Spatiotemporal changes at the northern limit of tree distribution in Quebec since 1970

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LIST OF ABBREVIATIONS

LRS	Latitudinal range shifts
LRS1	Latitudinal range shifts calculated using all plots
LRS2	Latitudinal range shifts calculated using weighted average in each longitudinal band
LRS_{50}	Latitudinal range shifts calculated at the 50th percentile
LRS_{90}	Latitudinal range shifts calculated at the 90th percentile
S3-S1	Latitudinal range shifts of saplings through time
T3-T1	Latitudinal range shifts of trees through time
S1-T1	Difference between relative position in the first decennial of saplings with respect to trees
S3-T3	Difference between relative position in the third decennial of saplings with respect to trees
MRNF	*Ministère des Ressources naturelles et de la Faune*
R^2	Coefficient of determination
USA	United States of America
sp.	Species
^{o}N	Degrees of latitude north of the Equator
^{o}W	Degrees of latitude west of the Prime Meridian
CC-Bio	Climate Change and Biodiversity Project
^{o}C	Degrees Celsius
CO_2	Carbon dioxide
km	Kilometers
m	Meters
%	per cent
e.g.	*Exempli gratia,* for example
GIS	Geographic information systems
DIL	Difference in Latitude
GAM	Generalized Additive Model

GLM	Generalized Linear Model
mm	Millimeters
DBH	Diameter at breast height
cm	Centimeter
S1	Saplings of the first decennial
S3	Saplings of the third decennial
T1	Trees of the first decennial
T3	Trees of the third decennial
p	Probability that the difference between sample means is larger than observed
>	Greater than
<	Less than
SE	Standard error
50th	50th percentile of latitude calculated using LRS1 or LRS2
90th	90th percentile of latitude calculated using LRS1 or LRS2

ABSTRACT

Forests are expected to undergo drastic changes in response to climatic warming. Northern tree species are of particular interest because species distribution models project important northward shifts in suitable climatic space and, consequently, increased climatic stress for species. Very few studies, however, have explored the interaction between recent warming and large-scale latitudinal distribution changes. The overall objective of this research was to determine whether tree range dynamics in Québec, Canada between 1970 and 2003 were consistent with the northward shifts in range limits predicted by climate change models. Latitudinal range shifts (LRS) and changes in site occupancy were quantified to reveal spatiotemporal signals of distribution change. Overall, five species of the 14 examined showed significant and consistent evidence for northward latitudinal shifts coinciding with increased occupancy of saplings in the northern part of their range. Most other species showed some evidence of northward or southward shifts, although trends were life stage specific and dependent on where and how range limits were calculated. Spatial differences between the distribution of trees and saplings within a single time period were generally not good indicators of observed temporal trends for saplings. Only long-term monitoring will tell whether these observed trends are just transient dynamics, will result in definitive northward shifts for most species or whether completely new patterns will emerge.

Keywords: Tree migration, Latitude, Northern range limit, Climate change, Quebec (Canada)

RÉSUMÉ

Les forêts changeront énormément au fur et à mesure que les changements climatiques progresseront. Les modèles de répartition d'espèces (SDM) prévoient qu'une augmentation des températures provoquera un déplacement important des niches climatiques des arbres vers le nord. Peu d'études cependant ont examiné l'interaction entre les déplacements latitudinaux potentiels à grande échelle des arbres et le réchauffement récent. L'objectif de cette recherche est de déterminer si la dynamique spatiotemporelle récente de l'aire de répartition de 14 espèces d'arbres du Québec entre 1970-2003 est conséquente avec les prédictions d'une migration vers le nord en réponse aux changements climatiques. Le déplacement de la limite de répartition (LRS) ainsi que les changements d'occupation de sites ont été quantifiés pour détecter si une réponse est déjà perceptible. Cinq espèces ont démontré un déplacement vers le nord de leur distribution qui correspond aux prédictions des modèles climatiques. Les tendances observées dépendent du stade de vie (arbres ou gaules) ainsi que de la position géographique et la méthode employée pour calculer les limites de répartition. La position relative des gaules et arbres n'était pas un bon indicateur des tendances temporelles observées pour les gaules. Seul un suivi à long terme de la répartition des arbres pourra confirmer si les tendances observées ne sont que transitoires, indiquent un réel déplacement des espèces vers le nord ou si des patrons complètement nouveaux émergeront.

Mots clés: Migration d'arbres, Latitude, Limite nordique de distribution, Changements climatiques, Québec (Canada)

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Results of Chapter 3 were presented at the International Union of Forest Research Organizations – Landscape Ecology conference in Bragança, Portugal in September 2010. Chapter 3 will be submitted for publication in Global Change Biology. The literature review in Chapter 2 will also be submitted at a later date to a journal that has yet to be decided.

This project is part of a larger research collaboration assessing the effects of climate change on Québec biodiversity (CC-Bio; http://cc-bio.uqar.qc.ca). The overall goal is to improve the current state of knowledge on the consequences of climate change for Québec flora and fauna.

Chapter 1 - INTRODUCTION

Climate change is expected to direct ecosystem dynamics in novel and unexpected ways. Rapid increases in temperature and important, but variable, changes in precipitation patterns will have great effect on many of the Earth's processes. As the effects of climate change become clearer, the consequences of such warming on biodiversity must be considered so that swift but informed decisions can be taken to minimize negative impacts on ecosystems.

Adaptation and mitigation tools are being devised to protect biodiversity and conserve resources. One rapidly advancing area of research includes projections of current species' distributions using bioclimatic enveloppes (Thuiller *et al.*, 2005b). These models associate variables such as temperature and precipitation with records of species observations and then use modelled scenarios of climate predictions to determine where a species' realised climatic niche will be in the future. Projections demonstrate that many species will face ameliorated conditions, especially in northern areas, suggesting a potential northward shift of species distributions for some species (Iverson and Prasad, 2008). A concern with these models is that too little ecological information such as migration rate is incorporated, producing either all (complete tracking of climate by species) or nothing (no tracking) scenarios. In contrast, process-based models (e.g. Phenofit, Morin *et al.*, 2007) use climatic and other environmental data to determine the probability of species occurrence (i.e. fundamental niche). Distribution data are employed only to calibrate the models and projected range shifts are determined based on known migration rates (Morin and Thuillier, 2009). These models suggest that range expansion will be much more moderate for most species. Knowing whether species will indeed be able to track their climatic niche is central to improve biodiversity-climate models and to devise adaptation strategies for climate change.

Warming is not a far off scenario yet to occur; temperature increases have already been observed since the start of the 20th Century (Hansen *et al.*, 2006). Consequently, biotic responses, such as northward migration of species or decline in parts of the range, have already been shown in several taxa including amphibians, birds, insects, mammals and plants (Parmesan and Yohe, 2003; Root *et al.*, 2003; Hickling *et al.*, 2006; Harsch *et al.*, 2009; Chen *et al.*, 2011). Most observations have been based on either tracking mobile species at specific locations (Wilson *et al.*, 2005) or measuring altitudinal range shifts over small distances using past distribution records when available (Lenoir *et al.*, 2008). Examining the range or distribution changes that have already taken place is a first step in quantifying the potential for species to track climate and can help improve both model predictions of species responses to climate change and ultimately our understanding of ecological processes in the face of rapid ecological shifts. Characterizing species' ranges by tracking distribution changes over large geographic areas, however, remains a challenge.

Trees are an informative indicator of range dynamics because of their intimate link with climate. Precipitation and temperature characterize factors like length of growing season and soil moisture availability, which directly influence where trees can establish and grow. As organisms with long life spans, range shifts in trees may be more reflective of long term dynamics because their immobility is expected to result in a time lag between when warming actually occurs and tree response (Davis, 1989). In temperate ecosystems, trees form the basis for many types of ecological classification because they directly influence species assemblages at similar or higher taxonomic levels (Olson *et al.*, 2001). Tree species may respond idiosyncratically to rapid climate change as a function of life history traits (e.g. dispersal rate) with great implications on community assemblages and biome composition (Davis, 1976). New arrangements of species in response to a warming climate may lead to different competitive dynamics, both in the understory (for shrubs and juveniles) and canopy levels (for mature and/or taller species).

Despite all the emerging research into distribution changes, examinations of historical latitudinal changes, particularly at range limit, have been limited for tree species. Because most trees in North America have wide latitudinal distribution, inconsistent methodology across the range in sampling tree species through time (Woodall *et al.*, 2008), or simply lack of data (Shoo *et al.*, 2006) or follow-up through time have prevented research of dynamics at range edges for a large number of species. Some studies have focused on the center or core of the range because they are more reflective of overall distribution patterns and less sensitive to inadequate sampling (Shoo *et al.*, 2006). Yet, it is at the northernmost extent of the range that climate change is expected to occur most rapidly and where species would be more limited by climate (Root *et al.*, 2003). Most evidence of range shifts for trees has come from either historical altitudinal records (Beckage *et al*., 2008) or the examination of the relative spatial distribution of trees and juveniles in the current time period (Woodall *et al.,* 2009; Zhu *et al.*, 2012). The latter more static approach has led mixed if not contradictory interpretations, with most trees seemingly able to track climate at the center of their range but not at the edges. To my knowledge, there is no broad scale documented historical record of latitudinal distribution shifts for trees in North America which could help validate the static approach. Also, most studies for trees (reviewed in the literature section below) have ignored the various processes including temporal shifts in tree occupancy patterns that could help explain observed trends in range shifts.

In this study, we examined the changes in the distribution patterns of 14 tree species with all or part of their range limit in Quebec, Canada over time (1970-2003). We proposed a comprehensive methodology to detect changing range dynamics for individual tree species by quantifying latitudinal displacement at defined geographic range limits (i.e. latitudinal range shifts) and changes in occupancy patterns within the range. Comparisons of historical data are invaluable in the context of contemporary climate change to inform resource managers of changing forest paradigms and support critical interpretation of models.

1.1. Objectives and Hypothesis

Warming has been well documented in the last 30 years and climate change models have predicted northward shifts in optimum conditions for tree species in Quebec. If species are tracking the climate, I hypothesized that changes in the distribution patterns of trees would already be detectable, especially at the northern distributional limit of individual species. The overall objective of this research was therefore to determine whether tree range dynamics in Québec, Canada between 1970 and 2003 were consistent with patterns of northward shifts predicted by climate change models. This was done by assessing tree distribution over time, directly comparing decade long inventories from 1970s and 1990s and indirectly, using the current distribution of juvenile trees as a precursor of future tree range dynamics. More specific hypotheses regarding the expected patterns were that: 1) latitudinal range limits would have shifted north in the 3rd decennial (1990-2003) compared to the 1st decennial (1970-1980); 2) northward latitudinal shifts would coincide with greater site occupancy in northern parts of the range in the 3rd decennial compared to the 1st decennial; 3) trees would show greater inertia than saplings; 4) since saplings can track the climate better than trees, the current latitudinal limit of saplings would be north of tree limits, indicating potential for northward migration; 5) observed changes in latitudinal range limits through time would corroborate observations of current spatial distribution of saplings in relation to trees.

Chapter 2 - LITERATURE REVIEW

2.1. Climate change and species responses

2.1.1. Recent and projected climatic change

As concerns about changing climate conditions mount, research is uncovering the link between emissions, temperature and precipitation. During the last 100 years, global average temperature increased by 0.74^{o}C (Pachauri and Reisinger, 2007). Increases in atmospheric CO_2 concentration show a positive relationship with increasing temperature, estimated around 1.0 to 2.5^{o}C per trillion tonnes emitted (Matthews *et al.*, 2009). Observed increases are not temporally and spatially consistent: Since 1980, average global temperatures have climbed 0.6^{o}C (Hansen *et al.*, 2006) with many of the warmest years on record since 1995 (Pachauri and Reisinger, 2007). Since the 1970s, this translates into a 40km poleward isotherm shift per decade in the Northern Hemisphere (Hansen *et al.*, 2006). It is also expected that disproportionately stronger warming will occur in the northern latitudes. Regionally, observations indicate that temperature has climbed by 0.8-1.6^{o}C in Quebec, with the strongest warming occurring in the Southwest (Yagouti, 2006; Yagouti *et al.*, 2008). Winter warming has been particularly strong; minimum nightly temperatures were 1.5-2.5^{o}C higher in only 45 years (Yagouti *et al.*, 2008). Future predictions estimate the magnitude of global temperature between 1.8-4.0^{o}C (Pachauri and Reisinger, 2007). Depending on the modelled scenario, the projected increase for Quebec by 2080 is 2.5-5.5^{o}C in the summer and 3.5-8.0^{o}C in the winter (Bourque and Simonet, 2008).

2.1.2. Species responses to climatic variability

2.1.2.1. Types of responses

Accelerating rate of temperature increase has considerable effects for plants in temperate ecosystems. Temperature and precipitation are important factors influencing expression of life history characteristics such as growth and survivorship. Strong changes in climate affect how physiological processes are regulated and expressed (Parmesan, 2006). Niche theory (Hutchinson, 1957) stipulates that species tolerate a given set of environmental conditions under which they can grow and persist. The fundamental niche describes the entire gradient of suitable factors whereas the realized niche is the actual set of conditions currently defining distribution at any given time period. Spatial analogs of niches are not static, varying as environmental gradients shift through time. Given the nature and magnitude of the changes underway, plants are responding according to their intrinsic characteristics through adaptation, change in phenology and range shifts.

Adaptation - Plants adapt to changes in precipitation and temperature as a function of their ecological and physiological requirements. While adaptation can occur without climatic influence, perturbations in ecological systems, such as warming, remain an important driver of changes in the expression of life traits, adapting to new climatic dynamics as their ecophysiological limits are approached or surpassed (Parmesan, 2006). Specific physiological tolerances to cold conditions are thought to restrict distribution at the northern edges (MacArthur, 1972). Increasing temperatures may decrease temperature stress for some species. As conditions warm, growth rate has been shown to accelerate (Gamache and Payette, 2005). Some of the possible reasons for increased growth rate are higher rates of respiration, photosynthesis and overall productivity (Hughes, 2000; Saxe *et al.*, 2001). Consequently, fitness optima may shift in favour of species with a high degree of phenotypic plasticity and high gene transfer (Davis and Shaw, 2001). Species with rapid reproductive maturity and high seed production would be favoured since they would be able to produce new generations quickly (Sexton *et al.*, 2009).

However, adaptation may be not enough; phenotypic and genotypic variability are the key to survivorship at a single location, limiting the adaptive potential of species with narrow environmental tolerances (Parmesan, 2006). Further, the projected rapid rate of climatic change may overwhelm species that are unable to adapt rapidly enough because of the conservation of characters defining niche tolerances (Saxe *et al.*, 2001). Yet, colonization of new areas may promote phenotypic responses to changing climate, promoting further colonization (Olivieri *et al.*, 1990). A study in the Swedish Archipelago showed that islands with younger populations showed more genetic variability than islands with intermediate aged populations and originated from multiple sources (Giles and Goudet, 1997). The reasons are two-fold; more individuals and enhanced gene flow to peripheral populations boosts adaptation in novel or underexploited areas (Davis and Shaw, 2001; Iverson *et al.*, 2004; Case *et al.*, 2005). Adaptation alone may not be enough for plants to adjust to new climatic paradigms (Parmesan, 2006) but may act in tandem with distributional shifts to track shifts in environmental tolerances (Davis and Shaw, 2001).

Phenology - Changes to the timing of phenophases are of particular interest because of their sensitivity to environmental cues (Bertin, 2008). In climates with strong seasonality, temperature thresholds trigger many processes such as flowering, bud burst and senescence (Rathcke and Lacey, 1985). Species react individualistically to conditions leading to differential response mechanisms (Davis et al., 1986). Advance in spring events and/or delay of fall event provide early clues of increasing climatic suitability at range margins. Spring and fall events have been well monitored over long time periods, providing key information into the response of many plant species to temperature, including trees. Climatic warming has influenced the advancement of vernal cues and the delay of autumnal events (Bertin, 2008). The amplitude of change in the timing of spring events is greater than the delay of fall events (Parmesan and Yohe, 2003; Cleland *et al.*, 2007; Doi and Takahashi, 2008). Advances of 3-20 days have been shown in the last century (Hughes, 2000; Root *et al.*, 2003; Primack *et al.*, 2004; Lavoie and Lachance, 2006;

Houle, 2007). Meta-analyses have shown even stronger advances ranging from 1-3 days per decade (Parmesan and Yohe, 2003). Early spring ephemerals have suggested the most rapid response, showing earlier flowering by 15-31 days in *Tussilago farfara* in Quebec (Lavoie and Lachance, 2006). The differential response may result from more contemporary studies showing accelerated changes since 1970 (Bertin, 2008). These trends are accentuated with increasing latitude because warming is stronger at high latitudes. Timing shifts have often associated with early spring climatic variables such as snowmelt and average temperature (Lavoie and Lachance, 2006). Phenological studies provide insight into potential shifts in distribution; however, concrete manifestations of the effects of the uncoupling of species associations (Hansen *et al.*, 2001; Houle, 2007) on colonization and establishment are difficult to interpret over broad spatial scales.

Range displacement – Range shifts are another notable response to changing climatic conditions (Davis and Shaw, 2001). Temperature controls many biological responses with warming, ameliorating physiological processes up to a limit. At northern ends of distribution, extreme cold and short growing seasons define range extent because of their effects on flowering and fruit production (Morin *et al.*, 2007). Three common reactions have been observed in response to change (Holt, 2003): 1) Contraction, one or more fronts recede resulting in an overall decrease in total area; 2) expansion, where one or more fronts advance leading to an overall increase in total area; or 3) shifts, where one edge advances while another one recedes causing no significant change in total distribution area. Changes occur continuously as a function of dispersal, colonization, establishment and extinction rates. At small scales, these shifts are mainly dictated by biotic controls such as competition and predators. At distribution-wide scales, climate and geographic barriers limit movement. Thresholds of viability are a function of a species' needs causing idiosyncratic changes. Large-scale influences such as climate tend to elicit a common reaction to changing paradigms (Beckage *et al.*,

2008) but may be dependant on the magnitude of change (Pucko *et al.*, 2011). Plants may be more indicative of long-term changes than animals because displacement is based on generational changes because of species' inertia (Bertin, 2008) and not annual ones (Penuelas and Boada, 2003).

2.1.2.2 Future projections

Plant distribution models based on climate and emission scenarios suggest reorganization of species composition and abundance. Most information is based on whether plants can fully track change with no dispersal limitations. Considering full migration, almost half of the tree species in eastern North America should experience a displacement of suitable climatic space by 100km to the north by 2100 (Iverson and Prasad, 1998). Similarly, four to nine species will see their projected ranges move completely from the USA into Canada. Consequently, there should be an increase in species richness, favouring northern climates the most (Iverson and Prasad, 2001). Once warming plateaus, it could take 300-500 years for major shifts to end (Overpeck *et al.*, 1991), but this may be unlikely given new competitive interactions and ecological conditions.

On the other hand, it is possible that warming will outpace trees' migrational capacity. Many of the models do not include life history traits such as dispersal, so potential displacements should be considered as overestimates (Pearson and Dawson, 2003). When taken into consideration, as many as one quarter of the plant species in Europe may become critically endangered (Thuiller *et al.*, 2005b). Moreover, in the same study, they found that many areas would experience important losses in species and as such, undergo rapid turnover in community composition. Losses are not expected to be spatially consistent, with high altitude areas experiencing a disproportionate amount of habitat loss (Engler *et al.*, 2011). With time, the course may reveal a "middle ground" trajectory where species will disperse and track changes at a rate determined by life history traits and, possibly, landscape fragmentation.

2.1.2.3 Past responses

Modelling future distributions is important for conservation and resource management given the magnitude of anticipated shifts in the realized niche (Clark and Fastie, 1998; Iverson *et al.*, 2004), but early reports suggest that species are unable to keep up over broad continental scales (Bertrand *et al.*, 2011). Incorporating information about past trends could ameliorate projections.

Paleoecological evidence - Evidence of changes in range distribution in response to climate variability have been documented throughout geologic time. Evidence of large scale shifts date to the start of the Holocene when the last major glaciation ended (Davis, 1976). Rapid warming caused the glaciers to recede at an accelerated rate, opening up new area for tree species at their geographic limit and ameliorating conditions for those at their physiological limit. According to pollen and fossil records, many species consequently shifted their northerly limit as temperatures warmed to near modern trends (Davis and Shaw, 2001; Binney *et al.*, 2009). The most rapid change in distributions are thought to have occurred several thousand years after warming commenced with displacements exceeding 100m per year (Davis, 1976; Clark and Fastie, 1998). Many species were found in different proportions and associates, showing different community composition than today (Overpeck *et al.*, 1992; Binney *et al.*, 2009). As time progressed, unique species responses shifted distributions along environmental and biotic gradients leading to observed modern arrangements (Davis *et al.*, 1986; Overpeck *et al.*, 1992; Binney *et al.*, 2009).

Modern changes - Studies of recent changes have generally been limited to small-scale examinations of distribution. Altitudinal observations have provided more definitive trends than latitudinal changes, yet still provide solid evidence for range shifts. A study of herbaceous and woody species in the French Alps found that their optimum altitude shifted on average by 29m when comparing 1905-1985 and 1986-2005 (Lenoir *et al.*, 2008) and that community composition shifted toward more lowland species (Lenoir *et al.*, 2010a). In California, vegetation survey transects spanning a 2km gradient showed an average increase of 65m between 1977 and 2007 with evidence of shifting at both ends of the distribution (Kelly and Goulden, 2008). Similarly, improved survival rates have been documented at higher altitudes than historical records for both juvenile and mature individuals of *Ceiba aesculifolia* (Valle-Diaz *et al.*, 2009).

Studies into recent changes in latitudinal distribution have been rather scarce and the trends unclear (Bertin, 2008). Observed changes in latitude are much slower due to the 1000-fold scale difference at which latitudinal changes occur relative to altitudinal changes (Hughes, 2000). More protracted studies have shown fluctuations in the spruce treeline of northern Quebec related to short term warming and cooling of the past millennia (Asselin and Payette, 2006) with more recent signs of upward progression in distribution (Gamache and Payette, 2005). Further, another study observed an increase in the number of deciduous saplings in the balsam fir and black spruce-feathermoss domains in Quebec between 1970 and 2000 (Crête and Marzell, 2006). Similarly, the same study found that the average age had decreased in the Yellow birch and balsam fir domains. Together, these findings suggest an upward shift in distributions of more southerly species.

Yet, not all systems show similar changes. A recent study in the eastern United States found that the limits of nearly 60% of tree species seedlings were located within their current range extent, suggesting potential contraction (Zhu *et al.*, 2012). In the French Alps, community composition did not change over broad latitudinal scales whereas composition changes over altitudinal scales accounted for about half the observed warming (Bertrand *et al.*, 2011). A regionalized study in New Hampshire showed minimal changes in community composition and even those observed could not be attributed to climate (Leak and Smith, 1996) suggesting that the most change may not occur at the range center. However, the trends may be different depending on treeline type. A comprehensive meta-analysis of latitudinal and distributional changes showed that roughly half of the studies experienced advancement in a direction corresponding with climate warming (Harsch *et al.*, 2009). Diffuse treelines demonstrated stronger displacement because of extension of the growing season and alleviation of severe winter conditions whereas abrupt treelines and krummholz growth forms showed little response.

2.2. Mechanisms involved in shifting distributions

There is a gap between what determines range area at different scales. At continental scales, plant distributions seem to be at mostly determined by large-scale variables, like climate (Morin *et al.*, 2007). However, at local scales, studies show that biotic variables determine spatial extent. The two scales however are related. In times of relative climatic stability, it is intuitive that biotic interactions, edaphic conditions, disturbance and land-use change would predominantly influence distribution. With climatic change underway, a combination of any or all of the above-mentioned factors are expected to direct shifts, possibly favouring or hindering migration into newly suitable habitat.

Undeniably, the relative influence of large and small-scale processes determine the magnitude of observed shifts. Determining shift importance starts out with understanding how small scale processes build into larger directional changes. One way to explain shifting range dynamics at smaller scales is to use a metapopulation approach whereby the landscape level of distribution is broken up into smaller interconnected populations. Dispersal, colonization and extinction rates will influence whether distributional area will increase, decrease or shift along with changes. With some exceptions, these mechanisms by which migration occurs are generally sequential with the time between and during each step determined by intrinsic life traits. Yet, as the pace of climate warming quickens, determinants of dispersal, colonization and extinction may be altered, confounding individualistic responses (Hampe, 2011). By using spatially refined explanations of displacement, ecologically sound interpretations of the effects of climate change may be constructed.

2.2.1. Dispersal

Dispersal is accomplished by seeds displaced from the mature parent tree to a separate location. Given the expected rate of change, dispersal is likely to be the most limiting factor in migration (Hampe, 2011). Paleoecological records based on pollen distributions show tree limits migrating rapidly upwards (Davis, 1976; Clark and Fastie, 1998). More recently, species invasions (Sakai *et al.*, 2001) and climate change have sparked research into the velocity of migration given human influence on the landscape. Many authors treat dispersal as coupled with establishment because it is difficult to assess on its own (Hanski, 1998; Cain *et al.*, 2000; Ehrlen and Eriksson, 2000). By evaluating dispersal based only on new recruits, temporal dispersal or persistence through time is ignored (e.g. seed bank) (Eriksson, 2000) which may become important for some species as climate ameliorates. Looking at dispersal through space and time reveals important insights into limitations of distribution patterns and how rapidly displacement may occur in times of climatic volatility.

Dispersal distance depends on various life traits and community characteristics influencing spatial and temporal dispersal such as seed characteristics, vectors and source strength. Seed morphology and size are important determinants of how far a seed can travel (Hewitt and Kellman, 2002). Seed size is inversely related to distance and quantity produced mainly because evolutionary pressures select structures best suited to a plant's associated vector given necessary physiological resources. Species that produce small seeds usually produce greater numbers increasing propagule pressure, increasing possibility of survival and reducing seed limitation (Jones and del Moral, 2009). However, the cost of producing many seeds comes at the expense of establishment success, possibly due to a trade off in nutrition for mobility (Hewitt and Kellman, 2002). While both factors are important, low seed production is thought to be relatively less important than establishment limitation in undisturbed ecosystems but becomes more so in newly opened habitat (Jones and del Moral, 2009). Further, larger seeds are more prone to seed predation because animals ingest them or stockpile them for hibernation (Hewitt and Kellman, 2004; Vittoz and Engler, 2007). Field evidence shows that intermediate-sized seeds, whether animal or wind dispersed, appear to be the best compromise between size and potential for establishment (Hewitt and Kellman, 2002).

Vectors are the associated modes of transport by which propagules are carried from one location to the next. They can be self, animal or environment mediated. Self-propelled seeds are an uncommon form of transport and usually are limited in their dispersal capacity (Vittoz and Engler, 2007). Animal mediated is considerably more common and estimates of dispersal rates vary with the associated animal. Larger (e.g. deer) and/or highly mobile (e.g. birds) animals have greater potential to move propagules large distances. Seeds dispersed by environmental factors such as wind or water are easier to predict because their trends can be modelled more accurately (Hewitt and Kellman, 2002). Behaviour makes it difficult to predict their trajectories so estimates of how far seeds are dispersed is variable. Dispersal by water is more limited and the likelihood of establishment for terrestrial plants is reduced. Like birds, wind has a high potential to disperse seeds over large expanses depending on its velocity (Greene *et al.*, 1999). However, seed characteristics will mainly determine how far a seed will go. Seed rain patterns are also different between animal mediated and wind mediated.

2.2.2. Colonization and establishment

The mechanisms by which seeds disperse to a new location vary between deterministic and stochastic processes. However, it is not sufficient for a seed to arrive in a new location; it must land in a physiologically suitable site. Colonization and establishment occur when seeds germinate and grow at a previously unobserved site. The distinction between the two is that colonization refers to germination success of an individual in a previously unoccupied area but may remain below the minimum number of individuals required to sustain a viable population. Establishment, on the other hand, is when a population exceeds the minimum viability threshold and a population is self-sustaining (Harper, 1977).

It is easier to assess factors that promote colonization and establishment by examining those that limit them. Two important categories have been focused upon in studies of colonization with respect to recruitment: seed and microsite limitation (Nathan and Muller-Landau, 2000). The importance, however, of each factor is not so easily determined. Seed limitation is determined by relatively low fecundity and/or low dispersal capacity negatively affecting the probability that a species can grow and thrive (Jones and del Moral, 2009). Even if a species is capable of growing in a given set of conditions, the size and number of viable seeds produced greatly influences the probability of successful germination. Evolutionary pressures have selected for characters suited to certain ecosystems. Wind dispersed species are not seed limited in newly opened habitat because of the relatively high number of propagules produced but instead limited by harsh conditions (Jones and del Moral, 2009). Further, species in undisturbed ecosystems produce fewer seeds because fewer resources are needed to assure survival (Turnbull *et al.*, 2000). Similarly, early successional species often have more dense seed banks than later ones (Clark *et al.*, 1999).

Collectively, source strength is a habitat-based measure of influence of abundance on successful colonization. It mediates the rate of dispersal as a function of the number of propagules produced and influences the density and dispersion of the seed rain pattern. Source strength is positively related to abundance of trees influencing propagule pressure on neighbouring patches.

Dispersal limitation is ultimately a question of source habitat (Iverson *et al.*, 2004). Low seed production and short distance dispersal have shown to sharply decrease the probability of establishment in spatially disjunct areas (Hewitt and Kellman, 2002).

Ecophysiological constraints determine which sites are suitable and unsuitable for establishment and growth in a microsite habitat matrix. Specific tolerances to a given set of light, edaphic and climatic conditions determine the presence of a given species, its relative abundance and its ability to persist over time (Lloyd *et al.*, 2003). It is expected that species with narrow environmental tolerances are more microsite limited than species defined by broad tolerances (Brown *et al.*, 1996). Also, fragmentation will confound the ability of some species to disperse adequately into increasingly disparate systems (Hewitt and Kellman, 2004). Factors that constrain establishment vary across distribution with the range of environmental tolerances exhibited by a given species. Leuschner *et al.* (2009) found that while the overall range of tolerances for a given species remained the same, the proportions of individuals varied across distribution as conditions toward the edge forced adaptive selection to less suitable habitats.

Colonization is also determined at a community level depending on their successional state. Competition from the receiving ecosystem will limit the ability of new species to enter and establish along with relative performance of an invading species (Ibanez *et al.*, 2009). Disturbed areas, either naturally or anthropogenically, may provide inroads for migrating species which were mainly temperature limited (Leithead *et al.*, 2010; Treyger and Nowak, 2011). In contrast, closed communities trade off in stability and ability to be colonized and negatively affect invasion success by migrants. Yet, they are conversely protected from potentially harmful introductions of exotic species. Also, the threshold at which species become established varies between populations; smaller populations require fewer introduced propagules to be present in order to establish (Drake and Lodge, 2004). Inertia of undisturbed forest communities to change may be explained by these dynamics (Leak and Smith, 1996; Pitelka *et al.*, 1997). However, landscapes are increasingly dominated by disturbance and fragmentation, limiting the ability of formerly undisturbed systems to resist new introductions. It remains to be seen whether native trees will be able to outcompete human-mediated changes in the race for survival.

2.2.3. Extinction

Extinction, in a metapopulation framework, implies localized disappearance of subpopulation patches rather than the wholesale extirpation of an entire species (Hanski, 1998). Seen this way, extinction acts as a range shaping mechanism continuously responding to different kinds of deterministic (e.g. habitat loss) and stochastic effects (e.g. environmental) (Brown *et al.*, 1996; Hanski, 1998). Extinction does not influence all populations equally: If trees do not respond immediately to warming, the rate at which extinction occurs is critical for changes in range area and the persistence of species during instability. When extinction rates exceed colonization rates, range contraction occurs defined by the difference between the two. Range collapse occurs when extinction rates far exceed colonization in a given time period such that the distribution area retracts rapidly to historical cores (Holt, 2003). Toward the extreme end of the environmental gradient, distributions become more disjunct and often show lower abundance (Brown, 1984). Extinction risk increases as the number of individuals or as patch area decreases because extreme events such as disease, bad mutations, severe weather events or habitat loss can remove individuals swiftly (Hanski, 1998; Holt, 2003).

Extinction processes act differently at the upper and the lower limits because of different limiting factors. Anderson (2009) found that lagomorphs showed faster displacement at the northern edge than the southern one in response to warming temperatures. Purves (2009) associated low regenerative and dispersive processes at the northern limit with harsh environmental conditions. Extinction processes tend to be more temporally punctuated than those favouring range expansions. Paleoecological records suggest that trees responded relatively suddenly to rapid cooling because soil processes were disturbed and physiological tolerances were exceeded (Davis, 1989). During rapid but steady changes, extinction at the rear edge may be less important, at least temporarily (Lenoir *et al.*, 2010b). Hampe and Petit (2005) suggest that rear edges of distribution may be stable due to refugia dotted around heterogeneous landscapes as seen in Quaternary distributions. Yet, the current accelerated rate of temperature increase may make species susceptible to extinction due to genetic conservatism (Holt, 2003). During the current warming period, doubling times of mortality have been positively correlated with temperature and water deficit in old growth forests in the southwestern USA (van Mantgem *et al.*, 2009). Effects stimulating background rates of mortality increase extinction risk as population levels decrease toward the minimum viable population threshold, making them more susceptible to stochastic extinction (Thomas, 1994).

2.3. Assessing recent changes across distribution

2.3.1. Altitude shifts versus latitude shifts

Distributional changes operate spatially in one, two (latitudinal and/or longitudinal displacement) or three dimensions (altitudinal shift). The magnitude of these changes is often calculated in one of the dimensions mentioned above. Altitudinal changes operate on a smaller scale than latitudinal changes because of the potential for faster rates of change. It is generally accepted that a 0.7^{o}C warming results in a 100m displacement in altitude whereas the same level corresponds to a 100km displacement in latitude (Bertin, 2008). Because of the scale, many more studies have been conducted in mountains than on broader latitudinal changes (Beckage *et al.*, 2008; Kelly and Goulden, 2008; Lenoir *et al.*, 2008; Lenoir *et al.*, 2009; Valle-Diaz *et al.*, 2009). Assessing these changes is important because they are easier to detect because of the scale and the sensitivity of montane plants. Further, heterogeneous landscapes, such as alpine habitats, may act as refugia for many species, serving as a buffer against catastrophic species losses while species adapt or conditions adjust to suit their tolerances (Hampe and Petit, 2005). However, alpine species are generally restricted in distribution and preferences, precluding the ability to make assumptions about species with more widespread ranges and ecological tolerances.

Latitudinal shifts may prove more important from a conservation standpoint than altitudinal dynamics. Alpine systems restrict how much species can track their physiological tolerances. The “escalator effect” (Marris, 2007) is experienced as species track their tolerances up a mountain. Eventually, they reach a limit coinciding with its maximum elevation. In eastern North America, the Appalachian mountain range is comparatively much lower in elevation than others around the World. Given the projected magnitude of warming, species may not find the necessary conditions for survival. Under those scenarios, many plants disappear from high elevation areas in the United States (Chambers, unpublished data; Beauregard, unpublished data). Thus the refugial effect that has proven important in the dispersal of tree species in North America (Davis, 1976; Davis and Shaw, 2001) may be limited from alpine systems in the near future. As a result, northerly displacement of the lower latitude range portions is more important for this area.

2.3.2. Testing for distribution changes

Studies into distributional changes have employed techniques generally falling into two categories: Comparison of composition over time (directly or indirectly) and associative modelling. Compositional changes can be assessed either by comparing presence/absence or changes in percent cover or abundance in a plot (Kelly and Goulden, 2008). Further subsequent analyses can be conducted but the basis remains the same. In ecological modelling, statistical models are most commonly used to associate presence or abundance with a specific response variable, such as latitude or climate (Thuiller *et al.*, 2005a). These models can be refined using life history characteristics (e.g. Anderson et al., 2009) improving the applicability of the results.

Many studies have compared current observed distribution with published historical trends (Kullman, 2002; Valle-Diaz *et al.*, 2009; Woodall *et al.*, 2009). It is often difficult to reproduce studies exactly as previously designed when methods are unclear or imprecise. However, particularly for Quebec, biological collections were most extensive at the beginning and middle of the 20th Century, making them valuable historical references (Delisle *et al.*, 2003). Published accounts are sometimes the best estimates available for deducing trends especially when referring to older sources. A study conducted in the eastern United States (Woodall *et al.*, 2009) using Little's (1971) digitized paper maps. To assess the changes over time, they compared the digitized maps to maps of tree presence plotted from the most current Forest Inventory Analysis data. From these, they calculated the difference between the southern or northern limit from these two references. The drawback of these assessments is their sensitivity to sampling effort. Older range maps are often based on soft evidence without a clear methodology making it difficult to repeat sampling. They also tend to miss areas where access is difficult or not commonly examined by other researchers (Woodall *et al.*, 2008). Many studies were conducted prior to the invention of hand-held global positioning devices and, as such, precise locations were not available. So, it is difficult to return to the exact area previously studied, and at best, studies like these provide a rough idea of the magnitude of change.

Several studies have examined changes in composition through surveys (Crête and Marzell, 2006; Pauli *et al.*, 2007; Kelly and Goulden, 2008; Lenoir *et al.*, 2008; Woodall *et al.*, 2009; Pucko *et al.*, 2011). Inventories are conducted either along transects or by establishing a network of quadrats. For comparison purposes, these sites can be resampled once or repeatedly, either at regular intervals for long term monitoring or irregularly for a snapshot of the breadth of change. Transects and quadrats are standard field designs for many contemporary studies. As such, they may or may not directly quantify shifts, depending on the extent and purpose of the study. In California, Kelly and Goulden (2008) resampled a transect established 30 years earlier along a wide elevational gradient and then extended linearly at specific intervals. They calculated a mean elevation weighted by cover taking into account relative species abundance. The mean was calculated for both time periods (1977 and 2007).

To assess spatial differences in species presence using seedlings, Woodall et al. (2009) examined changes in latitude at the edges and the center for 45 tree species in eastern United States. They calculated the difference in latitude (DIL) between presence of tree biomass and seedlings using data from the current inventory to estimate potential shifts. To assess the regenerative potential across the range, they calculated the ratio of a species' biomass or seedlings to the total amount of biomass or seedlings present in a given plot. From this, they assessed the outer range ratio by comparing the ratio of biomass or seedlings at the upper edge to those at the lower edge. All calculations were conducted with a Bootstrap approach to estimate the sampling error within the dataset by removing a random sample from the original data points and recalculating the desired statistic (Efron, 1979); in this case the mean. Sampling with replacement is conducted n times, n being the number of iterations at which the error levels off. An interesting feature of the DIL technique is that it does not make assumptions about the normal distribution making it suitable for species with non-normal, multi-modal responses. On the other hand, Woodall and colleagues only had information for one boundary for many species (southernmost for Northern species and northernmost for Southern species) because they did not use Canadian data. Consequently, calculations of their central position do not include the northernmost limit of many Northern tree species biasing calculations southward and precludes realistic interpretations of the results. For example, the central position of *Larix laricina* is calculated to be approximately 46°N. The extent of the range, however, ends in Northern Quebec (about 60°N) (Farrar, 1995) so this calculation is an underestimate. Further, calculating the central position assumes that abundance is highest there as per the abundant center hypothesis (Brown, 1984) which is not well supported in the literature (Sagarin and Gaines, 2002).

Lenoir *et al.* (2008; 2009) used a modelling approach to interpret both spatial and temporal changes in elevation. They obtained species data from surveyed plots along an elevational gradient in mountainous regions of Western France. In their 2008 study, they evaluated the difference in species optimum between two time periods (1905-1985 and 1986-2005) by evaluating species response curves using logistic regression (Guisan et al., 2002) to assess their response to elevation. In their 2009 study, they used contemporary data (1986-2006) to evaluate the altitudinal difference in optimum between seedlings and trees using generalized additive modelling (GAM) and generalized linear modelling (GLM) (Guisan *et al.*, 2002) to compare the outputs of the two. GAM and GLM calculate the probability that a species may occur at a given location. Thus, the optimum altitude was computed as the location of maximum likelihood of occurrence, following the abundant core hypothesis (Murphy *et al.*, 2006). If the response was revealed to be unimodal, then the relative probability of occupancy was calculated between seedlings and trees to assess whether there were any changes in the range dynamics. An advantage of this method is that it does not assume that the center of abundance lies necessarily in the center of the range, and thus lends itself to more sophisticated methods of interpreting range dynamics and displacement. A drawback of this method is that only species that showed unimodal response curves were considered. In larger scale studies (distribution-wide), multi-modal distribution centres may be more likely (Sagarin and Gaines, 2002) and thus reduce the number of species suitable for study particularly those with broad East-West distributions.

2.4. General remarks

As shown in this literature review, research into the biological response to the effects of climate change is advancing rapidly. The number of articles contributing to our knowledge base into responses is increasing every day. It is vital to understand how these dynamics interact to better mitigate impacts caused by human mediated climate change. However, information into the rate at which changes can be expected at the latitudinal limit of distributions has been confounded by bias or generalized lack of data. Yet, it is in this area that the greatest shifts are expected to occur. Changes are currently underway and it is crucial to understand past trends to better calibrate models of future projections of species habitat. By looking at historical data, a response may already by discernible in tree species at the northern edge of their distribution.

Chapter 3 - RECENT DISTRIBUTION CHANGES OF NORTHERN TREE SPECIES SUGGEST EARLY PATTERNS OF CLIMATE-RELATED SHIFTS[1]

Laura Boisvert-Marsh, Sylvie de Blois, Catherine Périé

Abstract

The effects of climate change are already detectable in many taxa and trees are no exception. Quantifying changes in the distribution of northern species is of particular interest because the strongest global warming is occurring at high latitudes and individuals are expected to be more sensitive to climatic stress at range limits. Climate suitability models project important northward displacement of suitable climatic space for some tree species over the next century. Most large-scale examinations of recent latitudinal range change have been limited because adequate spatiotemporal coverage is lacking. Nevertheless, comparisons of historical data are invaluable to inform resource managers of changing forest paradigms and support critical interpretation of models. The overall objective of this research is to determine whether northern tree range dynamics in Québec, Canada between 1970 and 2003 is consistent with the northward shifts predicted by climate change models. First, latitudinal range shifts (LRS) in northern limits were calculated spatially (e.g. across life stages) and temporally using two complementary methods. Second, changes in occupancy were quantified to ensure that observed shifts were actually based on expansion or filling in the north. Regardless of how the range limit was defined, 68% and 61% of the latitudinal differences at the 50th percentile and 90th percentile respectively showed higher sapling range limits in the third decennial than in the first. Overall, five species showed significant and consistent evidence for northern shifts coinciding with increased occupancy of saplings in the northern part of their range. Observed trends were species-specific, varying depending on where and

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how the range limit was calculated. Spatial differences between saplings and trees were not good indicators of temporal trends for saplings. As more data becomes available, these findings serve as a baseline for future studies to validate observed patterns.

Keywords: Tree migration, Latitude, Northern range limit, Climate change, Quebec (Canada)

3.1. Introduction

Trees are an informative indicator of range dynamics because of their intimate link with climate. Temperature and precipitation characterize factors like length of growing season and soil moisture availability, which directly influence where trees can establish and grow. Climatic warming has been particularly strong in northern latitudes (Yagouti *et al.*, 2008) and is projected to amplify through the next century (Pachauri and Reisinger, 2007; Bourque and Simonet, 2008). Northern range limits have generated much interest because individuals are hypothesized to be more sensitive to climatic disturbance and extreme events (Sexton *et al.*, 2009). Tree species at their northern limit are defined by marginal climatic conditions (Morin *et al.*, 2007) so alleviation of ecophysiological constraints should promote new growth in previously uncolonized areas. Species distribution models (SDM) project that temperature increases will elicit important rearrangements in species composition and abundance in the northern temperate and boreal forests promoting a northward shift of species distributions (Iverson and Prasad, 2008; McKenney *et al.*, 2011). It is unclear, however, whether species will migrate fast enough to follow their ecophysiological tolerances. Only using climatic variables in modelling does not take into account environmental constraints such as dispersal which are likely to mediate actual shifts (Hampe *et al.*, 2011). As the pace of change quickens through this century, and possibly beyond, there is a critical need to understand how climatic variability will direct individual species distributions.

Looking at recent distribution changes can provide essential insight into changing environmental paradigms. There is growing evidence linking observed distribution changes to warming temperatures and changing precipitation patterns in many different taxa (Parmesan and Yohe, 2003; Wilson *et al.*, 2005; Hickling *et al.*, 2006; Chen *et al.*, 2011). In trees, migrational patterns and amount of available literature vary depending on whether displacement along altitudinal or latitudinal gradients was calculated. Plants have shown upslope migration of their distributions corroborating with observed warming (Beckage *et al.*, 2008; Kelly and Goulden, 2008; Lenoir *et al.*, 2008). Smaller scale studies have shown that localized migration at northern range margins in some areas has occurred but this has not been consistent over broader scales. Protracted studies have shown fluctuations in the spruce treeline of northern Quebec related to short term warming and cooling of the past millennia (Asselin and Payette, 2006) with more recent signs of upward progression in distribution (Gamache and Payette, 2005). Further, another study observed an increase in the number of deciduous saplings in the *A. balsamea* and *P. mariana*-moss domains and a decrease in average age in the *Betula alleghaniensis* and *P. mariana* domains in Quebec between 1970 and 2003 (Crête and Marzell, 2006). Examinations of current abundance patterns in eastern North America suggest that many tree species have “signatures” amenable to northward migration (Murphy *et al.*, 2010). While these studies show patterns consistent with warming, there is a growing literature highlighting novel, unanticipated and sometimes contradictory changes (Lenoir *et al.*, 2010a). A recent study in the eastern United States found that for 74% of species presented juvenile northern range limits within the northern limit of mature trees, suggesting potential contraction (Zhu *et al.*, 2012). In the French Alps, community composition did not change over broad latitudinal scales whereas composition changes over altitudinal scales accounted for about half the observed warming (Bertrand *et al.*, 2011). While altitudinal trends appear to follow climate change hypotheses, it remains unclear if recent latitudinal shifts are detectable as of yet.

Large-scale latitudinal examinations in individual tree distributions at northern limits are lacking (but see Murphy *et al.*, 2010; Zhu et al., 2012). Many more studies have examined historical changes in altitudinal plant distributions because the compressed study scale and inherent sensitivity of montane plants makes shifts easier to detect (see Bertin, 2008; Harsch *et al.*, 2009; Chen *et al.*, 2011 for overview). Alpine species, however, are restricted in distribution and preferences, precluding the ability to make assumptions about species with more widespread geographic ranges and ecological tolerances. Moreover, dispersal, colonization and establishment processes are not the same along large-scale latitudinal gradients as compared to small-scale altitudinal ones because there is a thousand-fold scale difference at which latitudinal changes occur relative to altitudinal changes (Hughes, 2000). Even fewer studies have explored the temporal aspect of observed range limit changes in trees across broad scales because of insufficient data coverage (Shoo *et al.*, 2006), inconsistent methodology (Woodall *et al.*, 2008), and/or imprecise recording of survey locations (Tingley and Beissinger, 2009). To circumvent the lack of temporal data, several studies have compared juvenile tree distributions (e.g. seedlings or saplings) with mature tree distributions (Woodall *et al.*, 2009; Zhu *et al.*, 2012). Juvenile trees act as a surrogate for current conditions because of their recent emergence whereas mature trees are considered a surrogate for past conditions. What has not been highlighted is whether relative spatial position of juveniles with respect to trees will actually translate into sustained range extensions through time. Comparisons of historical data are invaluable in the context of contemporary climate change to inform resource managers of changing forest paradigms and support critical interpretation of models.

This study aims to assess changes in tree distribution over time directly, using inventories from the 1970s and 1990s, and indirectly, using juvenile trees as a precursor of future range dynamics. Warming is already underway with the strongest increases occurring in the last 30 years (Pachauri and Reisinger, 2007) so changes in distribution should already be detectable. Climate change is expected to shift optimum conditions northward for tree species. There are two objectives of this research: First, assess temporal changes in northern range limits in Quebec, Canada for tree species by estimating the magnitude of latitudinal displacement of mature trees and saplings. We refine recent research proposing this methodology with new data at the upper latitudinal limits, instead of at the range center to see if patterns are consistent (Woodall *et al.*, 2009). Moreover, we compare two different ways of calculating range limit differences to see if patterns are similar. Second, evaluate changes in site occupancy across the northern limit of distribution for individual tree species over time and between life stages. Occupancy patterns may provide different perspectives on how northern tree species are responding, even if absolute limits are unchanged or even receding. Using both occupancy and latitudinal shifts combined provide comprehensive insight into range margin dynamics. The overarching hypothesis is that given current patterns of warming, changes in occupancy and latitudinal range shifts will result in a northward shift in range limits for trees and saplings. More specifically, newly occupied sites will be in the northern portion of the study area. Saplings will be more sensitive to temperature fluctuations through time and, consequently, will exhibit larger increases in latitude than mature trees. Similarly, saplings will be found at higher latitudes than trees. Patterns of occupancy change and differences in latitudinal range limits combined will translate into range expansion for saplings and trees.

3.2. Methods

3.2.1. Study area

The study area covers the province of Québec, Canada, from 45^{0}N up to the commercial tree line around 53^{o}N, and from 80^{o}W to 61^{o}W, covering a surface of more than 761 000 km². This vast area is characterized by strong climatic gradients. Average annual temperature ranges from 6.5^{o}C in the south to -4.5^{o}C in the northern portion of the study area (Figure 3.1). Overall annual precipitation ranges from 730mm to 1500mm (Figure 3.2), decreasing from north to south and from east to west. Climate change is generally expected to bring much warmer and wetter conditions, but this pattern is spatially and seasonally variable (Bourque and Simonet, 2008). Regionally, observations indicate that temperature has climbed by 0.43°C on average in Quebec between 1965-1980 and 1985-2003, with the strongest warming occurring in the southwest (Appendix 1). Depending on the modelled scenario, the projected increase for Quebec by 2080 is 2.5-5.5°C in the summer and 3.5-8.0°C in the winter (Bourque and Simonet, 2008).

Physiographic regions include the Canadian Shield in the North, the Appalachian Mountains in the south, and the St-Lawrence Lowlands in between with its fertile soils developed from marine deposits originating from the Champlain Sea (Lemay, 2008). Elevation ranges from sea level to 1268m on the Mont-Jacques-Cartier in the southeast (Natural Resources Canada, 2009). Two major vegetation zones are part of the study area. The northern temperate zone includes the *Acer saccharum-Carya cordiformis* domain (14 500 km^2) to the extreme south of the province, the *A. saccharum-Tilia americana* domain (31 000 km^2), the *A. saccharum-Betula alleghaniensis* domain (65 600 km^2), and the *Abies balsamea-B. alleghaniensis* domain (98 600 km^2). The boreal forest zone to the north includes the *A. balsamea-Betula papyrifera* domain (139 000 km^2) and the vast *Picea glauca*-moss domain (412 400 km^2). The tree line separates the boreal zone from the Arctic zone with its low-lying vegetation. Because precipitation decreases westward, fires are more frequent in the western part of the study area and vegetation patterns tend to show also an east-west gradient (Saucier *et al.*, 2003).

3.2.2. Species data

Species data were provided by the Ministry of Natural Resources and Wildlife of Québec *(Ministère des Ressources naturelles et de la Faune;* MRNF). The data were obtained from their inventories of a network of permanent plots (*placettes-échantillons permanentes*) sampled by a specialized subgroup of the Ministry dedicated to collecting and analyzing forestry data (*Direction des inventaires forestiers*) (Boudreau and Philbert, 2011). The network covers the forested area of Québec considered commercially exploitable (under 53°N). Data collection started in 1970, taking 10-15 years to complete sampling of all plots. Three decennials have been completed and the fourth is expected to finish in 2018. The number of plots has changed throughout the inventory program as sampling needs and site characteristics change, but roughly 12 000 permanent plots are currently monitored.

In the inventory, two permanent plots (main and satellite) separated by 425 m are paired together as they represent one day of sampling for a field team. Precise geographic coordinates are taken for the main plot so it can be resampled even if plot markings are destroyed. All permanent plots are located to avoid major disturbances such as roads or intensive logging activities. Relatively minor natural and/or anthropogenic disturbances can be noted but major disturbances (fire, insect epidemic, or clear-cut) results in removal of the plots from the inventory and their replacement. Sampling density decreases along from south to north; sugar maple domain has 1 plot (satellite and main combined) per 26km^2, balsam fir domain has one plot per 104km^2 and the spruce-moss domain has 1 plot per 259km^2 (Crête and Marzell, 2006).

Trees and saplings are measured separately. According to the MRNF classification, a tree has a diameter at breast height (DBH) of at least 9.1cm whereas saplings range from 1.1 - 9.0cm DBH and are at least 1.3m tall. Trees are inventoried from a 400m^2 circular plot, individually numbered for tracking and their DBH measured to the nearest millimeter. Saplings are inventoried from a 40m^2 subplot at the center of the larger circular plot, classified within 2 cm classes (2, 4, 6, 8 cm classes), and then counted. Contrary to seedling data (<1 cm DBH), sapling data were collected since the start of the inventories. The smallest class of saplings (2cm, 1.1-3.0 cm DBH) is similar to the seedling definition used by

Woodall and colleagues (2009) and thus was retained in this study.

To reduce spatial autocorrelation, the main and nearby satellite plots were combined into one sampling unit. To assure consistent sampling effort and tracking through time, only plots sampled in both the 1st (1970-1980) and the 3rd (1990-2003) decennials were retained, resulting in a total of 3577 permanent plots for analysis (Fig 3.1). Sampling effort during the 1980s was not consistent with the other decennials and precluded repeated measures analysis.

Trees species were chosen based on several characteristics pertaining to data availability and distribution. 1) All or part of a species' northern range limit had to fall within the study area (i.e. under 53°N latitude). Visual inspection of the range extent was conducted (in order of decreasing importance) using maps from (Farrar, 1995), (Soper and Heimburger, 1990), (Flora of North America Editorial Committee, 1993+), and (Little, 1971). 2) Species had to be present in at least 50 plots to ensure a representative sample size. 3) Species had been assessed similarly for both decennials and life stages (see below). Fourteen species that met these criteria were chosen for analysis (Table 3.1). Lastly, all tables were checked for consistency and errors in data entry by mapping them in ArcGIS (ESRI, 2009).

3.2.3. Data analysis

We used two sets of evidence to detect changes in species distribution. We analyzed latitudinal shifts, and, as a complement, we investigated changes in occupancy patterns in plots over time.

Latitudinal shifts

For each species, four presence-only datasets (i.e. plots with at least one individual) were created; one for each life stage (saplings or trees) and decennial (1st or 3rd) with the latitudes of associated plots. Latitudinal shifts were assessed by: 1) calculating differences between the distribution of saplings and mature trees for a given species within the same time period. The assumption is that the range of saplings relative to trees can provide an indication on future range dynamics; 2) calculating observed differences in latitudinal distribution between 1970s and 1990s for saplings and for trees.

Two different algorithms were used to calculate latitudinal limits for comparison. For the latitudinal range shift (LRS1) method, the 50th and 90th percentile of latitude were calculated for all plots with saplings of the 1st decennial (S1), saplings of the 3rd decennial (S3), trees of the 1st decennial (T1) or trees of the 3rd decennial (T3). The observed difference between latitudes was then calculated across decennials for each of the different life stages to estimate range shifts over time (S3-S1, T3-T1; Equation 3.1)

$$LRS_{(\text{sapling or tree}),\, i} = y_{(\text{sapling or tree})3,\, i} - y_{(\text{sapling or tree})1,\, i} \quad \text{(Equation 3.1)}$$

where y is the calculated latitude. Similar calculations were done between life stages for a given time period (S1-T1, S3-T3; Equation 3.2)

$$LRS_{i,\, j} = y_{\text{Sapling}i,\, j} - y_{\text{Tree}i,\, j} \quad \text{(Equation 3.2)}$$

where i is the percentile of latitude (50th or 90th), j is the decennial (1st or 3rd) and y is the calculated latitude. The standard error was estimated using bootstrap resampling (Efron, 1979; Woodall *et al.*, 2009) where a random sample is removed from each population, a difference is calculated and repeated for n iterations. The standard error and subsequent t-statistic were calculated from n bootstrapped differences. The number of iterations (n=500000) was the level at which the standard error begins to even out. Significance was assessed to the 0.05 level.

The second algorithm (LRS2) took into account longitudinal variations of the northern latitudinal limit across the range and uses a moving window analysis. The study area was divided into 0.5° longitude-wide bands between the extreme western (80°W) and eastern limit (61°W) of Quebec, rounded to the nearest integer; a window of 2 bands (1°) spanning the latitudinal breadth (45°N-53°N) was used to calculate the 50th and 90th percentile of latitude in 0.5° steps so as to smooth out sharp differences in latitudinal limits from one band to the next. Bands without plots (i.e. 50th and 90th percentile equal to 0) were subsequently discarded. The average 50th and 90th percentile of latitude across the remaining longitudinal bands weighted by the number of plots present in each band were calculated for saplings of the 1st decennial (S1), saplings of the 3rd decennial (S3), trees of the 1st decennial (T1) and trees of the 3rd decennial (T3). Latitudinal distribution shifts were then calculated between the decennials (S3-S1, T3-T1; Eq. 3.1) and life stages (S1-T1, S3-T3; Eq. 3.2). A pooled variance was calculated and then used to compute 95% confidence intervals. Latitudinal differences along longitudinal gradients were significant if the upper and lower bounds on the interval did not intersect zero.

It is important to highlight that the 50th percentile of latitude does not necessarily reflect the median latitude of the entire north-south range, but reflects the median latitude in the study area. Most species have a substantial component of their range in the United States which was not included in the present research because of the lack of consistency in their temporal data (Woodall *et al.*, 2008). Given the distribution of our species, the 50th percentile in this study still represents the northern part of the range whereas the 90th percentile represents the extreme northern edge, where we would expect more variability. Using percentiles instead of absolute limits (i.e. 100th percentile) targeted the distributional core rather than the extremes.

Results from both LRS methods were combined based on their absolute value and significance, if applicable (Figure 3.3). Three general categories of responses emerged: 1) positive for one or both calculations (-0.03° and greater difference), 2) negative for one or both calculations (0.03° and less difference) or 3) one calculation was positive or negative but other was unchanged (between -0.03 and 0.03°) or of similar magnitude but opposite sign. Relative to the range of a species in the study area, positive latitudinal differences may result from these not necessarily mutually exclusive patterns: 1) thinning in the south (at lower latitudes), 2) filling in the north (at higher latitudes), 3) expansion of range limit (or dispersal) in the north. In all cases, this suggests patterns consistent with a northward migration of suitable conditions. In our study area, negative differences may result from: 1) filling in the south or 2) thinning in the north.

Occupancy

To complement latitudinal shift analysis and discern whether the observed range changes were due to true expansion or filling in of the current range, we also used as evidence changes in plot occupancy over time. First, we assessed changes in plot presence using range limits from the first decennial calculated using the first algorithm (LRS1) to check whether species were occupying in the third decennial more plots above (i.e. expansion) or below (i.e. filling in) their 1970s limit. The number of plots occupied 1) above the 50th and 2) 90th, and 3) below the 50th percentile of the first decennial were obtained for S1, S3, T1, and T3. Differences in absolute number of plots occupied were calculated between decennials (S3-S1, T3-T1). McNemar's Test for paired samples was conducted to see if the proportion of species presence in plots was statistically different ($p<0.05$) between the two decennials for a given life stage.

Second, changes in plot occupancy for saplings and trees were classified into three categories (Table 3.2) based on their presence or absence in a given decennial to evaluate at which latitudes changes are occurring (Zuckerberg *et al.*, 2009). 1) A gain is when a species is absent in the first decennial but present during the third. 2) A loss was considered when a species is present during the first decennial and absent during the third. 3) Maintained plots were classified as such when a given species was present in both decennials. Plots that were unoccupied in either decennial were excluded from the analysis. The number of sites, percentage of sites and the mean latitude of each category was calculated. A one-way analysis of variance was conducted to assess whether the means between the categories were different. A Tukey Honestly Significant Difference post-hoc test was performed to assess the difference between each of the categories and their statistical significance ($p<0.05$).

3.3. Results

3.3.1. Latitudinal shifts

Regardless of how the range limit was defined, 68% of the latitudinal differences at the 50th percentile showed higher sapling range limits in the third decennial than in the first ($S3\text{-}S1_{50}$; Table 3.3). Six of 28 calculated differences were significant, showing positive trend for saplings of four southern species (*Betula alleghaniensis, Acer rubrum, Fraxinus nigra,* and *Tsuga canadensis)* and negative trend for saplings of *Ostrya virginiana* (-0.0603°). The significant latitudinal shifts ranged from 0.0456 ° for *F. nigra* to 0.4275° for *A. rubrum*, or 5 to 47.5 km. At the 90th percentile, 61% of the latitudinal differences showed higher sapling range limits in the third decennial. Of the nine significant values, three confirmed the positive trend for *A. rubrum* and *F. nigra*, and the negative one for *O. virginiana*. At the northernmost part of their range*, Fagus grandifolia, Thuja occidentalis, Populus tremuloides*, and *Betula papyrifera* saplings also showed positive trend*,* whereas saplings of *Picea glauca* showed a negative one. The largest positive difference in saplings across decennials was *A. rubrum* averaging 0.3046° and 0.3302° (Average: 35.3km northward) at the 50th and 90th percentiles respectively for both LRS calculations. The way latitude was calculated influenced the findings, with only *A. rubrum* at the 50th percentile and *B. papyrifera* at the 90th percentile (Average = 0.4049°) showing consistently significant positive values across both algorithms. Sapling differences over time tended to be larger at the 90th than at the 50th but the trend was not significant ($LRS1_{90\text{-}50}$=0.0539, p=0.10324; $LRS2_{90\text{-}50}$=0.0306, p=0.1946) using a paired-test.

The spatio-temporal patterns for trees were more mixed than those for saplings. Although 54% of the differences were positive for trees at the 50th percentile, none was significant, suggesting inertia (T3-T1; Table 3.3). At the 90th percentile, only half of the differences were positive, and two were significant, both showing negative trend for *Picea rubens* and for *B. papyrifera*. Differences in tree responses through time were marginally significantly larger at the 50th percentile than the 90th percentile for range shifts over longitudinal gradients (paired-t-test; $LRS2_{90\text{-}50}$=-0.0248, p=0.0796).

Average northward shift of sapling distributions through time was 0.0363 and 0.0785° at the 50th and 90th percentile respectively whereas trees averaged 0.0006° and 0.0276° southward. When comparing tree shifts over time with those of saplings using a paired t-test, saplings demonstrated significantly larger shifts than trees at the 90th percentile for weighted latitudinal shifts (paired t-test; $LRS2_{90}$=0.1098, p=0.0361) while $LRS2_{50}$ and $LRS1_{90}$ were marginally significant (paired t-test; $LRS1_{90}$=0.0909, p=0.0796, $LRS2_{50}$=0.0544, p=0.0601).

The distribution of saplings relative to trees within the first decennial at the 50th percentile (S1-T1; Table 3.4) showed 54% positive values, with seven significant ones almost equally distributed between positive (saplings north of trees; four values) and negative (saplings south of trees; three values) trends. This showed that, at the beginning of the survey period, the median distribution of saplings of *Betula papyrifera, Picea mariana,* and *Picea rubens* in the study area was at higher latitude than the median distribution of trees of the same species. The converse was true for *F. nigra*, *T. canadensis*, and *P. glauca*. At the 90th percentile, 86% of differences between life stages (S1-T1) were negative and half were strongly negative (<-0.1°). Significant trends were maintained at the 90th percentile for all six species but not always in the same direction; an additional four also showed significant responses. Trees of *B. alleghaniensis*, *B. papyrifera, P. glauca, P. rubens, F. nigra, F. grandifolia, O. virginiana, P. tremuloides, and T. canadensis* showed significant northward distribution relative to saplings, the exception being *P. mariana.* The relative distribution of saplings in relation to trees (S1-T1) was not generally a good predictor of the observed trends for saplings in the later time period (i.e., S3-S1) but more so for trees (T3-T1) (Table 3.7). Three of four regressions between S1-T1 and T3-T1 were significantly positive. Only $LRS1_{50}$ was significantly positive ($LRS1_{50}$, R^2 adjusted= 0.4999, p=0.0028; Table 3.7b) whereas both calculations for range differences were significant for the 90th percentile ($LRS2_{90}$ R^2adjusted=0.2747, p=0.0315; $LRS1_{90}$ R^2adjusted = 0.2358, p=0.0449; Table 3.7b).

Compared to the first decennial, range limits of saplings were more often north of tree limits in the third decennial ($S3\text{-}T3_{50}$ - 71%; $S3\text{-}T3_{90}$ – 42%). Fourteen differences in range limits between saplings and trees were significant. Four species demonstrated consistent responses at the 50th and 90th, two positive (*A. rubrum, P. mariana)* and two negative (*O. virginiana, P. glauca*). At the 50th, sapling range limits were significantly north of tree limits for *P. rubens, F. grandifolia, T. occidentalis, P. tremuloides and B. papyrifera* while *F. nigra* was significantly south. At the extreme northern limits, apart from the four species with consistent trends mentioned above, saplings of *P. rubens, B. alleghaniensis* and *T. canadensis* were significantly south of tree limits.

When comparing 50th and 90th percentiles using a paired t-test, latitudinal differences between juvenile and mature trees were significantly larger at the 50th percentile for all calculations (S1-T1: $LRS1_{90\text{-}50}$=-0.1695°, p=0.0025, $LRS2_{90\text{-}50}$=-0.1746, p=0.001; S3-T3: $LRS1_{90\text{-}50}$=-0.1086°, p=0.01772, $LRS2_{90\text{-}50}$=-0.1192, p=0.0097). Differences between saplings and trees were generally smaller in the 3rd decennial than the 1st (Average 50th: 0.0422, Average 90th: 0.1003). At the extreme northern limit, mean shift of southern species was greater than northern species (6 of 8 – LRS_{90}), averaging 0.0231° more than northern species. On the other hand, average shift of northern species was greater than southern species at the range median (5 of 8 – LRS_{50}). Southern species shifted 0.0477° less than northern species at the 50th percentile, but variability in southern/northern differences was also greater. Only the S3-S1 calculation for $LRS1_{50}$ was significantly higher for southern species (Southern = 0.0489, Northern = -0.0356, t-test, S3-S1 LRS_{50}, p=0.0148).

3.3.2. Patterns of changes in occupancy

F. grandifolia and *P. tremuloides* saplings occupied significantly more plots in all areas while *Acer rubrum* occupied significantly more above the 50th and 90th percentiles. *B. alleghaniensis* occupied significantly more plots above the median while *B. papyrifera* occupied more above the 90th. Below the median of saplings, *O. virginiana, P. tremuloides and A. balsamea* occupied a significantly higher number of plots in the 3rd decennial while *A. saccharum* and *Thuja occidentalis* occupied fewer plots (Table 3.5). Only *P. glauca* demonstrated significantly fewer occupied plots above the 50th percentile. Trees of five species occupied significantly fewer plots in the third decennial below the median while three occupied more plots. *Fagus grandifolia, Tsuga canadensis* and *Acer rubrum* occupied more sites above either 50th or 90th percentiles. In addition to *Ostrya virginiana,* four of five northern species occupied significantly fewer sites above the 50th and/or 90th.

Tree occupancy was maintained at the highest latitudes for most species (8 of 14 sp.; Appendix 2, Table 1b). Only *B. papyrifera* underwent losses at the highest latitudes on average. The four southern species that demonstrated tree occupancy gains at upper latitudes of their range were *P. rubens, A. rubrum, Acer saccharum* and *T. occidentalis.* All 14 species of mature trees maintained occupancy in the higher proportion of sites. Saplings proportions on the other hand were more evenly split between either two or all three categories (Appendix 2, Table 1a). Species either had their highest median latitude in gains (7 of 14 sp.) or in the maintained sites (6 of 14 sp.), with *O. virginiana* being the exception. Gains in saplings of southern species were more commonly found at the highest latitudes (6 of 9 sp.) Only one northern species, *P. tremuloides*, experienced gains at the highest latitude on average while the other four showed maintained occupancy at the highest latitudes. Differences between the categories were often not significant, especially for saplings (Appendix 2, Table 2).

3.3.3. Species level trends

Table 3.6a-c summarizes trends across species and Figure 3.3 describes how these trends were summarized. Species showing significant and consistent evidence for northern shifts coinciding with increased occupancy of saplings in the northern part of their range (above 50th or 90th) include *B. alleghaniensis*, *A. rubrum*, and *F. grandifolia* for southern species, and *B. papyrifera* and *P. tremuloides* for northern species. Patterns for saplings of *F. nigra* and *T. canadensis* also show significant northern shift as do patterns for *T. occidentalis* but the latter with thinning in the south. *A. rubrum, P. tremuloides, B. papyrifera* and *T. occidentalis* demonstrated non-negligible (>10) occupancy gains in saplings above the latitudinal $T1_{90}$ limit and where trees were not already present. Of these species, none exhibited significant northward shifts in trees. Both saplings and trees of *A. saccharum* are thinning in the south but with no significant shift northward yet. For southern species, only *O. virginiana* shows evidence of southward shift as occupancy increases in the south and decreases in the north. Saplings of *P. glauca* also show southward shift because of thinning in the north. Interestingly, tree occupancy of *P. mariana* is decreasing strongly in the southern part of its range with no significant shift yet.

3.4. Discussion

This study quantified spatial and temporal changes in the distribution of 14 North-American tree species reaching northern limits in Quebec. We aimed to identify patterns of occupancy change and range limit displacement consistent with model predictions of northern shifts. Factors other than climate undoubtedly have influenced forest dynamics. For example, beech bark disease (Papaik *et al.*, 2005), a major ice event in 1998 (Hooper *et al.*, 2001) and spruce budworm outbreaks (Boulanger and Arseneault, 2004), among others, have all influenced local regeneration and stand dynamics within the time frame of our study. Natural disturbance was not explicitly isolated in this study in spite of its role in driving ecological shifts (Taylor and Chen, 2011) and successional trends cannot be ruled out, but both would not necessarily be directional. Altitudinal displacement was also not accounted for and could obscure patterns of latitudinal shifts. Whereas causality cannot be assumed, this study has shown that, at broad spatial scale, several tree species are showing early patterns of shifting distribution consistent with model predictions of northern shifts.

Although observed patterns frequently point towards northward shifts, they are also species-specific and vary with growth stage and the portion of the range that is being examined. This warrants caution about interpreting distributional patterns when only part of the range is being included, as is the case with most distributional studies. Range shifts encompass several dynamic processes including increased or decreased frequency within the current range and range extension due to dispersal outside of the current range limit. All these processes occur within the dataset that we examined and, as expected, patterns are stronger for saplings than trees. Whereas evidence of new sapling recruitment is consistent with a scenario of better reproduction and/or survival under improved environmental conditions, decreased frequency may be indicative of stress directly (because of physiological limits) or indirectly (for instance through increased competition) linked to climatic conditions. Both types of patterns may occur simultaneously in different parts of the range for the same species as suggested for instance by occupancy patterns for saplings of *B. papyrifera* or *P. mariana.*

Data from long-term monitoring like the one used in this study will need to be combined with more mechanistic approaches to untangle the different drivers of ecological shifts (e.g. Meier *et al.*, 2012), but already several observations support our interpretations. Southern species such as *A. rubrum* and *B. alleghaniensis*, which have demonstrated consistent evidence of northward shift in our study, have the ability to establish in the boreal forest (Barras and Kellman, 1998; Hewitt and Kellman, 2002). Near its calculated 90th limit in northwestern Quebec, eastern white cedar showed relatively strong recruitment since 1950 with higher proportions of recruitment in mixed boreal forest sites (Bouchard *et al.*, 2006). Warmer soils and lower soil moisture through increased evapotranspiration should accommodate the higher nutrient demands of temperate forest species at the northern edge of their range (Lafleur *et al.*, 2010), but may also cause stress in the south if some tolerance threshold is reached. If soil conditions are not limiting, tree growth will benefit from warming, as observed for the radial growth of *T. canadensis* which was shown to be significantly correlated with both temperature and precipitation variables in dendroclimatic analysis (Tardif *et al.*, 2001) and for which tree occurrence has increased in all but the northernmost (90th) part of its range in our study.

Not all species in our study displayed northward shifts due to expansion; reduced occupancy for some of the studied species (particularly, northern conifers and sugar maple) may be a product of increasing competition and/or warming stress. Competitive outcomes between species such as *A. saccharum* and *F. grandifolia* in temperate forest could be altered, with the latter appearing to be advantaged in the shared southern portion of their range where sugar maple showed signs of stress. In younger age classes, dominant radial growth shifted from *A. saccharum* to *F. grandifolia* in recent decades in Quebec (Beaudet *et al.*, 1999; Gravel *et al.*, 2011) possibly due to warming (Beaudet *et al.*, 1999). *A. saccharum* regeneration in the understory has decreased over much of southern Quebec (Brisson *et al.*, 1994), and although it can establish outside of its current range, it may have difficulty dispersing there (Kellman, 2004). *A. balsamea*, *P. rubens* and *B. papyrifera* have shown reduced competitive ability at small-scale ecotones in Vermont near their southern range limit (Beckage *et al.*, 2008). These findings are corroborated by this study; all three species decreased in occupancy in southern Quebec. Occupancy losses at southern range boundaries may exacerbate migration rates of northward expanding species by lowering competitive interactions (Meier *et al.*, 2012).

Species traits can determine whether species can disperse to newly available sites (Hampe, 2011). Interestingly, the two northern species that show strong evidence of northward shift are also the wind-dispersed, early successional, deciduous ones that regenerate in gaps (*B. papyrifera, P. tremuloides*). Other species showing similar trends, such as *A. rubrum* and *B. alleghaniensis,* may have also benefited from open sites. Gaps can definitely speed up turnover in sites at the northern limit of individual species' range or ecotones, which have recently become more climatically suitable (Bolte *et al.*, 2010; Leithead *et al.*, 2010; Treyger and Nowak, 2011). In a study in the boreal forest of northern Ontario, *A. rubrum* was five times more abundant in the understory gaps than in the overstory while northern species showed no difference in abundance between canopy and understory (Leithead *et al.*, 2010). In post-agricultural forests of southern Quebec, *A. rubrum* invasion peaked 12 years after field abandonment, the lowest of the four target species examined (D'Orangeville *et al.*, 2011).

Phenology and reproductive strategy could synchronously influence migration for certain species. We chose *A. rubrum* as a test species in preliminary analyses for this study, based on the hypothesis that longer growing seasons would be especially favourable since red maple germinates in the same season that seeds are produced, giving more time for saplings to establish and grow before winter sets in and therefore better chance at survival (Tirmenstein, 1991). In a growth chamber experiment with red maple, bud break occurred earlier in the spring, as long as chilling requirements were met, and leaf abscission was delayed in the fall (Norby *et al.*, 2003). *A. rubrum* turned out to be one of the species showing strong consistent patterns and one among four (the others being *B. papyrifera*, *P. tremuloides*, and *T. occidentalis*) for which we have evidence of expansion in sites not previously occupied by trees north of their 90th percentile. The reproductive strategy of *A. rubrum* is in contrast with that of the other maple in this study, *A. saccharum*, which does not germinate in the same season that seeds are produced (Burns and Honkala, 1990). While vegetative reproduction helps maintain isolated northern populations, species with strategies that include sexual reproduction, abundant seed production, long-distance dispersal, and early seedling establishment would presumably be better at keeping pace with a rapidly warming climate. Moreover, sexual reproduction can be stimulated by warming. In northern Quebec, *P. mariana* recently switched from krummholz (non-reproductive form) to seed producing straight forms just below the tree line (Lescop-Sinclair and Payette, 1995), a process which has repeated itself over centuries resulting in tree lines fluctuating with climate. This may translate into non-significant increases in tree frequency at the 90th in our data set, but not in successful sapling recruitment yet.

When data from long-time surveys is not available, information on the position of saplings relative to trees (i.e., S1-T1 and S3-T3) can be used to infer range dynamics (Woodall et al., 2009; Zhu et al., 2012). Our study provides a rare opportunity to validate the findings from such information on North American trees with observed range shifts. Using information from S1-T1, we would have correctly predicted the actual observed dynamics of saplings (S3-S1) 5 out of 14 times and of trees (T3-T1) 8 out of 14 times. This suggests that while relative sapling/tree distribution provides relevant information, it can also mask temporal trends and must be interpreted with care, at least when presence/absence are considered. Woodall *et al.* (2009) in the eastern United States examined distribution changes for 45 tree species by calculating the difference between latitudinal medians of tree biomass and seedlings using data from the current forest inventories. While most species in this study demonstrated strongly negative spatial differences at their extreme northern limit during the first decennial (i.e. 90^{th} percentile) (Table 3.4), Woodall found that 11 of 15 northern species showed significant potential northward expansion of 0.19^{o} on average. The average displacement for the ten species overlapping between the two studies is 0.0019^{o} whereas our study found that $LRS1_{50}$ (S3-T3) was 0.1051^{o} and $LRS1_{90}$ (S3-T3) was 0.0065^{o} for those same ten species. Only *P. tremuloides* and *B. papyrifera* showed similar shifts between the two studies. Also, *A. rubrum* demonstrated strong negative spatial differences between saplings and trees (-0.67^o; Table 3, Woodall *et al.*, 2009) but in our study showed strong northward progression of observed sapling limits over time (0.3046^o, Table 3.3) even beyond the limit of tree distribution. Similar to our study, Zhu et al. (2012) found that most tree species at their 95th percentile of distribution (76 of 92 species) in the eastern United States had sapling range limits at lower latitudes than trees, despite 62% of northern boundaries positively correlated with temperature increase. They explain this pattern by the fact that species traits and favourable temperatures may not be enough to overcome land use and successional changes. Range edges and centers are controlled by distinct demographic processes which drive change in distributional patterns through time (Purves, 2009; Sexton *et al.*, 2009). While relative position of juveniles and mature trees may be important to assess long-term range dynamics, it is difficult to generalize the results to all parts of the range and they will need to be corroborated with temporal data.

In summary, this study provided one of the rare opportunities to examine spatiotemporal trends of large-scale distribution changes and recent climate change using observations of latitudinal range shifts (LRS) and patterns of occupancy change. Five of 14 tree species exhibited significant directional distribution changes consistent with climate warming. Trends were species specific but it is difficult to generalize trends based on ecological or even functional groups because we did not have a complete or even random sampling of species. Further, results varied greatly depending on the location and method employed to characterize range limits. Static observations of the relative position of saplings with respect to trees were not necessarily good predictors of temporal trends, especially for saplings. New data is forthcoming in the next few years so this study sets the baseline for future long-term monitoring. Only time will tell whether these observations are just transient dynamics, indicative of definitive northward shifts or whether completely new patterns will emerge.

Table 3.1: Species list where species with their 90th percentile range limit below 49°N (calculated using all plots) are classified as southern and those with their 90th percentile range limit above 49°N (calculated using all plots) are classified as northern.

Southern species		Northern species	
Latin name	Common name	Latin name	Common name
Acer rubrum	Red maple	*Abies balsamea*	Balsam fir
Acer saccharum	Sugar maple	*Betula papyrifera*	Paper birch
Betula alleghaniensis	Yellow birch	*Picea glauca*	White spruce
Fagus grandifolia	American beech	*Picea mariana*	Black spruce
Fraxinus nigra	Black ash	*Populus tremuloides*	Quaking aspen
Ostrya virginiana	American hophornbeam		
Picea rubens	Red spruce		
Thuja occidentalis	Northern whitecedar		
Tsuga canadensis	Eastern hemlock		

Table 3.2: Change in occupancy categories as classified by presence/absence patterns per decennial

	1st decennial	3rd decennial
Gain	Absent	Present
Loss	Present	Absent
Maintain	Present	Present

Table 3.3: Latitudinal range shifts through time for each life stage (saplings: S3-S1, trees: T3-T1) calculated as the 50th and 90th percentile for all plots (LRS1) and across longitudinal gradients, weighted by the number of plots (LRS2)

	S3-S1 50th		S3-S1 90th		T3-T1 50th		T3-T1 90th	
	LRS1	LRS2	LRS1	LRS2	LRS1	LRS2	LRS1	LRS2
Southern species								
Betula alleghaniensis	0.0324	**0.0639**	0.0398	0.0074	0.02	-0.047	0.0179	0.0327
Picea rubens	0.0645	-0.0229	-0.0467	-0.011	-0.0161	0.0341	-0.1242	**-0.1649**
Acer rubrum	**0.1818**	**0.4275**	0.1538	**0.5065**	-0.0134	0.3692	0.07	0.0287
Acer saccharum	0.069	0.0611	0.0611	0.0681	0.0032	0.0019	0.0378	0.0308
Fraxinus nigra	0.0146	**0.0456**	0.1456	**0.2236**	-0.0326	-0.0925	0.0043	0.0713
Fagus grandifolia	0.0128	0.0123	-0.0006	**0.0652**	-0.036	0.1039	-0.0546	-0.0137
Ostrya virginiana	-0.085	**-0.0603**	-0.0802	**-0.041**	-0.002	-0.0743	-0.0269	-0.0308
Tsuga canadensis	0.0691	**0.0631**	0.081	0.0367	-0.0356	0.0076	-0.0216	-0.0515
Thuja occidentalis	0.081	0.0714	-0.0019	**0.0722**	0.0085	0.1298	0.013	0.0017
Northern species								
Populus tremuloides	-0.0413	0.0635	0.3004	**0.2789**	-0.1027	0.1633	-0.0961	-0.1171
Betula papyrifera	0.0408	0.0632	**0.4486**	**0.3612**	-0.0168	0.151	**-0.2725**	-0.1253
Picea glauca	-0.1098	-0.0575	0.0167	**-0.1734**	-0.0462	-0.2039	-0.0185	-0.0814
Picea mariana	-0.039	0.0257	-0.0171	-0.0346	0.108	0.5862	0.0654	0.0521
Abies balsamea	-0.0293	-0.0034	-0.0836	-0.1781	0.0025	0.0231	0.1503	0.0117

Table 3.4: Latitudinal range shifts between life stages of the same decennial (S1-T1 or S3-T3), calculated as the 50th and 90th percentile for all plots (LRS1) and across longitudinal gradients, weighted by the number of plots (LRS2)

	S1-T1 50th		S1-T1 90th		S3-T3 50th		S3-T3 90th	
	LRS1	LRS2	LRS1	LRS2	LRS1	LRS2	LRS1	LRS2
Southern species								
Betula alleghaniensis	-0.0632	-0.0903	**-0.1631**	**-0.1629**	-0.0508	-0.047	**-0.1412**	**-0.1883**
Picea rubens	0.0857	**0.0643**	-0.1669	**-0.214**	**0.1662**	0.0341	-0.0894	**-0.0601**
Acer rubrum	-0.0631	-0.0531	0.0027	-0.0935	**0.1321**	**0.3692**	0.0865	**0.3844**
Acer saccharum	-0.0495	-0.0587	-0.1114	-0.077	0.0163	0.0019	-0.0881	-0.0397
Fraxinus nigra	-0.0819	**-0.1103**	-0.2622	**-0.1659**	-0.0347	**-0.0925**	-0.1209	-0.0136
Fagus grandifolia	0.0347	0.0421	-0.0058	**-0.075**	**0.0835**	**0.1039**	0.0482	0.0038
Ostrya virginiana	-0.0016	0.0023	-0.1173	**-0.0855**	-0.0846	**-0.0743**	**-0.1705**	**-0.0957**
Tsuga canadensis	-0.0622	**-0.112**	-0.0545	**-0.1641**	0.0425	0.0076	0.0481	**-0.0759**
Thuja occidentalis	0.0591	0.0914	0.0017	-0.0543	**0.1315**	**0.1298**	-0.0133	0.0162
Northern species								
Populus tremuloides	0.023	0.0619	-0.0945	**-0.3008**	0.0845	**0.1633**	0.3021	0.09519
Betula papyrifera	**0.0918**	0.0458	**-0.454**	**-0.3521**	**0.1494**	0.151	0.2671	0.1344
Picea glauca	**-0.1656**	-0.1494	**-0.5139**	**-0.7302**	**-0.2291**	**-0.2039**	**-0.4787**	**-0.8221**
Picea mariana	**0.8357**	**0.6203**	**0.2992**	**0.4343**	**0.6892**	**0.5862**	**0.2168**	**0.3476**
Abies balsamea	0.0501	0.0362	-0.0396	-0.0132	0.0183	0.0231	-0.2735	-0.2029

Table 3.5: Change in number of sites over time occupied by either saplings or trees below or above the 50th percentile and above 90th percentile. Only calculated percentiles from the 1st decennial (S1 or T1) were used to see if number of occupied sites had changed. Bold values are significant ($p<0.05$).

	S3-S1			T3-T1		
	<50th	>50th	>90th	<50th	>50th	>90th
Southern species						
Betula alleghaniensis	19	**31**	10	**-58**	-15	-5
Picea rubens	-2	3	-6	-2	-10	-6
Acer rubrum	-17	**133**	**46**	**26**	19	**15**
Acer saccharum	**-48**	-4	7	**-14**	-3	4
Fraxinus nigra	7	5	1	3	-2	2
Fagus grandifolia	**49**	**55**	**10**	**43**	**16**	-2
Ostrya virginiana	**16**	5	1	-7	**-13**	-5
Tsuga canadensis	0	10	4	**17**	**14**	0
Thuja occidentalis	**-20**	-2	-2	**-20**	-10	-1
Northern species						
Betula papyrifera	-13	15	**41**	-21	**-52**	**-39**
Picea glauca	-2	**-41**	-3	-42	-20	-4
Picea mariana	12	-10	-4	**-151**	**-76**	-1
Populus tremuloides	**41**	**30**	**16**	-8	**-48**	**-15**
Abies balsamea	**41**	2	-4	**-95**	**-75**	-1

Table 3.6a-c): Summary of results for latitudinal range shifts (Table 3.3), changes in number of occupied plots (Table 3.5), proportions and average latitude of gain, loss, and maintained sites for saplings and trees (Appendix 2, Table 1) and Tukey HSD differences between occupancy categories (Appendix 2, Table 2).

a)	*Betula alleghaniensis*			*Picea rubens*			*Acer rubrum*			*Acer saccharum*			*Fraxinus nigra*		
Latitudinal Range Shifts (LRS)															
	50th	90th		50th	90th		50th	90th		50th	90th		50th	90th	
S3-S1	**+**	+		+	-		**+**	**+**		+	+		**+**	**+**	
T3-T1	*	+		*	**-**		+	+		*	+		-	+	
Change in number of occupied plots															
	<50th	>50th	>90th	<50th	>50th	>90th	<50th	>50th	>90th	<50th	>50th	>90th	<50th	>50th	>90th
S3-S1	+	**++**	+	*	*	*	-	**++**	**++**	**--**	*	*	*	*	*
T3-T1	**--**	-	*	*	-	*	**++**	+	**+**	**-**	*	*	*	*	*
Occupancy change															
Saplings	**Highest**	**Mid**	**Lowest**	**Highest**	**Mid**	**Lowest**	**Highest**	**Mid**	**Lowest**	**Highest**	**Mid**	**Lowest**	**Highest**	**Mid**	**Lowest**
Latitude	Gain	Loss	Maintain	Gain	Maintain	Loss	Gain	Maintain	Loss	Gain	Loss	Maintain	Gain	Loss	Maintain
Proportion	Gain	Loss	Maintain	Loss	Gain	Maintain	Gain	Maintain	Loss	Loss	Gain	Maintain	Gain	Loss	Maintain
Trees	**Highest**	**Mid**	**Lowest**	**Highest**	**Mid**	**Lowest**	**Highest**	**Mid**	**Lowest**	**Highest**	**Mid**	**Lowest**	**Highest**	**Mid**	**Lowest**
Latitude	Maintain	Gain	Loss	Gain	Loss	Maintain	Gain	Loss	Maintain	Gain	Loss	Maintain	Maintain	Gain	Loss
Proportion	Maintain	Loss	Gain	Maintain	Loss	Gain	Maintain	Gain	Loss	Maintain	Loss	Gain	Maintain	Gain	Loss
	Saplings	**Trees**		**Saplings**	**Trees**		**Saplings**	**Trees**		**Saplings**	**Trees**		**Saplings**	**Trees**	
Gain-Loss	+	++		++	*		**++**	+		+	++		++	+	
Gain-Maintain	++	*		*	**++**		**++**	**++**		++	**++**		++	*	
Loss-Maintain	*	**--**		--	**++**		--	++		*	++		*	--	
Summary															
Saplings	**Northward shift; filling north**			Ns;			**Northward shift; filling north**			Ns but positive**; thinning south**			**Northward shift**		
Trees	Ns but positive trend**; thinning south**			**Southward shift**			Ns but positive**; filling south and north**			Ns but positive; **thinning south**			Ns		

For Latitudinal Range Shifts (LRS) and Tukey differences, * indicates little or no change, + indicates positive difference while ++ indicates positive difference greater than 0.1

b)	***Fagus grandifolia***			***Ostrya virginiana***			***Tsuga canadensis***			***Thuja occidentalis***		
Latitudinal Range Shifts (LRS)												
	50th	90th		50th	90th		50th	90th		50th	90th	
S3-S1	+	**+**		**-**	**-**		**+**	+		+	**+**	
T3-T1	+	-		-	-		-	-		+	*	
Change in number of occupied plots												
	<50th	>50th	>90th	<50th	>50th	>90th	<50th	>50th	>90th	<50th	>50th	>90th
S3-S1	**++**	**++**	**+**	**+**	*	*	*	+	*	**--**	*	*
T3-T1	**++**	**+**	*	*	**-**	*	**++**	**++**	*	**--**	-	*
Occupancy change												
Saplings	**Highest**	**Mid**	**Lowest**	**Highest**	**Mid**	**Lowest**	**Highest**	**Mid**	**Lowest**	**Highest**	**Mid**	**Lowest**
Latitude	Gain	Loss	Maintain	Loss	Gain	Maintain	Maintain	Gain	Loss	Maintain	Gain	Loss
Proportion	Gain	Maintain	Loss	Gain	Loss	Maintain	Gain	Loss	Maintain	Maintain	Loss	Gain
Trees	**Highest**	**Mid**	**Lowest**	**Highest**	**Mid**	**Lowest**	**Highest**	**Mid**	**Lowest**	**Highest**	**Mid**	**Lowest**
Latitude	Maintain	Loss	Gain	Loss	Maintain	Gain	Maintain	Gain	Loss	Gain	Maintain	Loss
Proportion	Maintain	Gain	Loss	Maintain	Loss	Gain	Maintain	Gain	Loss	Maintain	Loss	Gain
	Saplings	**Trees**		**Saplings**	**Trees**		**Saplings**	**Trees**		**Saplings**	**Trees**	
Gain-Loss	*	--		*	-		++	--		++	++	
Gain-Maintain	+	**--**		+	*		*	*		*	++	
Loss-Maintain	+	-		+	*		--	++		**--**	-	
Summary												
Saplings	**Northward shift; filling everywhere**			**Southward shift; filling in south**			**Northward shift**			**Northward shift; thinning south**		
Trees	Ns**; Filling everywhere, highest in south**			Ns but negative trend; **thinning north**			Ns but negative trend**; filling everywhere except >90th**			Ns but positive trend**; Thinning south**		

For Latitudinal Range Shifts (LRS) and Tukey differences, * indicates little or no change, + indicates positive difference while ++ indicates positive difference greater than 0.1, - indicates negative difference while -- indicates negative difference greater than 0.1. For change in number of occupied plots, * indicates little change (0-9 plots), + indicates difference from 10-19 while ++ indicates difference greater than 20, - indicates negative difference between 10-19, while -- indicates negative difference greater than 20. Bold values are significant. For the summary, interpretations based on significant tests are in bold; Ns means non-significant LRS patterns.

c)	*Betula papyrifera*			*Picea glauca*			*Picea mariana*			*Populus tremuloides*			*Abies balsamea*		
Latitudinal Range Shifts (LRS)															
	50th	90th		50th	90th		50th	90th		50th	90th		50th	90th	
S3-S1	+	**+**		-	**-**		*	-		*	**+**		-	-	
T3-T1	+	**-**		-	-		+	+		*	-		+	+	
Change in number of occupied plots															
	<50th	>50th	>90th	<50th	>50th	>90th	<50th	>50th	>90th	<50th	>50th	>90th	<50th	>50th	>90th
S3-S1	-	+	**++**	*	**--**	*	+	-	*	**++**	**++**	**+**	**++**	*	*
T3-T1	--	**--**	**--**	--	--	*	**--**	**--**	*	*	**--**	**-**	**--**	**--**	*
Occupancy change															
Saplings	**Highest**	**Mid**	**Lowest**	**Highest**	**Mid**	**Lowest**	**Highest**	**Mid**	**Lowest**	**Highest**	**Mid**	**Lowest**	**Highest**	**Mid**	**Lowest**
Latitude	Maintain	Gain	Loss	Maintain	Loss	Gain	Maintain	Loss	Gain	Gain	Maintain	Loss	Maintain	Loss	Gain
Proportion	Maintain	Loss	Gain	Loss	Gain	Maintain	Maintain	Gain	Loss	Gain	Loss	Maintain	Maintain	Gain	Loss
Trees	**Highest**	**Mid**	**Lowest**	**Highest**	**Mid**	**Lowest**	**Highest**	**Mid**	**Lowest**	**Highest**	**Middle**	**Lowest**	**Highest**	**Mid**	**Lowest**
Latitude	Loss	Maintain	Gain	Maintain	Gain	Loss	Maintain	Loss	Gain	Maintain	Loss	Gain	Maintain	Gain	Loss
Proportion	Maintain	Loss	Gain	Maintain	Loss	Gain	Maintain	Loss	Gain	Maintain	Loss	Gain	Maintain	Loss	Gain
	Saplings	**Trees**		**Saplings**	**Trees**		**Saplings**	**Trees**		**Saplings**	**Trees**		**Saplings**	**Trees**	
Gain-Loss	**++**	**--**		-	+		-	--		+	--		--	*	
Gain-Maintain	*	**--**		--	**--**		**--**	**--**		*	**--**		**--**	--	
Loss-Maintain	**--**	++		*	**--**		**--**	**--**		-	-		**--**	--	
Summary															
Saplings	**Northward shift; filling in north**			**Southward shift; thinning in the north**			Ns but negative			**Northward shift; filling everywhere**			Ns but negative trend; **filling in south**		
Trees	**Southward shift; thinning in north**			Ns but negative trend			Ns but positive trend**: thinning below 90th, highest in south**			Ns but negative trend; **thinning in the north**			Ns but positive trend: **thinning highest the south**		

For Latitudinal Range Shifts (LRS) and Tukey differences, * indicates little or no change, + indicates positive difference while ++ indicates positive difference greater than 0.1, - indicates negative difference while -- indicates negative difference greater than 0.1. For change in number of occupied plots, * indicates little change (0-9 plots), + indicates difference from 10-19 while ++ indicates difference greater than 20, - indicates negative difference between 10-19, while -- indicates negative difference greater than 20. Bold values are significant. For the summary, interpretations based on significant tests are in bold; Ns means non-significant LRS patterns.

Table 3.7: Simple linear regression model predicting the latitudinal differences in range limits between a) saplings over time (S3-S1) and b) trees over time (T3-T1) calculated using one of two methods (LRS1 or LRS2) at the 50th and 90th percentiles, from the observed spatial differences between the northern latitudinal limits of saplings and trees of the first decennial (S1-T1).

	S1-T1 vs. S3-S1			
a)	Slope Estimate	Adjusted R^2	Residual Std. Error	p value
$LRS1_{50}$	-0.0505	-0.0561	0.078	0.5885
$LRS2_{50}$	-0.0624	-0.0725	0.121	0.7336
$LRS1_{90}$	-0.3046	0.097	0.1421	0.1477
$LRS2_{90}$	-0.0298	-0.0818	0.203	0.8982

	S1-T1 vs. T3-T1			
b)	Slope Estimate	Adjusted R^2	Residual Std. Error	p value
$LRS1_{50}$	0.1415	0.4999	0.0324	**0.0028**
$LRS2_{50}$	0.0796	0.1238	0.032	0.1179
$LRS1_{90}$	0.2736	0.2358	0.0882	**0.0449**
$LRS2_{90}$	0.1693	0.2747	0.0619	**0.0315**

Latitudinal range shifts calculated as the 50^{th} and 90^{th} percentile for all plots (LRS1) and across longitudinal gradients, weighted by the number of plots (LRS2). Bold values indicate significant regression models ($p<0.05$).

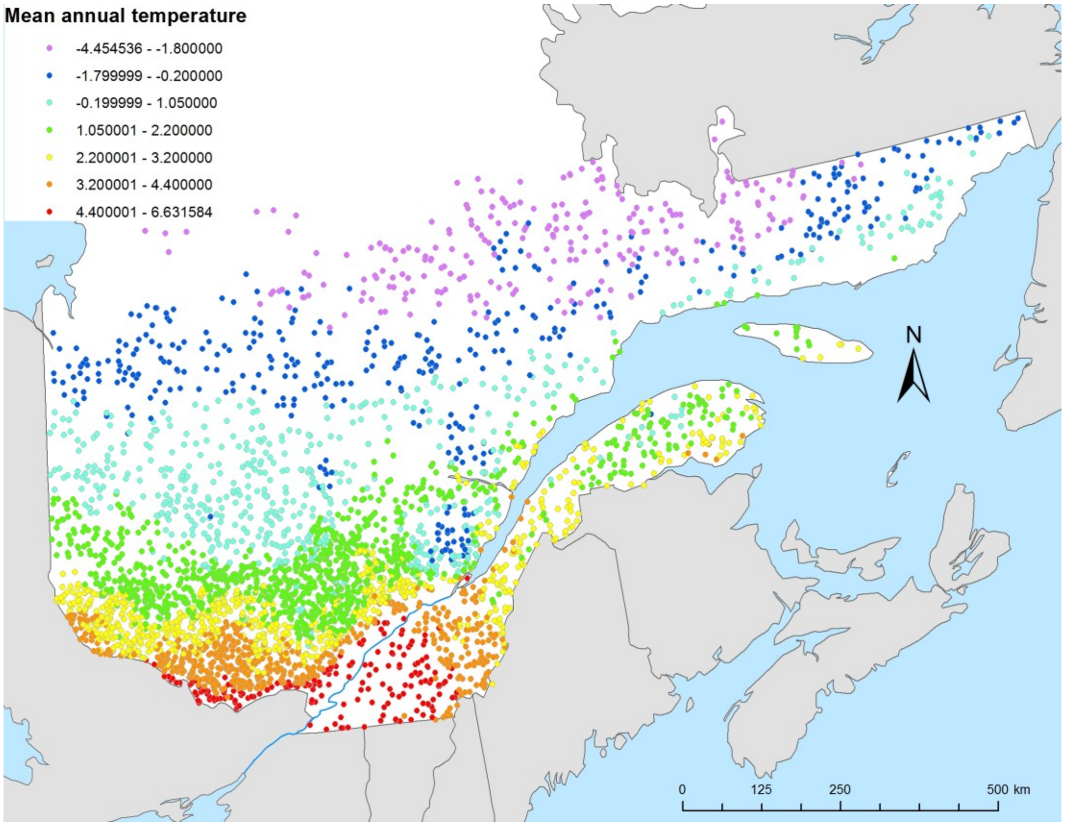

Figure 3.1: Mean annual temperature (at plot level) between 1965 and 2003. Values based on interpolated models from weather station data (Regnière and Saint-Amant, 2008).

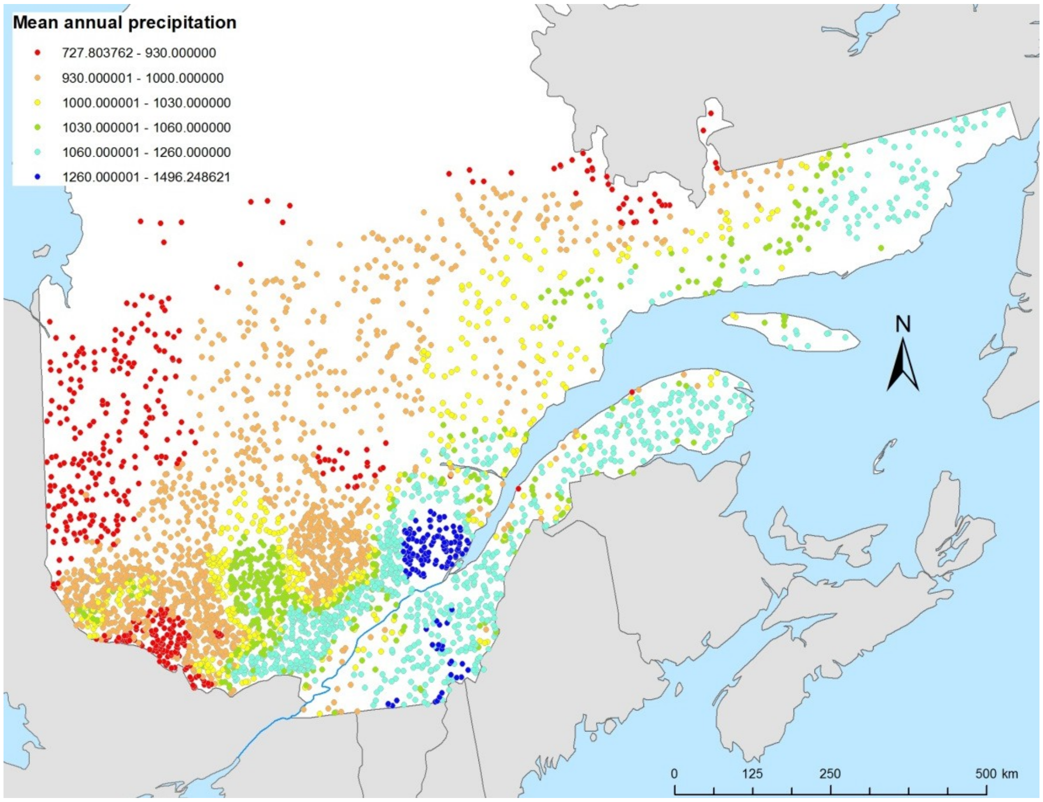

Figure 3.2: Mean annual precipitation (at plot level) between 1965 and 2003. Values based on interpolated models from weather station data (Regnière and Saint-Amant, 2008).

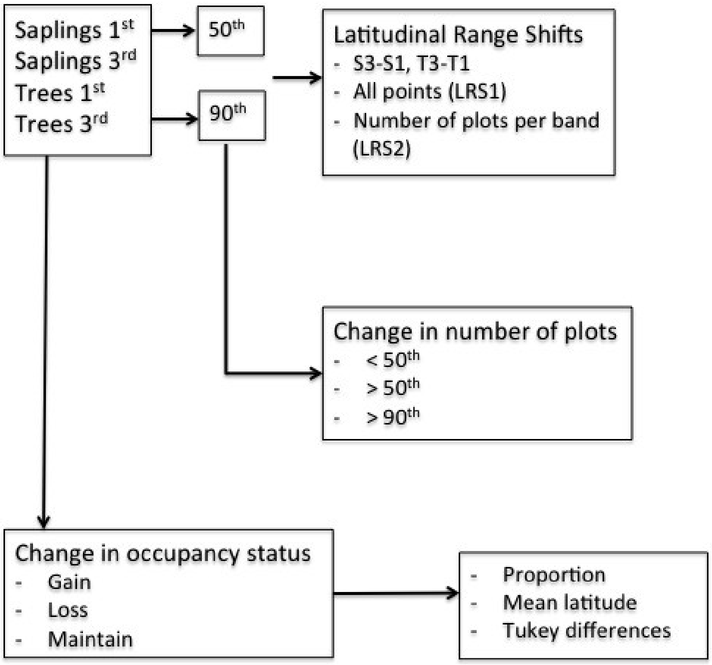

Figure 3.3: Flowchart of steps employed to summarize species range shifts

Chapter 4 - GENERAL CONCLUSION

This research provided a rare opportunity to investigate recently observed spatiotemporal trends of changing tree species distributions across large-scales. It is the first time that analyses of latitudinal range shifts have been coupled with changes in occupancy patterns to robustly interpret changes in northern distributions for trees. Both hypotheses about increasing range limits through time and greater plot occupancy were supported for some species; observed responses were species specific and difficult to group under a common ecological or functional response. Five species demonstrated significantly greater plot occupancy in the northern part of their sapling range in the third decennial while six species had sapling gains at the highest latitudes on average. Tree migration patterns varied depending on which life stage, portion of the range or method was examined. Nevertheless, 68% of the latitudinal differences at the 50th percentile and 61% of the latitudinal differences at the 90th percentile showed higher sapling range limits in the third decennial. Surprisingly, sapling range limits were mostly south of tree limits at the 90th percentile, especially in the first decennial and were not a good indicator of temporal trends for trees or saplings. Latitudinal range shifts calculated using S1-T1 would have correctly predicted the actual observed dynamics of saplings (S3-S1) and trees (T3-T1) 5 and 8 out of 14 times respectively. Overall, *B. alleghaniensis, A. rubrum, F. grandifolia, B. papyrifera* and *P. tremuloides* showed significant patterns of northward shifts due to higher latitudinal sapling limits and increasing occupancy in their northern area of distribution.

In future studies, this methodology could be repeated to confirm observed temporal trends. Not enough time elapsed between the two decennials for mature trees to show concerted directional trends. The fourth inventory of the Quebec forest inventory is expected to be completed by 2018 and will include signals of tree responses from some of the warmest years on record.

Also, incorporating data from the United States would provide a range-wide picture of how northern species are adapting. With the U.S. Forest Inventory Analysis now being conducted at regular intervals, sampling could eventually overlap with Quebec surveys. Combining these two potential studies will help confirm signals of changing ranges or uncover new emerging dynamics.

Even though the study area remains within the treeline, species will have to migrate into new biomes in order to maintain current range conditions. While the transition into the boreal forest seems feasible, migration into the tundra will undoubtedly be difficult and slow because of marginal soil conditions. Yet, in the tundra, boreal or temperate forest, not enough information is available describing what will happen when these species arrive. A proper balance of conservation and adaptive forest management over the short and long-term will be necessary to avoid overwhelming potentially stressed ecosystems.

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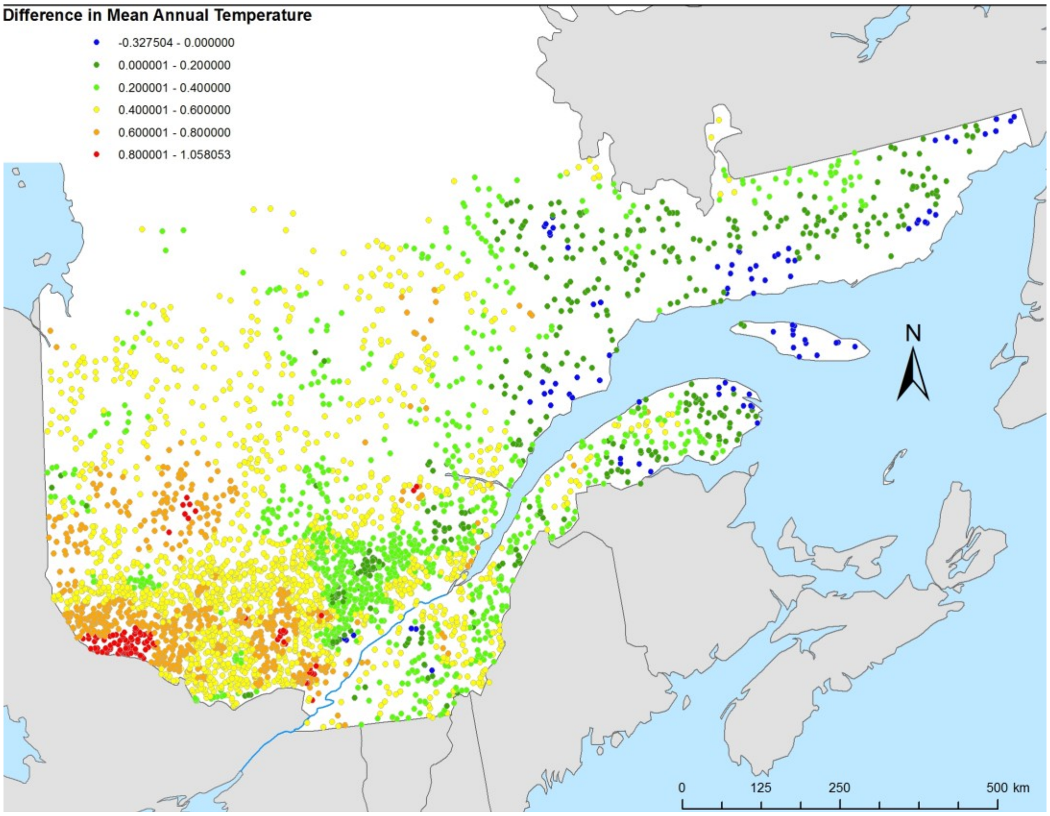
Appendix 1 - Plot level differences in mean annual temperature between 1965-1980 and 1985-2003 (average difference = + 0.4316^{o}C). Interpolated models based on weather station data (Regnière and Saint-Amant, 2008).



Appendix 2 – Supplementary results

Table 1: Percentage of plots and mean latitude for each occupancy category for a) saplings and b) trees. Values highlighted in bold are the highest mean latitude and highest percentage respectively for each species.

a)	**Gain**		**Loss**		**Maintain**	
	Latitude	%	Latitude	%	Latitude	%
Southern species						
Betula alleghaniensis	46.7099	46.76	46.6227	36.33	46.5896	16.91
Picea rubens	**46.7475**	42.98	46.6119	**44.74**	46.7188	12.28
Acer rubrum	**46.9125**	**37.24**	46.5898	25.81	46.7146	36.95
Acer saccharum	**46.506**	35.26	46.417	**40.74**	46.3919	24.00
Fraxinus nigra	**46.4759**	**37.21**	46.3205	32.56	46.2838	30.23
Fagus grandifolia	**46.3328**	**48.40**	46.3223	11.39	46.265	40.21
Ostrya virginiana	46.0362	**48.98**	**46.1336**	32.65	46.0064	18.37
Tsuga canadensis	46.1225	**40.70**	45.9378	29.07	**46.1267**	30.23
Thuja occidentalis	46.8175	25.00	46.5758	33.33	**46.8554**	**41.67**
Northern species						
Betula papyrifera	47.6663	32.66	47.3794	33.28	**47.7175**	**34.06**
Picea glauca	47.3095	38.39	47.4071	**46.25**	**47.442**	15.36
Picea mariana	48.0088	17.63	48.066	17.57	**49.2801**	**64.80**
Populus tremuloides	**47.366**	**51.43**	47.2886	37.67	47.3539	10.90
Abies balsamea	47.3289	17.16	47.4404	15.38	**47.7794**	**67.45**

b)	Gain		Loss		Maintain	
	Latitude	%	Latitude	%	Latitude	%
Southern species						
Betula alleghaniensis	46.7165	5.38	46.5339	11.24	**46.7605**	**83.39**
Picea rubens	**46.8124**	29.05	46.7771	31.62	46.5437	**39.33**
Acer rubrum	**46.8737**	11.67	46.8073	8.56	46.6891	**79.77**
Acer saccharum	**46.7972**	5.51	46.6128	7.21	46.4517	**87.27**
Fraxinus nigra	46.3962	17.84	46.3287	17.47	**46.4442**	**64.68**
Fagus grandifolia	46.0579	21.06	46.1766	8.20	**46.2631**	**70.73**
Ostrya virginiana	46.0603	12.27	**46.1332**	21.36	46.0837	**66.36**
Tsuga canadensis	46.1008	21.80	46.2676	10.53	**46.0982**	**67.67**
Thuja occidentalis	**46.8870**	5.99	46.6402	10.73	46.6931	**83.28**
Northern species						
Betula papyrifera	47.2230	7.93	**47.7117**	11.06	47.5254	**81.00**
Picea glauca	47.3742	28.27	47.2889	33.83	**47.9768**	**37.90**
Picea mariana	47.4637	7.84	47.5595	17.86	**48.6665**	**74.30**
Populus tremuloides	47.0276	14.32	47.2333	19.16	**47.3305**	**66.52**
Abies balsamea	47.5457	5.14	47.5378	11.26	**47.7171**	**83.60**

Table 2: Results of one-way analysis of variance and Tukey HSD tests for difference in latitudinal position of occupancy categories. Bold values are significant ($p<0.05$).

		Sapling Difference	p value	Tree Difference	p value
Betula alleghaniensis	Gain-Loss	0.0872	0.4263	0.1826	0.2111
	Gain-Maintain	0.1218	0.3671	-0.0441	0.8811
	Loss-Maintain	0.0347	0.9269	-0.2267	**0.0017**
Betula papyrifera	Gain-Loss	0.2895	**0.0006**	-0.4887	**0.0002**
	Gain-Maintain	-0.0490	0.8008	-0.3027	**0.0062**
	Loss-Maintain	-0.3386	**<0.0001**	0.1861	0.0732
Picea glauca	Gain-Loss	-0.0976	0.5988	0.0865	0.6250
	Gain-Maintain	-0.1325	0.6103	-0.6025	**<0.0001**
	Loss-Maintain	-0.0348	0.9646	-0.6890	**<0.0001**
Picea mariana	Gain-Loss	-0.0619	0.8954	-0.1019	0.7780
	Gain-Maintain	-1.2741	**<0.0001**	-1.1907	**<0.0001**
	Loss-Maintain	-1.2122	**<0.0001**	-1.0888	**<0.0001**
Picea rubens	Gain-Loss	0.1351	0.5641	0.0370	0.9242
	Gain-Maintain	0.0283	0.9890	0.2719	**0.0106**
	Loss-Maintain	-0.1068	0.8523	0.2349	**0.0269**
Acer rubrum	Gain-Loss	0.3235	**<0.0001**	0.0664	0.7345
	Gain-Maintain	0.2010	**0.0006**	0.1855	**0.0077**
	Loss-Maintain	-0.1225	0.0977	0.1191	0.2130
Acer saccharum	Gain-Loss	0.0892	0.1444	0.1845	0.2335
	Gain-Maintain	0.1149	0.0890	0.3462	**0.0003**
	Loss-Maintain	0.0257	0.8785	0.1618	0.0929
Fraxinus nigra	Gain-Loss	0.1555	0.4744	0.0675	0.8776
	Gain-Maintain	0.1921	0.3368	-0.0480	0.9003
	Loss-Maintain	0.0366	0.9632	-0.1155	0.5518
Fagus grandifolia	Gain-Loss	0.0106	0.9919	-0.1187	0.4340
	Gain-Maintain	0.0718	0.4124	-0.2038	**0.0014**
	Loss-Maintain	0.0613	0.7694	-0.0851	0.5859
Ostrya virginiana	Gain-Loss	0.0106	0.9919	-0.0729	0.7387
	Gain-Maintain	0.0718	0.4124	-0.0234	0.9593
	Loss-Maintain	0.0613	0.7694	0.0495	0.7486
Populus tremuloides	Gain-Loss	0.0760	0.7620	-0.2113	0.2050
	Gain-Maintain	0.0107	0.9978	-0.3080	**0.0085**
	Loss-Maintain	-0.0653	0.9249	-0.0967	0.5452
Tsuga canadensis	Gain-Loss	0.1848	0.3722	-0.1501	0.4182
	Gain-Maintain	-0.0041	0.9995	0.0026	0.9994
	Loss-Maintain	-0.1890	0.4049	0.1528	0.3173
Abies balsamea	Gain-Loss	-0.1094	0.5671	0.0084	0.9985
	Gain-Maintain	-0.4501	**<0.0001**	-0.1725	0.4093
	Loss-Maintain	-0.3407	**0.0003**	-0.1809	0.1358
Thuja occidentalis	Gain-Loss	0.2417	0.1297	0.2468	0.2262
	Gain-Maintain	-0.0379	0.9457	0.1940	0.2627
	Loss-Maintain	-0.2796	**0.0301**	-0.0528	0.8446