the investigation of the demography within the temperate-boreal ecotone was conducted for tree seedling recruitment for two stages (first year and older seedlings). As evidence for temperate tree migration should be detected first within these overlapping ecosystems, I again was interested in identifying the relative influence of a series of factors important to seedling recruitment; however, unlike what was done in the second chapter (transplanting seed), here in the third, I made inferences into the natural system. I hypothesized that boreal trees species were impeding the successful recruitment of temperate tree species through the imposition of priority effects. To evaluate this, I used a seedling distribution model that incorporated spatially explicit canopy and recruitment data from seven common tree species (*Abies balsamea, Betula papyrifera, Betula alleghaniensis*, *Acer saccharum*, *Acer rubrum*, *Populus tremuloides,* and *Fagus grandifolia*) to better identify the drivers (dispersal, substrate, and local neighborhood) of seedling recruitment with within three permanent plots that covered a cumulative area of approximately 34.4 Ha. I predicted that (i) boreal tree species would influence the spatial distribution of substrates within a stand, with which these substrated would then (ii) influence the seedling density of temperate tree species. Finally, I also predicted that seed dispersal would be limited, and thus magnifying priority effects imposed from boreal tree species.

It was found that boreal trees did in fact influence the distribution of substrates; in particular the presence of needle cover and decayed wood, which were both, deemed highly unfavourable substrates and affected seedling densities of all temperate tree species. Second, I found that seedling dispersal was highly localized, where mean dispersal for all trees occurred within very close proximity of parent trees. These results suggest that although long distance seed dispersal may be important in the context of species range migration (Clark *et al.,* 1998), it remains quite limited within the closed canopies which were assessed within this study. If we follow this in the context of keeping pace with climate change – for example, sugar maple must travel 4.9 km year^{-1} (Boisvert-Marsh *et al.,* 2014), using these values essentially means a seed should travel 196 km; assuming it takes approximately 40 years for the tree to reach reproductive maturity (Godman *et al.,* 1990) to compensate for the annual dispersal rate to reach maturity to produce another seed. Needless to say, this remains a far cry from the best long dispersal distances (Hewitt and Kellman 2002). As pointed out by a number of studies (Caspersen and Sprunoff 2005; Marx and Walters 2008; Kroiss and HillRisLambers 2015), substrates play a key role in influencing the success of tree seedling recruitment, however, I found that the relative benefits of one global "best" substrate did not exist, and was highly dependent on the species, recruitment stage, and site in question, suggesting that the recruitment niche of species is highly dependent on site factors. However, we did find that the cover of deciduous vegetation cover did provided the best predictor of tree seedling recruitment, which could suggest that either competition is providing benefits (i.e., reducing water stress) (Montgomery et al. 2010) or may provide a proxy for better understorey light conditions.

The results from this thesis highlight the fact that the rate of potential migration of temperate tree species into the boreal forest is expected to lag significantly behind the rate of climate change. The combination of the time required to adapt to future conditions (if at all), current species specific thresholds associated with germination and substrate favourability, and the monopolization of key resources by boreal tree species (i.e. priority effects) all point to little change in species distributions in the latitudinal context that are being reported more frequently (Vissault 2016; Sittaro *et al.*, 2017).

4.1 *Research Limitations*

As in any research conducted, a number of potential pitfalls and limitations are identified once the research has concluded. Here, I would like to point out a few, which I believe are important to highlight. An important limitation which is always present when conducting research is **Time.** A research focus within forest ecology sometimes requires long-term studies to make accurate conclusions or projections, which is especially difficult when the subject (tree) is currently experiencing its response (climate change). The response time can be especially long (i.e. growth, survival, adaptation). Albeit that in forest research one can get around such long temporal scales through the use of dendrochronology, however, these methods cannot be applied to the earliest of life cycle events and stages. In this thesis, I am limited to the conclusions being made as the number of time sensitive inputs or factors can change annually. First, the seeds used in this research were collected from one year, which could have an impact on the quality and viability associated with inter-annual variability, which is linked to environmental conditions incurred by the parent trees. Second, a common issue associated with time is that academic research being conducted in forest ecology, biology, and environmental sciences are constrained to the time periods of higher education, which typically limited to 2-6 years. Evidently, this is a much shorter time period than those necessary to witness many of the important processes (e.g. seed production, growth, survival). Ideally, following the seedlings transplanted beyond their current range (Chapter 2) for a number of decades would provide a much clearer picture of the influence, adaptability, and resilience of sugar maple to establish long term beyond its species range limit. Third, as is the case when investigating seedling recruitment there exists a potential for rapid pulsation (present vs. absent). In other words, arriving at a site to count the number of germinated seedlings one week (one month or one year), could be absent the following week, which is a considerable disadvantage particularly when conducting latitudinal studies. **Scale:** is another important limitation, which is often a common caveat to interpreting important findings. Although in this research I predominantly focus on the individual seed or seedling to make inferences into landscape scale processes (migration), being able to incorporate processes occurring at different scales (e.g. nutritional state of individuals to interpret health status) would prove beneficial. The use of twelve transplant sites in chapter 2 and three sites in chapter 3 would have potentially added benefit if I would have considered three or four times as many sites (i.e., including sites beyond the southern species range), which would allow for greater interpretation of the variability associated within the natural system. Ultimately, by including different scales one may potential increase the accuracy of key processes used in cross-scale modelling approaches (Talluto *et al.*, 2015). **Factors.** Although I feel that I was able to investigate a wide range of contributing factors at early life stages, which help contribute to our understanding of determining recruitment in the context of species migration (Figure 4.1). I did knowingly leave out a number, which undoubtedly are known to contribute to seedling demographics. These included but are not limited to: precipitation, herbivory, predation (granivory), nutrient content (within seedling and soil), pathogens (above and below ground), and growth, all of which have been previously determined to impact seedling recruitment (Brown and Vellend 2014; Tingstad *et al.,* 2015; Foster *et al.,* 2016; Benavides *et al.,* 2016; Walters *et al.,* 2016) (Figure 4.1).

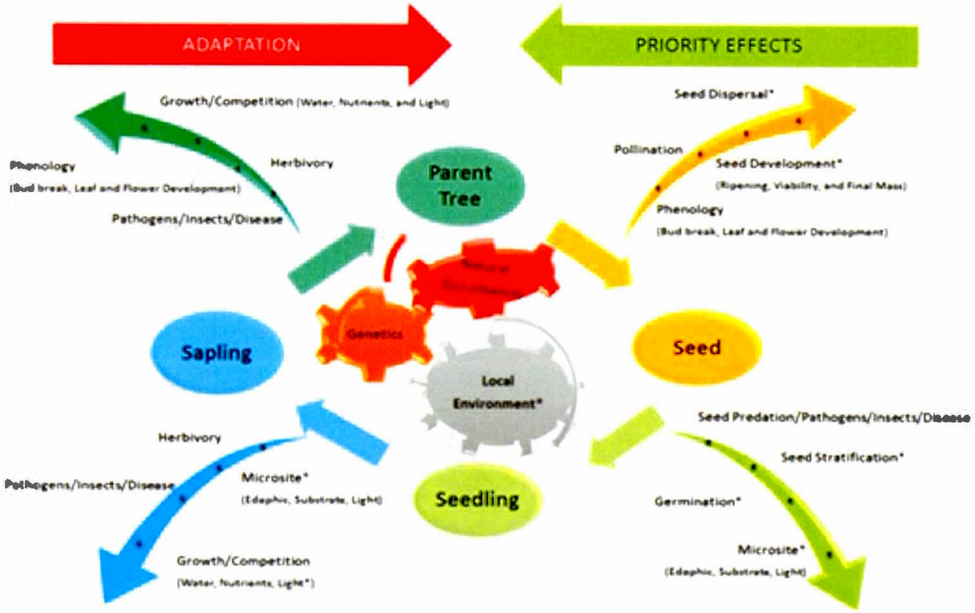


Figure 4.1. A conceptual framework for key life history cycle stages of a tree (parent tree-seed-seedling-sapling), which includes potential inhibiting factors to successfully reaching the next life stage. Additionally, the "inner" cogs infer the influence of overarching factors (natural disturbances, genetics, and local environment) that will simultaneously influence demographics. "Outer" arrows of adaptation and priority effects highlight supplemental factors influencing species migration. *Factors considered directly/indirectly within this thesis

4.2 *Speeding up Migration*

The results put forth in this thesis show strong evidence that sugar maple is currently constrained by its local adaptation to its environment, where its early life stages inhibiting rapid migration and is likely to continue in the future. In addition to the constraining effect local adaptation can have on slowing the migration of a potential invading species, it becomes even more constrained when resident species are imposing effects that further inhibit migration. As these two overarching factors (Figure 4.1) exist, human intervention may provide an opportunity to alleviate these potential stressors to some extent and speed up the natural process. **Assisted migration** – may provide an opportunity to improving tree species productivity and health by artificially moving (planting or seeding) a species to a more climatically friendly future location, which would by-pass a key constraint, dispersal; insufficient at overcoming a geographic barriers and insufficient distances obtained (Greene *et al.,* 2004; McLachlan *et al.,* 2007). The ethics of this management practice have been put into question in the past (Aubin *et al.,* 2011), however, it is a promising alternative as it is becoming increasingly evident that some tree species and certain populations are currently or will be in the future poorly adapted to conditions at their current locations (Hannah 2008). This alternative does not come without caveats, where placing species beyond certain physiological thresholds associated with the environment that would lead to significant declines in species health or adaptation that would make it a poor strategic option (O'Neil *et al.,* 2008). It thus will require careful consideration for picking an ideal target migration distance, which would ensure successful long term health prior to implementing an assisted migration practice (Williams and Dumroese 2013). **Forest management strategies** – favoring the recruitment of temperate tree species. Essentially, the removal of competing boreal trees, would reduce the amount of space inhabited (i.e. crowding) and minimize the delay of migration through the promotion of forest gaps; improving understorey canopy conditions (i.e., more light, and space) and favour recruitment of early successional species (Leithead *et al.,* 2010; Trever and Nowak 2011; Willis *et al.,* 2015; Walters *et al.,* 2016). Further, through the use of forest management, active and passive soil disturbance (i.e. scarification) could also improve the typically, cooler, poorer seed bed quality found within boreal stands (Moore et al. 1999), which would improve exposure of mineral soil that is often associated as a favourable substrate for recruitment (Solarik *et al.,* 2010; Lambert *et al.,* 2016). **Natural**

disturbances – may also provide a much needed boost for improving the ability of temperate tree species to migrate. It is expected that the intensity and frequency of disturbances to occur within the boreal forests of Canada, particularly for fire and insect outbreaks (dominant disturbance regimes in boreal forests of Canada), are expected to rise over the next century under climate change (Flannigan *et al.,* 2005; Price *et al.,* 2013). The northeastern boreal forests of Canada have already seen several large disturbance events over the past few decades causing considerable damage to the existing canopies (i.e. major ice storm, spruce budworm outbreaks, and fire). As with forest management practices discussed above, the removal of boreal canopy tree species will improve understorey conditions for facilitating the recruitment of temperate tree species. Again in the natural setting, the effect of a natural disturbance will be dependent on the type, size, severity, and historical regime of the disturbance and region in question, and thus will influence the species that will able to benefit (Fisichelli et al. 2013).

4.3 *Future Research*

Future research interested in looking at species response and fitness in regards to range shifts under climate change, will undoubtedly continue to face a difficult and daunting task, as the environment will be under constant flux. In order to better understand the driving factors controlling a tree species ability to adapt and adjust to future climatic conditions will require a number of considerable advances in a number of key research streams. Here I will outline some avenues, which I believe can greatly enhance our understanding of the driving factors influencing species range dynamics, tree life history stages, and their responses to climate change.

First, a more direct focus should be taken on identifying individual ***species specific thresholds*** associated growth, phenology, and fitness are critical (Figure 4.1). Detecting such tipping points associated with species specific physiological constraint(s) (e.g. optimum temperature for photosynthesis) to climate and their environment are critical in providing baselines for comparative assessments. Doing so will allow for a deeper understanding of how species performance and adaptive plasticity may play out in the future (Franks *et al.,* 2014). Identifying these thresholds should begin with those that may be controlling key life history stages (i.e. flower development, bud, break, seed production, seed viability, seed germination, growth, leaf development) as we see even within this thesis – where we investigated response of recruitment to a series of contributing factors (Figure 4.1).

Second, future research in parallel with determining species specific thresholds should also test **species response to potential future climate conditions or scenarios**. For example, Reich *et al.,* (2015) determined that artificially warming soil (+3.4°C) reduced the competitive ability of species at their southern range, while species at their northern cooler range limit experienced net photosynthetic and growth gains. Research that incorporates such forward thinking by simulating such plausible future environmental and climatic conditions will continue to provide invaluable information that could be used to better manage and maintain our forests in the future.

Third, future research should focus on ***increasing variability*** within studies. By including multiple sites, which represent a spectrum of environments a species is currently found or will be in the future provides opportunities to assess species variability to certain site specific variables (i.e., climate, edaphic factors). In the context of a species ability to withstand or respond to future environmental conditions will also require assessments that includee multiple life stages within their analysis (i.e. seedlings, saplings, and canopy trees) - as their response to changes will be depending on the stage in question (Fisichelli *et al.,* 2014; Putnam and Reich 2016). Essentially casting a wide net to identify a large amount of environmental variability associated with range limits, where it is crucial to include peripheral populations – provides considerable insight into the vulnerability or potential adaptability of a species. Currently, identifying the factors and their relative contribution as a constraint or facilitator still remain poorly understood (Clark *et al.,* 2014). As an increase in environmental variability is expected to occur with climate change (IPCC, 2014), a larger emphasis must be made within field assessments, particularly focused on measuring adaptive plasticity of a species in novel environment (i.e. more transplant studies) (Nicotra et al. 2010). These have been found to be extremely important for species fitness. For example, Morin and Chuine (2014) found that due to the variability associated with early spring development associated with leaf phenology could limit species migrations as there is an increased risk to frosting events at the northern range, while at the southern range limit the lack of stratification days limits recruitment of sugar maple. Essentially, different ecotones can create different factors that cause range limits, where only once these systems are better understood, a more profound explanation may be concluded or not.

Fourth, future research could focus on a better understanding the variability associated with ***species range genetics***. If gene flow is high enough and there is a strong enough selection for certain favourably genotypes and phenotypes, it may provide the necessary adaptive evolutionary rescue (Gonzales et al. 2013) to promote fitness in novel environments (Franks *et al.,* 2014; Aitken and Bemmels 2016; Anderson 2016). If a species is incapable of migrating at rates fast enough to maintain its climatic niche, the species will then need to persist in place, where the focus shifts from being able to move to being more resilient. One way this may be achieved is through epigenetics; changes in phenotypes caused modifications in gene expression, without the alteration of DNA itself (Berger *et al.,* 2009). The study of epigenetics in trees still remains relatively new, where tests across species and environments remains untested (Aubin *et al.,* 2016), however, having the ability to change rapidly could provide trees the best means of adaptation to deal with potentially hostile future local environments.

Finally, future research in the context of species migration requires a better understanding of the influence of ***edaphic factors*** (i.e. structure, porosity, moisture, biotic agents) on tree recruitment where there remains relatively few studies (Brown and Vellend 2014). For example, while boreal soils are known to be quite often nutrient poor (Collin 2017) and provide unfavourable microsites for temperate species (Chapter 3), we know little if this is due to the constraint associated with certain abiotic factors (soil pH, soil nutrient content) or if it is due to certain biotic agents being present/absent in the soil (e.g. pathogens, mycorrhizal fungi) (Kivlin *et al.,* 2013). Furthermore, an increased understanding of the relative contribution of factors already identified as causes for migration lags for tree species migration must continue, where dispersal (Clark *et al.,* 1998), fecundity, biotic interactions (Brown and Vellend 2014), microclimate (De Frenne *et al.,* 2013), growth (Foster *et al.,* 2016) are included (Figure 4.1).

It is unlikely that sugar maple will tap out to climate change, but it is definitely up against the ropes in its battle against climate change.

ANNEX A

Table A1.1. Pairwise comparisons for constant incubation temperature effect on seed originating from Tennessee, USA. Significant differences in bold (Fleming-Harrington, $\alpha \leq 0.05$).

	-1°C	0°C	1°C	3°C	5°C	7°C	9°C	11°C
0°C	0.9985							
1°C	0.5508	0.1544						
3°C	**<0.0001**	**<0.0001**	**<0.0001**					
5°C	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**				
7°C	**<0.0001**	**<0.0001**	**<0.0001**	0.7526	**0.0486**			
9°C	**<0.0001**	**<0.0001**	**<0.0001**	1.0000	**0.0004**	0.9341		
11°C	**<0.0001**	**<0.0001**	**<0.0001**	0.9089	**0.0163**	1.0000	0.9885	
13°C	**<0.0001**	**<0.0001**	**<0.0001**	0.9926	**0.0031**	0.9972	0.9999	0.9999

Table A1.2. Paired wise comparisons for constant incubation temperature effect on seed originating from <u>Kentucky, USA</u>. Significant differences in bold (Fleming-Harrington, $\alpha \leq 0.05$).

	-1°C	0°C	1°C	3°C	5°C	7°C	9°C	11°C
0°C	0.9998							
1°C	0.9930	1.0000						
3°C	0.9533	0.9990	1.0000					
5°C	0.6876	0.9387	0.9939	0.9996				
7°C	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**	**0.0014**			
9°C	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**	**0.0004**	1.0000		
11°C	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**	0.9546	0.9906	
13°C	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**	0.9026	0.9715	1.0000

Table A1.3. Paired wise comparisons for constant incubation temperature effect on seed originating from <u>Pennsylvania, USA</u>. Significant differences in bold (Fleming-Harrington, $\alpha \leq 0.05$).

	-1°C	0°C	1°C	3°C	5°C	7°C	9°C	11°C
0°C	0.9985							
1°C	0.5508	0.1544						
3°C	**<0.0001**	**<0.0001**	**<0.0001**					
5°C	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**				
7°C	**<0.0001**	**<0.0001**	**<0.0001**	0.7526	**0.0486**			
9°C	**<0.0001**	**<0.0001**	**<0.0001**	1.0000	**0.0004**	0.9341		
11°C	**<0.0001**	**<0.0001**	**<0.0001**	0.9089	**0.0163**	1.0000	0.9885	
13°C	**<0.0001**	**<0.0001**	**<0.0001**	0.9926	**0.0031**	0.9972	0.9999	0.9999

Table A1.4. Paired wise comparisons for constant incubation temperature effect on seed originating from Sherbrooke, Canada. Significant differences in bold (Fleming-Harrington test, $\alpha \leq 0.05$).

	-1°C	0°C	1°C	3°C	5°C	7°C	9°C	11°C
0°C	0.4063							
1°C	**0.0103**	0.8989						
3°C	0.1330	**<0.0001**	**<0.0001**					
5°C	**0.0077**	0.8729	1.0000	**<0.0001**				
7°C	**<0.0001**	0.0996	0.8907	**<0.0001**	0.9082			
9°C	**<0.0001**	**0.0121**	0.5025	**<0.0001**	0.5340	0.9996		
11°C	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**	
13°C	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**	1.0000

Table A1.5. Paired wise comparisons for constant incubation temperature effect on seed originating from Montmagny, Canada. Significant differences in bold (Fleming-Harrington test, $\alpha \leq 0.05$).

	-1°C	0°C	1°C	3°C	5°C	7°C	9°C	11°C
0°C	0.3220							
1°C	**<0.0001**	0.0961						
3°C	0.5302	**0.0004**	**<0.0001**					
5°C	**<0.0001**	0.0599	1.0000	**<0.0001**				
7°C	**<0.0001**	**<0.0001**	**0.0050**	**<0.0001**	**0.0088**			
9°C	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**	0.3217		
11°C	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**	**0.0005**	0.5242	
13°C	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**	0.2173	0.9999

Table A1.6. Paired wise comparisons for constant incubation temperature effect on seed originating from Ville-Marie, Canada. Significant differences in bold (Fleming-Harrington test, α ≤ 0.05).

	-1°C	0°C	1°C	3°C	5°C	7°C	9°C	11°C
0°C	0.0926							
1°C	**<0.0001**	**0.0103**						
3°C	0.9974	**0.0057**	**<0.0001**					
5°C	**<0.0001**	0.1383	0.9951	**<0.0001**				
7°C	**<0.0001**	**<0.0001**	0.2408	**<0.0001**	**0.0225**			
9°C	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**	**0.0001**		
11°C	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**	0.8347	
13°C	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**	0.9789	0.9999

Table A1.7. Paired wise comparisons for constant incubation temperature effect on seed originating from Rivière du Loup, Canada. Significant differences in bold (Fleming-Harrington test, α ≤ 0.05).

	-1°C	0°C	1°C	3°C	5°C	7°C	9°C	11°C
0°C	0.9156							
1°C	**<0.0001**	**<0.0001**						
3°C	**<0.0001**	**<0.0001**	**<0.0001**					
5°C	0.9274	1.0000	**<0.0001**	**<0.0001**				
7°C	**0.0051**	0.2616	**0.0098**	**<0.0001**	0.2994			
9°C	**<0.0001**	**<0.0001**	0.9574	**<0.0001**	**<0.0001**	0.2560		
11°C	**<0.0001**	**<0.0001**	0.1245	**<0.0001**	**<0.0001**	**<0.0001**	**0.0019**	
13°C	**<0.0001**	**<0.0001**	**0.0020**	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**	0.9365

Table A1.8. Paired wise comparisons for the overall warm shifting effect on seed germination. Significant differences in bold (Fleming-Harrington test, α ≤ 0.05).

	-1°C to 7°C	-1°C to 9°C	-1°C to 11°C	-1°C to 13°C	0°C to 7 °C	0°C to 9 °C	0°C to 11°C	0 °C to 13°C	1°C to 7°C	1°C to 9°C	1°C to 11°C	1°C to 13°C	3°C to 7°C	3°C to 9°C	3°C to 11°C
-1°C to 9°C	0.0015														
-1°C to 11°C	**<0.0001**	**<0.0001**													
-1°C to 13°C	**<0.0001**	**<0.0001**	0.9526												
0°C to 7 °C	0.0772	0.9999	**<0.0001**	**<0.0001**											
0°C to 9°C	**<0.0001**	0.9998	**<0.0001**	**<0.0001**	0.8633										
0°C to 11°C	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**									
0°C to 13°C	**<0.0001**	**0.0005**	**<0.0001**	**0.0138**	**<0.0001**	**0.0360**	**<0.0001**								
1°C to 7 °C	**<0.0001**	0.9932	**<0.0001**	**<0.0001**	0.6465	1.0000	**<0.0001**	0.1260							
1 °C to 9°C	**<0.0001**	**<0.0001**	**0.0258**	0.8145	**<0.0001**	**<0.0001**	**<0.0001**	0.9533	**0.0004**						
1°C to 11°C	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**	0.9999	**<0.0001**	**<0.0001**	**<0.0001**					
1°C to 13°C	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**	0.6036	**<0.0001**	**<0.0001**	**<0.0001**	0.9939				
3°C to 7°C	**<0.0001**	0.9932	**<0.0001**	**<0.0001**	0.6477	1.0000	**<0.0001**	0.1262	1.0000	**0.0004**	**<0.0001**	**<0.0001**			
3°C to 9°C	**<0.0001**	**<0.0001**	1.0000	1.0000	**<0.0001**	**<0.0001**	**<0.0001**	**0.0005**	**<0.0001**	0.2523	**<0.0001**	**<0.0001**	**<0.0001**		
3°C to 11°C	**<0.0001**	**<0.0001**	**0.0007**	**<0.0001**	**<0.0001**	**<0.0001**	1.0000	**<0.0001**	**<0.0001**	**<0.0001**	0.9863	0.2596	**<0.0001**	**<0.0001**	
3°C to 13°C	**<0.0001**	**<0.0001**	0.9980	1.0000	**<0.0001**	**<0.0001**	**<0.0001**	**0.0020**	**<0.0001**	0.4863	**<0.0001**	**<0.0001**	**<0.0001**	1.0000	**<0.0001**

Table A1.9. Paired wise comparisons for the overall cool shifting effect on seed germination. Significant differences in bold (Fleming-Harrington, α ≤ 0.05).

	7°C to -1°C	7°C to 0°C	7°C to 1°C	7 °C to 3°C	9°C to -1°C	9 °C to 0°C	9°C to 1°C	9°C to 3°C	11°C to -1°C	11°C to 0°C	11°C to 1°C	11°C to 3°C	13°C to -1°C	13 °C to 0°C	13°C to 1°C
7°C to 0°C	**0.0065**														
7°C to 1°C	1.0000	**0.0262**													
7°C to 3°C	0.9969	**<0.0001**	0.9573												
9°C to -1°C	1.0000	**0.0171**	1.0000	0.9804											
9°C to 0°C	**<0.0001**	0.2590	**<0.0001**	**<0.0001**	**<0.0001**										
9°C to 1°C	0.9992	0.2183	1.0000	0.5411	1.0000	**<0.0001**									
9°C to 3°C	**0.0002**	**<0.0001**	**<0.0001**	**0.0413**	**<0.0001**	**<0.0001**	**<0.0001**								
11°C to -1°C	**0.0002**	1.0000	**0.0009**	**<0.0001**	**0.0005**	0.8356	**0.0173**	**<0.0001**							
11°C to 0°C	1.0000	**0.0125**	1.0000	0.9899	1.0000	**<0.0001**	0.9999	**0.0001**	**0.0004**						
11°C to 1°C	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**	0.4596	**<0.0001**	**<0.0001**	**0.0007**	**<0.0001**					
11°C to 3°C	**0.0427**	**<0.0001**	**0.0103**	0.7023	**0.0179**	**<0.0001**	**0.0004**	0.9939	**<0.0001**	**0.0262**	**<0.0001**				
13°C to -1°C	0.1856	0.9996	0.4102	**0.0023**	0.3255	**0.0098**	0.8987	**<0.0001**	0.8787	0.2716	**<0.0001**	**<0.0001**			
13°C to 0°C	0.9984	**<0.0001**	0.9718	1.0000	0.9881	**<0.0001**	0.6016	**0.0337**	**<0.0001**	0.9942	**<0.0001**	0.6539	**0.0032**		
13°C to 1°C	0.9987	**<0.0001**	0.9747	1.0000	0.9895	**<0.0001**	0.6151	**0.0310**	**<0.0001**	0.9950	**<0.0001**	0.6365	**0.0035**	1.0000	
13°C to 3°C	1.0000	**0.0076**	1.0000	0.9906	1.0000	**<0.0001**	0.9997	**<0.0001**	**0.0002**	1.0000	**<0.0001**	**0.0225**	0.2127	0.9947	0.9955

Table A1.10. Paired wise comparisons for the warm shifting effect on seed originating from Tennessee, USA. Significant differences in bold (Fleming-Harrington, α ≤ 0.05).

	-1°C to 7°C	-1°C to 9°C	-1°C to 11°C	-1°C to 13°C	0°C to 7°C	0°C to 9°C	0°C to 11°C	0 °C to 13°C	1°C to 7°C	1°C to 9°C	1°C to 11°C	1°C to 13°C	3°C to 7°C	3°C to 9°C	3°C to 11°C
-1°C to 9°C	1.0000														
-1°C to 11°C	0.9730	1.0000													
-1°C to 13°C	0.3601	0.8678	0.9995												
0°C to 7 °C	0.2763	**0.0355**	**0.0013**	**<0.0001**											
0°C to 9°C	1.0000	0.9985	0.8047	0.1199	0.5743										
0°C to 11°C	1.0000	1.0000	0.9686	0.3376	0.2764	1.0000									
0°C to 13°C	0.9885	1.0000	1.0000	0.9978	0.0022	0.8742	0.9862								
1°C to 7 °C	0.3865	0.0614	0.0028	**<0.0001**	1.0000	0.7025	0.3875	**0.0044**							
1°C to 9°C	1.0000	0.9977	0.7829	0.1116	0.6351	1.0000	1.0000	0.8562	0.7560						
1°C to 11°C	0.9986	1.0000	1.0000	0.9860	0.0071	0.9613	0.9983	1.0000	**0.0135**	0.9525					
1°C to 13°C	0.4553	0.9228	0.9999	1.0000	**<0.0001**	0.1698	0.4310	0.9994	**<0.0001**	0.1585	0.9948				
3°C to 7°C	0.2553	**0.0320**	**0.0012**	**<0.0001**	1.0000	0.5437	0.2553	**0.0019**	1.0000	0.6048	**0.0063**	**<0.0001**			
3°C to 9°C	0.9938	0.7692	0.1980	0.0057	0.9886	0.9999	0.9943	0.2620	0.9970	1.0000	0.4427	**0.0095**	0.9845		
3°C to 11°C	1.0000	1.0000	0.9999	0.8324	**0.0494**	0.9994	1.0000	1.0000	0.0830	0.9990	1.0000	0.8967	**0.0446**	0.8246	
3°C to 13°C	1.0000	0.9991	0.8376	0.1411	0.5365	1.0000	1.0000	0.8995	0.6665	1.0000	0.9718	0.1970	0.5063	0.9999	0.9997

Table A1.11. Paired wise comparisons for the cool shifting effect on seed originating from Tennessee, USA. Significant differences in bold (Fleming-Harrington, α ≤ 0.05).

	7°C to -1°C	7°C to 0°C	7°C to 1°C	7 °C to 3°C	9°C to -1°C	9°C to 0°C	9°C to 1°C	9°C to 3°C	11°C to -1°C	11°C to 0°C	11°C to 1°C	11°C to 3°C	13°C to -1°C	13°C to 0°C	13°C to 1°C
7°C to 0°C	0.5121														
7°C to 1°C	0.9998	0.9877													
7°C to 3°C	0.0215	0.9987	0.3568												
9°C to -1°C	1.0000	0.4942	0.9997	**0.0198**											
9°C to 0°C	0.5774	1.0000	0.9930	0.9976	0.5595										
9°C to 1°C	0.7407	1.0000	0.9993	0.9737	0.7244	1.0000									
9°C to 3°C	0.0023	0.9467	0.0952	1.0000	0.0021	0.9289	0.7541								
11°C to -1°C	1.0000	05703	0.9999	**0.0288**	1.0000	0.6345	0.7898	**0.0034**							
11°C to 0°C	1.0000	0.9244	1.0000	0.1698	1.0000	0.9482	0.9872	**0.0327**	1.0000						
11°C to 1°C	0.0979	1.0000	0.7090	1.0000	0.0915	1.0000	0.9995	0.9997	0.1229	0.4557					
11°C to 3°C	**<0.0001**	0.0004	**<0.0001**	**0.0355**	**<0.0001**	**0.0003**	**<0.0001**	0.1496	**<0.0001**	**<0.0001**	**0.0052**				
13°C to -1°C	0.9997	0.9906	1.0000	0.3889	0.9996	0.9948	0.9995	0.1065	0.9999	1.0000	0.7365	**<0.0001**			
13°C to 0°C	0.8026	1.0000	0.9997	0.9641	0.7883	1.0000	1.0000	0.7204	0.8445	0.9933	0.9990	**<0.0001**	0.9998		
13°C to 1°C	1.0000	0.7413	1.0000	0.0600	1.0000	0.7951	0.9099	**0.0082**	1.0000	1.0000	0.2192	**<0.0001**	1.0000	0.9407	
13°C to 3°C	**<0.0001**	0.4557	**0.0058**	0.9929	**<0.0001**	0.4145	0.1893	1.0000	**<0.0001**	**0.0014**	0.8901	0.7405	**0.0067**	0.1719	**0.0002**

Table A1.12. Paired wise comparisons for the <u>warm shifting</u> effect on seed originating from <u>Kentucky, USA</u>. Significant differences in bold (Fleming-Harrington, α ≤ 0.05).

	-1°C to 7°C	-1°C to 9°C	-1°C to 11°C	-1°C to 13°C	0°C to 7°C	0°C to 9°C	0°C to 11°C	0 °C to 13°C	1°C to 7°C	1°C to 9°C	1°C to 11°C	1°C to 13°C	3°C to 7°C	3°C to 9°C	3°C to 11°C
-1°C to 9°C	1.0000														
-1°C to 11°C	0.9533	0.9973													
-1°C to 13°C	**0.0080**	**0.0018**	**<0.0001**												
0°C to 7 °C	0.9998	1.0000	1.0000	**0.0001**											
0°C to 9°C	0.9984	1.0000	1.0000	**<0.0001**	1.0000										
0°C to 11°C	0.4925	0.2386	**0.0043**	0.9873	**0.0486**	**0.0222**									
0°C to 13°C	**0.0007**	**0.0001**	**<0.0001**	1.0000	**<0.0001**	**<0.0001**	0.8157								
1°C to 7°C	1.0000	1.0000	0.9313	**0.0150**	0.9995	0.9964	0.6025	0.0016							
1°C to 9°C	0.5201	0.2607	**0.0053**	0.9879	0.0563	**0.0264**	1.0000	0.8227	0.6283						
1°C to 11°C	0.2000	0.0725	**0.0006**	0.9999	**0.0100**	**0.0039**	1.0000	0.9776	0.2804	1.0000					
1°C to 13°C	0.1053	**0.0328**	**0.0002**	1.0000	**0.0036**	**0.0013**	1.0000	0.9943	0.1595	1.0000	1.0000				
3°C to 7°C	0.9997	0.9893	0.3517	0.2434	0.8244	0.6866	0.9911	0.0541	0.9999	0.9925	0.8948	0.7721			
3°C to 9°C	0.9924	0.9274	0.1662	0.4715	0.5911	0.4273	0.9996	0.1460	0.9973	0.9997	0.9810	0.9352	1.0000		
3°C to 11°C	**0.0067**	**0.0014**	**<0.0001**	1.0000	**<0.0001**	**<0.0001**	0.9822	1.0000	**0.0126**	0.9829	0.9997	1.0000	0.2176	0.4346	
3°C to 13°C	0.1899	0.0670	**0.0005**	0.9998	**0.0088**	**0.0033**	1.0000	0.9725	0.2691	1.0000	1.0000	1.0000	0.8918	0.9806	0.9996

Table A1.13. Paired wise comparisons for the cool shifting effect on seed originating from Kentucky, USA. Significant differences in bold (Fleming-Harrington, α ≤ 0.05).

	7°C to -1°C	7°C to 0°C	7°C to 1°C	7°C To 3°C	9°C to -1°C	9°C to 0°C	9°C to 1°C	9°C to 3°C	11°C to -1°C	11°C to 0°C	11°C to 1°C	11°C to 3°C	13°C to -1°C	13°C to 0°C	13°C to 1°C
7°C to 0°C	1.0000														
7°C to 1°C	1.0000	1.0000													
7°C to 3°C	1.0000	1.0000	1.0000												
9°C to -1°C	0.9973	0.9992	0.9783	0.9996											
9°C to 0°C	1.0000	1.0000	1.0000	1.0000	0.9813										
9°C to 1°C	0.9983	0.9965	1.0000	0.9942	0.5206	1.0000									
9°C to 3°C	0.9369	0.9674	0.8160	0.9780	1.0000	0.8327	0.2039								
11°C to -1°C	1.0000	1.0000	1.0000	1.0000	0.9839	1.0000	0.9999	0.8438							
11°C to 0°C	0.9925	0.9972	0.9563	0.9985	1.0000	0.9618	0.4276	1.0000	0.9662						
11°C to 1°C	0.9945	0.9902	0.9997	0.9854	0.4360	0.9998	1.0000	0.1578	0.9996	0.3504					
11°C to 3°C	0.9995	0.9988	1.0000	0.9978	0.6142	1.0000	1.0000	0.2710	1.0000	0.5198	1.0000				
13°C to -1°C	1.0000	1.0000	1.0000	1.0000	0.9102	1.0000	1.0000	0.6247	1.0000	0.8559	1.0000	1.0000			
13°C to 0°C	1.0000	1.0000	1.0000	1.0000	0.9997	1.0000	0.9912	0.9819	1.0000	0.9989	0.9791	0.9965	1.0000		
13°C to 1°C	1.0000	1.0000	1.0000	1.0000	0.9896	1.0000	0.9998	0.8726	1.0000	0.9764	0.9989	0.9999	1.0000	1.0000	
13°C to 3°C	0.1396	0.1218	0.3105	0.1047	**0.0020**	0.3217	0.8928	**0.0002**	0.2950	**0.0012**	0.9525	0.8459	0.5143	0.0855	0.2232

Table A1.14. Paired wise comparisons for the warm shifting effect on seed originating from Pennsylvania, USA. Significant differences in bold (Fleming-Harrington test, α ≤ 0.05).

	-1°C to 7°C	-1°C to 9°C	-1°C to 11°C	-1°C to 13°C	0°C to 7°C	0°C to 9°C	0°C to 11°C	0°C to 13°C	1°C to 7°C	1°C to 9°C	1°C to 11°C	1°C to 13°C	3°C to 7°C	3°C to 9°C	3°C to 11°C
-1°C to 9°C	1.0000														
-1°C to 11°C	**<0.0001**	**<0.0001**													
-1°C to 13°C	**<0.0001**	**<0.0001**	0.9149												
0°C to 7°C	0.9122	0.9844	**0.0030**	**<0.0001**											
0°C to 9°C	0.9917	0.9203	**<0.0001**	**<0.0001**	0.0975										
0°C to 11°C	**<0.0001**	**<0.0001**	0.9526	1.0000	**<0.0001**	**<0.0001**									
0°C to 13°C	**<0.0001**	**<0.0001**	0.6629	1.0000	**<0.0001**	**<0.0001**	1.0000								
1°C to 7°C	**0.0011**	**0.0036**	0.9732	0.0612	0.41000	**<0.0001**	0.0899	**0.0141**							
1°C to 9°C	**<0.0001**	**<0.0001**	0.9598	1.0000	**<0.0001**	**<0.0001**	1.0000	1.0000	0.0981						
1°C to 11°C	**<0.0001**	**<0.0001**	0.9944	1.0000	**<0.0001**	**<0.0001**	1.0000	0.9999	0.2108	1.0000					
1°C to 13°C	**<0.0001**	**<0.0001**	0.3086	0.9999	**<0.0001**	**<0.0001**	0.9996	1.0000	**0.0020**	0.9995	0.9908				
3°C to 7°C	**<0.0001**	**<0.0001**	1.0000	0.8012	**0.0100**	**<0.0001**	0.8689	0.4872	0.9959	0.8833	0.9716	0.1858			
3°C to 9°C	**<0.0001**	**<0.0001**	0.7862	1.0000	**<0.0001**	**<0.0001**	1.0000	1.0000	**0.0266**	1.0000	1.0000	1.0000	0.6233		
3°C to 11°C	**<0.0001**	**<0.0001**	0.7317	1.0000	**<0.0001**	**<0.0001**	1.0000	1.0000	**0.0195**	1.0000	1.0000	1.0000	0.5596	1.0000	
3°C to 13°C	**<0.0001**	**<0.0001**	0.9815	1.0000	**<0.0001**	**<0.0001**	1.0000	1.0000	0.1377	1.0000	1.0000	0.9976	0.9325	1.0000	1.0000

Table A1.15. Paired wise comparisons for the cool shifting effect on seed originating from Pennsylvania, USA. Significant differences in bold (Fleming-Harrington test, α ≤ 0.05).

	7°C to -1°C	7°C to 0°C	7°C to 1°C	7°C to 3°C	9°C to -1°C	9°C to 0°C	9°C to 1°C	9°C to 3°C	11°C to -1°C	11°C to 0°C	11°C to 1°C	11°C To 3°C	13°C to -1°C	13°C to 0°C	13°C to 1°C
7°C to 0°C	0.8252														
7°C to 1°C	0.9107	1.0000													
7°C to 3°C	**<0.0001**	**0.0226**	**0.0135**												
9°C to -1°C	1.0000	0.9562	0.9847	**<0.0001**											
9°C to 0°C	0.6658	1.0000	1.0000	0.0529	0.8733										
9°C to 1°C	0.0739	0.9961	0.9873	0.5827	0.1835	0.9997									
9°C to 3°C	**0.0036**	0.7555	0.6470	0.9756	**0.0134**	0.8922	1.0000								
11°C to -1°C	0.9999	0.1947	0.2987	**<0.0001**	0.9963	0.1036	**0.0023**	**<0.0001**							
11°C to 0°C	0.9993	0.1163	0.1929	**<0.0001**	0.9863	0.0567	**0.0009**	**<0.0001**	1.0000						
11°C to 1°C	**<0.0001**	**<0.0001**	**<0.0001**	0.3030	**<0.0001**	**<0.0001**	**<0.0001**	**0.0018**	**<0.0001**	**<0.0001**					
11°C to 3°C	**<0.0001**	**<0.0001**	**<0.0001**	0.8379	**<0.0001**	**<0.0001**	**0.0018**	**0.0361**	**<0.0001**	**<0.0001**	1.0000				
13°C to -1°C	0.4186	1.0000	1.0000	0.1373	0.6713	1.0000	1.0000	0.9785	0.0377	**0.0184**	**<0.0001**	**<0.0001**			
13°C to 0°C	1.0000	0.9883	0.9972	**<0.0001**	1.0000	0.9496	0.2872	**0.0260**	0.9737	0.9320	**<0.0001**	**<0.0001**	0.8110		
13°C to 1°C	0.9569	1.0000	1.0000	**0.0047**	0.9954	1.0000	0.9530	0.4638	0.3898	0.2629	**<0.0001**	**<0.0001**	0.9999	0.9995	
13°C to 3°C	**<0.0001**	**0.0006**	**0.0003**	0.9999	**<0.0001**	0.0018	0.0838	0.4959	**<0.0001**	**<0.0001**	0.9066	0.9996	**0.0069**	**<0.0001**	**<0.0001**

Table A1.16. Paired wise comparisons for the warm shifting effect on seed originating from Sherbrooke, Canada. Significant differences in bold (Fleming-Harrington test, $\alpha \leq 0.05$).

	-1°C to 7°C	-1°C to 9°C	-1°C to 11°C	-1°C to 13°C	0°C to 7 °C	0°C to 9°C	0°C to 11°C	0°C to 13°C	1°C to 7°C	1°C to 9°C	1°C to 11°C	1°C to 13°C	3°C to 7°C	3°C to 9°C	3°C to 11°C
-1°C to 9°C	1.0000														
-1°C to 11°C	**<0.0001**	**0.0028**													
-1°C to 13°C	0.8443	0.9994	0.0898												
0°C to 7°C	0.5842	0.9791	0.4402	1.0000											
0°C to 9°C	0.0028	0.0666	1.0000	0.5885	0.9459										
0°C to 11°C	**<0.0001**	**<0.0001**	0.9811	**0.0002**	**0.0064**	0.5795									
0°C to 13°C	1.0000	1.0000	**0.0008**	0.9965	0.9402	**0.0283**	**<0.0001**								
1°C to 7 °C	0.2831	0.8524	0.7475	0.9999	1.0000	0.9962	**0.0291**	0.7256							
1 °C to 9°C	0.4059	0.9306	0.5852	1.0000	1.0000	0.9819	**0.0126**	0.8453	1.0000						
1°C to 11°C	**<0.0001**	**<0.0001**	0.9509	**<0.0001**	**0.0035**	0.4552	1.0000	**<0.0001**	**0.0171**	**0.0071**					
1°C to 13°C	**<0.0001**	**<0.0001**	**0.0204**	**<0.0001**	**<0.0001**	**0.0007**	0.7183	**<0.0001**	**<0.0001**	**<0.0001**	0.8403				
3°C to 7°C	0.1477	0.6824	0.8892	0.9979	1.0000	0.9997	0.0654	0.5164	1.0000	1.0000	**0.0403**	**<0.0001**			
3°C to 9°C	**0.0047**	0.0910	1.0000	0.6575	0.9635	1.0000	0.5654	**0.0414**	0.9980	0.9890	0.4433	**0.0007**	0.9999		
3°C to 11°C	**<0.0001**	**<0.0001**	0.1481	**<0.0001**	**<0.0001**	**0.0102**	0.9768	**<0.0001**	**<0.0001**	**<0.0001**	0.9936	1.0000	**0.0002**	**0.0103**	
3°C to 13°C	0.5325	0.9794	0.2378	1.0000	1.0000	0.8482	**0.0011**	0.9360	1.0000	1.0000	**0.0006**	**<0.0001**	1.0000	0.8889	**<0.0001**

Table A1.17. Paired wise comparisons for the cool shifting effect on seed originating from Sherbrooke, Canada. Significant differences in bold (Fleming-Harrington, α ≤ 0.05).

	7°C to -1°C	7°C to 0°C	7°C to 1°C	7°C to 3°C	9°C to -1°C	9°C to 0°C	9°C to 1°C	9°C to 3°C	11°C to -1°C	11°C to 0°C	11°C to 1°C	11°C to 3°C	13°C to -1°C	13°C to 0°C	13°C to 1°C
7°C to 0°C	0.0514														
7°C to 1°C	1.0000	**0.0219**													
7°C to 3°C	0.5349	**<0.0001**	0.7144												
9°C to -1°C	1.0000	0.0354	1.0000	0.6343											
9°C to 0°C	**0.0002**	0.9943	**<0.0001**	**<0.0001**	**0.0001**										
9°C to 1°C	1.0000	0.2184	1.0000	0.1584	1.0000	**0.0022**									
9°C to 3°C	**0.0135**	**<0.0001**	**0.0317**	0.9937	**0.0221**	**<0.0001**	**0.0010**								
11°C to -1°C	0.0898	1.0000	**0.0411**	**<0.0001**	0.0638	0.9816	0.3247	**<0.0001**							
11°C to 0°C	0.5946	**<0.0001**	0.7653	1.0000	0.6905	**<0.0001**	0.1948	0.9911	**<0.0001**						
11°C to 1°C	**0.0001**	0.9876	**<0.0001**	**<0.0001**	**<0.0001**	1.0000	**0.0012**	**<0.0001**	0.9652	**<0.0001**					
11°C to 3°C	**0.0076**	**<0.0001**	**0.0192**	0.9893	**0.0130**	**<0.0001**	**0.0004**	1.0000	**<0.0001**	0.9853	**<0.0001**				
13°C to -1°C	1.0000	0.1677	1.0000	0.2320	1.0000	**0.0014**	1.0000	**0.0021**	0.2580	0.2779	**0.0007**	**0.0010**			
13°C to 0°C	0.9890	**0.0001**	0.9985	0.9998	0.9958	**<0.0001**	0.8099	0.5711	**0.0003**	0.9999	**<0.0001**	0.4900	0.8865		
13°C to 1°C	0.7349	**<0.0001**	0.8734	1.0000	0.8159	**<0.0001**	0.2999	0.9665	**<0.0001**	1.0000	**<0.0001**	0.9490	0.4038	1.0000	
13°C to 3°C	0.9826	**<0.0001**	0.9973	0.9999	0.9929	**<0.0001**	0.7591	0.5584	**0.0002**	0.9999	**<0.0001**	0.4757	0.8493	1.0000	1.0000

Table A1.18. Paired wise comparisons for the warm shifting effect on seed originating from Montmagny, Canada. Significant differences in bold (Fleming-Harrington test, α ≤ 0.05).

	-1°C to 7°C	-1°C to 9°C	-1°C to 11°C	-1°C to 13°C	0°C to 7 °C	0°C to 9°C	0°C to 11°C	0°C to 13°C	1°C to 7°C	1°C to 9°C	1°C to 11°C	1°C to 13°C	3°C to 7°C	3°C to 9°C	3°C to 11°C
-1°C to 9°C	**0.0155**														
-1°C to 11°C	**<0.0001**	**<0.0001**													
-1°C to 13°C	**<0.0001**	0.1357	**0.0180**												
0°C to 7 °C	**0.0051**	1.0000	**<0.0001**	0.4400											
0°C to 9°C	**0.0017**	1.0000	**<0.0001**	0.5248	1.0000										
0°C to 11°C	**<0.0001**	**<0.0001**	0.9893	**<0.0001**	**<0.0001**	**<0.0001**									
0°C to 13°C	0.2379	0.9997	**<0.0001**	**0.0020**	0.9876	0.9579	**<0.0001**								
1°C to 7 °C	**0.0002**	0.9992	**<0.0001**	0.9077	1.0000	1.0000	**<0.0001**	0.7162							
1°C to 9°C	**<0.0001**	0.2186	**0.0245**	1.0000	0.5635	0.6471	**<0.0001**	**0.0057**	0.9490						
1°C to 11°C	**<0.0001**	**<0.0001**	0.4201	**<0.0001**	**<0.0001**	**<0.0001**	0.9991	**<0.0001**	**<0.0001**	**<0.0001**					
1°C to 13°C	**<0.0001**	**<0.0001**	0.5535	**<0.0001**	**<0.0001**	**<0.0001**	0.9999	**<0.0001**	**<0.0001**	**<0.0001**	1.0000				
3°C to 7°C	**<0.0001**	0.9938	**<0.0001**	0.9727	0.9999	1.0000	**<0.0001**	0.5402	1.0000	0.9871	**<0.0001**	**<0.0001**			
3°C to 9°C	**<0.0001**	**0.0001**	0.9543	0.8522	**0.0021**	**0.0028**	0.1398	**<0.0001**	0.0292	0.8622	**0.0028**	**0.0058**	0.0643		
3°C to 11°C	**<0.0001**	**<0.0001**	0.7986	**<0.0001**	**<0.0001**	**<0.0001**	1.0000	**<0.0001**	**<0.0001**	**<0.0001**	1.0000	1.0000	**<0.0001**	**0.0216**	
3°C to 13°C	**<0.0001**	**<0.0001**	0.9487	0.7889	**0.0009**	**0.0012**	0.1156	**<0.0001**	**0.0161**	0.8042	**0.0018**	**0.0038**	0.0388	1.0000	0.0156

Table A1.19. Paired wise comparisons for the cool shifting effect on seed originating from Montmagny, Canada. Significant differences in bold (Fleming-Harrington test, α ≤ 0.05).

	7°C to -1°C	7°C to 0°C	7°C to 1°C	7°C to 3°C	9°C to -1°C	9°C to 0°C	9°C to 1°C	9°C to 3°C	11°C to -1°C	11°C to 0°C	11°C to 1°C	11°C to 3°C	13°C to -1°C	13°C to 0°C	13°C to 1°C
7°C to 0°C	**0.0011**														
7°C to 1°C	1.0000	**0.0263**													
7°C to 3°C	0.9241	**<0.0001**	0.4059												
9°C to -1°C	1.0000	**0.0019**	1.0000	0.8664											
9°C to 0°C	**<0.0001**	0.7298	**<0.0001**	**<0.0001**	**<0.0001**										
9°C to 1°C	1.0000	**<0.0001**	0.9913	0.9982	1.0000	**<0.0001**									
9°C to 3°C	**<0.0001**	**<0.0001**	**<0.0001**	0.1144	**<0.0001**	**<0.0001**	**0.0011**								
11°C to -1°C	**0.0081**	1.0000	0.1134	**<0.0001**	**0.0128**	0.3894	**0.0005**	**<0.0001**							
11°C to 0°C	1.0000	**0.0014**	1.0000	0.9209	1.0000	**<0.0001**	1.0000	**<0.0001**	**0.0094**						
11°C to 1°C	**<0.0001**	0.9069	**<0.0001**	**<0.0001**	**<0.0001**	1.0000	**<0.0001**	**<0.0001**	0.6318	**<0.0001**					
11°C to 3°C	**0.0476**	**<0.0001**	**0.0018**	0.9723	**0.0283**	**<0.0001**	0.2321	0.9472	**<0.0001**	**0.0476**	**<0.0001**				
13°C to -1°C	0.7529	0.6251	0.9952	0.0089	0.8308	**0.0009**	0.3106	**<0.0001**	0.9047	0.7727	**0.0034**	**<0.0001**			
13°C to 0°C	0.9826	**<0.0001**	0.6144	1.0000	0.9605	**<0.0001**	0.9999	**0.0470**	**<0.0001**	0.9814	**<0.0001**	0.8863	**0.0247**		
13°C to 1°C	0.3715	**<0.0001**	0.0464	1.0000	0.2782	**<0.0001**	0.7767	0.6666	**<0.0001**	0.3687	**<0.0001**	1.0000	**0.0002**	0.9990	
13°C to 3°C	0.9928	**<0.0001**	0.6863	1.0000	0.9803	**<0.0001**	1.0000	0.0142	**<0.0001**	0.9921	**<0.0001**	0.7272	**0.0293**	1.0000	0.9923

Table A1.20. Paired wise comparisons for the warm shifting effect on seed originating from Ville-Marie, Canada. Significant differences in bold (Fleming-Harrington test, $\alpha \leq 0.05$).

	-1°C to 7°C	-1°C to 9°C	-1°C to 11°C	-1°C to 13°C	0°C to 7°C	0°C to 9°C	0°C to 11°C	0°C to 13°C	1°C to 7°C	1°C to 9°C	1°C to 11°C	1°C to 13°C	3°C to 7°C	3°C to 9°C	3°C to 11°C
-1°C to 9°C	**<0.0001**														
-1°C to 11°C	**<0.0001**	**<0.0001**													
-1°C to 13°C	**<0.0001**	0.8167	**0.0167**												
0°C to 7°C	0.8554	0.0980	**<0.0001**	**<0.0001**											
0°C to 9°C	0.0805	0.8211	**<0.0001**	**0.0038**	0.9976										
0°C to 11°C	**<0.0001**	**<0.0001**	0.9920	**<0.0001**	**<0.0001**	**<0.0001**									
0°C to 13°C	**<0.0001**	1.0000	**<0.0001**	0.7205	0.0724	0.7956	**<0.0001**								
1°C to 7 °C	**0.0009**	1.0000	**<0.0001**	0.2953	0.5192	0.9975	**<0.0001**	1.0000							
1°C to 9°C	**<0.0001**	0.0398	0.8036	0.9659	**<0.0001**	**<0.0001**	0.0531	**0.0195**	**0.0029**						
1°C to 11°C	**<0.0001**	**<0.0001**	0.8373	**<0.0001**	**<0.0001**	**<0.0001**	1.0000	**<0.0001**	**<0.0001**	**0.0067**					
1°C to 13°C	**<0.0001**	**<0.0001**	0.9802	**<0.0001**	**<0.0001**	**<0.0001**	1.0000	**<0.0001**	**<0.0001**	**0.0342**	1.0000				
3°C to 7°C	**0.0027**	0.9999	**<0.0001**	0.1807	0.6936	0.9998	**<0.0001**	0.9999	1.0000	**0.0012**	**<0.0001**	**<0.0001**			
3°C to 9°C	**<0.0001**	**<0.0001**	1.0000	**0.0049**	**<0.0001**	**<0.0001**	0.9998	**<0.0001**	**<0.0001**	0.5726	0.9678	0.9990	**<0.0001**		
3°C to 11°C	**<0.0001**	**<0.0001**	0.9998	**0.0002**	**<0.0001**	**<0.0001**	1.0000	**<0.0001**	**<0.0001**	0.1625	0.9999	1.0000	**<0.0001**	1.0000	
3°C to 13°C	**<0.0001**	0.0341	0.7125	0.9695	**<0.0001**	**<0.0001**	0.0292	0.0158	**0.0021**	1.0000	**0.0030**	**0.0179**	**0.0009**	0.4597	0.1035

Table A1.21. Paired wise comparisons for the cool shifting effect on seed originating from Ville-Marie, Canada. Significant differences in bold (Fleming-Harrington test, α ≤ 0.05).

	7°C to -1°C	7°C to 0°C	7°C to 1°C	7°C to 3°C	9°C to -1°C	9°C to 0°C	9°C to 1°C	9°C to 3°C	11°C to -1°C	11°C to 0°C	11°C to 1°C	11°C to 3°C	13°C to -1°C	13°C to 0°C	13°C to 1°C
7°C to 0°C	0.1305														
7°C to 1°C	0.2787	**<0.0001**													
7°C to 3°C	0.1497	**<0.0001**	1.0000												
9°C to -1°C	0.9950	**0.0012**	0.9889	0.9470											
9°C to 0°C	**<0.0001**	0.2747	**<0.0001**	**<0.0001**	**<0.0001**										
9°C to 1°C	0.9890	0.9498	**0.0024**	**0.0008**	0.2935	**0.0006**									
9°C to 3°C	**0.0001**	**<0.0001**	0.8132	0.9388	0.0443	**<0.0001**	**<0.0001**								
11°C to -1°C	**<0.0001**	0.4703	**<0.0001**	**<0.0001**	**<0.0001**	1.0000	**0.0024**	**<0.0001**							
11°C to 0°C	1.0000	0.1072	0.3433	0.1942	0.9978	**<0.0001**	0.9813	**0.0002**	**<0.0001**						
11°C to 1°C	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**	0.5078	**<0.0001**	**<0.0001**	0.3156	**<0.0001**					
11°C to 3°C	0.3365	**<0.0001**	1.0000	1.0000	0.9966	**<0.0001**	**0.0027**	0.5779	**<0.0001**	0.4098	**<0.0001**				
13°C to -1°C	0.2941	1.0000	**<0.0001**	**<0.0001**	0.0047	0.1025	0.9947	**<0.0001**	0.2174	0.2509	**<0.0001**	**<0.0001**			
13°C to 0°C	1.0000	0.5348	**0.0487**	**0.0203**	0.8362	**<0.0001**	1.0000	**<0.0001**	**<0.0001**	1.0000	**<0.0001**	0.0596	0.7841		
13°C to 1°C	0.9999	**0.0059**	0.9029	0.7629	1.0000	**<0.0001**	0.5739	**0.0101**	**<0.0001**	1.0000	**<0.0001**	0.9465	**0.0208**	0.9703	
13°C to 3°C	0.1143	1.0000	**<0.0001**	**<0.0001**	0.0007	0.1807	0.9524	**<0.0001**	0.3476	0.0927	**<0.0001**	**<0.0001**	1.0000	0.5195	**0.0042**

Table A1.22. Paired wise comparisons for the warm shifting effect on seed originating from Rivière-du-Loup, Canada. Significant differences in bold (Fleming-Harrington test, α ≤ 0.05).

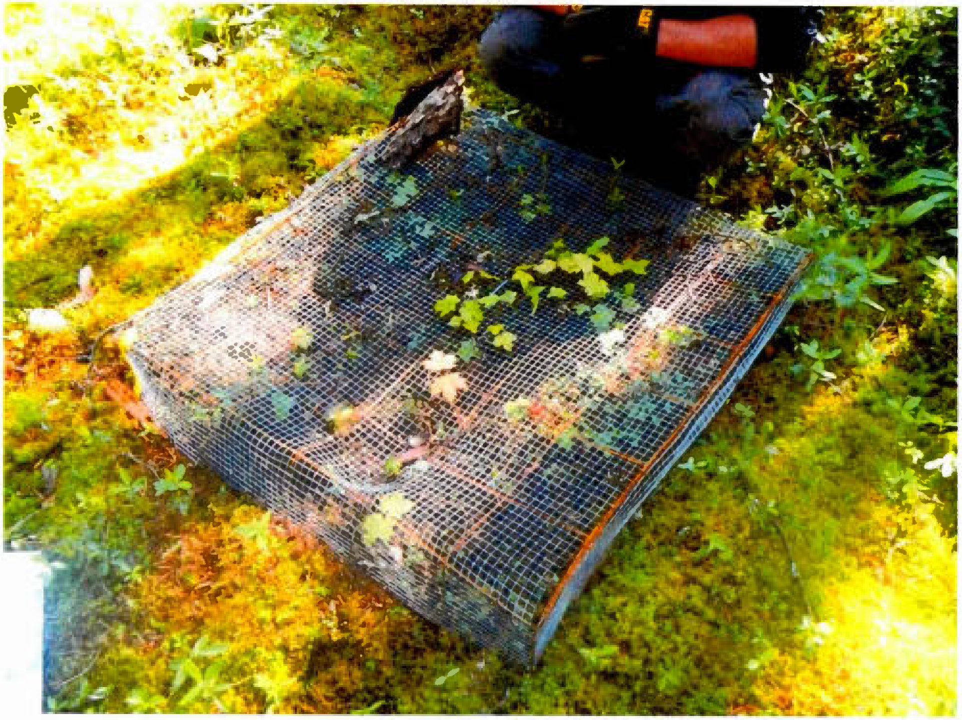
	-1°C to 7°C	-1°C to 9°C	-1°C to 11°C	-1°C to 13°C	0°C to 7 °C	0°C to 9 °C	0°C to 11°C	0°C to 13°C	1°C to 7°C	1°C to 9°C	1°C to 11°C	1°C to 13°C	3°C to 7°C	3°C to 9°C	3°C to 11°C
-1°C to 9°C	**<0.0001**														
-1°C to 11°C	**<0.0001**	**<0.0001**													
-1°C to 13°C	**<0.0001**	**0.0031**	0.4409												
0°C to 7°C	**<0.0001**	0.9996	**<0.0001**	0.2043											
0°C to 9°C	**<0.0001**	0.9863	**<0.0001**	0.3998	1.0000										
0°C to 11°C	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**									
0°C to 13°C	**<0.0001**	1.0000	**<0.0001**	**0.0441**	1.0000	1.0000	**<0.0001**								
1°C to 7°C	**<0.0001**	0.3794	**0.0177**	0.9944	0.9831	0.99988	**<0.0001**	0.8655							
1°C to 9°C	**<0.0001**	**<0.0001**	0.9938	0.9993	**0.0111**	**0.0315**	**<0.0001**	**0.0010**	0.5921						
1°C to 11°C	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**	1.0000	**<0.0001**	**<0.0001**	**<0.0001**					
1°C to 13°C	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**	1.0000	**<0.0001**	**<0.0001**	**<0.0001**	1.0000				
3°C to 7°C	**<0.0001**	0.9390	0.0004	0.6620	1.0000	1.0000	**<0.0001**	0.9998	1.0000	0.0952	**<0.0001**	**<0.0001**			
3°C to 9°C	**<0.0001**	**<0.0001**	0.9746	**0.0047**	**<0.0001**	**<0.0001**	**0.0075**	**<0.0001**	**<0.0001**	0.2365	**0.0017**	**0.0077**	**<0.0001**		
3°C to 11°C	**<0.0001**	**<0.0001**	0.1352	**<0.0001**	**<0.0001**	**<0.0001**	0.5275	**<0.0001**	**<0.0001**	0.0015	0.2795	0.5300	**<0.0001**	0.9824	
3°C to 13°C	**<0.0001**	**<0.0001**	0.9972	0.9949	**0.0028**	**0.0093**	**<0.0001**	**0.0002**	0.3914	1.0000	**<0.0001**	**<0.0001**	**0.0363**	0.2508	**0.0013**

Table A1.23. Paired wise comparisons for the cool shifting effect on seed originating from Rivière-du-Loup, Canada. Significant differences in bold (Fleming-Harrington test, α ≤ 0.05).

	7°C to -1°C	7°C to 0°C	7°C to 1°C	7 °C to 3°C	9°C to -1°C	9 °C to 0°C	9°C to 1°C	9°C to 3°C	11°C to -1°C	11°C to 0°C	11°C to 1°C	11°C to 3°C	13°C to -1°C	13°C to 0°C	13°C to 1°C
7°C to 0°C	**0.0009**														
7°C to 1°C	1.0000	**0.0078**													
7°C to 3°C	1.0000	**<0.0001**	0.9916												
9°C to -1°C	0.9036	0.3691	0.9956	0.3249											
9°C to 0°C	**<0.0001**	0.2756	**<0.0001**	**<0.0001**	**<0.0001**										
9°C to 1°C	1.0000	**0.0133**	1.0000	0.9784	0.9987	**<0.0001**									
9°C to 3°C	**0.0023**	**<0.0001**	0.0002	0.0575	**<0.0001**	**<0.0001**	**<0.0001**								
11°C to -1°C	**<0.0001**	1.0000	0.0001	**<0.0001**	**0.0345**	0.8745	**0.0003**	**<0.0001**							
11°C to 0°C	**0.0001**	1.0000	0.0015	**<0.0001**	0.1541	0.5420	**0.0027**	**<0.0001**	1.0000						
11°C to 1°C	**<0.0001**	0.0319	**<0.0001**	**<0.0001**	**<0.0001**	1.0000	**<0.0001**	**<0.0001**	0.3472	0.1043					
11°C to 3°C	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**	0.7876	**<0.0001**	**<0.0001**	**<0.0001**				
13°C to -1°C	0.2624	0.9519	0.6328	**0.0205**	0.9999	0.0007	0.7341	**<0.0001**	0.4141	0.7824	**<0.0001**	**<0.0001**			
13°C to 0°C	0.7967	**<0.0001**	0.4067	0.9985	0.0900	**<0.0001**	0.3096	0.6978	**<0.0001**	**<0.0001**	**<0.0001**	**0.0016**	**0.0001**		
13°C to 1°C	0.9994	**<0.0001**	0.9630	1.0000	0.1948	**<0.0001**	0.9261	0.1215	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**	**0.0087**	0.9999	
13°C to 3°C	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**	0.9684	**<0.0001**	**<0.0001**	**<0.0001**	1.0000	**<0.0001**	**0.0124**	**0.0002**

ANNEX B

Photo: 1m^2 regeneration plot cage. 216 cages were installed over 12 transplant sites.



ANNEX C

Table AC1: Summary of descriptive statistics for each of the study sites by tree species, seedling stages (1: first year seedlings, 2: older seedlings (≤30.0cm in height), and overstorey canopy trees (DBH> 10.0cm) for the measurement periods of 2015 and 2016. Tree seedling values reported are the number individuals over the entire site, while values in parenthesizes are the average per recruitment plot, and total basal area for canopy trees (m^2/Ha).

Site (Area)	Abitibi (4.0Ha)					Le Bic (10.4Ha)					Sutton (20.0Ha)				
Seedling Stage	1		2		Canopy Trees	1		2		Canopy Trees	1		2		Canopy Trees
Year	2015	2016	2015	2016		2015	2016	2015	2016		2015	2016	2015	2016	
Balsam Fir (ABBA)	252 (0.63)	18 (0.045)	563 (1.41)	372 (0.93)	1113 (5.82)	107 (0.10)	134 (0.13)	402 (0.39)	471 (0.46)	7362 (11.19)	39 (0.02)	17 (0.009)	68 (0.034)	70 (0.035)	2336 (3.24)
Red Maple (ACRU)	164 (0.41)	1048 (2.62)	454 (1.14)	370 (0.93)	237 (2.27)	614 (0.60)	11389 (11.12)	225 (0.22)	221 (0.22)	2103 (3.68)	Species Absent				
Sugar Maple (ACSA)	77 (0.19)	7 (0.018)	463 (1.16)	329 (0.82)	165 (2.68)	315 (0.31)	1920 (1.88)	612 (0.60)	241 (0.23)	495 (1.56)	1944 (0.97)	336 (0.168)	976 (0.49)	887 (0.44)	2821 (6.61)
Paper Birch (BEPA)	5 (0.01)	1 (0.003)	24 (0.06)	0 (0.0)	542 (8.02)	9 (0.001)	434 (0.424)	49 (0.05)	8 (0.007)	953 (2.04)	51 (0.02)	25 (0.013)	28 (0.014)	40 (0.02)	(1355) (3.36)
Yellow Birch (BEAL)	Species Absent					Species Absent					235 (0.12)	326 (0.163)	183 (0.09)	249 (0.12)	3085 (10.61)
American Beech (FAGR)	Species Absent					Species Absent					201 (0.10)	34 (0.017)	247 (0.12)	189 (0.09)	921 (1.97)
Aspen (POTR)	Species Absent					11 (0.01)	0 (0.00)	60 (0.05)	13 (0.05)	1949 (5.30)	Species Absent				
Total Analyzed	498 (1.25)	1074 (2.69)	1504 (3.76)	1071 (2.68)	2057	1056 (1.03)	13877 (13.55)	1348 (1.32)	954 (0.93)	12862	2807 (1.40)	738 (0.37)	2014 (1.00)	1435 (0.72)	10518

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