Biotic and abiotic effects on temperate tree range expansion at the boreal – temperate ecotone

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Abstract

The broad-scale effects of climate change on the distribution of species around the planet are relatively well understood, however our predictive powers of how species ranges will shift and re-organise are hampered by species' interactions with one another and their environments. An investigation into seedling emergence constraints of four northern temperate tree species beyond their realised geographical niche was conducted using the available literature and experimental manipulation of natural systems. Two iterations of the field experiment (2015/16 & 2016/17) allowed for development and evaluation of experimental design, particularly vertebrate herbivore exclosure design. Climatic variables were largely unimportant drivers of model species' ability to successfully emerge at experimental sites across Newfoundland, whereas biotic interactions impacted species-specific emergence, depending on reproductive strategies. Seed predation and canopy composition were among the most important biotic drivers of model species' emergence success.

Keywords: boreal forest, tree, ecotone, temperate forest, seed predation, seedling, Acer saccharum, Betula alleghaniensis, Fraxinus nigra, Thuja occidentalis, range expansion

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List of Acronyms

AIC	Akaike's Information Criterion
AICc	Corrected Akaike's Information Criterion
a.s.l.	above sea level
BDE	boreal – deciduous ecotone
BTE	boreal – temperate ecotone
ER	evidence ratio
GDD	growing degree days
GTREE	Global Treeline Expansion Experiment
LBC	large box cage
LRC	large round cage
NRCan	Natural Resources Canada
NTSC	National Tree Seed Centre
RH	relative humidity
SBC	small box cage
ZIB	zero-inflated binomial

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Co-Authorship statements

Evans P and Brown CD. 2017. The Boreal-Temperate Forest Ecotone Response to Climate Change. *Environ Rev,* **25**(4): 423-431. DOI: 10.1139/er-2017-0009.

PE and CDB conceived the review. PE collected the data, which was later supplemented by CDB. PE extracted information from the literature in consultation with CDB. PE wrote the first draft of the manuscript, which was then critically revised by both authors.

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PE, ED, and CDB conceived the study. PE and ED collected the data. PE executed the analyses in consultation with CDB and ED. PE and ED wrote the first draft of the manuscript, which was then revised by all authors.

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PE and CDB conceived the experiment. PE and CDB reviewed the literature and devised the experimental design. PE and others established first year experiment in 2015 and PE and AC collected 2016 data, set up the second year of the experiment, and collected all data in 2017. PE wrote the first draft of the manuscript and performed analysis in consultation with CDB and the manuscript was then reviewed by all authors.

Chapter 1: Introduction

1.1 Research Context

The implications that climate change holds for species' distributions and ranges have become an increasingly important topic of research and discussion spanning multiple disciplines. Many have forecasted a geographic re-distribution of species from scales ranging from global (Parmesan and Yohe 2003), to sub-continental (Iverson and Prasad 2002), to regional and local (Koca *et al.* 2006) perspectives. Others have focussed on other types of climate change induced shifts, such as changes in phenology (Walther *et al.* 2002) and evolutionary adaptive capacity (Davis and Shaw 2001). Exploring modern plant species' range dynamics is an optimal starting-point for trying to understand how global climate change will affect natural terrestrial systems. Trees, in particular, are important habitat-forming organisms (Thomsen *et al.* 2010), and their presence, absence, and abundance, coupled with the variety and type of plant species present at a biome spatial scale is both reflective of the current climatic regime and to some extent dictates the faunal assemblage within that biome.

Tree species range shifts have been occurring throughout the Quaternary Period as a result of changing climatic conditions. Such shifts have been recorded in the fossil pollen record, studies of which have revealed repeated southward and northward range shifts in concert with dramatic, large scale climatic swings during glacial events (Comes and Kadereit 1998), and shorter, more localised climate events such as the little ice age (Hupy and Yansa 2009). These shifts have been recorded around the world (Davis and

Shaw 2001), but it is a modern shift within the eastern North American portion of the boreal forest-temperate forest ecotone (BTE) that is of interest here.

The BTE is the transition zone wherein the northern extent of the temperate forest overlaps with the southern extent of the boreal forest; it occurs in eastern North America, northeastern Europe and eastern Asia (Goldblum and Rigg 2010). This transition occurs, generally, along a north-south gradient where both tree species diversity and average annual temperature decrease with increasing latitudes, with thermal conditions often considered as the primary factor determining the BTE location (Arris and Eagleson 1989). The eastern Asian portion takes some exception to this, and is rather more of an altitudinal gradient – and is therefore compressed – than a gradual latitudinal gradient (Ohsawa 1984, 1990). In North America the BTE is at its widest, and occupies a zonal band from southeastern Manitoba to the Gaspé Peninsula, Quebec and from western Minnesota to Cape Breton Island, Nova Scotia (Olson *et al.* 2001; Goldblum and Rigg 2010). Despite portions of the island of Newfoundland (herein Newfoundland) falling within the latitudinal zone inhabited by the BTE, expected species assemblages (Table 2.1) are not found here, due to the fragmented eastern coastline.

The dispersal barrier posed by the Gulf of St. Lawrence and the Cabot Strait may represent future distribution spatial losses for several northeastern species. McKenney *et al.*'s (2007) tree species redistribution model forecasted a generally northwestern shift in appropriate climate envelopes and a decrease in size of the same for the majority of the 130 tree species in their study. This extends the work by Iverson *et al.* (2008), which is limited in its predictive power for northern species' ranges due to truncation of study area at the US-Canada border, but which nevertheless also forecasts an overall north-eastward shift in future potential habitat for the majority of the 134 species in their study. As is covered to a greater extent in Chapter 2, there appears to be good agreement between forest distribution models that a northward shift of many North American tree species will occur, and that this will occur in a piecemeal fashion. Shifting species ranges will also move the BTE to a more northerly zonal band, and continued climate change is likely to produce climatically suitable niche space in Newfoundland for an increasing number of northern temperate species. Beyond the major dispersal barrier, this project investigates what other constraints will act upon tree species no longer limited by climate at their earliest life stages in Newfoundland.

1.2 Constraints on Species Range Shift

The Theory of Island Biogeography introduced the concept that an island geographically closer to a mainland source or species pool will, in general, possess greater species richness than if it were far from a mainland (MacArthur and Wilson 1967), which can alternatively be thought of as distance and history-dependent connectivity between communities (Barber *et al.* 2000). Wallace's Line, which separates the Malay Archipelago in two distinct ecozones, is a well-known example of this and shares similarities with the less dramatic and far less researched ecological boundary between the island of Newfoundland and Nova Scotia in eastern Canada (Olson *et al.* 2001). The Gulf of St. Lawrence-Cabot Strait seaway currently draws the far eastern dividing line between the boreal forest biome and the northeastern extent of the BTE in North America (Olson *et al.* 2001; Goldblum and Rigg 2010).

Deep water channels that persisted through repeated drops in sea-level now draw the dividing lines that make up Wallace’s Line (Mayr 1944), and a loose parallel can be seen here between Newfoundland and mainland Canada. The modern Cabot Strait separates the island from Nova Scotia to the southwest at a minimum distance of 110 km and it, as well as the narrower Strait of Belle Isle to the north, are likely to have remained submerged during the last glaciation (Shaw *et al.* 2002). The most recent bridging between Newfoundland and mainland Canada that is thought to have occurred was by ice, until approximately 14 ka and 12 ka, to the south and north respectively (Shaw *et al.* 2006). A post-glacial land-bridge seems unlikely given the island’s depauperate faunal assemblage (Strong and Leroux 2014), which is void of indigenous reptile or freshwater fish species (Dodds 1983). Examination of the island’s faunal species assemblage also indicates both the primary direction of terrestrial species influx (i.e., from the north) as well as the suspected methods of over-ice, or aquatic (i.e., swimming) dispersal. Similar assumptions cannot necessarily be made regarding Newfoundland’s predominantly boreal plant species assemblage.

The post-glacial floral recolonization of Newfoundland has not been extensively studied, but MacPherson's (1995) re-construction of tree species colonisation and range expansion on the island using the lake sediment pollen record provides an excellent overview. The primary direction of tree species expansion into post-glacial Newfoundland was from the southwest, beginning with the introduction of shrub birch (*Betula spp.*) followed closely by spruce (*Picea spp.*) and fir (*Abies balsamea* [L.] Mill.) before 10 ka and approximately around 10 ka, respectively (Anderson and Lewis 1992;

MacPherson 1995). Most of the remaining species that compose Newfoundland's forest canopy followed along the same route: arriving in southwestern Newfoundland and radiating from there. MacPherson's (1995) chronology extends from approximately 10.2 ka to the present and documents the arrival times of pine (*Pinus spp.*) at ~8.5 ka and ash (*Fraxinus nigra* Marsh.) at ~7 ka. Interestingly this chronology does not mention either of the maple species present on the island (*Acer rubrum* L, & *A. spicatum* Lam.), both of which are now common throughout large portions of the island (Farrar 1995). I have similarly been unable to find evidence of the mechanisms for tree species' dispersal to Newfoundland, however Macpherson (1995) does give mention to wind dispersal of pollen grains and for small-seeded boreal species, wind is the most likely candidate.

Beyond the initial long distance dispersal hurdle potentially barring temperate tree species' natural colonisation of Newfoundland under a warming climate regime, there is a complex suite of filters that also act to block successful colonisation. These filters can be individually difficult to overcome, or may combine through interactions to overwhelm species' adaptive abilities, and a more fulsome description and discussion on this topic takes place in Chapter 2 (Evans and Brown 2017). Newfoundland's boreal forest has been recognised as being in a transitionary state driven by climate change, pressures from anthropogenic activity and various introduced species, most notably moose (*Alces alces* L.; ESTR Secretariat 2014), which signals both opportunity and challenges for the establishment or expansion of temperate tree species range on the island. This project, however, investigates the role of seed predators (see Chapters 3 & 4) that have been found to impose significant herbivory filters on red maple (*Acer rubrum* L.) at early life history stages in Newfoundland (Kasimos 2007). Seed predation pressures are also exerted within the BTE when temperate species have attempted to colonise boreal coniferous stands (Brown and Vellend 2014).

Inappropriate soil conditions within future or fundamental climatic niche space represents another potentially challenging barrier to the successful colonisation of new, northern habitat for temperate tree species (McKenney *et al.* 2007; Lafleur *et al.* 2010). “Soil conditions” encompasses a wide range of characteristics and a comprehensive understanding of how soil conditions filter temperate tree species establishment upon emergence, including the interplay between the substrate, organic layer and mineral sub-soil and their constituent components is the scope of a separate project. Here, I am interested in how substrate properties, such as radicle/root penetrability (Wheeler *et al.* 2011), moisture retention (Cornett *et al.* 2000), temperature regimes (Burton and Bazzaz 1991), and the interplay with canopy composition act to filter northern temperate tree species emergence beyond their distributional ranges.

A further and more encompassing constraint may lie within the concept of ecological inertia, which has been defined by Orians (1975) as the capacity of an ecosystem to resist change, and by Westman (1978) as a community-level resistance to degradation due to some calamity, such as the introduction of a toxin. The change, in this case, could be due to the introduction of new species that may act as ecosystem engineers to change environmental variables in favour of their own perpetuation, rather than that of the native individuals (Jones *et al.* 1997; Crooks 2002). Ecological inertia could therefore be applied to a community’s ability to self-perpetuate in the face of changing conditions, and the boreal forest has been found to excel at resisting invasion of non-native species in a variety of ways (Loehle 2000; Collin *et al.* 2016). This in turn could be causing an immigration lag of temperate species into boreal forest stands, as discussed by Svenning and Sandel (2013), who refer to patches of suitable habitat for newly arriving species that become slowly expanding nodes that eventually connect to the originally occupied range. While biome-level resistance to invasion by exotic species is outside the scope of this work, I do aim to draw a link between forest canopy composition and substrate type as a means of qualifying biotic interactions that could serve as a proxy for ecological inertia at the micro-scale. This will allow me to investigate the subtle differences in a/biotic conditions in two common forest types in Newfoundland that lead to their respective assemblage and which may create the opportunity for the expansion of suitable temperate tree species habitat as the climate continues to change.

The goal of this work is to build on the current understanding of how abiotic and biotic factors constrain the range shifts of northern temperate tree species under changing climate regimes. Using a manipulative seed addition experiment in open-air field sites, I tested the emergence ability and capacity of four northern temperate tree species within and beyond their range against the following factors: (1) moss and leaf litter substrates under their corresponding conifer-dominated and mixed deciduous-coniferous canopies and the reciprocal, (2) alleviation of terrestrial vertebrate herbivory pressure, (3) forest canopy composition, and (4) climatic factors relevant to each model species. This work aims to address the earliest and most vulnerable life stages of the model species, and therefore will begin to reveal how these particular factors combine and interact to impact shifting species ranges.

1.3 Model Species

Four northern temperate tree species are being used in the present study – two of which are native to Newfoundland, and two of which have been introduced. Yellow birch (*Betula alleghaniensis* Britt.) and black ash (*Fraxinus nigra* Marsh.), reach their northern distributional limit in Newfoundland (Erdmann 1990; Wright and Rauscher 1990), whereas northern white cedar (*Thuja occidentalis* L.) and sugar maple (*Acer saccharum* Marsh.), are present in central and eastern Canada, but have not colonised the island (Godman *et al.* 1990; Johnston 1990).

Yellow birch has limited distribution on the island (Farrar 1995), and has long been noted as having poor reproductive success, even in ideal sites (Robertson 1945). Little work has been published on how this species' range is controlled on the island, but herbivory pressure by non-native moose has been described as a general limiting factor (McLaren *et al.* 2006). In mainland Canada, yellow birch is a well-studied commercially important species (Wood and Bormann 1974, Houle 1994, 1998). Emergence and early survival has been shown to be particularly sensitive to changes in substrate type and soil moisture (Linteau 1948, George and Bazzaz 1999) and seedling growth occurs best in mixed mineral/hummus soil over duff and exposed mineral soil (Wang 1965). More recent studies have confirmed that mineral soil is more likely to promote yellow birch emergence and survival (Caspersen and Saprunoff 2005), and that moss substrate is much less favourable (Lambert *et al.* 2015). However the permeability of a mossy substrate could promote yellow birch emergence over the barrier posed by leaf litter (Burton *et al.* 1969). For moss or leaf-litter substrate, the implications of canopy composition may become a dominant factor, where deciduous canopies pose the risk of smothering emergent birch seedlings (Burton *et al.* 1969). These limitations likely hold true in Newfoundland, but no publications make direct associations between specific substrate conditions or canopy compositions that exist on the island and the emergence success and seedling survival of this species. Similarly, it does not appear that publications exist focussing on seedling herbivory and seed predation pressures on yellow birch in Newfoundland's forests.

The other native species in this study, black ash, is of particular conservation concern in Canada (COSEWIC 2016) and across its range in North America due to the ongoing spread of the emerald ash borer (*Agrilus planipennis* Fairmaire). There is no evidence of this pest having reached Newfoundland yet and there is limited expectation that Newfoundland will become climatically well suited to this invasive pest in the next 30 years (Liang and Fei 2014). This can be viewed as a potential conservation opportunity, wherein understanding why the resident population of black ash is so geographically constrained to several small patches of habitat on the island's west coast (Farrar 1995) could allow for the assisted establishment of a refuge population of this threatened ash species. This species is poorly represented in the literature on germination and seedling survival limitations in the field, especially when literature concerning the emerald ash borer is omitted. From experimental germination studies carried out in the lab, Steinbauer (1937) and Vanstone (1974) clearly showed the importance of the warm followed by cold stratification requirements of this species, however it was difficult to find any publications experimentally testing the effects of limiting factors on emergence outside of a lab or tree nursery setting (but see Wright and Rauscher 1990). This is likely explained by the difficulty overcoming seed dormancy in this species (Bonner and Karrfalt 2008), a process that can take two years, making it a difficult species for typically time-constrained field studies. Ehrenfeld (2012) describes black ash as a species that is sensitive to drought, tolerant of a range of soil conditions and is seldom a dominant stand species, but also recognises the gaping lack of data on this species.

Sugar maple is well represented in the literature on a range of topics, and is a common model species in the ongoing discussion of a BTE shift in North America (Evans and Brown 2017). It is a characteristic species of this ecotone, and the factors limiting its passage from one life stage to the next are well studied. Sugar maple is known to preferentially germinate under cold temperature (≤5°C) conditions, often with measurable intra-specific variations in optimal germination temperature (McCarragher *et al.* 2011; Solarik *et al.* 2016). Caspersen and Saprunoff (2005) found that sugar maple was well adapted to emerging on a leaf litter substrate, which presents a nearly insurmountable barrier to smaller-seeded yellow birch. Maple seeds have been found to be highly vulnerable to predation beyond their distributional range (Kasimos 2007; Brown and Vellend 2014). Some experimental planting of sugar maple beyond its range has been done (e.g., Kellman 2004; Brown and Vellend 2014), however no such work has been published on experimental studies involving field emergence of this species in

Newfoundland. Despite this, sugar maple may be well suited to parts of Newfoundland, as the climate of the island is appropriate and it already inhabits areas that are geographically close (Farrar 1995), have similar soil types (Agriculture and Agri-Food Canada 2015) and are climatically similar (i.e., the Gaspé Peninsula and Cape Breton Island; Environment and Climate Change Canada 2017).

White cedar appears well-suited to make the leap to Newfoundland, for similar reasons as those given for sugar maple. Paul *et al.* (2014) hypothesised that white cedar's northern range boundary in Quebec (Farrar 1995) may be determined by late spring frost events or low annual growing degree days (GDD) that reduce seedling emergence and survival. Paul *et al.* (2014) did, however, reveal lingering climatological impediments to this species' success on the island, much of which has lower annual GDD and a shorter growing season than the marginal sites described (Agriculture and Agri-Food Canada 2013a, b). Yet the species' native range also includes areas with growing season traits similar to those on the island (Agriculture and Agri-Food Canada 2013c, d). White cedar emergence and seedling survival also appears to be impacted by substrate qualities (Cornett *et al.* 2000) and canopy type (Buda *et al.* 2011), although these factors have not been tested under open-air conditions in Newfoundland. It is unclear how white cedar is impacted by seed predation; Bartlett *et al.* (1991) found that predation did not seem to be a factor for this species' early life survival in Ontario, likely because its seeds are not differentiated from those of typical boreal species. However, at the sapling stage herbivory does become a limiting factor (Rooney *et al.* 2002).

According to models released by Natural Resources Canada (NRCan 2017), all four of these model species have suitable, yet unoccupied habitat across much of Newfoundland. The maximum entropy models used by NRCan employ only climatic variables in their calculations of probability of occurrence, which reinforces the assertions of Evans and Brown (2017) that non-climatic limiting factors are of increasing importance when climatic limitations are alleviated or absent.

1.4 Chapter Overviews

Chapter 2

This chapter serves as my literature review on the subject of the changes that have been studied and observed at the global boreal BTE due to changing climate regimes, in the academic literature. The goal of this review and synthesis was to unify research performed at locations within the BTE around the world into a meta-analysis, similar to that which Harsch *et al.* (2009) performed for the global Arctic and alpine treeline. We quickly realised, however, that changes occurring within the BTE have not been nearly so extensively studied as those occurring at treelines, and so one of the primary findings was the need for more research on several facets of this subject: (i) the need for research on a greater diversity of species, (ii) the need for more studies performed outside of North America, with particular focus on eastern Asia and European Russia, and (iii) the need for additional research performed in eastern North America, particularly in eastern Canada (Evans and Brown 2017). In the process of building a conceptual framework from the relevant literature, we were also able to identify potential drivers filtering out colonising tree species either at specific life history stages, or global filters that act on individuals across life stages. Of these, we were able to identify those that are not well understood and that require evidence to support their position in the framework.

Chapter 3

During the two years' worth of data collection for the research presented in this thesis, I came across several challenges in the design, construction and logistics of building herbivore exclosures. One problem in particular that caught my attention, and the attention of University of Guelph PhD student Emma Davis, was the possibility that small herbivore exclosure cages deployed in an environment that experiences a snowy winter may alter the microclimate within the cage confines. We installed temperature sensors within three cage designs at one site, and one cage design at three sites, to collect data between September 2016 and June 2017. From this data we explored whether cage design, size and/or material were impacting temperature or snow accumulation and duration. Our findings indicated that cages with lids, regardless of the size tested, shortened the period of snow-cover when compared to the controls, whereas finer mesh size and larger cage size were more often associated with microclimatic differences compared to the control setting. We concluded that while it may be difficult to design away the possibility of altering within-exclosure microclimate, installing temperature sensors as we did is a relatively cheap and simple way to accounting for a difference in microclimate caused by herbivore exclosures.

Chapter 4

The two-year experimental field-based manipulative seed addition experimental results are presented in the manuscript in Chapter 4. The experiment represents, to my knowledge, the first time anyone has experimentally tested the effects of multiple biotic and abiotic drivers on seedling emergence of multiple temperate tree species across the southern portion of Newfoundland. This project had two iterations, and was first implemented at five sites in 2015 and again at eight sites in 2016 for data collection in the 2016 and 2017 emergence years. Manipulative treatments were enforced both implementation years on pots sown with the seeds of the four model species used: sugar maple, yellow birch, black ash, and eastern white cedar. Treatments included protecting seeded pots from terrestrial vertebrate herbivory, filling pots with either leaf litter or mossy substrate, and placing pots under varying degrees of “boreal” (conifer dominated) or “mixed” (increasingly deciduous dominated) canopy types. All sites were within mature forest stands and treatments were carried out in full-factorial block design within sites, where each block contained all combinations of the herbivory and substrate treatment for each species. Climate sensor arrays were installed within each forest type at each site in 2016 to provide hourly air and soil temperature and soil moisture readings to determine whether microclimate variation might play some role in promoting or hindering seedling emergence. Emergence data for 2016 and 2017 were treated as a binary response (was there a seedling observed in a pot or not) and binomial response (how many seedlings emerged, given the number of seeds sown per pot), and each species’ data were analysed using two predictor variable categories: treatment and climate variables. Models created for each *species* x *response* x *predictor variable* for each emergence year were ranked using AICc table analysis.

The results reveal a mixture of seedling emergence patterns that match the results of those who have carried out similar experiments elsewhere, as well as some surprises. There appear to be distinct combinations of drivers acting on species according to life history strategies – here namely the size of each species' seed. The results from both years of this experiment support findings of experimental research within the home ranges of sugar maple and black ash that these species (or close analogues) suffer more due to seed predation than other species due to the size of their seed (De Steven 1991), whereas the smaller seeded birch and cedar emergence was reduced in the presence of smothering deciduous canopy cover, but responded unexpectedly well to a leaf litter substrate, contrary to others' findings (Caspersen and Saprunoff 2005). Graphical interpretation of emergence data correlation with climate variables revealed that only black ash emergence was well correlated with climatic variables, whereas climatic variables were unimportant for all other species.

Chapter 5

The final chapter frames the findings of Chapters 3 & 4 within the context outlined in the Introduction and Chapter 2. Focus is given to synergise the findings in Chapter 4 with the work done in Chapter 3 to explore how potential methodological issues regarding the use of small herbivore exclosures can be addressed. The overall objectives of the project are addressed and I summarise the relevance of this work to future studies of this kind both within Newfoundland and in other northern temperate forested settings.

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Chapter 2: The Boreal-Temperate Forest Ecotone Response to Climate Change

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Abstract:

A warming global climate will elicit changes in the distribution of plant species around the planet, and this will become most apparent where biomes converge. Climate exerts the strongest control over the geographic location of ecotones at the continental scale and many, including the boreal forest – temperate forest ecotone (BTE), are expected to shift to higher latitudes under climate change. Fine-scale drivers that define biome boundaries at the sub-continental scale are less well understood for many ecotones. We assembled studies addressing whether a modern distributional shift is occurring at the BTE and what biotic and abiotic factors are driving such a shift. Current research suggests a northward shift is occurring; yet, scant data are available to identify the processes involved. Abiotic and biotic factors are repeatedly identified as key drivers of change, though not all claims are evidence-supported and the interacting effects of these non-climatic factors are poorly understood.

Key words: ecotone, boreal forest, temperate forest, climate change, range shift.

2.1 Introduction

The global climate is warming at a faster rate at high latitudes than it is farther south (Stocker et al. 2013) and the effects of this change on forests are expected to be complex and varied. The implications of climate warming on plant distribution patterns seem, on the surface, to be obvious: as the climate at higher latitudes and elevations changes, plant distributions should shift in concert. Strong correlations between recent climate warming trends and latitudinal and elevational shifts in species' distributions have been found in many systems (Walther et al. 2005, Chen et al. 2011, Boisvert-Marsh et al. 2014), yet the complexity of species' responses are becoming increasingly apparent (Lafleur et al. 2010, HilleRisLambers et al. 2013) and the simplified view of a directional shift fails to appreciate the unevenness with which changes in regional climate are occurring (Walther et al. 2002). A commonality across biomes is the occurrence of time lags in climate-induced range shifts; these time lags appear to vary by species and geographic and topographic situation (Parmesan and Yohe 2003, Bertrand et al. 2011, Savage and Vellend 2014). Global-scale predictions of plant distribution patterns are therefore spatially general at best, and even regionalized inferences of future plant distributions based on climate predictions should be considered with caution (Walther et al. 2002).

The boreal forest biome has one of the largest geographic footprints of any terrestrial biome on the planet, encircling the globe in the northern latitudes (Olson et al. 2001). To date, range shift research in this biome has predominately focussed on the advance of boreal tree species into tundra or alpine habitats (i.e., treeline advance; see

Harsch et al. 2009), or the species-specific responses of temperate tree species (e.g., Zhu et al. 2012). An ecotone that has received less attention, yet which is a critical transition between two economically, culturally, and ecologically important biomes, is the southern boreal forest-northern temperate forest ecotone (herein referred to as BTE; Goldblum and Rigg 2010). The temperate forest biome is not nearly as expansive as the boreal forest, and so the BTE exists only in eastern North America, northern Europe and European Russia and eastern Asia (Pastor and Mladenoff 1992). The BTE is still largely intact in North America, contrary to Europe and eastern Asia where human activities such as agricultural expansion and logging have eliminated or modified large tracts of ecotone forest (Pastor and Mladenoff 1992, Goldblum and Rigg 2010), creating substantial hurdles to our understanding of this ecotone.

Pastor (2016) warns of the disassembly of the BTE, as plant species' shifts with climate will be asynchronous both spatially and phenologically with dependent fauna, causing the dismantling of ecological communities. In order to accurately predict the shift of the boundary between temperate and boreal forests, which has considerable implications for ecosystem function and processes, a continental and global understanding of the actual response of the BTE to recent warming is needed. To that end, we see three critical questions for which a synthesis is needed: 1) What determines the current position of the BTE? 2) How has this ecotone changed in the past? 3) How will the BTE change in the future? We approached these questions by synthesizing current knowledge on temperate tree species response to climate change at the boreal-temperate ecotone using a standardized, focussed literature search. Specifically, we investigated whether a modern distributional shift has occurred in the BTE across the globe, identified the most common biotic and abiotic factors involved in limiting or facilitating this shift, and assessed whether knowledge gaps exist for specific regions, species, and processes.

We had a number of expectations prior to our literature synthesis. Loehle (2000) showed that ecotone response to climate warming along a latitudinal transect would be slow, exhibiting a lag effect due to resistance of the retreating forest biome. At the BTE, we anticipated that lag would be due to a combination of abiotic and biotic factors: i) the porous structure of moss- and lichen-dominated boreal substrates would limit the germination and establishment of temperate tree species; and ii) the palatability of large-seeded temperate tree species (e.g., *Acer* species) would result in their preferential predation by small mammals in boreal forest sites. We also expected that range expansion of species with distributions that predominately occur in the BTE (rather than centred in the temperate forest biome; see Table 2.1) could be an early indicator of temperate forest shifts into historically boreal forest stands, as they are already established in marginal environments for temperate species. To our knowledge, this is the first global synthesis to date of the response of the boreal-temperate ecotone to recent climate change (but see Goldblum and Rigg 2010 for an excellent review on the North American portion of this ecotone). Such a synthesis is critical, given recent rapid climate change and subsequent ecosystem shifts and community re-organization occurring globally (Beckage et al. 2008, Hobbs et al. 2009, Jump et al. 2012, Trant and Hermanutz 2014).

Table 2.1: Typical tree species occurring in the BTE mixed-wood forest in North America and Eurasia (modified from Pastor and Mladenoff 1992). Since we are attempting to make global observations about this particular ecotone, a broad range of species belonging to each biome must be considered; however, even at the global scale, many of the genera are common among geographically disparate instances of the BTE.

North America	**Europe**	**Asia**
Boreal species		
Abies balsamea	*Betula pubescens*	*Abies nephrolepis*
Betula papyrifera	*Picea abies*	*Betula ermanii*
Picea glauca	*Pinus sylvestris*	*Betula platyphylla*
Picea mariana	*Populus tremula*	*Picea jezoensis*
Pinus banksiana	*Sorbus aucuparia*	*Populus davidiana*
Populus tremuloides		
Northern temperate deciduous species		
Acer saccharum	*Carpinus betulus*	*Acer mono*
Betula alleghaniensis	*Fagus sylvatica*	*Fraxinus mandshurica*
Fagus grandifolia	*Quercus robur*	*Pinus koraiensis*
Pinus strobus	*Tilia cordata*	*Quercus mongolica*
Tilia americana		*Tilia amurensis*
Tsuga canadensis		*Ulmus propinqua*

2.2 The BTE

Before we begin dissecting how this ecotone is changing, a clear picture of the general principles governing its location and spatial extent are needed. An over-arching theme of all ecotones is the inter-specific competition that takes place under considerable environmental stress, as these areas are typically where distributional range edges converge (see Table 2.1 for species list; Burns and Honkala 1990 and references therein). The North American BTE (Fig. 2.1a) offers some exception to this, as the BTE is wide enough here to host the majority of some tree species' distributional range (Pastor and Mladenoff 1992). The European BTE (Fig. 2.1b) is comparatively narrower, and much more fragmented due to anthropogenic activities. The latter can also be said about the Asian BTE, which compounds the difficult definition of the ecotone with its predominant occurrence along spatially distributed elevational gradients rather than a continuous latitudinal gradient (Fig. 2.1c; BTE not defined; Ohsawa 1990).

The BTE is located in the mid to high latitudes, which means it will be exposed to large increases in both mean annual temperature and annual precipitation over the next century (Stocker et al. 2013). These are important factors affecting the location of the BTE, although the exact combination of agents that act to define its location (e.g., climatic, topographical, edaphic, or otherwise) are not yet wholly understood (Goldblum and Rigg 2010, Graignic et al. 2014). Arris and Eagleson (1989) found a strong association between the mean annual -40˚C minimum isotherm and the BTE in North America, yet the same relationship was not as strong in Europe or Asia. Even so, there is ample evidence that at the continent scale, climate is the most significant factor determining the location of the BTE (Woodward and Williams 1987). To date, work on the current and future impact of the most recent warming on the BTE has been primarily regionally focused.

2.3 Contemporary BTE change

We reviewed the literature pertaining to the response of the boreal-temperate forest ecotone (methods summarized below), and revealed three key findings: 1) approximately one-third of the studied BTE species and communities had evidence of a distributional shift in the direction predicted by climate change (Supplementary Table 2.1); 2) while climate is a dominant driver of species' distributions in the BTE, non-climatic factors play a critical role in determining a species' ability to respond to changing climatic conditions; and 3) scant data are available on the response of the BTE to climate change or the mechanisms driving that response. Here, we discuss those findings further.

2.3.1 Literature synthesis of BTE response to recent climate change

We used the Scopus online database to search the literature published prior to February, 2015 using the search terms focussed on “temperate”, “boreal”, measures of range expansion, migration, or shifts (see Appendix 2.1 for full literature search methods and parameters). This search produced 1,095 titles, which were then scanned to identify articles relevant to the subject of this study, producing a list of 123 candidate papers. To ensure that as many relevant articles were included as possible, subsequent searches were performed on the Scopus database using search terms that included resurvey and elevational gradient studies, which we found were not captured by our initial search. We also searched specifically for climate-response studies on species whose ranges centre in the BTE, rather than belonging to one biome or another, identified by Pastor and Mladenoff (1992; see Table 2.1 for species list). These secondary searches produced a further 18 relevant publications. Finally, we scanned the reference lists of relevant publications for titles that the primary or secondary searches may have missed. This produced an additional 56 articles, raising the total of relevant articles in our study to 178.

Papers were individually evaluated to determine suitability for the current study. The response variable of interest was the detection, or lack thereof, of temperate tree establishment in boreal forest stands using experimental or observational methods. Studies needed to experimentally test or observe whether a range shift of ecotone-forming species was possible at or beyond the current BTE. We did not require the confirmation of range shift at the ecotone, as this would effectively omit many experimental studies that tested the possibility of range shift (e.g., Kellman 2004, Brown and Vellend 2014). Additionally, information was collected for each study on: (1) study design, (2) geographic location(s) of study site(s), (3) habitat type(s), (4) tree species studied, (5) life stage studied, (6) a/biotic variables studied, (7) measurement method(s), (8) important (a/biotic) drivers, (9) temporal duration of study, and (10) qualitative tree responses to climate (Supplementary Table 2.1). Elimination of studies from our database were designated as being due to subject, exposure, or response (see Koricheva et al. 2013). After the article scan, 62 candidate papers remained from the initial search. After a final reading of individual papers and the inclusion of the latest relevant publications as of December 2016, the final list of titles was cut to 27 papers (Fig. 2.1; Supplementary Table 2.1).

2.3.2 Have temperate tree species' ranges shifted northward?

Our synthesis indicated that nine of the 27 published studies detected through our methods provided evidence of a distributional shift of the BTE in the direction predicted by climate change (~33%). That ratio is lower than that found by Harsch et al. (2009) for the forest-tundra ecotone, where ~52% of treelines had shifted upward or northward with warming. When we compare our results to Harsch et al. (2009), some interesting contradictions are revealed between species at the southern and northern end of the boreal forest. Black and white spruce (*Picea mariana* and *Picea glauca*, respectively) are two common species in North American northern treeline research, both of which have been found to be shifting northwards with climate change (Lescop-Sinclair and Payette 1995, Payette 2007). This northward shift is often associated with a southern range contraction to form an overall distributional shift (Davis and Shaw 2001); however, Boisvert-Marsh et al. (2014) found that while many southern species had expanded beyond their northern ranges, neither black nor white spruce had experienced southern range contraction. They note that climate change and human-altered disturbance regimes in the BTE may be opening up niche space for boreal and temperate species alike.

At both the northern and southern edge of the boreal forest, it is interesting to look at the examples of ecotones that did not respond as predicted. The number of examples of a BTE shift in the opposite direction than expected in our search results was limited to one (Foster and D’Amato 2015), whereas the remaining studies reported that no shift had occurred as species’ distributions were simply static, or only shifts in abundance or species dominance were observed (Supplementary Table 2.1). In the boreal-tundra ecotone (treeline), the remaining 48% of treelines were predominantly static, showing no discernible response, and the authors hypothesized a combination of complex climatic constraints on treeline advance (e.g., ice damage, winter desiccation; Harsch et al. 2009) in combination with ecological time lags. We propose that the lack of BTE response to climate warming at the southern margin of the boreal forest is the outcome of ecological time lags driven by complex biotic and abiotic interactions.

2.4 Biotic and abiotic determinants of the current BTE location

While we stress that we are simply identifying observable trends in the limited research available on this topic, there are undeniably common themes that have emerged in our results – the strongest of which appears to be how changing climate regimes are affecting the BTE. The effect of climatic factors, particularly changes in temperature and precipitation regimes, on other biomes and ecotones around the world are better studied (Parmesan and Yohe 2003, Olivares et al. 2015). From these changes, some species stand to benefit from climate change in the form of expanding fundamental niches (Williams et al. 2014), while others are expected to have increasingly reduced available niche space (e.g., alpine meadows; Brandt et al. 2013). Sixteen of the 27 studies in our database demonstrated (11/27) or suggested (5/27) temperature as a factor in determining the position of the BTE (Supplementary Table 2.1 for this and all following enumerations). Half the studies (14/27) also suggested some other form of climatic control over the position of the BTE, which can be broken down into three groups: (i) precipitation or moisture availability, (ii) storm severity or wind throw events, and (iii) growing season length or timing of frost events.

Climate change could provide a common thread throughout the majority of the research our study uncovered; however, changes occurring in the global BTE are by no means solely climate-dependent, and the degree to which non-climatic a/biotic factors contribute to the observed changes is still poorly understood. Many studies tested, hypothesised, or made inferences to biotic interactions that could act as a negative feedback to northward shifts in the BTE (e.g., temperate sapling herbivory: Fisichelli et al. 2012, seed predation, soil biota: Brown and Vellend 2014). In some cases these interactions were quantified and were found to have the effect of slowing the northward advancement of southern temperate tree species. When the biotic interaction was herbivory, that slowing was often due to the higher nutritional value and better palatability of the seeds or foliage of deciduous tree species compared to predominantly coniferous boreal species (Kellman 2004, Fisichelli et al. 2012, Frelich et al. 2012). In contrast, biotic interactions can also result in a net positive feedback with regards to temperate tree species' northward advancement. Pest infestations in southern boreal stands have been found to increase the likelihood of a northward shift in the BTE at the regional scale by creating gaps that facilitate the establishment and often lead to dominance of southern species at the local scale (Grundmann et al. 2011, Boisvert-Marsh et al. 2014).

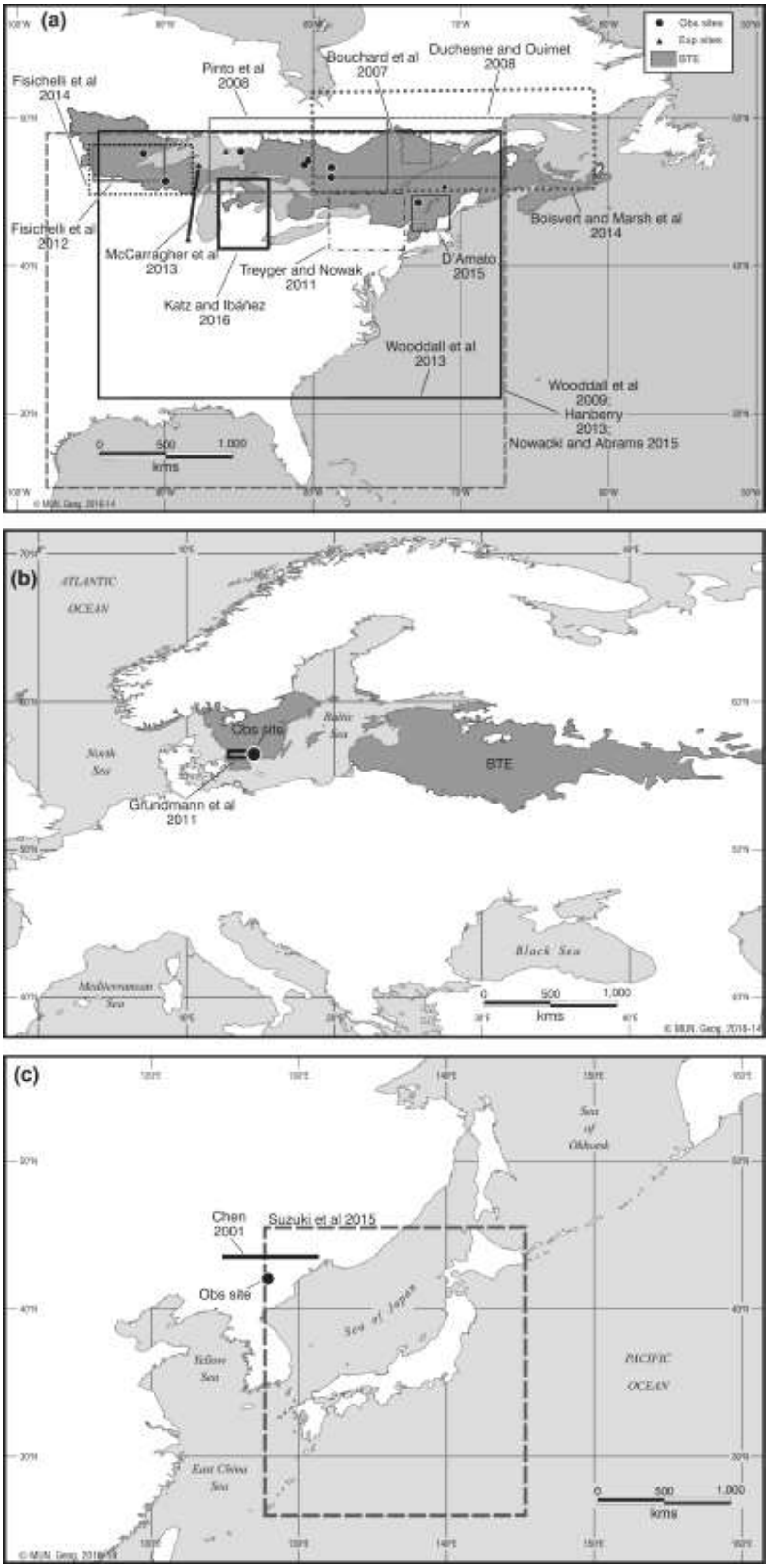
While biotic interactions can be difficult to monitor and measure, proving problematic to separate from climatic drivers (see Brown and Vellend 2014), abiotic non-climatic factors such as edaphic qualities and disturbance regimes are better understood. Lafleur et al. (2010) argues that while climate change will likely lead to northward shifts in tree species ranges of boreal and temperate species alike, this progression will be piecemeal and uneven due to species-specific edaphic constraints. Empirical evidence supporting Lafluer et al.'s (2010) argument is emerging. Edaphic factors are well represented in the research found in the present study; there are a wide range of soil characteristics cited as contributing factors in determining the location of the BTE including moisture and temperature (Goldblum and Rigg 2005), the interplay between moisture and nitrogen content (Pastor and Post 1988), nutrient content (Bai et al. 2011), pH (Fisichelli et al. 2013), and texture and depth to parent material (Lee et al. 2005). Researchers suggest that temperate species' ability to track a warming climate will be constrained by shallow, coarse, poorly drained, and acidic soils.

A critical point that has emerged from our synthesis is that no single variable has stand-alone effects on tree species distributions; instead, the response of BTE tree species to climate change is the result of the interacting effects of multiple drivers. To further complicate the story, those drivers cannot always be categorized as abiotic or biotic, climatic or non-climatic. Soil is an excellent example; a combination of biotic (e.g., soil biota) and abiotic (e.g., moisture capacity) drivers, soil characteristics can have immensely complex influences on tree species' abilities to track changing climate (Brown and Vellend 2014, Lankau et al. 2015, Katz and Ibáñez 2016) with feedbacks between newly arriving tree species and the soils they encounter (e.g., increasing soil fertility through increased nitrogen input; Pastor and Post 1988). Disturbance regimes are also the result of complex interactions between climatic and non-climatic factors (e.g., temperature and fuel load) or biotic and abiotic variables (e.g., climate-induced range expansion of herbivores). The disruption of these regimes can have far-reaching consequences on species composition that must be considered when contemplating the modern composition of the BTE, and its future (Nowacki and Abrams 2015). The message, then, is that any study of a species distributional response to climate change must not only incorporate climatic and non-climatic factors, but also the interactions between them.

2.4.1 Constraints on life history stages

Many factors that act to constrain the northward expansion of temperate tree species into boreal stands reoccur frequently in the literature, and act as filters that weed out potential colonising tree species at different life stages. In organising them into a conceptual framework (Fig. 2.2), one can view the normal life-cycle of a given tree species that has the chance to establish a population in an area it previously did not inhabit. This population will, under normal conditions, begin with the arrival of seeds in a new location which must then germinate, survive, and propagate. At each life stage, filters can have different levels of impact on or relevance to a new colonising population given its genetics, demographics, physical setting, and proximity to disturbance and vectors of dispersal. Global filters act on a given tree species at all life stages. It is important to note that many of the filters in our conceptual framework are hypothesised in the literature, not directly supported by evidence. The inclusion of unsupported filters is meant to draw focus to areas that we have found to be under-represented in the literature to date, and serve as a roadmap for future work to address knowledge gaps in our understanding of which and how drivers interact with species occurring in the BTE. Additionally, more work is needed in order to solidify the relationships between known drivers and those yet to be revealed, as well as to quantify their influence on the location of the BTE under the influence of global warming.

A general constraint that was not captured by our literature review, but is an increasingly important consideration when researching species range shifts, is the potential for phenological mismatch between plant species and their pollinators


(a)
Obs sites
Exp sites
BTE
Fisichelli et al 2014
Pinto et al 2008
Bouchard et al 2007
Duchesne and Ouimet 2008
Fisichelli et al 2012
McCarragher et al 2013
Treyger and Nowak 2011
Katz and Ibáñez 2016
D'Amato 2015
Boisvert and Marsh et al 2014
Wooddall et al 2013
Wooddall et al 2009; Hanberry 2013; Nowacki and Abrams 2015
0
500
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kms
© MUN. Geog. 2016-14
(b)
ATLANTIC OCEAN
North Sea
Baltic Sea
Obs site
BTE
Grundmann et al 2011
Black Sea
Mediterranean Sea
0
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© MUN. Geog. 2016-14
(c)
Sea of Okhotsk
Chen 2001
Suzuki et al 2015
Obs site
Sea of Japan
Yellow Sea
PACIFIC OCEAN
East China Sea
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Figure 2.1: The spatial extent of the BTE and distribution of studies in (a) North America, (b) Europe, and (c) Asia. The North American BTE was assembled here using Nearctic mixed forest terrestrial ecoregions from Olson et al. (2001) and closely resembles the outline of Goldblum & Rigg's (2010) boreal-deciduous ecotone (BDE). The European BTE is represented here using the Sarmatic Mixed Forest Ecoregion from Olson et al. (2001), which matches earlier descriptions of the Hemiboreal zone outlined by Ahti et al. (1968). Studies show small and large-scale observational and experimental studies, with linked study sites indicated.

(Memmott et al. 2007), dispersers (Tylianakis et al. 2008), and pests (Schweiger et al. 2008). This is a complex issue that could affect how the BTE shifts with climate change. Asynchrony between the phenology of specialist insect herbivores and their host tree could lead to some alleviation of herbivory stress (Asch and Visser 2007), whereas asynchrony between insect herbivores and the migration timing of their avian predators could result in un-checked insect outbreaks (Venier and Holmes 2010). These and other examples of how phenological mismatch could simultaneously maintain and disrupt current species range status-quo offer a glimpse of the intricate, multi-trophic interactions that can confound climate change-induced range shifts.

2.5 Historical context of range shift in the BTE

The prevailing notion that climate-related factors, primarily temperature, precipitation and seasonality (Woodward and Williams 1987), are the most important controls on the distribution of vegetation is not new, and can certainly be applied to the modern and historical location of the BTE (Mather and Yoshioka 1968, Allen and Hoekstra 1990, Pastor and Mladenoff 1992). Historical ecotone shifts have been recreated using palynological and macrofossil evidence across North America (Jackson et al. 1997, Hupy and Yansa 2009) and Europe (Amon et al. 2012, Douda et al. 2014) during the warming period since the last ice age. Evidence that as recently as 126 ka the North

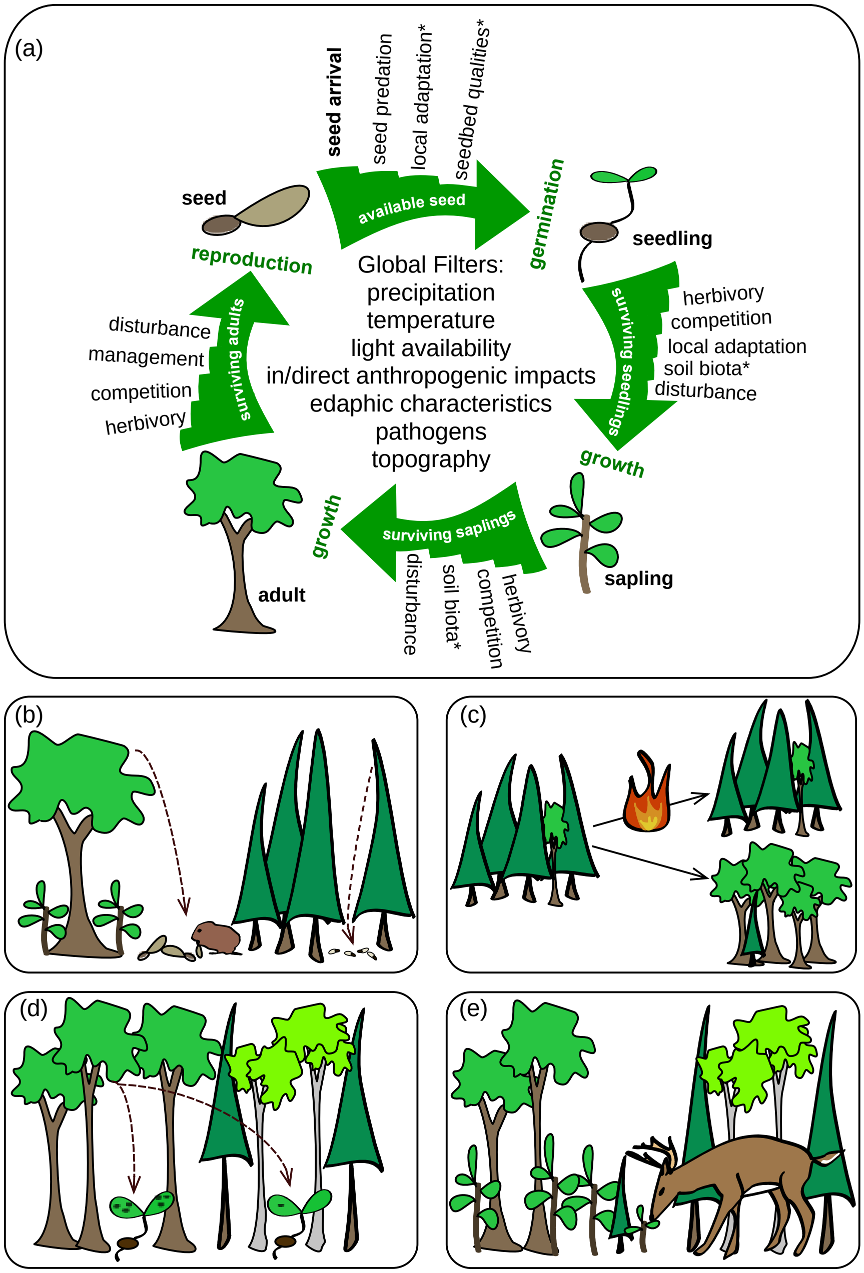

Figure 2.2: (a) Conceptual framework showing filters acting on potential colonising tree species at the BTE, each of which reduces the number of individuals available for the next demographic stage. Filters were assembled from the 27 most relevant papers pulled from the literature in the present study, with an adjacent asterisk (*) representing filters that were inferred, hypothesised, or were otherwise not supported with evidence in studies encountered and therefore in particular need of research. Specific filters (or their removal) are depicted to show: (b) preferential seed predation of temperate species by boreal vertebrates (Brown and Vellend 2014), (c) the impact of fire suppression on forest successional pathways and subsequent canopy composition (e.g., Drever et al. 2006), (d) the escape from pathogens with increased

distance from conspecific individuals (Katz and Ibáñez 2016), and (e) increased browse pressure on more palatable temperate species in boreal stands (Fisichelli et al. 2012).

American temperate biome was located at least 500 km further north than it is today in response to 6-7˚C higher average temperatures (Fréchette and de Vernal 2013) could serve as a regional maxima for the potential of future warming to be reflected by a drastic northward shift of the BTE. The rate of tree species range shift and recolonization after the last glacial maximum is widely contested with some authors suggesting a maximum rate of 2,000 m yr^{-1} (Giesecke et al. 2011) and others a maximum of less than 250 m yr^{-1} (Cheddadi et al. 2013), reflecting the general agreement that the rate of movement varied among species. The disassembly of this ecotone is therefore expected to mirror the process of its assembly as it occurred on a species-by-species basis, due to the species-specific responses to climate change (Pastor 2016).

2.5.1 Projected changes in the BTE

During our literature review, we opportunistically identified forest modelling or simulation studies dealing specifically with forest dynamics at the BTE. The majority of studies predicted northward shifts of southern temperate species at the expense of boreal species, with a minority of temperate species projected to retain their current range or suffer range contractions (Chen 2002, Koca et al. 2006, Iverson et al. 2008, Hickler et al. 2012). Most of the modelling studies we found dealt with the North American and European BTE, with fewer studies dealing with the eastern Asian portion of the BTE. Because we found little data on field studies of the Russian BTE, we specifically searched for modelling papers addressing the Russian BTE (or hemiboreal/boreo-nemoral zone sensu Ahti et al. 1968), which revealed predictions of northward shifting species ranges, aligning with projections of other regions of the BTE globally (Sykes 2001, Zhang et al. 2009). Additional Russian studies modelled future states of the Russian boreal forest (e.g., Nadezda et al. 2006, Brazhnik and Shugart 2015), or focussed on the future of Russian forests as a whole (e.g., Tchebakova et al. 2009, Kicklighter et al. 2014, Shuman et al. 2014, Schaphoff et al. 2016).

Many regional, community-scale studies have revealed evidence suggesting that recent climate change has affected the BTE location by influencing growth patterns (Goldblum and Rigg 2005), shifting tree species distribution (Weng and Zhou 2005, Beckage et al. 2008, Tang and Beckage 2010), re-positioning temperate species' competitive standing (Bolte et al. 2010), and increased northern recruitment success of temperate species (Leithead et al. 2010). However, these studies often focus on a narrow subset of species out of necessity, due to the often monumental task of collecting adequate data upon which to base firm conclusions for large groups of species (see Iverson and Prasad 2002). Likewise, many regional-scale models have been designed to test the implications of future climate change scenarios on the BTE, with northward and upward shifts being common predictions (Weng and Zhou 2005, Koca et al. 2006, Tang and Beckage 2010, Shuman et al. 2014). When combined, regional projections do encompass the global BTE in a piecemeal fashion; however, we are aware of no study that deals directly with the question of how current climate change will affect the BTEs globally.

Currently, to specifically deal with how the BTE may respond to climate change at the global scale one must refer to studies using global scale models to investigate how climate change will affect vegetation distribution (e.g., Haxeltine and Prentice 1996, Alo and Wang 2008, Warszawski et al. 2013), as inclusion of the BTE is implicit. Predictions can also be informed by historical BTE responses to periods of climate flux, which provide useful insight into how even relatively small changes in a climatic regime have produced ecotonal shifts (Hupy and Yansa 2009) and can serve as a recent historical analogue to modern change at the regional scale. Beyond predicting forest distributional response to climate change, modelling studies in the literature appear to have the purpose of informing policy (Hickler et al. 2012, Steenberg et al. 2013, Bright et al. 2014), combinations of changing climate and non-anthropogenic disturbance regimes (Scheller and Mladenoff 2008, Vanderwel and Purves 2013), or multiple climate scenarios (Iverson and Prasad 2002, Iverson et al. 2008), while others have narrowed in on BTE dynamics at the regional scale (Koca et al. 2006, Anyomi et al. 2012).

2.6 Research needs

We identified significant geographic gaps in BTE research globally. Studies in the highly human-influenced portions of the BTE that exist in Europe and eastern Asia may be lacking due to the difficulty in locating the natural BTE. Bolte et al. (2010) conducted research in a reserve in southern Sweden, and took great care in researching the historical land-use patterns that could have left an imprint on their study area. In north-eastern China, where the east Asian portion of the BTE exists, land-use change has occurred more recently and much more rapidly than in Europe. Rapid population growth over the past half century has produced expanding demand for cleared agricultural land and building supplies and has left a characteristic mark on the forested landscape (Yu et al.

2014). Research on BTE response to climate change is growing fastest in North America; yet, knowledge gaps remain. Data on the North American portion of the BTE has the best geographical coverage, yet eastern Canada remains under-researched. There, a fragmentary coastline creates geographic barriers between sites with amenable climatic conditions for southern temperate tree species expansion into typically boreal-forested regions, and creates logistical challenges for field research.

A holistic understanding of the processes controlling the location and configuration of the BTE is needed. Our review of the literature has identified numerous factors that may facilitate or constrain a shift in the BTE. We anticipate these factors will produce a piecemeal ecotone shift, controlled by local and regional non-climatic factors. While we are moving towards gaining a big-picture understanding of the North American BTE, which has relatively abundant empirical data compared to the other regions, we cannot directly apply predictions informed by North American data to other regions with unique combinations of confounding factors and traits. The three broad regions where the BTE exists – North America, Europe and eastern Asia – also have significant ecological differences; historical colonisation patterns and geography account for much of the tree species richness gradient from high diversity in east Asian forests to lower diversity in Europe (Latham and Ricklefs 1993). At the surface this gradient may seem like yet another complicating factor; however, it also presents a unique opportunity for a direct comparison between how shifts of species-rich ecotones compare with those that are relatively species-poor between the same two biomes.

Moving forward, expanding the focus of research on this topic to include more work in eastern Canada and within the European and Asian ecotones will not only i) allow for a better grasp of spatial differences in rates and morphology of change at the global scale, but ii) through the role of ecotones as bellwethers for climate change (Wasson et al. 2013), the BTE may also offer a glimpse of how biomes around the world may respond to a changing climate. However, the interaction between ecological features and climatic and other (a/biotic) factors is still not clearly understood and clouds our ability to make accurate predictions of future ecological states due to the multitude of global and local conditions that must be taken into consideration and the temporal longevity of the systems under study (Woods 2014). It is our opinion that such ecological complexity can only be disentangled through field experimentation (e.g., Kellman 2004, Brown and Vellend 2014) and future research efforts in the BTE should focus on quantifying a/biotic effects on species distributions at their range limits. Scale factors become important considerations here as well, as field experiments are often only able to identify local drivers due to the inherent limitations of time and resources. Therefore, questions surrounding how local drivers can be scaled to explain regional or continental changes must also be addressed. Despite these challenges, our findings do suggest that the quantity and scope of research on this topic is growing at an accelerating pace and will likely continue to do so in the coming years.

2.7 Conclusions

We set out with a number of expectations for our review of current research addressing the response of the BTE to climate change. Those expectations were met in that we uncovered a complex story involving disturbance, biotic interactions, and abiotic characteristics. We did not anticipate that we would only gain an understanding of small pieces of the full story of the historic, current, and future BTE, and only in geographically discrete regions. We lack a holistic understanding of the ecotone globally, which is critical for predictions of species' distributions. What we do know is that, under various circumstances and conditions, the components required for temperate tree expansion into boreal forest stands include: a favourable disturbance regime, suitable substrate, predator satiation or absence, presence of symbiotic organisms, and release from pathogens, in addition to the suitable environment created via climate change. The absence of one or more of these conditions will likely result in a time lag between the creation of favourable environmental conditions beyond temperate tree species' current distributions and their response to that warming via population advance.

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Chapter 3: Small herbivore exclosure cages alter microclimate conditions

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Highlights

- Small herbivore exclosures of varying size and design can create microclimates
- Temperature and snow accumulation differed between exclosures and controls
- Small exclosures with large gauge material had the least impact on microclimate
- Monitoring temperature within exclosures can reduce chances of Type I & II errors

Abstract

Small herbivore exclosures are a popular means of experimentally assessing the impacts of herbivory on the germination, growth, and survival of various plant species. The degree to which small exclosures modify microclimatic conditions relative to control plots has, however, received relatively little attention and is rarely quantified. Inadvertent microclimatic effects have the potential to either confound or enhance the detection of significant experimental results that may be due to herbivory or to a combination of herbivory and microclimate modification. We anticipate that areas experiencing seasonal snow accumulation may be particularly prone to microclimate modification by small exclosures and that the selection of exclosure material and design influences the magnitude of the effect.

Mean, minimum, and maximum temperatures during the period of initial snow accumulation and melt, as well as the number of snow covered days, were measured in three geographically distinct environments to test for the effects of exclosure application and design. Measurements recorded under three exclosure designs of various sizes and materials were evaluated relative to control plots.

All three of the cage designs caused some degree of microclimate modification, the extent of which was dependent on cage design, material selection, and study site location. Overall, we found that small cages made of large gauge material had the least effect on microclimatic conditions. Significant variability in the magnitude of the effects between study sites with different climates and degrees of tree canopy cover suggests that the effects of exclosure application cannot easily be generalized to different locations.

The detection of microclimate modification in all exclosure designs and experimental settings highlights the value of temperature monitoring in herbivore exclosure studies, and stresses the importance of selecting cage designs and materials with care. Differences in soil-level air temperatures, such as those found in our study, have the potential to affect the performance of sensitive and/or juvenile plants growing within the small exclosure environment. The relative ease and low cost of temperature monitoring should make separating the effects of microclimate modification from herbivory a feasible option in future exclosure studies.

3.1 Introduction

Climate and edaphic characteristics are the dominant drivers of species distributions, yet it is becoming increasingly apparent that plant and animal distributions are also shaped by local intra- and inter-specific biotic interactions (HilleRisLambers et al., 2013) such as competition (Tingstad et al., 2015), predation (Brown and Vellend, 2014; Johnson and Fryer, 1996), facilitation (Bruno et al., 2003), and mutualisms (Nuñez et al., 2009). Sessile terrestrial plants are unable to effectively evade herbivores, and are therefore vulnerable to herbivory and seed predation by vertebrates and invertebrates. Predicting the magnitude of the effects of biotic interactions on a species' ability to respond to climate change is challenging given that biotic interactions are inherently tied to local abiotic environmental gradients. Experimental field studies are necessary to tease apart biotic and abiotic (i.e., climatic, edaphic) processes controlling the distributions of species (HilleRisLambers et al., 2013). The methodologies employed in this ongoing investigation have, however, received little scrutiny thus far.

The use of herbivore exclosure devices in field experiments has become a popular means of assessing the effects of herbivory, by both post-dispersal seed predators and plant herbivores, on recruitment and plant community dynamics. Such effects are of strong interest in conservation biology, where plant-herbivore interactions between native and introduced species are often important (Boyd et al., 2017; Forsyth et al., 2015; Hager and Stewart, 2013; Thompson et al., 1992), and for forestry and horticultural applications, where herbivory and seed predation can constrain productivity (Leadem et al., 1997; Marsh et al., 1990). The benefits of using exclosures in field-based herbivore-plant interaction research are obvious: exerting control over a natural system by experimentally manipulating conditions in the field can isolate the impacts of a group of herbivores on a selected area and/or plant species, whereas observational studies must rely more heavily on inference. However, exclosure studies have been criticised for not addressing fundamental interactions between herbivore groups and the species they consume, and instead apply a binary filter on a complex relationship (Hester et al., 2000). Nevertheless, exclosure studies produce consistent responses among prey species the vast majority of the time (Sih et al., 1985). The prevalence of significant effect size, as well as the immutable importance of herbivore-plant interactions research (Humphrey, 1998), explains the continued popularity of herbivore exclosure studies, despite often being logistically challenging.

Alternatives to using herbivore exclosures in experimental herbivore-plant interaction studies are uncommon in the literature. Lab-based research focussed on herbivore-plant interactions can be practical when looking at herbivore-induced reactions in plants (e.g., Roslin et al. 2008; Hartley and DeGabriel 2016), or when a plant and its respective herbivore specialist can be tested in a lab (e.g., Bates et al. 2000); however, these options are not always feasible and such research often requires field-based experimental data collection. Camera traps, a method borrowed from wildlife studies (Kucera and Barrett, 2011; Trolliet et al., 2014), have been effectively used in herbivore-plant interaction studies to identify herbivores (Nuñez et al., 2008) and observe their behaviour (Jansen et al., 2012). Their use in plant-focussed research remains limited (Burton et al., 2015), however, due to their inability to quantify aspects of herbivore-plant interactions such as the extent of damage caused by browse pressure (Brodie et al., 2012; Kuijper et al., 2009).

The design of herbivore exclosures must be scaled to the consumers of interest in a given study, such that a wide range of sizes, designs, and materials are commonly employed (Table 3.1). Though there exists an extensive body of literature regarding the effects of large herbivores on various plant species (e.g., McLaren et al. 2009; Kain et al. 2011; Ellis and Leroux 2017), our focus in this study is on herbivore exclosure cages intended to exclude small vertebrate animals (e.g., Mittelbach and Gross 1984; Côté et al. 2005; Brown and Vellend 2014). The majority of literature describing the use of exclosures (Bowers, 1993; Fraser and Madson, 2008; Olofsson et al., 2004; Young et al., 1997) provides adequate information for the replication of their designs and deployment techniques and this is supplemented by forestry (Leadem et al., 1997) and field operations manuals (O'Keefe and Alard, 2002). Yet, the body of literature evaluating design considerations of herbivore exclosures appears sparse.

Although the materials used in vertebrate exclosure cages appear largely consistent (Table 3.1), the impact of material and design selection on the conditions within and in immediate proximity to the exclosure has, to our knowledge, not been investigated under snowy winter conditions. Tree guard effects on microclimate conditions have been investigated during the growing season (e.g., *Prunus* plantation, south of France, Bergez and Dupraz, 2000; *Eucalyptus-Banksia-Allocasuarina* woodland, southwestern Australia, Close et al., 2009; experimental *Quercus* plantation, southwestern Washington, Devine and Harrington, 2008), however the influence of this type of

Table 3.1: A sample of the variety of designs and range of sizes of herbivore exclosures used in herbivory studies. “Open or closed” refers to the exclosure’s top; Ø refers to a diameter measurement.

Type	Target species group	Dimensions of exclosure	Open or closed	Materials used	Habitat; location	Duration	
Cage	Small rodents	20 x 20 x 5 cm	Assumed closed	6 mm wire mesh	Old-field habitat; Southwestern Michigan, USA	July 1983	(1)
Cage	Small rodents	20 x 20 x 20 cm	Closed	1 cm hardware cloth, stainless steel nails	Mixedwood Appalachian forest; Southern Quebec, Canada	Oct 2012 – April 2013	(2)
Cage	Small rodents	25 cm x 36 cm Ø	Closed	1.25 cm^2 hardware cloth, PVC pipe, metal flashing	Scientific reserve within mixedwood plains ecozone; South-central Ontario, Canada	August-October 2013	(3)
Cage	Small vertebrates	90 x 90 x 60 cm	Closed	6.4 mm galvanised wire mesh	Boreal forest; South-central Quebec, Canada	June-August 2001	(4)
Cage	Aquatic reptiles and fish	90 cm Ø x 122 cm	Closed	5 x 10 cm welded wire fencing, rebar, wire ties	Lake and shoreline habitat; Southern Texas, USA	June-Sept 1996	(5)
Net	Avi-fauna	Varied	Closed	20 mm black nylon netting, bamboo stakes	Tropical rainforest; Southern Yunnan Province, China	April-May 2004	(6)
Cage	Rodents and large mammals	4 m Ø x 1.5 m	Closed	Wire fencing (dimensions unspecified)	Tropical wet forest; Costa Rica	Feb 2001 – July 2002	(7)
Fence	Deer	12 x 12 x 2 m	Open	2 m posts and10 x 10 cm	Mixed conifer-angiosperm forest; Southern South	July 2004 – July	(8)

				mesh	Island, New Zealand	2006	
Fence	Moose	15 x 15 x 3 m	Open	Wire fencing (dimensions unspecified), cedar posts	Boreal forest; Isle Royale, Michigan, USA	Approx. 1950 – 1988	(9)
Fence	Moose	15 x 15 m	Open	Materials and dimensions unspecified	Boreal forest; East-central Newfoundland, Canada	1976 – 1987	(10)

Citations: (1) Mittelbach and Gross (1984), (2) Brown and Vellend (2014), (3) Cassin and Kotanen (2016), (4) Côté *et al.* (2005), (5) Smart *et al.* (1998), (6) Meng *et al.* (2012), (7) DeMattia *et al.* (2004), (8) Forsyth *et al.* (2015), (9) Pastor *et al.* (1993), and (10) Thompson *et al.* (1992).

exclosure on snow and over-winter conditions appears yet to be studied. Researchers who manipulate highly localised temperature regimes to observe plant responses (e.g., International Tundra Experiment) have developed methods to maximise control over temperature ranges within an enclosure (Chapin and Shaver, 1985; Henry and Molau, 1997; Marion, 1996). However, we assert that in small herbivore exclosure experiments, the alteration of microclimate conditions is an inadvertent outcome of the methodologically standard practise of placing a barrier between small herbivores and their potential prey. This is problematic because differences in plant performance between control and exclosure plots are typically attributed solely to the effects of herbivory, when unanticipated and unaccounted for differences in microclimate may confound these results.

Microclimate modification within small herbivore exclosure cages (hereafter, ‘cages’) could occur in various settings, however we posit that unintended effects are likely most pronounced when cages are deployed in areas that experience seasonal snow accumulation. Slight temperature differences within exclosures could affect initial snow accumulation and the later release from snow cover, with consequences for the performance of vegetation. For example, small changes in the duration of snow cover can significantly affect the germination, growth, and survival of juvenile plants, which can benefit from the protection provided by snow cover (Renard et al., 2016). Alternatively, exclosure walls may reduce surface wind speeds, or act as snow fences, leading to increased snow accumulation in their immediate vicinity (Wipf and Rixen, 2010). In an effort to quantify the effects of cages on microclimate conditions, we deployed field experiments in three geographically distinct environments to test whether (1) the onset of winter, marked by the first accumulation of snow lasting 24 hours, occurred later and was marked by colder temperatures within cages than without, (2) spring thaw, marked by the last period of snow cover on the ground lasting 24 hours, occurred earlier and was marked by colder temperatures within cages than without, and (3) the number of snow-covered days during the winter was fewer within cages than surrounding areas. Further, we investigated how construction material and design influenced the degree of microclimate modification. Alteration of microclimate conditions within cages has important implications for the temperature regimes facing seeds and seedlings, particularly regarding the timing and duration of freeze-thaw cycles. Our goal is to offer the first, to our knowledge, direct evidence of small herbivore exclosure cage effects on microclimates to serve as an example for researchers employing these cages in similar climatic settings.

3.2 Materials and Methods

3.2.1 Study areas

Our experimental study was conducted in three locations (“Eastern”, “Central”, and “Western” sites) across Canada under three distinct canopy types (Fig. 3.1). We chose a broad range of geographic and ecological settings to assess whether cage design would emerge as a well-defined predictor of temperature variation and microclimate creation despite the anticipated strong site effect in the three study ecosystems.

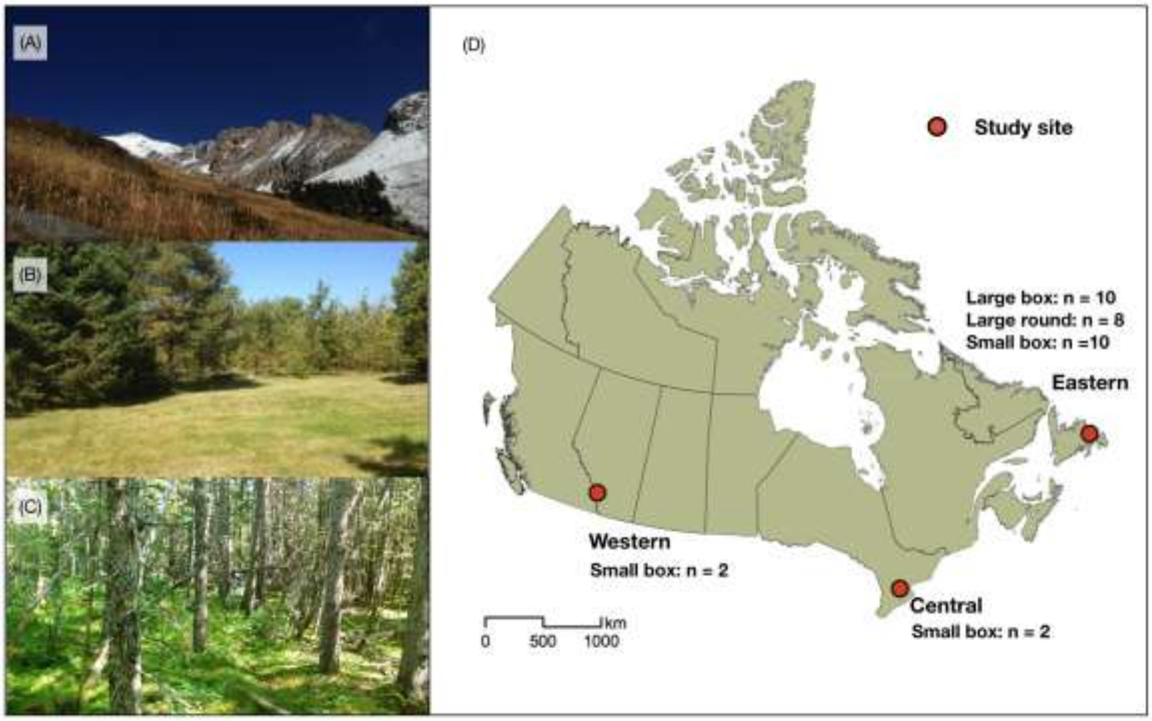

Figure 3.1: The three study sites; (A) Western, within an alpine treeline in Kananaskis Country, Alberta; (B) Central, in a meadow University of Guelph Arboretum, Guelph, Ontario; and (C) Eastern, in a mixed broadleaf-coniferous forest near Clarenville, Newfoundland and Labrador. The number and type of exclosures tested are noted for each study site (D).

3.2.1.1 Eastern Site

The “Eastern” field site (Fig. 3.1; 48°11’47.07” N, 54° 1’31.81” W; 55 m a.s.l.) is located in the northeastern portion of the island of Newfoundland, Canada. The site lies at the bottom of a shallow northwest-southeast valley approximately 2 km northwest of Clarenville, NL, and has an overall shallow gradient (< 2%) of northward aspect. The dense canopy cover (mean 92%) is composed of black spruce (*Picea mariana*), paper birch (*Betula papyrifera*), tamarack (*Larix laricina*), red maple (*Acer rubrum*), and balsam fir (*Abies balsamea*), in order of decreasing abundance. The average annual temperature at the nearest weather station (Lethbridge, NL; 48°21’00” N, 53°54’06” W; 15.2 m a.s.l.; 19.5 km from site) is 4.7°C, with an average annual snowfall of 223.5 cm

(Environment Canada, 2011). This area records an average snow depth by the end of April of 2 cm, and has an average daily minimum temperature above 0°C from May until October.

3.2.1.2 Central Site

The “Central” field site is located in a grassy meadow at The Arboretum, University of Guelph, in southwestern Ontario (Fig. 3.1; 43°32’32.92” N, 80°13’10.43” W; 328 m a.s.l.). The exclosures were situated in a flat area with no tree canopy cover, although nearby buildings and trees created a windbreak within the study area. Historical climate normals for the area (1981-2010; available from the Waterloo, ON, weather station; 43°27’00” N, 80°23’00” W, 317 m a.s.l.; approximately 25 km from field site) indicate mean annual temperatures of 7°C and a mean annual snowfall of 159.7 cm (Environment and Climate Change Canada, 2011). Winter snow accumulation typically begins in November or December (mean December snow depth of 5 cm) and the spring melt is typically complete by the end of March (average month-end snow depth of 1 cm).

3.2.1.3 Western Site

The “Western” field site is near Highwood Pass in Peter Lougheed Provincial Park, southwestern Alberta, Canada (Fig. 3.1; 50°34’11.53” N, 114°56’54.88” W; 2215 m a.s.l.). The area is a treeline ecotone environment with Engelmann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*) as the dominant tree species. The site has a south-southwest aspect and a steep slope (27%). The nearest long-term weather station (Kananaskis Pocaterra; 50°42’45.02” N, 115°07’12.06” W; 1610 m a.s.l.; 20 km from the study area) indicates that the mean annual temperature is 1.1°C and mean annual snowfall is 255 cm. Snow accumulation can occur year-round but is heaviest from September to May. Mean September snowfall is 8.7 cm, and month-end snow depth is 3 cm in April (Environment and Climate Change Canada, 2013).

3.2.2 Data collection & analysis

At the Eastern site, temperature data were collected at two hour intervals using Onset® HOBO® dataloggers (Onset Computer Corporation, Cape Cod, MA, USA): 8k Pendant® Temp/Light Loggers and 8k Pendant® Temp Loggers were attached to wooden stakes inserted into the ground such that the sensor was no more than 10 cm above the ground surface. At the Central and Western sites, U-12 temperature loggers with temperature sensors attached were used to collect temperature data at two hour intervals. The loggers were encased in waterproof containers, the sensor cables were buried, and the temperature sensors were placed on the exposed soil surface. Within-cage temperature loggers were placed in the centre of the cage in all cases. The duration of temperature recordings varied between the sites (see Table 3.2) but captured the onset and release from snow cover in all cases.

Three cage designs were tested at the Eastern site, with 10 replicates of each; one of these designs was common to all three sites, with two replicates at both the Central and Western sites. The small box cage (SBC) design (Fig. 3.2a), tested at all sites, was derived from the Global Treeline Expansion Experiment (GTREE; Brown et al. 2013) and was a closed-top design measuring 18 cm (h) x 56 cm (l) x 33 cm (w) with 1.27 cm (½”) hardware cloth. At the Central and Western sites, sensors were placed in two replicates of the SBC type, paired with two control sensors. The effects of cage material and design on microclimate modification were also tested in 10 replicates of the SBC design at the Eastern site (Fig. 3.2a). In addition, the Eastern site included two “large” designs, the closed-top large box cages (LBCs; Fig. 3.2b), which measured 50 cm (h) x 122 cm (l) x 81 cm (w) and were encased in 6.35 mm (¼”) hardware cloth, and the large round cages (LRCs; Fig. 3.2c), which had open tops and measured 92 cm (h) x 56 cm diameter (Ø) and were constructed from 2.54 cm (1”) gauge chicken wire. Both of the larger cage designs were adapted from Leadem et al. (1997) to suit local conditions in Newfoundland – specifically the predominance of shallow, rocky soils. Ten replicates of each cage type were tested at the Eastern site, but sensor battery failure in two LRCs meant that cage type had data for only eight replicates (Table 3.2).

Cages at the Eastern site were a minimum of 2 m from the nearest neighbouring cage, or control sensor, with cage types randomly distributed. Cages were intentionally placed on level ground so that all cage edges were flush with the forest floor. Canopy cover and composition above control sensors was consistent with their nearest neighbour cage sensors, and control sensors were placed on similarly even terrain to the cages. At the Central site, replicates were 1 m apart in open canopy, and the control sensor was placed adjacent to the cage (within 50 cm). At the Western site, cage and control sensors were similarly placed, with one pair of cage and control located under closed canopy and one in open canopy.

We defined the onset of winter as the first accumulation of snow lasting at least 24 hours, and the release from winter as the last day with an accumulation of snow lasting at least 24 hours, a slight modification of the snow-season described by Danby and Hik

(2007). Snow covered days were defined as 24 hour periods in which the temperature variance of a control sensor was ≤ 1°C (Danby and Hik, 2007). Total snow-covered days for the duration of each of the data collection periods was summed for individual cage and control sensors, and these values were used to perform our analysis. To account for differences in the timing of onset and release from winter conditions between locations, we analysed temperature data from control and caged sensors for the 30 days following the onset of winter and for 15 days before and after the spring thaw for all cage types (Table 3.2). We based these periods on the first and last control sensor reading showing snow-cover, respectively.

All statistical analyses and data visualizations were conducted in R (R Core Team, 2016). We tested to see whether dependent variables i) mean temperature values, and ii) summed snow-covered days (Table 3.2), were significantly influenced by the categorical caged/control variable for SBCs using mixed-effects models (lme4 package; Bates et al. 2015). Using a mixed-effects model allowed us to account for inter-site variation, which was not our variable of interest, through the inclusion of “site” as a random effect. The same tests were performed for the LBCs and LRCs using general linear models, as no random variable was required. The significance of cage effect on any of the temperature variables or snow cover duration was determined by comparing the associated p-value from a t-distribution to $\alpha = 0.05$. Coefficients of determination (R^2; Johnson, 2014; Nakagawa and Schielzeth, 2013) were also determined for each model (MuMin package; Barton 2016) as a measure of how much variance the presence or lack of a cage explained and to determine the magnitude of the site-effect in the SBC models. Both marginal and

Figure 3.2: (A) Small, closed-top box cage design deployed in all sites, constructed of 1.3 cm (½”) mesh hardware cloth with dimensions of 18 cm (h) x 56 cm (l) x 33 cm (w). Open-top cage also pictured, but not included in analysis. (B) Closed-top, LBC design with dimensions of 50 cm (h) x 122 cm (l) x 81 cm (w) and (C) open-top, LRC design constructed with 2.54 cm (1”) chicken wire with dimensions of 92 cm (h) x 56 cm Ø, both deployed only in the Eastern site.

Table 3.2: Date ranges of the onset and spring thaw conditions by study site and cage type (N = number of replicates) for the September 2016 – May 2017 study duration. Mean temperatures and number of snow-covered days with standard deviations are provided for each cage treatment, location and period.

Site	Cage Type	N	Data collection period	Onset of winter period Spring thaw period	Mean daily temperature (°C); *standard deviation*	Mean daily maximum temperature (°C); *standard deviation*	Mean daily minimum temperature (°C); *standard deviation*	Mean number of snow-covered days; *standard deviation*
Eastern	Control	10	Oct 29, 2016 – May 24, 2017	Dec 3 – Jan 2	-1.45; *0.296*	-0.53; *0.330*	-2.01; *0.893*	140.6; *10.3*
				April 24 – May 23	3.06; *0.206*	6.94; *1.83*	0.98; *0.301*	
Eastern	Small box	10	Oct 29, 2016 – May 24, 2017	Dec 3 – Jan 2	-2.28; *0.911*	-0.76; *0.315*	-4.04; *1.71*	120.1; *22.4*
				April 24 – May 23	3.48; *0.434*	7.75; *1.73*	0.92; *0.285*	
Eastern	Large box	10	Oct 29, 2016 – May 24, 2017	Dec 3 – Jan 2	-3.68; *0.144*	-0.91; *0.121*	-6.71; *0.203*	62.0; *34.3*
				April 24 – May 23	3.48; *0.638*	7.41; *1.63*	0.66; *0.634*	
Eastern	Large round	8	Oct 29, 2016 – May 24, 2017	Dec 3 – Jan 2	-0.81; *0.410*	-0.29; *0.212*	-1.38; *0.624*	140.5; *9.3*
				April 24 – May 23	3.31; *0.278*	7.26; *1.40*	1.03; *0.418*	
Central	Control	2	Dec 11, 2016 – Feb 27, 2017	Dec 12 – Jan 11	0.27; *0.658*	0.42; *0.542*	0.10; *0.776*	51.5; *17.7*
				Jan 28 – Feb 27	0.75; *0.305*	2.79; *0.726*	-0.48; *1.01*	
Central	Small box	2	Dec 11, 2016 – Feb 27, 2017	Dec 12 – Jan 11	0.29; *0.156*	0.58; *0.074*	0.04; *0.284*	40.0; *11.3*
				Jan 28 – Feb 27	0.84; *0.160*	3.77; *0.545*	-0.59; *0.563*	
Western	Control	4	July 1, 2016 – 9 Aug, 2017	Sept 21 – Oct 20	2.27; *1.200*	10.58; *4.778*	-0.58; *2.046*	224.3; *25.8*
				17 May – 15 June	3.54; *0.482*	10.19; *1.744*	0.89; *0.648*	
Western	Small box	2	July 1, 2016 – 9 Aug, 2017	Sept 21 – Oct 20	2.84; *3.466*	10.65; *11.926*	0.29; *1.541*	222.5; *14.8*
				17 May – 15 June	3.85; *4.085*	10.99; *11.457*	0.77; *1.467*	

conditional R^2 values were calculated for SBC models, to determine variance explained by the cage effect alone (marginal), and with both cage and site effects accounted for (conditional).

3.3 Results

3.3.1 Small box cage

The mixed-effects model indicated that mean daily minimum temperatures recorded during the winter onset period ($p = 0.031$), and mean daily temperatures recorded during the spring thaw period ($p = 0.003$), were significantly colder and warmer, respectively, within cages compared to control sensors (Table 3.3). Neither model explained a great deal of the variation in the data, however, as the marginal R^2 values for all SBC models were ≤ 0.08. Differences in microclimate conditions between SBC and control sensors were small, compared to the dramatic differences in local climate found at the three sites from which temperature data was collected. Inclusion of the site variable as a random effect substantially increased the explained variance of the models as indicated by the much higher conditional R^2 values in Tables 3.3 & 3.4 relative to marginal R^2. This negative variation in minimum temperature from minimum temperatures recorded by control sensors may be primarily due to the data recorded at the Eastern site. There, SBC sensors were consistently colder than their controls (Fig. 3.3; mean minimum temperatures 2.03°C colder) and took up to 14 days longer than controls to become snow-covered (Fig. 3.4). By contrast, there were brief, but consistently positive differences in temperatures recorded by caged sensors across sites compared to the respective control means during the spring thaw period (Fig. 3.3; see Supplementary Figure 3.4 for greater detail).

Sensors within the SBCs recorded significantly fewer snow-covered days than their respective control settings ($p = 0.028$; Table 3.3). We consistently found fewer snow-covered days within cages across sites, with the largest difference in mean number of snow-covered days occurring at the Eastern site (20 days) and the smallest at the western site (2 days; Table 3.2). The timing of cage sensor exposure compared to control sensor exposure varied by site, with Western and Central cage sensors becoming exposed within 1-2 days of their respective controls, and Eastern SBC sensors becoming exposed up to 5 days earlier than their controls (Fig. 3.4).

3.3.2 Large box cage

Large box cages, constructed with the smallest gauge hardware cloth of the three cage types, posed the greatest barrier to snow accumulation within their confines (Fig. 3.4). Sensors in LBCs recorded significantly colder mean, maximum, and minimum temperatures than control sensors during the 30-days following winter onset ($p < 0.001$, $p = 0.003$ & $p < 0.001$, respectively), indicating greater exposure (i.e., less snow cover; Table 3.3). The average daily temperature at ground level within LBCs was 2.23°C colder than the control temperature, with average daily temperature ranges 4.32°C greater than the immediate surroundings (Table 3.2), which tended to have warmer maximum and much warmer minimum temperatures (+0.38 & +4.70°C, respectively).

Table 3.3: Number of temperature sensors (N), parameter estimates (PE) with standard errors (SE), and goodness-of-fit (R^2; explained over total variance for LBC & LRC models, marginal & conditional for SBC mixed-effects models) showing the difference in mean temperature variable values each cage type had with respect to the control value in each seasonal period. Standard error of random effect variance is given for models containing random effects. Significant parameter estimates ($\alpha = 0.05$) are shown in bolded text.

Dependent Variable Fixed Variable	N	Winter onset					Spring thaw				
		PE	SE	R^2	Conditional R^2	Random effect SE	PE	SE	R^2	Conditional R^2	Random effect SE
Mean temperature											
Small box	14	-0.461	0.297	0.011	0.875	± 0.508	**0.433**	0.132	0.018	0.952	± 0.505
Large box	10	**-2.222**	0.104	0.960	-	-	0.433	0.212	0.180	-	-
Large round	8	**0.644**	0.166	0.470	-	-	**0.259**	0.114	0.233	-	-
Maximum temperature											
Small box	14	-0.136	0.688	0.000	0.916	± 0.507	0.997	0.608	0.016	0.830	± 0.524
Large box	10	**-0.534**	0.079	0.374	-	-	0.467	0.776	0.019	-	-
Large round	8	0.243	0.135	0.160	-	-	0.319	0.786	0.010	-	-
Minimum temperature											
Small box	14	**-1.249**	0.548	0.078	0.573	± 0.549	-0.066	0.154	0.001	0.791	± 0.526
Large box	10	**-2.010**	0.205	0.933	-	-	-0.321	0.222	0.099	-	-
Large round	8	0.632	0.373	0.144	-	-	0.051	0.169	0.005	-	-

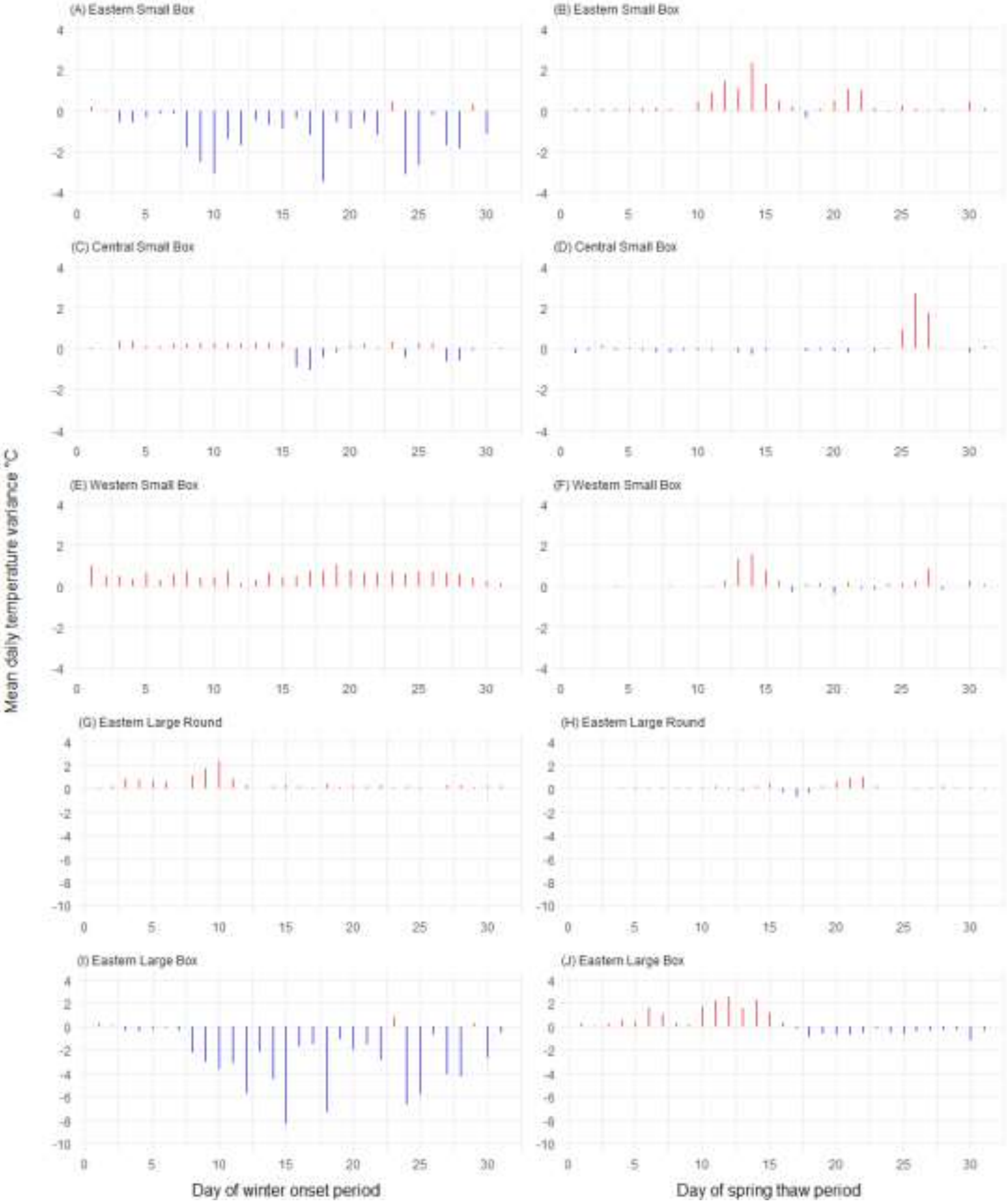

Figure 3.3: Averaged caged sensor temperature variation from the mean control sensor temperature for the winter onset and spring thaw periods at each site. Blue and red line segments indicate mean daily within-cage temperatures colder and warmer, respectively, than mean daily control temperatures. Cage designs at the Eastern site possessing tops had similar negative temperature variations during the winter onset period (A & I) with a warm temperature variation 'bump' almost mid-way through the spring thaw period (B & J); the latter also appearing in the Western data (F). Central SBC and Eastern LRC types show very little variation during either period (C, D, G & H), and Western cages were consistently warmer than controls during winter onset (E). Detailed temperature variation plots for individual cages can be found in Supplementary Figures 3.1-3.4. Plots created using ggplot2 (Wickham, 2009).

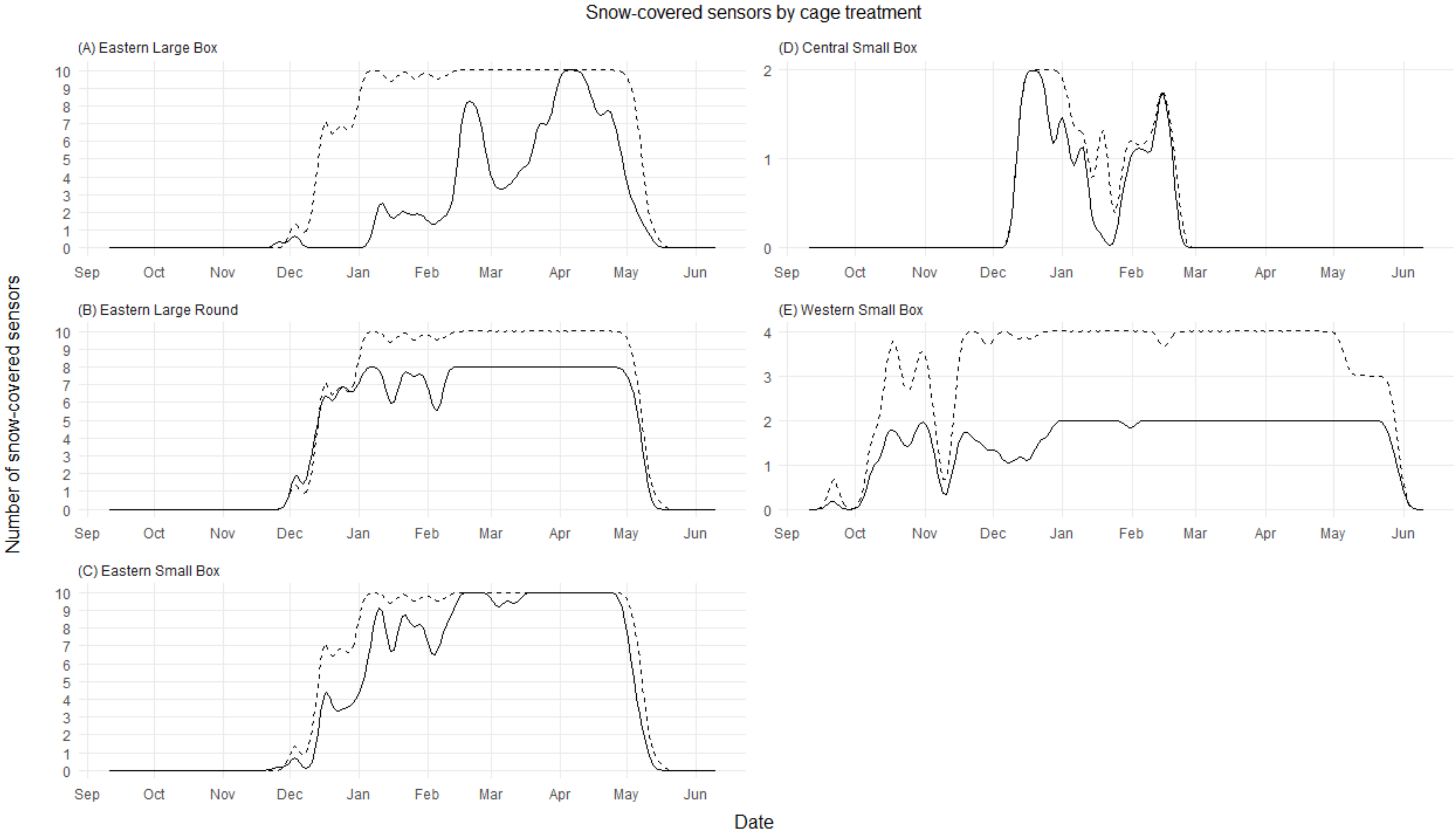

Figure 3.4: Smoothed plots showing the number of sensors under each cage type treatment compared to their controls that were snow-covered throughout the maximum duration of our data collection. Solid lines represent sensors within cages, dashed lines represent control sensors. The number of snow-covered days recorded by Eastern control sensors was far greater than those recorded by LBC sensors (A; average 141 & 62 snow-covered days, sd = 10.3

& 34.3, respectively). LRC sensors were much more closely aligned with control sensors, (average 141 days, sd = 9.3 & 10.3, respectively). The range of snow-covered days recorded by Eastern control and large round sensors (B) was also similar (Mid-Range = 138 ±18 & 140 ±12, respectively); LBC sensors (A) recorded a much larger range of snow-cover duration (MR = 70 ±48). The range of snow-covered days recorded in Eastern SBCs (C) mostly overlapped with Eastern controls (MR = 119 ±31 & 138 ±18), but recorded a lower mean number of snow-covered days (120, sd = 22.4 vs 141, sd = 10.3). The overall winter season was much shorter at the Central site (D); control sensors there recorded an average 52 snow-covered days (sd = 17.7, MR = 52 ±13). The Western site (E) experienced a much longer winter season, where control sensors recorded an average 224 snow-covered days (sd = 25.8, MR = 215 ±28). SBCs at the Central (D) and Western (E) sites had snow-cover conditions closer to their controls than their Eastern counterparts; sensors in those cages recorded a mean 40 and 223 snow-covered days (MR = 40 ±8 and 223 ±11, & sd = 11.3 and 14.8, respectively). Two sensors within LRCs failed during the data collection period, leaving only 8 LRC sensors to the 10 control sensors (B); at the Western site, four control sensors were placed compared to the 2 SBC sensors (E). Plots created using ggplot2 (Wickham, 2009).

The delayed onset of snow cover by up to 64 days was apparent within most LBCs and was followed by a relatively brief period of nearly uniform snow-cover (Fig. 3.4). A similarly brief period of consistent low temperature variability between caged sensors and the mean control sensor temperature occurred during approximately the first half of April 2017 (Fig. 3.3; see Supplementary Figure 3.1 for individual cage data). An average of 62 (sd = 34.3) snow-covered days were recorded by sensors within LBCs throughout the data collection period (November 2016 – May 2017), far fewer than the mean number of snow-covered days that control sensors experienced (141 days, $p < 0.001$, sd = 10.3; Table 3.4). During the subsequent spring thaw period, the presence of LBCs did not significantly impact any of the temperature variables we investigated (Table 3.3), with mean daily, and mean daily maximum temperatures in LBCs 0.42°C and 0.47°C warmer, respectively, and mean daily minimum temperatures 0.32°C colder than their immediate surroundings (Table 3.2). The lack of statistical difference between LBCs and ambient temperatures during the spring thaw is interesting considering that the sensors within the LBCs became snow-free much earlier than the control sensors (Fig. 3.4). Possible explanations for the difference in R^2 values between the three cage-type models include the difference in canopy type under which cages were placed (Supplementary Figure 3.5), or that snow cover within the LBCs had at that point reached a similar depth to the control setting by the spring thaw period (Fig. 3.4).

3.3.3 Large round cage

The open-top design of the LRC was meant to facilitate the passage of snow to the ground and allow for natural accumulation rates that would be as similar as possible to the control setting. This is apparent in Figure 3.4, which shows the similar timing of winter onset between these cages and their immediate surroundings; winter onset within cages was delayed by 1 day in most cases and 10 days in one outlier case. Sensors within LRCs also recorded an identical mean of 141 (sd = 9.3) snow-covered days to control sensors and had a more confined range of 128-152 days compared to control sensors' 120-156 days. LRCs were the only cage type to have a non-significant difference in the mean number of snow-covered days recorded by caged sensors compared to the control setting (Table 3.4). Nevertheless, these cages enabled microclimatic warming such that mean daily temperatures over the 30 days following winter onset were significantly warmer than control sensors ($p = 0.001$; Table 3.3). The difference in mean daily temperatures within the cages against control sensors was +0.64°C ($p = 0.001$; Table 3.3), and the mean daily maximum and minimum differences were +0.24 and +0.63°C ($p > 0.05$ for both; Table 3.3), respectively. Figure 3.3 shows the relatively small temperature variance between LRCs and their surroundings during both the winter onset and spring thaw periods (see Supplementary Figure 3.2 for individual cage temperature variance).

The mild warming effect that LRCs provided was also observed during the spring thaw period across all temperature variables, though again only mean daily temperature was significantly warmer ($p = 0.037$; Table 3.3). In all cases during this time, the mean daily temperature within all LRCs was less than 0.5°C warmer than ground-level temperatures in the immediate surroundings. These mildly warmer temperatures, including the mean daily temperature variable ($p = 0.037$), are well reflected in Figure 3.4, which shows near-identical timing of snow-melt between the LRC and control sensors.

Table 3.4: Number of temperature sensors (N), parameter estimates (PE) with standard errors (SE), goodness-of-fit (R^2; explained over total variance for LBC & LRC models, marginal & conditional for SBC mixed-effects models) showing the difference in mean snow-cover duration experienced within each cage type compared to the control setting. Standard error of random effect variance is given for SBC model. Significant parameter estimates ($\alpha = 0.05$) are shown in bolded text.

Cage type	N	Snow-covered days				
		PE	SE	R^2	Conditional R^2	Random effect SE
Small box	14	**-14.706**	6.328	0.007	0.961	± 0.504
Large box	10	**-73.850**	11.708	0.701	-	-
Large round	8	-22.600	15.570	0.110	-	-

3.4 Discussion

Our findings indicate that cage design and material selection influence the microclimatic conditions created by small herbivore exclosure cages (Table 3.5). Testing the effects of three cage types on ground-level air temperatures revealed that mesh gauge and overall cage size affect snow accumulation and melt processes. Additionally, deploying the same cage type (SBCs) in three geographically distinct locations demonstrated that the substantial inter-site variability was far greater than the variation attributable to our primary variable of interest: the effect of the exclosure itself on temperature and snow cover. Despite this and acknowledging that the low number of replicates at the Western and Central sites limits the strength of our evidence, we did see lower minimum and warmer mean temperatures during winter onset and spring thaw, respectively, which should at the very least be cause for concern that this methodological tool may unintentionally alter microclimate conditions.

Table 3.5: Results summary addressing three primary hypotheses addressed in manuscript (significant results shaded).

Outcome	Large box	Large round	Small box
H_a 1. The onset period of snow cover will begin later and be colder in cages than controls			
Later	Yes	No	No
Colder	Yes	No	Yes
H_a 2. The spring thaw period will occur earlier and be colder in cages than controls			
Earlier	Yes	No	No
Colder	Yes	No	No
H_a 3. There will be fewer snow covered days in cages than controls			
Fewer	Yes	No	Yes

3.4.1 Cage design

Differences between control and exclosure temperature readings were largest in the LBC design. The smaller mesh gauge (¼”) and large overall size of the LBC likely caused it to act as a snow fence, slowing the accumulation of snow within the exclosure and exposing the cage interior to the temperature extremes occurring above the snow pack. Temperature readings in the LRCs, which had a larger mesh (1” chicken wire) and open tops, were more comparable to control temperatures but caused a slight warming effect. The warming effects of the LRCs may have been caused either by the greater heat-conducting properties of the cage material or the higher snow accumulation within the cage that further insulated the soil surface (Wipf and Rixen, 2010). Finally, the SBC appeared to allow snow to accumulate relatively unimpeded, but differences were noted in the overall duration of snow cover between sites. The SBCs were lidded like the large box design but had a larger mesh size (½”) and were smaller in size. While it is possible that the near-natural rate of snow accumulation in the SBCs was due to their design and/or material type, it is also possible that other unmeasured factors, such as early vs. late season snow type (Jiusto and Weickmann, 1973), played an important role. Marsh et al. (1990) noted that snow fencing is a common problem for small mammal exclosures made of 0.85 cm (⅓”) mesh hardware cloth.

Based on the differences between the microclimatic effects of the various cage types, it is clear that cage design is an important consideration for herbivore exclosure experiments. Choosing a design that is as small as possible with the largest suitable mesh size appears to provide the least influence on microclimate conditions. The latter condition corroborates the findings of Bergez and Dupraz (2000) who found increased ventilation holes in tree guards limited their effect on air temperature. Such design choices will have to be made in accordance with the aims of the research study (weighing potential microclimatic effects against increased efficiency in predator and herbivore exclusion) and logistical and financial constraints.

3.4.2 Inter-site variability

In addition to differences between cage types, notable differences were found in the microclimate effects of cages between study sites. The results of the mixed-effects model for the SBCs demonstrated that most of the difference in the temperature variabilitywas in fact related to inter-site variability, as shown in the large conditional R^2 values, and by Figure 3.3. Given the distinct climates of the study sites, it is unsurprising that they also experienced different temperature regimes throughout the winter. Across sites, the mean temperature difference between exclosures and controls ranged from -0.83-0.57°C during winter onset and from 0.09-0.42°C during spring thaw, highlighting the spatial variability in the effect of cages on ground-level temperatures. It is also possible that some of the variability between study sites was due to differences in canopy cover, which varied between locations.

Canopy cover provided by mature trees in forested areas moderates temperature extremes that occur in more exposed environments (Chen et al., 1999). The Central site, a grassy meadow with no canopy cover, showed the smallest differences between cage and control plots. In contrast, the SBCs at the Eastern site were located under dense canopy cover and showed the greatest variation between SBCs and controls of the three sites (Supplementary Figures 3.3 & 3.4), and the number of snow-covered SBCs dropped considerably mid-winter under coniferous canopy whereas the controls did not (Supplementary Figure 3.5). These data suggests a possible interaction between cages and canopy cover and composition, and that the cage effects are stronger in more sheltered areas where the microclimate is also modified by the forest canopy. This variability in cage-effect between canopy types (Supplementary Figure 3.5) mirrors the variability in snow accumulation and ablation rates between open and closed canopies (Varhola et al., 2010) and within forest stands of varying density (Davis et al., 1997; Veatch et al., 2009), and may be attributable to unmeasured factors such as wind exposure, latitude, elevation, or inter-annual snowfall variability. The combination of several factors could produce differences in the number of snow-covered days. For instance, wind-driven snow would much more readily accumulate to cover a cage, regardless of material type or snow crystal size, in an open field rather than in a closed-canopy forest, and may remain longer due to the compacting force of the wind (Knuth et al., 2010). This is possible to infer from the Western site open canopy sensor data (Fig. 3.4; Supplementary Figure 3.5), which were collected at a wind-exposed, high-elevation area, and where we saw earlier, later and more consistent snow cover than control sensors. This was likely not observed at the Central site due to the location being relatively low elevation and well-sheltered from the wind by nearby trees and buildings.

3.4.3 Implications

Exclosure experiments are used to assess the effects of animal activity on factors such as seed germination and seedling survival. Evidence suggests that exclusion of small herbivores and granivores often leads to greater seed (Brown and Vellend, 2014) and plant (Bowers, 1993) survival. However, our findings indicate that depending on the cage design and setting, the perceived effects of herbivory and seed predation could be entangled with differences in microclimate within the exclosure compared to reference plots. Unlike studies employing enclosures specifically designed to create microclimatic conditions, such as those using open-top chambers (OTCs; Leadley and Drake 1993; Hollister and Webber 2000; Bokhorst et al. 2013), studies employing small herbivore exclosure cages do so to measure biotic interactions between predator (e.g., small mammalian granivores) and prey (e.g., seeds). Our findings are not without precedent; Lawson et al. (1994) measured environmental and biological metrics in an insect herbivore exclosure experiment during the 1991 and 1992 growing seasons and found that exclosures (mesh sizes ranging from 1.0 x 0.13 mm to 3.0 x 3.0 mm) had warmer air temperatures than their surroundings. Interestingly, Lawson et al. (1994) also found that exclosures inhibited rainfall from reaching their test plant, similar to our finding that regardless of cage size or material, the presence of a lidded exclosure appears to inhibit snow accumulation. Contrary findings have also been reported; Nelson and Rieske (2014) measured the effect of insect sleeve exclosures on microclimate and on new growth and found that while there was variation in within-exclosure temperature between different cage sizes, no difference occurred between exclosures and controls.

Our study is unique in that our primary focus is on the effect of small herbivore exclosure cages on microclimate during the winter period. This is of particular relevance for studies occurring in areas with snow accumulation and those involving the germination and success of juvenile plants. The spring thaw period can provide important germination cues (e.g., *Acer saccharum*; Godman et al. 1990), and a cage-induced early thaw could interfere with germination phenology. Snow also provides an important layer of insulation for juvenile plants, protecting them from otherwise harmful temperature extremes. Plants commonly found in areas with harsh winter climates are hardened to survive extended periods of freezing temperatures and freeze-thaw cycles; however, increasing the frequency of these cycles can have a weakening effect on plant hardiness (Sanders-DeMott et al., 2017). Exposure to increased freeze-thaw cycles has been found to negatively impact seedling emergence and survival (Connolly and Orrock, 2015), and the loss of buffering capacity against freezing temperatures offered by the snowpack can enable damage to small or shallow root systems (Schaberg et al., 2008). Our findings show that the application of lidded cages had the effect of reducing the number of snow-covered days, increasing the risks associated with exposure to extreme cold temperatures and increased freeze-thaw cycles to the plants within.

3.4.4 Recommendations

Each of the tested cage designs showed some degree of microclimate modification, and the degree and intensity of modification varied between cage types and study locations. We recommend, therefore, that experiments employing small herbivore exclosure cages assess microclimate effects over the course of the study, or that control treatments are designed such that they produce similar microclimate changes without preventing access by the herbivores of interest.

Exclosure experiments are labour and time intensive, and the relatively low cost and ease of installing temperature sensors makes microclimate monitoring worthwhile. Monitoring can reveal potential unintended effects of the experimental treatment (e.g., Lamb et al. 2005), thereby confirming whether the significant effects of excluding small herbivores and seed predators are indeed related to the exclusion of consumers, or perhaps more importantly, highlighting instances where methodological techniques must be refined to disentangle microclimate effects from herbivore exclusion. Routine microclimate monitoring will also make it possible to synthesize the effects of geographic setting, climatic regime, and cage design using meta-analysis at a later time (Gerstner et al., 2017).

3.5 Conclusion

Field-based experimental ecology research is inherently made difficult by the requirement to balance logistical and cost constraints with the need to control factors of scientific interest to the best of our abilities. Where our abilities have the potential to fall short, however, efforts should be made to account for potential sources of error. Here, we have presented evidence indicating that small herbivore exclosure cages can have a direct influence on ground-level air temperatures, and could thereby indirectly influence the health and/or survival of plant species within their confines. The unintended effects that cages can have on air temperature and snow-cover timing and duration are important for plants at early life stages, which may be of particular relevance to horticulturalists and foresters, for whom herbivory protection is a common concern (Cadenasso and Pickett, 2000; Marsh et al., 1990). We suggest taking the simple and cost-effective step of monitoring this environmental variable in order to reduce the potential for type I or type II errors in herbivore exclosure research.

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Chapter 4: Biotic factors act as seedling emergence filters for northern temperate tree species in a beyond-range field experiment

Evans P, Crofts A and Brown CD. Biotic factors act as seedling emergence filters for northern temperate tree species in a beyond-range field experiment (in preparation for submission to Ecological Monographs).

Abstract:

Changing climatic regimes are causing increasing temperatures, changing precipitation patterns and are subsequently expected to impact the spatial distribution of plants. The distribution of plants at the scale of continents broadly conforms to the climatological regimes at play, however in scaling down to the regional and landscape context, the influence of climate becomes confounded by complex and interacting biotic and abiotic factors. These factors have often been cited as important variables in determining the locations of biome overlap, such as the boreal forest-temperate forest ecotone (BTE). This ecotone exists as a broad latitudinal swath between the boreal and temperate forest biomes in the eastern half of North America. While the impact of non-climatic factors on the location of the BTE have been investigated within the ecotone, few studies focus on how these same factors are shaping the colonisation of the southern boreal forest by northern temperate tree species forest as part of a potential northward shift of the BTE. The effects of seed and seedling herbivory, substrate composition and canopy composition on seedling emergence of four northern temperate tree species were investigated in a beyond-range seeding experiment spanning across the southern portion of the island of Newfoundland, Canada. Two small-seeded tree species, *Betula alleghaniensis* and *Thuja occidentalis,* and two tree species with large seeds relative to typical boreal forest species, *Acer saccharum* and *Fraxinus nigra*, were chosen to represent a range of reproductive strategies. The potential impact of microclimate on seedling emergence, based on the natural climatic variation across experimental sites was also evaluated.

The results of this experiment show a reproductive strategy-dependent emergence response; large seeds and seedlings appear more vulnerable to predation, while small seeds are more vulnerable to smothering. Canopies with greater representation of deciduous species posed a significant barrier to small seeds that produce small seedlings, while the food-rich reward of the larger seeds made for attractive targets to granivorous vertebrates. This work represents a first glimpse at the challenges northern temperate tree species will face if they are to colonise the southern boreal forest and track changing climates as is broadly expected.

Keywords: emergence, seed herbivory, range expansion

4.1 Introduction

Species range shifts are expected to result from a changing climate regime, however only insofar as their inherent biotic and abiotic limitations will allow (Lafleur et al. 2010, Parmesan and Hanley 2015). The implications of climate change will, for many species, mean areas at their current range edges may become environmentally suitable, or unsuitable (Iverson and Prasad 2002, McKenney et al. 2007). Yet, in many cases a climatological approach alone is not enough to understand how range expansion will proceed, and does not elucidate the complexities with which species range shifts are, and will be, occurring (HilleRisLambers et al. 2013, Evans and Brown 2017). Biotic interactions are important modifiers of climate-induced distributional shifts (Brooker et al. 2007, Zarnetske et al. 2012, Urban et al. 2013), however disentangling climate and non-climatic effects along the gradients that range edges typically occur along is difficult. Competing abiotic factors of soil and climate for example, each a multi-faceted driver of species ranges on their own, must also be understood with the third dimension of soil microbiota and soil-climate-biotic feedback interactions (Lafleur et al. 2010). Soil is just one example of many complex interactions; the list includes interacting climate-pest species (Logan et al. 2003), climate-disturbance regimes (Rocca et al. 2014), and plant-pollinator phenological mismatching (Hegland et al. 2009), to name a few. The goal of this work is to build an understanding of how northern temperate tree species' establishment in boreal forest stands is affected by constraining abiotic and biotic factors. This work is unique in that it takes place in a relatively isolated island boreal system that will share increasingly similar climatic conditions to their historic distributions.

Species life history strategies are selected for and adapted to the pressures exerted upon them by the system in which they persist. As species, such as trees, attempt to colonise new systems in response to climate change, the strategies that succeeded in their historic distribution may not be well suited to the new conditions. For example, producing large seed in a boreal forest community in which small seeds are the norm may be detrimental to seed survival due to predation selection (Zhang et al. 2005). Trees are important habitat-forming organisms (Thomsen et al. 2010) and their presence, absence, and abundance, coupled with their associated herbaceous plant communities, is reflective of the current climatic regime and, to some extent, dictates the faunal assemblage within that biome.

Tree species range shifts have occurred throughout their evolutionary history, evidenced in the fossil pollen record, and more recently in the lake sediment record. Repeated southward and northward range shifts have been documented in concert with dramatic, large scale climatic swings during glacial events (Comes and Kadereit 1998), and shorter, more localised climate events such as the little ice age (Hupy and Yansa 2009). Such range shifts have been recorded globally (Davis and Shaw 2001), including a modern shift currently occurring at the biome-level, causing the boreal forest to shift northward as temperate tree species invade the boreal forest trailing edge at the boreal-temperate forest ecotone of North America (reviewed in Chapter 2) and northern edge boreal forest trees invade the tundra and alpine regions at the forest – tundra ecotone (Harsch et al. 2009).

The boreal-temperate ecotone (BTE) is the transition zone wherein the northern extent of the temperate forest overlaps with the southern extent of the boreal forest; it occurs in eastern North America, north-eastern Europe and eastern Asia (Goldblum and Rigg 2010, Evans and Brown 2017). This transition generally occurs along a north-south gradient where both tree species diversity and average annual temperature decrease with increasing latitudes, with thermal conditions often considered the primary factor determining the ecotone's location (Arris and Eagleson 1989). In North America, the BTE is at its widest, and occupies a zonal band from southeastern Manitoba to the Gaspé Peninsula, Quebec and from western Minnesota to Cape Breton Island, Nova Scotia (Olson et al. 2001, Goldblum and Rigg 2010). Despite portions of the island of Newfoundland (herein, Newfoundland) falling within the BTE latitudinal zone and possessing similar climatic characteristics to mainland areas of the BTE, expected species assemblages are not found there. The most parsimonious explanation for this pattern is the approximately 110 km of ocean that isolates southwestern Newfoundland from Cape Breton Island, the eastern-most distributional range of many temperate tree species (Farrar 1995). However, as this dispersal barrier becomes functionally smaller due to anthropogenic transport of propagules, an increase is expected in the potential for successful species colonisation events.

Colonising tree species face a variety of barriers that act to filter out individuals from an establishing population, but few studies have tied together biotic and abiotic variables within the same study to test these filters in novel habitats (Rustad 2008). To this end, the following hypothesis has guided this study: tree seedling emergence success at or beyond the range edge will be driven by biotic and abiotic drivers, the combination of which will depend on species' traits. A description and investigation of known germination constraints of the species used in this study can be found in Chapter 1. We tested explicit, species-specific predictions of the controls on early life stage processes using manipulative seeding field experiments within and beyond four model temperate tree species population distributions, (see Table 4.1): (1) *F. nigra* seeds must avoid desiccation and predation long enough to mature and break dormancy, with final germination ability depending heavily on over-winter temperatures, and pre-emergence temperature and moisture availability (Vanstone 1974). (2) *A. saccharum* germination is sensitive to seed predation (Brown and Vellend 2014), temperature (Solarik et al. 2016), available moisture, and can be achieved under complete canopy cover and on various substrate types (Godman et al. 1990). (3) *B. alleghaniensis* germination benefits from exposure to light, warm temperatures (Karrfalt 2008), adequate moisture (Erdmann 1990) and permeable germination surfaces (Burton et al. 1969). (4) *T. occidentalis* germination requires near constant moisture and high temperatures (Curtis 1959, Johnston 1990) along with an appropriate, moisture-bearing seedbed (Bartlett et al. 1991, Cornett et al. 2000). Our work aims to address the earliest and most vulnerable life stages of tree species, and therefore will begin to reveal how these particular factors impact shifting species ranges.

Table 4.1: Outline of predicted species emergence responses to treatment variables for each emergence year.

Species	Emergence year	Driver variables							
		XHerb	SubM	%DecC	Smoist	Stemp	Atemp	WSmoist	WStemp
A. saccharum	2016	↑	X	X	NA	NA	NA	NA	NA
B. alleghaniensis	2016	X	↓	↓	NA	NA	NA	NA	NA
T. occidentalis	2016	X	↓	↓	NA	NA	NA	NA	NA
A. saccharum	2017	↑	X	X	↑	↓	↓	X	X
B. alleghaniensis	2017	X	↓	↓	↑	↑	↑	X	X
F. nigra	2017	↑	X	X	↑	↑	↑	↑	↑
T. occidentalis	2017	X	↓	↓	↑	↑	↑	X	X

Notes: XHerb: exclusion of vertebrate herbivores; SubM: leaf litter substrate; %DecC: percent deciduous canopy cover; Smoist: soil moisture; Stemp: soil temperature; Atemp: Air temperature; Wsmoist: over-winter soil moisture; WStemp: over-winter soil temperature. Arrows indicate direction of response with bold arrows suggesting magnitude of response; X represents no predicted response. NA's are given when the predictor variable was not used, or data were not available for that variable for that year, respectively.

4.2 Methods

4.2.1 Study Area

Newfoundland is projected to see widespread increases in mean temperature and annual precipitation by mid-late century (Finnis 2013, Natural Resources Canada 2015). Mean annual precipitation and temperature are expected to rise across Atlantic Canada, with Newfoundland tracking or exceeding the Maritime provinces' rate of precipitation and temperature increases, respectively (Natural Resources Canada 2015). Southern Newfoundland could see a mean annual temperature increase of 1.5-3.1˚C, a rise in annual growing degree days (GDD) of 108-211 (T_{base}=10°C) and an annual frost-free period increase of 27-35 days by 2070 (Finnis 2013). Newfoundland's geographic position combined with its climate change projections make it an ideal location for studying potential forest composition change as a result of climate change, especially given the already abundant diversity of tree species introduced to the island through anthropogenic means, particularly in the island's urban centres (Environmental Design and Management Ltd. 2006). Modern tree species range shifts have not been studied in Newfoundland in the context of a changing climate (Evans and Brown 2017), and the island's physical separation from mainland North America creates a confluence of confounding variables affecting possible species range shifts.

The field experiment took place across Newfoundland (47˚10′N - 49˚21′N and 53˚23′W - 58˚15′W; Fig. 4.1; Supplementary Table 4.1). Seasonal average temperatures and annual precipitation amounts vary across the island, with a smaller summer temperature range than winter temperature range across study sites (Supplementary 4.2). The strong maritime influence on the island's climate maintains an even distribution of precipitation throughout the year, with infrequent droughts that are generally not severe (Atlantic Climate Centre and Environment Canada 2006). Newfoundland has distinct regional climates due to the island's geographic position, shape, area (approximately 106,000km^2), and topography (Damman 1983). These climatic variations are captured by the range of plant hardiness zones found on the island, between 3a-6a (Agriculture and Agri-Food Canada and Government of Canada 2000). Its forests are typically described as boreal, and have been given their own designation as the Newfoundland Boreal Ecozone (ESTR Secretariat 2014).

Five sites were established across Newfoundland during an initial implementation of this experiment in 2015 (Fig. 4.1). These and a further three sites (N = 8) were established across Newfoundland in 2016 (Fig. 4.1) using data collected from the 2015 implementation to inform and update experimental design. Methods and results from the initial experiment were analysed and appear alongside those for the 2016 implementation to show the progression of the experiment. Sites were selected based on a range of criteria (site characteristics described in Supplementary Table 4.1): (1) on public (Crown) land that would not be logged for a minimum of three years, or on Provincial (i.e., Provincial Parks), or private lands with permission from the land owner, (2) were within 1 km of a publically accessible road, and (3) contained stands of mature boreal coniferous forest ("boreal" forest type; forest type selection described below) and mixed coniferous-deciduous forest ("mixed" forest type) with no evidence of recent harvesting in close proximity. Sites with non-native tree species present were avoided.

4.2.2 Experimental Design

The experimental design allowed for the manipulation of i) herbivore access to tree seed and seedlings and ii) substrate, or seedbed composition under iii) boreal or mixed canopy composition forest type (see Supplementary Table 4.1 for stand composition data). Forest type was distinguished after extensive searching and assessment of field sites based on canopy composition and substrate characteristics. Substrate refers to the top of the organic layer (i.e., the seedbed) and soil represents the organic and mineral components below that. Boreal forest stand canopies had a minimum ⅔ (~66%) proportion of coniferous species of the total and mixed stand canopy composition was at least ½ deciduous species. Mixed stands also often contained canopy species more commonly associated with forests within the BTE, such as white pine (*Pinus strobus* L.), yellow birch (*Betula alleghaniensis* Britt.), black ash (*Fraxinus nigra* Marsh.) and red maple (*Acer rubrum* L.), all of which are native to Newfoundland (Farrar

1995, Forestry and Agrifoods Agency 2015). Mixed stands were further required to have predominantly broadleaf-litter dominated substrate (rather than needle leaf litter) and less than 30% moss substrate cover, whereas boreal forest stands were selected with greater than 60% moss cover substrates.

Ten planting blocks were established at each study site, split evenly between boreal and mixed forest stands (Fig. 4.2). We employed a full factorial experimental design each year of the two-year experiment by reciprocally transplanting soil between boreal and mixed forest blocks, such that each block had pots of each treatment for each species under each canopy type (Fig. 4.2). Five replicate blocks containing this combination of treatments were established under each canopy type. Seedling surveys generally took 1-2 days per site and were conducted over the 2016 and 2017 growing seasons. Surveys were conducted in May and late August/early September in 2016 and in May, June, July, August and September in 2017. Each pot was inspected closely for the presence of seedlings, seedling and seed (if found) health and general pot condition.

4.2.2.1 Substrate composition & stand characteristics:

Forest floor substrate was reciprocally swapped between forest types within each site. Using a soil knife, the first 10-15 cm of soil was removed from the forest floor and inserted into peat pots (14.5 x 12.5 cm), making efforts to maintain the soil structure during removal and transport. Pots of soil were then either re-inserted into the ground in place, or transported to and planted in the other stand type; this way the local and foreign substrate type were tested under either canopy type. A control treatment with no pot was also initiated to test for any effect of the pot itself on seedling emergence; pot rims (top ⅓ of peat pot) were inserted into the soil to contain the planted seeds but the forest substrate was otherwise left undisturbed.

Canopy cover and canopy composition to the species level was recorded during site establishment in 2015 and 2016 by averaging readings taken in each cardinal direction at each block using a spherical densiometer (Forest Densiometers, Rapid City, SD, USA) to allow canopy cover and composition to be treated as a continuous variable in the analyses (Supplementary Table 4.2).

4.2.2.2 Herbivory exclusion:

Half of pots deployed in both 2015 and 2016 were placed within cages meant to limit seeds’ exposure to small terrestrial vertebrate herbivores. Of the 36 pots in each 2015 experimental block, half were placed within exclosures measuring 50 (h) x 122 (l) x 81 cm (w) and encased in 6.4 x 6.4 mm hardware cloth (Fig. 4.3a). In 2016 the design of the cages changed to an open-top design, which is different from other exclosure cage designs that have been used (Coté et al. 2003, Munier et al. 2010), but similar to designs where the differential impact of rodent versus bird granivores was being evaluated (Howe et al. 2002). This new design was adopted after issues surrounding snow- and leaf-litter accumulation were identified with the 2015 cage design. The issues encountered in using the closed-top cage design specifically revolved around the blockage of leaf-litter and snow entering the cage (described in detail in Chapter 3), requiring the two years’ data to be analysed separately. Half of the 24 pots at each 2016 experimental block were placed within exclosures that were 92 (h) x 56 cm diameter (Ø) cylinders of 2.5 cm galvanized chicken wire with a 31 (h) x 56 cm Ø cylinder of 6.4 x 6.4 mm hardware cloth wrapped around the bottom third of the chicken wire in order to deter small vertebrates (Fig. 4.3b). A strip of flexible plastic was attached to the top portion of the cage in an effort to keep out climbing vertebrates. Neither cage type was designed to withstand interactions with large herbivores, such as moose, or to prevent access to invertebrates.

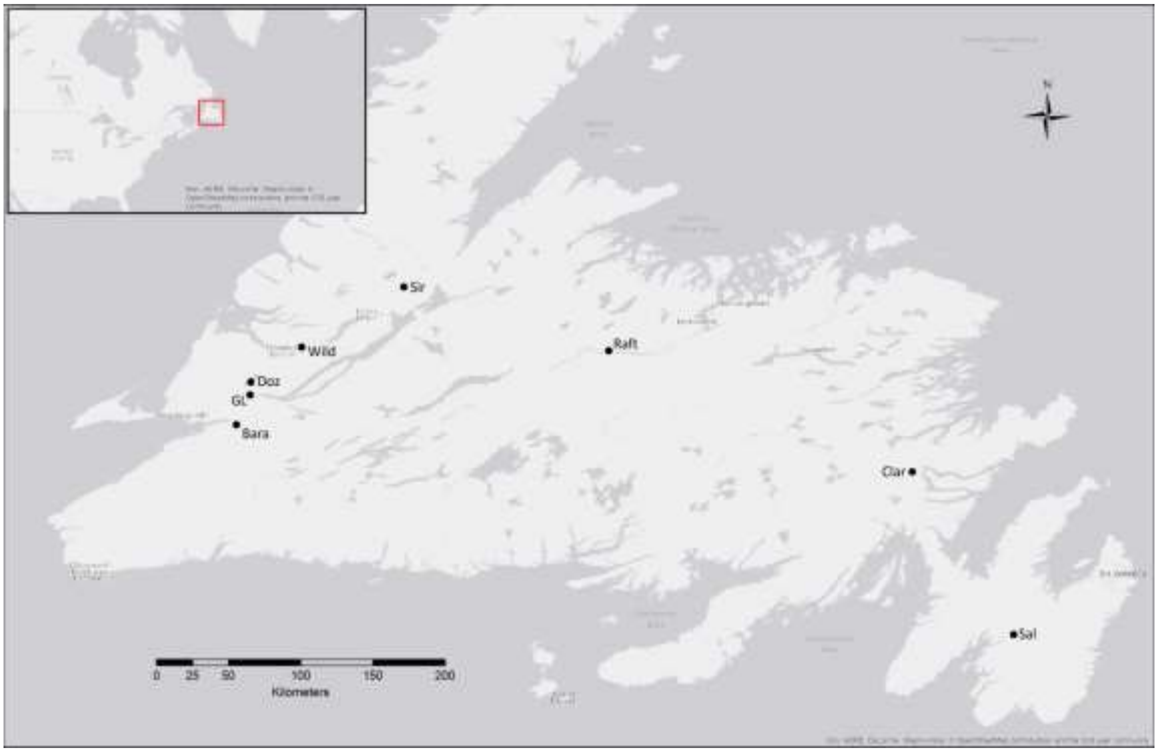

Figure 4.1: Study site locations across the island of Newfoundland. Sal, Clar, Raft, Sir, and Bara were established in 2015 and Doz, GL and Wild, in addition to the original five sites established during the 2015 field season. The 2016 sites were concentrated in the island's southwest, which has the highest tree canopy species diversity of any region in the province (Farrar 1995).

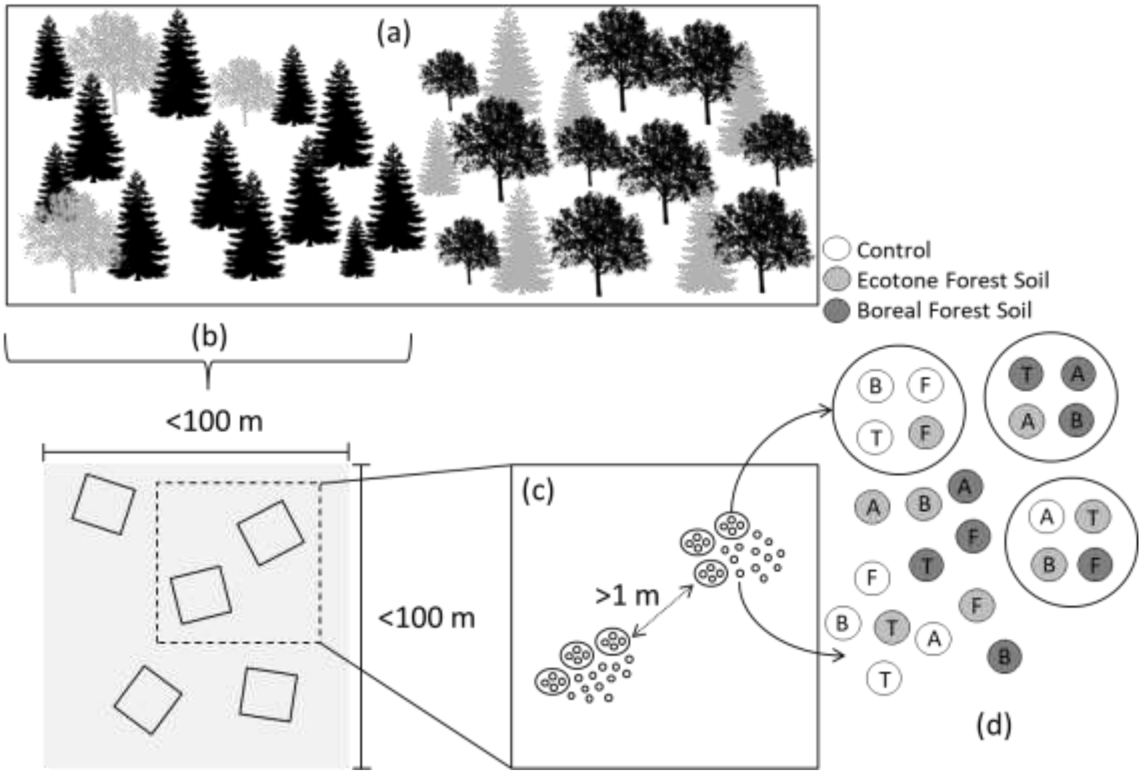

Figure 4.2: Experimental design diagram showing (a) conceptualised difference in canopy composition between boreal and ecotone forest-types (left and right, respectively) and (b) planting block layout shown within one of the two forest types within each site. Blocks are approximately 2 x 2 m in dimension, spaced at least 1 m apart (c). The blocks in (c) show the round open-top cages deployed in 2016 and contain 24 pots per block, rather than the closed-top box cages deployed at each block in 2015, which had 36 pots. Each species was planted in a caged or control pot containing boreal or ecotone soil, or in a control pot, which were the top ⅓ of a pot seated into the local soil (d). F = *F. nigra*, B = *B. alleghaniensis*, A = *A. saccharum*, and T = *T. occidentalis.*

Figure 4.3: Pictures showing (A) 2015 cage type and block layout, with 36 pots, half of which are within the cage, and (B) 2016 cage type and block layout with 24 pots, half of which are within the three cages (four pots per cage). Both blocks depicted in photos are in boreal forest stands.

4.2.2.3 Seeding:

Pots were seeded between September 12th-19th, 2015 and October 15th-22nd, 2016, within the natural seed-fall period of all model species (Burns and Honkala 1990). In 2015, each block contained two pots each sown with 5 *A. saccharum* and 10 *T. occidentalis* seeds and one pot each sown with 5 *F. nigra* and 10 *B. alleghaniensis* seeds per treatment combination for a total of 36 seeded pots per block. These numbers were standardised for the 2016 seed sowing; 10 seeds of each species was sown into one pot per treatment combination, reducing the number of pots to 24 per block. Seed was obtained from the National Tree Seed Centre (NTSC; Fredericton, NB, Canada) from seed sources in New Brunswick and Nova Scotia. Attempts were made to use highly viable seed stock from regions with climates as similar to Newfoundland as possible to maximise local adaptation to the potentially difficult climatic conditions model species would encounter in Newfoundland (Supplementary Table 4.3).

Initially, our experimental design included provenance treatments for *A. saccharum* and *T. occidentalis* to investigate whether seed source would imbue additional climatic adaptations for the climate beyond those species' natural distribution. Seeds for these model species were sourced from areas in either 'warm' plant hardiness zones (>4) or 'cold' hardiness zones (<4; Agriculture and Agri-Food Canada 2000) in order to see whether variations in adaptation in the parent individuals would be beneficial for seed germination under a more challenging climate, as others have investigated (e.g., McCarragher et al. 2011, Solarik et al. 2016). It quickly became apparent that the design of the overall project was becoming unwieldy, so this treatment was not ultimately used and all *A. saccharum* and *T. occidentalis* seeds were treated the same.

4.2.2.4 Climate:

Two climate sensor arrays were installed at each site under both canopy types to provide continuous environmental monitoring in October, 2016 using Onset® HOBO® Data Loggers Micro Station Logger with Smart Temperature Sensor, Soil Moisture Smart Sensor and Temperature & RH (relative humidity) Sensor (Onset Computer Corporation, Cape Cod, MA, USA). These arrays were assembled onto masts approximately 1 m tall and sampled air and soil temperature, relative humidity and soil moisture at 1 hour intervals from the time of seeding (October, 2016) through the end of the 2017 growing season (final data collection was in September, 2017).

4.2.3 Model species

To address the suitability of potential range-expanding tree species to novel habitats, we focus here on four tree species whose early life history strategies vary drastically: i) two species that produce large seeds relative to boreal species, one native to Newfoundland, *F. nigra*, and one native to mainland Canada, but only found in Newfoundland as an ornamental, sugar maple (*Acer saccharum* Marsh.); and ii) two small seeded species, again a native species, *B. alleghaniensis*, and another common ornamental, eastern white cedar (*Thuja occidentalis* L.). The model species used in this experiment are representative species of the BTE, each having significant portions of their native distributions falling within the geographic area of this ecotone (Evans and Brown 2017).

A. saccharum produce large seed relative to typical boreal species (0.050-0.142 g/seed; Olson and Gabriel 1974), which allows for vigorous germination (Yawney and Clayton 1968), but also makes the seeds highly vulnerable to predation in a boreal setting (Brown and Vellend 2014). *F. nigra* produces seed possessing a large samara, but immature embryo that requires specific climatic conditions over periods sometimes spanning two years under natural conditions in order to mature and break dormancy (Vanstone 1974), which allows abundant time for dispersal, predation and/or seed desiccation. *B. alleghaniensis* and *T. occidentalis* share several early life history traits; they are both small-seeded species (0.501-1.63 mg/seed, and approximately 1.31 mg/seed, respectively; Johnston 1990, Karrfalt 2008). The potential dispersal-related benefits of this reproductive strategy are partially offset by the lack of resources and resultant fragility of their respective seedlings, both of which have been found to require specific substrates to promote successful germination (Cornett et al. 2000, Caspersen and Saprunoff 2005) and are known to be limited due to smothering under leaf litter (Burton et al. 1969, Buda et al. 2011). The combination of reproductive strategies offered by these species will allow me to experimentally test the germination capacity of this representative suite of species to combinations of known relevant drivers that exist across Newfoundland (see Chapter 1 for further discussion on species traits). They are also well suited to the climatic conditions found on much of the southern portion of Newfoundland, having already colonised areas with similar climates in mainland Canada.

4.2.4 Statistical analyses

We performed the data analyses to test the species-specific effects of combinations of experimentally imposed and naturally occurring environmental conditions on the presence and abundance of emergent seedlings. Seedling emergence count data were collected in May and September, 2016, and monthly from mid-May to mid-September, 2017. Seedlings were counted as having emerged if the radicle had breached the seed coat. Seedling emergence was recorded as both: (1) a Bernoulli presence/absence response ("presence" data), and (2) a binomial proportion response, which was the number of seedlings that emerged in a pot out of the total number of seeds that could have germinated ("abundance" data). Partitioning the response variable into *pass/fail* and *x passes/y potential passes* (similar to Tsuyuzaki et al. 2014), allowed for the identification of variables (see Table 4.1 & Supplementary Table 4.2 for predicted responses and explanatory variable details, respectively), or combinations thereof, driving whether the seedlings emerged at all, and conditions that promoted the greatest number of emergent seedlings in a given pot, respectively (Zuur et al. 2009). Evidence of seed and seedling herbivory, were recorded qualitatively.

During seedling emergence surveys in 2017, we observed and counted naturally occurring first-year *Betula* sp. (*B. alleghaniensis* & *papyrifera*) seedlings in pots not seeded with *B. alleghaniensis* (n = 1,440). The total number of naturally occurring birch seedlings counted over the course of the 2017 growing season at each block was divided by the total number of pots not sown with *B. alleghaniensis* seeds within each block (n = 18), to give the background rate of naturally occurring *Betula* sp. contamination. The resultant background rate was rounded up to the nearest integer and subtracted from each pot seeded with *B. alleghaniensis* to correct for background contamination within the corresponding block (Elderd 2003, Donohue et al. 2005). This correction was only applied to the 2017 emergence data due to the infrequency of site visits in 2016, which did not allow for accurate tracking of naturally occurring *Betula* sp. emergence.

All statistical analyses were performed using model selection based on corrected Akaike Information Criterion (AICc; Hurvich and Tsai 1989, Akaike 1998, Burnham and Anderson 2004) for small sample sizes. Following Burnham and Anderson (2003, 2004), we considered models with ΔAICc ≤ 2 have essentially as much explanatory power as the top ranked model (i.e., ΔAICc $= 0$), models with a ΔAICc between 4 & 7 are considerably weaker, and models with ΔAICc > 7 have very little support. We erred on the side of caution by employing the small-sample AICc method of model selection, as many of the global models fitted to our species-specific datasets were at or near the $n/K > 40$ approximate threshold, at which AICc begins to converge to AIC (Burnham and Anderson 2004).

We analysed presence and abundance data for the 2016 and 2017 emergence years separately, fitting generalised linear mixed-effects models with a binomial error structure and logit link for the presence, and zero-inflated binomial (ZIB) models for abundance response variables with treatment explanatory variables (herein: treatment analysis). Full species 2016 and 2017 emergence year datasets were used for *response variable* x *treatment analysis*, for each species that emerged in each year.

All possible combinations of our treatment variables were fitted to data for each species for each emergence year to test our predictions that biotic and abiotic drivers that are important for these model species' emergence within their respective distributional ranges would be important in the novel system under study (Table 4.2; Supplementary Table 4.2; Murtaugh 2007, Symonds and Moussalli 2011). The models created for all hypothesis testing included the block within site random nested term to account for the hierarchical structure of our experimental design, and each model set included a model with only this random nested term (i.e., hereafter the Null model; Table 4.2; Bolker et al. 2009). This made for a total of eight candidate models including the Null model. For models in which substrate type was included as an explanatory variable, an additional random variable designating each pot as either "treatment" or "control" was also included to account for possible variability introduced by the substrate treatment itself.

Data for the canopy composition explanatory variable was scaled by subtracting the variable mean from each value and dividing that result by its standard deviation using the base package in R (R Core Team 2016) in order to account for the difference in scales between categorical and continuous variables (Supplementary Table 4.2). There is the risk here of finding importance in variables with little support due to small datasets, as outlined in Freedman's Paradox (Freedman 1983), however the variables used in the model set reflect important ecological relationships for these species elsewhere, thus allowing us the assumption that they should still be important in the novel environments represented in this study at this early life stage. All analyses were carried out using The R Project statistical software (version 3.3.2; R Core Team 2016) packages nlme (Pinheiro et al. 2017), mctest (Ullah and Aslam 2017), glmmTMB (Magnusson et al. 2017, Brooks et al. 2017), and bbmle (Bolker and R Core Team 2016). Pseudo-R^2 values for binomial models were calculated after McFadden (1973).

A confidence set of best-supported models was created for each combination of *species* x *response variable* for each emergence year, and was populated by fitted models with a ΔAICc < 2. We removed models containing pretending variables (sensu Anderson 2007), or uninformative parameters (sensu Arnold 2010) from our confidence sets (Supplementary Tables 4.4 & 4.5). Models that contained variables with parameter estimates that reached zero within the range of their standard errors were omitted from the confidence set, as these variables were considered unimportant and uninformative. This process of confidence set creation is a somewhat similar analytical methodology to those employing AIC weights to perform model averaging (Burnham and Anderson 2003, Richards 2005, Burnham et al. 2011, Symonds and Moussalli 2011), however the weaknesses of this approach are well outlined by Galipaud et al. (2014) and Cade (2015), and our primary objectives from this study are to provide evidence-based descriptive analyses to serve as a baseline for future hypothesis generation in this subject and geographic area.

Using full 2017 emergence datasets for each model species, climate variables of known importance, as outlined in our predictions, were analysed graphically. Conditional density plots were generated from the raw presence and abundance data using the graphics package in R (version 3.3.2; R Core Team 2016) in order to identify whether important relationships between climate variables and seedling emergence for these model species elsewhere were also important in this novel system. This procedure was chosen over attempting to model the data, as our climate data sampling design was too coarse to differentiate specific climate drivers from possible site effects.

Table 4.2: Full candidate model set applied to presence and abundance data for each model species' germination data for each year in which germination occurred. Predictor variables refer to the percent deciduous canopy cover (%DecC), protection from or exposure to vertebrate herbivory (XHerb), and whether the seeds were sown onto mixed or boreal forest substrate (SubM). All models were given the nested random terms grouping Blocks within their respective Sites, to account for correlations due to geographic proximity.

Model No.	Predictor variables
1	1 + (1 | Site/Block)
2	%DecC + (1 | Site/Block)
3	XHerb + (1 | Site/Block)
4	SubM + (1 | Site/Block)
5	XHerb + %DecC + (1 | Site/Block)
6	XHerb + SubM + (1 | Site/Block)
7	SubM + %DecC + (1 | Site/Block)
8	%DecC + SubM + XHerb + (1 | Site/Block)

4.3 Results

4.3.1 Within-year and inter-annual effects:

Seedlings emerged consistently across the two annual iterations of the experiment (Table 4.3), but with considerable variation in the success species experienced across sites (Table 4.4). Three of the four model species experienced greatest success at the Sir site in 2016 (excluding *F. nigra*, which did not germinate that year). In 2017, emergence was greatest at the Clar site for the same three species, while *F. nigra* was most successful at the Bara site. This inter-site variation in emergence success meant that the 2017 emergence data for these three model species (minus *F. nigra*) were subsetted for treatment analysis. The overall rate of seedling emergence for any species did not exceed 14% either year and was as low as 0.7% for *T. occidentalis* in 2016 (Table 4.3).

Several notable changes in overall abundance of seedlings took place from year to year for *A. saccharum* and *B. alleghaniensis*, which rose by 4.1% and fell by 2.4%, respectively. For *A. saccharum*, this apparent rise in overall abundance of emergent seedlings took place at just two sites (Doz & Clar; Table 4.4), while the proportion of seedlings at all other sites did not reach above 4% of sown seeds. Further, though we recorded 39% of the seeds sown at the Doz site having germinated, none survived to the end of the 2017 growing season, whereas of the 63.5% of seeds that were recorded to have germinated at the Clar site, 17.4% survived to September, 2017. A possible explanation for the decline in overall emergence success of *B. alleghaniensis* is the fact that emergence data for 2017 were corrected for background contamination, which was not done for 2016 data. *F. nigra* had surprisingly strong emergence results in both response categories. Emergence abundance results were highest in areas of natural regeneration success for *F. nigra* on the island (Farrar 1995), with greatest abundance of seedlings at western sites (Bara = 123) and lowest at the eastern-most site (Sal = 24). *T. occidentalis* emergence, while still the lowest of any model species, jumped from a total of 32 in 2016 to 98 in 2017, despite a reduction in the number of seeds sown in 2016 by 1,200. Increases in the abundance of *T. occidentalis* seedlings were observed at every site common to both study years except the Sir site, at which declines in abundance of emergent seedlings were observed for all species with 2 years of emergence data.

Table 4.3: Showing proportion of total (%) and total number (N) of pots in which seedlings were found (Presence) and emergent seedlings observed (Abundance) in both emergence years for each species. Numbers shown for *B. alleghaniensis* are corrected for background contamination from naturally occurring birch seed in 2017 only.

	2016				2017			
Species	Presence		Abundance		Presence		Abundance	
	%	N	%	N	%	N	%	N
A. saccharum	29.0	600	8.8	3,000	25.0	480	13.9	4,800
B. alleghaniensis	28.0	300	5.4	3,000	10.4	480	2.0	4,800
F. nigra	-	-	-	-	61.0	300	26.3	1,500
T. occidentalis	15.0	600	0.7	6,000	15.8	480	2.0	4,800

Table 4.4: Proportion (%) of seeds of each model species that emerged at each site in each germination year. The number of seeds sown at each site per species varied in 2015 (600 each for *A. saccharum* & *B. alleghaniensis*, 300 for *F. nigra*, and 1,200 for *T. occidentalis*), but remained constant at 600 seeds/species/site in 2016. Seeds sown in the 2015 year are represented in the 2016 emergence year with the exception of *F. nigra*, which emerged in 2017 due to the lengthy seed maturation process. Proportions given for *B. alleghaniensis* are corrected for background contamination from naturally occurring birch seed.

Species	2016					2017							
	Bara	Sir	Raft	Clar	Sal	Bara	GL	Doz	Wild	Sir	Raft	Clar	Sal
A. saccharum	7.5	12.3	11.3	11.8	1.0	1.8	2.0	39.0	3.2	0.5	0.2	63.5	0.8
B. alleghaniensis	5.3	8.6	1.2	4.8	4.7	0.1	2.8	3.3	0.1	2.5	2.5	11.3	7.6
F. nigra	-	-	-	-	-	41.0	-	-	-	34.0	23.0	25.7	8.0
T. occidentalis	0.8	1.1	0.3	0.8	0.8	2.8	3.2	1.2	0.7	1.8	1.5	3.8	1.3

Evidence of an effect attributable to our substrate treatment was generally weak, with the exception of the models fit to the 2016 *B. alleghaniensis* presence and abundance datasets. The standard deviations of the random pot treatment/control term in the top models fit to *B. alleghaniensis'* presence and abundance datasets (sd = 0.7074 & 0.4000, respectively) were greater than and nearly equal to the parameter estimates for the substrate treatment, respectively (Supplementary Tables 4.4 & 4.5), in 2016.

4.3.2 Herbivore exclusion:

Emergence was positively associated with the absence of terrestrial vertebrate herbivores for most combinations of *species* x *response variable* in either emergence year (Tables 4.5 & 4.6). Models containing this variable also tended to have the largest pseudo-R^2 values, particularly for *A. saccharum* (up to 0.15; Fig. 4.4a,d). Support for the importance of herbivory for *F. nigra* was less clear (Fig. 4.4g), particularly for its presence response variable (pseudo-R^2 = 0.01-.03), for which no model in the treatment analysis confidence set was greater than 4 AICc units away from the Null model (ER_0 = 6.2-14.3). There was limited evidence of a herbivore effect on *B. alleghaniensis*, and *T. occidentalis* emergence. Herbivory emerged as the most important explanatory variable for *B. alleghaniensis* and *T. occidentalis* in 2016 (Fig. 4.4b,c) in explaining the presence of seedlings (pseudo-R^2 = 0.05 for both), and for explaining the abundance of seedlings when paired with substrate effects for *B. alleghaniensis* (pseudo-R^2 = 0.07), or on its own for *T. occidentalis* (pseudo-R^2 = 0.04). Exclusion of small terrestrial vertebrate herbivores became less important for both small seeded species' emergence in 2017, being more often negatively correlated with emergence (*T. occidentalis*; Fig. 4.4f), or of questionable importance given the parameter estimate's standard error (*B. alleghaniensis*; Fig. 4.4e; Supplementary Table 4.5).

The qualitative observations made at each site visit support the importance of the herbivory treatment that emerged in the models, presented above. In 2016, observations of missing seeds were made for 80% of uncaged pots containing *A. saccharum* during the May visit. Uncaged *A. saccharum* pots fared slightly better in May 2017, when 55% of uncaged *A. saccharum* pots were observed with missing seeds, indicating better over-winter survival of seeds on the forest floor. During the June 2017 site visit, only 3% of uncaged *F. nigra* pots seeded in 2015 were observed having missing seeds. The true number is likely far greater, as some pots were lost due to moose trampling or were obliterated by snow crushing, which disproportionately affected uncaged pots (n = 38) over caged pots (n = 15). Pots seeded with *F. nigra* in 2016 suffered far greater seed loses, 53% of uncaged *F. nigra* pots were observed to have been missing seeds. Several pots seeded in 2015 were also missing for *A. saccharum* and *T. occidentalis* (n = 12), and *B. alleghaniensis* (n = 7). All pots for species that emerged in 2017 were accounted for (N = 480 each). Due to time constraints, we did not make observations for whether seeds were missing for *B. alleghaniensis* or *T. occidentalis*, as their seeds were too small to easily relocate.

Damage observed to seeds and seedlings that was considered to have been performed by invertebrates was also recorded, and was particularly evident for *A. saccharum*. Invertebrate damage was recorded if only part of the seedling was damaged (e.g., hypocotyl bitten in half, part or whole cotyledons or leaves eaten; e.g., Meiners and

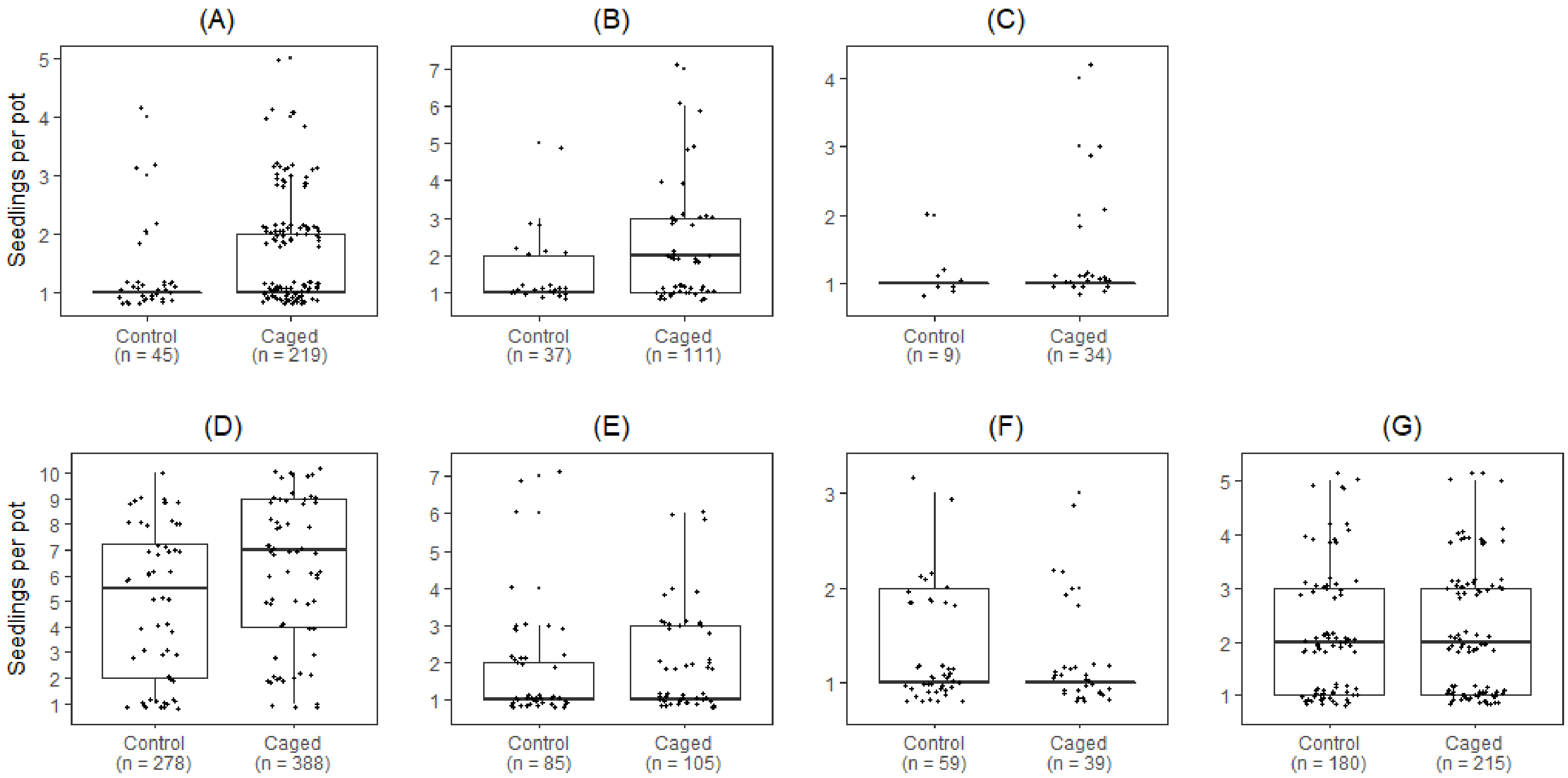

Figure 4.4: Mean number of seedlings per pot with jittered points showing data spread for (A) *A. saccharum* 2016, (B) *B. alleghaniensis* 2016, (C) *T. occidentalis* 2016, (D) *A. saccharum* 2017, (E) *B. alleghaniensis* 2017, (F) *T. occidentalis* 2017, and (G) *F. nigra* 2017 emergence data. 2016 and 2017 emergence data are for pots under closed- and open-top cages, respectively, and their controls. Total numbers of seedlings observed for each species in each emergence year are listed below each panel. Although these seedlings emerged in different years, panels A-C & G represent seeds that experienced the same herbivore exclusion treatments, whereas seeds represented in panels D-F were enclosed within the re-designed herbivore exclosures.

Handel 2000), or if only part of the seed was damaged (e.g., holes in seed coat, cracked seed coat with all or part of the radicle or cotyledons eaten; e.g., Nystrand and Granström 2000). While invertebrate herbivory was not specifically a driver of interest to our study, suspected invertebrate damage was observed in up to 41% of caged and 32% of uncaged *A. saccharum* pots in 2017, which appeared to be the primary targets of invertebrate herbivores.

4.3.3 Substrate composition:

Top models contained substrate effects for *B. alleghaniensis* abundance data (Table 4.6) for 2016 emergence year data and 2017 *T. occidentalis* presence and abundance data (Table 4.5 & 4.6, respectively). *T. occidentalis* emergence data from 2016 would not converge when fit with the substrate treatment variable and random pot treatment/control variable, thereby cutting the number of treatment analysis models to four. Model convergence issues were due to the low overall emergence success of *T. occidentalis* in 2016 (N = 43; Table 4.3), over half of which occurred in mixed forest substrate treatment pots (n = 26; Fig. 4.5).

Substrate type was also important in determining whether *F. nigra* seedlings would be present and in what abundance in 2017 (Table 4.5 & 4.6). Contrary to *B. alleghaniensis* and *T. occidentalis*, which were positively correlated with mixed forest substrate in the 2016 and 2017 emergence years, respectively, *F. nigra* was negatively correlated with mixed forest substrate in 2017 (Tables 4.5 & 4.6; Supplementary Tables 4.4 & 4.5). The actual difference was small for all three species. When comparing the mean number of seedlings per seedling-containing pot (i.e., non-zero data) for the 2016 *B.*

alleghaniensis and 2017 *F. nigra* and *T. occidentalis* emergence data, the difference in mean number of seedlings in a mixed forest vs. boreal forest pot was 0.6 (mixed = 2.22, boreal = 1.65), 0.1 (mixed = 1.34, boreal = 1.23), and -0.5 (mixed = 1.90, boreal = 2.39) seedlings, respectively. Looking at the raw 2016 emergence data for *T. occidentalis*, seedlings occurred in 7% of pots containing mixed forest substrate, compared to 4% of pots containing boreal forest substrate (Fig. 4.5); the odds were equally even in 2017 (odds ratio = 1.3). The odds of finding a *B. alleghaniensis* seedling on either substrate type was essentially even in 2016 (OR = 1.0), however in 2017 there was a greater chance of finding *B. alleghaniensis* seedlings in boreal over mixed substrate pots (OR = 0.75). A similar correlation existed in 2017 for *F. nigra* seedlings, which were just over half as likely to occur on mixed forest substrate over boreal substrate (OR = 0.58). Confidence sets for *A. saccharum* did not include substrate effects for either emergence year.

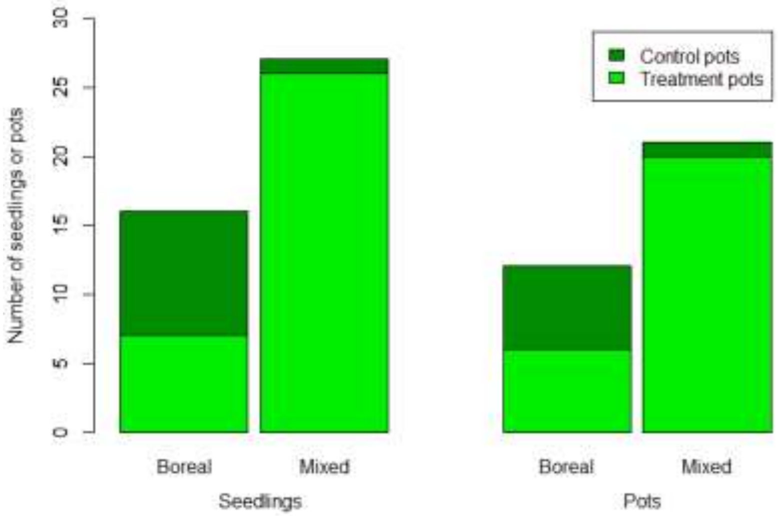

Figure 4.5: 2016 *T. occidentalis* seedling abundance (left) and presence (right) by substrate type. In mixed substrate control (1) and treatment (20) pots, 1 and 26 seedlings occurred, respectively; in boreal substrate control (6) and treatment (6) pots, 9 and 7 seedlings occurred, respectively.

4.3.4 Stand characteristics:

The presence and abundance of small-seeded *B. alleghaniensis* and *T. occidentalis* were both negatively correlated with increasingly deciduous canopy composition in 2017 (Fig. 4.6c,d). There was not enough evidence to support a correlation in our models between either of the small-seeded species' emergence response variables and canopy composition in 2016, despite *B. alleghaniensis* and *T. occidentalis* seedlings emerging in greater numbers in boreal forest stands (n = 106 & 35, respectively) than mixed forest stands (n = 42 & 8, respectively). The evidence of a negative correlation between both *B. alleghaniensis* response variables and canopy composition was relatively strong (ER_0 = 258.8-647.6), but much weaker for *T. occidentalis* response variables (ER_0 = 1.4-9.6) in 2017, however in neither case was there enough evidence to greatly improve the log likelihood of the explanatory models over Null models (pseudo-$R^2 < 0.04$; Tables 4.5 & 4.6). The total number of *A. saccharum* seedlings was nearly even under mixed canopy (n = 142) and boreal canopy (n = 122) in 2016, however emergence was better under boreal (n = 376) than mixed (n = 290) canopy in 2017. The presence of the canopy cover variable in the confidence set models for *F. nigra* is not well borne out when that species' abundance data are displayed graphically (Fig. 4.6a). There appeared to be little evidence of canopy composition influencing either *F. nigra* seedling presence or abundance, as the numbers were essentially even between boreal (85 pots containing 204 seedlings) and mixed (98 pots containing 191 seedlings) stands.

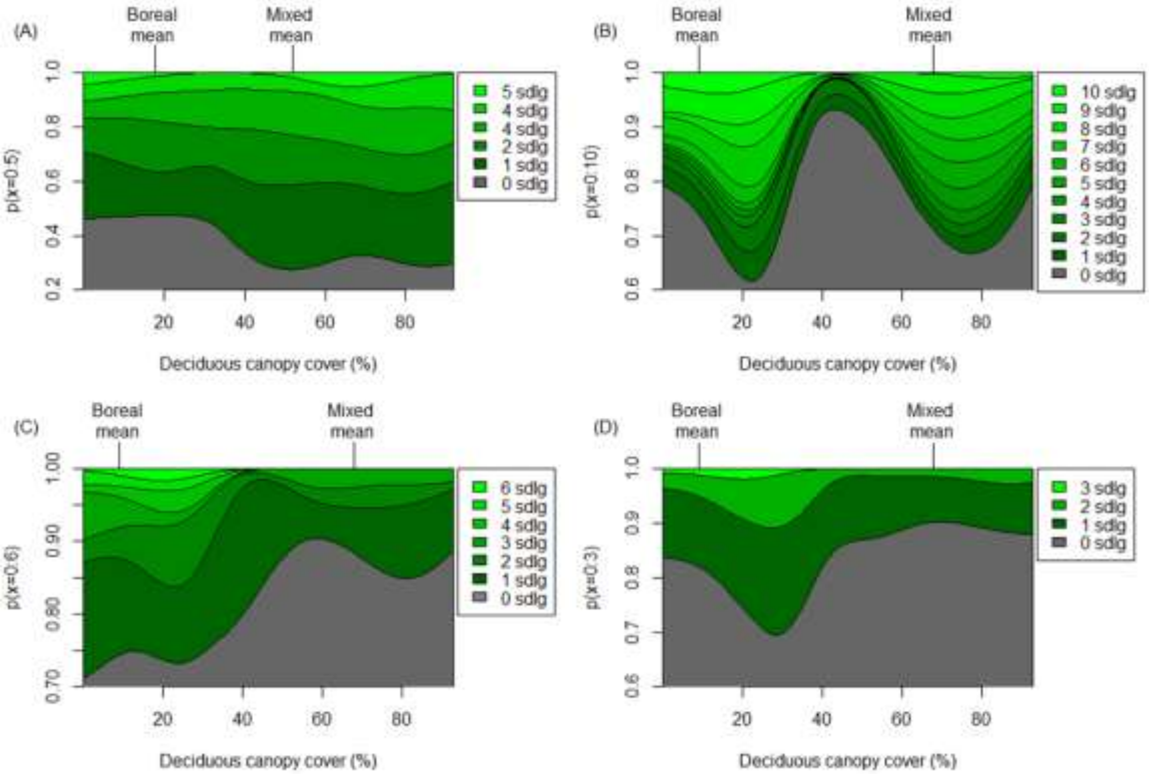

Figure 4.6: Conditional density plots using 2017 emergence data to show the probability of finding (A) 0-5 *F. nigra*, (B) 0-10 *A. saccharum*, (C) 0-6 *B. alleghaniensis*, and (D) 0-3 *T. occidentalis* seedlings per pot under increasing deciduous canopy cover. Emergence data for *B. alleghaniensis* is adjusted for background contamination. Also shown are the mean percent deciduous canopy composition of for blocks established in 2015 (A) and 2016 (B-D). The negative association between deciduous canopy cover and *B. alleghaniensis* and *T. occidentalis* emergence is evident in panels C & D, whereas no clear relationship appears for *F. nigra*. The majority of *A. saccharum* emergence took place at only two sites (Clar & Doz), which had mean deciduous canopy compositions of 14 & 8% (boreal forest), and 74 & 72% (mixed forest), respectively.

4.3.5 Climate:

The inherent limitations of cost and time did not permit more than two replicate climate sensor arrays per site. Yet, even with this limitation, we were able to make observations about the microclimatic variations across the province during 2017, which revealed surprising differences in the timing of the transition spring to summer air temperature. The Bara site warmed up much more quickly than its nearest neighbours (see Fig. 4.1), with mean air temperatures 2.4-3.1°C and 1.3-1.4°C warmer than Doz and GL in May and June, respectively. Differences in microclimate within sites was generally small; in both May and June, boreal and mixed forest stands differed in mean air temperature by 0.1°C. Soils in mixed forest stands did tend to warm up faster than in boreal stands, going from a mean 0.02°C warmer in May to 0.4°C warmer in June, which is not easily explained by a difference in air temperature or soil moisture – which remained virtually unchanged between the forest types.

The *a priori* list of climate variables graphically explored using the 2017 emergence data for each species revealed few obvious relationships that could be easily differentiated from possible site effects. Only the data for *F. nigra* emergence revealed clear relationships between the abundance of seedlings and climate variables relevant to *F. nigra* emergence success (Fig. 4.7). *F. nigra* emergence success appears well correlated with conditions seeming to improve along an east to west gradient (see Fig. 4.1). This gradient is reinforced by the emergence success of this species at the Sir site (n = 102), at which both HOBO® sensor masts failed in February, 2017. Emergence data for *A. saccharum, B. alleghaniensis,* and *T. occidentalis* did not appear well correlated with any of the three climate variables investigated (Fig. 4.8). Emergence of *A. saccharum* seedlings at Clar and Raft varied dramatically, despite similar climatic conditions leading up to the initial pulse of newly emerged seedlings in late May, 2017 (Fig. 4.8a,d,g). *B. alleghaniensis* emergence was similarly poorly correlated with climate variables, and showed an opposite trend to what was expected, where sites that experienced lower mean temperatures leading up to the initial pulse of new seedlings were locations of greater emergence success than those with higher temperatures (Fig. 4.8h). Similar to data for *F. nigra*, the lack of climate data from the Sir site, at which a total of 11 *B. alleghaniensis* seedlings were observed further reinforces this trend, as the nearest weather station to the Sir site (Cormack, NL; 16 km away) reported a mean temperature of 7.7°C for the 19th May – 17th June, 2017 period (Environment and Climate Change Canada 2017a). By the 11th June – 10th July, 2017 period preceding the initial pulse of new *T. occidentalis* seedlings, mean values for the climate variables investigated were evenly spread across variable ranges (Fig. 4.8c,f,i) with no discernable east-west or north-south gradient. It is unlikely that inclusion of climate and emergence data from the Sir site, at which a total of 11 *T. occidentalis* seedlings were observed, would have changed this.

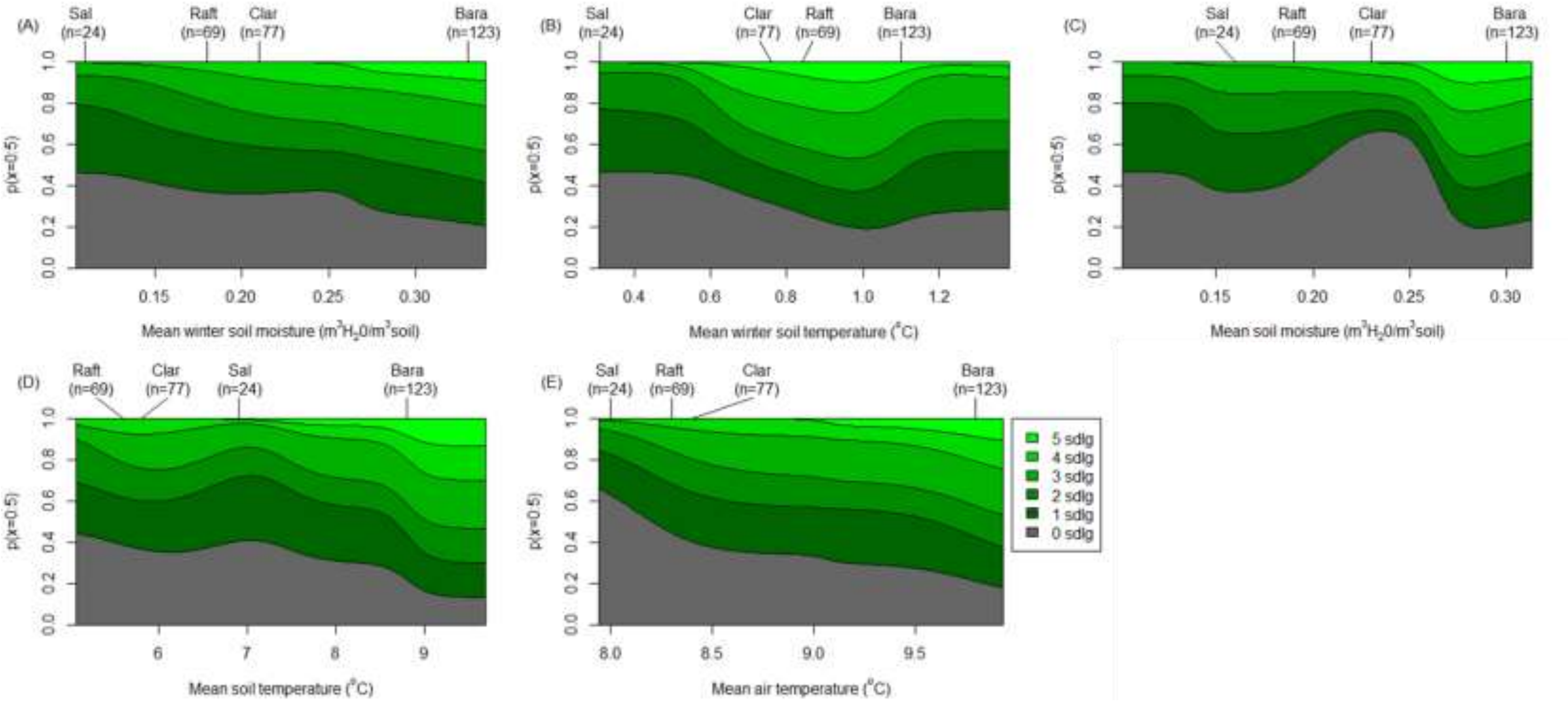

Figure 4.7: Conditional density plots showing probability of 1-5 *F. nigra* seedlings occurring per pot in 2017 by (A) mean winter soil moisture, (B) mean winter soil temperature, and mean soil moisture (C), soil temperature (D), and air temperature (E) for the period of 19th May – 17th June, 2017. Winter climate variables were averaged between first and last weeks with an average air temperature below 0°C (starts 28th of November, 2016 for all sites, ends 2nd of April, 2017 for Bara & Sal, 23rd of April, 2017 for all other sites). Mean values for climate variables at each site are indicated by the position of the sites above each panel. Total number of seedlings observed at each site is also given below site names.

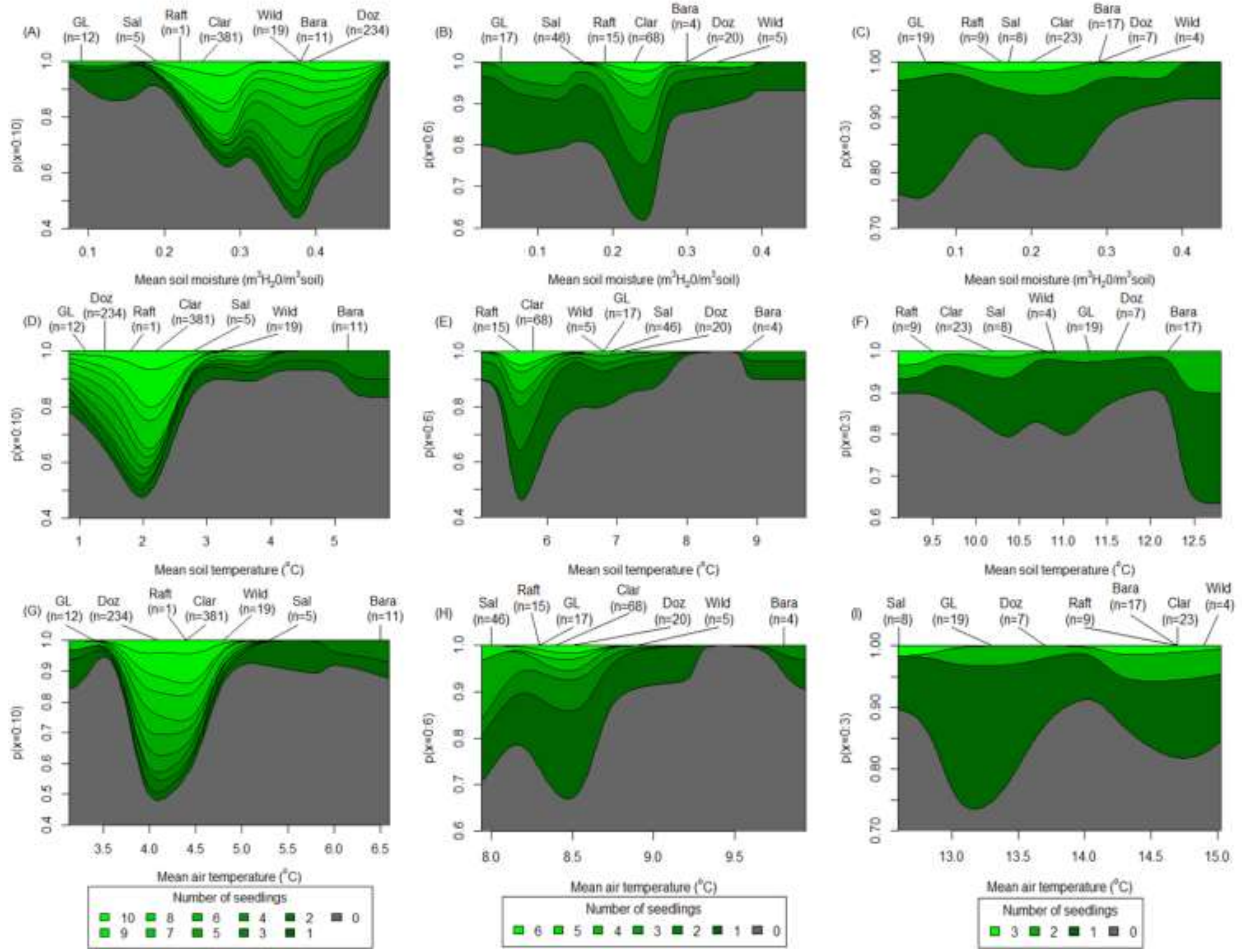
(A)
GL (n=12)
Sal (n=5)
Raft (n=1)
Clar (n=381)
Wild (n=19)
Bara (n=11)
Doz (n=234)
p(x=0:10)
Mean soil moisture (m³H₂0/m³soil)
(B)
GL (n=17)
Sal (n=46)
Raft (n=15)
Clar (n=68)
Bara (n=4)
Doz (n=20)
Wild (n=5)
p(x=0:6)
Mean soil moisture (m³H₂0/m³soil)
(C)
GL (n=19)
Raft (n=9)
Sal (n=8)
Clar (n=23)
Bara (n=17)
Doz (n=7)
Wild (n=4)
p(x=0:3)
Mean soil moisture (m³H₂0/m³soil)
(D)
GL (n=12)
Doz (n=234)
Raft (n=1)
Clar (n=381)
Sal (n=5)
Wild (n=19)
Bara (n=11)
p(x=0:10)
Mean soil temperature (°C)
(E)
Raft (n=15)
Clar (n=68)
Wild (n=5)
GL (n=17)
Sal (n=46)
Doz (n=20)
Bara (n=4)
p(x=0:6)
Mean soil temperature (°C)
(F)
Raft (n=9)
Clar (n=23)
Sal (n=8)
Wild (n=4)
GL (n=19)
Doz (n=7)
Bara (n=17)
p(x=0:3)
Mean soil temperature (°C)
(G)
GL (n=12)
Doz (n=234)
Raft (n=1)
Clar (n=381)
Wild (n=19)
Sal (n=5)
Bara (n=11)
p(x=0:10)
Mean air temperature (°C)
(H)
Sal (n=46)
Raft (n=15)
GL (n=17)
Clar (n=68)
Doz (n=20)
Wild (n=5)
Bara (n=4)
p(x=0:6)
Mean air temperature (°C)
(I)
Sal (n=8)
GL (n=19)
Doz (n=7)
Raft (n=9)
Bara (n=17)
Clar (n=23)
Wild (n=4)
p(x=0:3)
Mean air temperature (°C)
Number of seedlings
10 8 6 4 2 0
9 7 5 3 1
Number of seedlings
6 5 4 3 2 1 0
Number of seedlings
3 2 1 0

Figure 4.8: Conditional density plots showing probability of 0-10 *A. saccharum* (A, D, G), 0-6 *B. alleghaniensis* (B, E, H), and 0-3 *T. occidentalis* (C, F, I) seedlings occurring per pot in 2017 by mean soil moisture (A, B, C), soil temperature (D, E, F), and air temperature (G, H, I). Periods from which means were taken are 24th April – 23rd May, 2017 for *A. saccharum*, 19th May – 17th June, 2017 for *B. alleghaniensis*, and 11th June – 10th July, 2017 for *T. occidentalis*. Mean values for climate variables at each site are indicated by the position of the sites above each panel. Total number of seedlings observed at each site is also given below site names.

Table 4.5: Results shown for treatment variable analysis of presence data for all model species for each germination year for models with ΔAICc ≤ 10 that did not contain pretending variables. Direction of treatment effects and the number of observations in model sets (N) are shown; the left-most column refers to the models shown in Table 4.2. Data structure for all species was a Bernoulli response and models were binomial with a logit link function. Predictor variable treatments are labelled as follows: XHerb = small terrestrial herbivore exclusion, SubM = mixed canopy forest substrate, and %DecC = percent deciduous canopy cover. ΔAICc & AICc weights (AICcw) are given, evidence ratios (ER) calculated for top model over second ranked model and each model over the Null model (ER_0), and pseudo-R^2 (McFadden 1973) is calculated for each model.

	Species	Year	Model structure	N	Predictor			k	Log Likelihood	ΔAICc	AICcw	ER	ER_0	R^2
					XHerb	SubM	%DecC							
3	*A. saccharum*	2016	Binomial	588	↑			4	-270.0	0	0.45	1.1	4.8×10^{19}	0.15
5					↑		↑	5	-269.1	0.2	0.39		4.3×10^{19}	0.15
6					↑	↑		6	-269.6	3.2	0.09			
8					↑	↑	↑	7	-268.8	3.7	0.07			
1			Null					3	-316.4	90.7	<0.001			
3	*A. saccharum*	2017	Binomial	480	↑			4	-140.2	0	0.41	1.7	2.9	0.01
1			Null					3	-142.2	2.1	0.15			
3	*B. alleghaniensis*	2016	Binomial	293	↑			4	-152.8	6.3	0.031	2.7	731.4	0.05
1			Null					3	-160.5	19.5	<0.001			
2	*B. alleghaniensis*	2017	Binomial	480			↓	4	-222.9	0	0.46	1.1	280.5	0.03
5					↑		↓	5	-221.9	0.2	0.42		258.8	0.03
1			Null					3	-229.6	11.3	0.002			
3	*T. occidentalis*	2016	Binomial	588	↑			4	-111.9	0	0.71	2.6	89.6	0.05
1			Null					3	-117.4	9.0				
2	*T. occidentalis*	2017	Binomial	480			↓	4	-202.9	0	0.31	1.3	3.6	0.01
5					↓		↓	5	-202.2	0.6	0.23		2.7	0.01
7						↑	↓	6	-201.5	1.3	0.16		1.9	0.02

8					↓	↑	↓	7	-200.8	1.8	0.12		1.4	0.02
1			Null					3	-205.3	2.6	0.08			
8	*F. nigra*	2017	Binomial	300	↑	↓	↑	7	-176.0	0	0.27	1.3	5.0	0.03
5					↑		↑	5	-178.4	0.5	0.21		3.9	0.02
3					↑			4	-179.7	1.2	0.15		2.8	0.01
6					↑	↓		6	-177.9	1.7	0.12		2.2	0.02
7						↓	↑	6	-178.2	2.2	0.09			
2							↑	4	-180.5	2.6	0.07			
1			Null					3	-181.8	3.3	0.05			

Table 4.6: Results shown for treatment variable analysis of abundance data for all model species for each test year for models with ΔAICc ≤ 10 that did not contain pretending variables. Direction of treatment effects and the number of observations in model sets (N) are shown; the left-most column refers to the models shown in Table 4.2. Data structure for all species was a proportional binomial response, weighted with the number of seeds sown per pot. With the exception of the *F. nigra* data, when full datasets were used, inclusion of a zero-inflation factor greatly improved model fit (denoted by ZIB). Predictor variable treatments are labelled as follows: XHerb = small terrestrial herbivore exclusion, SubM = mixed canopy forest substrate, and %DecC = percent deciduous canopy cover. ΔAICc & AICc weights (AICcw) are given, evidence ratios (ER) calculated for top model over second ranked model and each model over the Null model (ER_0), and pseudo-R^2 (McFadden 1973) calculated for each model.

	Species	Year	Model structure	Model weight	N	Predictor			k	Log Likelihood	ΔAICc	AICcw	ER	ER_0	R^2
						XHerb	SubM	%DecC							
3	*A. saccharum*	2016	ZIB	5	588	↑			5	-452.8	0	0.42	1.2	9.4 x 10^{19}	0.06
5						↑		↑	6	-452.0	0.4	0.34		7.7 x 10^{19}	0.10
6						↑	↑		7	-451.8	2.1	0.14			
8						↑	↑	↑	8	-451.2	2.9	0.10			
1			Null						4	-499.8	92.1	<0.001			
5	*A. saccharum*	2017	ZIB	10	480	↑		↓	6	-417.5	0	0.64	3.0	1.1 x 10^{4}	0.02
2								↓	5	-419.7	2.2	0.21			
1			Null						4	-426.6	14.0	<0.001			
6	*B. alleghaniensis*	2016	ZIB	10	293	↑	↑		7	-240.6	0	0.71	2.5	2.4 x 10^{6}	0.07
1			Null						4	-258.5	29.5	<0.001			
5	*B. alleghaniensis*	2017	ZIB	10	480	↑		↓	6	-353.6	0	0.49	1.7	647.6	0.02
2								↓	5	-355.2	1.1	0.29		377.7	0.02
1			Null						4	-362.2	13.0	<0.001			
3	*T. occidentalis*	2016	ZIB	10	588	↑			5	-135.9	0	0.70	2.5	54.6	0.04

1			Null						4	-141.0	8.1	0.01			
8	*T. occidentalis*	2017	ZIB	10	480	↓	↑	↓	8	-251.6	0	0.29	1.3	9.6	0.02
5						↓		↓	6	-254.0	0.5	0.23		7.3	0.02
7							↑	↓	7	-253.0	0.6	0.22		7.2	0.02
2								↓	5	-255.4	1.4	0.15		4.7	0.01
3						↓			5	-256.5	3.6	0.05			
1			Null						4	-258.0	4.6	0.03			
8	*F. nigra*	2017	Binomial	5	300	↑	↓	↑	7	-445.7	0	0.55	2.2	6.6 x 10^3	0.03
6						↑	↓		6	-447.5	1.6	0.25		3.0 x 10^3	0.02
7							↓	↑	6	-448.2	2.9	0.13			
4							↓		5	-450.0	4.5	0.06			
1			Null						3	-458.7	17.7	<0.001			

4.4 Discussion

Our spatially-extensive field experiment suggests that the four model temperate tree species' distributions are not limited by their incapability to germinate in mature boreal or mixed canopy forest stands, evidenced by successful seedling emergence across all experimental sites in insular Newfoundland. Such evidence supports the over-arching goal of this research, to identify probable drivers beyond climatic variables influencing future distributions of our model species in a range-edge and beyond-range setting, and compare those to known drivers within species' ranges. That each species was able to successfully germinate beyond their current distributional range also provides indirect evidence that these species' climatic niche extends well beyond their respective realised niche space, at least for the demographic stages studied here. We have provided empirical evidence for each of our model species' abilities to overcome early life stage a/biotic hurdles in environments beyond their current distribution. The seedling emergence patterns resulting from the two iterations of this experiment presented, in many cases, evidence that supported our *a priori* hypotheses; large-seeded tree species were more vulnerable to seed predation, while small-seeded species were sensitive to canopy composition. Other findings, however, were unexpected, given what is known about these species' germination requirements under natural conditions elsewhere. Here, we will explore these species-specific drivers and constraints on temperate tree range expansion in boreal forest stands

4.4.1 Boreal-temperate ecotone and unfilled niche space

A striking finding was the apparent lack of correlation between model species' emergence patterns and climatic variables. *F. nigra* emergence was correlated, weakly, with climatic variables, and many of these match well with known germination requirements for this species. The site at which *F. nigra* emergence was poorest (Sal) had the lowest mean air temperature and mean soil moisture for the 30 day period leading up to the initial pulse of newly emerged seedlings in mid-June, 2017, as well as the lowest mean over-winter soil moisture. These associations fit well with typically boggy, water-saturated site characteristics where *F. nigra* is commonly found within its mainland range (Gates 1942, Wright and Rauscher 1990). One surprising correlation seemed to occur between greater *B. alleghaniensis* emergence and lower mean air temperatures for the 19th May – 17th June, 2017 period. Overall, 93% of the total number of seedlings observed in 2017 occurred at sites with mean temperatures of 7.7-8.6°C for the 19th May – 17th June, 2017 period, indicating other factors were dominant in driving emergence in this species, as typically *B. alleghaniensis* germination is optimal under temperatures of 20-23°C (Perala and Alm 1990).

Though this is based on only a single year of data, three of the model species were also able to germinate in 2016, in similar numbers to 2017 (Table 4.3). The graphical comparison of 2017 emergence data with climate variables (Fig. 4.7 & 4.8), paired with the overall emergence results appears to confirm that portions of Newfoundland are within the climatic envelope of these BTE species, however their widespread establishment has not occurred here (Pastor and Mladenoff 1992). Despite the stage apparently being set for colonisation of the island by a larger suite of temperate tree species than naturally dispersed here (MacPherson 1995), either the monumental challenge of crossing the Cabot Strait has proven insurmountable without human intervention, or else other competing factors have barred the establishment of viable populations of most temperate species on the island.

4.4.2 Vertebrate predation constrains large-seeded tree establishment

A. saccharum emergence was well explained by protection from terrestrial vertebrate herbivory in both study years. This followed our expectations that *A. saccharum* would be targeted by terrestrial vertebrate granivores looking for the larger, more food-rich seeds, which has been observed within (Hsia & Francl, 2009) and at the edge (Brown & Vellend, 2014) of its native distribution in mainland Canada. The large size of *A. saccharum* seeds and seedlings also made it easy to observe damage, which was often consistent with invertebrate herbivory patterns (Nystrand and Granström 2000, Meiners and Handel 2000). This was also the case with *F. nigra* seeds and seedlings, although overall observations of seed and seedling herbivory were lower for that species.

Our initial assumptions were that *F. nigra* would be vulnerable to seed predation given its large seed size relative to most of the species present at our sites and their duration on the forest floor before germinating. This assumption was based on work done with other species with similar seed sizes (De Steven 1991, Hulme and Hunt 1999), as it appears no research has been done to directly study the effects of post-dispersal seed predation on this species' reproductive success within its range, or at the range edge. This assumption was borne out, insofar as our analysis pointed to our herbivory treatment as being among the most important of the treatment variables, however Figure 4.4g shows that the effect size overall was limited. Unlike *A. saccharum*’s 2017 emergence data, *F. nigra* was more consistent across sites (Table 4.4), however while both species experienced greater emergence success within exclosures at most sites (in either year for *A. saccharum*), both species did experience greater success outside of exclosures at several sites.

The herbivory treatment effect was evident in 2016 and 2017 emergence year models for the small-seeded model species, despite that these species’ seeds are not readily differentiable in size from those of typical boreal tree species (Bartlett et al. 1991, Bonner and Karrfalt 2008). This is certainly not unprecedented, *B. alleghaniensis* and *T. occidentalis* have been observed suffering from post-dispersal seed predation in their home ranges (Kelly et al. 2001, Larouche et al. 2011). The variability in the importance of the herbivory treatment between the 2016 and 2017 seedling emergence years (Fig. 4.4) might reflect inter-annual variation in naturally occurring seed production, changes in the efficacy of our herbivory treatment with the altered exclosure design, inter-annual variation in the invertebrate seed predator population, or some other unmeasured variable. Regardless of the specific cause, our initial assumptions that these species would not suffer from vertebrate seed herbivory were not well supported by our data. Further investigation into whether these small-seeded species with limited distributions on the island are suffering from seed predation disproportionately to locally more abundant tree species with similar sized seeds is warranted.

4.4.3 Canopy-seedbed interactions

The delay in spring canopy closure may have benefitted *B. alleghaniensis* seeds under increasingly deciduous canopies due to the integral role light exposure plays in breaking seed dormancy (Yelenosky 1961). The differences observed in spring soil temperatures between boreal and mixed forest stands is likely evidence that greater solar radiation was reaching the forest floor in mixed forest stands due to increased canopy openness before spring leaf flush of deciduous trees (Lieffers et al. 1999). Pots were seeded both years in the middle of leaf-fall (September, 2015 and October, 2016), and while we can hypothesise that the competing smothering effect of leaf litter likely cancelled out any beneficial spring light transmission for the 2017 germination year, it is curious that this effect was absent in 2016. This smothering effect also showed up in the models fit to the 2017 emergence data of *T. occidentalis*, despite that in 2016, the only pots containing 4 seedlings (the greatest number of seedlings found in any pot that year) were found in areas with less than 50% deciduous canopy cover and few seedlings were found in areas with greater than 50% deciduous canopy cover. Seedling abundance for both species was highest in 2016 under 60-80% total canopy cover, and 85-95% in 2017. This is within the range of what others have found. Linteau (1948) observed greatest germination of *B. alleghaniensis* under partial and complete canopies over open canopies, and Cornett et al. (2001) found that while *T. occidentalis* germination was negatively impacted by leaf litter, they saw favourable germination under >70% total canopy cover.

One of the most surprising results from our treatment variable analysis was the positive correlation between *T. occidentalis* emergence and mixed forest substrate in

2017, as well as the lack of evidence supporting any correlation between *B. alleghaniensis* emergence and a specific substrate type. The relative success of these species on a predominantly leaf litter seedbed, which has poor moisture-bearing capacity (Linteau 1948, Buda et al. 2011), may be partially explained by the generally low density of maples (*Acer* sp.) at any of the experimental sites, which shed leaves that tend to mat and therefore create a hard, dry barrier for the small seedlings (Burton et al. 1969). An alternative hypothesis would be that while the moisture retaining qualities of leaf-litter are poor, early summer in Newfoundland is characterised by an average 81-104 mm precipitation and relatively cool temperatures (Environment and Climate Change Canada 2017b), perhaps reducing the risk of seedling desiccation. Regardless, the conditions under which *T. occidentalis* seedlings emerged most successfully in 2017 – on leaf litter substrate under predominantly boreal canopy – are rare under natural conditions, and this poses questions about whether range expansion throughout Newfoundland will be possible.

A. saccharum emergence was notably more successful at the Doz and Clar sites than the others and had mean May air temperatures of 4.1 & 4.4°C, respectively, an ideal temperature for *A. saccharum* germination (Solarik et al. 2016). These temperatures were in line with the Raft and Wild sites, at 4.4 & 4.8°C respectively, yet only 1.5 & 0.7% of *A. saccharum* seeds managed to emerge there (Fig. 4.8g). *A. saccharum* emergence followed expectations as a species known for its shade tolerance (Godman et al. 1990), showing best emergence under 80-95% canopy cover in both 2016 and 2017. The effect of canopy composition featured in the confidence sets for the *A. saccharum* 2016 presence and 2016/17 abundance dataset treatment analyses, however the large relative standard error surrounding this variable's 2016 parameter estimates (Supplementary Tables 4.4 & 4.5), and the change in effect direction between models fit to 2016 and 2017 abundance datasets (Table 4.6) calls its actual importance into question. While there appears to be limited literature discussing the effects of canopy composition on *A. saccharum* seedling emergence, a study by Reinhart et al. (2012) suggested that seedling recruitment of *A. saccharum* was greater near heterospecific individuals than conspecifics.

Predictably, *A. saccharum* emergence was unaffected by substrate in this experiment, which is in line with what others have found elsewhere (Barras and Kellman 1998, Kellman 2004). Caspersen and Saprunoff (2005) found that *A. saccharum* recruitment was significantly limited on leaf litter substrate, however their study included a wider variety of comparison substrates of which moss was a negligible component. Tying together the dual effects of substrate type and canopy composition was similarly of little importance in the confidence sets for *A. saccharum*, offering little evidence of an interaction leading to a possible smothering effect.

F. nigra appeared uninhibited by increasing canopy cover; the likelihood of finding five seedlings in a pot in 2017 was greatest in pots with 70-80% total canopy cover. While the treatment model analysis suggests that there was some positive association with increasingly deciduous canopy cover, this correlation is relatively weak when the models are displayed graphically (Fig 4.6a) and when the coefficients are inspected (Supplementary Tables 4.4 & 4.5), however not so weak as to declare it an uninformative parameter (Arnold 2010). One possible explanation for this positive correlation comes back to the higher levels of solar radiation that would be reaching the ground in the spring due to delayed deciduous canopy closure, as light is often one of the necessary ingredients in breaking seed dormancy (Vanstone 1974, Bonner and Karrfalt 2008).

The importance of a deep organic layer is apparent in the literature regarding where *F. nigra* is found within its natural distribution (Gucker 2005). The moisture retention properties of soils with deep organic layers of partially decomposed moss (Turetsky et al. 2012) may explain *F. nigra*'s preferential emergence on mossy substrates over leaf litter substrates, characteristic of the boreal forest stands. The fact that this association did not extend to a correlation between *F. nigra*'s emergence patterns and canopy composition, where the average number of *F. nigra* seedlings per pot was 1.3 and 1.4 in mixed and boreal stands, respectively, was likely due to the similarity in soil moisture conditions during the 2017 growing season and the 2016/17 winter, differing by at most 0.04 mean m^3_{H2O}/m^3_{soil} between boreal and mixed forest stands.

4.4.4 Further research

Some elements of this study limited our ability to offer predictions of how emergence of temperate tree species might be controlled by specific drivers across Newfoundland, such as the limited climate data, the change in our terrestrial vertebrate exclosure design between study years, the low number of data collection site visits in 2016 that limited our ability to track emergence of seedlings, and purposely broad definitions used for the different substrate types tested in this experiment. Our two emergence years' datasets would have been more comparable, had the experimental design remained consistent, between the herbivore exclosure cage designs and number of data collection site visits, for instance; however the 2015 implementation was intended as a learning experience and it would have been irresponsible to not apply valuable methodological lessons gleaned from it. While the low emergence rates do represent challenges to the inferential power of any analysis we performed, this is not uncommon in field-based manipulative germination experiments (De Steven 1991, Ronnenberg et al. 2008), especially when planting seed beyond their natural distribution range (Brown and Vellend 2014).

Since the primary focus of this research was to further generate research on the topic of temperate tree range expansion to and within Newfoundland, there are many questions that easily spring from our results. We would initially pose the question of whether terrestrial vertebrate predators are the only limiting herbivory-related factor, or whether invertebrate herbivores pose a greater barrier to successful germination for temperate tree species in Newfoundland as they do in other areas where they are exotics (Pigot and Leather 2008). This question could be addressed using carefully combined herbivore exclusion methods to differentiate the impacts of herbivory by invertebrates (e.g., Saska et al. 2014) and vertebrates (e.g., Brown and Vellend 2014), or herbivory impacts within functional groups (e.g., Moore and Swihart 2008, Lobo et al. 2009, Pufal and Klein 2013). Notable here as well were the prevalence of slugs observed within our test pots; Nystrand and Granström (2000) found that slugs were the most important herbivores in their boreal Swedish study area for emergent seedlings. Evidence that damage and mortality of newly emerged seedlings were caused by slugs, such as the physical presence of slugs in test pots and slime trails near seedlings, was consistent with that described by Nystrand and Granström (1997) may pose a serious establishment barrier for introduced and native tree species alike (Moss and Hermanutz 2010). The prevalence of seed and seedling herbivory that was observed at all sites, across species and during both germination years made it abundantly clear that further experimentation with these species to differentiate the effect of different herbivore groups is necessary. Given that our second cage design (implemented in 2016) did not effectively omit avifauna from entering the exclosures and predating upon the enclosed seeds, the effects of this herbivore group on temperate tree species germination could also be studied further in Newfoundland. From our results, we would expect the herbivore group responsible for posing the greatest barrier to germination would change, depending on seed size and germination phenology.

Our two large seeded model species, *F. nigra* and *A. saccharum*, suffered differently from both seed and seedling herbivory; the latter can likely be explained by the timing of their respective germination. Where *A. saccharum* emerged in May, before much of the forest floor herb layer had emerged (personal observation), the seedlings are the first new growth to attract the attention of herbivores, *F. nigra* seedlings emerged in June, after the forest floor herb layer had flushed out. This problematic “early-bird” phenology for *A. saccharum* may persist as rising spring temperatures across Newfoundland (Natural Resources Canada 2015) is likely to induce a phenological shift to earlier emergence for both forest herb layer species as well as for *A. saccharum*

(Walther et al. 2002). This phenological synchrony is also likely to persist between the herbivorous species feeding on *A. saccharum* seedlings and their emergence period, as has been shown in other tree species-insect herbivore systems (Schwartzberg et al. 2014). One of the ways that *A. saccharum* is known to deal with this dilemma within its home range is through well-synchronised masting years, which allow a pulse of seedlings to survive the early life-stage herbivory filter by satiating their herbivorous enemies (Schnurr et al. 2002).

The different cage designs may also have been responsible for the lack of any negative correlation between the small seeded model species and deciduous canopy composition in the 2016 emergence year. The initial cage designs, installed in 2015 had 'lids' of hardware mesh that effectively omitted any leaf litter from reaching the ground within the cages. This unintended barrier eliminated any potentially smothering effect that could have occurred within cages, which likely washed out any potential effect deciduous canopy cover may have had in 2016. Therefore, the importance of the herbivore exclusion treatment effect observed in *T. occidentalis* and *B. alleghaniensis'* 2016 emergence data may have indirectly been due to protection from smothering, rather than or in combination with protection from herbivory.

4.5 Conclusions

We have shown that for all species, but particularly for species with large seeds relative to the native flora, seed predation poses an effective barrier to seedling emergence across Newfoundland. This cannot be as easily overcome as within-range populations, where seed abundance during high production years can satiate predators, allowing some propagules to escape (Kellman 2004). It is apparent that there are sufficient substrate types for germination to occur in mature forested stands of varying compositional complexities in Newfoundland, but that further work needs to be done to investigate substrate and soil qualities in relation to canopy composition to identify linkages between the above and below ground nutrient flows (Wardle et al. 2004) and seedling emergence, survival, and growth. Finally, while climatic variables did not appear well correlated with emergence success of most of our model species, these may become more important at later life stages, such as promoting growth rates adequate to escape moose herbivory (McInnes et al. 1992), and adequate GDD for healthy seed production (Sykes et al. 1996). Further research investigating these and other temperate tree species' survival, growth, and transition between crucial life stages is needed to understand how isolated boreal forest systems may become colonised by southern tree species with a changing climate.

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Chapter 5: Conclusion

Evidence of the importance of non-climate biotic and abiotic interactions in species range shifts under anthropogenically driven climate change has been mounting for several decades (Walther *et al.* 2002; Parmesan and Hanley 2015). Apparent in the recognition of the importance of these interactions is a need for greater experimental and observational research in order to compliment the growing body of literature regarding future species distributions under various climate change projections (e.g., Iverson and Prasad 2002; Iverson *et al.* 2008; Lawler *et al.* 2009). As outlined in Chapter 2, ecotones represent ideal systems for this type of research given the inherent state of stress that members from each biome-specific community experience. When the alleviation of climate-driven limiting factors does not induce a consistent pattern of response, as we have seen in the boreal forest – temperate forest ecotone (BTE), the natural inclination is to ask why.

I identified several geographical areas for which data on possible tree species range shifts within the BTE are scarce, including Europe and European Russia, eastern Asia, and eastern Canada. The fragmentary coastline, glacial history and geographical isolation of Newfoundland means that likely habitable areas for BTE-dwelling tree species on the island have been effectively omitted from many species' ranges due to the dispersal barrier imposed by the Cabot Strait and Gulf of St. Lawrence. The anthropogenic facilitation of propagule dispersal to an otherwise unreachable island with a climate capable of supporting a wider diversity of plant species than currently live there will not necessarily mean range expansion or establishment in Newfoundland (Qian and

Ricklefs 2006). Biotic and abiotic hurdles must be overcome in order to establish viable populations of incoming species and parsing the relative importance of these hurdles, which I have shown in Chapter 4 can vary widely among species from the same ecosystem, is important in expanding our understanding of tree species range shifts.

The methods that are employed to model the effects of climatic drivers on plant species' distributions are often put under scrutiny (e.g., Jaeschke *et al.* 2012; Morin and Thuiller 2009; Fischer *et al.* 2014), and comparisons are drawn between projected species distributions and long-term occurrence datasets (Araújo *et al.* 2005), or experimental data (Davis *et al.* 1998) in order to quantify the success rate of these projections. This methodological analysis has also been performed for field experimental methods that are used to make direct observations on species range shift in manipulated systems (Brown 1992; Cleland *et al.* 2007). Chapter 3 was inspired by observations made over the course of my project and explores the possibility that small herbivore exclosure cages are capable of modifying microclimatic conditions by affecting temperature regimes and snow accumulation within their confines. The annual climatic cycle for which plant species in areas that experience snowy winters are adapted includes factors such as local snowfall amounts and duration, as well as plant species' tolerance to early winter and early spring freeze-thaw cycles (Sakai and Larcher 2012; Connolly and Orrock 2015). The buffering capacity of snow against large temperature swings is well understood, but a lack of natural snow accumulation within herbivore exclosures before, during and following a snowy winter season can have consequences for plants within cages (Schaberg *et al.* 2008). My results indicated that the variance in temperature and snow-cover duration between within-cage and control plots was dependent on cage material, design, and size. Smaller cages made of large gauge material had the least impact on temperature variables, while cages without an open top had least impact on snow-cover duration. It may be difficult to overcome this experimental design challenge, but monitoring exclosure-induced microclimates using temperature sensors may prove to be an easy and effective way to account for this potential source of error.

The results of the main experiment in this thesis are laid out in Chapter 4. I tested climatic, biotic, and abiotic factors that could potentially form a germination bottleneck for four model northern temperate tree species, effectively truncating the establishment of new populations in novel territory. The challenges in the passage of model species from seed to seedling represent the initial post-dispersal barriers to range expansion for northern temperate tree species into the boreal forest under conditions that exist in Newfoundland. The vulnerability of model species to dangers posed by seed predation, substrate type, and canopy composition reveal differences in the ease with which some species are able to germinate in boreal systems beyond their range over others according to reproductive strategies (i.e., seed size). The lack of climate variable importance in the results presented in Chapter 4 could be interpreted as indirect evidence that this work was conducted within unfulfilled climatic niche space of the model species for this life stage transition. Future research delving more deeply into one or more of these a/biotic drivers is called for, as is continuing study focussing on a/biotic drivers limiting northern temperate tree species' transitions between later life stages beyond their modern distributional ranges.

Of particular interest is under what conditions these species might manage to overcome future, changing herbivory threats. All of the model species in the current study are highly palatable to herbivores that inhabit Newfoundland, such as moose (McLaren *et al.* 2006; Fisichelli *et al.* 2012), snowshoe hare (*Lepus americanus,* Erxleben; Davis et al. 1998), and beavers (*Castor canadensis,* Kuhl; Johnston 2017), which tend to forage preferentially on trees that are sapling sized or larger. Relating climatic variables to growth and development, and carbon sequestration, of these and other temperate tree species and comparing these to native species would provide further insights into the appropriateness of Newfoundland's climate for establishment of viable populations of non-native southern species.

Further work could also be done to differentiate the effects that soil and substrate have on my model species' emergence ability, as has been done elsewhere by looking at a greater variety of seedbed types (Caspersen and Saprunoff 2005), relating species distributions to soil horizons and structure (Demers *et al.* 1998), and connecting canopy gaps to seedbed suitability (LePage *et al.* 2000). The presence of beneficial soil biota can allow established seedlings to thrive where otherwise they might languish (Stinson *et al.* 2006; Leigh Jr 2010). While I did not investigate the soil biota present at the test sites in this study, it is possible that beneficial soil biota relevant to mainland temperate tree species in Newfoundland may not be present, which would have implications for growth and nutrient exchange (Van Der Heijden *et al.* 2008).

The context within which the majority of species distributional shift research takes place is shaped by the narrative of global climate change (Iverson and Prasad 2002;

Walther *et al.* 2002; Parmesan and Yohe 2003; Alo and Wang 2008; Lawler *et al.* 2009). The work presented in this thesis follows a now common understanding (Walther 2003; Brooker *et al.* 2007; Zarnetske *et al.* 2012; Urban *et al.* 2013) that, while tree species redistributions may be primarily driven by changing climate regimes, careful field-based experimental and observational work will help us discern other drivers that are arguably of equal importance in shaping distributional shifts. Geographic, demographic, and taxonomic gaps in research on this topic need to be explored and a/biotic drivers investigated to understand how viable populations of tree species may or may not establish beyond their current range edge.

Others have shown that the climatic envelopes for the four model species used in Chapter 4 extend well beyond their realised distributional range, a discrepancy that is expected to become increasingly pronounced under climate change (McKenney *et al.* 2007). I have shown that for four northern temperate tree species to germinate beyond their distributional range, seed size is a good predictor of the conditions under which species are successful. Despite the challenges model species faced in this experiment and the low number of seeds sown per site compared to average seed rain for these species within their native ranges (Burns and Honkala 1990), successful seedling emergence and survival did occur. Therefore, the combination of limiting factors preventing the establishment of a viable population beyond the distributional range of any of my model species on the island is not yet known. The work presented in this thesis represents the first attempt to understand what factors might prevent seedling emergence for these four northern temperate tree species on the island using the methodology explained in Chapter

4. I am hopeful this will lead to further investigation into these and other limiting factors' effects on potential future range expansion of northern temperate tree species to and within Newfoundland.

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Supplementary Materials

Chapter 2

Appendix 2.1: Literature search full methods

Our primary search tool for this study was the Scopus online database, which was used to search the literature published prior to December, 2016 using the search term:

(ALL (temperate) AND ALL (boreal) AND TITLE-ABS-KEY (tree) AND TITLE-ABS-KEY (expansion OR migration OR shift*))

This search produced 1,095 titles, which were then scanned to identify articles relevant to the subject of this study, producing a list of 123 candidate papers. Subsequent searches were conducted to ensure all relevant papers were captured in our database. Subsequent searches were performed on the Scopus database in order to capture additional studies as outlined in the literature review methods using the following search terms:

(TITLE-ABS-KEY (plant* OR veg* OR tree) AND TITLE-ABS-KEY (temperate OR boreal) AND TITLE-ABS-KEY (resurvey* OR resample* OR revisit* OR "temporal change"),

(TITLE-ABS-KEY (tree OR sapl* OR seedl* OR plant) AND TITLE-ABS-KEY (forest) AND TITLE-ABS-KEY (temperate) AND TITLE-ABS-KEY (range AND expansion) OR TITLE-ABS-KEY (range AND shift)), and

(TITLE-ABS-KEY (latitud* OR elevation* OR alpine) AND TITLE-ABS-KEY (shift OR expan*) AND TITLE-ABS-KEY (tree) AND TITLE-ABS-KEY (temperate))

The requirement for study locations to be within portions of the BTE in North America, Europe or eastern Asia was important to avoid dilution of our results by data from studies focussing on deciduous forest-conifer forest boundaries to the south of the spatial extent of the BTE. Alpine forest zones occurring close to the BTE, but not within its extent – as in the southern Appalachian Mountains – can resemble the BTE in terms of tree species composition; however, they were excluded as they were not located within our spatial definition of the BTE in North America or Europe (see Fig 3.1a & 3.1b). One area that presented somewhat of a challenge in this respect was the BTE in eastern Asia, which predominately occurs along spatially distributed elevational gradients rather than a continuous latitudinal gradient (Ohsawa 1990). Therefore, species composition (outlined in Table 2.1 by Pastor and Mladenoff 1992) was relied upon as a proxy for relevance to this study for this portion of the BTE, if authors did not explicitly identify the BTE as a focus of their work.

Supplementary Table 2.1: Studies extracted from the literature based on relevance to the subject of shifts occurring in the modern boreal-deciduous ecotone, and the qualitative findings contained therein.

Authors	**Year**	**Country**	**Study design**	**Study temporal range (years)**	**Life stages studied**	**Habitat-type(s) under study**	**Northward/Upward temperate tree range expansion**	**Observation of increasing temperate species dominance at range edge**	**Important climate drivers**	**Other drivers of range dynamics?**
Xiongwen	2001	China	obs*	9	Sapling – adult	Temperate mixed evergreen coniferous and broadleaf deciduous forest		Yes, infilling, change in abundance	Decrease in annual precipitation, climate change (hypothesised)	Forestry plantations, logging (hypothesised), land-use change (hypothesised), soil moisture content (inferred)
Kellman	2004	Canada	exp	11	Seed – sapling	Hardwood uplands, boreal lowlands transition zone, Great Lakes-St Lawrence hardwood forest and southern boreal forest	Yes, when planted		Climate warming (hypothesised)	Light availability, seed predation (inferred), canopy disturbance/canopy gaps, available mycorrhizal fungus (inferred)
Goldblum & Rigg	2005	Canada	obs	5	NA	Northeastern deciduous on rocky till upland sites and spruce and fir on wet, cool lowland sites		Yes, increased growth	Temperature, precipitation (quantity & type), climate change	Soil qualities (inferred)
Friedman & Reich	2005	USA	obs	100-120	Sapling – adult	Productive and unproductive forest stands, uplands and forest reserves in Arrowhead Region, Minnesota	Yes	Yes, dominance shift	NA	Anthropogenic influence on disturbance regime (logging for fire), pest infestations (hypothesised), organic layer conditions (hypothesised)
Drever et al.	2006	Canada	obs	Approx. 90	Adult	Sugar maple-yellow birch bioclimatic region; Great Lakes-St. Lawrence forest, subpolar continental climate		Yes, change in dominance	Long-term natural climate cycles (Little Ice Age - present; hypothesised), drought	Time-since-fire, fire suppression, pest infestations (inferred), wind-throw (inferred), soil texture, soil moisture and nutrient content (inferred), logging, topography

Authors	Year	Country	Study design	Study temporal range (years)	Life stages studied	Habitat-type(s) under study	Northward/Upward temperate tree range expansion	Observation of increasing temperate species dominance at range edge	Important climate drivers	Other drivers of range dynamics?
Bouchard et al.	2007	Canada	obs	62	Adult	Mixed woods forest zone (balsam fir / white birch and balsam fir / yellow birch bioclimatic domains)	No, (decline at limit)	Yes, infilling	Temperature, humidity (both hypothesised)	Spruce budworm outbreak severity & frequency, succession
Beckage et al.	2008	USA	obs	43	Sapling – adult	Maple-beech-yellow birch transitioning to spruce-fir-paper birch with elevation	Yes		Temperature (particularly warmer winters), precipitation	Elevation, canopy turnover
Pinto et al.	2008	Canada	obs	190	Sapling – adult	Great Lakes - St. Lawrence forest region, boreal forest region in central-northern Ontario		Yes, shift in dominance	NA	Logging, pest infestations, forest management practices, inadequate reproduction (all hypothesised), land clearing
Duchesne & Ouimet	2008	Canada	obs	36	Sapling – adult	Deciduous, coniferous and mixed forest zones of southern Quebec	No		Climate warming (inferred)	Logging, pest infestations, natural disturbance (windthrow, fire, ice storms),
Woodall et al.	2009	USA	obs	6	Seedling – adult	Eastern continental US; temperate and mixed forest zones	Yes		Climate change (hypothesised)	NA
Leithead et al.	2010	Canada	obs	Approx. 40	Sapling – adult	Transitional Great Lakes - St. Lawrence forest	Yes		Temperature (hypothesized), climate change (hypothesised)	Canopy gap size and age, light availability, disturbance regimes
Bolte et al.	2010	Sweden	obs	4	Sapling – adult	Plateau crossed with small boulder ridges, nutrient poor, acidic soil; boreo-nemoral transition forest		Yes, infilling, increasing abundance	Temperature, drought, wind-throw, climate change (hypothesised)	Pest infestations, gap dynamics

Authors	Year	Country	Study design	Study temporal range (years)	Life stages studied	Habitat-type(s) under study	Northward/Upward temperate tree range expansion	Observation of increasing temperate species dominance at range edge	Important climate drivers	Other drivers of range dynamics?
Amatangelo et al.	2010	USA	obs	Approx. 50	Sapling – adult	Mesic hemlock, mesic hardwood, hardwood 'dry-mesic', and pine-hardwood 'dry' forest types across Wisconsin		Yes, dominance shift	Decreasing temperature & precipitation, lengthened growing season, increasing and decreasing growing degree days, climate change (hypothesised)	Fire suppression (inferred), deer browsing (inferred), logging (inferred), edaphic qualities (soil moisture important), understorey composition, succession
Bai et al.	2011	China	obs	44	Sapling – adult	Broad-leaved to tundra vertically zonated forest gradient under monsoonal influence	No	Yes, dominance shift	Temperature, precipitation, climate change (hypothesised)	Elevation, edaphic factors (hypothesized)
Grundmann et al.	2011	Sweden	obs	NA	Adult (assumed)	Near-natural mixed spruce-beech forest stand on moss, lichen and bouldery substrate		Yes, increased growth	Precipitation, temperature, wind-throw, climate change (hypothesised)	Pest infestations, competition
McCarragher et al.	2011	USA	exp	2	Seed – seedling	Temperate to mixed BTE forest type, continental climate		Yes, shown experimentally	Temperature, climate change (hypothesised)	Intra-specific genetic variation (inferred)
Treyger & Nowak	2011	USA	obs	30	Sapling	Northeast mixed forest, Adirondacks highland forest, eastern broadleaf forest, mid-west broadleaf forest		Yes, increased infilling, recruitment of southern species	Temperature, precipitation, growing season length, soil moisture (hypothesised), changing animal communities (hypothesised), phenological changes (hypothesised)	Invasive species interactions (hypothesised), anthropogenic disturbances

Authors	Year	Country	Study design	Study temporal range (years)	Life stages studied	Habitat-type(s) under study	Northward/Upward temperate tree range expansion	Observation of increasing temperate species dominance at range edge	Important climate drivers	Other drivers of range dynamics?
Fisichelli et al.	2012	USA	obs	6	Sapling	Upland mesic stands with mixed forest, northern Minnesota	No	Yes, increased growth with warming	Temperature, drought (hypothesized), climate change (hypothesised)	Browse intensity, light availability
Leithead et al.	2012	Canada	obs	22	Sapling – adult	Old-growth white pine transitional forest	Yes		Temperature (inferred), precipitation (hypothesised)	Canopy gap size & age, light availability, soil temperature (hypothesised), fire suppression (inferred)
Hanberry	2013	USA	obs	45	Sapling – adult	Northern mixed forest, eastern broadleaf forest, southern mixed forest, prairie/savannah, prairie		Yes, dominance shift	Climate change (hypothesised)	Anthropogenic influences on disturbance regimes (fire suppression & forestry practices; both inferred), deer browse (hypothesised)
Brown & Vellend	2014	Canada	exp	3	Seed – seedling	East-facing elevational gradient from low-elevation sugar maple dominant to high-elevation spruce-fir forest	No		Temperature, growing season length (both hypothesised)	Soil source, seed predation, elevation, fungal infection, soil-nutrient availability (hypothesized), beneficial fungal interactions (hypothesized), intra-specific genetic variation (hypothesized)
Boisvert-Marsh et al.	2014	Canada	obs	33	Seedling – adult	Province of Quebec, south of "commercial treeline" at 52°N, including boreal and mixed forest	Yes		Temperature, precipitation, winter storm severity, climate change (all hypothesised)	Pest infestations, logging, powerline installation, gap dynamics (all hypothesized)

Authors	**Year**	**Country**	**Study design**	**Study temporal range (years)**	**Life stages studied**	**Habitat-type(s) under study**	**Northward/Upward temperate tree range expansion**	**Observation of increasing temperate species dominance at range edge**	**Important climate drivers**	**Other drivers of range dynamics?**
Fisichelli et al.	2014	USA	obs	3	Seedling – sapling	Temperate to boreal transition forest south and southwest of Lake Superior	Yes		Temperature, frequency/timing of frost events (hypothesized), climate warming (hypothesized)	Elevation, light availability, nutrient availability, canopy openness, understory competition (all hypothesised)
Suzuki et al.	2015	Japan	obs	8	Sapling – adult	Secondary and old-growth forests across the Japanese archipelago	Yes		Temperature, precipitation (hypothesised), distribution and depth of snow cover (hypothesised), long-term climate cycles/climate change (hypothesised)	Historic land-use & anthropogenic influences, succession, historical disturbance regime (all hypothesised)
Foster & D'Amato	2015	USA	obs	27	Adult	Low elevation northern temperate forest transitioning to high elevation boreal forest in the White Mountains and northern Green Mountains	No		NA	Latitude, slope aspect, recovery of red spruce (hypothesised), uncompetitive hardwood species (hypothesised), changing land-use patterns (hypothesised)
Danneyrolles et al.	2016	Canada	obs	125-155	Adult	Northern limit of the Great Lakes – St. Lawrence forest region in Quebec over undifferentiated or rocky till		Yes		Topography, logging, spruce budworm
Katz & Ibáñez	2016	USA	exp	4	Seedlings	Temperate forest to temperate-boreal mixed forest in Michigan				Disease, herbivory, inter-specific mutualism (hypothesized)

*Acronyms used in the table are as follows: obs = observational and exp = experimental study; *Abies balsamea* = AB; *Abies nephrolepis* = AN; *Acer mono* = AM; *Acer saccharum* = AS; *Acer rubrum* = AR; *Betula papyrifera* = BP; *Betula alleghaniensis* = BA; *Fagus sylvatica* = FS; *Fagus grandifolia* = FG; *Larix laricina* = LL; *Larix olgensis* = LO; *Picea abies* = PA; *Picea glauca* = PG; *Picea jezoensis* = PJ; *Picea mariana* = PM; *Pinus koraiensis* = PK; *Pinus resinosa* = PR; *Pinus strobus* = PS; *Populus balsamifera* = PB; *Populus tremuloides* = PT; *Tsuga canadensis* = TC.

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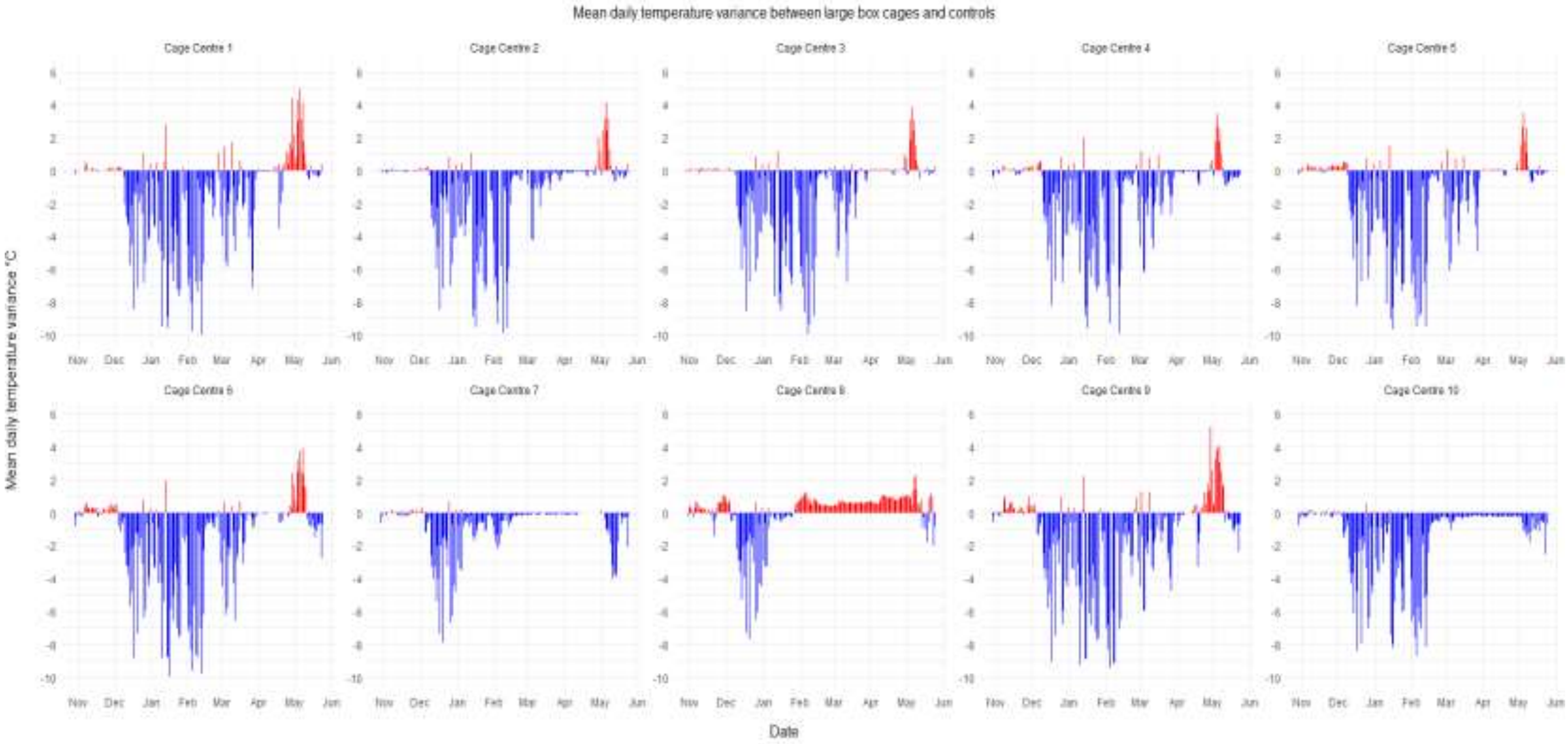
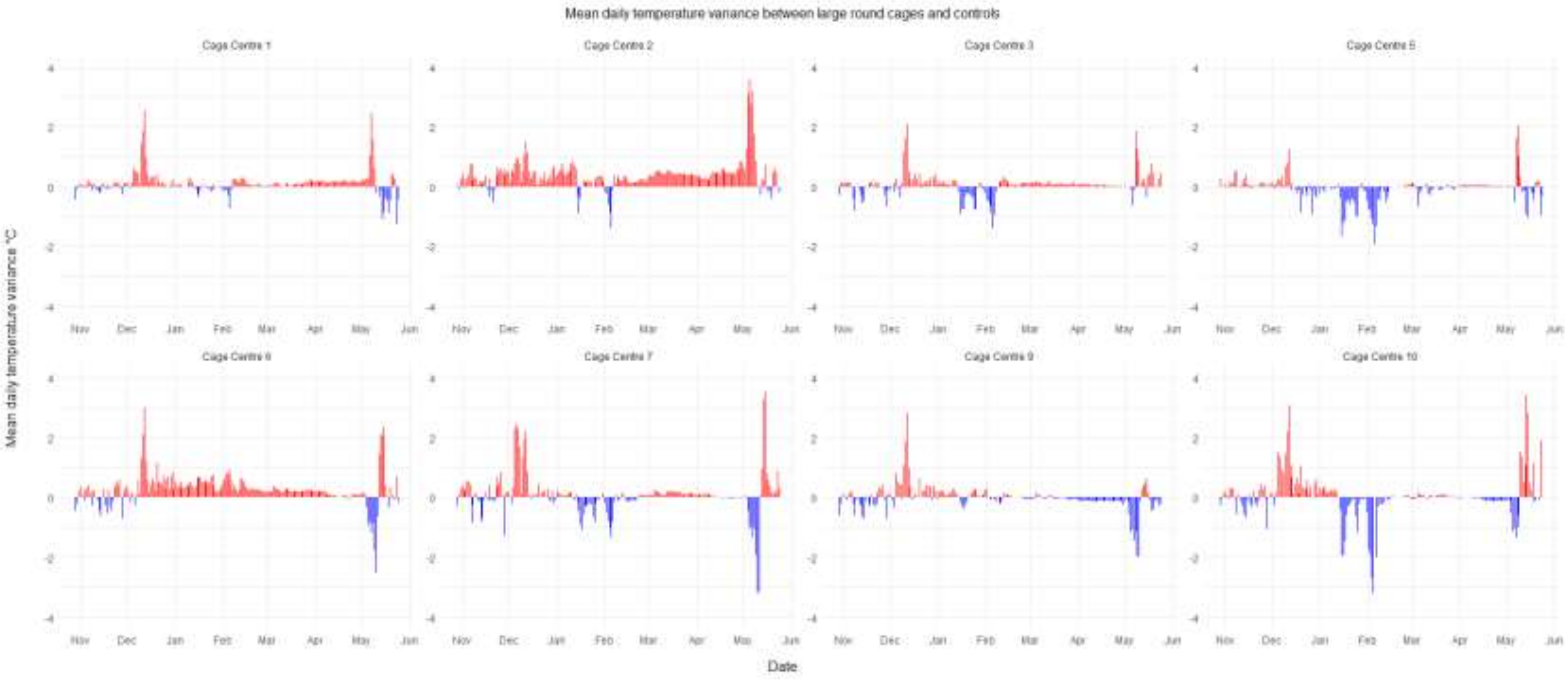
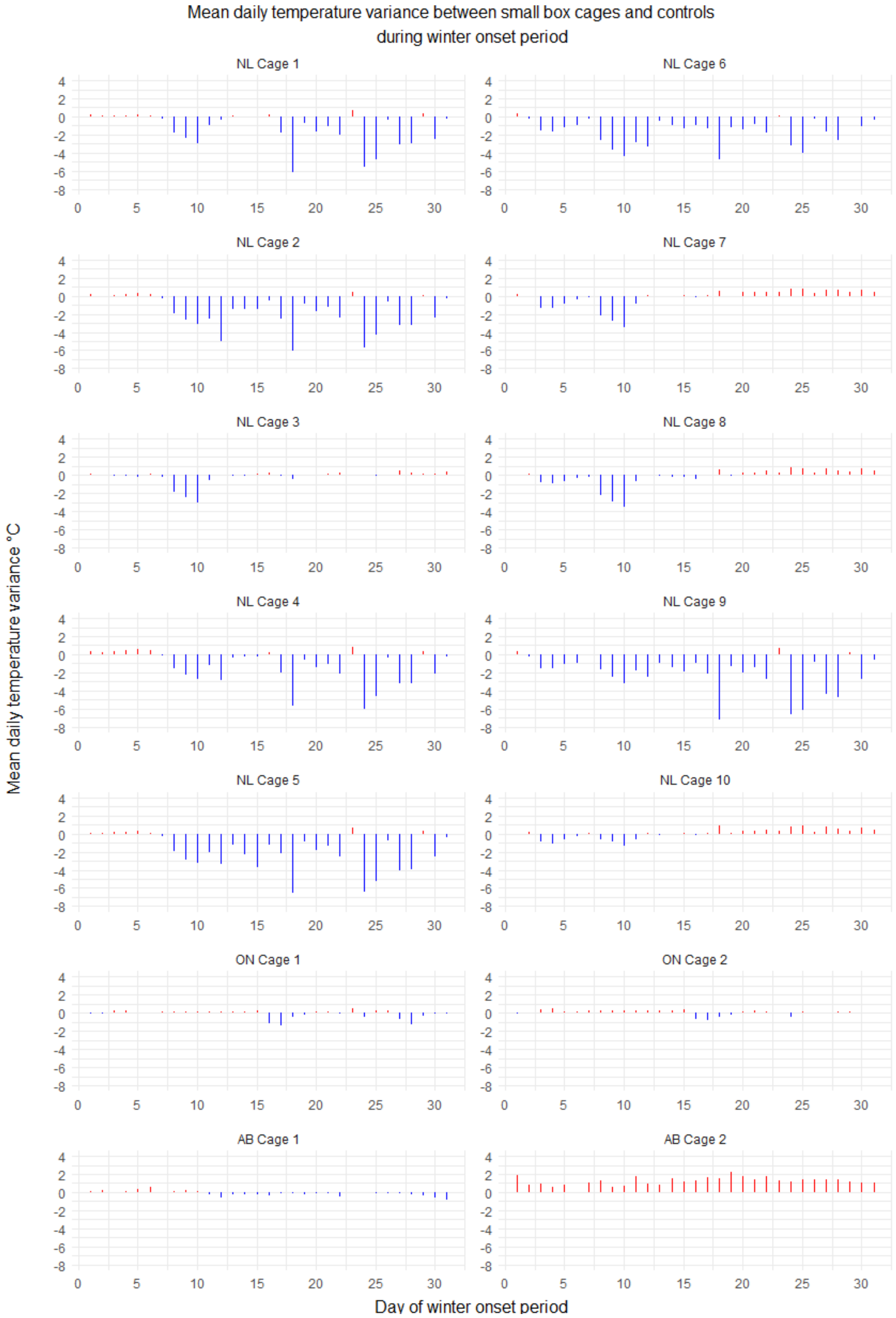
Chapter 3



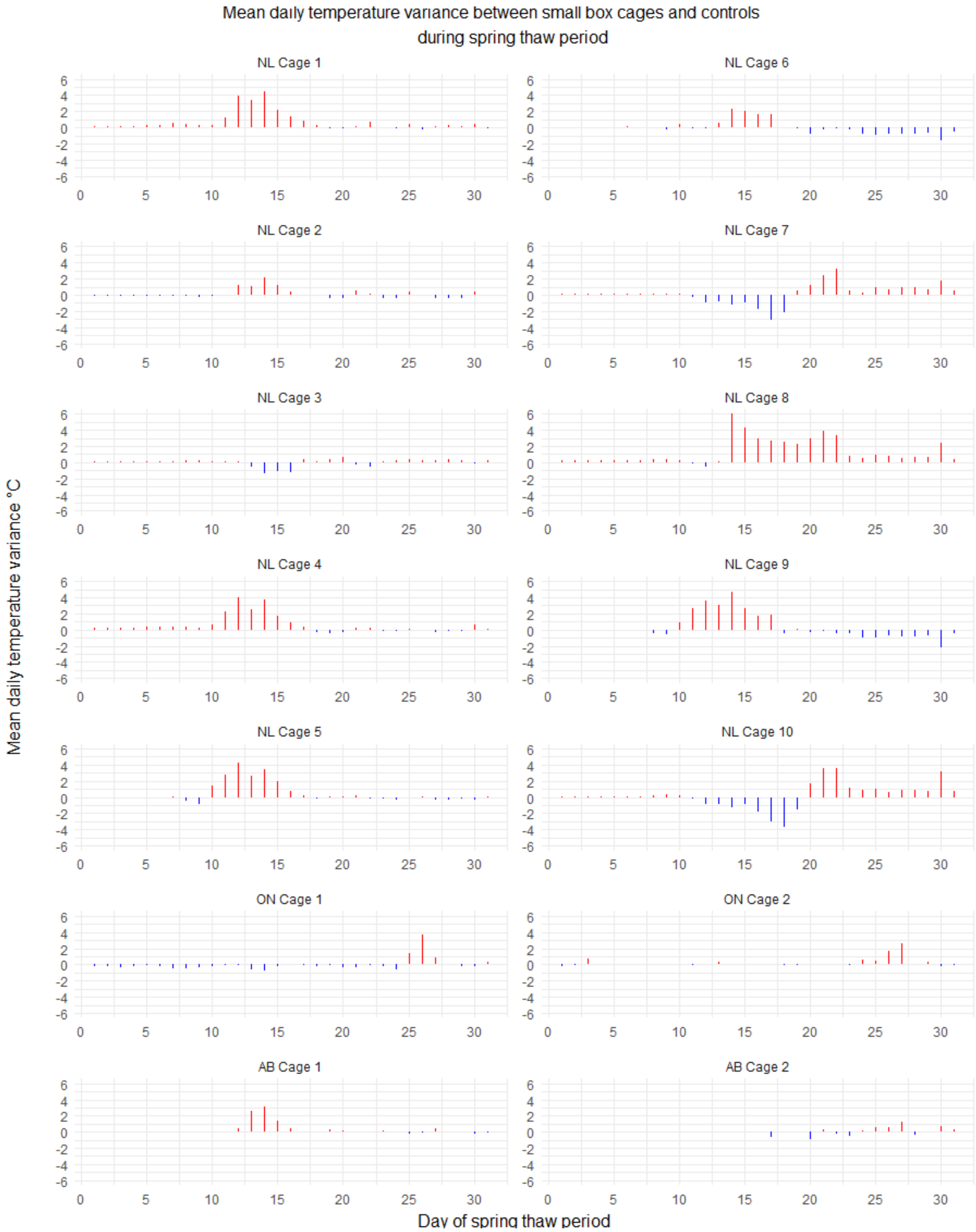
Supplementary Figure 3.1: Individual large box cage sensor temperature variation from the mean control sensor temperature throughout the data collection period. Blue and red line segments here indicate when mean daily temperatures recorded by caged sensors were colder and warmer than mean daily temperatures recorded by control sensors, respectively. All cage sensor data show similar negative temperature variation during the month of December during which time the sensors were left exposed to ambient air temperature – dipping as much as 9 degrees lower than the control mean temperature – while control sensors were insulated by snow cover (Fig 3.4). With two exceptions (cages 7 & 10) there is a similarly uniform positive temperature variation around the start of May, when snow-melt had already occurred in many cages – before any control sensors had been uncovered (Fig 3.4). Plots were created using ggplot2 (Wickham 2009) in R (R Core Team 2016).



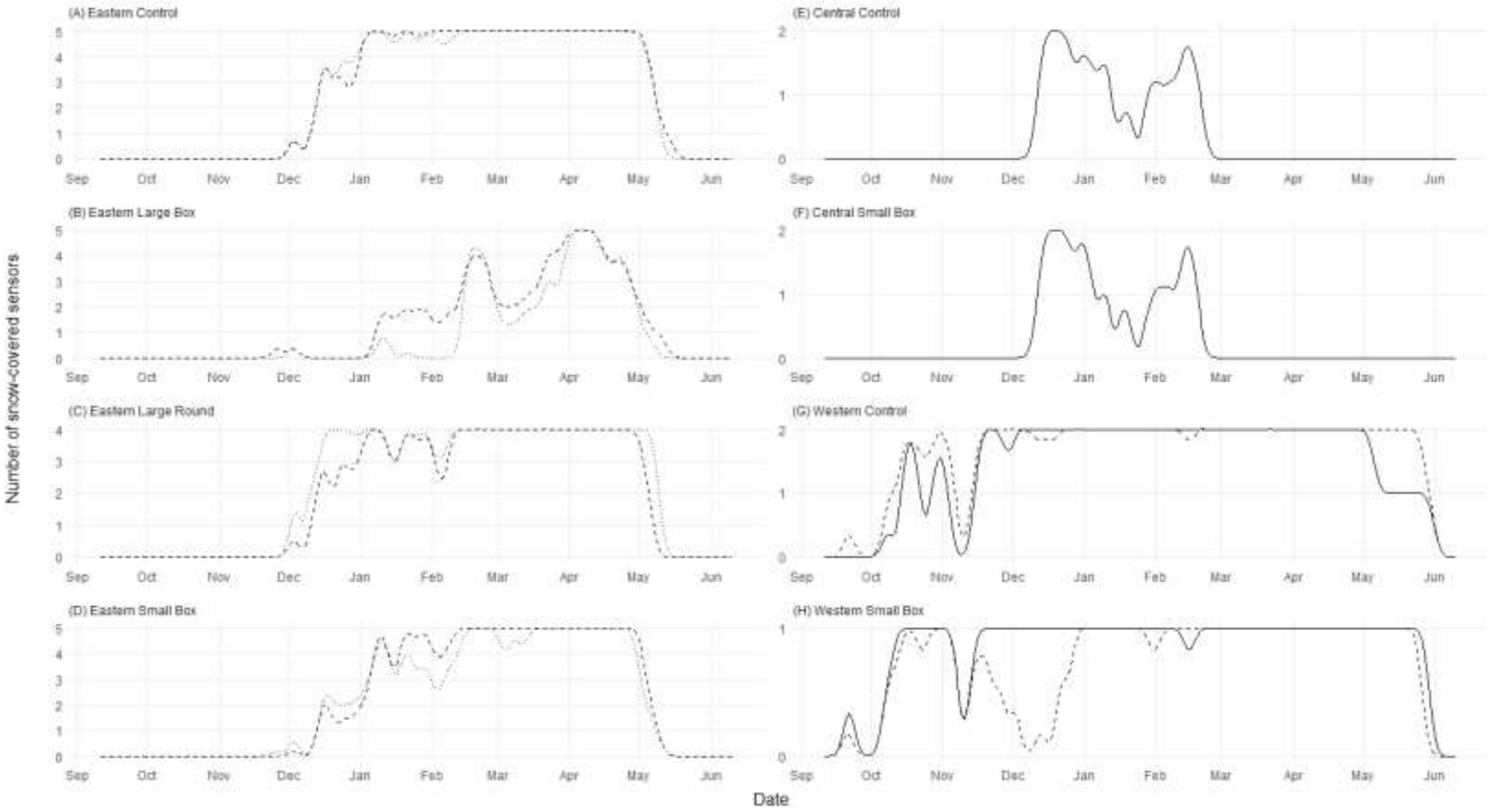
Supplementary Figure 3.2: Individual large round cage sensor temperature variation from the mean control sensor temperature throughout the data collection period. Blue and red line segments here indicate when mean daily temperatures recorded by caged sensors were colder and warmer than mean daily temperatures recorded by control sensors, respectively. The reverse trend to what occurred in the large box cages is shown during the winter onset period for the large round cages where a consistent positive temperature anomaly was observed. With the exception of what we interpret to be several brief periods of sensor exposure, all cages of this type appear to be largely consistent with the control mean throughout the winter, mostly varying < ±1°C. The spring thaw period is characterised in all cages by a positive temperature anomaly, which is consistent with the significant finding of mildly warmer mean daily temperatures within the cages during this period. Plots were created using ggplot2 (Wickham 2009) in R (R Core Team 2016).



Supplementary Figure 3.3: Individual small box cage sensor temperature variation from the mean control sensor temperature during the winter onset period at each site. Blue and red line segments indicate when mean daily temperatures recorded by caged sensors were colder and warmer than mean daily temperatures recorded by control sensors, respectively. Plots were created using ggplot2 (Wickham 2009) in R (R Core Team 2016).



Supplementary Figure 3.4: Individual small box cage sensor temperature variation from the mean control sensor temperature during the spring thaw period at each site. Blue and red line segments indicate when mean daily temperatures recorded by caged sensors were colder and warmer than mean daily temperatures recorded by control sensors, respectively. Plots were created using ggplot2 (Wickham 2009) in R (R Core Team 2016).



Supplementary Figure 3.5: Smoothed plots showing the number of sensors under each cage type treatment and controls that were snow-covered throughout the maximum duration of our data collection. Solid lines represent sensors under open canopy, dashed lines under coniferous canopy and dotted lines under mixed deciduous-coniferous canopy. The number of snow-covered days between Eastern control sensors (A) and large round sensors (C) aligned closely, (average 141 snow-covered days, sd = 10.3 & 9.3, respectively). LBC sensors (B) recorded far fewer snow-covered days, (average 62 days, sd = 34.3). The range of snow-covered days recorded by Eastern control (A) and large round sensors (C) was also similar (Mid-Range = 138 ±18 & 140 ±12, respectively); LBC sensors (B) recorded a much larger range of snow-cover duration (MR = 70 ±48). The range of snow-covered days recorded in Eastern

SBCs (D) mostly overlapped with Eastern controls (MR = 119 ±31), but recorded a lower mean number of snow-covered days (120, sd = 22.4). The overall winter season was much shorter at the Central site (E, F); control sensors there recorded an average 52 snow-covered days (sd = 17.7, MR = 52 ±13). The Western site (G, H) experienced a much longer winter season, where control sensors recorded an average 224 snow-covered days (sd = 25.8, MR = 215 ±28). SBCs at the Central (F) and Western (H) sites had snow-cover conditions closer to their controls (E & G, respectively) than their Eastern counterparts; sensors in those cages recorded a mean 40 and 223 snow-covered days (MR = 40 ±8 and 223 ±11, & sd = 11.3 and 14.8, respectively). Plots created using ggplot2 (Wickham, 2009).

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Chapter 4

Supplementary Table 4.1: Outline of the general site location, elevation, aspect, plant hardiness zone (Agriculture and Agri-Food Canada 2000), basic climate characteristics (Agriculture and Agri-Food Canada 2013a, b; Environment and Climate Change Canada 2017), and forest composition.

Site Name:	**Bara**		**Clar**		**Raft**		**Sal**	
Forest type:	Mixed	Coniferous	Mixed	Coniferous	Mixed	Coniferous	Mixed	Coniferous
Established:	2015		2015		2015		2015	
Approximate Location:	Barachois Pond Provincial Park		Clarenville		Rafting Newfoundland		Saint Catharine's	
Nearest weather station (distance in km):	Stephenville Airport (23)		Port Blandford (20)		Grand Falls (18)		Holyrood (37)	
Average annual temp (˚C)	5.0		5.0		4.5		6.3	
Average summer high (˚C)	20.6		23.2		22.7		21.9	
Average winter low (˚C)	-10.7		-12.1		-13.3		-7.8	
Average annual precipitation (mm)	1340.4		988.3		1098.9		1015.0	
GDD (T_{base}= 5˚C)	1387.5		1428.7		1408.6		1488.1	
Frost-free period (days)	157		N/A		134		130	
Aspect (%):	-11 WSW	-3 W	-2 NNE	0	-24 WSW	1 NNE	-31 N	-13 NNE
Mean Canopy Cover (%):	96	92	93	91	90	90	89	NA
Mean Deciduous CC (%)[ǂ]:	65	24	74	14	51	10	70	NA
Mean Boreal CC (%)[ǂ]:	33	69	20	79	42	81	20	NA
Tree species present:	AB, BA, BP, *Pinus strobus*	AB, AR, BA, BP, PG, PM, SD	AB, AR, BP, LL, PG, PM, SD	AR, BP, LL, PG, PM,	AB, AR, AS, BP, PG, PM,	AB, BP, PG, PM, *Populus tremuloides, Prunus pensylvanica*	AB, BA, BP,	AB, PM, BP, BA
Eco-region (Damman, 1983):	Western Forest		Central Forest		Central Forest		Avalon Forest	
Sub-region (Damman, 1983):	St. George's Bay		Northcentral		Northcentral		NA	
Plant hardiness zone:	5a		5a		4b		5b	

AB = *Abies balsamea*, AR = *Acer rubrum*, AS = *Acer spicatum*, BA = *Betula alleghaniensis*, BP = *Betula papyrifera*, LL = *Larix laricina*, PG = *Picea glauca*, PM = *Picea mariana.*

ǂ Due to overlapping layers of canopy, values may not sum to 100% or total mean canopy cover in all cases.

Site Name:	**Sir**		**Doz**		**GL**		**Wild**	
Forest-type:	Mixed	Coniferous	Mixed	Coniferous	Mixed	Coniferous	Mixed	Coniferous
Established:	2015		2016		2016		2016	
Approximate Location:	Sir Richard Squires Provincial Park		Beaver Pond cottage development area		Grand Lake access road		Wild Cove Pond Road, north of Corner Brook	
Nearest weather station (distance in km):	Cormack (16)		Gallants (10)		Gallants (7)		Corner Brook (9)	
Average annual temp (˚C)	3.2		3.7		3.7		5.2	
Average summer high (˚C)	21.4		21.6		21.6		21.6	
Average winter low (˚C)	-14.3		-13.7		-13.7		-10.6	
Average annual precipitation (mm)	1263.5		1159.8		1159.8		884.5	
GDD (T_{base}= 5˚C)	1155.2		1213.4		1213.4		1473.7	
Frost-free period (days)	82		79		79		146	
Aspect (%):	-1 ENE	-4 SW	-13 SE	2 NWN	-19 NNE	-8 ENE	-14 E	-21 ENE
Mean Canopy Cover (%):	92	91	96	88	98	95	92	90
Mean Deciduous CC (%)[ǂ]:	56	1	72	8	76	3	76	8
Mean Coniferous CC (%)[ǂ]:	36	91	25	81	23	91	19	83
Tree species present:	AB, AR, AS, BP	AB, BP, PM	AB, BA, BP, PM, SD	AB, AR, BP, PM, *Prunus pensylvanica*, SD	AB, BA, BP, PM	AB, BA, BP, PM	AB, AR, BA, BP, *Fraxinus nigra*, PM, *Prunus pensylvanica*, SD	AB, AR, BA, BP, PM, *Pinus strobus Prunus pensylvanica*, SD
Eco-region (Damman, 1983):	Central Forest		Western Forest		Western Forest		Western Forest	
Sub-region (Damman, 1983):	Northcentral		Corner Brook		St. George's Bay		Corner Brook	
Plant hardiness zone:	4a		4b		4b		5a	

AB = *Abies balsamea*, AR = *Acer rubrum*, AS = *Acer spicatum*, BA = *Betula alleghaniensis*, BP = *Betula papyrifera*, LL = *Larix laricina*, PG = *Picea glauca*, PM = *Picea mariana*, SD = *Sorbus decora.*

ǂ Due to overlapping layers of canopy, values may not sum to 100% or total mean canopy cover in all cases.

Supplementary Table 4.2: Treatment variables used in mixed-effects models analysing 2016 and 2017 emergence data, with descriptions, category, units, level of measurement (see Fig. 4.2) and variable type. Climatic variables were not applied to 2016 emergence data, as sensors were only installed at test sites in the fall of 2016 and certain climatic variables were only applied to specific model species, reflecting their known relevance to those species (Table 4.1).

Variable Description	Category	Units	Level	Type	Germination year	Applicable species
Herbivory treatment (caged or control/exposed)	Treatment	Levels	Block	Factor	2016, 2017	All
Substrate type (ecotone or boreal substrate)	Treatment	Levels	Block	Factor	2016, 2017	All
Deciduous canopy cover	Treatment	%	Block	Continuous	2016, 2017	All
Mean soil temperature	Climatic	°C	Canopy type	Continuous	2017	All
Mean soil moisture	Climatic	m^3H_2O/m^3Soil	Canopy type	Continuous	2017	All
Mean air temperature	Climatic	°C	Canopy type	Continuous	2017	All
Mean winter soil moisture	Climatic	m^3H_2O/m^3Soil	Canopy type	Continuous	2017	*F. nigra*
Mean winter soil temperature	Climatic	°C	Canopy type	Continuous	2017	*F. nigra*

Notes: (1) non-winter climate variables are for the 30 day period preceding the greatest number of newly emergent seedlings recorded: 24th April – 23rd May, 2017 for *A. saccharum*, 19th May – 17th June, 2017 for *F. nigra* & *B. alleghaniensis*, and 11th June – 10th July, 2017 for *T. occidentalis*. (2) winter climate variables were averaged between first and last weeks with an average air temperature below 0°C (starts 28th of November, 2016 for all sites, ends 2nd of April, 2017 for Bara & Sal, 23rd of April, 2017 for all other sites).

Supplementary Table 4.3: Germination test data for each species ordered from the NTSC each year (Canada Forest Service - Atlantic Forestry Centre 2016) with predicted approximate number of viable seeds sown as a proportion of the season total and pot total. In several cases seeds were assembled from multiple provenances due to the size of this project and in those cases the seeds were homogenised by hand mixing prior to being sown into pots.

Species	Year sown	Year collected	NTSC Germination rate (%)	NTSC test year	Average viability (%)	N viable seed/ N seed sown	N viable seed/ N seed per pot
A saccharum	2015	2002	56.0	2014	51.0	1,530/3,000	2/5
		2006	51.0	2008			
		2006	39.0	2008			
		2006	54.0	2008			
		2008	55.0	2009			
B. alleghaniensis	2015	2000	80.5	2010	78.5	2,355/3,000	7/10
		2006	76.5	2007			
F. nigra	2015	2009	67.0	2010	60.1	901/1,500	3/5
		2009	53.0	2010			
		2009	56.0	2010			
		2013	56.0	2014			
		2013	65.0	2014			
		2013	55.0	2014			
		2013	69.0	2014			
T. occidentalis	2015	2008	88.0	2009	84.5	5,070/6,000	8/10
		2011	81.0	2011			
A. saccharum	2016	1999	84.0	2014	81.5	3,912/4,800	8/10
		2002	74.0	2014			
		2002	83.0	2014			
		2002	85.0	2014			
B. alleghaniensis	2016	2015	92.0	2016	92.0	4,416/4,800	9/10
T. occidentalis	2016	2002	70.0	2013	70.0	3,360/4,800	7/10

Supplementary Table 4.4: Coefficients table for treatment variable analysis of presence datasets showing parameter estimates with standard errors (SE) for confidence set models.

	Species	Year	Model structure	N	Variable parameter estimates (SE)				Substrate Treatment variance	Within-Site variance	Between-Site variance
					Intercept	XHerb	SubM	%DecC			
3	*A. saccharum*	2016	Binomial	588	-2.6415 (0.6082)	2.1901 (0.2570)				0.8531	1.4668
5					-2.6493 (0.6202)	2.1889 (0.2564)		0.2553 (0.1922)		0.8185	1.5425
3	*A. saccharum*	2017	Binomial	480	-3.1210 (1.2158)	0.7656 (0.3872)				4.959	8.912
5					-3.1413 (1.2391)	0.7622 (0.3879)		-0.3717 (0.3922)		4.940	9.308
6	*B. alleghaniensis*	2016	Binomial	293	-2.3242 (0.7142)	1.2827 (0.3350)	0.0212 (0.3224)		0.5005	1.2373	0.5074
8					-2.3288 (0.7128)	1.2835 (0.3351)	0.0264 (0.3241)	-0.0398 (0.2457)	0.4661	1.2472	0.4952
3					-1.9461 (0.4076)	1.1930 (0.3191)				0.9920	0.3442
2	*B. alleghaniensis*	2017	Binomial	480	-1.6428 (0.2917)			-0.5326 (0.1440)		0.2621	0.4700
5					-1.8240 (0.3267)	0.3409 (0.2498)		-0.5366 (0.1460)		0.2905	0.4797
3	*T. occidentalis*	2016	Binomial	588	-4.8226 (0.6848)	1.3683 (0.4434)				3.083	4.491x10^{-9}
5					-4.8452 (0.6952)	1.3698 (0.4436)		-0.1428 (0.3632)		3.1500	2.61x10^{-9}
2	*T. occidentalis*	2017	Binomial	480	-1.8571 (0.2579)			-0.3179 (0.1471)		0.1967	0.2920
5					-1.7120	-0.3181		-0.3190		0.1938	0.2975

					(0.2820)	(0.2631)		(0.1471)			
7					-2.1161 (0.3114)		0.4634 (0.2786)	-0.3965 (0.1576)	1.016×10^{-9}	0.2322	0.3034
8					-1.9706 (0.3312)	-0.3224 (0.2647)	0.4661 (0.2792)	-0.3980 (0.1577)	1.467×10^{-9}	0.2298	0.3091
8	*F. nigra*	2017	Binomial	300	0.5807 (0.4712)	0.5789 (0.2820)	-0.6308 (0.2967)	0.4164 (0.2152)	2.399×10^{-9}	0.8866	0.7121
5					0.2569 (0.4374)	0.5653 (0.2784)		0.3388 (0.2054)		0.8047	0.6915
3					0.2687 (0.4524)	0.5657 (0.2785)				0.8995	0.7480
6					0.5555 (0.4883)	0.5791 (0.2820)	-0.5537 (0.2949)		1.465×10^{-9}	1.024	0.7791

Supplementary Table 4.5: Coefficients table for treatment variable analysis using abundance datasets. Zero-inflated binomial (ZIB) model intercept and standard error (SE) values given for confidence set models.

	Species	Year	Model structure	Model weight	N	ZIB Intercept (SE)	Variable parameter estimates (SE)				Substrate Treatment variance	Within-Site variance	Between-Site variance
							Intercept	XHerb	SubM	%DecC			
3	*A. saccharum*	2016	ZIB	5	588	-1.0095 (0.2848)	-3.6656 (0.5366)	1.9187 (0.1921)				0.5137	1.1394
5						-1.0092 (0.2784)	-3.6803 (0.5463)	1.9235 (0.1927)		0.1926 (0.1530)		0.5152	1.1942
5	*A. saccharum*	2017	ZIB	10	480	-1.3647 (0.2509)	-4.4948 (1.0630)	0.3135 (0.1507)		-0.6403 (0.2818)		3.193	7.570
6	*B. alleghaniensis*	2016	ZIB	10	293	-1.4872 (0.6215)	-4.5688 (0.5348)	1.1744 (0.2296)	0.5067 (0.2080)		0.1600	1.5484	0.3557
8						-1.4776 (0.6031)	-4.5759 (0.5286)	1.1752 (0.2301)	0.5156 (0.2084)	-0.1325 (0.2357)	0.1572	1.5720	0.3259
5	*B. alleghaniensis*	2017	ZIB	10	480	0.2308 (0.2371)	-3.0481 (0.3955)	0.3476 (0.1966)		-0.5377 (0.1300)		0.2254	0.7396
2						0.2440 (0.2312)	-2.8659 (0.3779)			-0.5233 (0.1324)		0.2540	0.7372
3	*T. occidentalis*	2016	ZIB	10	588	-0.0355 (0.5232)	-6.4864 (0.7857)	1.4074 (0.4346)				3.488	4.572x10^{-9}
5						-0.0298 (0.5258)	-6.5114 (0.7957)	1.4023 (0.4347)		-0.1720 (0.3788)		3.566	3.772x10^{-9}
8	*T. occidentalis*	2017	ZIB	10	480	-0.3537 (0.4884)	-3.7534 (0.3901)	-0.3854 (0.2391)	0.5310 (0.2463)	-0.4182 (0.1554)	1.404 x10^{-9}	0.4191	0.1677
5						-0.2129 (0.4604)	-3.3676 (0.3545)	-0.4090 (0.2416)		-0.3320 (0.1477)		0.3732	0.1610
7						-0.3142 (0.4970)	-3.9055 (0.3853)		0.5465 (0.2465)	-0.4228 (0.1543)	8.530x10^{-10}	0.3949	0.1626
2						-0.1718 (0.4783)	-3.5130 (0.3552)			-0.3319 (0.1452)		0.3354	0.1535

8	*F. nigra*	2017	Binomial	5	300		-1.1391 (0.3572)	0.2838 (0.1277)	-0.5797 (0.1341)	0.2644 (0.1393)	$7.242x10^{-10}$	0.5629	0.5111
6							-1.1423 (0.3668)	0.2838 (0.1277)	-0.5536 (0.1335)		$9.535x10^{-10}$	0.5904	0.5441

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